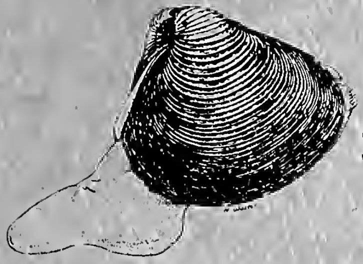

PROCEEDINGS OF THE SECOND INTERNATIONAL *CORBICULA* SYMPOSIUM

SPECIAL EDITION NO. 2 OF THE *AMERICAN MALACOLOGICAL BULLETIN*

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AMER. MALAC. BULL. SPECIAL EDITION NO. 2
June 1986

PREFACE

The Second International *Corbicula* Symposium was held in Little Rock, Arkansas, June 21-24, 1983. The meeting was sponsored by and the majority of support for publication of these proceedings was provided by grants from the Electric Power Research Institute, Palo Alto, California and the Nuclear Regulatory Commission, Washington D. C. Arkansas Power and Light Company kindly acted as host of this meeting. The Symposium Organizing Committee (Louise Russert Kraemer, Robert West, Robert McMahon, Jack Mattice, Paul Hayes, and Joseph C. Britton) express our sincere gratitude to these organizations for their assistance.

The Little Rock meeting was for the specific purpose of stimulating dialogue between basic and applied scientists with respect to *Corbicula* biofouling and control. Additional aspects of the basic biology of *Corbicula* were also considered. About 40 papers were presented by the participants, and several *Corbicula* and power plant "tutorials" were provided in informal evening sessions. The last day of the meeting was highlighted by two panel discussions, the first devoted to basic biology and the second devoted to biofouling and control. (A summary of each panel discussion appeared in Volume 8(2) of The *Corbicula* Newsletter.) The delivered papers, informal rap sessions and panel discussions focused on many topics, most of which are formalized in the papers which appear in these proceedings. A few topics, however, have received only modest coverage herein, but are likely to continue to be issues of *Corbicula* biology or control in the years to come. The first, an issue of basic science, has to do with the number of species of *Corbicula* now in North America. There is increasing biochemical evidence supporting the concept of two species of *Corbicula* in North American fresh waters (e.g., see McLeod's paper herein), but ecological data presented at the meeting suggests that the situation may not be conclusively settled by biochemical evidence alone. Jerry Landye raised the question of a *Corbicula* fishery at the Little Rock meeting. Since that time (and independent of his presentation) I have received numerous inquiries concerning *Corbicula* fisheries or aquaculture for human or livestock consumption. This may be another direction future *Corbicula* work may lead. Another issue, one of applied biology, addresses the most appropriate mechanism for *Corbicula* control in industrial water supplies. Several papers herein discuss various methods for *Corbicula* control. There seems to be an increasing feeling among the industrial community that there is no single-most appropriate measure. Effective *Corbicula* control is highly site-specific. What works at Site A may not be effective at Site B. Control efforts must focus on the one or combination of measures most effective for the specific industrial operation.

Most of you who attended the Little Rock Symposium have communicated to me that you found the Symposium useful, intellectually stimulating, and a smoothly run meeting. There are several reasons for this positive reaction, all of which are the results of attention given by members of the Local Organizing Committee. Louise Russert Kraemer and Bob West were perhaps the most visible, and each clocked hundreds of hours working on many

details that eventually culminated in an efficient and successful meeting. Nancy Rogers of the University of Arkansas' Division of Continuing Education must also be commended on effective management of registration and pre-meeting preparations. Many staff members of Arkansas Power and Light Company contributed time and energy before and at the meeting to insure its success. To all of you go our sincere appreciation.

As with the first *Corbicula* Symposium Proceedings, manuscripts submitted for this volume received peer review. All papers were read by at least two independent reviewers. I would like to express my appreciation to each of the following persons who graciously provided time and expertise to serve as reviewers:

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I am especially indebted to Robert Prezant, who was willing to accept the formidible task of Managing Editor for these Proceedings. Bob received the reviewed manuscripts, sent them for additional reviews, negotiated with the printer, marked all manuscript copy for printing, and, in essence, served as overseer in the transition from manuscript to printed page. He has also served as the primary liason between the Symposium Organizing Committee and the American Malacological Union. Finally, I am appreciative to the Executive Committee of the American Malacological Union, who agreed to publish these proceedings under the AMU name, and thereby insured a distribution for the document significantly greater than would have been possible by private publication.

Joseph C. Britton
February, 1985

HISTORICAL REVIEW OF ASIATIC CLAM (*CORBICULA*) INVASION AND BIOFOULING OF WATERS AND INDUSTRIES IN THE AMERICAS

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ABSTRACT

Severe biofouling problems with Asiatic clams (*Corbicula*) were first reported in the United States in 1956. Clam infestations were reported in 1961 in irrigation canals, and numerous reports of clams biofouling irrigation canals in the west have appeared in subsequent years.

The first verified excursion of Asiatic clams beyond the Rocky Mountain barrier occurred when they were discovered in the Tennessee River in 1959. Since that time there have been numerous reports of range extensions into other river systems, including headwater streams. Clams have caused severe biofouling problems in water intakes, pumps, and industrial and power plant cooling water (heat rejection) systems.

The current range extension in the Americas includes 35 of the contiguous United States. The range extension of *Corbicula "leana"* and *"fluminae"* to Argentina, in South America, was reported in 1981.

This paper provides a historical review of Asiatic clam (*Corbicula*) invasion and nuisance problems in the Americas, principally the United States. The First International *Corbicula* Symposium (Britton *et al.*, eds., 1979) provided considerable information on the invasion and nuisance of *Corbicula* in North America. Mattice (1979), Goss *et al.* (1979), and especially Mattice, Eng, and Collier (1979) identified resources on this problem. Isom (1975-1982) provided an updated bibliography on mollusks, including *Corbicula*. Ralph Sinclair initiated a "*Corbicula*Communication" (1971a), as did Fox, for example, in 1970, and later the *Corbicula Newsletter* became an additional source of information. McMahon (1982) provided a comprehensive review of the introduction, invasion, and spread of *Corbicula* in the United States.

Ingram (1956) was the first to develop a reporting system to indicate mollusk nuisance encountered in the water works field to assist the American Water Works Associations task group on biological infestation of purified waters. Until 1956 the principal mollusk problem was with the "faucet snail" *Bythinia tentaculata* (Linnaeus), a nuisance in some water supplies (Ingram, 1956).

The macroinvertebate and mollusk nuisance problem in water supplies is an old one (see Isom 1971). Kraepelin (1885) reported macroinvertebrates inhabiting water pipes at Hamburg. Whipple *et al.* (1927) cited incidents of biological nuisance in Rotterdam, Hartford, Boston, and Brooklyn. The National Electric Light Association (1926) reported restrictions in flow due to vegetable and animal growths in conduits. Control used was periodic manual cleaning of condensers and pipes and , in one instance, backwashing of condensers.

Clarke (1952), Feigina (1954), Ingram (1956-1959), Ray (1962), Krishnamoorthi and Rajagopalan (1967), and Morton (1975) recorded fauna associated with nuisances in drinking water supplies. Feigina (1959), Gruver (1968), Goss and Cain (1975), Goss *et al.* (1979), Isom (1971, 1976), Kirpichenko *et al.* (1962), Mattice (1979), Mikheev (1961), Sinclair (1964), Sinclair and Isom (1961,1963), Van Benthem Jutting (1953), and others have recognized nuisance mollusk problems in steam electric station water systems, hydrotechnical installations, and various industries.

HISTORY OF *CORBICULA* INVASION IN THE U.S.

Ingram (1959) first reported the potential *Corbicula* nuisance problems with the prophetic statement that, "...Asiatic clams are seen as potential pests and a threat of continued nuisance...". Ingram reviewed nuisance problems to the date including Coachella Valley Water District's water supply transported 198 km by open canal from the Colorado River at Imperial Dam. The water supply of the Metropolitan Water District of Southern California reported clam infestations in 1958. Dundee and Dundee (1958) extended the known range of *Corbicula* outside coastal areas of the west and central California to an irrigation canal in Phoenix, Maricopa County, Arizona, in June 1956. Prokopovich (1969) reported that in 1952, only one year after completion of the Delta-Mendota Canal, *Corbicula* caused serious operational problems at the Tracy Pumping Station, Tracy, California. Sinclair and Isom (1963) reviewed these early papers and records. From 1963-1970, Fox (1970) reported to the Western Society of Malacologists the invasion of the clams in the west, and in the east from published accounts.

As the clam nuisance spread continued in the western area of the U.S., *Corbicula* was found downstream of Pickwick Dam on the Tennessee River, km 327-332, October 21, 1959 (Sinclair and Ingram, 1961). Heard (1964) recorded the range

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extension of *Corbicula* to Florida, and Sickel (1973) to areas of Georgia. Other range records can be found in Sinclair (1971). However, essentially none of these papers indicate any problem with nuisance aspect of the *Corbicula* range extensions. Following the report of Fuller and Powell (1973) on the finding of *Corbicula* in the Savannah, Pee Dee, and Delaware River systems, there was a spate of complaints about *Corbicula* nuisance in power plants and industries in the Atlantic Coastal drainages, which were confirmed by Foster and Box (1976). Coincidental with the spread of *Corbicula* to the southeastern and Atlantic Coastal states was its spread to the middle and northen Interior Basin. Thomerson and Myer (1970) and Eckblad (1975) reported range extension and power plant problems with *Corbicula* on the Mississippi River at Granite City, Madison County, Illinois, and Lansing, Iowa. Subsequintly, the author discussed and visited with personnel of Commonwealth Edison Company of Illinois about real and potential problems associated with *Corbicula* in power plants throughout their system (personal communications).

Corbicula spp. are now in the northern Mississippi River drainage basin in the St. Croix River east of St. Paul and north of Hastings, Minnesota (personal communication). Clarke (1981) reported *Corbicula* in Lake Erie, and Scott-Wasilk (1982) reported *Corbicula* in a sewage plant outfall area "within the Bay Shore Station thermal plume," Ohio. Scott-Wasilk also reported that *Corbicula* occurred in the thermal plume of the Monroe Power Plant, Michigan, on the western shore of Lake Erie.

Sinclair (1971) and McMahon (1982) reviewed the spread of *Corbicula*. Ituarte (1981) Reported the introduction of *Corbicula* to the "Argentine" and South America which is further indication of its adaptability.

ASIATIC CLAM NUISANCE PROBLEMS

If not the first, the most significant early problem with Asiatic clams was in the Delta-Mendota Canal, a part of the California Central Valley project, which is about 188 km long (Anonymous, 1963; Prokopovich and Herbert, 1965). They reported the number of live and dead clams in shallow sediments (15-30 cm) was 25,000-65,000/0.092 m^2 in some places. The clams contributed significantly to the deposition of 17,330 cubic meters of sediments in 48.2 km of the canal. Prokopovich (1969) noted that not only was shell deposition a problem, but also the fact that clams clasticized suspended materials in their mucus (forming sediment bars) which was also a major contributor to the clam problem in the Delta-Mendota Canal. Eng (1979) reported population dynamics of Asiatic clams in this canal and also noted problems.

Sinclair and Isom (1961, 1963) compiled and discussed various aspects of *Corbicula* biology, spread, nuisance, control, benefits, and economic value in Phillipine and Asian habitats. Their 1961 report relates the first nuisance incidents with *Corbicula* in U.S. power plants and industries. They reported that on the Tennessee River a large number of small cooling-water pipes became sluggish with clams at several electric power stations. Two wheelbarrow loads of clams were removed from one condenser inlet water box and clams had plugged the inlets on about half of the tubes. Most of the clams were small, ranging from about 12.7-22.0 mm in size, some clams occured throughout the raw water service and the fire protection systems.

The only control measure instituted was flushing the line at regular intervals, with future plans to chlorinate the water as a control measure since it was the only practical approach to the problem at that time.

Sinclair and Isom (1961, 1963) further reported the problems that sand and gravel companies had with Asiatic clams in concrete aggretates. One sand and gravel company executive stated, "Seeing moving concrete can be unnerving" (Sinclair and Isom, 1963). Problems with clams migrating to the surface of poured concrete resulted in many gravel "beds" being abandoned.

Since the publication by Sinclair and Isom (1963), I have probably received 1,000 telephone calls or letters of inquiry concerning *Corbicula* nuisance problems. Only a few of these inquiries have ultimately been reported in the literature. Most inquires were from power companies and engineering consulting firms trying to solve immediate problems. Other inquiries were from sand and gravel companies, the Environmental Protection Agency (EPA), the Nuclear Regulatory Commission (NRC), Department of the Interior agencies, including the Bureau of Reclamation, chemical companies and vendors, State agencies, individuals reporting clam mortalities or nuisances, and individuals interested in location, utilization, and suitability of clams for food or aquaculture.

Corbicula problems have been widespread in industries and power plants over the years (Goss and Cain, 1975; and Goss *et al.,* 1979); however, with the shutdown of Arkansas Nuclear One (ANO) on September 3, 1980, due to waterline clogging with *Corbicula* shells, the issue received National attention. Following this shutdown, the Nuclear Regulatory Commission (NRC) issued IE Bulletin 81-03: "Flow Blockage of Cooling Water to Safety System Components by *Corbicula* sp. (Asiatic Clam) and *Mytilus* sp. (Mussel)," (Anonymous, 1981) which mandated licensees determine if they had a real or potential problem with Asiatic clams. This shutdown, and the resultant NRC bulletin, alerted scientists and engineers about the problems and essentially everyone in the power industry became cognizant of the potential for *Corbicula* fouling. NRC noted that *Corbicula* or *Mytilus* were significant to reactor safety"... because (1) the fouling represented an actual common cause failure, i.e., inability of safety systems redundant components to perform their intended safety functions, and (2) the licensee was not aware that safety components were fouled." Mollusk blockage problems were subsequently reported at Brunswick and Sequoyah unit 1.

The information sought by IE Bulletin 81-03 surveys should be very helpful to the industry when published by the NRC. They will also provide information on the distribution of *Corbicula* nationally in relation to nuclear power stations.

Initial testing for *Corbicula* as required by IE Bulletin 81-03 costs untold numbers of dollars. If one assumes an outage cost of $50,000 per hour per 1,000 megawatt unit, times roughly 79 operative units in the U.S., plus 50-60 under construction, these costs alone would be $3.5 million for the first evaluation and perhaps $1 million in the plants under construction. Need for continued re-evaluation of these plants due to *Corbicula* nuisance points to the tremendous economic burden caused by this clam. Other industries have similar problems with Asiatic clams that power plants do, although in most cases safety systems are not as critical. The combined outages, reductions in efficiency, capital investment in equipment, labor, and chemical control of *Corbicula* probably for exceed $1 billion annually in the U.S.

There are several unstated but common "threads" among the papers reviewed that may be of interest: (1) In most, if not all instances, problems have been the result of clams growing in the plant/industry water system, since most have water supplies that have screens with openings smaller than clams found within the systems; (2) based on the few studies that reported quantitative sampling of Asiatic clams, the average "carrying capacity" of Interior Basin streams over a long period of time is 100-200 sexually mature clams/m² (Bickel, 1966).

Based on 1,187 TVA samples from 1971-1976 in the upper Tennessee River, the *Corbicula* population mean was 93.5/m². Results from hundreds of samples from 1969-1979 revealed 131 *Corbicula*/m² in the middle Tennessee River. Sickel and Chandler (1981) reported 200 *Corbicula*/m² from the lower Cumberland River (km 106-113) in the spring of 1980. Gardner *et al.* (1976) found much higher mean densities of *Corbicula* in the Altamaha River, Georgia, when sexually immature clams were included in their samples. However, average density of first year, second year, and third year sexually mature *Corbicula* was about 70/m² each in 1979 and 1975, or a total of 210/m². When sexually immature clams were included in the data, an average density of 9,257/m² was reported in July 1974. Eng (1979) and Sickel (1979) also reported high densities from California and Georgia, respectively. Gottfried and Osborne (1982) reported 212 *Corbicula*/m² for Wekiva River, Florida, 1966-1967.

Ingram *et al.* (1964) reported 1,400-2,900 *Corbicula*/m² from the "main canal" near Parker, Arizona, in May 1963, only 16 months after the canal had been cleaned.

Data from Villadolid and Rosario (1930) on *Corbicula* taken from tributaries to Laguna de Bay, Phillipines, indicated densities from 45-235/m² which appeared to decline with altitude.

Rodgers *et al.* (1977) reported a mean population density of 18-29 *Corbicula*/m² from the New River, Virginia, at Glen Lyn which may have been low due to its recent invasion or perhaps the relatively low alkalinity (39 mg/L as $CaCO_3$) or lack of food. this should be a good reference river for comparing with more eutrophic streams and canals. There are other meager quantitative data, but they were unavailable to the author as of this writing. However, I suggest that more than 200 *Corbicula*/m² may constitute a potential for severe nuisance problems, 100-200/m² moderate problems, and fewer than 100/m² indicates potential for minor problems. These values should be derived from at least two years preoperational and two years post operational data, or four or more successive years of recorded data.

MEDIATION (METHODS) OF *CORBICULA* SPREAD

Disagreements continue about how freshwater mussels were/are dispersed. The abailable data on historical records of Unionidae should be applicable to analysis of spread of *Corbicula*. Even though Unionidae have a fish host(s), similar claims are being made as to their dispersal as those for *Corbicula*. My evaluation of the role of natural dispersion of *Corbicula* vs. distribution by man is as follows.

The role of birds should be discounted as a significant dispersal factor in the spread of Unionidae or *Corbicula*. Juvenile Unionidae have byssal attachment organs, as do *Corbicula*, and would have been dispersed by birds or waterfowl, as has been attributed to the spread of *Corbicula* McMahon (1982). However, all historical evidence is to the contrary. There are no records of endemic, Cumberlandian Unionidae, for example, outside their known ranges. Not even a relic shell record from contiguous watersheds has ever been reported. If aquatic birds, or even aquatic mammals, were a factor in mussel dispersal, it would seem logical to expect at least a few relic shell records to document these events from the thousands of years of opportunity.

McMahon (1982) raises the possibility of *Corbicula* being spread in "fish digestive tracts." In my opinion, this avenue of spread is without merit. Gut contents of several fish species that had consumed *Corbicula*, included freshwater catfish, drum, sunfish, and carp, have never revealed even a shred of *Corbicula* tissue. This was the case regardless of whether the shells were crushed or not. Thompson and Sparks (1977) discounted the dispersal of *Corbicula* by the intestinal tracts of migratory waterfowl.

Invasive Unionidae such as *Anodonta* were absent from the long historical record of the Tennessee River and tributaries as were a number of big river or "Ohioan" species upstream of Muscle Shoals prior to impoundment. A number of *Anodonta* and other genera now occur in impoundments upstream and downstream of Muscle Shoals. Unionid species have parasitic glochidia which are transported by fish. *Corbicula* do not have this type distribution due to lack of a parasitic life stage. Jenkinson (1979) concluded that *Corbicula,* as a result of their "non-swimming, pelagic, veliger larval stage," are dispersed unidirectionally as a result of water currents.

Corbicula did not get to North America from its native Asiatic habitat by natural distributional means. *Corbicula* did not cross the western mountain barrier and get into the Tennessee River by natural means of dispersal. The author's observations since 1959 and the historical records for Unionidae strongly suggest spread of *Corbicula* has been by two, and only two methods, by human mediation and passive dispersal by water currents. Early studies on Unionidae indicated that locomotion is not a significant factor in bivalve dispersal because of their highly random movements.

BENEFICIAL USES OF *CORBICULA*

In conclusion a short review of Asiatic clam benefits are presented. These benefits range from the intangible such as their use in aquaria and by sportsmen for fish bait, to their local harvest and use as food for human consumption.

History of *Corbicula* for use as food for humans, domestic animals, and wildlife is documented to the extent that we can note their benefits, but not to the extent that we can juxtapose their benefits against costs of their nuisance.

Villadolid and Rosario (1930) reported that *Corbicula manilensis* from the Laguna de Bay and its tributaries in the Phillipines were used extensively as a protein source for domestic ducks, for native "laboring class" inhabitants, and that in some cases shells were "burned" for the manufacture of commercial air-slaked lime, this was also a practice in China.

Miller and McClure (1931) reported on human consumption of *Corbicula manilensis* known in the vernacular as "Wong Sha Hin" (yellow sand clam). When found on/in mud the clams were known as "Nai Hin" or "mud clams" which were a dark color and had an inferior taste to yellow sand clams.

Caution is noted about use of raw clams for human food. Sinclair (1971) (from Cheng, 1964; Sandground and Bohne, 1940; and Van Benthem Jutting, 1953) noted that in its native range the clam is the intermediate host for Echinostome trematodes. Clams should be well cooked before eating, like pork and some fish, etc.

Gonzales and Bersamin (circa 1956) reported that *Corbicula* were a better source of dietary calcium than either oysters or clams (Paros) *Soletellina elongata* Lamarck.

Cahn (1951), Sinclair and Isom Sinclair (1963), reported that in Japan *Corbicula sandai* was protected by law which provided for a closed season and size limit. Cahn (1951) also discussed the *Corbicula japonica* fishery (for a synopsis see Sinclair and Isom, 1963, page 28).

Fox (1970) (see Mattice et al., 1979, for other Fox citations) reported that from 1963-1968, 2,240,822 pounds of *Corbicula* were sold in California for bait at a value of $234,448. Other papers relating the value of *Corbicula* as bait include Sickel et al. (1980), and Sickel and Chandler (1981). There was a large *Corbicula* fish bait industry in the lower Tennessee River prior to massive mortalities in the summer of 1977. *Corbicula* were sold for about two cents each by collectors, and four cents each by wholesalers.

There is certainly a lot of opportunity to exploit the *Corbicula* resource commercially. Historically, exploitation of "wild" populations has provided control to the extent of overharvesting and in many cases, unfortunately, to the point of extinction. Whether or not exploitation of *Corbicula* will control their nuisance will be one more interesting aspect of dealing with this introduced bivalve.

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Although this review is not all inclusive, the following persons are recognized as contributing to the awareness of the *Corbicula* problems and providing insight into solutions of the nuisance of *Corbicula*: William Marcus Ingram, Ralph M. Sinclair, Jack Mattice, Ralph Olen Fox, and N. P. Prokopovich.

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THE ZOOGEOGRAPHY AND HISTORY OF THE INVASION OF THE UNITED STATES BY *CORBICULA FLUMINEA* (BIVALVIA: CORBICULIDAE)[1]

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ABSTRACT

A survey of the collections of *Corbicula fluminea* housed in 26 museums was collated with distributional information from state agencies, private collections, and available literature to determine the present zoogeographic distribution and chronology of the invasion of these exotic bivalves in the United States waters. Results revealed *C. fluminea* is presently found in 33 states. An analysis of the historical zoogeography of *C. fluminea* in the United States indicates that man is the principal agent of its dispersal into new drainage systems and that no large-scale geographic features act as a significant barrier to dispersal. Two long-distance dispersal events have occurred in the United States; from the western states to the Ohio River in 1957, and an infestation in the Escambia River, Florida, in 1960. Accounts of the zoogeography of *C. fluminea* in each affected state are presented, as is a detailed chronology of the invasion of the United States.

Bivalves in the genus *Corbicula* Mühlfeld, 1844 were introduced into North America sometime during or before the 1920's (Counts, 1981a). Our earliest record for bivalves in the genus is at Nanaimo, Vancouver Island, British Columbia and was collected in 1924 (Counts, 1981a) The first collection of *C. fluminea* (Müller), 1774) in United States was made along the banks of the Columbia River near Knappton, Pacific County, Washington in 1938 (Burch, 1944). Since that first discovery in United States waters, *C. fluminea* has invaded nearly every major river system of the country and now threatens the Great Lakes (Clarke, 1981).

Several investigators have published summaries concerning the spread of *Corbicula fluminea* in the United States. Fox (1969-1971) presented yearly updates on its spread in which he gave new stream and state records for the year of the report. Sinclair (1961) published an annotated bibliography on *C. fluminea* in the United States which also described, in a general way, the invasion of these bivalves. Sinclair and Isom (1961, 1963) described the invasion of the Tennessee River system, and Dundee (1974) reported the zoogeography of *C. fluminea* in the United States using literature reports as well as some museum records. Britton and Morton (1979) discussed the systematics of *C. fluminea* in the United States and gave some zoogeographic data chiefly in the form of records from the Texas Christian University Museum. However, their emphasis was almost entirely systematic rather than zoogeographic.

Much of the published literature on *Corbicula fluminea* in the United States is comprised of new locality reports, i.e. new infestations of streams, lakes, or industrial water facilities. The only synthesis of these reports is that of McMahon (1982) in which he attempted to chronicle the invasion and subsequent spread of *C. fluminea* in the United States and draw conclusions about the manner by which it has successfully infested North American waters. However, his description lacked many literature reports and did not include the extensive resources of the malacological collections held in zoological museums of the United States.

The present paper describes the zoogeography of *Corbicula fluminea* in the United States and reports on the chronology of the invasion using both distributional literature and museum collection records.

TAXONOMY

There is some debate as to how many species of bivalves in the genus *Corbicula* are currently present in the United States. Corbiculid clams in this country have been reported using the taxa *Corbicula fluminea, Corbicula leana* Prime, 1864, *Corbicula manilensis* (Philippi, 1844), and *Corbicula sinensis nomen dubium*. While McLeod and Sailstad (1980) and Hillis and Patton (1982) have presented electrophoretic evidence for two species, their studies are as yet inconclusive. Thus, I will use the taxon *C. fluminea, sensu*

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Britton and Morton (1979), for all populations of corbiculid bivalves reported in this study.

MATERIALS AND METHODS

Zoogeographic records for *Corbicula fluminea* were obtained from the malacological collections of the museums listed below. Also included are records provided by several state environmental agencies. An acronym for each institution or agency, as it appears in the results section of this paper, are given in parentheses. The museums are: the Academy of Natural Sciences, Philadelphia (ANSP); the California Academy of Sciences, San Francisco (CAS); the Cincinnati Museum of Natural History (CMNH); the Dallas Museum of Natural History (MNHD); the Delaware Museum of Natural History, Greenville (DMNH); the Field Museum of Natural History, Chicago (FMNH); the Florida State Museum, University of Florida, Gainesville (FSM); the Fort Worth Museum of Science and History (FWM); the Houston Museum of Natural Science (HMNS); the Illinois State Museum, Springfield (ISM); the Marshall University Malacological Collection, Huntington, West Virginia (MUMC); the Milwaukee Public Museum (MPM); the Mississippi Museum of Natural Science, Jackson (MMNS); the Museum of Comparative Zoology, Harvard University, Cambridge, Massachusetts (MCZ); the Museum of Northern Arizona, Flagstaff (MNA); the National Museums of Natural Science, Ottawa, Canada (NMNS); the North Carolina State Museum of Natural History, Raleigh (NCSM); the Ohio State University Museum of Zoology, Columbus (OSUM); the Peabody Museum of Natural History, Yale University, New Haven, Connecticutt (PMNH); the San Diego Museum of Natural History (SDMNH); the Santa Barbara Museum of Natural History (SBMNH); the Stanford University Museum, Stanford, California (SU); the State Biological Survey of Kansas, Lawrence (SBSK); the Thomas Burke Memorial Washington State Museum, University of Washington, Seattle (TBWSM), the United States National Museum of Natural History (USNM); the University of Cincinnati Geological Museum (UCGM); and the University of Oklahoma Museum, Norman (UOM). Museum records from the Texas Christian University Museum (TCU) were published by Britton and Morton (1979).

Other distributional records were provided by C. Dale Snow, Oregon Department of Fish and Wildlife (ODFW), Alan C. Buchanan and Ron D. Oesch, Missouri Department of Conservation (MDC), and Robert Singleton, Arkansas Department of Pollution Control and Ecology (ADPC). Gary A. Coovert (GAC), Dayton, Ohio and David Metty (DM), Cincinnati, Ohio generously provided records from their private collections. Constance E. Boone (CEB) of HMNS provided additional information on Texas populations. R. Tucker Abbott (RTA) and Robert Bullock (RB), University of Rhode Island, and Russell Jensen (RJ) provided Florida records. Richard L. Reeder, University of Tulsa, provided Oklahoma records and Steven L. Coon (SLC) and James J. Hall (JJH) provided records for southern California and North and South Carolina, respectively. Stavros Howe (SH) provided information on Delaware populations.

All information concerning locations of populations of *Corbicula fluminea* gathered from these sources was collated with the available zoogeographic literature and placed in a computerized data base at the University of Delaware. Categories of encoded information were month and year of collection or first report of the population, body of water infested, state, county, nearest city to population site, locations and catalog numbers of museum specimens, literature report citations, and latitude and longitude. Records were then sorted by state, year, and major drainage.

All records were assembled into individual state accounts and, the zoogeography of the species was plotted on base maps for each state. Year records were used to plot chronologic maps of the invasion of the United States waters.

RESULTS

The review of museum records and literature reports revealed that *Corbicula fluminea* now inhabits the waters of 33 states. An account of the zoogeography of these bivalves in individual states is presented below. Following the name of each body of water infested by *C. fluminea* is the acronym for the record source or literature citation.

ALABAMA

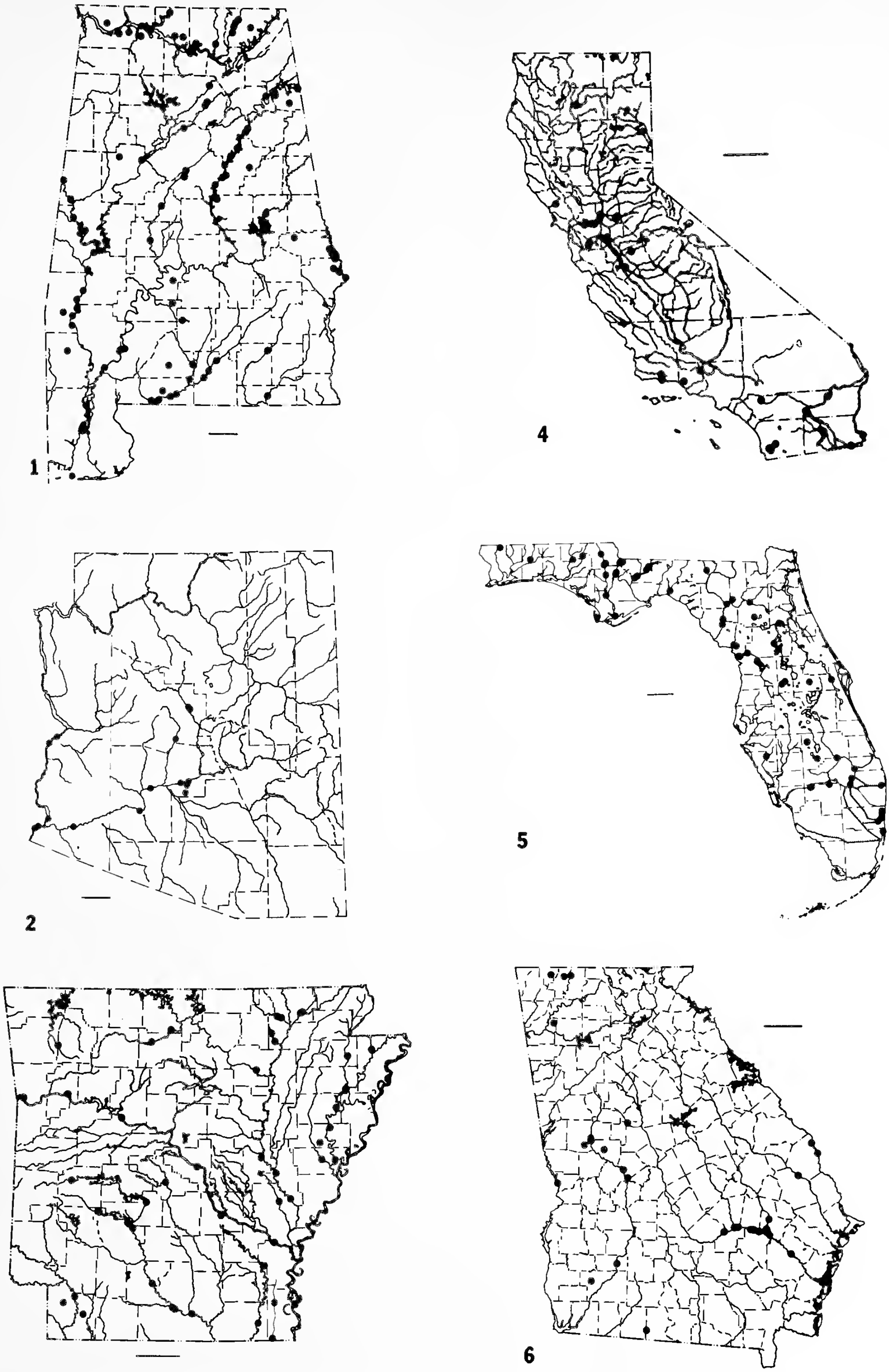
(Fig. 1)

Corbicula fluminea was first reported in Alabama in the Mobile River in 1962 (Hubricht, 1963). In the fall of 1964 it was found in the Alabama River (Hubricht, 1965) and the following year it appeared in the Cahaba and Tombigbee rivers and in Sucanochee Creek (Hubricht, 1966).

Shealy (1966) reported predation of *Corbicula fluminea* by the Alabama map turtle, *Graptemys pulchra* Baur, in the Conecuh River of the Escambia River system. This predation did not significantly reduce the *C. fluminea* population in that stream.

Jenkinson (1979) reported the occurrence of *Corbicula fluminea* in the main streams and tributaries of the Chattahoochee and Tallapoosa rivers in east-central Alabama in 1973. He noted that the population in Saugahatchee Creek, a tributary of the Tallapoosa River, is apparently thriving in waters receiving effluents from a textile mill, a sewage treatment plant, and runoff from the experimental ponds of Auburn University. *C. fluminea* was usually found in clay and sand substrata in these streams.

Corbicula fluminea has been found in the following waters of Alabama: Alabama River (MCZ; USNM; Hubricht, 1966), Big Cedar Creek (OSUM), Big Nance Creek (OSUM), Black Warrior River (FMNH; MCZ; OSUM; TCU), Buck Creek (OSUM), Burnt Corn Creek (OSUM), Cahaba River (OSUM; Hubricht, 1966), Cedar Creek (OSUM), Chattahoochee River (Jenkinson, 1979), Choctawhahatchee River (FSM), Conecuh River (OSUM; UF; Shealy, 1976), Coosa River (DMNH; NMNS; OSUM; USNM), Cypress Creek (USNM), Dauphin Island (USNM), Drivers Branch (FSM), Elk River (FSM), Escambia River (Hubricht, 1963), Flint River (FSM), Gantt Lake (FSM), Indian Creek (OSUM), Limestone Creek (OSUM), Little Cypress Creek (OSUM), Little Uchee Creek (OSUM; Jenkinson, 1979), Locust Fork (NMNS), Mobile River (Hubricht, 1966), Mud Creek (FSM), Murder



Figs. 1 - 6. Zoogeographic distribution of *Corbicula fluminea* in Alabama (1), Arizona (2), Arkansas (3), California (4), Florida (5), and Georgia (6). Scale bar = 50 km.

Creek (OSUM), Neely Henry Lake (Britton and Morton, 1979), North River (OSUM), Okatuppa Creek (FSM), Paint Rock River (DMNH; FSM; MCZ; OSUM; USNM), Pea River (FSM), Peckerwood Creek (OSUM), Piney Creek (OSUM), Santa Bouge Creek (FSM), Saugahatchee Creek (Jenkinson, 1979), Second Creek (OSUM), Sucarnochee Creek (Hubricht, 1966), Sepulga River (FSM), Tallapoosa River (Jenkinson, 1979), Tennessee River (ISM; NMNS; OSUM), Terrapin Creek (OSUM), Tombigbee River (MCZ; OSUM; USNM; Hubricht, 1963, 1966), Town Creek (OSUM), Tubbs Creek (FMNH), and Uchee Creek (Jenkinson, 1979).

ARIZONA

(Fig. 2)

Dundee and Dundee (1958) made the first report of *Corbicula fluminea* in Arizona from collections made at Papago Park, Phoenix in 1956. Keup *et al.* (1963) later reported *C. fluminea* from Main Canal near Parker.

Minickley *et al.* (1970) found that *Corbicula fluminea* was a food of three species of buffalo fishes *(Ictiobus bubalus [*Rafinesque*], Ictiobus cyprinellus [*Valenciennes*]* and *Ictiobus niger [*Rafinesque*])* in Apache and Roosevelt lakes in central Arizona. Veligers, juveniles, and small adults were consumed by these fishes. Rinne (1974) noted that the highest densities of *C. fluminea* in these lakes occurred on rock rubble slopes and increased directly with the complexity (numbers of components) of the substrata. He also noted that numbers of these clams increased with depth and position downlake from inflow areas with high turbidity.

Bequaert and Miller (1973) reported *Corbicula fluminea* to be common in the Colorado, Gila, and Verde rivers by 1972. Dundee (1974) also reported *C. fluminea* from Lake Meade in the Colorado River drainage.

Corbicula fluminea reported from the following Arizona waters: Agua Fria River (Bequaert and Miller, 1973), Colorado River (ANSP; NMNS; Bequaert and Miller, 1973), Gila River (Bequaert and Miller, 1973), Lake Martinez (SBMNH; SDMNH), Salt River (CAS; SDMNH; Dundee and Dundee, 1958), Verde River (DMNH; MNA), and several irrigation systems (MCZ).

ARKANSAS

(Fig. 3)

Fox (1970a) reported *Corbicula fluminea* from the St. Francis River in the northeastern portion of the state where densities of these clams reached 21/yd². He also reported *C. fluminea* from the lower Ouachita River in the southwestern portion of the state. These were the first published reports of *C. fluminea* in Arkansas.

Kraemer (1976) found *Corbicula fluminea* in the Arkansas River at river mile 43. Kraemer (1977) later reported these bivalves at river mile 171 and said that they were ubiquitous from below Ft. Smith downstream to Lock and Dam No. 3. Kramer (1976) believed it is unlikely that *C. fluminea* invaded the Arkansas River before the mid-1960's.

Corbicula fluminea has also been reported from the Buffalo River (Kraemer, 1978, 1979), Chamagnoll Creek and the Caddo River (Britton and Morton, 1979) as well as from the White River (Kraemer, 1980).

Corbicula fluminea is reported from the following Arkansas waters: Arkansas River (Kraemer, 1977), Bayou Bartholomew (ADPC), Black River (MCZ; OSUM), Boeuf River (ADPC; OSUM), Buffalo River (ADPC; OSUM), Caddo River (ADPC; TCU), Chamagnoll Creek (TCU), Coon Bayou (OSUM), LaGrue Bayou (FSM), L'Anguille River (OSUM), Little River (MCZ), Madison - Mariana Diversion Canal (OSUM), Maniece Bayou (OSUM), McKinney Bayou (OSUM), Mississippi River (OSUM), Ouachita River (ADPC; FSM; OSUM; TCU), Red River (OSUM), Saline River (FSM), St. Francis River (OSUM, Spring River (OSUM), Strawberry River (ADPC; OSUM), and White River (FSM; OSUM; USNM; Kraemer, 1980).

CALIFORNIA

(Fig. 4)

Corbicula fluminea was first discovered in California in the Sacramento River north of Pittsburg in 1945 (Hanna, 1966). It apparently spread from this region to foul many of the canals surrounding the San Francisco Bay estuary and the Central Valley. It has been reported from Mayberry Cut and the Contra Costa Canal (Ingram, 1959), and the South Bay Aqueduct (Morgester, 1967).

Invasion of the Delta-Mendota Canal in the Central Valley has been well documented. prokopovich and Hebert (1964) and Prokopovich (1969, 1970) noted that an increased deposit of clastic sediments was attributable to these bivalves binding susupended sediments with mucus and in their feces as well as decreasing water flow as a result of mounds of dead shells.

Eng (1975) reported on the biology of *Corbicula fluminea* in the Delta-Mendota Canal in a detailed study for the California Academy of Sciences. Eng (1976) also found the oligochaete, *Chaetogaster limnaei* von Baer, 1827, living and feeding on the lateral grooves of the gills of *C. fluminea* from the Delta-Mendota Canal. Of those clams examined in March 1974, 87% were infested. Less than 3% were infested in other months. These oligochaetes were believed to be commensal. In a later paper, Eng (1979) discussed the population dynamics and growth of these bivalves in the Delta-Mendota Canal. Behrens (1975) reported the survival and growth of these bivalves in beverage containers and, in one instance, a locked fishing tackle box, taken from the canal.

Sigfried *et al.* (1980) discussed the occurrence of *Corbicula fluminea* in the San Francisco Bay estuary in 1976 when conditions were dry. *C. fluminea* dominated the benthos with the bivalve *Macoma balthica* (L. 1758) the amphipods *Corphium stimpsoni* and *C. spinicoine,* nematodes, and a spinonid polychaete, *Boccardia ligerica*. They determined that the factors controlling the size and composition of the benthos were salinity and sediment composition. They further reported that the population of *C. fluminea* peaked in March and noted that previous studies (Fisk and Doyle, 1962; Hazel and Kelley, 1966) showed population peaks in January. Their estimates of population densities for the estuary ranged from 2,000 m^{-2} to 14,500 m^{-2} as compared with the 312 m^{-2} estimate of Fisk and Doyle (1962) for 1960-1961.

Carlton (1973) discovered *Corbicula fluminea* in Stow Lake, Golden Gate Park, San Francisco. This represented the first finding of these bivalves on the peninsula.

Corbicula fluminea was discovered in the Imperial Valley of southern California in 1953 (Fitch, 1953). It has since fouled many of the major aqueducts and reservoirs in this portion of the state including the Colorado Aqueduct (Fox, 1970a), the Los Angeles Aqueduct (Fox, 1972), the San Jacinto Reservoir (Fox, 1972), Lake Jennings (Richardson et al., 1970), and Lake Matthews (Fox, 1972). The Coachella Water District (Fitch, 1953) and the Gene and Hayfield pumping plants of the Colorado Aqueduct have also experienced biofouling by *C. fluminea*. Fox (1970b) and Bequaert and Miller (1973) reported that the bivalve had infested the Salton Sea basin and had crossed into the Baja of Mexico.

Richardson et al. (1970) noted that the blue catfish, *Ictalurus furcatus* (LeSueur) commonly fed on *Corbicula fluminea* in Lake Jennings. They did not believe, however, that *I. furcatus* would appreciably limit the size of *C. fluminea* populations where the two species are found together.

Corbicula fluminea is found in the following California waters: Alamao Canal (SDMNH), All American Canal (CAS), Anaheim Bay (SBMNH), Coachella Valley Water District (CAS; FMNH), Cahuma Lake (SBMNH), Colorado Aqueduct (DMNH; USNM), Columbia River (CAS), Delta-Mendota Canal (DMNH; TCU; Eng, 1979; Prokopovich, 1969), Dyer Canal (Morgester, 1967), El Capitan Reservoir (Fast, 1971), Evans Lake (ANSP; DMNH), Lake Casitas (SLC), Lake Jennings (Richardson *et al.*, 1970), Lake Murray (TCU), Lake Piru (SLC), Livermore Canal (Morgester, 1967), Mayberry Cut (CAS: Ingram, 1959), Merced River (SBSK), Mokelumne Aqueduct (CAS), Mokelemne River (PMNH, SDMNH, SU), Owens River (Fox, 1972), Potatoe Slough (CAS), Russian River (CAS), Sacramento River (ANSP, CAS, GAC, TCU, USNM; Hanna, 1962, 1966), Salinas River (TCU), Salton Sea (CAS, SBMNH), San Diego City Water Works (SBMNH), San Francisco Bay (CAS), San Jacinto Reservoir (Fox, 1970a), San Joaquin River (ANSP, CAS, SBMNH, SU), San Luis Reservoir (TCU), Santa Ana River (ANSP), Santa Barbara Harbor (SBMNH), Shasta Lake (CAS), South Bay Aqueduct (Prokopovich, 1968), Stanislaus River (OSUM), Stow Lake (Carlton, 1973), Tolumne River (CAS, Ingram, 1959).

DELAWARE

Although *Corbicula fluminea* has been reported on the Delmarva peninsula from states surrounding Delaware (Stotts *et al.*, 1977; Counts, 1981b) no reports of the species within the geopolitical borders of the state have yet appeared in the literature. The present report represents the first published record of *C. fluminea* in Delaware.

Nanticoke River (SH).

FLORIDA

(Fig. 5)

The earliest reports of *Corbicula fluminea* in Florida are those of Heard (1964, 1966). Heard (1964) reported *C. fluminea* in the Apalachicola, Chipola, and Withlacoochee rivers. He later hypothesized that upon the completion of the Cross-Florida Barge Canal, *C. fluminea* could move across the state to inhabit the St. Johns River system (Heard, 1966). This hypothesis has since been proved correct. Gifford (1974) found *C. fluminea* in the Cross-Florida Barge Canal and reported that these bivalves reached a biomass of 500 g live tissue/m^2.

Schneider (1967) found *Corbicula fluminea* in the Escambia River during a survey by the Florida State Board of Health in 1960. He believed these bivalves invaded the Escambia River sometime in 1957. *Corbicula fluminea* was found in the Apalachicola River, near the Chattahoochee River in 1961. By 1967, *C. fluminea* ranged from the Escambia River near Century to the Withlacoochee Inglis.

Clench (1970) found that *Corbicula fluminea's* range extended into the Caloosahatchee River - Lake Okeechobee system. He hypothesized that their presence in the system may lead to the spread of *C. fluminea* throughout all of southern Florida.

Deaton (1981) found *Corbicula fluminea* in the Ochlocknee River in waters of about 0.1 ppt S and in association with the native unionid bivalve *Lampsilis claibornensis* (Lea, 1938).

Corbicula fluminea has been found in the following Florida waters: Apalachicola River (DMNH; FSM; OSUM; Heard, 1964; Schneider, 1967), Aucilla River (OSUM), Calossahatchee River (DMNH; OSUM; Clench, 1970), Chipola River (FMNH; FSM; Heard, 1964), Chochtawahatchee River (FSM), Cypress Creek Canal (OSUM), Escambia River (OSUM; Schneider, 1967), Ft. Lauderdale Canal (USNM), Grassy Lake (OSUM), Holmes Creek (FSM), Ichetucknee River (FSM), Indian Prairie Canal (DMNH), Kissimmee River (FSM), Lake Buena Vista (RJ), Lake Hippochee (MCZ; OSUM; Clench, 1970), Lake Jackson (OSUM), Lake Lucy (FSM), Lake Okeechobee (ANSP; DMNH; FSM; MNHD; OSUM), Lake Oklawaha (FSM), Lake Palatlakaha (FSM), Lake Talquin (FSM), Lake Tsala (ANSP), Main Canal (FSM), Mayakka River (OSUM), Middle River Canal (OSUM), Mosquito Creek (USNM), North Mosquito Creek (OSUM), Ochlocknee River (FSM; OSUM; Heard, 1966), Oklawaha River (FSM; OSUM; USNM), Rocky Creek (FSM), St. Joe Bay (FSM), St. Johns River (OSUM; RTA), Santa Fe River (FSM), Sky Lake (OSUM), Spring Creek (FSM; OSUM; USNM), Steinhatchee River (DMNH), Suwannee River (FSM), Waccassa River (FSM), Wekiva River (RB), Withlacoochee River (MCZ; USNM), and Yellow River (FSM).

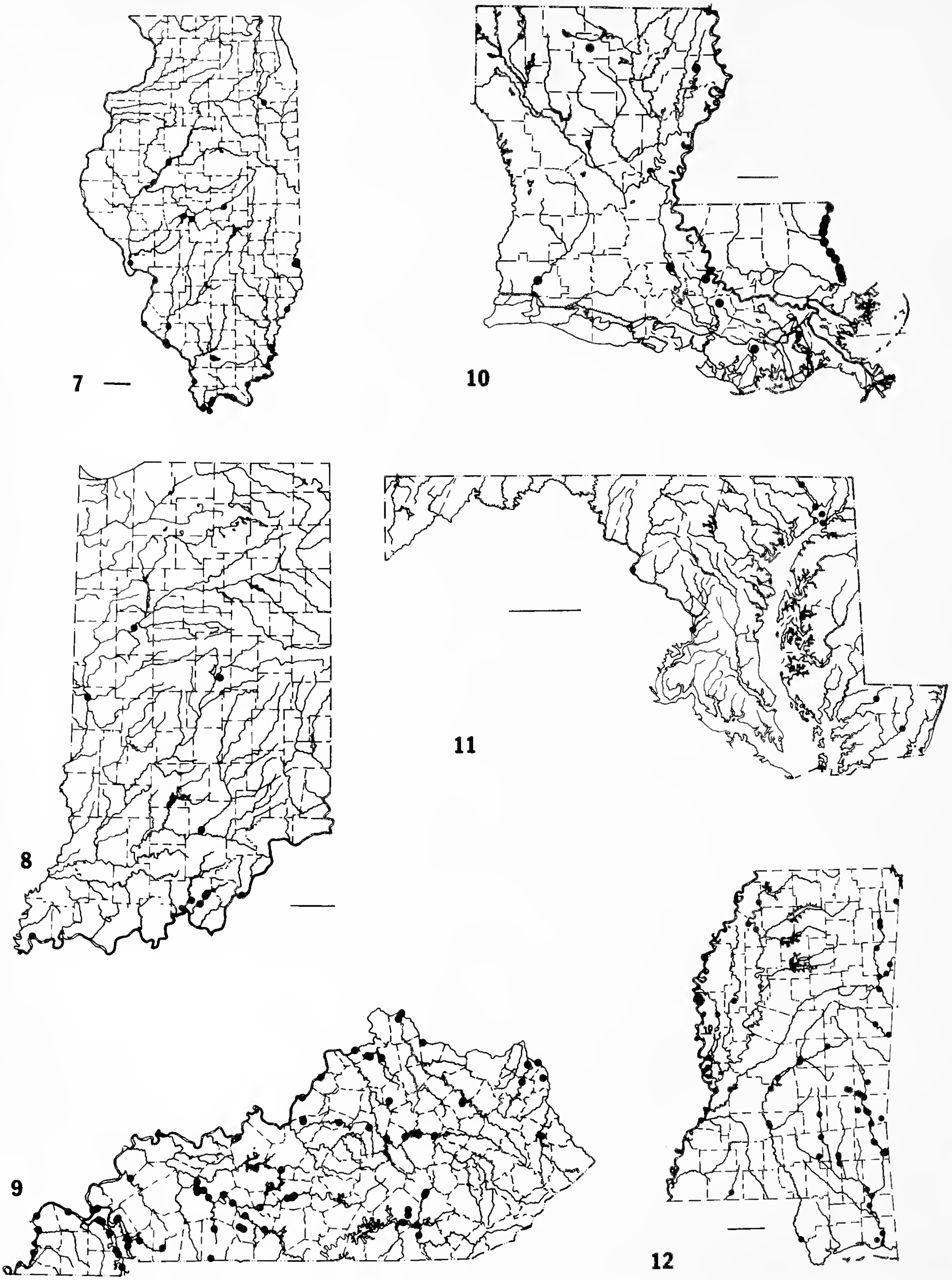
GEORGIA

(Fig. 6)

The first specimens of *Corbicula fluminea* reported in Georgia were collected from the Altamaha River in 1971 near river mile 116 (Sickel, 1973). Later, in 1971, populations were also found in the Ocmulgee and Flint rivers (Sickel, 1973). The Flint River and the Altamaha River populations were found in association with *Lampsilis anodontoides floridensis* (Lea, 1852), *Lampsilis uniominatus* (Simpson, 1900), and *Quincuncina infucata* (Conrad, 1834) in coarse sand substrata (Sickel, 1973).

Sickel (1976) reported that the Altamaha River population increased to a density of more than 2500/m^2 between 1971 and 1974. However, Gardner *et al.* (1976) reported densities of 10000/m^2 in 1974 in some localities in the Altamaha River. These population increases were accompanied by a decline in populations of unionid bivalves (Gardner *et al.*, 1976).

Fuller and Powell (1973) reported *Corbicula fluminea* in the Savannah River in 1972. Fuller and Richardson (1977) noted the success of *C. fluminea* in that river and reported that these bivalves actively uproot unionid bivalves.



Figs. 7 - 12. Zoogeographic distribution of *Corbicula fluminea* in Illinois (7), Indiana (8), Kentucky (9), Louisiana (10), Maryland (11), and Mississippi (12). Scale bar = 50 km.

Walker (1982) reported mass mortalities of *Corbicula fluminea* in the Towaliga River, a tributary of the Ocmulgee River, in 1981. He believed a similar mortality occurred in the same stream in 1980. However, no causitive factor was identified for these mass mortalities.

Corbicula fluminea has been found in the following Georgia waters: Altamaha River (DMNH; FSM; OSUM; Gardner *et al.*; Sickel, 1973, 1976, 1979), Chattahoochee River (USNM), Chickamauga Creek (OSUM), Chickasawhatchee River (FSM), Coahulla Creek (OSUM), Consauga River (OSUM), Flint River (OSUM; USNM; Sickel, 1973), Lake Allatoona (OSUM), Little Ocmulgee River (OSUM), Ocmulgee River (OSUM; USNM; Sickel, 1973, 1979), Ogeechee River (FSM), Ohoopee River (FSM; OSUM; USNM), Oostanula River (OSUM), Potatoe Creek (OSUM), Pound Creek (OSUM), Savannah River (FSM; Fuller and Powell, 1973), Towaliga River, and Withlacoochee River (FSM).

HAWAII

Corbicula fluminea has been sold as food in Kailua, Oahu Island in the Open Market (Burch, 1978). Burch (1978) reported that several shipments have been intercepted by the Department of Agriculture Plant Quarantine Office. These clams were imported from the Orient and from California. As yet, however, no populations have been reported from the streams of Hawaii.

IDAHO

The only report of *Corbicula fluminea* in Idaho is that of Ingram (1959). He noted the presence of a population in the Snake River at the Wasington-Idaho border.

ILLINOIS

(Fig. 7)

The oldest record of *Corbicula fluminea* in Illinois is that of Fetchner (1962) for Massac County along the Ohio River. Parmalee (1965) later reported the spread of *C. fluminea* in the Ohio River of Illinois and found specimens at 18 localities in the rivers and streams of the southern border counties including the Mississippi, Ohio, and Wabash rivers. Parmalee believed that *C. fluminea* became established in the Ohio River in Illinois in 1961 and that populations in the three rivers of the state were descendents of populations from the Cincinnati Reach of the Ohio River (Keup *et al.*, 1963). Populations in the Wabash River were the youngest being approximately 2 years old in 1964 (Parmalee, 1964). Substrata for the Illinois populations reported by Parmalee varied from silt-sand and mud slab-like cobbles. However, densest populations were found in sand substrata.

Thomerson and Myer (1970) reported large populations of *Corbicula fluminea* inhabiting the cooling system of the Granite City Steel Company's plant at Granite City in 1969. The intake pipe for the plant's water system was at Lock and Dam 27 of the Chain and Rocks Canal of the Mississippi River. They believed *C. fluminea* became abundant at that site in 1966. Specimens from this locality were later used to determine the effects of potassium on larval and adult *C. fluminea* by Anderson *et al.* (1976).

Thompson and Sparks (1977) found populations of *Corbicula fluminea* in the Illinois River and noted that waters are generally warmer in areas where the bivalves are found. They believed the clams became established sometime between 1970 and 1971.

Klippel and Parmalee (1979) found that *Corbicula fluminea* were the most frequently recovered bivalve in Lake Springfield of the Sangamon River. Lake Springfield is an impoundment constructed in 1935 and *C. fluminea* probably became established there in the 1970's.

Lewis and Brice (1980) commonly found *Corbicula fluminea* in the Kankakee River. The location at which *C. fluminea* was abundant did not receive thermal discharge, a condition that has been credited with the success of the northern populations in Minnesota (Cummings and Jones, 1978).

Corbicula fluminea has been reported from the following Illinois waters: Crab Orchard Lake (Thompson and Sparks, 1977), Illinois River (OSUM; Thompson and Sparks, 1977), Kankakee River (Lewis and Brice, 1980), Kaskasia River (Thompson and Sparks, 1977), Mississippi River (OSUM; Thomerson and Myer, 1970), Ohio River (FMNH; ISM; NMNS; OSUM; Fetchner, 1962), Saline River (OSUM), Sangmon River (Klippel and Parmalee, 1979; Thompson and Sparks, 1977), and Wabash River (FMNH; ISM; OSUM).

INDIANA

(Fig. 8)

Fox (1969) reported *Corbicula fluminea* in the Ohio River of southern Indiana. No specific locality information was reported. Taylor (1982) collected *C. fluminea* in three of seven localities in Big Indian Creek, a tributary of the Ohio River. No other published reports of *C. fluminea* in Indiana are known.

Metty (Personal communication, 1979) found *Corbicula fluminea* in the East Fork of the White River near the Indiana-Ohio state line.

Corbicula fluminea has been found in the following Indiana waters: Big Indian Creek (MUMC), Blue River (OSUM), Ohio River (OSUM), Salt Creek (OSUM), Stoney Creek (OSUM), Wabash River (OSUM), and White River (DM).

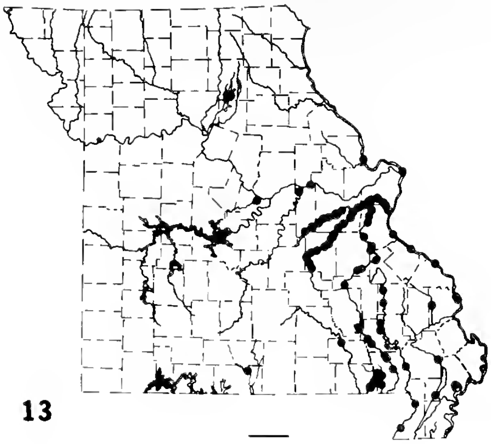
IOWA

The only report of *Corbicula fluminea* in Iowa is that of Eckcald (1975). It was found in the thermal effluent from an electric power generating station at Lansing in 1974. Eckbald believed the oldest clams at this site were 2 years old. They reached a density of 200/m^2 in some areas.

KENTUCKY

(Fig. 9)

The first report of *Corbicula fluminea* in Kentucky is that of Sinclair and Isom (1961) who reported the collection of specimens at the Shawnee Steam Plant at Paducah on the Ohio River in 1957. This initial collection was later described by other investigators (Bates, 1962a, b; Stein, 1962) and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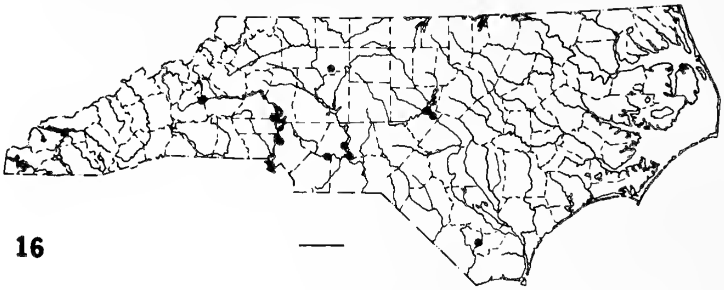
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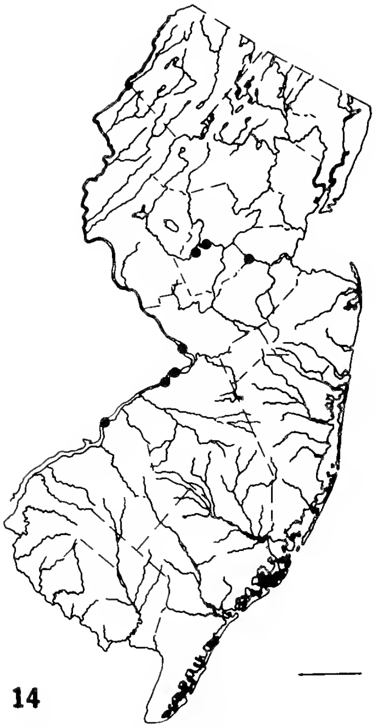
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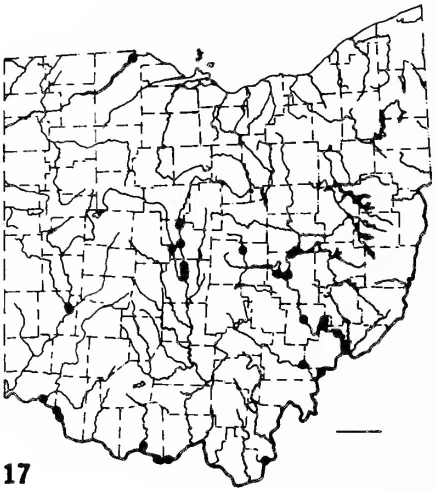
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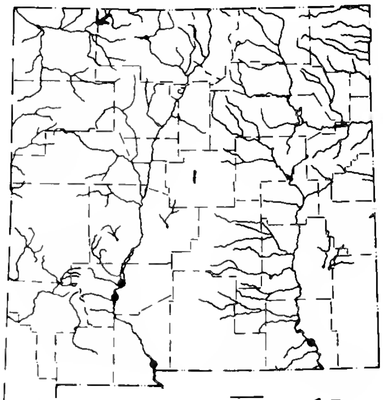
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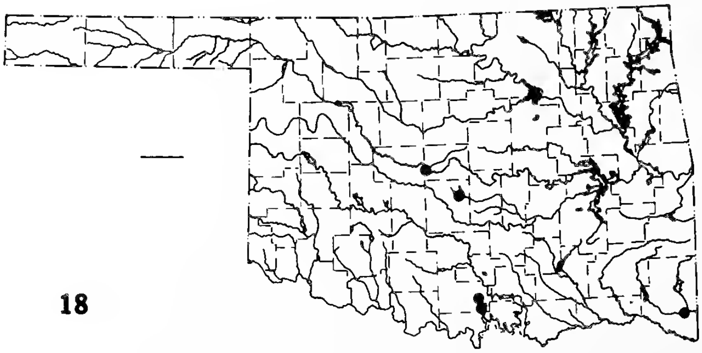
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Figs. 13 - 18. Zoogeographic distribution of *Corbicula fluminea* in Missouri (13), New Jersey (14), New Mexico (15), North Carolina (16), Ohio (17), and Oklahoma (18). Scale bar = 50 km.

also represents the first collection of *C. fluminea* east of Arizona.

Bates (1962a) noted the presence of *Corbicula fluminea* in the Tennessee River at Kentucky Reservoir and in a later paper (Bates, 1962b) reported the presence of populations in the Green River. Stein (1962) reported the collection of more than 200 specimens from the Ohio River at Dayton, Kentucky, that were living in filamentous green algal mats.

Bickel (1966) described the ecology of *Corbicula fluminea* in the Ohio River at Louisville and noted that spring mortalities seemed to be an annual occurrance.

Branson and Batch (1969) reported the occurrence of *Corbicula fluminea* in the Kentucky and Red River systems and noted that the first infestation of the Red River probably occurred sometime after 1966. In 1968 they reported the collection of specimens in the Cumberland and Tennessee Rivers (Branson and Batch, 1971)

Williams (1969) described populations of *Corbicula fluminea* from the Green and Tennessee Rivers and reported that these bivalves contituted 99% of all living mussels collected in those rivers. He further reported on the collection of *C. fluminea* from the Green River at Mammoth Cave National Park in 1968. Similar collections by Bates (1962b) failed to reveal the presence of *C. fluminea* at that locality in 1962. Isom (1974) noted the continued presence of *C. fluminea* in the Green River.

Blankenship and Crockett (1972) reported the first occurrence of *Corbicula fluminea* in the Rockcastle River for collections made in 1968 at Livingston.

Sickel *et al.* (1980) and Sickel and Chandler (1981) reported on mass mortalities of *Corbicula fluminea* populations in the Cumberland River in 1978 and noted similar occurrences in Barkley Lake. They further discussed the possible commerical exploitation of *C. fluminea* populations as a fish bait.

Taylor (1980) reported *Corbicula fluminea* in Tygarts Creek in Carter and Greenup counties of eastern Kentucky. Substrata at his collection localities varied from mud covered by algal mats to shale rubble and sand.

Sickel and Lyles (1981) noted the first occurrence of the presumed commensal *Chaetogaster lymnaei* with *Corbicula fluminea* living in Barkley Lake. The oligochaete was found on the gills and foot with an incidence of infestation greater than 80%.

Corbicula fluminea has been found in the following waters of Kentucky: Buck Creek (OSUM), Coal River (MUMC), Cumberland River (FMNH; OSUM; Branson and Batch, 1971; Sickel and Chandler, 1981; Sickel and Lyles, 1981), Dix River (Branson and Batch, 1971), Eagle Creek (MUMC), Elkhorn Creek (MUMC), Floyds Fork (DMNH; MUMC; OSUM), Gasper River (OSUM), Green River (FWM; MCZ; MUMC; NMNS; OSUM; USNM; Bates, 1926b; Williams, 1969), Kentucky River (OSUM; Branson and Batch, 1969), Licking River (CMNH), Little River (OSUM), Mississippi River (FMNH), Mud River (OSUM), Nolin River (MUMC), Ohio River (OSUM; Bickel, 1966; Sinclair and Isom, 1961; Williams, 1969), Red River (OSUM; Branson and Batch, 1969), Rockcastle River (FWM; OSUM), Salt River (OSUM), Silver Creek (Branson and Batch, 1969), Slate Creek (MUMC; OSUM), Tennessee River (Sickel *et al.*, 1981), Tradewater River (OSUM), and Tygarts Creek (MUMC).

LOUISIANA

(Fig. 10)

Stein (1962) made the first report of *Corbicula fluminea* from Louisiana waters. These bivalves were collected in the Mississippi River in 1961. However, no precise locality data were published concerning these specimens and none accompanied the specimen's collection label (OSUM 4416). Dundee and Harman (1963) found *C. fluminea* in benthic samples taken from the Calcasieu River in 1961 and from Bayou Magasille and Bayou Sorrel in 1962.

Gunning and Suttkus (1966) found *Corbicula fluminea* throughout the lower Pearl River system and speculated, based on shell measurements, that it became established in the Pearl River in 1959. *Corbicula fluminea* was abundant in sand, gravel, silt, and mixtures of these substrata types in the Pearl River (Gunning and Suttkus, 1966).

Kuckyr and Vidrine (1975) reported *Corbicula fluminea* to be the most abundant of 21 species of bivalves collected in the Tensas River of southern Louisiana. Vidrine and DeRouen (1976) found that *C. fluminea* inhabited most of the streams of the Bayou Teche system of southeast Louisiana.

Corbicula fluminea has been reported from the following Louisiana waters: Bayou Cocodrie (Vidrine and DeRouen, 1976), Bayou Magasille (Dundee and Harman, 1963), Bayou Sorrel (HMNH; Dundee and Harman, 1963), Calcasieu River (Dundee and Harman, 1963), Mississippi River (OSUM), Pearl River (FMNH; USNM; Gunning and Suttkus, 1966), Red River (*Corbicula* Newsletter, 1982), Tensas River (Kuckyr and Vidrine, 1975), and an unnamed creek in Lincoln Parish (FSM).

MARYLAND

(Fig. 11)

Stotts *et al.* (1977) made the first report of *Corbicula fluminea* from Maryland. Specimens were collected at Susquehanna Flats of the northern reaches of the Chesapeake Bay on silt-sand to hard substrata near Turkey point and Havre-de-Grace. Stotts *et al.* (1977) noted the *Corbicula fluminea* have been in the bay since 1975. Nichols and Domermuth (1981) noted that populations of *C. fluminea* are present in the Susquehanna River at Conowingo Dam. These clams may have been the population of origin for those populations at Susquehanna Flats.

Dresler and Cory (1981) reported the discovery of *Corbicula fluminea* in the Potomac River at the center of Washington, D. C. (RM 89) to the mouth of Piscataway Creek (RM 84.5) in 1976. They further discussed the fouling of the Potomac Electric Power steam generating station that was so seriously infested that live clams, dead shells, and silt build-up caused operational problems.

Counts (1981b) made the first report of *Corbicula fluminea* in waters of the Eastern Shore. Specimens were found in the Wicomico River at Salisbury. No fouling problems have been associated with Eastern Shore populations.

Records for *Corbicula fluminea* in Maryland include: Chesapeake Bay (Stotts *et al.*, 1977), Nasawango Creek (USNM), Potomac River (OSUM; USNM; Dresler and Cory, 1980), Susquehanna River (Nichols and Domermuth, 1981), and Wincomico River (Counts, 1981b).

MICHIGAN

The only report of *Corbicula fluminea* in Michigan is that of Clarke (1981). Specimens were found on sand substratum in 1.3 m of water approximately 305 m south of the mouth of Sandy Creek. No other bivalves were found at this locality. Scott-Wasilk, (Personal communication, 1983) reported that these bivalves are living in a thermal plume from a power station and have survived the winters since their discovery. Other specimens from this locality are in the collection of OSUM and USNM.

MINNESOTA

Corbicula fluminea has been reported from only one locality in Minnesota. Specimens were found in a small lake that received thermal effluent from Northern States Power Company Blackdog electric generating station, and others were found in the channel of the Minnesota River downstream from the plant (Cummings and Jones, 1978). Live specimens that were collected at these sites were approximately 3 years old. The shells, both live and dead, varied in height from 6 to 44 mm and were thought to represent individuals ranging in age from 1 to 5 years old. Although the proportionately large number of empty shells suggested a mass mortality, no causative agent could be identified.

MISSISSIPPI

(Fig. 12)

Heard (1966) first discovered *Corbicula fluminea* in Mississippi in the Yazoo River at Vicksburg in 1963. Heard also reported on populations in the Coldwater and Leaf rivers. Grantham (1967) reported *C. fluminea* in the Chickasawhay, Pascagoula, and Pearl rivers. Grantham (1969) later reported *C. fluminea* in the Big Black, Deer, Leaf, Tennessee, and Tombigbee rivers.

Cooper and Johnson (1980) found *Corbicula fluminea* in Grenada Reservoir of the Yalobusha River during studies conducted there between 1973 and 1976. Leard *et al.* (1980) collected *C. fluminea* from the Big Black, Chickasawhay, Chucky, Coldwater, Leaf, and Pearl rivers and from Steel Bayou and Black Creek.

King and Miller (1982) reported *Corbicula fluminea* to be most abundant bivalve species in the Tombigbee River near Columbus. Hartfield and Cooper (1982) reported *C. fluminea* to be absent in the southern part of the state between, but not including, the Pascagoula and Pearl rivers and streams that drain into the lower Mississippi River; Bayou Pierre, Buffalo Bayou, and the Homochitto River.

Corbicula fluminea is reported from the following Mississippi waters: Allan Branch (FMNH), Amite River (MMNS), Bear Creek (MMNS), Big Black Creek (MMNS), Big Black River (FMNH; MMNS; Leard *et al.*, 1980), Bouge Phalia River (FSM), Buckatunna Creek (FMNH; FSM), Buttahatchie River (MMNS; OSUM), Chickasawhay River (FMNH; FSM; OSUM; Grantham, 1967), Chunky River (FMNH; FSM), Coldwater River (Heard, 1966; Leard *et al.*, 1980), Leaf River (FMNH; FSM; MMNS; OSUM; Heard, 1966; Leard *et al.*, 1980), Mississippi River (MMNS; OSUM), Moss Creek (FMNH), Okatibee Creek (USNM), Okatoma Creek (MMNS), Pascagoula River (MMNS; Leard *et al.*, 1980), Pearl River (MMNS; OSUM; USNM; Leard *et al.*, 1980), Shubuta Creek (FMNH), Souinlovey Creek (FMNH), Steel Bayou (Leard *et al.*, 1980), Sunflower River (FSM), Talahala Creek (MMNS), Tibbee Creek (FMNH; MMNS), Tombigbee River (MMNS; OSUM), Woodward Creek (FMNH), Yalobusha River (Cooper and Johnson, 1980), Yazoo River (FMNH; USNM; Heard, 1966), and Yockanookany River (MMNS).

MISSOURI

(Fig. 13)

Fox (1969) reported *Corbicula fluminea* from the Mississippi River of Missouri. Oesch (Personal communication, 1979) reported the species from the St. Francis, Gasconade, Osage, and Meramec rivers. Buchanan (Personal communication, 1979) found *C. fluminea* from the Big and Bourbuese rivers as well as in the little Black River system.

Corbicula fluminea is reported from the following Missouri waters: Big Creek (MDC), Big River (ACB; MDC; OSUM), Black River (DMNH; FMNH; MDC; MNHD; OSUM), Bourbeuse River (ACB; MDC; OSUM), Bryant Creek (MDC), Cane Creek (MCZ; MDC; OSUM), Gasconade River (MDC), Little Black River (ACB), Little River Canal (MCZ; OSUM), Logan Creek (ACB), Meramec River (MDC; OSUM), Mississippi River (MDC; OSUM; Fox, 1969), Missouri River (RDO), Moreau River (MDC), Osage River (MDC; SBSK), St. Francis River (DMNH; MDC), Thomas Hill Reservoir (MDC), and Whitewater River (MDC).

NEVADA

There is but a single report of *Corbicula fluminea* in Nevada. Ingram (1959) took specimens from Lake Meade of the Colorado River.

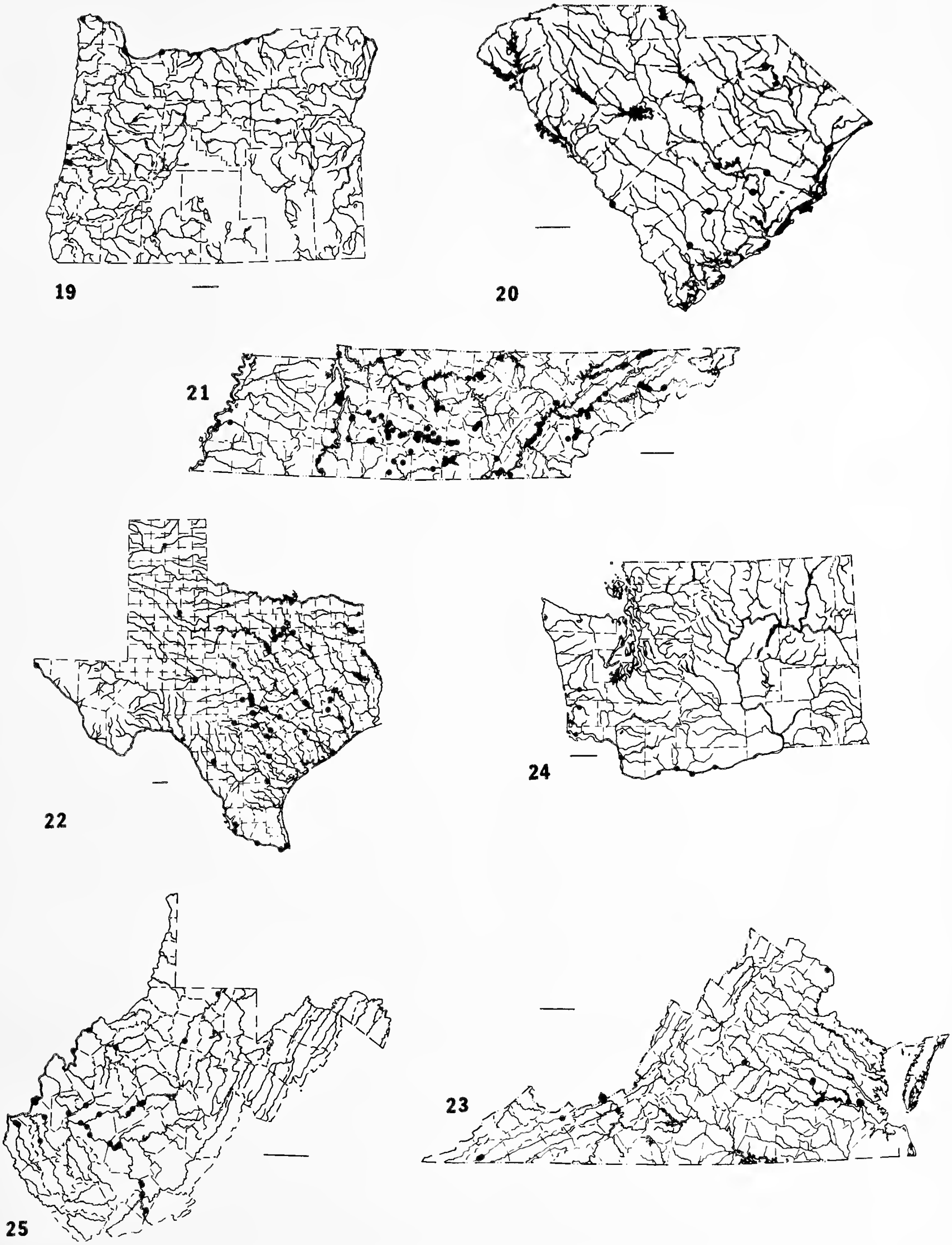
NEW JERSEY

(Fig. 14)

The first report of *Corbicula fluminea* in New Jersey was made by Fuller and Powell (1973) who recorded its presence in the Delaware River between Trenton and Philadelphia. Bivalves seemed to prefer muddy and fine gravel substrata.

Crumb (1977) reported on the colonization of the Delaware River by *Corbicula fluminea* and noted the extension of its range between Trenton and Burlington. Crumb hypothesized that *C. fluminea* invaded the Delaware River sometime during, or before, 1971 and noted that it was usually found in sand or coarse sediments, as reported by Fuller and Powell (1973). He also found that the bivalve *Sphaerium transversum* (Say) was common in the Delaware River until the expansion of the population of *C. fluminea. Corbicula fluminea,* with *Limnodrilus* spp., *Procladius culiciformis,* and *Peloscolex ferox* dominated the benthic community at his collection sites.

Trama (1982) reported a population of *Corbicula fluminea* in the Raritan River. Populations were successful in both the tidal and non-tidal portion of the river as well as in the North and South Branches of the river.



Figs. 19 - 25. Zoogeographic distribution of *Corbicula fluminea* in Oregon (19), South Carolina (20), Tennessee (21), Texas (22), Virginia (23), Washington (24), West Virginia (25). Scale bar = 50 km.

Other specimens of *Corbicula fluminea* from the Delaware River are in ANSP.

NEW MEXICO
(Fig. 15)

The only published account of *Corbicula fluminea* in New Mexico is that of Metcalf (1966). Clams were found in the West Drain, a drainage ditch, in the Mesilla Valley, a part of the Rio Grande drainage. The affected portion of the ditch flows between Texas and New Mixico in a north - south direction from El Paso, Texas to Radium Springs, New Mexico and crosses the state line in several places.

Records of *Corbicula fluminea* in New Mixico waters are: Caballe Reservoir (USNM), Elephant Butte Reservoir (USNM), Pecos River (USNM), and Rio Grande (MNHD; USNM; Metcalf, 1966).

NORTH CAROLINA
(Fig. 16)

The earliest report of *Corbicula fluminea* in North Carolina was made by Fox (1971). He reported specimens taken at the Allen Steam Station at Lake Wylie of the Catawba River system in 1970. Fuller and Imlay (1976) later reported *C. fluminea* in Lake Waccamaw, and speculated that the population became established only where the habitat was severely disturbed by man.

Records of *Corbicula fluminea* in North Carolina waters are: Cape Fear River (NCSM), Catawba River (JJH; NCSM; Fox, 1971) Eden River (JJH), Little River (NCSM), Long Mountain Island Lake (USNM), Richardson Creek (NCSM), Rocky River (OSUM), Uhwarrie River (MCZ), and Waccamaw River (OSUM; Fuller and Imlay, 1976).

OHIO
(Fig. 17)

Pojeta (1964) first reported *Corbicula fluminea* in the Ohio River from collections made in 1962. Horning and Keup (1964) later reported a decline of the *C. fluminea* population in the Cincinnati Reach of the Ohio River. They attributed this mass mortality to the severe winter of 1962-1963 during which the river was ice-covered for seven days. Keup *et al.* (1963) also noted the spread of *C. fluminea* to points above Cincinnati at RM 465.5. Three years later, *C. fluminea* had spread to Marietta at RM 172 (ORSANCO, 1966). Taylor (1980) found *C. fluminea* along the entire length of the Ohio River from the Ohio-Pennsylvania state line to just below the mouth of the Scioto River.

The most recently reported infestation of Ohio waters occurred in the Maumee River at the Davis Besse Nuclear Power Station, Toledo (Scott-Wasilk *et al.*, 1983).

Corbicula fluminea has been reported from the following waters of Ohio: Brush Creek (DM), Hocking River (OSUM), Licking River (OSUM), Little Muskingum River (OSUM), Maumee River (Scott-Wasilk *et al.*, 1983), Meigs Creek (OSUM), Miami River (OSUM), Muskingum River (DMNH; MCZ; OSUM), Ohio River (MUMC; OSUM; USGM; ORSANCO, 1966), Olentangy River (DM; OSUM), Olive Green Creek (OSUM), Scioto River (FMNH), and Stillwater River (GAC).

OKLAHOMA
(Fig. 18)

Few reports have appeared in the literature concerning the occurrence and distribution of *Corbicula fluminea* in Oklahoma. Clench (1970) first reported *C. fluminea* in the state from Lake Overholser collections made in 1969. Britton and Morton (1979) reported *C. fluminea* from Lake Texoma and Lake Thunderbird. White (1977) commented that the Lake Texoma population experienced a reduction in numbers due to the droughts of 1975 - 1976 and 1976 - 1977. He also noted that gravel and rip-rap habitats seemed to provide greater protection from desiccation than did sand substrata when water levels fluctuate. White and White (1977) found that *C. fluminea* from Lake Texoma cannot withstand more than a few days of aerial exposure and suggested that controlled water draw-down during the winter months may be used as a control method in reservoirs and other impoundments.

Oklahoma records for *Corbicula fluminea* include the following bodies of water: Arkansas River (RLR), Caddo Creek (UOM), Little River (RLR), North Canadian River (OSUM; TCU; Clench 1972; O'Kane *et al.*, 1977), and Red River (TCU; UOM).

OREGON
(Fig. 19)

Although Ingram (1948) did not report *Corbicula fluminea* from Oregon, he did report the species as being collected along the north bank of the Columbia River, Pacific County, Washington. Hence, it is not unreasonable to assume that *C. fluminea* was also present in Oregon during the 1940's. In a later paper Ingram (1959) mentions populations in the Williamette River and it's confluence with the Columbia River.

Fox (1969) noted that the entire Columbia River Basin of Oregon was infested and reported the presence of *Corbicula fluminea* in the Umpqua River for the first time.

Snow (personal communication, 1979) noted that *Corbicula fluminea* is an important item in the diet of the white sturgeon, *Ancipenser transmontanus* Richardson, in Oregon.

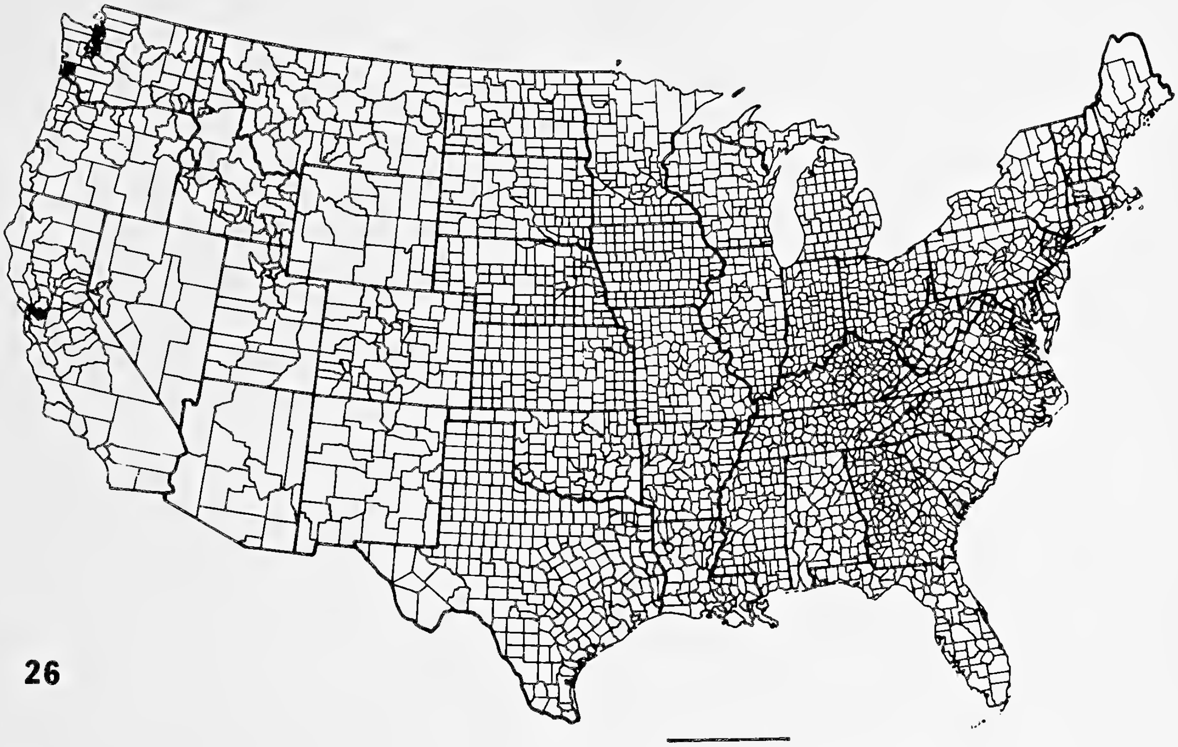
Corbicula fluminea has been reported from the following waters of Oregon: Columbia River (MCZ; NMNS; ODFW; USNM), John Day River (ODFW), Suislaw River (ODFW), Smith River (ODFW), Umpqua River (Fox, 1969), and Williamette River (Ingram, 1959).

PENNSYLVANIA

Corbicula fluminea has been reported only from the Ohio River at Pittsburgh (Taylor, 1980). Although the species is found in the Susquehanna River below Conowingo Dam, Maryland, it has not yet moved upstream into Pennsylvania (Nichols and Domermuth, 1981). No other records, other than those for the Delaware River, which is a part of New Jersey, have been reported for the state.

SOUTH CAROLINA
(Fig. 20)

The first published report of *Corbicula fluminea* in South Carolina is that of Fuller and Powell (1973). They found "gapers" and living specimens in the Pee Dee River on hard



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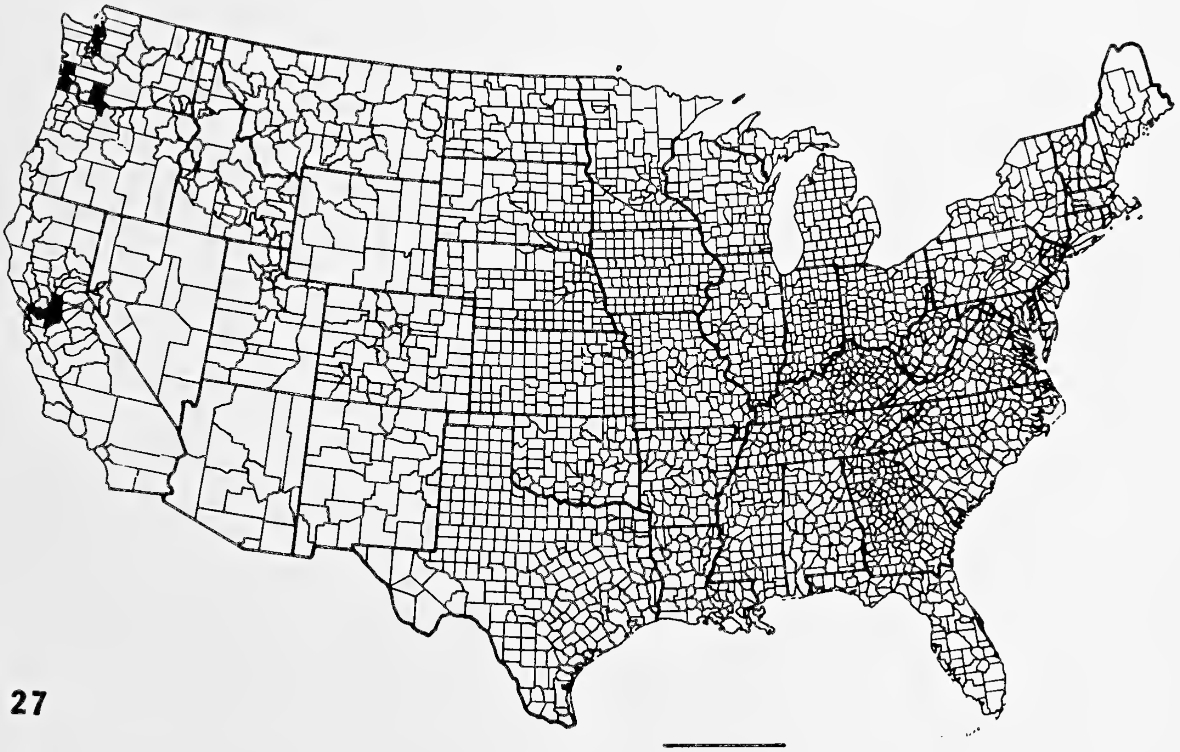

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Figs. 26 - 27. Chronologic zoogeographic distribution of *Corbicula fluminea* by United States counties. 1938 - 1945 (26). 1946 - 1950 (27). Scale bar = 500 km.

clay and sand substrata in 1972. They further reported populations found in 1973 in the Savannah River near Augusta, Georgia. Fuller later reported *C. fluminea* to be abundant in the Cooper River (Fuller, 1974) and in the Santee-Cooper River systems (Fuller, 1976).

Fuller and Imlay (1976) found numerous living and dead specimens of *Corbicula fluminea* below the confluence of the Waccamaw River with the Intracoastal Waterway. Fuller (1978a) later noted the establishment of a population in the Intracoastal Waterway in Georgetown County.

The infestation of the Savannah River Power Plant by *Corbicula fluminea* has received wide attention in the literature. Tille *et al.* (1978) noted severe yearly infestations at the plant and reported on irradication experiments using gamma irradiation. Boozer and Mirkes (1979) discussed the association of *C. fluminea* with *Musculum partumenium* (Say, 1822) in the sedimentation basin at the plant. Harvey (1981) reported on the recolonization of the plants reactor water cooling system and noted that the pumps, reactor basins, pump wells, and emergency cooling system must be cleaned every 10 months to keep them free of these bivalves.

Corbicula fluminea has been found in the following waters of South Carolina: Cooper River (TCU; USNM), Edisto River (OSUM), Hartwell Reservoir (JJH), Intracoastal Waterway (Fuller, 1978a; Fuller and Powell, 1973), Lake Keowee (JJH), Little Pee Dee River (Kool *et al.*, 1981), Pee Dee River (Coney *et al.*, 1983; Fuller and Powell, 1973), Salkahatchie River (OSUM), Santee River (OSUM; Fuller, 1976), Savannah River (TCU), and Waccamaw River (Fuller and Powell, 1973).

TENNESSEE

(Fig. 21)

The first account of *Corbicula fluminea* in Tennessee appears in Sinclair and Isom (1961) and described the infestation below Pickwick Dam of the Tennesse River in 1959. By 1961, *C. fluminea* had also invaded the Cumberland River of Tennessee (Sinclair and Isom, 1961). By 1962, *C. fluminea* had infested the Johnsonville Steam Plant on the Kentucky Reserevoir and public and industrial water supplies as well as a sand and gravel quarry at Chattanooga (Sinclair and Isom, 1963). Introduction of *C. fluminea* into the Tennessee River occurred sometime after 1958. A survey of mussels of the Kentucky Reservoir by Bates (1962a) did not reveal their presence in 1985.

Sinclair (1964) discussed infestations of the sand and gravel industries of the Tennessee and Cumberland rivers and described the deleterious effects of *Corbicula fluminea* in freshly poured concrete.

Isom and Yokley (1968) found *Corbicula fluminea* at 10 stations in the Duck River between river miles 71 and 242.5 in 1965. Clench and Stansbery (1969) later reported the infestation of the Nolichucky River southeast of Warrensburg and noted that these populations were found living in beds of angular limestone, loose limestone rocks, gravel, sand, and sandy mud substrata.

Isom (1971) reported *Corbicula fluminea* from the Fort Loudoun Reservoir of the Tennessee River in 1970, and later (Isom, 1972) reported an infestation at the Nickajack Dam site first noted in 1965 before completion of the dam.

Isom *et al.* (1973) found *Corbicula fluminea* in the Elk River basin during studies made in 1965 to 1967. Van der Schalie (1973) further noted the presence of *C. fluminea* in the Duck and Buffalo rivers, tributaries of the Tennessee River and noted that they are commonly eaten by mink and muskrat, thus replacing the once-numerous unionid bivalves as a food source for these mammals.

Goss and Cain (1977) discussed the history of biofouling by *Corbicula fluminea* at the Tennessee Valley Authority's Johnsonville Steam plant as well as the fouling of Brown's Ferry Nuclear Plant in late 1974. They also discussed various techniques used to control these bivalves at industrial facilities.

Eagleson and Morgan (1977) reported the growth rates of populations of *Corbicula fluminea* in the Clinch River and two small tributaries, Grassy Creek and Bear Creek, near Oak Ridge in 1975 - 1976.

Corbicula fluminea has been found in the following waters of Tennessee: Barren Fork River (OSUM), Big Bigby Creek (OSUM), Big Hickory Creek (OSUM), Big Rock Creek (OSUM), Big Swann Creek (OSUM), Buffalo River (ANSP; FSM; OSUM), Clinch River (ANSP; OSUM; USNM), Collins River (OSUM), Cumberland River (OSUM; Sinclair and Isom, 1963), Duck River (ANSP; MCZ; OSUM), East Rock Creek (OSUM), Elk River (FSM; MCZ; OSUM), Emory River (OSUM), Fall Creek (OSUM), Flat Creek (OSUM), Fountain Creek (OSUM), Garrison River (OSUM), Greenlick Creek (OSUM), Holston River (ANSP; USNM), Harpeth River (OSUM), Hatchie River (OSUM), Lick River (FSM; OSUM), Little Duck River (OSUM), Little Tennessee River (SBSK), Mississippi River (SBSK), Nine Mile Creek (OSUM), Nolichucky River (ANSP; DMNH; FSM; MCZ; OSUM), North Fork Creek (OSUM), Notchy Creek (OSUM), Obey River (OSUM), Paint Rock River (OSUM), Piney River (OSUM), Red River OSUM), Rich Creek (OSUM), Richland Creek (OSUM), Rutherford Creek (OSUM), Sequatchie River (OSUM), Shoal Creek (USNM), Sinking Creek (OSUM), South Chickamauga Creek (OSUM), Stones River (OSUM), Sugar Creek (OSUM), Tellico River (OSUM), Tennessee River (ANSP; FMNH; MCZ; NMNS; OSUM; USNM; Sickel *et al.*, 1981), and Weekly Creek (OSUM).

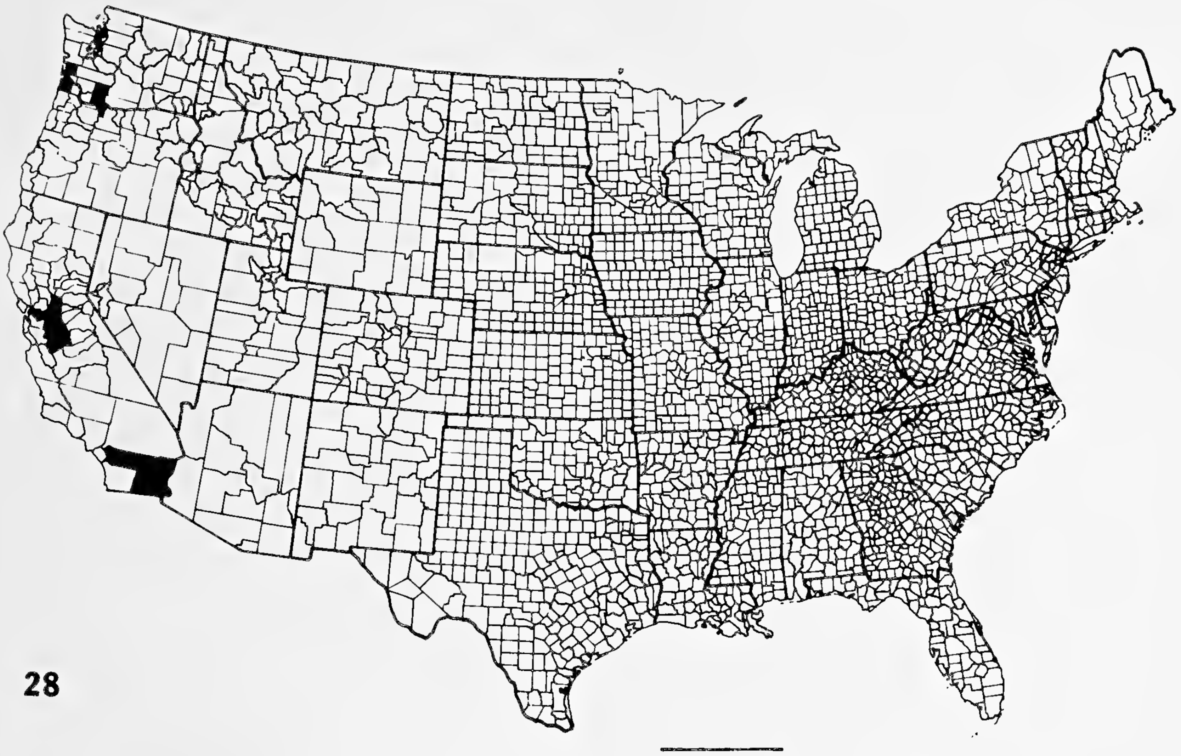
TEXAS

(Fig. 22)

Metcalf (1966) first reported *Corbicula fluminea* in Texas. This first population was located in the Rio Grande at El Paso. These bivalves were believed to have invaded the Rio Grande in 1964 or earlier (Metcalf, 1966). Since its initial discovery, *C. fluminea* has extended its range downstream to Monte Alto Reservoir and Falcoln Lake (Murray, 1971a).

Corbicula fluminea has also invaded the Colorado River system. specimens reported from this river have nearly all been reported from reservoirs. Murray (1971b) reported *C. fluminea* from Lake Lyndon B. Johnson. O'Kane *et al.* (1977) reported infestations in Lake Inks and Lake Travis. Britton and Murphy (1977) found *C. fluminea* at Marble Falls, Austin, and Bastrop.

Three instances of power plant fouling by *Corbicula fluminea* occurred in Texas (McMahon, 1977; O'Kane et *al.*, 1977; Baker, 1978). In all three cases infestations required



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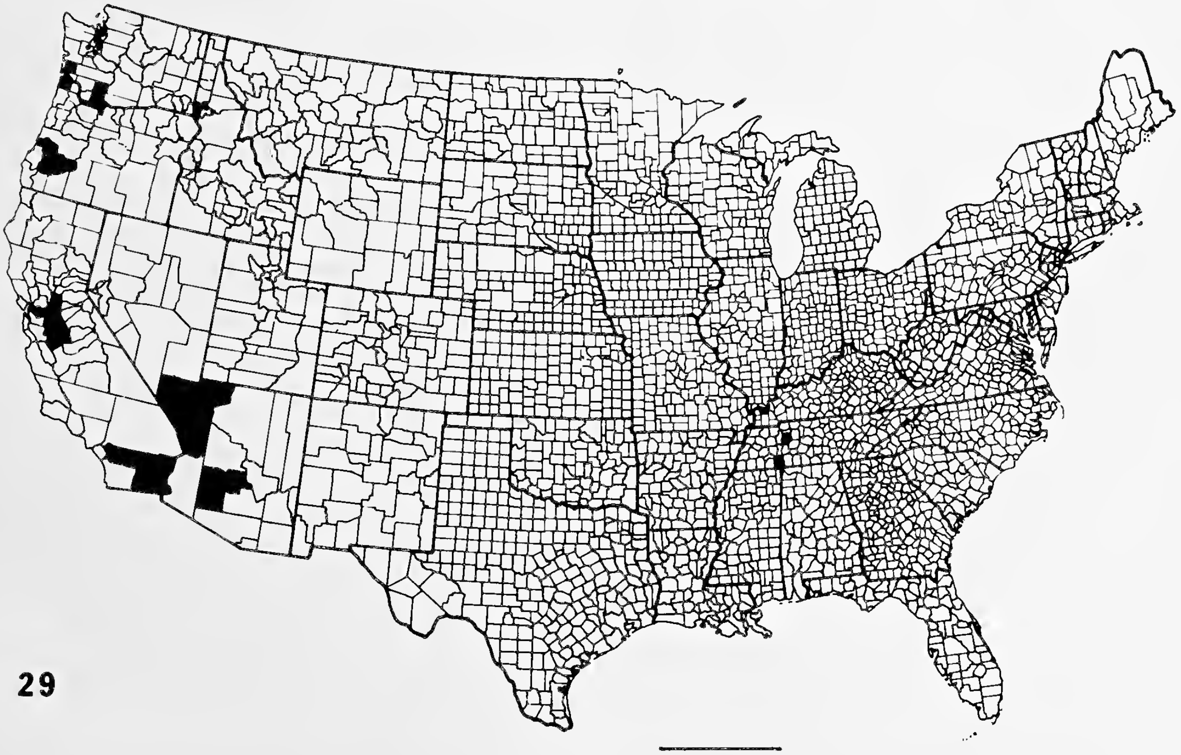

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Figs. 28 - 29. Chronologic zoogeographic distribution of *Corbicula fluminea* by United States counties. 1951 - 1955 (28). 1956 - 1960 (29). Scale bar = 500 km.

the shut-down of the plant to remove the clams and restore normal operation.

Britton and Murphy (1977) reported that *Corbicula fluminea* is a food of the fishes *Lepomis microlophus (Gunther)* and *Minytrema melanops* (Rafinesque) in Lake Benbrook and *Aplocinotus Grunniens* (Rafinesque) in Eagle Mountain Lake.

Hillis and Patton (1982) examined the morphology and genetic variability of populations in the Brazos River system. It was their opinion that two species of bivalves in the genus *Corbicula* may have been introduced into North America. Their evidence is, however, preliminary and they are unable to refer the presumed second species to a taxon with certainty. Britton (1982) reviewed the biogeography and ecology of *C. fluminea* in Texas and also discussed the possibility of two species being in the state.

Corbicula fluminea is reported from the following waters of Texas: Angelina River (TCU; UOM), Big Cypress River (Pool and McCullough, 1979), Blanco River (OSUM; Horne and MacIntosh, 1979), Brazos River (HMNS; OSUM; TCU; UOM; Britton and Morton, 1979), Colorado River (HMNS; TCU; Baker, 1978; Britton, 1982; Britton and Murphy, 1977), Concho River (Baker, 1978), Guadelupe River (UOM; Britton and Murphy, 1977), Johnson Creek (Britton, 1982), Little Brazos River (OSUM), Llano River (UOM), Nueces River (Britton, 1982; Britton and Murphy, 1977; Murray, 1971a, 1978), Pecos River (Britton, 1982), Perdernales River (CED), Red River (Britton and Murphy, 1977), Rio Grande (HMNS; OSUM; SBMNH; Britton, 1982; Metcalf, 1966; Murray, 1971a), Sabine River (Pool and McCullough, 1979), San Antonio River (CEB), San Gabriel River (Hillis and Patton, 1982), San Jacinto River (MCZ; TCU; CEB; Hillis and Patton, 1982), Spring Creek (OSUM), Trinity River (TCU; Aldridge and McMahon, 1978; Britton and Murphy, 1977; Evans *et al*., 1979; McMahon, 1977), and White River (Britton, 1982; Fontanier, 1982)

VIRGINIA

(Fig. 23)

Diaz (1974) made the first report of *Corbicula fluminea* in Virginia. Specimens were taken in the James River between RM 80, at Richmond, and RM 45. He also found populations at the confluence of the Appomattox and James rivers. Clams were usually found on clay-silt substrate. Diaz (1974) suggested that the triclad *Dugesia trigrina* may be a predator of *C. fluminea* in the James River estuary. Shell measurements indicated the James River was probably invaded by *C. fluminea* in 1968 or earlier (Diaz, 1974).

Rodgers *et al*. (1977) reported the presence of *Corbicula fluminea* in the New River. In a later paper Rodgers *et al*. (1978) calculated the upstream rate of invasion to be 14.4 km/yr. The population dynamics, ecology, and control of *C. fluminea* in the New River was discussed in detail by Cherry *et al*. (1980).

Corbicula fluminea has infested three power stations in Virginia: the Twelfth Street Generating Station of the Virginia Electric and Power Company, Richmond (Diaz, 1974); the Glen Lyn Power Plant (Rodgers *et al*., 1977, 1978; Graney *et al*., 1980; Cherry *et al*., 1980); and the Potomac Electric Power Company's generating station at Alexandria (Dresler and Cory, 1980). *C. fluminea* has also been found in the collecting ponds of cooling towers at the Allied Chemical Company plant at Hopewell (Diaz, 1974). The thermal effluent of the Glen Lyn plant has been implicated in the maintenance of a stable population in the New River (Rodgers *et al*., 1978; Graney *et al*., 1980).

Corbicula fluminea has been found in the following waters of Virginia: Appomattox River (USNM), Chickahominy River (DMNH), Clinch River (MCZ; OSUM; USNM), James River (MPM; OSUM; SBMNH; USNM; Diaz, 1974), New River (Rodgers *et al*., 1977), and Potomac River (Dresler and Cory, 1980).

WASHINGTON

(Fig. 24)

The first report of *Corbicula fluminea* in the United States was made from collections on the banks of the Columbia River, Pacific County, in 1938 (Burch, 1944). Ingram (1949) also reported *C. fluminea* from the north bank of the Columbia River near Knappton-- the same population originally described by Burch (1944). Fox (1971), commenting on this discovery, noted that Burch's materials were composed of dead, drift shells and that the water of the Columbia River where they were collected is saline. Fox (1971) further reported *C. fluminea* in the Columbia River from near Knappton upstream to Richland.

Records for *Corbicula fluminea* in Washington include: Chehalis River (CAS; DMNH; NMNS; USNM) and Snake River (USNM).

WEST VIRGINIA

(Fig. 25)

The earliest report of *Corbicula fluminea* in West Virginea was that of Thomas and MacKenthum (1964). They found *C. fluminea* in the Kanawha River at two localities and believed the clams became established populations of *C. fluminea* from the Kanawha River not far from the localities of Thomas and MacKenthum (1964). *C. fluminea* was collected at five stations and found in association with unionid bivalves where substrata was usually pebbly, the water clarity good, and stream flow variable (Taylor and Morris, 1978).

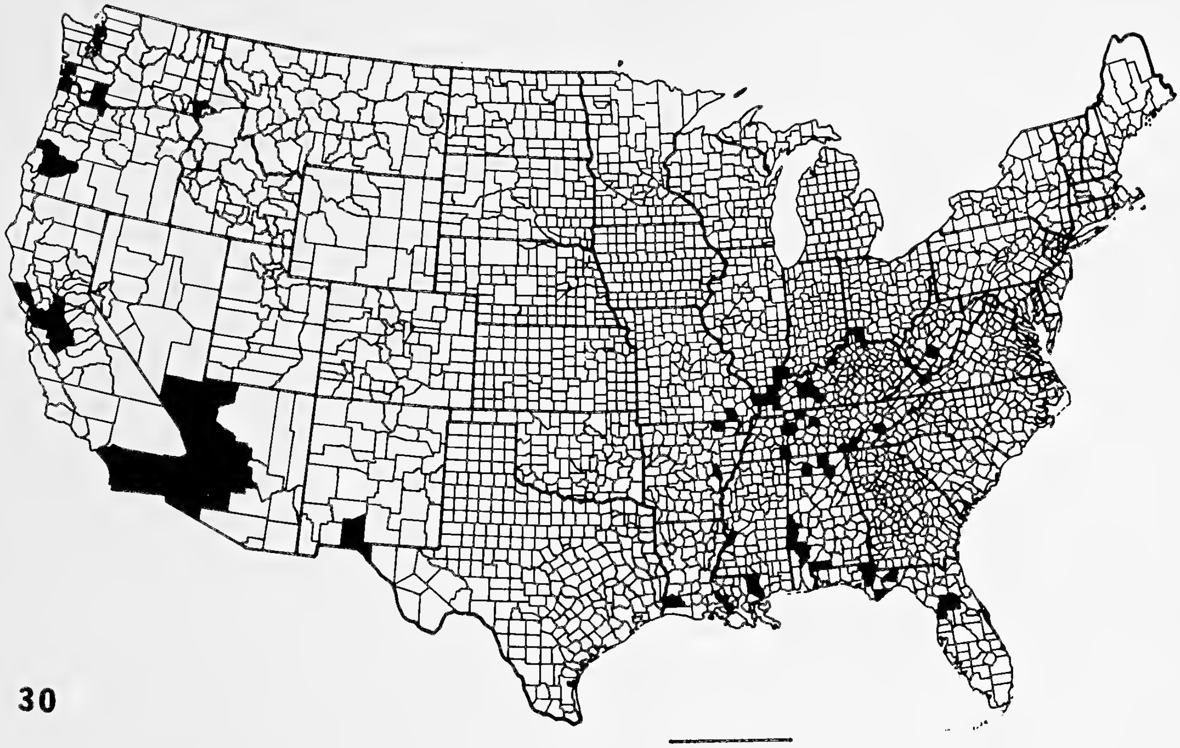
Taylor and Counts (1977) reported populations in the Ohio River and noted they were preyed upon by the Northern Raccoon, *Procyon lotor* (Linné).

Markham *et al*. (1980) found that *Corbicula fluminea* was the most abundant bivalve in the New River from the Virginia - West Virginia state line downstream to the mouth of Meadow Creek, a distance of Approximately 55 km.

Taylor and Hughart (1981) reported *Corbicula flumiea* in the Elk River from its confluence with the Kanawha River upstream to Sutton Dam, Braxton County. The bivalve was found at all localities in association with unionid mussels.

Zeto (1982) reported the presence of *Corbicula fluminea* in the Monogahela and West Fork rivers. Joy and McCoy (1975) studied the correlation between shell and visceral characters in a population of *C. fluminea* from a riffle in the Mud River.

Records of *Corbicula fluminea* in West Virginia waters include: Beach Fork Creek (MUMC), Big Seven Mile Creek (MUMC; OSUM; Taylor and Hughart, 1981), Guyandotte River (MUMC), Hughes River (MUMC), Kanawha River (DMNH; MCZ; MUMC; OSUM; USNM; Mor-



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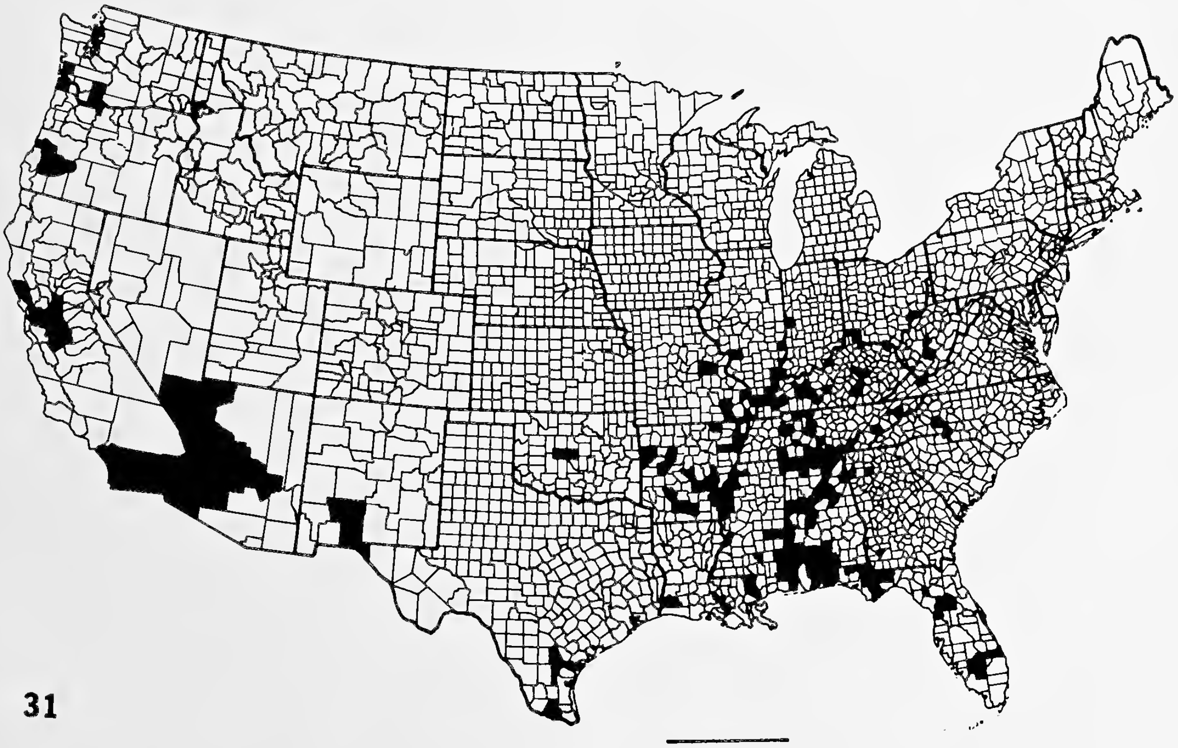

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Figs. 30 - 31. Chronologic zoogeographic distribution of *Corbicula fluminea* by United States counties. 1961 - 1965 (30). 1966 - 1970 (31). Scale bar = 500 km.

ris and Taylor, 1978; Thomas and MacKenthum, 1964), Monongahela River (Zeto, 1982), Mud River (MUMC), New River (OSUM; Markham *et al.*, 1980), Ohio River (DMNH; MUMC; OSUM; Taylor and Counts, 1977), Pocatalico River (MUMC), Twelve Pole Creek (MUMC), and West Fork River (Zeto, 1982).

WISCONSIN

Corbicula fluminea was discovered in the St. Crox River, near Hudson, in the summer of 1977 (Cummings and Jones, 1978; Fuller, 1978b; Mathiak, 1979). This is the only locality, thus far, for these bivalves that has been reported for the state. Since they were not living in a thermal plume, it is not known whether they have survived winters since their discovery.

The Chronology of invasion of the United States by *Corbicula fluminea* is presented in Table 1 and graphically in Figs. 26-33. Records presented in Table 1 represent only the first account of *C. fluminea* in a particular body of water in a given state. Figures 26-33 present the complete distribution of *C. fluminea* in the form of records for the counties from which specimens have been collected and/or reported. Collections and reports cited in Table 1 are not necessarily the first appearance of *C. fluminea* in a body of water but rather represent the earliest documented detection.

DISCUSSION

Several hypotheses have been offered to explain the introduction of *Corbicula fluminea* into North America. The first states that the introduction was made by Chinese immigrants who arrived on the west coast during the Gold Rush of the late 1840's (Fox, 1970a). These immigrants played a prominant role in the development of the American west as laborers in construction projects (such as the Transcontinental Railroad) and in agriculture. Their migrations, coupled with a traditional use of corbiculid clams as food (Miller and McClure, 1931) and their penchant for settling in "China Towns" (although this was more a result of highly restrictive laws governing the Chinese in the western states at the time) suggest that they were the first to introduce *C. fluminea* into North America. It is also significant that the majority of the Chinese who immigrated to the west came from, or had family origins in, Kwangtung Province in the Pearl River Basin (of which Canton is the principal city) (Fox, 1971; Morton, 1973) where Cantonese have a traditional industry centered around the harvest and consumption of corbiculid clams (Miller and McClure, 1931).

It is unclear, however, how Chinese immigrants were able to transport live *Corbicula fluminea* to the west coast of North America in significant numbers. Voyages from China to the western American coast in the mid 1800's involved the use of slow sailing vessels, and the trip could take as along as 180 days. Further, Caucasian ship captains and crews were distrustful of the Chinese and, in many cases, locked these passengers below decks with food and water just adequate for subsistance during the voyage. It is difficult to imagine significant amounts of water being spared for clams transported as a seed stock. Unless the Chinese were frugal with their water rations, or corbiculids were able to withstand long periods of only damp conditions, it is doubtful that many of them arrived in North America in a viable condition by this route. There were also many Chinese immigrants to the Hawaiian Islands and the eastern coast of the United States during this same period. Populations of *C. fluminea* have only just now been found in the Islands, and none was discovered east of the Rocky Mountains before 1957. Considering the number of active malacologists of the period, it would seem likely the *C. fluminea* would have been discovered in the United States before 1938.

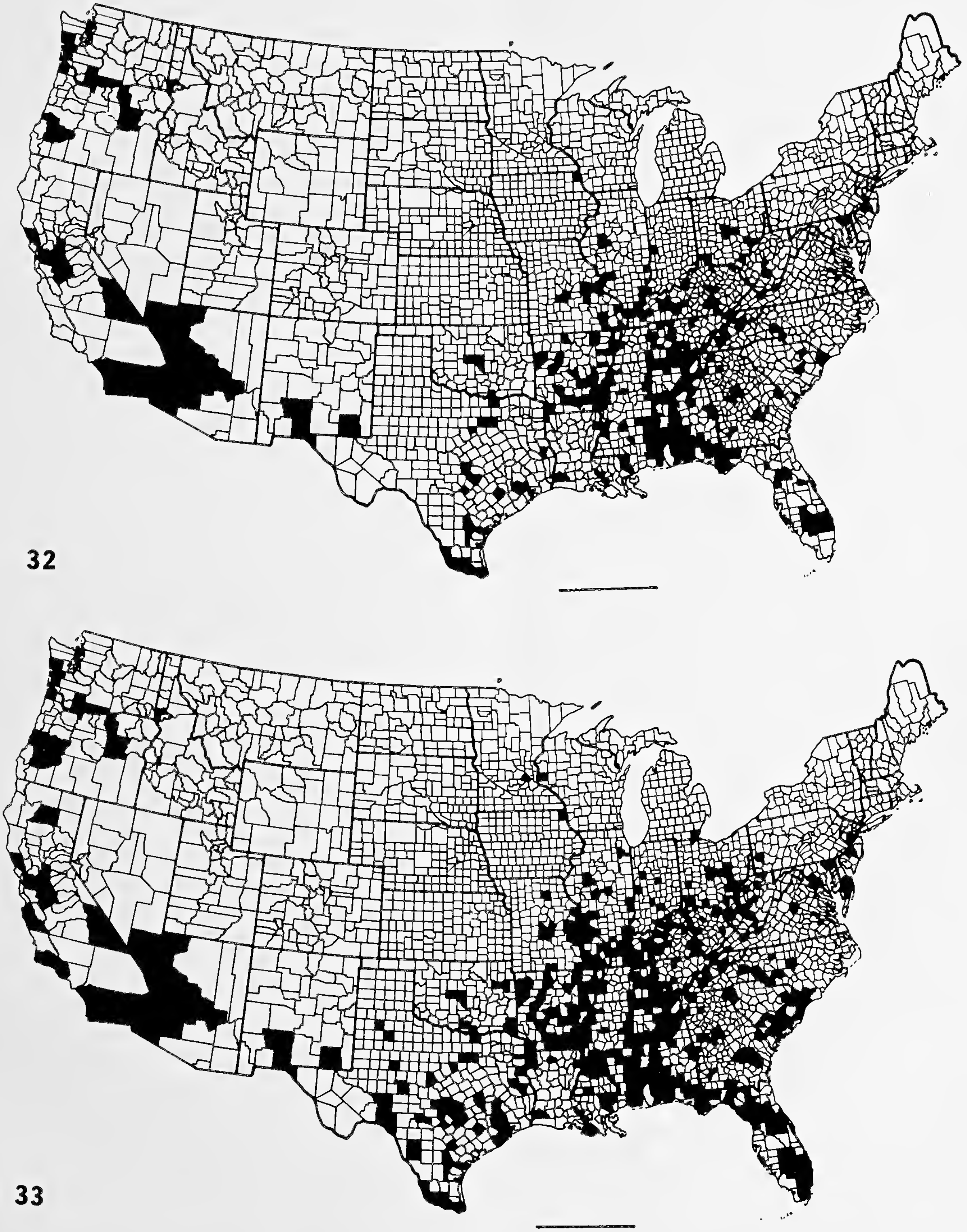
A second possibility for the introduction of *Corbicula fluminea* to the Pacific Coast is their importation from the Orient with the Giant Pacific Oyster, *Crassostrea gigas* (Thunberg, 1793). Morton (1977) reported that *C. fluminea* enters the Hong Kong area in shipments of *C. gigas* that are imported to seed oyster beds. Abbott (1974) reported that large numbers of *C. gigas* are imported into the western coasts of the United States, Canada, and Mexico, and it is conceivable that *C. fluminea* entered North American waters by this route. However, no information is available concerning the first importation of *C. gigs*.

The third hypothesis also involves the Chinese. During the mid- and late 1930's, mainland China was beset with national and international hostilities. During that period, many Chinese immigrated to the United States. This period would allow more favorable shipboard conditions for the successful transport of *Corbicula fluminea* to North America. Treatment of passengers was somewhat improved over that of the 1840's and the time necessary to traverse the Pacific Ocean was shorter. This is the theory subscribed to by Britton and Morton (1979) and seems to be most attuned to what is known about the early history of *C. fluminea* in North America. Although Counts (1981b) noted that *C. fluminea* were collected as dead shells in British Columbia in 1924, before the immigrations of the 1930's, this hypothesis best explains the method of early introductions. The details of introduction, however, are still unclear.

Earliest introduction of *Corbicula fluminea* into United Staes waters was at Knappton, Pacific County, Washington (Burch, 1944) (Fig. 34). McMahon (1982) suggested that *C. fluminea's* present zoogeographic distribution is the result of this single introduction and possibly two subsequent, long-distance introductions to the Ohio River at Paducah, Kentucky, in 1957 (Sinclair and Isom, 1961) and to Lake Overholser, Oklahoma, in 1969 (Clench, 1972).

Introduction of *Corbicula fluminea* into the Ohio River in 1957 is indeed a dramatic leap across the continent. Until its discovery at Paducah, *C. fluminea* appeared to spread eastward across southern Washington into the Snake River and across southern California into the Colorado River Basin of Arizona and Nevada (Figs. 34 - 36). The transcontinental leap to the Ohio River (Fig. 37), therefore, seems to be the result of human activity, although the exact manner by which it was transported is unknown.

Introduction into Lake Overholser is not as dramatic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Figs. 32 - 33. Chronologic zoogeographic distribution of *Corbicula fluminea* by United States counties. 1971 - 1975 (32). 1976 - 1983 (33). Scale bar = 500 km.

as depicted on the map of McMahon (1982). In reality, *Corbicula fluminea* was collected in the Black and White rivers in Arkansas in 1964 (MCZ 260919; OSUM 13992), in the St. Francis River in 1966 (OSUM 20142), and in the Ouachita River at Camden (OSUM 20409) and at Arkadelphia (FSM-U) in 1969 (Figs. 38 - 39); the year of Clench's (1972) Lake Overholser discovery. Kraemer (1971; 1976) reported significant populations of *C. fluminea* in the Arkansas River, of which the North Canadian River (and hence Lake Overholser) is a tributary, before 1964. Records indicate that *C. fluminea* was well established in the Arkansas River drainage, and in the rivers of Arkansas generally for at least five years before its appearance in Oklahoma and was very likely in the Fort Smith, Arkansas vicinity, on the Arkansas - Oklahoma state line, before collections were made at Lake Overholser. It is possible that a long distance introduction was made into Lake Overholser from the Ohio - Mississippi basin and that occurrence of populations in the Arkansas River reported by Kraemer (1971) was the result of normal downstream migration. An upstream dispersal in the Arkansas - Canadian river system terminating at Lake Overholser is not temporally different from similar upstream movements by *C. fluminea* in the Ohio River system.

Examination of the upstream range extension records for *Corbicula fluminea* in the Ohio River reveal that after the initial discovery at Paducah, Kentucky in 1957 (Sinclair and Isom, 1961), these bivalves were collected at Ghent, Kentucky, in 1961 (OSUM 6585), at Cincinnati, Ohio in 1963 (OSUM 9275), at Marietta, Ohio in 1966 (ORSANCO, 1966), and at Pittsburgh, Pennsylvania in 1979-1980 (Taylor, 1980). *C. fluminea* was also collected in the Kanawha River, West Virginia in 1963 (Thomas and MacKenthum, 1964). In view of these records, McMahon (1982) was incorrect in stating that *C. fluminea* reached its upstream limit in the Ohio River system with the establishment of the Kanawha River population in 1963. Collections of *C. fluminea* have also been made in the Monongahela River at Morgantown, West Virginia, (Zeto, 1982) and in the Olentangy River, Delaware County, Ohio, in 1972 (OSUM 33900), demonstrating that these bivalves are still expanding their upstream range in the Ohio River system. Populations reported in the New River at Glen Lyn, Virginia (Rodgers *et al.,* 1979), may also reflect the upstream range extension of *C. fluminea*.

More dramatic than the Lake Overholser population expansion was the extablishment of a population in the Escambia River, near Century, Florida, in 1960 (Schneider, 1967). It seems unlikely that this population was established by naturally mediated dispersal.

Corbicula fluminea has a short-term planktotrophic veliger stage (Sinclair and Isom, 1963; Goss and Cain, 1977). While a velum is present, Sinclair and Isom found no evidence that this organ is used to keep larvae suspended in the water column. They also noted the presence of an apical swim plate but could not demonstrate that this is used for swimming. Eng (1979) found that *C. fluminea* larvae in the Delta - Mendota Canal are essentially benthic, and that a pediveliger stage is released by the parent that broods larvae in a marsupium located in the inner gills. Both Sinclair and Isom (1963) and Eng (1979) observed that the larvae, though benthic, can be transported in turbulent water.

Kraemer (1979) described the development of a byssus in *C. fluminea* after marsupial release and observed that Arkansas River larval populations frequently attach themselves to sand grains with this structure. McMahon (1982) reported populations of *C. fluminea* in Texas similarly attached to sand grains frequently entangled in algal mats. Stein (1962) found adult *C. fluminea*, in algal mats in Cincinnati, Ohio, in 1962.

McMahon (1982) argued that the rate of invasion by *Corbicula fluminea* is higher when moving downstream than moving upstream. However, by 1959, *C. fluminea* had expanded its range from Paducah, Kentucky, into the Tennessee River upstream to Pickwick Dam and had been collected in 1960 at Metropolis, Illinois, in the Ohio River (Table 1; Figs. 37 - 38). Establishment of the population in the Escambia River would have required an extremely high rate of downstream transport by natural means. In view of a short larval life span, it is doubtful larvae could remain suspended in the water column for periods of time sufficient to make possible migration from the Ohio River to the lower Mississippi River. Larvae may have attached byssally to logs or filamentous algal mats and then be transported downstream but this mode of travel seems doubtful since logs or mats would tend to become entangled in vegetation near the river's banks.

Transport of *Corbicula flumiea* by barges seems most likely. Larvae could attach themselves to barges that in turn could be towed downstream within the time necessary to link the Ohio River infestation with that in the Escambia River. However, once established in the lower reaches of the Mississippi River, *C. fluminea* would have to reach the Escambia River. While transport in the gastrointestinal tract of migratory waterfoul is biologically impossible for any length of time (Thompson and Sparks, 1977b), short term transport by birds is likely.

Mackie (personal communication, 1979) has found that sphaeriid bivalves may survive ingestion by migratory waterfowl only if they are regurgitated after a few hours. McMahon (1982) noted that larval *Corbicula fluminea*, byssally attached to sand grains enmeshed in filamentous green algae, could become attached through entanglement on the feet of wading birds or migratory ducks and subsequently be transported to a new locality. However, McMahon (1982) logically points out the long-distance transport does not seem likely since these flights would result in death of the bivalves by desiccation. Thus, transport of *C. fluminea* from the lower Mississippi Valley to the Escambia River could have been accomplished only by flights of short duration. Such flights should have deposited *C. fluminea* in streams between the Mississippi and the Escambia rivers. The chronological record of *C. fluminea's* invasion (Table 1) and collection records do not indicate that this happened. Hartfield and Cooper (1982), for example, noted that in spite of *C. fluminea's* presence in this region of the United States for over 20 years it is still absent from the rivers and streams that empty into the lower Mississippi River.

Chronological records for invasion of the United States by *Corbicula fluminea* (Table 1) indicate that in all probability the Escambia River population was established by a long-distance dispersal event, as was the Paducah, Kentucky, population, and not by natural dispersal mechanisms.

McMahon (1982) believed that the Appalachian Mountains are a significant barrier to the eastward migration of *Corbicula fluminea* into streams below the fall line of the east coast. However, he also suggests that invasion of the New River at Glen Lyn, Virginia, by *C. fluminea* in 1975 was the result of the species crossing the Appalachian Mountains from North Carolina into Virginia. In view of *C. fluminea*'s long history in the Kanawha River, and that streams confluence with the New River in West Virginia, it is more likely that infestation resulted from an upstream migration either naturally or anthropogenically mediated. There is little doubt that the demonstrated rapidity of *C. fluminea*'s dispersal across the United States argues against the proposal that large physiographic features are dispersal barriers of any consequence in the extension of the bivalve's geographic range. Neither the Mojave Desert nor the Rocky Mountains appeared to present any significant barrier to dispersal.

Water temperature would appear to offer the most significant barrier to northward dispersal of *Corbicula fluminea*. Northernmost records for the species (Table 1) are artificial situations in which *C. fluminea* lives in water warmed by thermal effluent from industrial or power generating facilities. The population in Wisconsin (Cummings and Jones, 1978; Fuller, 1978b; Mathiak, 1979) does not live in such industrially warmed waters. No further reports or collections of the St. Croix River population have been made.

Water temperature has been implicated in mass mortalities of *Corbicula fluminea* populations. Sinclair and Isom (1963) reported one in a Tennessee River population at Wolfe Island (RM 195.2) in April 1961, and another in the Cumberland River (RM 100) during this same period. Horning and Keup (1964) found a decline in the population in the Cincinnati Reach of the Ohio River between 1962 and 1963 that they attributed to severe winters in which the river was ice-covered for several days. However, this population has since recovered and the severe winters of 1977 and 1978 have not significantly reduced their numbers (Taylor, personal communication, 1979).

Sinclair and Isom (1963) reported that mass mortality of *Corbicula fluminea* populations in the Tennessee River blocked the intake pipe screens of the Chattanooga, Tennessee, water treatment plant. This occurred during late August and early September 1962 and suggested that some physicochemical factor, other than low temperature alone, may have been responsible for the deaths. Britton and Morton (1979) reported four instances of mass mortalities in the Trinity River, Texas, which they attributed to flooding.

The infestation of streams by *Corbicula fluminea* has been implicated as a contributing factor in the demise of native unionid mussels (Gardner *et al.*, 1976; Cherry *et al.*, 1980). *C. fluminea* has been observed physically dislodging unionid mussels from the substratum in the Savannah River of Georgia and South Carolina (Fuller and Richardson, 1977). It is doubtful, however, that these activities play a significant role in competition for space and hence a decline of native unionid species. Instead, it would appear that *C. fluminea* is able to adapt to a wide variety of habitats, especially those stressed by pollution, r-selection regimes (MacArthur and Wilson, 1967), while native bivalve species are more adapted to stable, k-selection habitats.

Britton and Morton (1979) discussed r- versus k-selection in *Corbicula fluminea* and found that these bivalves have both r- and k-selective features but, in the majority of cases, r-selection seems to be dominant. Sickel (1979) also discussed what he believed to be a shift from r- to k-selection strategy in the Altamaha River, Georgia, population.
While Britton and Morton (1979) concede that no species is probably wholly r- or k-selected, it does seem likely that the rapid growth of *C. fluminea* populations and the concomittant decline of unionid populations is a function of r-selected species *(C. fluminea)* cohabitating with k-selected species (unionids) in waters that have become polluted. Since unionid bivalves have a parasitic larva that must attach to a host fish in order to metamorphose into an adult, polluted waters may cause these fish to leave and the unionids, unable to complete their life cycle, become moribund. Conversely, *C. fluminea's* life cycle requires no intermediate host species and is therefore independent of fish for successful recruitment of new individuals into the population. Sickel (1979) hypothesized that a lack of one year-old *C. fluminea* in the Altamaha River in 1976 may have been due to r-selective pressures that favored individuals who diverted energy into growth rather than reporduction. His alternative hypothesis stated that growth rates of large cohorts in 1973 - 1974 was decreased by crowding pressures, i.e. intense competition for both food and space, thereby diverting energy into those activities from reproductive processes (Sickel, 1979).

Kraemer (1979) noted that in an altered habitat, such as the Arkansas River, physicochemical factors seemed to be far more important to the success of *Corbicula fluminea* than they would in an unaltered habitat. In an unaltered habitat, such as the Buffalo River, Arkansas, interspecific competition between unionids and *C. fluminea* may shift between r- and k-selective strategies from one season of the year to another.

In either case, an r-selective regime would operate against the generally k-selected unionid mussels and allow the generally r-selected *Corbicula fluminea* to successfully invade a new habitat. The r-, k-selection scheme seems to offer the best explanation for the phenominal success of *C. fluminea*'s invasion of North American waters.

Man has unquestionably been primarily responsible for the rapid transcontinental dispersal of *Corbicula fluminea* in the United States. They may be transported long distances in sand and gravel dredged for making concrete (Sinclair and Isom (1963). They are harvested in California to be sold as bait to sport fisherman (Fox, 1970) or in pet shops (Abbott, 1975). A clam purchased from a bait shop or pet store could easily be discarded in a local stream. The shock of hitting the water's surface, when used as bait, could easily stimulate gravid *C. fluminea* to release brooded veliger larvae resulting in the infestation of a previously uninfested stream (Clarke, Personal communication, 1982). The common habit of fishermen of throwing unused bait overboard after fishing would also be sufficient to infest a stream or lake.

The use of *Corbicula fluminea* by man has surely made man the vetor responsible for the current zoogeography of the species in North America.

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Table 1. Chronology of invasion of United States waters by *Corbicula fluminea*. Figures 26-33 depict the course of the invasion. All records are for only the first documented detection of *C. fluminea* in a body of water in a particular state.

Year	State	Body of Water/Locality/Reference
1924	British Columbia	Vancouver Island near Nanaimo/ USNM 363020
1938	Washington	Columbia River/ Knapton/ CAS 32360
1945	California	Sacramento River/ N of Pittsburg/ CAS 42926
1946	California	Mayberry Cut/ CAS 32369
		Mokelumne Aqueduct/ Middle River/ CAS 32237
		Potatoe Slough/ Near Lodi/ CAS 37271
		San Joaquin River/ Canal E fo Los Banos/ SBMNH 32378
1950	California	Delta-Mendota Canal/ Near Tracy/ Eng, 1975
1952	California	Tolumne River/ CAS 43671
	Washington	Snake River/ USNM 595265
1953	California	All American Canal/ Imperial Valley/ CAS
		Colorado Aqueduct/ Mecca/ USNM 613968
1956	Arizona	Salt River/ Papgo Park, Phoenix/ Dundee and Dundee, 1958
1957	Kentucky	Ohio River/ W of Paducah/ Sinclair and Isom, 1961
1958	California	Salton Sea/ Imperial Co./ Sinclair and Isom, 1961
1959	Idaho	Snake River/ Idaho - Washington State line/ Ingram, 1959
	Nevada	Colorado River/ Lake Meade/ Ingram, 1959
	Oregon	Smith River/ Douglas Co./ ODFW
		Williamette River/ Multnomah Co./ Ingram, 1959
	Tennessee	Tennessee River/ Below Pickwick Dam/ USNM 636118
1960	California	San Jacinto River/ San Jacinto Reservoir/ Fox, 1970
		Stanislaus River/ SE of Ripon/ OSUM 23646
	Illinois	Ohio River/ Metropolis/ FMNH 103678
	Florida	Escambia River/Near Century/ Schneider, 1967
1961	Alabama	Tennessee River/ Wheeler Reservoir/ NMNS 20569
	Arizona	Colorado River/ Lake Martinez/ SBMNH 4456
	California	Russian River/ Somona Co./ CAS 37639
	Florida	Appalachicola River/ Near Apalachicola/ Schneider, 1967
	Kentucky	Green River/ Above Paradise/ Bates, 1962b
	Louisiana	Calcasieu River/ RM 66/ Dundee and Harman, 1963
		Mississippi River/ Unknown/ OSUM 4416
	Tennessee	Cumberland River/ Near Stone River / Sinclair and Isom, 1963
1962	Alabama	Escambia River/ Near Century/ Hubricht, 1963
		Mobile River/ Hubricht, 1963
	Arizona	Agua Fria River/ NE of Rock Springs /Bequaert and Miller, 1973
	California	South Bay Aqueduct/ Alamenda Co./ Prokopovich, 1968
	Florida	Withlacoochee River/ Inglis/ MCZ 237952
	Louisiana	Bayou Magasille/ Assumption Par./ Dundee and Harman, 1963
		Bayou Sorrel/ Iberville Par./ Dundee and Harman, 1963
	Ohio	Ohio River/ Pojeta, 1966
1963	Kentucky	Mississippi River/ Wickliffe/ FMNH 123601
	Louisiana	Pearl River/ Wilson's Slough/ Gunning and Suttkus, 1966
	Mississippi	Yazoo River/ Vicksburg/ FMNH 137777
	Texas	Rio Grande/ El Paso/ Britton, 1982
	West Virginia	Kanawha River/ Chelyan/ Thomas and Mackenthum, 1964
1964	Alabama	Alabama River/ Hubricht, 1965
		Big Nance Creek/ Near Leighton/ OSUM 11488
		Indian Creek/ SW of Huntsville/ OSUM 12848
	Arkansas	Black River/ Pocahontas/ MCZ 260919
		White River/ S of Clarendon/ OSUM 13992
	California	El Capitan Reservoir/ E of San Diego/ Fast, 1971
	Florida	Chipola River/ E of Clarksville/ Heard, 1964
	Illinois	Wabash River/ E of Rising Sun/ ISM
	Indiana	Ohio River/ Mt. Vernon/ OSUM 14399
	Kentucky	Tennessee River/ Below Kentucky Dam/ MCZ 268647
	Missouri	Castor River/ Between Dexter and Sikeston/ MCZ 268300
	New Mexico	Rio Grande/ West Drain, Mesilla Valley/ Metcalf, 1966
	Tennessee	Sequatchie River/ NNE of Whitwell /OSUM 24223
1965	Alabama	Cahaba River/ Hubricht, 1966
		Suncanochee Creek/ Hubricht, 1966
	California	Dyer Canal/ Alamenda Co./ Prokopovich, 1968
		Livermore Canal/ Alameda Co./ Prokopovich, 1968

Table 1. (continued)

Year	State	Body of Water/Locality/Reference
	Florida	Ochlocknee River/ NW of Tallahassee/ Heard, 1966
	Tennessee	South Chickamauga Creek/ Chattanooga/ OSUM 24146
	Virginia	Clinch River/ North Tazewell/ MCZ 268583
1966	Alabama	Black Warrior River/ Below Lock 16 Dam/ OSUM 19084
		Coosa River/ Below Logan-Martin Dam/ OSUM 9005
		Locust Fork/ N of Cleveland/ NMNS 65722
		Town Creek/ NE of Leighton/ OSUM 22086
	Arkansas	St. Francis River/ S of Marked Tree/ OSUM 20142
	Kentucky	Cumberland River/ Kuttawa/ FMNH 179981
		Silver Creek/ At Kentucky Reservoir/ Branson and Batch, 1969
	Mississippi	Chickasawhay River/ Near Merril/ Grantham, 1967
		Coldwateer River/ Cohoma Co./ Heard, 1966
		Leaf River/ McClaine/ Heard, 1966
	Tennessee	Harpeth River/ NE of Forest Home/ OSUM 22078
		Richland Creek/ W of Pulaski/ OSUM 22087
1967	Alabama	Cypress Creek/ Near Florence/ USNM 756753
		Limestone Creek/ E of Peels Corner/ OSUM 42261
		Paint Rock River/ Above Trenton/ DMNH 30382
	Florida	Escambia River/ E of Century/ OSUM 23450
		Suwanee River/ NW of Bell/ FSM
		Kentucky River/ Camp Daniel Boone/ Branson and Batch, 1969
		Red River/ At Kentucky River/ Branson and Batch, 1969
		Rockcastle River/ Livingston/ OSUM 22251
	Mississippi	Bear Creek/ Tishomingo State Park/ MMNS 1565
	Missouri	Black River/ Hendrick/ FMNH 156605
	Tennessee	Duck River/ ESE of Shelbyville/ MCZ 280464
		Elk River/ S of Estill Springs/ MCZ 271671
1968	Alabama	Terrapin Creek/ Ellisville/ OSUM 28041
	Arkansas	Ouachita River/ Camden/ OSUM 20409
	California	Columbia River/ Imperial Co./ CAS 38784
	Georgia	Oostanula River/ E of Amuchee/ OSUM 28050
	Indiana	Wabash River/ N of Newport/ OSUM 39346
	Kentucky	Nolichucky River/ SE of of Warrensburg/ MCZ 276636
	Mississippi	Mississippi River/ W of Gunnison/ MMNS 1642
	Missouri	Little River Canal/ SE of Gideon/ MCZ 268205
	Tennessee	Buffalo River/ N of Napier/ OSUM 34272
		Nolichucky River/ SE of Warrenburg/ OSUM 23398
1969	Alabama	Elk River/ NNW of Elkmont/ FSM
		Flint River/ Madison Co./ FSM
		Mud Creek/ NW of Hollywood/ FSM
	Arizona	Verde River/ W of Camp Verde/ MNA 24.397
	Arkansas	Little River/ Near Mississippi River/ MCZ 280465
	California	Lake Jennings/ Near San Diego/ Richardson *et al.*, 1970
		Santa Ana River/ Riverside/ ANSP 342789
	Florida	Lake Hippochee/ Glades Co./ OSUM 25210
	Kentucky	Gasper River/ WNW of Bowling Green/ OSUM 23060
	Mississippi	Bouge Phalia River/ E of Arcola/ FSM
		Sunflower River/ NE of Indianola/ FSM
		Tombigbee River/ Leard *et al.*, 1969
	Missouri	Meramec River/ Times Beach/ MDC 3850
		Mississippi River/ New Madrid/ OSUM 26398
		St. Francis River/ Dunklin Co./ MDC 6300
	Oklahoma	North Canadian River/ Lake Overholser/ OSUM 35789
	Tennessee	Red River/ NE of Adams/ OSUM 23079
	Texas	Nueces River/ Lake Corpus Christi/ Murray, 1971a
	West Virginia	Elk River/ E of Big Chimney/ OSUM 23118
		New River/ Gauley Bridge/ OSUM 23425
1970	Alabama	Conecuh River/ FSM
		Gantt Lake/ N of Andalusia/ FSM
		Santa Bouge Creek/ NW of Franklin/ FSM
		Sepulga River/ S of Brooklyn/ FSM
	Arkansas	Arkansas River/ RM 50 - 283/ Kraemer, 1971

Table 1. (continued)

Year	State	Body of Water/Locality/Reference
	Florida	Lake Okeechobee/ Port Myaca/ DMNH 29055
		Yellow River/ E of Millington/ FSM
	Georgia	Chickasawahatchie River/ W of Newton/ FSM
		Lake Allatoona/ Cherokee Co./ OSUM 36761
	Illinois	Mississippi River/ Granite City/ Thomerson and Myer, 1970
	Kentucky	Dix River/ Near High Bridge/ Branson and Batch, 1971
	Mississippi	Buckatunna Creek/ SE of Buckatunna/ FSM
		Chunky Creek/ NNW of Enterprise/ FSM
		Okatibee Creek/ Meridian/ USNM 707708
	Missouri	Gasconade River/ Below Fredrickson /MDC 2300
	North Carolina	Catawba River/ Lake Wylie/ Fox, 1971
	Tennessee	Stones River/ E of Nashville/ OSUM 27086
1971	Florida	Indian Prairie Canal/ Glades Co./ DMNH 47308
	Georgia	Altamaha River/ RM 116/ Sickel, 1973
		Coahulla Creek/ Prater Mill/ OSUM 27377
		Consanga River/ Beaverdale/ OSUM 27379
		Flint River/ Sickel, 1973
		Little Ocmulgee River/ E of Reynolds /OSUM 39966
		Ocmulgee River/ At Oconee River/ Sickel, 1973
	Mississippi	Pearl River/ Ross Barnett Dam/ OSUM 27113
	New Jersey	Delaware River/ Trenton/ Fuller and Powell, 1973
	Ohio	Licking River/ S of St. Louisville/ OSUM 26860
		Muskingum River/ Lowell/ DMNH 51690
	Washington	Chehalis River/ Raymond/ DMNH 56395
1972	Alabama	Choctawahatchee River/ NE of Geneva/ FSM
		Little Uchee Creek/ NW of Ft. Mitchell/ OSUM 41538
		Pea River/ E of Perry/ FSM
	California	Owens River/ Inyo Co./ Fox, 1972
	Florida	Holmes Creek/ WSW of New Hope/ FSM
		St. Joseph Bay/ SE of Port St. Joe/ FSM
	Georgia	Savannah River/ NNE of Milhaven/ Fuller and Powell, 1973
	Missouri	Osage River/ Miller Co./ MDC 5550
	Ohio	Olentangy River/ Delaware Reservoir /OSUM 33900
	Oregon	John Day River/ Grant Co./ ODFW
	South Carolina	Pee Dee River/ SE of Society Hill/ Fuller and Powell, 1973
	Tennessee	Fall Creek/ Anchor Mill/ OSUM 33791
	Texas	Trinity River/ Lake Grapevine/ TCU 357
1973	Alabama	Little Cypress Creek/ NNW of Jackson/ OSUM 34860
		Peckerwood Creek/ N of Marble Valley/ OSUM 36004
	Arkansas	Buffalo River/ Buffalo River State Park/ OSUM 41571
	California	Stow Lake/ Golden Gate Park, San Francisco/ Carlton, 1973
	Florida	Lake Tsala/ Hernando/ ANSP 332593
		Wekiva River/ Seminole Co./ RCB
	Mississippi	Yalobusha River/ Grenada Reservoir/ Cooper and Johnson, 1980
	New Mexico	Pecos River/ Eddy Co./ USNM 709229
	South Carolina	Intracoastal Waterway/ At Waccamaw River/ Fuller and Powell, 1973
		Waccamaw River/ Horry Co./ Fuller and Powell, 1973
	Tennessee	Clinch River/ ESE of Tazewell/ ANSP 335725
		Halston River/ Knoxville/ ANSP 335735
		Obey River/ Dale Hollow Reservoir/ OSUM 35788
		Paint Rock River/ Swaim/ OSUM 335720
	Texas	Guadelupe River/ Canyon Lake/ Britton and Murphy, 1977
	Virginia	Appomattox River/ Near Hopewell/ USNM 711390
		James River/ Near Hopewell/ SBMNH 43037
1974	Alabama	Big Cedar Creek/ NE of Shepardsville/ OSUM 35450
		Cedar Creek/ NE of Furman/ OSUM 35221
		North River/ E of Samantha/ OSUM 36723
	Arkansas	Bouef River/ W of Lake Village/ OSUM 35977
		Spring River/ S of Ravenden/ OSUM 36642
	Florida	Main Canal/ Palm Beach Co./ FSM
	Georgia	Ogeechee River/ SW of Halcyon Dale/ FSM
		Potatoe Creek/ W of Thomston/ OSUM 35161

Table 1. (continued)

Year	State	Body of Water/Locality/Reference
	Illinois	Illinois River/ Kampsville/ Thompson and Sparks, 1977
	Iowa	Mississippi River/ Lansing/ Eckbald, 1975
	Mississippi	Buttahatchie River/ Lowndes Co./ OSUM 36251
	Tennessee	Emory River/ NE of Harriman/ OSUM 36769
		Little Tennessee River/ Near Telico/ SBSK 988
		Mississippi River/ Fulton/ SBSK 990
	Texas	Angelina River/ Sam Rayburn Lake/ TCU 1177
		Brazos River/ Pecan Plantation/ TCU 2983
		Colorado River/ Marble Falls/ Britton and Murphy, 1977
	Virginia	Chickahominy River/ Lanexa/ DMNH 98701
1975	Alabama	Dauphin Island/ USNM 76536
		Drivers Branch/ SE of Talladega/ FSM
		Second Creek/ W of Rogersville/ OSUM 36350
	Arkansas	Coon Bayou/ W of Winchester/ OSUM 39680
		Maniece Bayou/ NNW of Bradley/ OSUM 39682
		Mckinney Bayou/ NW of Garland City/ OSUM 39676
		Mississippi River/ ESE of Lake Village/ OSUM 39666
		Red River/ E of Bradley Lake/ OSUM 39958
	California	Lake Murray/ San Diego/ TCU 3028
	Florida	Lake Jackson/ Sebring/ OSUM 36827
		Mayakka River/ Mayakka State Park/ OSUM 37965
	Illinois	Saline River/ E of Equality/ OSUM 36832
	Kentucky	Buck Creek/ NW of Ula/ OSUM 38072
		Floyd's Fork/ E of Brooks/ DMNH 106659
	Louisiana	Tensas River/ Madison Par./ Kuckyr and Vidrine, 1975
	Maryland	Chesapeake Bay/ Susquehanna Flats/ Stotts *et al.*, 1977
	Missouri	White Water River/ Bollinger Mill/ MDC 7601
	North Carolina	Waccamaw River/ Lake Waccamaw/ Fuller and Richardson, 1976
	Ohio	Scioto River/ S of Delaware/ FMNH 171650
	Oklahoma	Red River/ Lake Texoma/ TCU 1580
	South Carolina	Santee River/ Lake Marion/ OSUM 36568
	Texas	Red River/ Lake Texoma/ Britton and Murphy, 1977
		San Jacinto River/ Lake Houston/ MCZ 293569
	Virginia	New River/ Glen Lyn/ Rodgers *et al.*, 1977
	West Virginia	Mud River/ Cabell Co./ Joy and McCoy, 1975
1976	Alabama	Neely Henry Lake/ Britton and Morton, 1979
		Tubbs Creek/ SW of New Mt. Hope/ FMNH 197886
	Arkansas	Caddo River/ Near Amity/ ADPC 155
		Chamagnoll Creek/ Calion/ TCU 3004
	California	Cachuma Lake/ Santa Barbara Co./ SBMNH 48084
		Salinas River/ Monterey Co./ TCU 3018
		San Luis Reservoir/ N of Basalt Hill/ TCU 3017
		Shasta Lake/ Shasta Co./ CAS 57374
	Indiana	Salt Creek/ Monroe Reservoir/ OSUM 48532
	Louisiana	Bayou Cocodrie/ Terrenbonne Par./ Vidrine and DeRouen, 1976
	Mississippi	Noxubee River/ S of Macon/ FMNH 197887
		Tibbee Creek/ N of Tibbee/ FMNH 197860
	Missouri	Big Creek/ Sam Baker State Park/ MDC 157
	North Carolina	Little River/ Town Creek Mound/ NCSM P211
		Uwaharrie River/ SE of Albemarle/ MCZ 280461
	Ohio	Miami River/ Dayton/ OSUM 38475
		Stillwater River/Dayton/ GAC 762
	Oregon	Siuslaw River/ Lane Co./ ODFW
	South Carolina	Cooper River/ Lake Marion/ TCU 2999
	Tennessee	Barren Fork River/ McMinnville/ OSUM 40922
		Big Bigby Creek/ Canaan/ OSUM 40726
		Big Rock Creek/ Verona/ OSUM 40747
		Big Swan Creek/ SE of Centerville/ OSUM 40727
		East Rock Creek/ NNE of Verona/ OSUM 41552
		Flat Creek/ SW of Rally Hill/ OSUM 40741
		Fountain Creek/ SE of Columbia/ OSUM 40740
		Garrison River/ WSW of Bugscuffle/ OSUM 40913

Table 1. (continued)

Year	State	Body of Water/Locality/Reference
	Tennessee (con't)	Greenlick Creek/ SE of Williamsport/ OSUM 40719
		Lick Creek/ Branton Ford/ OSUM 40731
		Liepers Creek/ NE of Williamsport/ OSUM 40723
		Little River/ N of Maryville/ OSUM 40931
		Little Duck River/ Manchester/ OSUM 40920
		North Fork Creek/ SE of Unionville/ OSUM 40911
		Notchy Creek/ SE of Madisonville/ OSUM 40928
		Piney River/ NW of Centerville/ OSUM 40733
		Rich Creek/ S of Wilhoit Mills/ OSUM 40893
		Sinking Creek/ S of Halls Mill/ OSUM 40898
		Sugar Creek/ S of Shelbyville/ OSUM 40915
	Texas	Blanco River/ At San Marcos River UOM
		Johnson Creek/ S of Ozona/ Britton, 1982
		Pecos River/ N of Rio Grande/ Britton, 1982
1977	Alabama	Burnt Corn Creek/ Brewton/ OSUM 42021
		Murder Creek/ Evergreen/ OSUM 42259
		Piney Creek/ W of Peets Corner/ OSUM 42100
	Florida	Aucilla River/ Taylor Co./ OSUM 42021
		Kissimmee River/ SE of Okechobee/ FSM-U
		Oklawaha River/ E of Silver Springs/ OSUM 41184
		St. Johns River/ SE of Geneva/ OSUM 45832
		Steinhatchee River/ Dixie-Taylor Co. Line/ DMNH 125738
	Georgia	Ohoopee River/ SSW of Reidsville/ FSM
		Withlacoochee River/ Brookes-Lowndes Co. Line/ FSM
	Illinois	Kaskaskia River/ Near Baldwin/ Thompson and Sparks, 1977
		Sangamon River/ Lake Sangchris/ Thomas and Sparks, 1977
	Kentucky	Mud River/ NE of Beechland/ OSUM 41495
		Tygarts Creek/ Below Cascade Cave / MUMC 848
	Mississippi	Big Black River/ NW of Edwards/ FNMH 198384
	Missouri	Big River/ NW of House Springs/ OSUM 41133
		Bourbeuse River/ Noser Hill/ OSUM 42666
	North Carolina	Richardson Creek/ Union Co./ NCSM P256
	Ohio	Hocking River/ NE of Stewart/ OSUM 41395
		Little Muskingum River/ ENE of Marietta/ OSUM 39712
		Meigs Creek/ NW of Beverly/ OSUM 40198
		Olive Green Creek/ NW of Beverly/ OSUM 40260
	Texas	Big Cypress Creek/ Lake of the Pines/ Pool and McCullough, 1979
		Concho River/ Lake Nasworthy/ Baker, 1978
		Sabine River/ Murvaul Reservior/ Pool and McCullough, 1979
	West Virginia	Beech Fork Reservoir/ Cabell Co./ MUMC 857
	Wisconsin	St. Croix River/ Near Hudson/ Fuller, 1978b
1978	Arkansas	Bayou Bartholomew/ Near Jones River/ ADPC 51
		L'Anguille River/ NE of Mariana/ OSUM 41492
		Madison-Mariana Diversion Canal/ ENE of Tuni/ OSUM 43050
		Strawberry River/ S of Smithville/ ADPC 108
	Florida	Lake Oklawaha/ Rodman Dam/ FSM 26512
	Georgia	Chattahoochee River/ Near Columbus/ USNM 79558
	Indiana	Big Indian Creek/ Near Crandall/ MUMC 1559
		Blue River/ N of Wyandotte/ OSUM 45780
		White River/ E of Mendora/ DM 562
	Maryland	Potomac River/ Washington, D. C. area/ Dresler and Cory, 1980
	Minnesota	Minnesota River/ Near Burnsville/ Cummings and Jones, 1978
	Mississippi	Allan Branch/ N of Enterprise/ FMNH 201527
		Moss Creek/ SE of Caichael/ FMNH 201525
		Shubuta Creek/ NW of Shubuta/ FMNH 201514
		Souinlovey Creek/ N of Pachuta/ FMNH 201521
		Woodward Creek/ E of Cooksville/ FMNH 201524
	Missouri	Cane Creek/ Butler Co./ MDC 1325
		Little Black River/ Butler Co./ ACB

Table 1. (continued)

Year	State	Body of Water/Locality/Reference
	Missouri (con't)	Moreau River/ Jefferson City/ MDC 5222
	North Carolina	Rocky River/SE of Oakboro/ OSUM 42192
	Oklahoma	Caddo Creek/ N of Ardmore/ UOM
	Tennessee	Collins River/ E of McMinnville/ OSUM 43806
	Texas	Llano River/ Llano Co./ UOM
	West Virginia	Big Seven Mile Creek/ Cabell Co./ MUMC 1144
		Guyandotte River/ Midkiff/ MUMC 1221
1979	Alabama	Chattahoochee River/ Below Uchee Creek/ Jenkinson, 1979
		Saugahatchee Creek/ NW of Auburn/ Jenkinson, 1979
		Tallapoosa River/ Upstream of Lake Martin/ Jenkinson, 1979
		Uchee Creek/ At Chattahoochee River/ Jenkinson, 1979
	Arkansas	Saline River/ W of Owinsville/ FSM 29553
	California	Lake Casitas/ Near Ojai/ SLC
		Lake Piru/ Near Filmore/ SLC
		Merced River/ Merced/ SBSK 1777
	Florida	Lake Lucy/ Groveland/ FSM 26687
		Lake Palatlakaha/ SW of Cleremont/ FSM 26772
		Lake Talquin/ W of Tallahassee/ FSM 26932
		Mosquito Creek/ E of Chattahoochee / USNM 809640
		Spring Creek/ SE of Mariana/ FSM 30097
		Waccasassa River/ Levy Co./ FSM
	Georgia	Pound Creek/ Lake Meriwether/ OSUM 45570
	Indiana	Stoney Creek/ SE of Noblesville/ OSUM 43620
	Kentucky	Coal River/ Boyd Co./ MUMC 1526
		Salt River/ SSE of Waterford/ OSUM 44764
	Maryland	Wicomico River/ Salisbury/ Counts, 1981b
	Missouri	Thomas Hill Reservoir/ Macon Co./ MDC 7537
	North Carolina	Cape Fear River/ Lee Co./ RS
	Pennsylvania	Ohio River/ Pittsburgh/ Taylor, 1980b
	Tennessee	Big Hickory Creek/ SW of McMinnville/ OSUM 39044
		Shoal Creek/ SSW of Pulaski/ USNM 795588
		Weakly Creek/ SE of Unionville/ OSUM 40908
	Texas	Pedernales River/ Near Johnson City/ CEB
		San Antonio River/ Karnes Co./ CEB
		Spring Creek/ NNW of West Field/ OSUM 45887
1980	Arkansas	La Grue Bayou/ S of Dry Lake Dam/ FSM 29141
	Florida	Ichetucknee River/ Ichetucknee State Park/ FSM 26905
		Rocky Creek/ N of Sink Creek/ FSM 28350
		Santa Fe River/ At Olustee Creek/ FSM 27817
	Illinois	Kankakee River/ Custer Park/ Lewis and Brice, 1980
	Kentucky	Eagle Creek/ Sparta Bridge/ MUMC 1666
		Little River/ S of Hopkinsville/ OSUM 49287
	Michigan	Lake Erie/ ENE of Monroe/ OSUM 49999
	Mississippi	Big Black Creek/ Jackson Co./ MMNS 1054
		Pascagoula River/ Three Rivers/ MMNS 1078
		Steel Bayou/ Near Fitler/ Leard *et al.* 1980
		Tallahala Creek/ Forest Co./ MMNS 981
		Yockanookany River/ Leake Co./ MMNS 1295
	Missouri	Bryant Creek/ Ozark Co./ MDC 1175
		Missouri River/ Merman/ RDO
	North Carolina	Eden River/ Near Winston-Salem/ JJH
		Mountain Island Lake/ Near Lucia/ USNM 809473
	South Carolina	Hartwell Reservoir/ Anderson-Oconee Cos./ JJH
		Lake Keowee/ Oconee-Pickens Cos./ JJH
	Texas	Little Brazos River/ SE of Law/ OSUM 48170
		White River/ White River Lake/ Fontanier, 1982
	Virginia	Potomac River/ Alexandria/ Dresler and Cory, 1980
	West Virginia	Monongahela River/ Morgantown/ Zeto, 1982
		Pocatalico River/ Sissonville/ MUMC 1586
		Twelve Pole Creek/ Shoals/ MUMC 1587
		West Fork River/ NE of West Milford/ Zeto, 1982
1981	Florida	Cypress Creek Canal/ NE of North Lauderdale/ OSUM 49853
		Lake Buena Vista/ Orange Co./ RJ
		Middle River Canal/ Lauderdale Lakes/ OSUM 49849

Table 1. (continued)

Year	State	Body of Water/Locality/Reference
	Florida (con't)	Sky Lake/ North Miami Beach/ OSUM 49910
	Georgia	Chickamauga Creek/ Ringgold/ OSUM 50521
		Towaliga River/ Downstream of High Falls Lake/ Walker, 1982
	Kentucky	Nolin River/ White Mills/ MUMC 3029
		Slate Creek/ E of Owingsville/ MUMC 3106
		Tradewater River/ S of Sullivan/ OSUM 50808
	Maryland	Susquehanna River/ Conowingo Dam/ Nichols and Domermuth, 1981
	Mississippi	Amite River/ Amite Co./ MMNS 1450
	New Jersey	Raritan River/ Near New Brunswick/ Trama, 1982
	Oklahoma	Arkansas River/ Ft. Gibson Dam/ RLR
		Little River/ N of Goodwater/ RLR
	South Carolina	Edisto River/ ENE of Canadys/ OSUM 48840
		Salkahatchie River/ NE of Yemassee / OSUM 48840
	Tennessee	Hatchie River/ NE of Rialto/ OSUM 50462
	Texas	San Gabriel River/ Circleville/ Hillis and Patton, 1982
	West Virginia	Hughes River/ E of Cisco/ MUMC 3184
1982	Delaware	Nanticoke River/ Near Seaford/ SH
	Kentucky	Elkhorn Creek/ S of Stamping Ground/ MUMC 3224
	Maryland	Nassawango Creek/ Near Snow Hill/ USNM 804416
	Ohio	Maumee River/ Toledo/ Scott-Wasilk *et al.*, 1983

BIOFOULING OF POWER PLANT SERVICE SYSTEMS BY *CORBICULA*

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ABSTRACT

Corbicula sp. foul the service water systems at nuclear power plants because the environment within these systems is compatible with the ecological requirements of the species. To reduce fouling by *Corbicula*, components of service water systems and operating procedures that enhance the potential for fouling need to be identified. Factors important in mediating biofouling of service water systems appear to be screening potential, minimum and maximum velocities and the operational procedures employed during power plant biofoulant control and downtime. These conclusions are based on the results of a categorical model we used to correlate information from power plants with that on *Corbicula* life history. Power plant parameters in the model include temperature, dissolved oxygen concentration, screen and strainer size, maximum and minimum velocities, and elements of the biofouling control procedures. Parameters for *Corbicula* include tolerances to temperature, dissolved oxygen, biofouling control chemicals, velocity preferences, and optimal temperatures for each life stage and behavior.

The freshwater clam, *Corbicula* sp., has effectively fouled service water systems in nuclear power plants. After the Arkansas Nuclear One, Unit 2, power plant was shut down because clams blocked flow through the containment air coolers the Nuclear Regulatory Commission (NRC) issued a bulletin (I&E Bulletin 81-03) requiring power plant operators to examine for the presence of *Corbicula* in their power plants and in the environment near the plants. Information was collected from 87 sites, which included 151 units; 73 of these units were operating and 78 were planned or under construction.

Data on the distribution of *Corbicula* near the plants was collected as 1) present in plant, 2) present in vicinity, 3) present in waterbody, or 4) not present. The NRC staff defined "present in plant" as live organisms, shells or shell fragments in or having been found in the circulating water system, service water system, or fire protection system. The intake structure was not considered part of the plant. "Present in vicinity" was defined as in or having occurred in the areas near the plant that are subjected to plant related aquatic biological monitoring programs. "Present in the waterbody" was defined as in or having occurred in the water from which the plant obtains cooling water or a connecting body of water from which colonization of the area in which the plant occurs is probable. "Not present" was defined as not reported in the waterbody and the probability of future colonization unlikely.

A review of the responses to I&E Bulletin 81-03 showed *Corbicula* was reported present in the plant at 10 sites, which included 17 operating units (Masnik, unpubl. ms. NRC, Wash. D.C.) *Corbicula* was reported in the vicinity but not in the plant of 5 sites, including 10 operating units. Two sites, with three units, reported *Corbicula* in the waterbody but not in the plant vicinity. *Corbicula* was reported not present in the plant, vicinity or waterbody at 33 sites with 43 operating units.

For plants planned or under construction, *Corbicula* was reported as present in the vicinity of 27 sites including 41 units and present in the waterbody at 31 sites with 51 units. The organism was reported not present for 17 sites with 27 units.

Corbicula was present in 23% of the currently licensed units in the United States. However, when the percent occurrence was calculated based on *Corbicula* occurrence in the vicinity and waterbody, in-plant occurrence increased to 57%.

These data illustrate 1) the effectiveness of *Corbicula* to invade and foul the service water systems of power plants if found in the environment around the power plant and 2) the environment within these systems is compatible with the environmental requirements of *Corbicula*. In order to obviate *Corbicula* fouling in service water systems of power plants, *Corbicula* must be 1) prevented from entering the system or 2) the environment of the system must be made incompatible with the ecological requirements for growth and survival of *Corbicula*. The purpose of this review is to detail *Corbicula* characteristics that enhance their ability to service water systems. The methods and techniques to survey for and control the *Corbicula* fouling are not complete as of this review and we do not suggest that total prevention of *Corbicula* fouling is possible.

CORBICULA CHARACTERISTICS AND POWER PLANT CONDITIONS

We used a categorical model to correlate information from power plants with that of *Corbicula* life history. Power plant parameters in this model include temperature, dissolved oxygen concentration, size of screens and strainers, maximum and minimum velocities and elements of biofouling control and operational prodedures. Paramenters for *Corbicula* include tolerance to temperature, dissolved oxygen and biofouling control chemicals, velocity preferences, optimal temperatures for each life stage and behavior. The correlations between *Corbicula* and power plant service water systems that appear to promote or allow *Corbicula* fouling are 1) larva size and size of screens and strainers, 2) larvae settling and in-plant flow velocities and patterns, 3) larva-substrate requirements and silt buildup, 4) growth potential and water temperature, and 5) avoidance behavior and intermittent antifoulant application.

LARVA SIZE AND SIZE OF SCREENS AND STRAINERS

The offspring of *Corbicula* are retained in the brood chamber of the adult from the egg to the juvenile stage, at which time they are released (Britton and Morton, 1982). During the breeding season, an adult can contain thousands of pre-release juveniles, releasing 300-400 juveniles per day (Britton, 1982; Aldridge and McMahon, 1978). When released the larvae are not typical molluscan veligers, but rather pediveligers more adapted for crawling than swimming (Britton, 1982). However, pediveligers can be carried by ambient currents some distance downstream of the adult population (Britton, 1982; Eng, 1979).

Figure 1 illustrates the relationships between larvae size and screening and strainer capability that must occur to prevent *Corbicula* from entering the service water systems of the power plant. When breeding populations of *Corbicula* occur in or near the intake structure of a power plant, the water intake system can entrain *Corbicula* into the plant. The obvious control measure is screening or straining. However, to maintain the cooling requirements of a power plant, large volumes of water are required. Screen mesh-size is generally limited to no less than 0.3 cm and in-system strainers are too large to restrict the passage of *Corbicula* pediveligers or small juveniles (Goss and Cain, 1977). The approximate size of the *Corbicula* pediveliger in 220m (Sinclair and Isom, 1961; Aldridge, 1976; Aldridge and McMahon, 1978; Britton and Morton, 1982). *Corbicula* pediveligers in the intake water of a power plant wil not be screened at the intake or by strainers incorporated into the service water system. The use of smaller intake screens and strainers of present design is probably not practical because of the large volumes of water required for operation of nuclear power plants.

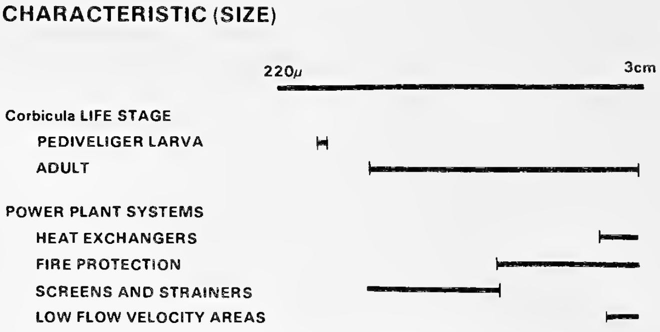

Fig. 1. Categorical model illustrating correlation between *Corbicula* larva size and power plant system screening potential.

LARVAE SETTLING AND IN-PUT FLOW VELOCITIES AND PATTERNS

Juveniles, released from the adult, quickly settle onto the surrounding substratum (Britton, 1982) unless they are moved by ambient currents. High velocity flows may prevent juveniles from settling or may dislodge juveniles before they are large enough to survive in currents that can move them (Eng, 1979).

We were not able to locate data correlating the ability of *Corbicula* larvae to settle with ambient flow velocities. Eng

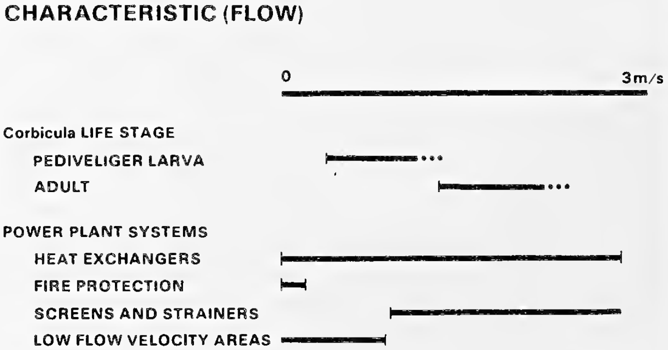

Fig. 2. Categorial model illustrating correlation between *Corbicula* flow requirements and in-plant flow velocities.

(1979) studied *Corbicula* populations in the Delta-Mendota Canal in California. Flow velocities in the canal averaged 1.2 mps. Sickel (1976) observed substratum preference of *Corbicula* pediveligers. The preferred velocity for *Corbicula* larvae settlement on the substrata tested was about 0.3 mps, however larval settlement may occur in currents less than this.

Using these observations (Eng, 1979; Sickel, 1976) and the fact that fouling potential in power plant service water uptake varies, we assumed there are preferred and upper flow limits for settlement of *Corbicula* larvae. Figure 2 illustrates the correlation between settling requirements and in-plant flow velocities that allow settlement of *Corbicula* pediveligers in the service water system. Data from operating power plants indicate that the pediveligers settle in low-flow areas. Then, as the populations grow, some of the organisms may move from low-flow to higher-flow areas and be carried with the water to other locations in the plant where larger individuals may block condenser tubes or smaller-diameter intake pipes in the service water system.

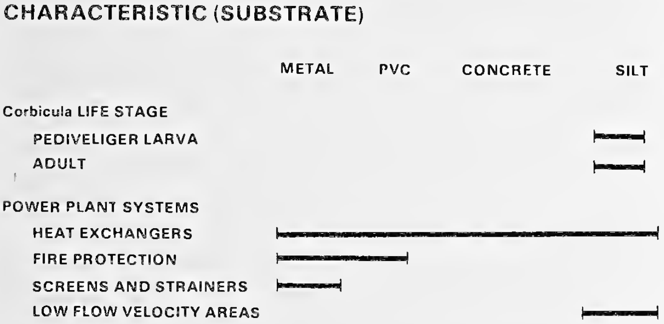

Fig. 3. Categorical model illustrating correlation between suitable substrate for *Corbicula* and substrates that occur in power plant service water systems.

LARVA-SUBSTRATUM REQUIREMENT AND SILT BUILDUP.

Corbicula seem to prefer sandy or gravel substrata, but are also found in larger rock or in mud or silt (Britton, 1982). *Corbicula* densities in a waterbody will vary with the substratum type (Eng, 1979). In service water systems, *Corbicula* appear to be associated with accumulations of silt or corrosion products. It is not clear, at this time, if this association is causitive or incidental. The larvae may initially settle preferentially in areas of silt, or their settling may result in siltation. Another explanation is that larvae and silt may settle at the same location independent of one another. Materials found in power plant service water systems are not a preferred substratum for *Corbicula* settlement or growth, but there is no indication that larvae cannot settle on the kinds of materials found in the service water system, in the absence of silt. However, if suitable substratum for *Corbicula* pediveliger settlement does not occur in the plant, then the incidence of *Corbicula* in the plant may be reduced.

Figure 3 illustrates the correlation between suitable substrate for *Corbicula* and available suitable substratum in service water systems. Most service water "plumbing" is constructed with metal or concrete; however, low flow areas or "dead legs" provide areas were silt and larvae can accumulate. These silted areas can serve as substrata for *Corbicula* to initially settle and grow. Additionally, pitted surfaces on service water systems may promote or allow *Corbicula* settlement.

GROWTH POTENTIAL AND WATER TEMPERATURES

Corbicula juveniles grow rapidly after they are released from the adult. Depending on the water temperature when the pediveliger is released, juveniles can grow to 10 to 18 mm shell length in a few months (Britton, 1982; Aldridge and McMahon, 1978). This rapid growth characteristic may contribute to the effectiveness of *Corbicula* as a biofouling organism. *Corbicula* become sexually mature very young and are fecund. Estimates for size at maturation range from 6 mm to 13 mm shell length (Heinsohn, 1958; Sinclair and Isom, 1963; Alderidge and McMahon, 1978). If the clams inside the power plant are able to grow at the same rate as those in nature, then it is possible for clams that have infested a power plant as a result of the spring spawning season to begin reproducing in the fall. Clams also reach reproductive size before they are large enough to become trapped in the smaller-diameter pipes in the service water system. Therefore, potentially reproducing populations may become widely distribution within the plant in a short period.

Corbicula can tolerate a wide range of water temperatures. Mattice and Dye (1976) reported that for continuous exposures the upper tolerance limits for 50% of the clam tested was between 24°C and 34°C when acclimation temperatures ranged from 5°C to 30°C. Lower tolerance limits were between 2°C and 12°C for acclimation temperatures ranging from 15°C to 30°C. Goss *et al.* (1979) reported similar tolerance, with variation dependant on acclimation temperatures and *Corbicula* size. Figure 4 illustrates the correlation between temperature tolerance of *Corbicula* and the occurrence of warm water in service water systems. Water temperatures in the service water systems are conducive to

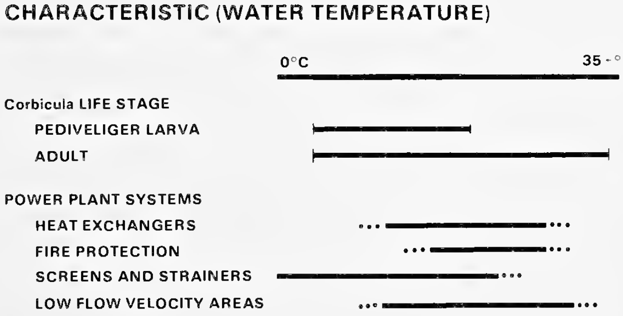

Fig. 4. Categorical model illustrating correlation between temperature tolerances of *Corbicula* and water temperatures in power plant service water systems.

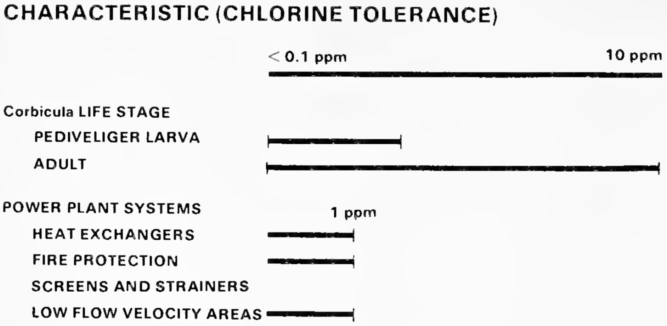

Fig. 5. Categorical model illustrating the correlation between chlorine tolerance of *Corbicula* and chlorine exposures (concentration, time and frequency) expected in power plant service water systems.

the growth and reproduction of *Corbicula* and probably enhance the potential for *Corbicula* occurrence and fouling at nuclear power plants.

Power plant service water systems include areas where the circulating raw water is warmed by plant operations. The water temperatures are usually within the range of tolerance for *Corbicula*. The warmed water can increase the growth potential of pediveligers and juveniles that have invaded the plant. This growth over a short period of time would increase the fouling problems associated with *Corbicula*.

AVOIDANCE BEHAVIOR AND INTERMITTENT ANTIFOULANT CONTROL

A characteristic of mollusk bivalves is their ability to "clam-up" in response to environmental stimuli. Bivalves avoid inimical environmental conditions by retreating into their shells and respiring anaerobically for extended periods of time. This behavior allows adult *Corbicula* to avoid antifoulant control measures such as chlorination. Mattice *et al.* (1982) reported that, given the U.S. Environmental Protection Agency's regulation limits on chlorine in power plant discharges (USEPA 1980), the use of chlorine has proven to be ineffective in controlling clam fouling at power plants. They reported adult *Corbicula* can tolerate target concentrations of 10 mg/L total residual chlorine for up to 30 min. Chlorination practices at Tennessee Valley Authority plants that include continuous chlorination during the clam breeding season have been somewhat successful (Goss and Cain, 1977). However, residual levels are difficult to maintain in static systems, like fire protection systems. Burial in silt may provide some additional protection from intermittently chlorinated water. Figure 5 illustrates the correlation between chlorine tolerance of *Corbicula* (including their ability to avoid chlorinated water for extended periods) and the chlorine levels expected in power plant service watersystems. Tolerance of *Corbicula* to chlorine is a function of both concentrations and exposure time. The tolerance levels illustrated in Figure 5 and generally consistant with exposure resulting from chlorination schedules generally used at freshwater cooled power plants, e.g. usually less than 2 hrs during a 24-hr period.

It is unlikely that standard chlorination practices alone will control *Corbicula* fouling because adults can avoid short-term exposure to toxic levels of chlorine, discharge regulations prevent use of chlorine at concentrations and for periods of time sufficient for effective control and during the larval release season, chlorination in the plant must be continuous to control infestation by larvae.

CONCLUSIONS

The freshwater clam *Corbicula* sp. is common in the aquatic environments near nuclear power plants in the United States. These clams readily move from the ambient environment to the environment of the service water system in the power plant as pediveligers and small juveniles. Portions of the service water system environment are compatible with the ecological requirements of *Corbicula*. Once in place in the power plant, the ability of *Corbicula* to grow and potentially reproduce and to avoid control measures for short periods allow *Corbicula* to effecively foul these plant systems. Effective control will require changing the environment of the service water system so *Corbicula* pediveligers either cannot enter or become established, grow and reproduce in the power plant service water system. Environmental changes may include dewatering of redundant systems during maintenance schedules, ensuring that systems on stand-by are filled with antifoulant treated water, antifoulant treatment of the entire service water system during *Corbicula* spawning, or enhanced flow through all service water system components. Control will probably be plant specific, and may even require different controls for different system components within the same plant.

ACKNOWLEDGMENTS

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ENGINEERING FACTORS INFLUENCING *CORBICULA* FOULING IN NUCLEAR SERVICE WATER SYSTEMS

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ABSTRACT

Corbicula fouling is a persistent problem in the service water systems of nuclear power plants. An understanding of the biological characteristics of *Corbicula* and the engineering characteristics of service water systems is important in developing effective detection and control methods. A data base of *Corbicula* fouling was compiled from nuclear and non-nuclear power stations and other industrial users of large volumes of raw water. The data base was analyzed to identify engineering factors common to service water systems that are conducive to fouling by *Corbicula*. Bounds on several engineering parameters such as flow velocity and water temperature which support *Corbicula* growth are given. Service water systems found in BWR and PWR reactors are listed and those that show fouling are identified. Systems that have fouled include residual heat removal heat exchangers, containment coolers and turbine-bearing lube oil coolers. Possible safety implications of *Corbicula* fouling are discussed for specific service water systems. Recommendations are given on how to minimize the potential for *Corbicula* fouling.

Fouling of service water systems due to the presence of the asiatic clam, *Corbicula*, is a persistent problem in the nuclear and non-nuclear power industries. Fouling of nuclear service water systems is especially critical because many service water cooling loops are required for safe shutdown of the reactor. This paper identifies engineering factors that have commonly occurred where *Corbicula* were found in nuclear service water system piping. The safety implications of service water system fouling are discussed and recommendations are given to reduce the potential for *Corbicula* fouling.

Many of the factors which influence fouling were identified from first-hand accounts given by utility personnel who have witnessed fouling incidents involving *Corbicula*. A second source of information was utility responses to IE Bulletin 81-03, "Flow Blockage of Cooling Water to Safety System Components by *Corbicula* sp. (Asiatic Clam) and *Mytilus* sp. (mussel)." This Bulletin was issued by the Office of Inspection and Enforcement of the U.S. Nuclear Regulatory Commission to all operating plants and plants under construction. Other information was obtained from the published literature on *Corbicula*.

The conclusions presented in this report are not necessarily those of the U.S. Nuclear Regulatory Commission and are not intended to infer any regulatory position on the part of the NCR.

NUCLEAR SERVICE WATER SYSTEMS

Nuclear service water systems are designed to provide cooling water to reactor and auxiliary system components during both normal and accident conditions. The water source is raw water taken directly from a river, lake, or ocean (Haried, 1982). The circulation water system, which cools the main turbine condensers, is considered separate from the service water systems.

Service water systems of both boiling water reactors (BWRs) and pressurized water reactors (PWPs) are divided into two general categories -- essential and nonessential systems. Each system handles a different type of cooling load.

Generally, the essential service water system cools components within the reactor and auxiliary buildings that are nuclear-related and are required for safe shutdown. The essential service water system may also be referred to as the emergency equipment cooling water (EECW) system, the service water (SW) system, or the essential raw cooling water

(ERCW) system. Cooling loops served by the essential service water system are classified as safety related.

The nonessential service water system, in general, cools components within the turbine-generator building that are non-nuclear related and are not required for safe shutdown of the reactor. In some plants this system is referred to as the raw cooling water (RCW) system or the auxiliary cooling water system. Cooling loops served by the nonessential service water system are classified as nonsafety related.

The fire protection system is a non-nuclear safety system that often draws its water from the service water system or from the service water intake bay. Because *Corbicula* fouling has occurred in the fire protection system, this system will be discussed along with the service water systems.

Initial fouling control for both BWRs and PWRs occurs in the service water intake structure. Large chunks of floating debris such as driftwood and ice are removed by the trash racks at the opening of the intake structure. After entering the intake, water passes through self-cleaning traveling screens which remove debris greater than 13 mm in diameter. Downstream from the service water pumps, the water passes through basket strainers which remove particles greater than 3 mm in diameter. Therefore, *Corbicula* up to 32 mm in diameter which have been found inside service water heat exchangers (Goss and Cain, 1976) have come in as larvae and have found suitable conditions for growth inside service water systems piping. Thus, an effective means of controlling *Corbicula* inside service water systems must address control of *Corbicula* larvae in the service water.

ENGINEERING FACTORS INFLUENCING *CORBICULA* FOULING

The engineering factors discussed here have occurred commonly where *Corbicula* have been found in service water system piping. These factors often interact to emulate environmental conditions known to support *Corbicula* growth in their natural environment. The factors are: 1) flow velocity, 2) water temperature, 3) silt and corrosion products, 4) system redundancy and intermittent use, 5) valve leaks, 6) chlorination effectiveness and system reliability, and 7) component size.

FLOW VELOCITY

Low-velocity flow appears to be a major factor supporting the settlement and growth of *Corbicula* larvae in service water systems. Power plant personnel indicate that velocities up to 0.30 mps may be sufficiently low to allow *Corbicula* larvae to settle. In addition, *Corbicula* may attach to piping by secreting a byssal thread (Sinclair, 1963). Once the larvae settle and attach, minor increases in velocity will not detach them. It is possible that settled larvae may create eddies which result in silt deposition, thus compounding the fouling problem.

Low-velocity flow also provides an ideal environment for the deposition of silt and other suspended particles. Fluid velocities in municipal water systems are typically kept above 1 mps to prevent silting. At one nuclear plant, levels of suspended solids in the service water reached as high as 10,000 ppm during peak run-off periods. Silt deposits provide an environment in which *Corbicula* may grow, and the silt layer protects the young *Corbicula* larvae from chlorine levels that would be toxic if in direct contact with the larvae.

Unlike stagnant water conditions, low-velocity flow provides a continuous supply of food and dissolved oxygen to clams in the piping system. Thus, low-velocity flow not only allows clams to settle and attach to internal surfaces of the service waste system, it also provides food and oxygen needed for their growth.

Eddies and backwater conditions occur at or near abrupt changes in flow path geometry in the service water system and cause low-velocity flow. Low-velocity flow conditions exist in service water inlet structures (Fig. 1), at inlets to heat exchanger waterboxes, and where there are sudden changes in pipe diameter. Low velocity may also occur in lines with leaking or partially open valves.

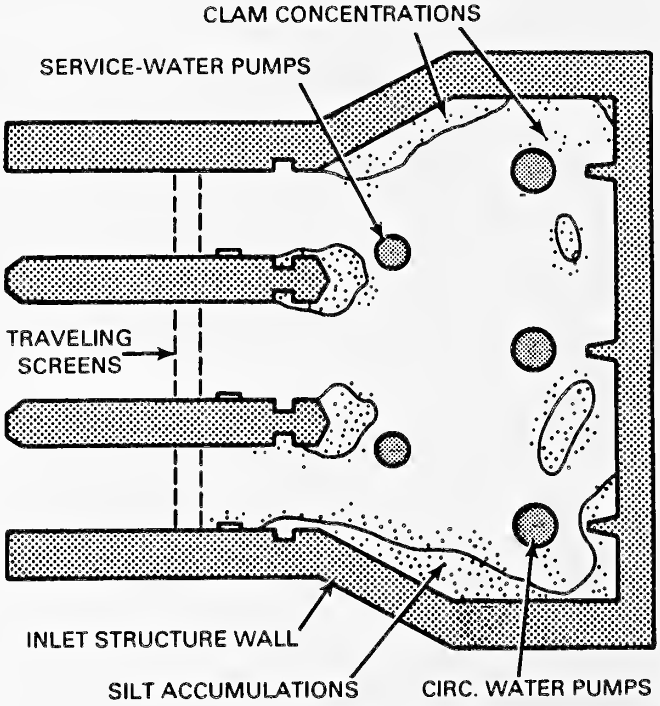

Fig. 1. A Typical Inlet Structure Design Showing Areas Where Clams and Silt have Deposited (Smithson, 1981).

WATER TEMPERATURE

Water temperature is a major factor that determines whether service water cooling loops will support *Corbicula* growth. Although thermal tolerance limits of *Corbicula* are dependent on acclimation temperature and life stage, the upper limit appears to be between 31 and 35°C, and the lower limit between 2 and 4°C (Mattice *et al.*, 1982). Optimum temperatures for *Corbicula* growth are in the mid 20°C range (Mattice *et al.*, 1982). At many plants, the water temperature of the service water source is above 2°C for most of the year. Also, the retention period of water held in redundant heat exchangers or systems which see intermittent use is generally long enough for the service water to reach room temperature (approximately 20°C).

Seasonal temperature extremes affect the population dynamics of *Corbicula* in the service water source. Low water temperatures have been known to cause severe winter kills in *Corbicula* populations (Bickel, 1966). The greatest population increases and most severe fouling problems have occurred in the southern United States where winter temperatures of the water source typically remain above 2°C.

SILT AND CORROSION PRODUCTS

Fouling caused by silt and corrosion products (primarily iron-oxide) is often found in conjunction with clams and relic shells in carbon steel service water piping. Although these fouling mechanisms may exacerbate clam fouling, similar environmental conditions are known to promote all three types of fouling independently. Two utilities have replaced portions of their carbon steel service water and fire protection system piping with stainless steel piping to minimize corrosion. No further corrosion problems have been reported from them to date.

As stated previously, low velocity flow conditions that allow settlement of *Corbicula* also allow deposition of other suspended particles such as silt. Silt and mud deposits provide a natural substratum for *Corbicula* growth, and can act as a buffer between clam larvae and chlorinated service water. Silt deposits exhibit a chemical demand for free chlorine, and a layer of silt covering clams may also reduce the rate of chlorine diffusion into the layer where the clams are located. Therefore, the residual chlorine level in the water may be several times higher than that to which the buried clams are exposed. Because of the differences in exposure, residual chlorine levels known to kill clam larvae when in direct contact may prove ineffective in controlling clam larvae protected by a layer of silt.

At least two methods can be used to remove silt from piping systems. The Vermont Yankee nuclear plant, for example, has used a chemical dispersant to flush mud and silt from its circulating water system (Electric Light and Power, 1978). The dispersant increases the wettability of mud and silt and allows normal water turbulence to keep the particles suspended so they can be flushed away. The use of some dispersants may, however, be restricted to closed cycle cooling water systems due to the discharge limits imposed on these chemicals. High velocity flushing is another method of removing silt from piping systems.

Corrosion products are often found along with deposits of silt and *Corbicula*. Although the interaction between corrosion products, silt and *Corbicula* is not completely understood, there are definite correlations between the presence of silt and corrosion products as well as the correlations between silt and *Corbicula* deposits, as previously discussed.

Two mechanisms believed to cause corrosion of carbon steel in the presence of silt deposits are electrochemical reactions and the presence of sulfides. Electrochemical corrosion in carbon steel piping results from a nonuniform distribution of dissolved oxygen (Bacon, 1978). This renders the area exposed to low oxygen concentration anodic with respect to areas of higher oxygen concentration. Thus, areas where silt has deposited may become oxygen deficient cells where electrochemical corrosion can occur. One utility noted that pitting and corrosion in their fire protection system is more prevalent on the bottom, inside surface of piping where silt and organic matter has deposited. Chemical analysis of the corrosion product revealed the presence of sulfides, the second corrosion mechanism, which are known to cause accelerated pitting corrosion in carbon steel piping. Sulfides could result from decomposition of organic matter by sulfate reducing bacteria in fire protection and cooling water systems.

Other effects of corrosion are reduced flow area and increased surface roughness, both of which restrict the flow-carrying capacity of piping. Increased surface roughness, in particular, may provide a more suitable surface for attachment by clam larvae and increase the thickness of the boundary layer which further promotes the settlement of silt and clams. Thus, silting, corrosion products, and *Corbicula* all contribute to degraded flow conditions in the service water system.

SYSTEM REDUNDANCY AND INTERMITTENT USE

Many components in redundant systems are used intermittently and often exhibit low flow and/or stagnant conditions. Several utilities indicated that fouling typically occurs in systems with low flow, intermittent flow, or stagnant conditons for extended periods of time.

Redundant cooling loops are provided in the essential service water system and in some nonessential service water cooling loops to ensure continuous cooling in the event that one of the redundant coolers fails. Typical cooling loops with redundant heat exchangers are the containment cooling units, component cooling (or closed cooling) units, and turbine-bearing lube oil coolers. Systems used intermittently include those which provide cooling or service water on demand only. Examples of such systems are containment cooling units, residual heat removal heat exchangers (or decay heat removal heat exchangers), and the fire protection system. Containment cooling units, for example, are only in service when the temperature inside the reactor containment vessel exceeds a specified temperature. Many heat exchangers only receive flow during scheduled testing performed on a weekly, monthly, or even yearly basis.

Both redundant systems and intermittently used systems are typically maintained full of service water and in a standby condition. Plant technical specifications call for periodic flow testing to ensure the operability of these systems. Several utilities have increased the frequency of their flow tests after finding *Corbicula* in the systems. Although more frequent flow testing may work to flush the system of silt and small clams, it is possible that increased flow testing provides a fresh supply of food and water to the clams more frequently, thus providing a more habitable environment for *Corbicula* trapped in protected areas of the system.

An apparently effective means of controlling *Corbicula* in redundant and intermittent-use systems is to schedule flow tests coincident with service water chlorination. Thus, when flow testing is completed, the systems are filled with chlorinated service water and returned to standby condition. Because service water flow bypasses systems in the standby mode, failure to chlorinate during flow testing means that systems which would benefit most from chlorination may never be chlorinated. Since finding *Corbicula* in their redundant and intermittent use systems, several plants have implemented such schedules and have noted success.

VALVE LEAKS

Valve leaks are another cause of low-velocity, continuous flow. Although these leaks may be minor from an engineering standpoint, the flow may be great enough to provide clams with a continuous supply of food and oxygen. There is evidence that *Corbicula* may be less tolerant of reduced oxygen levels than other fresh water molluscs (McMahon, 1979). As oxygen levels fall below saturation, oxygen uptake by *Corbicula* rapidly decreases to approximately ten percent of that at saturation. Factors such as Clam respiration, the oxygen demand of bacteria, and formation of corrosion products reduce dissolved oxygen levels in stagnant service water. Leaking valves, supplying food and dissolved oxygen, appear to be a primary cause of *Corbicula* growth in redundant and intermittent use systems which are assumed to be stagnant.

Two basic types of valve leaks are actual valve malfunctions, and leaks within the design specifications of the valve. Valve malfunctions may be corrected with increased maintenance, but design allowable leaks are a result of manufacturing tolerances. Valves in the service water system may normally allow leaks of up to 10% of the design flow when they are in the closed position. Of the different valve types, butterfly valves appear to have the highest potential for leakage.

At one plant the combination of an open inlet valve and a closed but leaking outlet valve allowed *Corbicula* and silt to deposit in the inlet waterbox of a redundant turbine-bearing lube oil heat exchanger. The open inlet valve allowed silt and clams to enter the heat exchanger and settle in the waterbox. The leaking outlet valve provided a continuous flow (approximately 4 L per minute) of fresh water to the clams and allowed further deposition of clams and silt. The inlet water temperature was approximately 16ºC. The combination of a continuous low velocity flow of warm service water and the accumulation of silt provided conditions which permitted *Corbicula* growth. The heat exchanger was in standby condition for approximately 9 months during which time clams and silt accumulated to a depth of 7 to 10 cm. This fouling incident was discovered during a scheduled, visual inspection of the turbine-bearing lube oil heat exchanger. During this inspection the on-line turbine-bearing lube oil heat exchanger was found to be completely free of *Corbicula* and silt deposits. The high velocity flow through the on-line heat exchanger kept silt and young clams from settling there. Plant personnel speculated that the weekly chlorination (30 minutes at 1 ppm residual chlorine) was ineffective in controlling clams which entered in the larval stage because of the protective layer of silt.

CHLORINATION EFFECTIVENESS AND SYSTEM RELIABILITY

Chlorination effectiveness and the reliability of chlorination systems are important factors in controlling *Corbicula* larvae. Chlorination has been shown to be one of the most effective means of controlling *Corbicula* larvae (B.G. Isom, unpub. manuscript, TVA). However, if chlorination is not properly scheduled or if residual chlorine levels are not high enough to kill clam larvae, *Corbicula* may not be kept to a nuisance level. Also, mechanically unreliable chlorination systems can effectively halt all chlorination while the system is down for repair. During this downtime, *Corbicula* larvae can enter the service water system and settle in protected areas.

As mentioned previously, chlorination may be most effective when scheduled to coincide with clam spawning seasons (Goss and Cain, 1976) and flow testing or flushing. Continuous chlorination at 0.5 to 1.0 ppm total residual chlorine for one or two 3 week periods during the spawning season is required to control clam larvae (B.G. Isom, unpub. manuscript, TVA). *Corbicula* spawning periods are greatest in the spring and fall, although they are dictated somewhat by environmental conditions (primarily water temperature). Continuous chlorination, however, may be an unreasonable control method given the current EPA regulations on chlorine discharge from power plants (Mattice *et al.*, 1982). This conclusion assumes that the service water effluent is not dechlorinated before returning to the source waterbody.

The Tennessee Valley Authority (TVA) has implemented a program of continuous chlorination of essential service water systems which are in service during the clam spawning seasons. The TVA program calls for chlorinating the service water to a total residual chlorine level of 0.6 to 0.8 ppm. The program also requires the nonessential service water systems to be chlorinated to the same level for two 3 week periods corresponding to the beginning and end of the clam spawning season. During these periods a small continuous flow of chlorinated service water is established through all main fire system headers normally exposed to raw service water. This ensures that when chlorination has been completed, the fire protection system will remain in standby condition, filled with chlorinated service water. The TVA clam control program also includes straining all raw water through 0.8 mm mesh screens.

Correct measurement of free residual chlorine levels is also a factor which impacts the effectiveness of a chlorination system. As mentioned previously, silt and other suspended particles in service water have a chemical demand for chlorine. This factor makes free residual chlorine levels both time and space dependent. Free residual chlorine levels which are measured near the point of injection will be unrealistically high in comparison to levels measured at service water components farther down stream. For this reason free residual chlorine should be measured downstream from all components where chlorination is required.

Unreliable chlorination systems can also be a major factor in allowing larval *Corbicula* to become established in service water system piping. Although plant technical specifications may call for chlorination at specified times during plant operation, the chlorination system is not mechanically "required" for safe operation. Utility personnel indicate that often chlorination systems do not receive the same level of maintenance attention as do other systems more critical to plant operation. Thus, plants have remained in operation for several months with the chlorination system out of service. One severe fouling incident related to chlorination system reliability, although not involving *Corbicula*, occurred in a salt water cooled plant. Severe fouling of the residual heat removal (RHR) heat exchangers by oysters was directly attributed to the chlorination system being out of service for an extended period.

One utility noted a correlation between the amount of maintenance required by their diaphram type chlorination pumps and whether hypochlorite solution is injected upstream or downstream from the main service water pumps. They noted that chlorination systems which inject hypochlorite solution downstream from the service water pumps have a higher incidence of pump diaphram failure than similar pumps in systems where hypochlorite solution is injected directly into the service water intake structure. This difference has been attributed to the fact that injection downstream of the service water pumps requires pumping against a back pressure of approximately 345 kPa. This pressure, while not unusual for raw water systems, is high enough to shorten the operating life of these particular diaphram-type injection pumps.

COMPONENT SIZE

Corbicula fouling most often manifests itself in small diameter components in the service water and fire protection systems. One utility indicated that fouling from *Corbicula*, silt, and corrosion products is most prevalent in pipes of 100 mm and smaller diameter, with chronic fouling occurring in pipes 50 mm and smaller. An example is fouling of the 76 mm supply lines to their reactor building cooling units. This utility has replaced much of its small diameter carbon steel piping with stainless steel piping. They have also replaced service water system piping less than 25 mm in diameter with 25 mm stainless steel piping.

Several utilities have indicated that heat exchangers with tube diameters of 13 mm and less foul more readily than heat exchangers with larger diameter tubes. Pump motor room coolers have frequently fouled with buildups of silt, corrosion, and *Corbicula*. These coolers typically have supply piping less than 100-mm in diameter.

There is some question as to whether *Corbicula* actually settle and grow in these small diameter components or whether these are simply the locations where adult clams and relic shells accumulate after being carried into the system. One utility noted that fouling in heat exchangers consisted largely of relic shells and speculated that the clams had grown elsewhere in the system and after dying had been flushed into the heat exchangers. There is evidence that as the number of clams in low velocity areas increases, some of the clams are forced into high flow areas and are carried through the system until they lodge in constricted areas (J.S. Mattice, unpub. manuscript, EPRI). Areas where clams are typically found are on heat exchanger tube sheets and behind inlet valves to intermittent use systems in standby mode.

NUCLEAR SAFETY IMPLICATIONS OF *CORBICULA* FOULING

Corbicula fouling of the essential and nonessential service water systems both directly and indirectly affects the overall safe operation of nuclear power plants. Fouling of the essential service water system directly affects reactor safety because when essential cooling is interrupted during reactor shutdown, an alternate emergency cooling path must be established. Similarly, fouling of certain nonessential service water cooling loops may indirectly affect reactor safety by causing an unscheduled reactor shutdown and thus requiring cooling from safety related essential service water cooling loops.

An example of essential service water heat exchangers which have been fouled by *Corbicula* and which may directly impact reactor safety are the containment fan cooling units (Sometimes called containment cooling units or reactor building cooling units) which are common to PWR plants. The containment fan cooling units are designed to remove heat from the containment building during both normal and accident conditions. In Westinghouse PWRs there are a total of five units which operate in parallel (Masche, 1971). During normal operation a maximum of four units are required to remove the design heat load. Therefore, during normal operation one of two cooling units are in standby mode. Other PWR designs also have four to five units with one or two on standby during normal operation.

During normal operation, if containment cooling requirements are not met because of flow blockages, reactor power would have to be reduced to bring the containment temperature down. During accident conditions, severe fouling of the coolers would require that alternate containment cooling be established. Fouling of containment cooling units with *Corbicula* has, in fact, forced the shutdown of a nuclear plant while the coolers were cleaned and restored to their design capacity.

Turbine-bearing lube oil coolers are an example of nonessential service water heat exchangers that have fouled with *Corbicula*. As the name implies, turbine-bearing lube oil coolers provide cooling to the turbine-bearing lubricating oil. Turbine-bearing lube oil typically begins to lose its lubricating ability at temperatures above 150ºC. The temperature of the turbine-bearing lube oil is therefore monitored and if flow blockage of both the online and backup lube oil coolers causes it to exceed the allowable temperature (somewhat below the 150ºC maximum), a turbine trip would be initiated. If the cause of the turbine trip was not readily apparent or if it were not possible to clean these heat exchangers while the reactor was on line, a reactor shutdown would follow.

Upon initiation of shutdown, initial reactor cooling in a PWR is achieved by dissipating heat through the steam generators and discharging steam to the condensers by means of the turbine steam bypass system. The residual heat removal system (RHR) begins removing heat from the reactor when the reactor water temperature and pressure have dropped to approximately 177°C and 2.75 MPa, respectively. The RHR heat exchangers are cooled by the component cooling loop which is in turn cooled by the component cooling water heat exchangers. The component cooling water heat exchangers are cooled by service water and are part of the essential service water system. Therefore, although the turbine-bearing lube oil coolers are not safety related, their fouling could cause a reactor shutdown which relies on safety related service water systems for cooling.

ENGINEERING RECOMMENDATIONS TO MINIMIZE *CORBICULA* FOULING

Many actions can be taken to reduce *Corbicula* fouling to a nuisance level. Some methods such as low-level, continuous chlorination during *Corbicula* spawning seasons could be used to control establishment of clam larvae in the plant. Continuous chlorination, however, may not be possible given the current EPA regulations on chlorine discharge from power plants (Mattice *et al.*, 1982). Adult *Corbicula* are best controlled by physically removing them from the intake structure and internal surfaces of the service water system.

Conditions that promote *Corbicula* settlement and growth are costly and should be avoided. Fouling can be monitored and controlled in several ways. Systems in standby condition during plant operation should be chlorinated during flow tests, and visual inspections of the system internals should be performed during outages. Areas such as intake structures, heat exchanger waterboxes and other low-velocity flow areas should be visually inspected during outages for accumulations of *Corbicula*. Also, many heat exchangers in nuclear service water systems have no individual flow metering devices. Installation of such devices would provide early detection of fouling problems during operation without visual off-line inspections.

During extended outages, service water cooling loops that are not required for removing residual heat from the reactor or other essential cooling could be dewatered. Buildup of silt and corrosion products in the service water and fire protection system should be minimized. Leaky valves or those that do not operate correctly should be repaired to avoid low-velocity flow conditions. The installation of fine mesh strainers, either at the service water pump discharge or at the inlets to heat exchangers, can greatly reduce the occurrence of flow blockages due to *Corbicula* fouling. Finally, the chlorination system should be maintained with the same level of care as the essential service water system, because effective chlorination indirectly affects the safety related cooling functions of the essential service water system.

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Utilities and nuclear plants that provided information are not identified unless requested by the utility. This is to honor the request of many utilities that they remain anonymous.

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CORBICULA CONTROL AT THE POTOMAC RIVER STEAM ELECTRIC STATION ALEXANDRIA, VIRGINIA

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ABSTRACT

The successful colonization of the freshwater tidal Potomac River by the Asiatic clam has resulted in severe macrofouling problems at the Potomac Electric Power Company's (PEPCO) Alexandria, Virginia Station. Planktonic veligers and small clams entered the plant through the traveling screens, settled, and attached in slow velocity areas. Fouling problems occurred when clams died and their shells clogged condenser tubes.

Studies were conducted to ascertain seasonal growth rates of *Corbicula* in relation to station fouling and to monitor the effects of thermal effluent on *Corbicula* populations. Growth rates, as determined by increases in shell height, were inversely related to size. Mean cumulative increases in shell height were 9.8 and 7.9 mm for size class III and IV clams, respectively. *Corbicula* growth rates were not significantly different among control and thermally-influenced stations. Based upon traveling screen mesh size of 10 mm, clams ≤ 10 mm could enter the plant and grow, within 1 season, to a size where they could clog condenser tubes. However, on the basis of plant operational data and in-plant sampling, it was concluded that biennial physical removal was a successful control method.

Corbicula sp., the Asian clam has increased rapidly in ecological and economic significance since its first sighting in the United States in 1938 (Burch, 1944 as cited in Mattice, 1983). Since its introduction, the range of the Asiatic clam has expanded to include most of the freshwater drainage basins in the United States (Mattice and Dye, 1976). Its high fecundity, incubatory egg, and planktonic veliger's ability to infest raw water supplies has resulted in considerable biofouling problems for the power industry (Sinclair and Isom, 1963; McMahon, 1977).

The United States Geological Survey first found *Corbicula* concentrations in the tidal freshwater portions of the Potomac River in 1977 (Dressler and Cory, 1980). Within two years, clams were found fouling intake and condenser areas of the Potomac Electric Power Company's Potomac River Steam Electric Station (SES) in Alexandria, Virginia. Planktonic veligers and small clams (≤10 mm) apparently entered the plant through the traveling screens, settled, and attached in slow velocity areas behind the traveling screens. Fouling problems occurred when the clams died and their shells wedged within condenser tubes. Losses at the Potomac River SES due to *Corbicula* fouling were divided into three areas: (1) the efficiency loss due to higher condenser backpressures; (2) the megawatt losses due to inability to achieve a full load; and (3) the outage losses associated with cleaning the condensers. Physical removal of clams during scheduled overhauls was implemented to control *Corbicula* fouling.

The Potomac River SES was inspected several times during 1979 for *Corbicula* infestations. Clams were found in the intake area behind the traveling screens, at the base of the circulating water pumps, and lodged in tube openings in the condenser waterboxes. Size distribution analyses of the clams showed most were smaller in diameter than the condenser tube openings. The Raw Service Water lines were inspected in 1981 and no *Corbicula* were found.

Studies were conducted by PEPCO's Water and Land Use Department during 1980 and 1981 to provide supporting data for *Corbicula* control methodology. The objectives of these studies were: (1) to ascertain the seasonal growth rate of *Corbicula* in relation to the potential for power plant fouling; and (2) to monitor the effects of the thermal effluent on *Corbicula* populations in the vicinity of the Potomac River SES.

METHODS AND MATERIALS

The Potomac River SES, located in Alexandria, Virginia, has five coal-fired steam turbine generators with a net capacity of 508 Megawatts. Water is withdrawn from the

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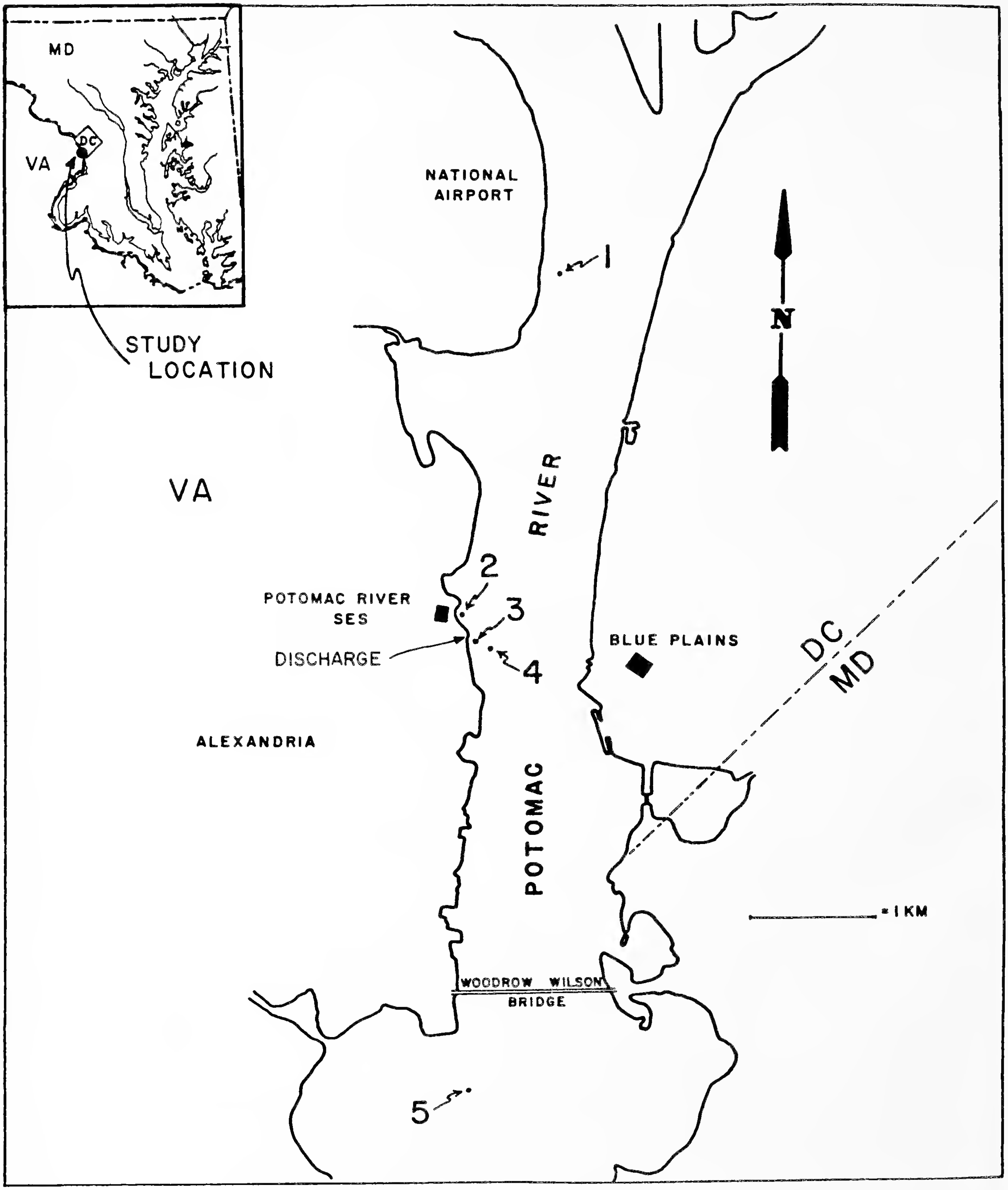

Fig. 1. Location of Potomac River SES in Alexandria, Virginia, and 1981 *Corbicula* study locations.

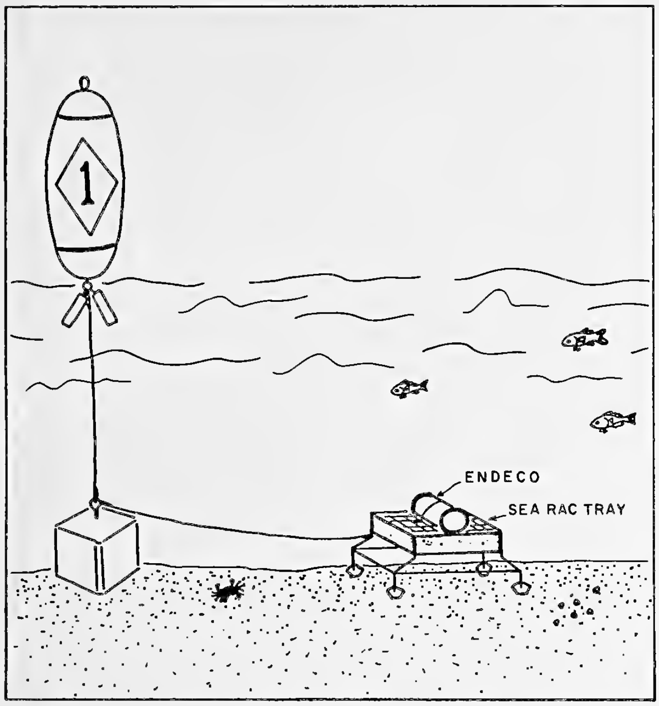

Fig. 2. Underwater platforms used to hold *Corbicula* for growth studies in the Potomac River, May through October, 1981.

Potomac River for once-through condenser cooling. Maximum plant cooling water flow is 19.8 m³/sec. The cooling water is intermittently chlorinated 3 times daily maintaining in-plant total residual chlorine concentration of 0.20 mg/*l* for 15 min. The heated effluent is discharged approximately 300 m downstream of the intake. Partial recirculation of discharge water occurs as a result of tidal action.

The Potomac River at Alexandria is relatively shallow (0-4 m deep). Net freshwater flow averages 1,980 m³/sec and ranges from 19.8 m³/sec to 2,547 m³/sec.

Growth and survival of tray-held *Corbicula* were monitored monthly at 5 stations in the vicinity of the Potomac River SES, May through October 1981 (Fig. 1). Station 1 was located 3 km upstream of the thermal discharge; Stations 3 and 4 were directly in the thermal discharge; Station 5 was 4 km downstream of the thermal discharge. Station 2 was located in the intake area and was subject to thermal recirculation.

Corbicula were placed in oyster trays secured to underwater platforms (Fig. 2). The underwater platforms were constructed of polyurethane-coated steel angle and rod stock and measured 46 x 46 x 36 cm. The platforms were connected with stainless steel cable to a 30 x 30 x 30 cm concrete block which was, in turn, attached to an identifying buoy. The trays were constructed of vinyl-coated stainless steel wire with hinged tops and measured 45 x 41 x 13 cm. Each tray was divided into two compartments and lined with expanded polyethylene mesh for separation of *Corbicula* size classes.

Corbicula were dredged from the Potomac River below the confluence of the Potomac and Monacacy Rivers, near Dickerson, Maryland. Clams were randomly selected, measured, and sorted into size classes. Size class determinations were based on shell length (after Sickel, 1973, as cited in Gardner et al., 1976; see Table 1, Gardner e*t al.*, 1976). Only size class III (13.5-18.5 mm) and IV (≥ 18.5 mm) clams were used because of insufficient numbers of smaller *Corbicula*.

Twenty-five class III and one-hundred size class IV *Corbicula* were placed in each compartment. *Corbicula* shell height and length were measured monthly to determine growth. Shell dimensions were determined according to McMahon (1977). Shell height to length ratios averaged 0.97 ± 0.05 (n = 500); therefore only height was presented.

Percent mortality was calculated by dividing the number of dead clams by the total number of dead and live clams.

Temperature was recorded continuously at each station using Endeco Type 109 Recording Thermographs. Surface and bottom dissolved oxygen concentrations were determined monthly using the azide modification of the Winkler titration (APHA, 1980). Conductivity (Beckman RS-5 meter) and turbidity (H. F. Instruments, model PRT-15) also were measured monthly at each station.

Means and standard deviations were calculated using the small sample size approximation in Sokal and Rohlf (1969). Analysis of variance (ANOVA) was used to test for station or time effects on shell height for size classes III and IV.

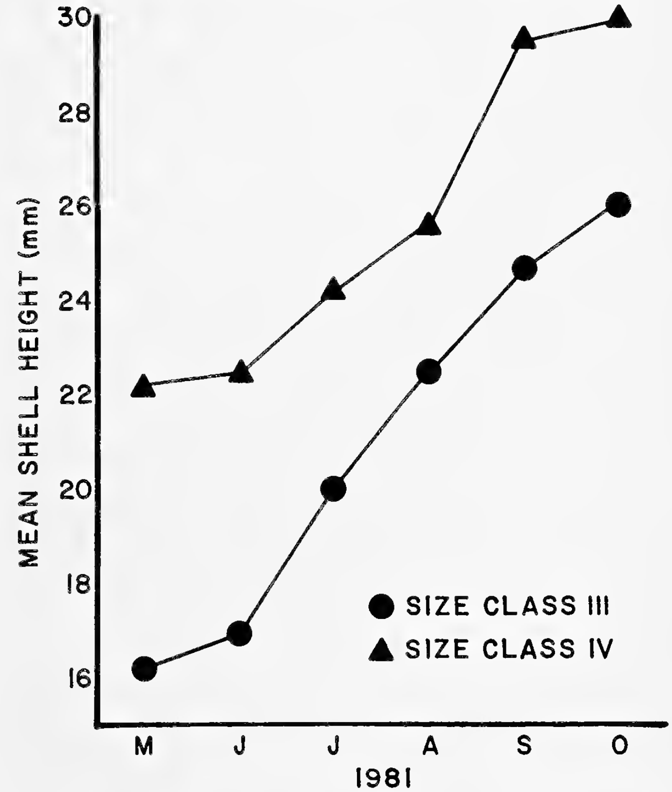

Fig. 3. Changes in mean shell heights of tray clams in the vicinity of the Potomac River SES, May through October, 1981. Clam height data from all stations are combined.

RESULTS AND DISCUSSION

Corbicula growth, as determined by increases in shell height, generally was continuous throughout the study for size class III and IV clams (Fig. 3). Cumulative increases in shell height among size class III *Corbicula* ranged from 39% at Station 5 and 74% at Station 3 with an overall mean increase of 61% (Table 1). Shell height for size class III clams increased an average of 9.8 mm from May through October, 1981 (Table 2). Mean monthly increase was 2.0 mm. Minimum and maximum increases in shell height for size class III *Corbicula* occurred in June and July, respectively. Decreases in mean shell height were noted in June at Station 1 and September at Station 5. The June decrease at Station 1, in addition to smaller increases in shell height at other stations, probably resulted from field measurement errors, since little clam mortality occurred. However, September decreases at Station 5 were attributed to reduced sample size resulting from cumulative mortality.

Cumulative increases in shell height among size class IV *Corbicula* ranged from 31% at Station 4 to 41% at Station 5, with a mean increase of 35% (Table 1). Shell height increased an average of 7.9 mm among size class IV clams at all stations throughout the study (Table 2). Mean monthly increase was 1.6 mm. Smallest and largest increases in shell height occurred in June and September, respectively. Decreases in shell height were observed in June at Station 3, August at Station 5, and in October at Station 4. The June decrease in shell height, in addition to the low rate of growth at other stations during this month, probably resulted from field measurement errors, since little mortality occurred. However, decreases during August and October were attributed to reduced sample size resulting from cumulative mortality.

Growth studies conducted at the Potomac River SES from June through October, 1980 yielded results similar to those obtained in this study (PEPCO, 1981). Mean cumulative shell height increases for size class III *Corbicula* were 7.6 mm for 4 months in 1980 and 9.8 mm for 5 months in 1981. Mean monthly increases in shell height were 1.9 and 2.0 mm during 1980 and 1981, respectively. No data were obtained for size class IV *Corbicula* in 1980. Other researchers also have reported similar growth rates. Auerbach *et al.* (1978) monitored *Corbicula* growth at the Kingston Steam Electric Plant, Tennessee from May through October, 1976. Cumulative growth of cage-confined clams was 6.5 mm and 7.5 mm at the station intake and discharge, respectively. Britton et *al.* (1979) reported *Corbicula* growth rates of 0.67, 0.58, and 0.47 mm per month for 3 clam groups ranging from 14-21 mm, 21-24 mm, and 24-32 mm, respectively.

Analyses of Variance were performed to determine the effects of location and time on *Corbicula* shell height for both size classes (Table 3). Monthly changes in mean shell height were significantly different (p = 0.05) for size classes III and IV clams. However, station effects were not significantly different (p = 0.05) for either size class. Station-related thermal effects were not a source of variance. Temperatures between stations varied less than 2°C throughout the study.

Table 1. Cumulative percent change in mean *Corbicula* shell height in the vicinity of the Potomac River SES, May through October, 1981.

Size Class	Measurement Date (Month)	Station					Average
		1	2	3	4	5	
III	Jun	−2.1	6.3	2.8	9.4	4.8	4.2
	Jul	20.5	24.4	26.7	32.7	16.1	24.1
	Aug	37.1	45.3	43.3	46.3	23.2	39.0
	Sep	60.4	58.9	64.8	56.8	18.2	51.8
	Oct	67.6	62.0	74.4	64.2	39.4	61.5
IV	Jun	3.1	1.3	−6.0	1.6	4.6	0.9
	Jul	9.7	4.2	−0.7	17.7	14.2	9.0
	Aug	14.2	16.1	11.2	24.3	11.7	15.5
	Sep	34.0	30.0	25.9	34.8	40.8	33.1
	Oct	34.5	33.9	33.9	30.5	40.8	34.7

Table 2. Monthly changes in mean shell height (mm) of *Corbicula* in the vicinity of the Potomac River SES, May through October, 1981.

Size Class	Measurement Date (Month)	Station					Average
		1	2	3	4	5	
III	Jun	−0.38	1.00	0.44	1.54	0.8	
	Jul	3.68	2.90	3.83	3.82	1.85	
	Aug	2.68	3.34	2.65	2.24	1.18	
	Sep	3.74	2.19	3.44	1.71	−0.83	
	Oct	0.36	0.49	1.55	1.22	3.50	
	TOTAL	10.08	9.92	11.91	10.53	6.50	9.79
	MEAN	2.02	2.08	2.38	2.01	1.30	1.96
IV	Jun	0.70	0.29	−1.37	0.35	0.97	
	Jul	1.50	0.65	1.21	3.51	2.06	
	Aug	1.01	2.64	2.73	1.44	−0.53	
	Sep	4.47	4.12	3.36	2.28	6.20	
	Oct	0.11	0.86	1.84	−0.94	0.00	
	TOTAL	7.79	8.56	7.77	6.64	8.70	7.88
	MEAN	1.56	1.71	1.55	1.33	1.74	1.58

Table 3. Analysis of variance for mean monthly changes in *Corbicula* shell height in the vicinity of the Potomac River SES, May through October, 1981.

		SIZE III HEIGHT			
Source	SS	df	MS	F	P>F
Date	18.60534	4	4.65133	3.11	0.044 *
Station	3.19342	4	0.79835	0.53	0.7123 NS
Error	23.89350	16	1.49334		
		SIZE IV HEIGHT			
Source	SS	df	MS	F	P>F
Date	48.64721	4	12.16180	7.09	0.0018 *
Station	0.53838	4	0.13459	0.08	0.9878 NS
Error	27.44674	16	1.71542		

* Significant at P=0.05.

Table 4. *Corbicula* survival in the vicinity of the Potomac River SES, May through October, 1981.

Size Class	Month	Station									
		1		2		3		4		5	
		Live	Dead	Live	Dead	Live	Dead	Live	Dead	Live	Dead
III											
	May	25		25		25		25		25	
	Jun	25	0	26	0	25	0	24	1	23	2
	Jul	25	0	20	6	22	3	21	3	13	11
	Aug	13	11	17	3	13	9	16	5	3	10
	Sep	11	2	14	3	11	2	14	2	2	0
	Oct	11	0	12	1	11	0	14	0	2	0
IV											
	May	100		100		100		100		103	
	Jun	96	4	88	11	89	11	93	5	103	0
	Jul	80	5	68	10	66	15	64	21	63	28
	Aug	27	43	48	10	32	33	31	21	5	49
	Sep	18	7	43	2	23	7	26	4	1	3
	Oct	18	0	36	0	18	0	18	3	1	0

Corbicula survival was similar for size classes III and IV until August (Table 4). Large mortalities were observed among both size classes in August; moreover, those for size class IV were substantially greater. The large number of *Corbicula* mortalities paralleled observations of Water and Land Use personnel conducting ichthyoplankton sampling within the study area. Numerous *Corbicula* viscera were observed in the water column during July and August. These occurrences of mortality coincided with maximum ambient water temperatures (30°C) in the Potomac River, as indicated by Endeco temperature data. However, this temperature-mortality relationship was not supported by reported upper thermal tolerance limits of 34°C for *Corbicula* (Mattice and Dye, 1976).

Cumulative survival for size class III and IV clams averaged 38% and 18%, respectively, at all stations (Table 5). Survival at Stations 1, 2, 3, and 4 was not substantially different among size classes. However, cumulative survival at Station 5 was only 8% (Table 5).

CONCLUSIONS AND SUMMARY

Corbicula growth, determined by increases in shell height, generally was continuous throughout the 6 month study. Increases in clam shell height were inversely related to size; smaller clams grew faster. Mean cumulative increases in shell height for size classes III and IV were 9.8 and 7.9 mm, respectively. *Corbicula* growth was not influenced by station location. Growth at control and thermally influenced stations was not significantly different ($p = 0.05$).

Survival of experimental, as well as natural, *Corbicula* populations in the Potomac River was poor during the 1981 study.The period of greatest clam mortality coincided with the period of maximum river temperature. However, this temperature-mortality relationship was not supported by reported thermal tolerance data for *Corbicula*.

Table 5. Cumulative survival of *Corbicula* in the vicinity of the Potomac River SES, May through October, 1981.

Size Class	Measurement Date (Month)	Station					Average
		1	2	3	4	5	
III	May	100	100	100	100	100	
	Jun	100	104	100	96	92	
	Jul	100	90	88	80	52	
	Aug	52	59	52	64	12	
	Sep	44	55	44	44	8	
	Oct	44	49	44	44	8	
							37.8
IV	May	100	100	100	100	100	
	Jun	96	88	89	93	100	
	Jul	80	68	66	64	51	
	Aug	27	48	32	31	5	
	Sep	18	43	23	26	1	
	Oct	18	36	18	18	1	
							18.2

Similar trends for growth and survival were found for 1980 and 1981. Mean monthly growth rates were 1.9 mm and 2.0 mm for size class III *Corbicula* during 1980 and 1981, respectively. Large clam mortalities were observed in August during both years in test populations.

Although *Corbicula* spp. has successfully inhabited the Potomac River in the vicinity of the PEPCO Potomac River SES since 1977, the results of this study indicated that the plant's thermal effluent has not influenced clam growth and survival during the spring, summer, or fall. In addition, it appeared unlikely, on the basis of the small Delta T discharged by the plant (1-2°C), that clam populations in the vicinity have been enriched and maintained by increasing temperatures to within the clam's lower thermal tolerance range during the winter.

Clams ≤ 10 mm potentially could enter the plant through the traveling screens (mesh size of 10 mm) and grow 8-10 mm, within 1 season, to a size at which they could clog condenser tubes (17-19 mm). However, on the basis of plant operating data and in-plant sampling, it was concluded that biennial physical removal (every 18 mos) was a successful control method. Size frequency distributions of *Corbicula* in the plant indicated that the clams do not grow to a sufficient size to cause fouling problems. Plant operating data also shows that condenser efficiency has not been affected by *Corbicula* fouling.

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A MECHANICAL STRAINER DESIGN FOR *CORBICULA* FOULING PREVENTION IN THE SERVICE WATER SYSTEM AT ARKANSAS NUCLEAR ONE, UNIT 2

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ABSTRACT

Reduced flow in small safety grade lube oil coolers was found to be caused by accumulations of the Asian clam *Corbicula* sp. in the service water supply lines. Installation of conventional, nuclear-grade strainers was the preferred solution, but the twelve month delivery schedule on vendor designed nuclear components forced consideration of other means of obtaining strainers.

In response, Arkansas Power and Light Company contracted qualified consultants and welders to design and fabricate "clam traps" from standard piping components. Strainers were completed within nine months and installed during the next refueling outage. These strainers were designed with provisions for periodic flushing and cleaning as well as passive removal of clams and debris. This design with plant specific modifications may be applied to other utilities with similar problems.

Arkansas Power & Light Company (AP&L) operates a two unit nuclear power plant, Arkansas Nuclear One (ANO), on Dardanelle Reservoir near Russellville, Arkansas. Reservoir water is the primary cooling source for ANO's service water system. This system is designed to stringent nuclear standards to assure safe plant operation in the event of postulated design accidents such as a loss of reactor coolant, earthquake, floods, etc.

Water is withdrawn from the reservoir for once through cooling during normal plant operation. Traveling screens (9.5 mm mesh) and basket strainers (4.7 mm mesh) are provided in the intake structure to remove large debris. Historically, shock chlorination was used to control biological fouling. However, because of chlorination equipment reliability problems and the method used, control of organisms and biologicaly induced corrosion was not totally effective.

Many heat exchangers in a nuclear power plant are used only during emergencies or to allow safe plant shutdown. Except during monthly surveillance flow tests, supply piping to these exchangers had low flows of fresh water due to leaking isolation valves, and thus provided an ideal environment for growth of *Corbicula* and deposition of river silt (Neitzel *et al.*, 1984) In the past *Corbicula* passed through the intake screens in the larval stage and burrowed into silt deposits. Buried in these deposits, the clams were largely immune to intermittent chlorination, and were free to grow and multiply. Adult clams and clam debris subsequently broke loose and clogged various coolers and inlet headers, which required plant shutdown to remove the debris.

Seven small pump oil coolers were found to be most susceptible to plugging by clams, silt and other debris. Being at the lowest elevation of the service water system and in a low flow area, a large amount of debris accumulated in the water supply piping. In January, 1982, the "B" Low Pressure Safety Injection (LPSI) pump oil cooler was found clogged with clams and debris. It was determined that susceptibility to clam plugging was greatest in the small diameter 0.5-0.75 inch (12.7-19.0 mm) supply tubing on the cooler. As part of an overall upgrade program which included piping replacement, chemical cleaning, and additional chlorination, AP&L decided to install straining devices in the supply lines to "B" LPSI cooler and six other similar coolers as soon as possible. The target date for installation was September 1982, the next refueling outage.

DESIGN APPROACH

Initially, efforts were made to buy nuclear grade simplex or duplex type strainers. However, procurement of vendor-design nuclear grade strainers was estimated to require a minimum of twelve months. Since strainers were needed within six months for installation during the next refueling outage, AP&L was forced to consider other means of obtaining them.

The next option considered was purchasing strainers fabricated for another utility with a cancelled nuclear plant. However, due to site specific requirements of nuclear plants and type of strainers available, this option was not feasible.

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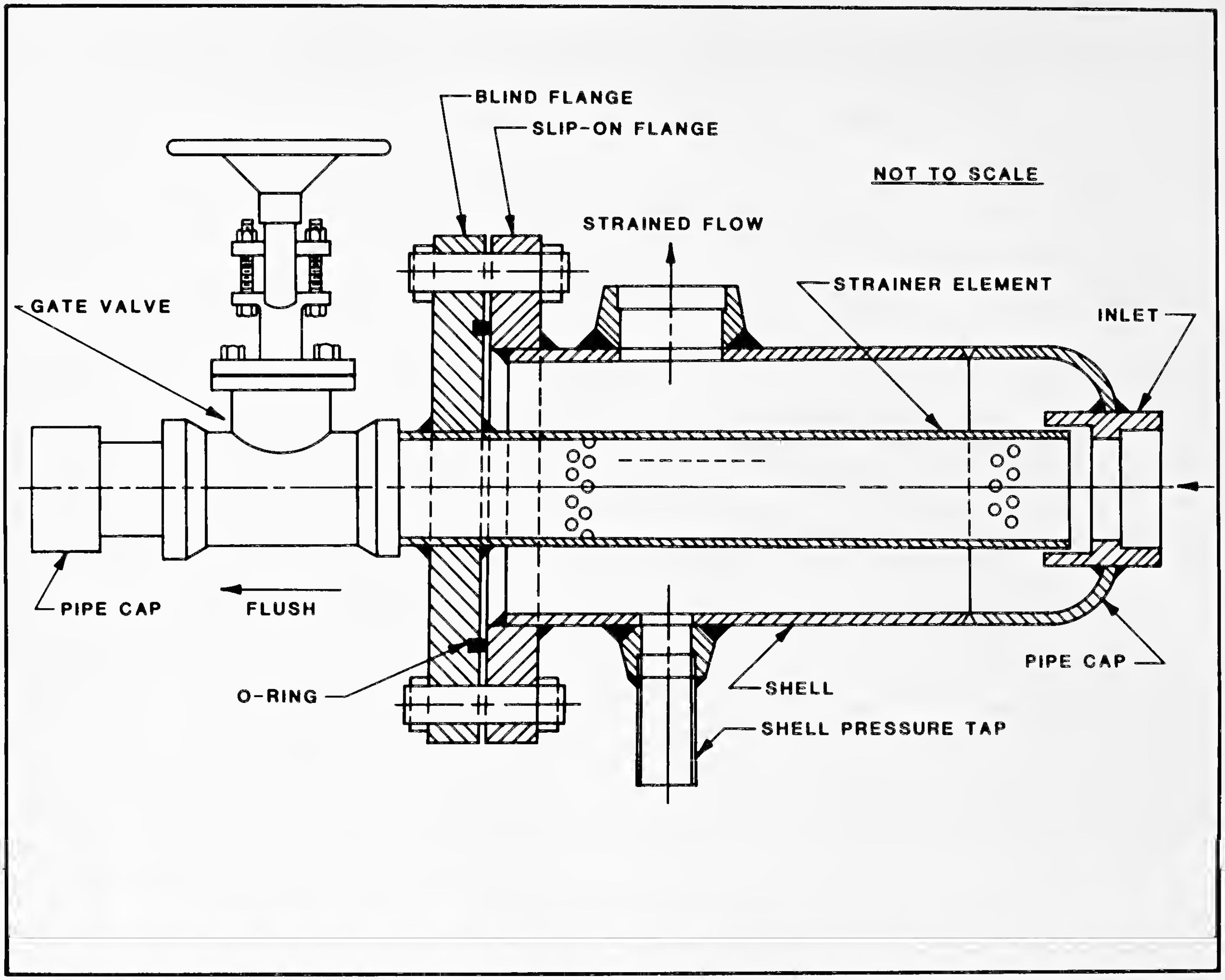

Fig. 1. Nuclear service strainer assembly (section).

It was determined that nuclear grade strainers similar to "clam traps" used by the Tennessee Valley Authority in fossil fueled power plants (Goss and Cain, 1975) could be fabricated using standard nuclear grade piping, valves, and fittings. A conceptual design prepared by AP&L was qualified to meet nuclear requirements by a consultant. Nuclear qualified welders available in-house fabricated the strainers. This option proved to be cost-effective, feasible and achievable within the time limitations.

STRAINER DESIGN REQUIREMENTS

Strainers were designed to remove debris larger than 0.25 inch (6.4 mm) diameter which could clog cooler inlet piping. The strainer open area was five times the inlet area to prevent excessive pressure drop. Design temperature and pressure were 130°F (55°C) and 150 PSIG (1034 KPa), respectively. Stresses due to internal pressure, thermal expansion, deadweight, and seismic forces were considered. Provisions for on-line flushing of the strainer element, and off-line cleaning were provided. The design also included provisions for differential pressure measurement across the strainer.

STRAINER DESIGN AND OPERATION

The strainer (Fig. 1) is basically an arrangement of standard piping components positioned to form an inner pipe and an outer pipe aligned along their centerlines (Paulsen, *et al.*, 1982).

The inner pipe is drilled with a staggered arrangement of 0.25 inch (6.4 mm) holes to serve as the strainer element. The outer pipe serves as the shell and pressure boundary. The inlet end of the shell is sealed with an assembly of a standard butt-weld pipe cap and an integrally welded socket weld coupling. The opposite end is a bolted flange connection with slip-on and blind flanges. The strainer element penetrates the blind flange, is welded on both sides, and connects on the outside to a flush valve. A "sockolet" is welded to the side to provide the outlet connection. An additional sockolet connection is provided on the shell to allow for pressure drop measurements.

In operation, water laden with clam shells and other debris flows through the inlet into the inner strainer tube assembly. Water flows circumferentially into the outer plenum while the debris is retained by the strainer element. The strained water then exits through the outlet nozzle in the shell. Periodically, based on pressure drop through the component, the flush valve is opened and system pressure forces the accumulated debris to drain through the valve. For cleaning and maintenance, the flush end assembly including the blind flange, flush valve, and strainer element is removable in one piece. Blind flanges are maintained as spare parts for use if work on the strainer element is required.

ASME BOILER AND PRESSURE VESSEL CODE REQUIREMENTS

Certain sections of the ASME Boiler and Pressure Vessel Code were used for design of the strainers (ASME, 1980). Strainers were designed in accordance with Section III, Nuclear Components. Materials for the strainers were in accordance with Section II. Welding requirements were in accordance with Section IX. Fabrication and installation of the strainers were in accordance with Section XI.

Code symbol stamping is normally required for vendor supplied equipment (i.e. "N", "NPT"). However, since components were fabricated by AP&L per Section XI requirements, the code symbol ("NA") was not required to be stamped on the strainers.

To avoid classification as a pressure vessel under the ASME Code, Section VIII, 5 inch (13 cm) schedule 40 pipe was used for the strainer shell. Under the ASME Code, the strainers are considered to be piping components. In this fashion, the design of the strainers did not have to meet Section VIII rules and requirements, and thus did not require the "U" code symbol stamp.

INSTALLATION

Strainers were installed in the September 1982 refueling outage, some nine months after project inception . Due to extensive system measurements and checking for fit, installation of strainers was accomplished with only minor clearance problems.

RESULTS

To date (August 1985), installed strainers have served their intended purpose. As well as preventing clam fouling of associated coolers, the effectiveness of other control measures (piping replacement, chemical cleaning, continuous chlorination) may be determined from the frequency, type, and amount of biological material collected. In addition, several leaking isolation valves have been or will be replaced in the service water system, removing the low water flows necessary for clam survival in normally stagnant water lines.

The total cost for the study, design, fabrication and installation of seven strainers and associated instrumentation was $254,000 for a total installed cost of $36,300 per strainer in 1983 dollars. The total includes a material cost of $25,400. Comparable strainers purchased from a vendor would be in the range of $20,000 to $25,000, each.

CONCLUSION

A mechanical clam fouling prevention system has been designed, fabricated and installed to protect small safety grade lube oil coolers at ANO-2. The strainer is readily adaptable to any nuclear utility, and can be much cheaper and obtained faster than strainers purchased from vendors. The design approach may be used for other nuclear - grade components as well.

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DEVELOPMENT OF A *CORBICULA* CONTROL TREATMENT AT THE BALDWIN POWER STATION

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ABSTRACT

A successful treatment was developed to prevent condenser fouling by *Corbicula* at the Baldwin Power Station. Initially, sodium-meta-bisulfite ($Na_2S_2O_5$) was utilized to create anoxic conditions in the intake basins during scheduled outages. Results were favorable, however, $Na_2S_2O_5$ may not have been solely responsible for *Corbicula* mortalities since mortality rates could not be replicated in controlled laboratory experiments. It was hypothesized that hydrogen sulfide formed during anoxic conditions in the intake basin may have contributed to *Corbicula* mortalities. Treatments which utilized $Na_2S_2O_5$ and H_2S gas proved to be a successful means of *Corbicula* control. Aeration of the intake basin effectively neutralized the treatment chemicals prior to discharge. A permanent chemical distribution system was installed in the intake basins and annual treatment costs were less than $1,000 per unit. Condenser fouling was eliminated since the annual treatments prevented clams from growing larger than the inside diameter of the condenser tubes. Growth and settling rates, and shell length frequencies of *Corbicula* were examined during the development and evaluations of the treatments. Observations on the distribution of *Corbicula* in the intake basins have some implications on future designs and operations of intake structure which may reduce *Corbicula* accumulations.

Asiatic clams [*Corbicula fluminea* (Müller)] began causing problems for electric utilities in the 1950's (Goss *et al.*, 1979). In the next two decades the number of power plants plagued by *Corbicula* increased as *Corbicula* became more widely distributed. The small size (200 μm) and abundance of the larvae make it difficult to screen *Corbicula* from the intakes of power plants or other large water users. Larvae are capable of growing to 25 mm shell size within a year (Dreier and Tranquilli, 1981), and clams of this size can cause blockages in heat exchangers and small pipes. Controls are further complicated by the clam's resistance to biocides which control other fouling organisms.

Corbicula control programs may differ depending upon the type water system affected and which life stage of *Corbicula* causes problems. Treatments of affected water systems will vary depending upon the volume and velocity of water, pipe size, and possible regulations upon the final discharge of treated water. The differences in physical size and chemical tolerances of various life stages of *Corbicula* must also be considered in developing control programs. It is unlikely that a single control program would be effective for all water systems and all life stages of *Corbicula*.

A treatment to control condenser fouling problems resulting from an accumulation of *Corbicula* within the intake basin was developed by Illinois Power Company at the Baldwin Power Station. This treatment may be effective in other power plants with similar condenser cooling systems and problems. The treatment methodology was developed through a series of experiments conducted in the intake basin. This paper describes the stages in development of the treatment and observations on distribution, growth, and settling rates of *Corbicula*.

DESCRIPTION OF *CORBICULA* PROBLEM

The Baldwin Power Station is located in southwestern Illinois and is owned by Illinois Power Company. The station consists of three 600 MW coal-fired generating units. Cooling water is provided by a 810 hectare perched pond which receives make-up water from the Kaskaskia River. Each generating unit has a separate intake basin with 9.5 mm mesh traveling screens. Pumps for the condenser cooling water, service water and fire protection systems are located in the intake basin. In 1975 the severity of condenser fouling by *Corbicula* increased in all three units. The condenser problems resulted from chronic levels of tube fouling as well as short episodes of severe fouling (Smithson, 1981). The source of *Corbicula* was identified as the intake basin where shells had accumulated to a depth of one meter.

STRATEGY FOR CONTROL TREATMENTS

The 9.5 mm mesh traveling screens should have

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prevented larger clams from entering the itake basin, so the accumulation was assumed to have resulted from larvae or juveniles settling and growing in the intake basin. The large volume of water entering the intake basin and the small size of the larvae precluded continual chemical treatment or screening. Since entry of larvae could not be prevented, emphasis was directed toward preventing them from growing large enough to plug the 7/8'' condenser tubes.

Each generating unit and corresponding intake basin were taken out of service at least once each year for scheduled maintenance. This period offered an opportunity to treat the intake basin under static water conditions since no pumps were in operation. A treatment applied during the scheduled outages would be effective if it killed recently recruited clams before shells reached a size capable of fouling condenser tubes. The treatment had to be capable of being neutralized prior to being discharged to the reservoir.

Fast (1971) reported that *Corbicula* were restricted to shallow depths in a California reservoir by hypolimnetic stagnation. Laboratory experiments by Paparo (1976, personal communication to W. S. Brenneman, Illinois Power Company) also suggested *Corbicula* was susceptible to oxygen depletion. Thus, creation of anoxic conditions in the intake basin during scheduled outages appeared to offer an effective treatment. Sodium-meta-bisulfite ($Na_2S_2O_5$) was the oxygen scavenger selected to create anoxic conditions. This chemical is non-toxic and used in preservation of human food. The anoxic effects are neutralized by aeration.

DEVELOPMENT OF THE TREATMENT

The recommended treatment evolved from a series of treatments which extended over four years. This section discusses some of the events and observations which lead to the recommended treatment.

Six months prior to the first treatment divers removed most of the *Corbicula* from the intake basins with a large submersible trash pump. The first experiment with the $Na_2S_2O_5$ treatment was made during a scheduled outage in October 1976. SCUBA was used to inspect the intake basin for the distribution and abundance of *Corbicula* prior to this and all following treatments. The pretreatment inspection revealed densities up to 1600/m^2 in low velocity areas. A saturated solution of water and sodium-meta-bisulfite ($Na_2S_2O_5$) was siphoned to the bottom of the intake basin and distributed by a diver. A cage containing 200 adult *Corbicula* was used to assess the treatment effectiveness. Dissolved oxygen (DO) was depleted from the bottom one meter of the intake basin within minutes of the treatment. Twenty-four hours later the DO was still depleted and a post-treatment inspection was made. Most of the clams were alive but several appeared stressed and had tightly closed their shells on their foot. A similar response was observed by Anderson et al. (1976) when *Corbicula* was exposed to potassium at concentrations greater than 120 mg/l. At the end of the week all the caged *Corbicula* were dead.

Based upon the success of the first treatment, another unit was treated during an outage in December 1976. The treatment was identical to the first, but the $Na_2S_2O_5$ did not deplete the DO. Additional $Na_2S_2O_5$ was added, but DO was still in excess of 4 mg/l. This treatment was probably unsuccessful because the colder water contained higher levels of DO and lowered the metabolic rates of *Corbicula*.

Variable effectiveness in the next of treatments prompted laboratory duplication of the treatments. In the first intake basin treatment, enough $Na_2S_2O_5$ (87 mg/l) had been added to theoretically deplete oxygen from the entire water volume. This treatment was successful but similar concentrations of $Na_2S_2O_5$ in one liter beakers did not cause any mortalities. However, there was a major difference in the actual concentration *Corbicula* were exposed to in the intake basin as compared to the well-mixed laboratory beaker. In the intake basin the $Na_2S_2O_5$ mixture was siphoned to the bottom and its greater density kept it near the bottom. Dissolved oxygen profiles indicated the effects were limited to the bottom one meter. If all the $Na_2S_2O_5$ remained in the bottom one meter, the concentration would have been approximately 900 mg/l, rather than 87 mg/l which would have resulted from complete mixing.

Concentrations of $Na_2S_2O_5$ from 1,650 to 3,330 mg/l produced high mortalities of *Corbicula* in laboratory treatments. This suggested that the toxic effect of high concentrations of $Na_2S_2O_5$, or the various oxides of sulfur formed from it, may have contributed to mortalities as much as oxygen depletion alone. This was supported by another laboratory treatment in which *Corbicula* survived DO levels of 0.4 mg/l or less for five days. The intake basins were treated with 180 to 400 kg of $Na_2S_2O_5$ which would have resulted in a concentration of 900 to 2000 mg/l if all the $Na_2S_2O_5$ remained in the bottom one meter. At these concentrations, the combination of oxygen depletion and $Na_2S_2O_5$, or the sulfur oxides formed from it, were fatal to the clams.

A hydrogen sulfide (H_2S) smell was noted during the inspections following several successful treatments. The anoxic layer at the bottom of the intake basin created conditions where the H_2S could occur. It was not determined if the H_2S resulted from the sulfur bacteria acting upon the excess sulfates or if it was formed directly from the $Na_2S_2O_5$. Since H_2S is highly toxic to most life forms, adding more H_2S to the anoxic layer offered a potential for increasing the treatment effectiveness. The H_2S could also be easily neutralized by aeration prior to discharging the treatment water.

Hydrogen sulfide was added in the next experimental treatment after the anoxic zone had been created by the $Na_2S_2O_5$. A gas diffuser was placed in the siphon hose and the flow of additional $Na_2S_2O_5$ treated water dispersed the H_2S. This treatment resulted in over 95% mortality within 48 hours. The addition of H_2S to later experiments increased the effectiveness in cooler water and reduced the time the intake basin had to remain undisturbed in warmer weather.

RECOMMENDED TREATMENT

The following recommended treatment resulted from the four years of experimental treatments. The treatment uses 158 to 210 g/m^3 of $Na_2S_2O_5$ and 2.4 to 3.7 g/m^3 of H_2S. The effectiveness of $Na_2S_2O_5$ as an oxygen scavenger can be increased by adding 0.26 g/m^3 of cobalt chloride as a catalyst. After one half of the $Na_2S_2O_5$ has been injected into the bottom of the intake basin, H_2S is mixed with the remaining amount. Water in the intake basin should remain undistrubed for 60 to 72 hours after the treatment. If the temperature is below 21°C, then the larger amounts of $Na_2S_2O_5$ and H_2S should be used, and the intake basin should stand undisturbed for an additional 36 hours.

Plastic pipes were permanently installed on the floor of the intake basin to distribute the chemicals and provide aeration to neutralize the treatment prior to discharge. The annual cost to treat each unit was less than $1,000. A more complete description of the treatment methodology is provided by Smithson (1981).

EVALUATIONS OF TREATMENTS

Treatments effectiveness was evaluated from samples of clams collected in the intake basin and by comparing condenser fouling problems of treated and untreated units. The percentage of live clams in pretreatment samples were compared with recently killed clams from posttreatment samples and provided an immediate indication of treatment effectiveness. The size of live clams collected prior to a treatment indicated the success of the previous treatment and the growth of newly recruited clams. If the previous treatment was successful, live *Corbicula* in the intake basin should all be newly recruited and relatively small. An abundance of larger shells would indicate that the previous treatment was ineffective or the period between treatments was too long and recruited clams had grown large enough to plug condenser tubes. Comparisons of shell sizes from treated and untreated intake basins indicated that shells from the treated intakes were not large enough to plug main condenser tubes, but in untreated intakes 78% could plug condenser tubes (Fig. 1).

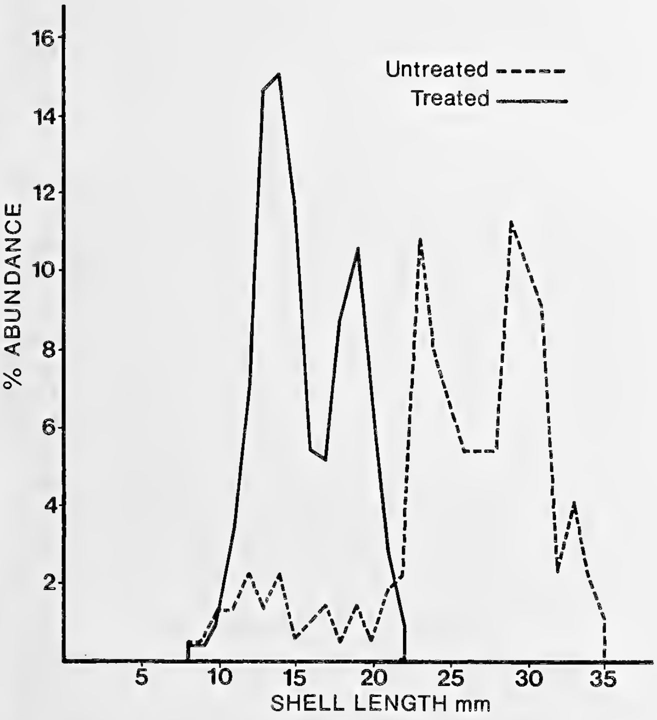

Fig. 1. Percent abundance of *Corbicula* by shell lengths from a treated and untreated cribhouse.

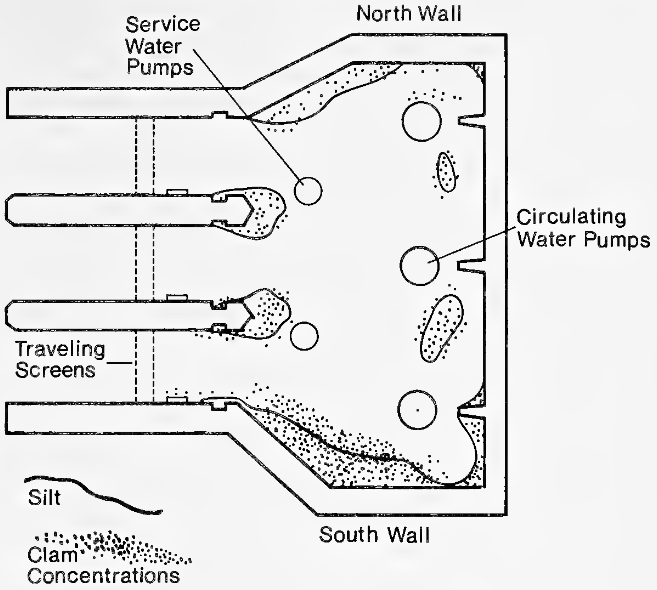

Fig. 2. Typical distribution of *Corbicula* and silt on floor of cribhouse.

The pretreatment inspections also provided an opportunity to assess the abundance of *Corbicula* in the intake basin. Prior to any treatments, *Corbicula* had accumulated to a depth of one meter, but after several years of treatments the accumulations were usually less than 7 cm and were composed mostly of relic shells.

Condenser fouling problems were reduced in treated units. The unit with the longest history of treatments has had only one minor problem of condenser fouling since treatments began in 1976. An untreated unit experienced episodes of severe condenser pluggage each summer until treatments were started.

DISTRIBUTIONS WITHIN THE INTAKE BASIN

Distribution of *Corbicula* in intake basins was noted during sample collections and has some implications on design and operating practices of intake basins which could reduce problems with *Corbicula*. The distribution of *of Corbicula* and silt was not uniform, but was strongly associated with low velocity areas (Fig. 2). Clam abundance in the intake basin appeared to result from larvae or juvenile clams settling in low velocity areas and growing. When these clams reached maturity they released additional larvae and accumulation was compounded. The increased abundance of larvae in the intake basin also presented a greater threat to service water and fire protection systems which draw water from the intake basin. Attachment by byssal threads was never observed in the intake basin, circulating water piping, or in condensers.

The uneven distribution of *Corbicula* illustrates the importance of eliminating low velocity areas in designing new intake structures. Rounding the corners of intake basins and creating a 45° slope where the walls meet the floor might reduce the areas where *Corbicula* accumulate. Installation of high pressure water nozzles to periodically flush areas where silt and clams accumulate could be retrofitted into existing intake basins or incorporated in new disigns. Water flushed through the chemical distribution lines (Smithson, 1981) reduced the silt accumulation in the intake basin.

Episodes of condenser fouling may result from changes in *Corbicula* distribution which subject them to pump entrainment. McMahon (1979) cited an example where *Corbicula* within an intake basin may have moved out of the sediments in response to environmental stress and were pumped into the condensers. An untreated intake basin at the Baldwin Power Station experienced severe episodes of condenser pluggage by *Corbicula* in early summer each year. The episodes generally occurred when water temperature first exceeded 32°C that year. These higher temperatures may have stimulated *Corbicula* to seek cooler areas and their movement exposed them to higher velocities areas where they were entrained by circulating water pumps.

Episodes of severe condenser fouling could also result from changes in the number of circulating water pumps being used. Intake basins usually contain several circulating water pumps. The number of pumps in operation may vary with inlet water temperature and the number of generating units in operation. When a pump is taken out-of-service the velocity in that area is reduced and may provide an area where *Corbicula* can accumulate. If these pumps are out-of-service for an extended period, they may entrain the accumulated *Corbicula* when restarted. This problem also applies to any infrequently used pump located in an area where *Corbicula* settles and accumulates.

SETTLING, GROWTH AND PREDATION

The treatment strategy assumed that *Corbicula* or juvenile clams were entering, settling, and growing in the intake basin and annual treatments would kill clams before they grew large enough to plug condenser tubes. In conjunction with the development of a treatment, a study was conducted to assess the growth and settling rates of larvae and juveniles and the effects of predation on small *Corbicula*.

Trays (38 x 34 x 15 cm) filled with a mud-gravel substrate were placed at the bottom of the intake canal. Trays were covered with a wire screen (12 mm aperture) which formed an inverted V-shaped roof over the tray. The wire screen simulated the intake screens which early life stages pass through to settle in the intake basin. Two of the four trays were completely enclosed by the wire mesh, and two trays had the mesh removed from the ends to allow predator access. The trays were 15 cm above the canal bottom to prevent entry by larger clams and were in the canal from April until November.

The mean density of *Corbicula* in November was 270/m² in the completely covered trays and 50/m² in open-ended trays. The lower density in the open-ended trays may have been due to fish predation on the small clams. Minckley et al (1970) found buffalo fishes consumed large numbers of *Corbicula*. Sule *et al*. (1981) found *Corbicula* were regularly consumed by bluegill (*Lepomis machrochirus*), freshwater drum (*Aplodinotus grunniens*), and channel catfish (*Ictalurus punctatus*). These species are abundant in Baldwin Cooling Pond and may have accounted for the lower densities in the incompletely covered trays. Predator absence in intake basins may contribute in part to the higher densities of *Corbicula* observed there.

The height of the sides of the tray above the lake bottom and the 12 mm mesh should have precluded the entry of larger clams; thus; *Corbicula* in the trays must have been recruited as larvae and grew. Britton et al (1979) found considerable recruitment of juvenile *Corbicula* through 10 mm opening in the lids of 19 liter buckets. The size range of the *Corbicula* in the trays also indicated they had settled as larbae and grew. The shell lengths in November ranged from 5 to 22 mm with a mean length of 16.8 mm. The range and mean shell length were similar to those reported for caged young-of-year *Corbicula* from the intake canal of nearby Lake Sangchris (Dreier and Tranuilli, 1981). The shell lengths of the Lake Sangchris clams ranged from 9 to 25 mm with a mean length of 18.1 mm.

The growth rate of larvae in the trays was useful in determining the timing of treatments of prevent *Corbicula* from reaching a size which wold plug condenser tubes. The maximum size obtained by November was 22 mm, and based upon this growth rate, an annual fall treatment should prevent incoming larvae from reaching a problem size. Outages of fossil-fueled generating units in power plants are typically scheduled during the spring and fall. Fall treatments are the most effective since they occur after the reproductive season. Recruitment of *Corbicula* to intake basins should remain relatively low until larvae are released during the following spring.

SUMMARY

A variety of measures may be needed to control *Corbicula* fouling in the various water systems in power plants. The control treatment described in this paper was successful in controlling condenser fouling problems at the Baldwin Power Station and has been patented by Illinois Power Company. The treatment consisted of the addition of an oxygen scavenger ($Na_2S_2O_5$) followed by an injection of H_2S into the intake basin during the annual scheduled outage of the generating unit.

Corbicula entered the intake basin through the traveling screens as larvae and settled in low velocity areas where they accumulated and grew. Annual fall treatments were sufficient to prevent the incoming larvae from becoming large enough to plug 7/8" condenser tubes between treatments.

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CORBICULA FOULING AND CONTROL MEASURES AT THE CELCO PLANT, VIRGINIA

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ABSTRACT

Corbicula fluminea infestation was initially reported in May 1981 and increased substantially by the fall at the Celco Plant, Celanese Corporation, Narrows, Virginia, as clam numbers at the river pumphouse station increased from 2,529/m² on 7/13/81 to 269,105/m² by 9/29/81. Infestation in the plant increased throughout 1982 as clam numbers at the pumphouse increased from 2,465 to 23, 869/m² from 4/13/82 to 11/29/82. Spring spawning was documented on 6/8/82 and 5/25/83 at river temperatures of 17-22 and 14-17 C, respectively. Spawning was continuous throughout the summer and fall of 1982 and 1983 although a major fall spawn was observed at river temperatures of 8-22 C (10/11 to 11/29/82) and 16-24 C (9/29/83). In-plant continuous chlorination ($\geqq$ 0.50 mg/L) for four weeks at the major spring and fall spawning periods was implemented in 1982 and continued in 1983 to reduce the incidents of clogged air conditioning condensers, oil cooling heat exchangers, industrial condensing-recovery complexes and power generating units. Other anti-fouling efforts used included the removal of clam-laden sediment at the pumphouse and periodic flushing of water holding towers and dead pipe spaces within the plant. Benthic macroinvertebrate collections were made in the New River upstream, adjacent to and downstream of the plant before continuous chlorination was implemented and during the two years of its use. No discernible impact of continuous chlorination for clam control was observed on the invertebrate populations sampled in the river. Literature data suggested that fish populations in the New River area influenced by chlorination would avoid these discharges. Continuous chlorination had a positive effect in reducing the number of clam fouling incidents within the plant in 1983 since only six of the seven incidents reported were due to clam shells and not live clams.

The incidence of the Asiatic clam [*Corbicula fluminea* (Müller)] as a biofouling pest in power plant and other industrial installations has increased alarmingly in the Southeastern United States during the past decade. After *Corbicula* was first discovered in 1938 in the Columbia River near Knapton, Oregon (Burch, 1944), the Asiatic clam was found in the Ohio River near Paducah, Kentucky in 1957 (Sinclair and Isom, 1963). By 1961, it was found in the Upper Ohio and Kanawha River Drainage at Chelyan, West Virginia (Thomas and MacKenthun, 1964). A subsequent collection was made in 1973 by Joy and McCoy (1975) in the Kanawha River, and Rodgers *et al.* (1977) calculated an upstream invasion of *Corbicula* in the New River to Glen Lyn, Virginia at ∿ 15 km/year. *Corbicula* and other mollusk fouling occurrences in the Southeastern United States were initially reported and reviewed by Sinclair and Isom, 1963; Sinclair, 1964 and 1971; Isom, 1971; McMahon, 1977, 1982; Cherry *et al.*, 1980. *Corbicula* were reported in the Savannah River, South Carolina by 1972 (Fuller and Powell, 1973) and resulted in fouling disturbances thereafter in power generating facilities at the Savannah River Project (R. S. Harvey, personal communication).

The initial documentation of *Corbicula* in the New River was reported at the Glen Lyn Plant in October, 1976, with densities in uninfluenced and thermally influenced areas of 20-30 clams/m² of river substratum (Rodgers *et al.*, 1977). Since then, proliferation of *Corbicula* densities had reached a high of 11,522/m² in the thermally influenced area of the Glen Lyn Plant in February, 1978 (Cherry *et al.*, 1980) *Corbicula* fouling has been controlled by routine physical

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maintenance of condenser systems. The diameter of the condenser tubes (∿19 mm) allows most adult clams to pass through unimpeded. In addition, the Glen Lyn Plant does not warm the intake of the travelling screens at the pumphouse for deicing purposes which inhibits successful overwintering of clams at this location. Consequently, *Corbicula* population densities do not reach unusually high numbers in non-thermally influenced areas (e.g. at the pumphouse) during the winter when New River temperatures approach 0 C.

The Celco Plant, located ∿11 km upstream from the Glen Lyn Plant, was probably initially inundated with *Corbicula* from the massive, 1978 spawn resulting in fouling incidents in 1981. From shell sizes up to 31 mm, clams were calculated to be ∿3 years old in condenser systems fouled with *Corbicula* by spring 1981. After the initial fouling occurrence in May 1981 in raw water-fed air conditioning units at the Celco Plant, numerous (e.g., two to three per month) fouling occurrences of *Corbicula* had occurred in plant processing condenser systems (i.e. power production turbines, oil and air coolers, acetone recovery, calcium chloride refrigeration, and production of distilled water). As a result of these problems, a study was designed to evaluate the clam populations in and around the Celco Plant beginning in May 1981 and ending in November 1983.

The objectives of this study were to: (1) measure *Corbicula* numbers and gravid condition of adults at the pumphouse and the thermal discharge stations in the New River Celco Plant; (2) evaluate the removal of river sediment at the plant pumphouse as a clam control procedure; (3) determine the effect of continuous chlorination upon *Corbicula* within the plant for a four-week period during peak spawning periods in spring and fall; (4) identify clam infestation areas within the plant and provide maintenance for clam control; and (5) evaluate potential environmental effects of chlorinated

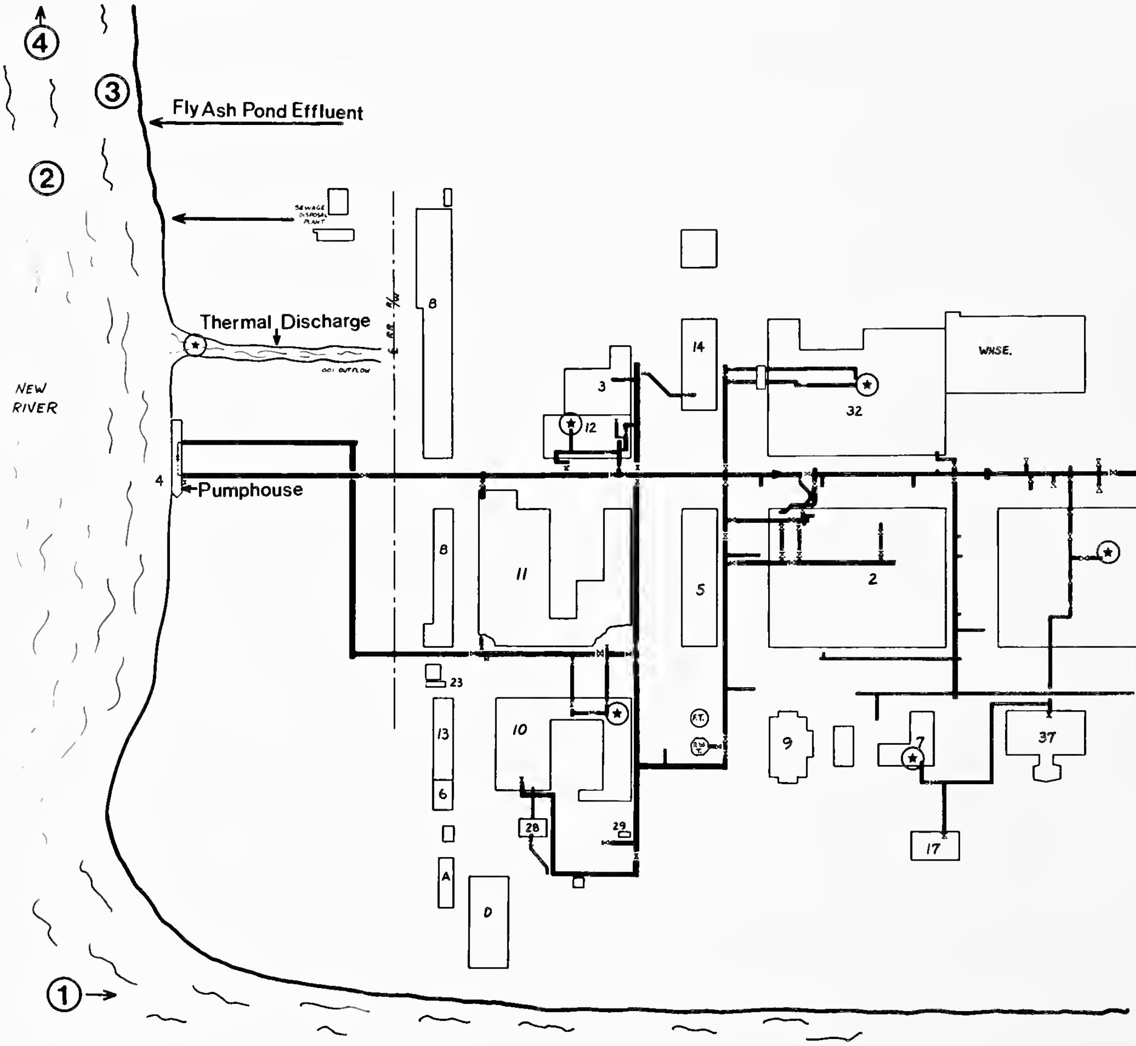

Fig. 1. Sampling stations for *Corbicula* at the pumphouse and thermal discharge stations of the Celco Plant and chlorine sampling stations (denoted by *) within the plant. Numbers within each building represent the identification of each production unit while thick lines to and from each building are raw river pipe lines. Invertebrate sampling stations in the New River are designated as 1-4.

discharges in the New River from a field study of benthic, macro-invertebrates and literature review of fish.

MATERIALS AND METHODS

PLANT SITE

The Celco Plant is located along the New River at Narrows, Virginia. New River water is used to: (1) air condition offices, process control rooms and some production areas; (2) recover acid and acetone using river water for condenser cooling; (3) provide fire control; and (4) cool turbine generators in power production, calcium chloride chillers, and stills for distilled water. River water is pumped from the pumphouse through 0.92 and 0.61-m lines into the plant by six centrifugal pumps at 188,000 L/min. The chlorination system is approximately 30 m from the pumphouse, and chlorinated water flows throughout the plant (Fig. 1).

CORBICULA SAMPLING

Asiatic clams were sampled by Ponar dredge at five locations: 150 m upstream from the plant; at the pumphouse; at the thermal discharge station (120 m downstream from the pumphouse); and 75 and 150 m downstream from the discharge on June 24, 1981. Thereafter, clam sampling was emphasized at the pumphouse and thermal discharge stations from July 13, 1981 through November 29, 1983 once each month or at two to three-month intervals during the spring to fall (Fig. 1). At these stations, *Corbicula* samples were taken four times during 1981 and five times each during 1982 and 1983. Clam samples were taken $\sim$5 m away from the pumphouse from one end to the other. Clams at the discharge station were collected by wading and removing 0.25 m^2 areas of sediment. All samples were reported as per m^2 of clam numbers.

GRAVID CONDITION OF CORBICULA

Fifty adult clams ($\geqq$ 10 mm) were evaluated microscopically using a dissecting microscope for developing larvae in the gill marsupia during each field sampling effort. Data were evaluated as the percent of clams sampled with incubating larvae in the marsupia of gills.

REMOVAL OF RIVER SEDIMENT (MUCKING PROCESS)

In mid-June, 1982, much of the clam-infested sediments at the pumphouse of the Celco Plant was siphoned or removed by a suction (bilge-"mucking") pump and emptied into a dumpster in order to reduce the accumulated sediment and clam population at the pumphouse. "Pre-mucking" data for clam densities at the pumphouse refer to river sediment conditions prior to sediment removal while "post-mucking" data indicate clam density measurements after this operation.

MONITORING OF CHLORINE CONCENTRATIONS

Several stations in the Celco Plant were monitored for chlorine residuals (Fig. 1). These included: Buildings 10 and 12 (375 and 275 m away from the chlorinator, respectively), followed by Buildings 1 and 32 (590 and 460 m, respectively), and the Office-Computer Complex Building which was farthest away (790 m). During continuous four-week chlorination periods, chlorine residuals were measured by amperometric titration at each station. Chlorine measurements were taken daily during the continuous, four-week chlorination periods at the discharge channel. The New River water depth and the volume of effluent water released from the plant in the discharge station were measured daily due to a special NPDES (National Pollutant Discharge Elimination System) variance permit obtained from the State Water Control Board in Richmond, Virginia. The following dilution factors were incorporated into calculations of the daily chlorinated water discharge which resulted in an overall calculated chlorine residual of $\leqq$ 0.01 mg/L TRC (total residual chlorine) into the New River:

$$\frac{\textit{Plant Outfall Flow (MGD) X Measured TRC mg/L in Plant Outfall}}{\textit{Daily New River Flow (MGD as millions of gallons/day}} \leq 0.01 \text{ (TRC)}$$

IDENTIFICATION OF CLAM INFESTATION AREAS WITHIN THE PLANT

Dead water pipe lines were identified within the plant that had become obsolete and were removed. Water towers used for emergency fire control or production were drained and sediment was analyzed for potential juvenile and adult clam habitation each spring and fall during 1982 and 1983.

BENTHIC MACRO-INVERTEBRATE SAMPLING IN THE NEW RIVER

Environmental effects of chlorine were determined by establishing sampling stations in similar riffle habitats at the following locations using a 0.092 m^2 Surber Sampler (Fig. 1):

Station 1: above the Celco Plant $\sim$0.5 km above the U.S. 460 bridge or 2 km above Station 2;
Station 2: just below ($\sim$0.1 km) the waste water effluent of the Celco Plant;
Station 3: just below the fly ash effluent of the Celco Plant, $\sim$0.5 km below Station 2;
Station 4: $\sim$1.0 km below Station 3.

On each of the ten sampling dates (September and October 1981, and May 1982 before the first four-week continuous chlorination; and on August, September, October 1982, and four times in 1983 - after four, 28-day continuous chlorination treatments for *Corbicula* control), three macroinvertebrate samples were collected at each of the above stations. River water depth was less than 0.3 m during each sampling effort. Samples were immediately preserved in 70% ethanol and taken to the laboratory for identification. Organisms were identified to genus level, counted and recorded by sample replicate, and later evaluated in terms of taxon diversity (Shannon-Wiener) per sample and station, percent similarity between stations, and major taxonomic groups by station.

REVIEW OF LITERATURE ON CHLORINE TOXICITY AND AVOIDANCE RESPONSES OF FISH

To evaluate the potential impact of continuous chlorination discharges upon the fish community in the New River, daily TRC concentrations from the thermal discharge station were compared to chlorine toxicity data in the literature for known New River fish species. Forty-eight fish species have been identified and evaluated in the New River relative to thermal discharges at the Glen Lyn Plant (Stauffer *et al.*, 1976). Potential fish avoidance and toxicological consequences of chlorine from studies at the Glen Lyn Plant (Cherry *et al.*, 1977; 1982; Cherry and Cairns, 1982; Giattina *et al.*, 1981) were compared to other data (e.g., Heath, 1977; Seegert *et al.*, 1979).

RESULTS

PRE-MUCKING OPERATION-1981 TO SPRING, 1982

PRELIMINARY SAMPLING

After the initial incident of *Corbicula* fouling at the Celco Plant on May 28, 1981, preliminary sampling showed clam numbers of 215/m^2 at 150 m upstream of the plant, 2,529/m^2 at the pumphouse, 272/m^2 at the thermal discharge station, 1,204/m^2 75m downstream of the thermal discharge, and 1/m^2 150 m downstream of the thermal discharge. Temperatures at these stations were 25, 26, 38, 29, 29 C, respectively. Oldest clams ($\sim$31 mm) were considered to be recruits from the Glen Lyn Power Plant in 1978; no clams were found to be less than 9 mm in shell length. Clam densities were highest at the pumphouse and at 75 m downstream from the thermal discharge from the plant.

CORBICULA NUMBERS AND GRAVID CONDITION AT THE PUMPHOUSE

Numbers (per m^2) at the pumphouse varied from 2,529 in July to 9,742 in August to a high of 269,105 in September, and then declined to 41,788 in November, 1981 (Table 1). The high densities in August and September, 1981 were due primarily to the large number of young clams $\leqq$ 1 mm in shell length (84 and 78% of the samples, respectively). The percent of adult clams with eggs in the gonadal tissue was high for both months (96 and 76%, respectively) while the percent with incubating larvae in the marsupia was low (14%). No young clams $\leqq$ 1 mm in shell length were found in the other three sampling efforts. The relatively high number of clams

Table 1. Number (per m^2) of *Corbicula fluminea* in juvenile and adult clam shell length classes (early juveniles $\leqq 1$ mm, juveniles to early adults >1 to $\leqq 10$ mm, and adults >10 mm) at the pumphouse station of the Celco Plant, Narrows, Virginia. The occurrence of early juvenile clams sampled from the river sediment are compared to New River temperature (mean and ranges in C) of two weeks at and prior to each of the sampling efforts along with the gravid condition (larvae in gills, $n = 50$) of adult clams.

Sampling Date	Water Temperature (C)		Shell Length of clams in mm			Total	% Adults w/ larvae in Gills
	Mean	Range	$\leqq 1$	>1 to $\leqq 10$	>10 to 31		
			Pre-Mucking Period[a]				
7/13/81	23.5	21-27	0	184	2,345	2,529	14
8/5/81	25.2	24-27[b]	8,242	321	1,179	9,742	12
9/29/81	18.7	17-22[c]	207,030	59,374	2,701	269,105	14
11/11/81	12.6	10-17	0	40,248	1,540	41,788	0
4/13/82	9.3	6-12	0	2,408	57	2,465	0
6/8/82	19.9	17-22	545	6,680	215	7,440	50
			Post-Mucking Period[a]				
7/19/82	24.3	23-25[b]	7,479	1,800	570	9,849	20
10/11/82	20.0	18-22[c]	13,741	1,344	1,375	16,460	30
11/29/82	9.9	8-12[c]	21,993	640	1,236	23,869	0
5/25/83	16.5	14-17	127	1,401	684	2,212	65
6/14/83	20.0	19-23[b]	3,486	1,597	2,250	7,333	85
8/10/83	26.0	24-27	25	2,326	1,046	3,397	65
9/29/83	19.4	16-24[c]	7,225	3,581	830	11,636	80
11/29/83	9.0	7-11	70	2,649	2,339	5,058	57

[a] Pre-Mucking period occurred before New River sediment was removed by a bilge-pump mucking process at the pumphouse station while post-mucking occurred after removal of a substantial amount of the sediments.

[b] Indicates the mean and range (previous two weeks prior to each sample) of New River daily temperatures during the major spring spawning season.

[c] Indicates the mean and range (previous two weeks prior to each sample) of New River daily temperatures during the major fall spawning season.

Table 2. Number (per m^2) of *Corbicula fluminea* in juvenile and adult clam shell length classes (early juveniles ≦ 1 mm, juveniles to early adults >1 to ≦ 10 mm, and adults > 10 mm) at the thermal discharge station of the Celco Plant, Narrows, Virginia. The occurrence of early juvenile clams sampled from the river sediment is compared to effluent temperatures (mean and ranges in C) of two weeks at and prior to each sampling effort along with the gravid condition (larvae in gills, n = 2-50) of adult clams.

	Water Temperature (C)		Shell Length of Clams in mm				
Sampling Date	Mean	Range	≦1	>1 to ≦10	>10 to 31	Total	% Adults w/ larvae in Gills
			Pre-Mucking Period[a]				
7/13/81	36.6	31-40	0	95	177	272	14
8/5/81	36.7	31-40	0	51	608	659	10
9/29/81	30.9	31-28[a]	2,199	1,255	1,096	4,530	6
11/11/81	29.2	25-33	0	1,217	317	1,584	0
4/13/82	28.0	22-30	0	520	418	938	0
6/8/82[c]	—	—	—	—	—	—	—
			Post-Mucking Period				
7/19/82	38.5	37-41[b]	976	741	469	2,186	10
10/11/82	33.2	28-39	0	387	424	811	15
11/29/82[c]	—	—	—	—	—	—	—
5/25/83[c]	—	—	—	—	—	—	—
6/14/83	34.0	32-37[a]	317	285	50	652	40
8/10/83	38.6	36-41	0	2	1	3	0
9/29/83	31.7	31-34	0	3	3	6	0
11/23/83	32.0	29-34	0	1	1	2	0

[a] Indicates the mean and range (previous two weeks prior to each sample) of thermal discharge temperatures during the major spring spawning week.

[b] Indicates the mean and range of thermal discharge temperatures during the major fall spawning season.

[c] High river water levels prevented sampling of clams.

in November was attributed to the clams spawned in September. Clams from 1-10 mm in shell length in November were 40,248/m^2 which represented 96% of the total. The gravid condition of clams at the pumphouse station was low in the November sample (15 and 0% of adults with eggs in gonadal tissue or larvae in marsupia, respectively). Mean water temperatures (two weeks prior to and during sampling) at peak spawning collections in 1981 were 25.2 and 18.7 C, respectively.

On April 13, 1982, clam numbers at the pumphouse station were 2,465/m^2 and increased to 7,440/m^2 by June 6, 1982 (Table 1). Clams ≦ 1 mm in length were not found in the April sample but represented 7.4% of the sample in June. The gravid condition of adult clams (eggs and larvae, respectively) sampled in 1982 ranged from 75 and 0% in April to 100 and 50% in June. The release of juvenile clams as determined in the sediment, was initally identified when water temperature reached 17-22 C ($\bar{x}$ = 19.9 C).

CORBICULA NUMBERS AND GRAVID CONDITION IN THE THERMAL DISCHARGE

Numbers (per m^2) in the thermal discharge station increased from 272 in July to a high of 4,530 in September and declined to 1,584 in November, 1981 (Table 2). Spawning resulted in the collection of clams ≦ 1 mm in length in September, 1981, when 2,199/m^2 (48.5% of the total sample) was obtained. This was the only time in 1981 when young clams ≦ 1 mm in length were sampled as mean, two-week water temperature was 30.9 C. The gravid condition in the November sample was low (6% in gonads and 0% in gills).

No spring spawning activity in the thermal effluent was recorded in June 1982 since high water conditions prevented adequate sampling (Table 2). Discharge temperatures ranged from 22 to 30 C during the April and June sampling efforts. The gravid condition of clams in the thermal effluent was low in the April sample (61 and 0% for eggs and larvae, respectively) showing no potential of larval release from adults.

POST-MUCKING OPERATION - SUMMER 1982 TO FALL 1983

CORBICULA NUMBERS AND GRAVID CONDITION AT THE PUMPHOUSE

After removal of the sediment at the pumphouse and thermal discharge stations in 1982, *Corbicula* numbers at the pumphouse ranged from 9,849 in July to 16,460 in October to 23,869 in November (Table 1). Early summer spawning of *Corbicula* had occurred by July 19, 1982 when 7,479/m^2 of ≦ 1 mm in length were sampled in pumphouse sediment. This amount represented 76% of the total July sample as newly spawned individuals. River water temperatures ranged from 23-25 C. The gravid condition of clams in July

1982 was 90% (eggs) and 30% (larvae) in adults. A major spawning of *Corbicula* was observed from October 11 through November 29, 1982 in which 13,741/m^2 and 21,993/m^2 clams ≦ 1 mm in size were sampled from sediments. This abundance of clams ≦ 1 mm represented 83 to 92% of the overall sediment sample taken in October and November, 1982, respectively. The gravid condition (eggs and larvae, respectively) of adult clams ranged from 100 and 30% in October to 30 and 0% in November, 1982. During fall spawning, river water temperatures ranged from 18-22 C in October to as low as 8.0 C in November 1982.

In 1983, clam numbers ranged from a low 2,212/m^2 in May to a high of 11,636/m^2 in September (Table 1). The highest number of clams sampled corresponded to the release of juvenile clams (∿1 mm) in June (3,486/m^2) and September (7,225/m^2). The percent of adults with larvae in the gills was also high (65 to 80%) during these months of high spawning activity. Water temperature in June ranged from 19-23 C and in September, 16-24 C. Spawning was essentially over by November 29 when river temperatures were 7-11 C.

CORBICULA NUMBERS AND GRAVID CONDITION IN THE THERMAL DISCHARGE

Corbicula numbers (per m^2) in the thermal discharge station ranged from 2,186 in July to 811 in October, 1982 (Table 2). River conditions were too high to sample in November. Slight spawning in the thermal discharge station was observed at a temperature of 37-41 C (976/m^2 for clams ≦ 1 mm in length) during the July sampling effort but could not be compared to the June sampling effort due to high river conditions. The gravid condition of *Corbicula* sampled in July 1982 was 90 and 10% (eggs in gonads and larvae in marsupia). In 1983, the number of clams sampled markedly decreased from June (652/m^2) to November (2/m^2). Slight spawning was observed in June when water temperature was 32-37 C.

OBSERVATIONS BETWEEN PRE- AND POST-MUCKING SAMPLING

Sediment removal process at the Celco Plant pumphouse was approximately 70% effective from patches of sediments to bare rock substrate observed from the upper floor of the pumphouse. A four-fold decline in juvenile and adult clams (≧ 1-31 mm) was observed immediately after sediment removal in July 1982 when compared to June 1982 (Table 1). Adult clams (≧ 10 mm), however, rapidly increased after July 1982 to numbers by June 1983 which were similar to those obtained in July to September, 1981.

CHLORINE RESIDUALS MEASURED IN THE CELCO PLANT AND THERMAL DISCHARGE

Biocidal effectiveness was a function of the rate of chlorine gas application, water temperature, and distance of sampling stations from the chlorinator (Table 3). Measurement of TRC was always lowest at the thermal discharge station

Table 3. Summary of mean total residual chlorine (TRC) measurements in mg/L at selected sampling stations in the Celco Plant at the chlorinator rate of 200 to 525 lbs per day in the 0.61 and 0.92-m water lines of the plant. Data were taken from several sampling periods on August 26, 1982 to November 1, 1983. Numbers in parentheses represent the water temperature measured at each sampling station in C.

	Total Residual Chlorine (TRC) in mg/L at Sampling Stations					
Chlorine (lbs/day)	Thermal Discharge	Bldg 12	Bldg 10	Bldg 32	Bldg 1	Office Bldg
	AUGUST 26, 1982					
200	0.02	a	a	a	a	a
	(33)					
400	0.06	0.30	0[b]	0[b]	0[c]	a
	(33)	(27)	(24)	(23)	(26)	
525	0.12	0.85	0.77[d]	0.52[d]	0[c]	a
	(34.5)	(27)	(24)	(24)	(27)	
	SEPTEMBER 21, 1982					
525	0.18	0.90	0.59	0.76	0[c]	a
	(29)	(22)	(18)	(18)	(18)	
	NOVEMBER 1, 1982					
250	0.10	0.34	0.37	0.30	0.30	0.16
	(28.5)	(17.0)	(16.0)	(17.5)	(15.0)	(15.5)
450	0.24	0.65	0.75	0.60	0.66	0.38
	(27.5)	(17.5)	(16.0)	(17.5)	(15.0)	(16.0)
500	0.27	a	a	a	a	a
	(28.0)					
	NOVEMBER 16, 1982					
200	0.02	0.46	0.11	0.26	0.16	0.13
	(21)	(13)	(9)	(9)	(10)	(10)
350	0.23	1.22	0.29	0.60	0.46	0.36
	(21)	(13)	(10)	(9)	(10)	(10)
300	0.06	a	a	a	a	a
	(21)					
	JULY 17, 1983					
325	0.10	0.21	0.25	0.20	0.21	0.13
	(33)	(27)	(23)	(33)	(23)	(23)
500	0.18	0.55	0.36	0.47	0.45	0.27
	(33)	(27)	(23)	(23)	(23)	(23)
	JULY 22, 1983					
325	0.08	0.35	0.34	0.33	0.32	0.25
	(37)	(30)	(26)	(25)	(25)	(25)
500	0.21	0.67	0.60	0.55	0.56	0.36
	(37)	(30)	(26)	(25)	(25)	(25)
	NOVEMBER 1, 1983					
325	0.06	0.58	0.06	0.30	0.27	0.15
	(39)	(18)	(15)	(15)	(15)	(15)
500	0.20	0.12	0.19	0.63	0.61	0.38
	(29)	(18)	(15)	(15)	(15)	(15)

[a] TRC measurements were not taken at this station.

[b] Water line was not flushed adequately to obtain a TRC measurement.

[c] Chlorinated river water was not passing through the condenser when sample was taken.

[d] Water line was flushed for 30-60 min prior to TRC measurement.

which was farthest from the chlorinator. When TRC was 0 mg/L, problems in river water circulation or lack of condenser use were the reason for no chlorine detection. As the chlorination rate was increased from 200 to 525 lbs/day during this period, biocidal effectiveness increased. However, a greater chlorine application rate was needed in August and September 1982 (maximum rate of 525 lbs/day) to achieve the same biocidal effect in November 1982 (350-450 lbs). In 1983, chlorine application varied from 325 to 500 lbs/day depending upon the river flow rate. In most sampling stations within the plant, TRC concentrations were attempted to be ≧0.50 mg/L. The office building, which was farthest from the chlorine application point, had the lowest TRC concentration (≧0.38 mg/L).

No violation of the special variance permit occurred in 1982-1983. As river flow rates declined to less than 1200 MGD (million gallons/day) chlorine application was reduced to 350 lbs/day. By measuring the TRC in the thermal discharge or plant outfall, and applying it to the plant outfall rate and flow rate of the river, calculated TRC had to be ≦ 0.01 mg/L. For example, if the plant outfall was 60 MGD the measured TRC was 0.18 mg/L when the New River flow was 1200 MGD, then:

$$\frac{60 \text{ MGD} \times 0.18 \text{ mg/L TRC}}{1200 \text{ MGD}} = 0.009 \text{ mg/L TRC}$$

When comparing chlorine residuals at Bldgs 12, 10, 32 and 1 in the August-September 1982 samples with those in November 1982, effective biocidal exposures of 0.90 to 0.52 mg/L were obtained at 525 lbs/day (Table 3). Similar TRC levels (0.75-0.60 mg/L, were obtained in the same stations at 450 lbs/day on November 1 with even higher TRC levels at 350 lbs/day (1.22-0.46 mg/L) on November 16, 1982. The high and low discrepancies on November 16, 1982, between Bldgs 12 and 10 (1.22 and 0.29 mg/L, respectively) were due to shifts in chlorinator flow between the 0.61 and 0.92-m lines that fed these sampling stations.

The mean temperature at Bldgs 12, 10, 32 and 1 decreased steadily at the four sampling dates from August 26 to November 16 (25, 19, 16.4, and 10.5 C, respectively). The decline in New River water temperature in the plant processing stations from summer to fall conditions should have resulted in lower chlorine usage during the fall to provide the same degree of biocidal activity as that needed during the summer. However, less chlorine (325 lbs/day) was used daily during the summer due to low New River flow. Similar daily adjustments in the chlorination from 325 to 500 lbs/day were needed in the 1983 chlorination schedules due to river fluctuations. Maximum chlorination output (500 lbs/day) only occurred for 35% of each 28-day period. Therefore, TRC released into the thermal effluent varied daily from ≧0.06 to 0.02 mg/L. This maintained permit limitations of ≦0.01 mg/L TRC released into the thermal discharge station.

Chlorination was highly effective in controlling *Corbicula* infestation. Where dozens of fouling incidents occurred in 1982, only seven were reported in 1983. Only one was due to clogging by live clams; all others were the result of clam shells.

IDENTIFICATION OF CLAM INFESTATION AREAS WITHIN THE PLANT

Several obsolete water pipe lines were identified and removed. The water holding tower for emergency fire control was drained and sediment was removed. On the roof of Bldg 10, three holding towers used for production purposes were drained after each major spring and fall spawning period determined from clam analysis at the pumphouse station. During May 1983, numerous juvenile clams (~ 1-2 mm) were found in the tower sediment.

AQUATIC BENTHIC MACRO-INVERTEBRATE COMMUNITY STUDIES

Each of the four sampling stations appeared to be comprised of "healthy" aquatic macro-invertebrate communities for all six sampling periods. That is, diversity of organisms was consistently high at all stations. The mean number of taxa per station was relatively high for the 1981-1983 combined samples, ranging from 21.5 at Station 1 to 23.1 at Station 2 (waste water outfall) and 22.1 to 21.4 at Stations 3 and 4, respectively (Table 4). The mean

Table 4. Total number of invertebrate taxa from 3 replications per station and averages before and after 4-week continuous chlorination and for all years combined (1981-1983). The rank assigned to each station represents the degree of taxa abundance by assigning a number from 1 to 4 to each station relative to the lowest and highest number of taxa, respectively.

Date of Sample	STATION 1	2	3	4
Before Four-Week Continuous Chlorination				
September 1981	27	25	28	29
October 1981	33	35	34	27
May 1982	20	22	24	28
AVERAGE	26.7	27.3	28.7	28.0
After Four-Week Continuous Chlorination				
August 1982	23	26	21	22
September 1982	16	22	19	16
October 1982	22	21	19	14
July 1983	20	17	17	22
September 1983	20	23	22	23
October 1983	16	20	18	19
November 1983	18	20	19	14
AVERAGE	19.3	21.3	19.3	18.6
Combined Average Before and After Chlorination	21.5	23.1	22.1	21.4
Range	16-33	17-35	17-34	14-29
Average Rank	2.05	3.10	2.35	2.50

Table 5. Shannon Wiener diversity of invertebrates per sampling station and average diversity before and after continuous chlorination and for all years combined (1981-1983). The rank assigned to each station represents the degree of diversity between stations by assigning a number from 1 to 4 for each station relative to the lowest to highest diversity, respectively.

Date of Sample	STATION			
	1	2	3	4
Before Four-Week Continuous Chlorination				
September 1981	3.495	3.040	3.000	2.868
October 1981	3.420	3.280	3.000	3.570
May 1982	2.695	3.380	2.716	2.449
AVERAGE	3.203	3.233	2.905	2.962
After Four-Week Continuous Chlorination				
August 1982	2.888	3.662	3.134	3.333
September 1982	3.359	3.537	0.031	1.717
October 1982	3.339	3.738	2.387	1.665
July 1983	2.994	2.705	2.520	2.919
September 1983	3.005	3.296	2.985	3.384
October 1983	3.220	3.325	2.529	3.415
November 1983	3.132	3.013	2.291	2.457
AVERAGE	3.134	3.325	2.697	2.698
Combined Average Before and After Chlorination	3.155	3.298	2.759	2.778
Range	2.695-3.495	2.705-3.662	2.291-3.134	1.665-3.570
Average Rank	2.8	3.2	1.6	2.4

Shannon-Weiner diversity index values for the 1981-1982 combined samples were also high, ranging from 2.767 at Station 4 to 3.440 at Station 2 (Table 5). In view of these trends, the high number of taxa and diversity indices observed indicated that the macroinvertebrate assemblages upstream, adjacent to and downstream from the Celco Plant were diverse.

When comparing mean taxa and diversity of organisms before and after four-week continuous chlorination, the following trends were observed. Stations 2 and 3, which were potentially influenced by TRC, had an average of 23.1 and 22.1 taxa, respectively, after chlorination compared to 27.3 and 28.7 taxa before chlorination (Table 4). A similar decline, however, was also seen in Stations 1 and 4 that had no TRC influence. Mean taxa (before and after chlorination, respectively) declined from 26.7 to 21.5 in Station 1 and 28.0 to 21.4 in Station 4. After chlorination, diversity at Station 2 ranged from 2.705 to 3.738 with an average for 1982-1983 of 3.325 which was higher than the other stations (Table 5). These high values were probably the result of organic enrichment from the waste water discharge. Stations 2 and 3 were closest to chlorinated influence but showed little difference relative to the total number of taxa, rank of taxa between stations, and diversity of invertebrates in the uninfluenced Stations 1 and 4.

No major differences were observed between chlorine influenced Stations 2 and 3 with regard to the percent composition of invertebrates by order (Table 6). The greatest percent abundance values (calculated as the mean percent abundance value per station by groups) were associated with Ephemeroptera (15.6), Trichoptera (26.1), and Gastropoda (21.5). This was consistent with the fact that the New River, a wide shallow river with relatively high primary productivity, is composed of benthic feeders that graze on periphyton or filter seston.

The Ephemeroptera in the New River were primarily collector-gatherers and scrapers, which feed on attached plants. These numbers were relatively high in Stations 1, 2, and 3 with mean percent abundance values of 17.0, 17.6 and 18.0, respectively, from 1981-1983 (Table 6). Ephemeroptera at Station 4 had an average percent abundance of 9.9.

Gastropods, which also feed on attached algae, comprised the second highest average percent abundance values of 24.2, 28.3, 35.4 and 16.4 for Stations 1, 2, 3, and 4, respectively (Table 6). The percent abundance for Stations 2 and 3 was somewhat lower than those for the uninfluenced stations; these differences may be due to the replacement of the functional (trophic) category that gastropods occupy at Stations 1 and 4 and by mayflies at Stations 2 and 3.

Trichoptera in the New River are principally filter-feeders, feeding on organic particles and smaller organisms drifting with the current. Their abundance comprised an average of 26.1% of all 4 stations, with a range from 16.4 at Station 4 to 28.3 at Station 2 (Table 6).

When comparing changes in the percent abundance of insect orders before and after chlorination, the following results were observed. The decline in ephemeropterans and trichopterans after chlorination was coincidental to the increase in *Corbicula* densities, even in Station 1 upstream from the Celco plant. At Stations 2 and 3, *Corbicula* and gastropods increased after chlorination while ephemeropterans and trichopterans declined. Dipteran densities declined in all stations in mid to latter 1982 but increased in 1983 (Table 6).

DISCUSSION

CORBICULA NUMBERS AT THE PUMPHOUSE

The potential for *Corbicula* infestation at the New River pumphouse station and fouling within the Celco Plant was realized from May 28, 1981 through August 1982, as evidenced by field population numbers and by many in-plant fouling occurrences. From the initial occurrence of clam fouling in the air conditioning units of the process control room in Bldg 10, disruptions from clogged condensers occurred through 1981 and progressively increased in spring and early summer of 1982 in units in addition to air conditioning (e.g., condenser systems in turbine generators, circulating air and oil coolers, distilled water systems in Stokes Stills, carrier calcium chloride chillers, acetone recovery units).

The source of *Corbicula* fouling was identified at the Celco pumphouse where clam populations developed to unusually high numbers. Part of this proliferation at the New River pumphouse station may have been due to deicing of

Table 6. Average percent abundance of selected insect orders by station before and after four-week continuous chlorination and for 1981-1983 combined.

		Percent Composition						
Date of Sample	Sampling Station	Ephemeroptera	Trichoptera	Coleoptera	Diptera	Gastropoda	Pelecypoda	Other
		Before Four-Week Continuous Chlorination						
1981-1982 Average	1	23.6	24.4	6.7	8.0	30.6	0.2	13.2
	2	14.4	31.1	11.2	18.4	11.3	9.3	15.5
	3	21.5	32.3	5.3	16.5	11.0	8.2	10.5
	4	18.6	20.3	9.1	11.0	29.2	12.5	8.4
		After Four-Week Continuous Chlorination						
1982 Average	1	10.5	25.5	15.5	1.8	29.8	11.1	21.3
	2	26.7	26.7	9.2	4.0	16.1	13.1	13.4
	3	13.5	22.6	8.0	2.1	28.4	19.9	13.5
	4	7.0	7.1	5.8	1.0	33.9	43.3	7.1
1983 Average	1	17.2	21.9	16.5	2.8	25.7	11.2	5.5
	2	13.2	27.3	12.7	6.8	23.5	14.0	2.6
	3	18.6	48.4	5.0	8.8	12.9	5.0	1.5
	4	9.3	19.7	11.1	6.7	27.1	21.9	4.4
Overall Average After Chlorination (1982-1983)	1	14.3	22.6	16.1	2.4	27.4	10.7	5.7
	2	19.0	27.0	11.2	5.6	19.5	13.6	3.3
	3	16.7	37.3	6.3	5.8	19.5	11.4	3.2
	4	8.3	14.5	8.8	4.2	30.0	31.1	3.1
		Average Percent Abundance by Station for 1981-1983						
	1	17.0	24.2	13.2	4.1	28.4	21.0	5.8
	2	17.6	28.3	11.1		17.5	13.1	3.6
	3	18.0	35.4	6.0	9.0	17.0	12.7	3.9
	4	9.9	16.4	8.8	6.2	23.1	28.1	3.6
		Average Percent Abundance for Each Taxonomic Group for All Stations Considered Collectively						
		15.6	26.1	9.8	7.2	21.5	18.7	4.2

the travelling screens during the winter months with heated water which was released into the immediate New River sediment (4-8 C). This practice could have enhanced Asiatic clam proliferation in the New River sediments when seasonally ambient winter temperatures reached O C which could have suppressed their development. Mattice and Dye (1976) reported 2 C as the lower temperature where *Corbicula* could not be acclimated. Cherry *et al.* (1980) reported that clams residing in stations outside the thermal discharge of the Glen Lyn Power Plant (several miles downstream of the Celco Plant) were erradicated during the winter when river temperature dropped below 2 C. The semi-fine, granular sediments, which were well aerated from the New River flow and continuous Celco Plant pumping activities, served to harbor and promote clam development in water temperatures several degrees above freezing in the immediate vicinity of the pumphouse.

Clam numbers were highest in the immediate vicinity of the Celco Plant pumphouse station, probably due to heated water released into the station from the travelling screen deicing procedures in the winter. Although adult clam numbers were reduced by 4 and 2-fold, respectively, over the winter to following spring of 1981-1982 and 1982-1983, sufficient numbers were available each spring to allow for a great amount of larval production during the spring spawning season. The clam population at the Celco Plant was extremely high regarding clam numbers in comparison to clams sampled downstream at the Glen Lyn Plant (Cherry *et al.*, 1980). The highest number of clams collected at the Glen Lyn Plant in the thermally discharged channel in February 1978 was 11,522/m^2 which was much less than the highest obtained in this study (269,105/m^2).

CORBICULA SPAWNING ACTIVITY

Corbicula spawning has been reported during the spring and fall or continual in some localities (Britton, in press). Eng (1979) found spawning to be biannual from mid-April through May and from mid-August through September in the San Joaquin River system, California, while Sickel (1979) found *Corbicula* to have a strong spring spawn and a weaker fall spawn with lesser but continuous spawning in between.

Spawning of clams in the Savannah River, South Carolina appears to be continuous from April to November (R. S. Harvey, personal communication). In 1981, we noted major spawning activity by August 5, 1981, since 84.6% of the young clams in the sediment were ≦1 mm in size and were not found in the previous sampling effort of July 13, 1981 (Table 1). By September 29, 1981, spawned larvae (≦1 mm) comprised 76.9% of the sample or 207,030/m² of sediment at the pumphouse station. Between August 5, 1981, and September 29, 1981, clams ≦ 1 mm in size had increased by 25-fold in the pumphouse sediment (8,242 vs 207,030/m², respectively). Spawning in the fall of 1981 was essentially over by November 11, 1981, after peak spawning had probably occurred by September 29, 1981 or soon thereafter.

Clam spawning was generally continuous from June 8, 1982 to October 29, 1982 and May 25, 1983 to November 29, 1983 (Table 1). Initial spawning activity generally occurred at 17-22 C and 14-17 C in the spring of 1982 and 1983, respectively. The greatest number of newly spawned clams (≦1 mm) in the sediments occurred from July 19 through November 29, 1982 which suggested that no two peak spring and fall spawns had occurred. In 1983, however, two major spawns were evident during June 14 and September 29. These data have made it difficult to gauge major spawning conditions with river temprature. Determining the major fall spawning activity was even more difficult since highly abundant juveniles in the sediment were obtained at 17-22 C in 1981, 8-12 C in 1982 and 16-24 C in 1983. At the Celco Plant, monthly monitoring of juvenile clams in the sediments has been established in order to decide when to commence with a 28-day continuous chlorination after a major output of juvenile clams has been determined during spring and fall months.

Determination of spring and fall spawning seasons of *Corbicula* in the thermal discharge station cannot be identified. The number of juvenile clams sampled in the sediment was low during the three months when larvae ≦1 mm were found in 1981-1983 (Table 2). Water temperature ranges were high during the previous two weeks prior to sampling (e.g., 31-38 C in September, 1981, 37-41 C in July, 1982 and 32-37 C in June, 1983). Most likely, young juveniles were either transported from areas of lower temperature at the pumphouse located above this station or from infested sites within the plant allowing juveniles to grow in the heated effluent.

PRE- AND POST-MUCKING SEDIMENT PROCESS

Removal of sediments at the Celco pumphouse station appeared to have a positive effect in reducing adult clam densities in the New River. It appeared that the removal of sediment disrupted many clams but for only a short period of time. In general, a four-fold decrease in adult clam (≧ 10 mm) numbers was noted between sampling of July 1981 (pre) to July 1982 (post-mucking) (Table 1). Following 4 months after sediment removal adult clam numbers were almost the same between pre- and post-mucking activities when comparing data from November 11, 1981 and November 1982 (1,540 and 1,236/m, respectively). Although the overall amount of sediment removed at the pumphouse was ~ 70% effective, sampling of clams in sediment patches where mucking efforts had missed showed a recovery of adult densities by Novemer 1982 relative to the pre-mucking samples. Since the sediment removal process was only temporary it is not recommended as a future clam control procedure at other industrial installations.

The regularity of sediment removal at the pumphouse has not been decided. The overall mucking procedure is a time consuming process (e.g., two weeks) since sediments were removed in an area along the length of the pumphouse (45 m) to a distance of 30 m outward into the river. Clam numbers were highest within the first 10 m adjacent to the pumphouse with numbers diminishing rapidly thereafter (e.g., 335-2,345/m² at 10 m to 134-201/m² at 30 m). A repeat of sediment removal on a two-year basis is not being considered unless a return of high sediment deposition adjacent to the pumphouse becomes evident.

COMPARISON OF THERMAL DISCHARGE TRC CONCENTRATION TO FISH AVOIDANCE AND TOXICITY

Biocidal effective levels of total residual chlorine for a four-week continuous chlorination period have been assumed to be ≧0.50 to 1.0 mg/L (B. G. Isom, personal communication). It was difficult to maintain a chlorinated residual of 0.50 mg/L TRC throughout the plant even when the New River was high for appropriate dilution capabilities. At buildings nearest the chlorinator, Bldg 12 (275 m away), TRC was as high as 1.22 mg/L while at the farthest building (Office-Computer Building, 790 m away) TRC dropped to 0.36 mg/L (Table 3). Clam fouling problems were most frequent at the Office-Computer Building of Celco where chlorinated residuals were lowest. The maximum residual measured in the thermal discharge station was 0.27 mg/L TRC with a calculated - dilution factor ≦0.01 mg/L TRC entering the New River. TRC measurements 50 m below the effluent in the New River were not detectable due to the rapid dissipation of the chlorinated discharge with the assimilative capacity of the New River. Chlorine measurements through the 130-m distance of the thermal discharge channel to the New River confluence showed ~ 50% reduction in TRC.

The effects of TRC during continuous 28-day application were assumed to have minimal if any effects upon the fish populations in the New River near the Celco Plant because of rapid chlorine dissipation. The highest concentrations of TRC measured at the Celco Plant in the thermal discharge (0.27 mg/L and within the New River (≦ 0.01 mg/L - after calculated dilution factors) downstream of the plant can be avoided by fish. A majority of the fish species tested at the Glen Lyn Laboratory have avoided TRC between 0.05 - 0.20 mg/L TRC (Cherry and Cairns, 1982). Rainbow trout (*Salmo gairdneri*) have been reported to have a 48-hr LC50 response of 0.09-0.16 mg/L TRC to intermittent chlorination (Heath, 1977). However, no rainbow trout are found in this part of the New River or at the Glen Lyn Plant (Stauffer et al., 1976; Hocutt, 1974). Besides, rainbow trout have been reported to avoid "continuous" chlorination exposures for one-hour periods in the laboratory at 0.05-0.10 mg/L TRC

(Cherry et al., 1982). Even though TRC was continuously released daily into the thermal discharge station, chlorine concentrations would usually vary from one day to the next from $\geqq$0.06 to 0.27 mg/L. Some days, TRC was not detectable when the chlorinator malfunctioned. Since there was considerable manipulation of the Celco chlorinator during the four-week dosing period, the release of TRC into the New River was not at a constant rate, and at most times fluctuated on a daily or semi-daily basis depending upon the river flow.

For selected fish species inhabiting the New River, intermittent chlorine, acute toxicity values (TRC with high combined residual in mg/L) ranged from 1.50-2.37 for carp (*Cyprinus carpio*), 0.41-0.65 for spotfin shiner (*Notropis spilopterus*), 1.23-3.00 for bluegill (*Lepomis macrochirus)*, 1.15-2.87 for white bass (*Morone chrysops*), 0.65-0.78 for channel catfish (*Ictalurus punctatus*), 0.36-1.09 for white sucker (*Catostomus commersoni*), to 1.26-2.03 for mosquitofish (*Gambusia affinis*) (Seegert et al., 1979; Cherry et *al.*, 1982). Other reviews by Mattice and Zittel (1976) and Turner and Thayer (1979) provided toxicity data on continuous, 96-hour chlorine exposures which are not environmentally realistic to the fluctuating TRC released at the Celco Plant. The above toxicity concentrations of TRC, along with avoidance capability indicate that no harmful effects should occur for fish from the Celco Plant TRC effluent that approached the 0.01 mg/L calculated level in the immediate New River receiving system. In addition, no documentation of fish kills have been reported from the 28-day continuous procedures during 1982-1983.

Acute effects of chlorinated residuals to aquatic, benthic invertebrates ranged from 0.009 mg/L for *Isonychia*, 0.396 mg/L for *Hydropsyche*, to 0.502 mg/L for *Stenonema* (Gregg, 1974). Acute toxicity of chlorine to snails (*Nitocris* and *Physa*, respectively) ranged from 0.044 and 0.258 mg/L (Mattice and Zittel, 1976). Since the chlorination residuals were not detectable at Stations 2, 3, and 4, it is assumed that the continuous TRC released has no measurable impact upon these invertebrate communities, especially when diversity was highest at the two stations closest to potential chlorine influence.

BENTHIC INVERTEBRATE SAMPLING

Benthic invertebrate sampling in the New River, three times before continuous chlorination and seven thereafter during 1981-1983, showed no observable impact of residual chlorine on the invertebrate communities in the stations sampled immediately within the Celco Plant (Tables 4-6). Station 2 was closest to the potential influence of chlorinated discharge; however, diversity of aquatic invertebrates was higher (3.325) after chlorination than before (3.233). Taxon diversity indices between pre- and post-chlorination were similar at Station 3 (e.g., 2.905 versus 2.697, respectively). Diversity values at Station 4 (~ 1.0 km below Station 3) were as comparable before and after chlorination (2.962 to 2.698, respectively); however, chlorinated effluent had been completely diluted within the first 50 m of the river before reaching this station. The average abundance of insect orders and other invertebrates had changed due to seasonal differences after chlorination or due to high numbers of *Corbicula* having been collected downstream in Station 4 which influenced low diversity indices (Tables 5-6). It is difficult to determine whether the reduction in diversity at this station was due to natural clam invasion or from Celco Plant discharges. Since *Corbicula* have only recently invaded this river system, the shift to lower diversity downstream for selected insect taxa may have been attributed to the increase in *Corbicula* densities. In all stations sampled upstream, within and downstream of the Celco Plant, a corresponding increase in clams resulted in a decline in many major insect groups especially at Station 4 during 1982. During 1983, however, clam densities in the New River declined downstream at Station 4 from 43.3% in 1982 to 21.9% in 1983. Insect orders (Ephemeroptera, Trichoptera, Coleoptera, Diptera) showed a major increase in abundance in 1983.

DISCUSSION OF OTHER APPROACHES FOR *CORBICULA* CONTROL

Use of mollusk biocides may have detrimental effects upon fish and invertebrate fauna in the New River receiving system below the thermal discharge station and so was dismissed. Bayer 73 (2-hydroxy-5, 2' dechlor-4' nitro benzanilide) has been reported to produce a 24-hr TL_m of 0.18 mg/L to bluegill sunfish (Sinclair and Isom, 1963). The ability of *Corbicula* to "clam up" and thus "avoid" the toxic consequences of these molluscides may result in far greater ecological hazards to the other biota in the receiving system.

The potential of heated water backflushing through the Celco Plant was not attempted due to production protocol and the concern for clogging of production systems with dead clam shells. Use of industrial anti-flocculants to remove sediment accumulation was not attempted. We assumed that Asiatic clam infestation occurs in dead pipe spaces where the clam can congregate into sediments, not within rapidly flowing pipe lines. Other industrial biocidal chemicals (hypobromous acid in addition to reduced chlorination) are available and are effective for slime (e.g., bacterial, fungal, algal accumulations) control, but their usefulness for *Corbicula* biocidal effectiveness is unknown. The use of a counter-current pump system has merit in reducing sediment and detrital (and potential clam larvae and shells) material at the initial pumphouse installations, but the cost in implementing and maintaining this pumping system relative to *Corbicula* control may be too high due to the high daily water volume used by the plant. More research in the above arenas is recommended before any can be utilized as supportive measures of chlorine in controlling the Asiatic clam.

A major concern at the Celco Plant is that no holding ponds exist between the thermal discharge and the river. If ponds were available, they could dilute the chlorinated residual before it enters the New River. For this plant, a biocidal agent needed is one with highly ephemeral characteristics that can be diluted, absorbed, precipitated or assimilated as a consequence of the assimilative capacity of the New River. Total residual chlorine has been selected as the most appropriate biocidal agent currently available since it meets the above specifications. The use of chlorine as a biocidal agent for *Corbicula* control is suggested for industrial installations that lack holding ponds to the receiving river system if a data base of chlorine toxicity with avoidance behavior of fish and/or concurrent invertebrate field surveys are available.

SUMMARY

Proliferation of *Corbicula* in the New River at the Celco Plant pumphouse station, Celanese Corporation, Narrows, Virginia, resulted in a major infestation of larval clams with biofouling disruptions in production and air conditioning condenser systems during 1981-1982. Production procedures such as deicing practices of travelling screens at the pumphouse probably allowed *Corbicula* to survive adequately during the winter and propagate in spring. Dead pipe spaces and reserve river water holding towers within the plant enabled the clam to proliferate further resulting in biofouling incidents in production and air conditioning condenser systems. These systems either have been removed or periodically flushed twice each year to remove sediment and juvenile clam presence. During 1983, six of the seven major clam fouling incidents were due to dead clam shells which showed that continuous 28-day chlorination had a positive effect in minimizing *Corbicula* infestation after four treatments in 1982-1983. Control measures for *Corbicula* carried out in 1981-1983 included documentation of spawning occurrences in the New River sediment coupled with four-week continuous chlorination at a target, in-plant concentration of ≧0.50 mg/L TRC to minimize larval clam infestation. Much of the sediment accumulation at the river pumphouse had been removed by a mucking-bilge pump operation in order to reduce the dense, resident clam population from releasing larvae into the plant. However, this procedure had a short-term effect of four months in reducing the adult clam population in the river sediment. The overall approach by the Celco Plant for *Corbicula* control is both traditional and different. Continuous chlorination for four weeks at anticipated peak, biannual spawning seasons normally has been used to ensure clam biocidal effectiveness. Concommittent field sampling of macro-invertebrate populations found upstream, adjacent to and downstream from the plant, to ensure that residual chlorine released from the plant was not harmful to the biota in the New River is unique. Review of fish responses to chlorinated residuals (e.g., avoidance behavior relative to toxicity concentrations of chlorine) in the literature has shown no effect (e.g., documented fish kills) from the use of chlorine to control *Corbicula* at the Celco Plant other than potential avoidance reactions.

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ASIATIC CLAM CONTROL BY MECHANICAL STRAINING AND ORGANOTIN TOXICANTS

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ABSTRACT

Corbicula (Asiatic Clams) control technologies include mechanical/physical, chemical, and biological controls. Large in-line strainers have been used successfully to filter adult clams from circulating water systems. Fine mesh screens with 0.5 mm mesh have recently been evaluated in the United States for the protection of fish eggs and larvae. Screens with 0.2 mm mesh may be feasible to screen clam larvae for small flow rates. Very fine mesh screens require very low flow velocities resulting in large intake structures. The Electric Power Research Institute (EPRI) has investigated the effectiveness of tributyl tin fluoride (TBTF) pellets to control clam larvae, juveniles, and adults by conducting preliminary tests at Murray State University. The test results show TBTF to be highly toxic to all stages of *Corbicula*.

Asiatic clams (*Corbicula*) are spreading rapidly through the United States, causing flow blockage and reliability problems in many freshwater circulating and service water systems. The Nuclear Regulatory Commision (NRC) has recently requested plant operators to determine whether the Asiatic clams are present, to measure the flow rates in systems that have clams, and to outline future preventative and detection methods. The clams in once-through cooling systems are usually found at the bottom of the intake structure, in the intake tunnels, at the condenser water boxes, in the condenser tubes, in fire-protection lines, and in the discharge canals. In closed-cycle systems, clams often accumulate in cooling tower basins and cooling ponds.

Control techniques include mechanical/physical, chemical, and biological controls (Mattice 1983). Biological control by predators have not yet proven to be effective. Chemicals such as chlorine have been used with some success. Oxygen scavengers such as sodium-bisulfite and hydrogen sulfide have been used to control clams at intakes. Chemicals have not been widely used because of environmental regulations. At some plants, clams are removed physically on a periodic schedule. However, physical removal has not proven to be very effective and should be used in combination with other mechanical and chemical controls. Thermal backwash is one of the most promising physical controls. However, existing freshwater power plants are usually not equipped with thermal backwash capabilities because of the recent advent of the Asiatic clams problem.

The Electric Power Research Institute (EPRI), under Project RP1689-9, is monitoring the performance of several mechanical straining systems at existing power plants and has investigated the use of tributyl tin fluoride (TBTF) pellets to locally control Asiatic clams in pipelines or intake bays.

This paper discusses the results of these investigations in order to transfer these technologies to power plant application.

MECHANICAL STRAINING

To exclude clam larvae from entering cooling water systems, mesh openings as small as 0.2 mm (200 μm) are required. Very fine mesh screens with openings as small as 0.001 mm (1 μm) have been used in tertiary wastewater treatment plants. The flow velocities associated with these very fine mesh screens are about 0.3 cms (0.01 fps) with the

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screen traveling continuously at about 15 mpm (50 fpm). Very fine mesh screens are not practical to use in screening circulating water systems because they would require many screens and very large intake structures. However, for makeup or service water systems, fine mesh (0.2 mm) screening is operationally feasible, although costly.

Recently, a fine mesh screen (Mussalli *et al.*, 1981) with mesh of 0.5 mm (500 μm) and 50 percent open area has been tested successfully for the protection of fish eggs and larvae at the Big Bend Station of Tampa Electric Company. The screen operated continuously with flow velocities of 15 cms (0.5 fps) and 30 cms (1 fps) and at speeds ranging from 2 mps (7 fps) to 8 mps (28 fps). The encouraging test results have resulted in the incorporation of screens with 0.5 mm mesh for fish eggs and larvae protection at the Big Bend Station in Florida and at the Prairie Island Nuclear Station on the Mississippi River. Another traveling screen of a center flow design with 1 mm mesh (1000 μm) has also been operating successfully at the Barney Davis Station of Central Power and Light in Corpus Christi, Texas. The mesh is nylon with about 50 percent open area.

Continuously traveling screens with 0.2 mm mesh either of metallic or synthetic fabric and designed with low approach velocities of about 3 to 6 cms (0.1 to 0.2 fps) could be operationally feasible for small flow rates. This concept, however, should be tested in situ prior to prototype application and would result in large intake structures requiring five to ten times more traveling screens than conventionally used.

In-line strainers located between the pump and the condenser or heat exchangers also can be used to control juvenile and adult clams (Mussalli and Diaz-Tous, 1983). This technology is of German and French origin and has recently begun to be used in the United States. Currently, there are large strainers in ten U.S. power plant cooling water pipelines. For a large diameter pipe (up to 2.8 m; 110 in.) with a capacity of 15.5 m³/s (245,000 gpm), a debris filter of a perforated stainless steel screen (mesh size ranges from 2.8 mm (1/9 in.) to 9.5 mm (3/8 in.) concentrically aligned within a steel casing as shown on Figure 1 can be used. The filters can be installed inside the turbine building at the pump house or in the yard between the pump and the condenser employing a variety of mounting positions.

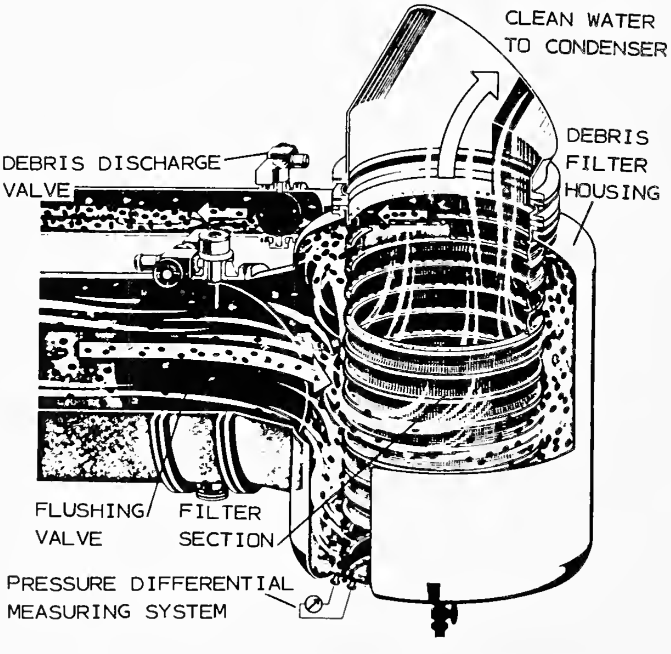

Fig. 1. Cutaway drawing of a typical amertap debris filter.

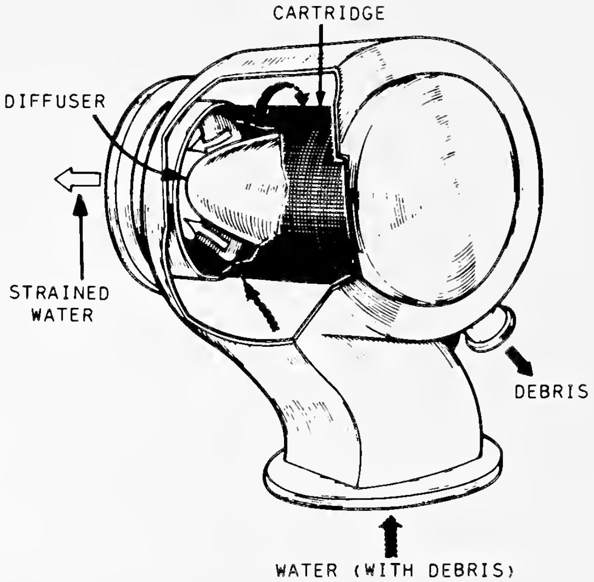

Fig. 2. Shellfish strainer. Source: Beaudrey/COGENEL.

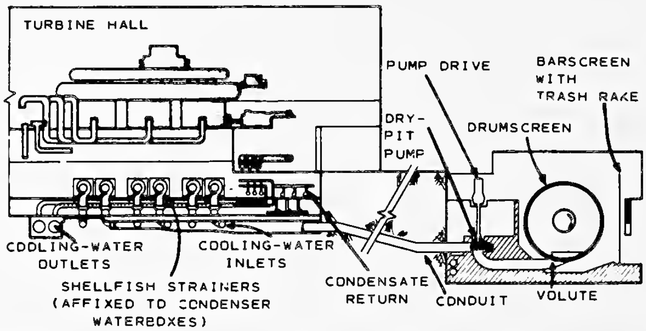

Fig. 3. Integrated filter strainer design at the Paluel Nuclear Station (France).

The ability of these filters to remove entrained debris and biogrowth (such as mussels, barnacles, and Asiatic clams) has been demonstrated at several power plant locations including Southern Califorina, North Carolina, Ohio, and Connecticut.

The French also have used self-cleaning strainers that can be installed at the entrance to the water box. The strainer has a volute-shaped shell as shown in Figure 2. One feature of this design is the absence of moving parts.

The integrated filter/strainer design to supplement intake screening as it is used at the Electricite de France Paluel

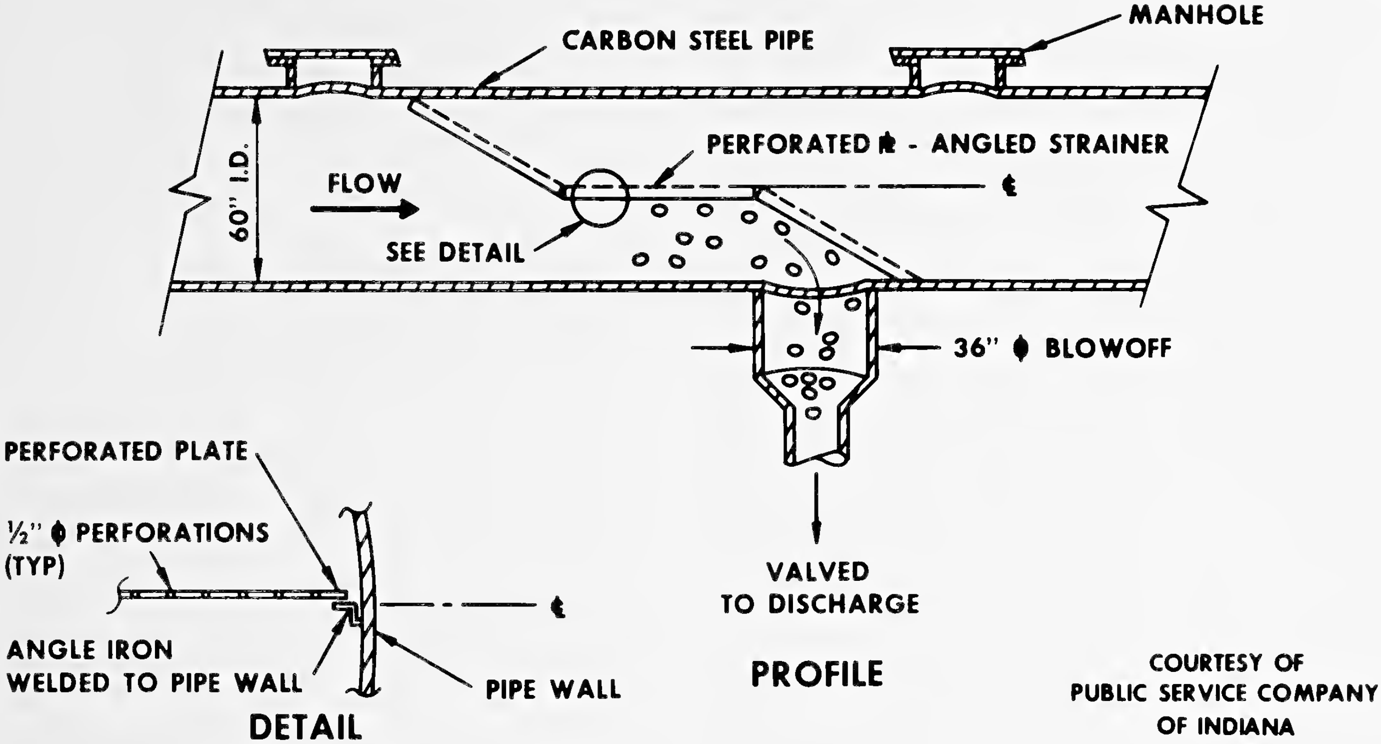

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Fig. 4. Angled strainer for Asiatic clams.

(1300 MW PWR) Nuclear Station is shown in Figure 3.

One advantage of the filter/strainer is that it improves condenser performance when used in conjunction with a tube cleaning system.

Public Service of Indiana at its Cayuga Station has devised an in-line angled strainer to divert adult clams to a blowoff bypass, as shown in Figure 4. This design is simple and has been operating successfully. It is adaptable, however, to clean circulating water flows such as in closed-cycle systems where debris is a minimum.

The Electric Power Research Institute is monitoring the performance of several large filters of German design at the South Bay Station of San Diego Gas & Electric Corporation, at Sammis Staion of Ohio Edison Company, at the Nueces Bay Station of Central Power and Light, and at the Jack Watson Station of Mississippi Power Company. Another filter of French design used to filter seaweed and grasses is also being monitored in Puerto Rico to determine any operational problems and solutions.

OGRANOTIN TOXICANTS

Tributyl tin fluoride (TBTF) in parts per billion or parts per trillion concentration may provide an economical mechanism for controlling clam larvae; in higher concentrations, TBFT may kill adult clams in intake structures and makeup ponds. The TBTF pellets can be located in low velocity areas of intake structures where clams congregate, in service water pipe laterals, in fire protection pipes, and can be dispersed in cooling ponds. The organotins will leach out slowly to locally treat clams in the flow. The advantage of a controlled release mechanism lies in its simplicity of application and low maintenance cost. The effects on the environment will be minimized, because only a small localized volume of the flow will be exposed to organotin.

Under Project RP-1689-9, EPRI sponsored preliminary tests to determine the effectiveness of TBTF pellets on *Corbicula* (Asiatic clams) larvae and adults in flowing and static conditions (EPRI 1984). Continuous flow and static tests were conducted at Murray State University in 1983. The compound tested in this EPRI study was a porous plastic matrix containing 30 percent by weight of TBTF and designated ECOPRO 1330-S by Environmental Chemicals, Inc. The solubility of TBTF in water at 20°C is only 0.4 mg/l, but within the plastic matrix the TBTF hydrolyzes to tributyl tin oxide (TBTO), which has a solubility of about 10-40 mg/l (Himel 1983).

The ECOPRO 1330-S contained ferric oxide to give it a density slightly greater than that of water. It was provided as cut or ground pellets of irregular shape, ranging from 3 to 6 mm in diameter. According to Himel (Personal Communication), the release rate of TBTO from freshly prepared pellets when placed in water would decrease for several weeks, then increase slightly to a constant rate that would be maintained for approximately 2 years. This constant release rate under continuous flow, unsaturated conditions, was estimated to be 0.285 μg/min/g pellet. Calculated concentrations of TBTO used in this EPRI study were based on this estimated release rate.

CONTINUOUS FLOW TEST. This test exposed clam larvae and adults to water that was briefly in contact with

TBTF pellets in a continuous flow system to simulate a water intake or cooling water system in a power plant. The objective was to determine the lethal concentration at which 50 percent of test animal die (LC_{50}) of larvae and adult *Corbicula*.

In these tests filtered lake water was pumped at a constant rate through containers with different amounts (by weight) of TBTF pellets and allowed to flow into 6-liter glass tanks containing adult *Corbicula*. Concurrently, a small fraction of the treated water was diverted into 10 ml tissue culture dishes containing juvenile clams ranging in age from 1 to several weeks from the time of release. The continuous flow of water provided a constant concentration of TBTO under uniform conditions at 20°C (±0.5°).

The continuous flow system with the chemical containers is shown in Figure 5. Six containers were used with combinations of the following weights of pellets: 27.7 g, 15.6 g, 8.76 g, 4.92 g, 2.77 g, 0.0876 g and a control with no pellets. Flow rates were adjusted to either 250 ml/min or 300 ml/min. The calculated concentrations of TBTO in each test based on expected release rate and volume of low are presented in Table 1. Typical continuous flow test results are given in Tables 2 and 3.

Water supplied for all tests was obtained from Kentucky Lake, Tennessee River, from where it was pumped about 50 m into the Hancock Biological Station of Murray State University where the tests were conducted. The water was filtered to remove large zooplankton and sediment, but small phytoplankton remained to provide food for the clams. A constant level reservoir tanks of 285 l (75 gal) was used to maintain a constant head for the gravity flow system. A heater in the tank maintained the temperature at 20°C (±0.05°) Aeration maintained the dissolved oxygen concentration near saturation.

Larval and early juvenile *Corbicula* are microscopic, ranging in length from 0.225 to 0.25 mm. Because of their small size and mobility they require special handling techniques for bioassay studies. Generally, larvae or juveniles must be kept in containers separate from adults because adults may release additional larvae during the test and these might become confused with original test individuals at a similar development state. A convenient method of exposing the juveniles was developed for the tests. Treated water was diverted at a T-connector (as shown in Figure 5) through tubing, and pumped by Buchler peristatic pumps into 10 ml tissue culture dishes at a rate sufficient to maintain good mixing but not so great as to wash out the juvenile clams.

Initially, each test was planned to be conducted for 96 hours, and the 96 hour LC-50 and 95 percent fudicial limits calculated using Probit Analysis (Finney 1964). However, as the study progressed it became evident that the high variability in mortality made it necessary to extend some of the tests in an attempt to obtain 100 percent mortality at the highest concentration. Statistical analysis was accomplished by using the SAS program (SAS 1989) at the Murray State University Computing Center. Where only one intermediate concentration occurred between 100- and 0-percent mortality, the data could not be analyzed by the probit method. Tables 2

Table 1. Weights and calculated concentrations of TBTF pellets at each flow rate used in tests.

	Volume of Flow			
	250 ml/min		300 ml/min	
	Concentration			
Weight(g) of ECOPRO	µg/l	log(µg/l)	µg/l	log/(µg/l)
27.7	31.6	1.50	26.3	1.42
15.6	17.8	1.25	14.8	1.17
8.76	10.0	1.00	8.33	0.92
4.92	5.62	0.75	4.67	0.67
2.77	3.16	0.50	2.63	0.42
0.867	1.00	0.00	—	—
0.0867	0.10	-1.00	—	—
0.0	0.0	—	—	—

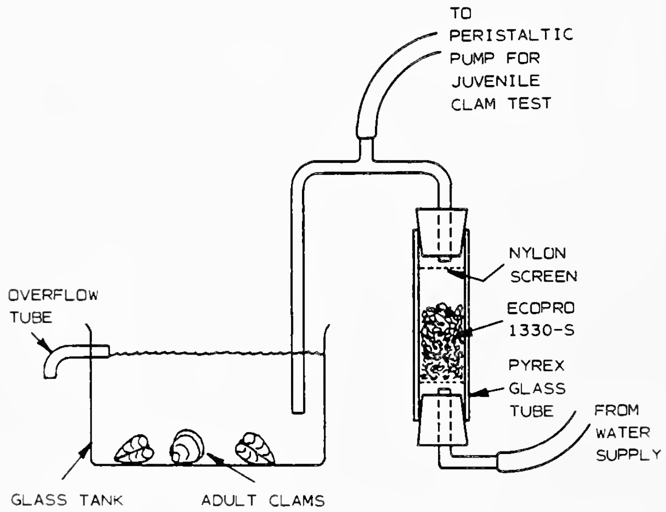

Fig. 5. Continuous flow system with chemical container and exposure tank for adult clams.

Table 2. Adult clam mortality during continuous exposure to TBTO from September 20 to October 7, 1983.

		Number of Dead Clams				
Calculated Dose (µg/1)	Number of Clams	24 hrs	48 hrs	72 hrs	96 hrs	192 hrs
31.6	10	0	4	8	10	10
10.0	10	0	0	0	0	10
3.2	10	0	0	0	2	4
1.0	10	0	0	0	0	1
0.1	10	0	0	0	0	0
0.0	10	0	0	0	0	0

Note: 8 day LC-50: 2.4 µg/l; 8 day LC-99: 60.5 µg/l.

and 3 present the typical results of the continuous flow tests. Where data were sufficient for statistical analysis, the LC-50 and LC-99 are given at the bottom of the table.

The time required for adult clams to succumb is longer than for juveniles, but low concentrations in the range for 5 to 20 μg/l appear to be lethal. These data indicate a high toxicity of TBTO to *Corbicula.*

STATIC TEST. This test exposed clam larvae and adults to water in contact with TBTF pellets under static conditions, to simulate a situation in which a bag or canister of pellets is placed in a tank, screenwell, crib-house, fire protection piping, etc, and filled with water. The objective of this test was to estimate a diffusion rate of TBTF from pellets using information on toxicity determined in the continuous flow testing.

Five 6-liter glass tanks were each filled with 4 liters of lake water. In Tanks 1 and 2, 0.5 g of ECOPRO 1330-S was placed in a section of PVC pipe with both ends opened and covered with nylon mesh which allowed water to circulate through the pipes while retaining the ECOPRO pellets. In Tanks 3 and 4, one end of a "U" shaped PVC was open, and the other end closed with a PVC cap with 0.5 g of ECOPRO 1330-S held in the capped end by a mesh nylon screen. In this configuration the TBTO would have to diffuse 40 cm through stagnant water before contacting the water in the tank holding the clams. Tank 5 was used as a control with no TBTO pellets.

Table 3. Juvenile clam mortality during continuous exposure to TBTO from September 29 through October 3, 1983.

Calculated Dose (μg/l)	Number of Clams	Number of Dead Clams			
		24 hrs	48 hrs	72 hrs	96 hrs
31.6	20	9	16	20	20
10.0	20	4	10	19	19
3.2	20	2	2	3	8
1.0	20	0	0	1	1
0.1	20	0	0	0	0
0.0	20	0	0	0	0

Note: 4 day LC-50: 3.5 μg/l; 4 day LC-99: 17.4 μg/l.
95% fiducial limits: LC-50: 2.6-4.8; LC-99: 10.4-51.3

Table 4. Adult clam mortality during exposure to TBTO under static conditions.

Tank No.	Numbers of Clams	Number of Dead Clams Days of Exposure								
		1	2	3	4	5	7	22	27	40
1	10	0	0	0	0	10	—	—	—	—
2	10	0	0	0	0	10	—	—	—	—
3	10	0	0	0	0	0	0	0	0	0
4	10	0	0	0	0	0	0	0	2	2
Control	10	0	0	0	0	0	0	0	0	0

Note: Tanks 1 and 2 with 0.5 g ECOPRO in open 5-cm long PVC pipe

Tanks 3 and 4 with 0.5 g ECOPRO in 40 cm-long "U" shaped PVC pipe closed at one end where the chemical was located.

Ten adult clams were placed in each tank, and gentle aeration was provided to maintain sufficient dissolved oxygen and circulation. Juvenile clams were placed in 10 ml tissue culture dishes which were placed in 50 ml Pyrex beakers and carefully submerged in the tanks.

In the typical static test, 15 juveniles (1 to 2 weeks old) and 10 adults were placed in each tank. Clam mortality occurred only in Tanks 1 and 2. After 24 hours most of the veliger larvae in Tanks 1 and 2 were dead and development of the surviving larvae had stopped. One juvenile was dead in Tank 2. In 48 hours all of the veligers were dead in both tanks, and two juveniles were dead in Tank 2. After 96 hours two juveniles were dead in Tank 1, and six in Tank 2. Adult clams were moribund and had an accumulation of thick mucus around the edge of the shells. After 120 hours all the adults and juveniles were dead in Tanks 1 and 2.

No deaths occurred in Tanks 3 and 4 even after 31 days. At that time the "U" stoped pipe in Tank 4 was tilted emptying some of the accumulated TBTO into the tank. Five days later two adult clams were dead. The undisturbed Tank 3 showed no signs of toxicity after 40 days (Table 4).

These static tests demonstrate that circulation is required to dissolve and distribute TBTO from ECOPRO 1330-S. Diffusion alone would not be sufficient to treat a stagnant body of water with TBTO from ECOPRO. Some water movement is necessary.

ORGANOTIN TOXICANTS TEST SUMMARY. The observed response of *Corbicula* to TBTO indicates certain characteristics which make TBTO a favorable molluscicide. In general, if a toxic substance is also irritating, such as chlorine, the clams tend to close and avoid contact with the substance for as long as possible. This results in a long treatment period before the clams begin accumulating a toxic dose. In the case of TBTO, however, at low concentrations of 1 to 10 μg/l the clams remained open and continued siphoning water. Perhaps this allows an accumulation of a lethal dose more rapidly. In fact, increasing the concentration above 30 μg/l might not decrease the time for 100-percent mortality because clams would remain closed much of the time.

The lake water used in the tests contained many small rotifers and protozoa. These were rapidly killed at concentrations estimated to be greater than 1 μg/l. At concentrations near 0.1 μg/l the activities of the microfauna appeared normal.

Tributyl tin oxide is highly toxic to *Corbicula* adults, juveniles, and larvae. At low concentrations (1 to 10 μg/l) it apparently causes little or no avoidance response. This allows the clams to accumulate a lethal dose rapidly.

The variability in the results, small sample size, and apparent decline in release rate of TBTO from ECOPRO 1330-S during the tests precluded a precise determination of the concentrations required to control *Corbicula.* If the estimated release rates used to calculate the concentration of TBTO were reasonably correct, then a continuous exposure to 10 to 30 μg/l for 1 to 2 weeks would kill 100 percent of adult and juvenile *Corbicula*. The juveniles would succumb more quickly than the adults. Larval development and transformation was stopped at concentrations below 10 μg/l.

TBTO from ECOPRO 1330-S requires some water circulation to be effective in controlling *Corbicula*. The circulation speeds solution and distribution of TBTO. The diffusion rate from ECOPRO pellets in static water was not sufficient for lethal concentration of TBTO to travel 40 cm in 40 days.

The EPRI study demonstrated the extreme toxicity of tributyl tin oxide to *Corbicula*, which warrants further investigations of the potential of TBTO as an agent for controlling *Corbicula* in industrial and electric power facility water systems. It was recommended to EPRI that a more extensive study be conducted before or concurrently with an actual trial application of ECOPRO 1330-S in a power plant water system.

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CORBICULA POPULATION MORTALITIES: FACTORS INFLUENCING POPULATION CONTROL

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ABSTRACT

Several factors potentially affecting population density in *Corbicula fluminea* are reviewed. These include thermal and oxygen tolerance, silt loads, acidic waters, pollution, bacterial and viral infections, parasites, predators, interspecific competition, genetic changes, and intraspecific competition. All of these factors may influence clam densities and population structure in certain cases. However, it is hypothesized that overpopulation with its attendant strain on energy supplies and stress on individuals is the major cause of the commonly observed mortalities while genetic change through the process of selection may be a major factor in establishing different life history characteristics in different populations.

Since the discovery of *Corbicula fluminea* (Müller) in the United States in 1938 (Burch, 1944), there have been numerous reports of its range extension and population increases. Concomitantly there have been reports of high mortalities during which many dead clams were observed floating ashore or being caught on screens of industrial water intakes (Sinclair and Isom, 1963).

Several explanations are generally given to account for the rapid population growth observed when *Corbicula* invades a new region. These include high fecundity of monoecious individuals, free-living planktonic larvae, absence of naturally adapted predators, and the ability to exploit a variety of habitats. As one would expect in an organism with these attributes, *Corbicula* frequently becomes the dominant benthic species shortly after invasion, increasing to densities of thousands per m^2 in only a few years (Gardner *et al.*, 1976; Eng, 1979; Sickel, 1979). This rapid population growth obviously cannot continue indefinitely, and the subsequent population may demonstrate varying degrees of success in terms of density, size distribution and ability to survive as native species adapt to its presence. The focus of this paper is on the period of adaptation which follows the initial invasion by several years or decades. A review of some of the possible factors of population control is presented with an emphasis on mass mortalities. Several case histories are presented from the Tennessee and Cumberland Rivers and their respective reservoirs Kentucky and Barkley Lakes.

ETIOLOGY OF *CORBICULA* MORTALITIES

Various factors have been proposed to account for the regulation of *Corbicula* populations and the reported mass mortalities at different times and in different situations. Proposed factors include excessively high or low temperature, low dissolved oxygen, silt, acidic waters, pollution, bacterial or viral infections, parasites, predators, competition, and genetic changes.

THERMAL AND OXYGEN TOLERANCE

Generally, high temperatures contribute to low dissolved oxygen levels in bottom waters of rivers and lakes because of the lowered solubility of oxygen and the increased respiratory demands. McMahon (1979) demonstrated that *Corbicula fluminea* is poorly adapted to high temperature and low oxygen. In his experiments, clams were severely stressed above 25 - 30°C, and Mattice and Dye (1975) indicated a long-term thermal tolerance of 34°C. They reported a lower temperature limit of below 2°C. Both high temperature with reduced oxygen and low temperature may be related to recent mortalities in the Tennessee, Cumberland, and Ohio Rivers. Horning and Keup (1964) reported a decline of *Corbicula* from 290/m^2 to from 0 - 10/m^2 in 1963 in the Ohio River at Cincinnati. They speculated that the cold winter during which the Ohio River was frozen over for 7 days was the cause of the die-off.

The winter of 1977 in western Kentucky was unusually cold, and ice up to 7.5 cm thick covered the embayments of Kentucky Lake. During the week prior to February 5, 1977, the lake level was lowered about .6 m. This broke up much of the ice and exposed the shoreline to freezing temperatures. On 5 February at the Murray State University Hancock

Biological Station, many dead *Corbicula* bodies were observed washing ashore. The tissue appeared fresh, and examination revealed completely intact bodies with no eggs or larvae in the gills, no developing eggs in the gonads, and no crystalline styles. Some gill water tubes were filled with clumps of clay. It was assumed that these washed in as a result of the churning action of the waves along shore rather than entering the living clam and contributing to death. The cause of death was probably exposure to freezing temperatures, and the bodies were probably beaten from the shells by wave action although no shells were observed.

On 4 April 1978 an extensive bed of *Corbicula* was discovered in the channel at a depth of 20 m at Cumberland River mile 67.0 in Barkley Lake, Kentucky. This bed consisted of mostly large clams 35 - 45 mm in length at a density of 400/m^2. About 10% of the clams were recently dead with tissue just beginning to decay, and about 20% of the total were old empty shells. Less than 10% were juveniles under a year old. A continuous decline in numbers occurred with extensive mortalities observed until November 1981 at which time there were no more live clams (Table 1).

Table 1. *Corbicula* at Cumberland River mile 67.0, Barkley Lake, Kentucky.

Date	Density Alive (No./m^2)	% Alive
4 April 1978	400	90
16 July 1978	333	?
4 March 1979	160-200	?
18 August 1979	172	55
6 March 1980	200	?
21 May 1980	65	18
25 October 1980	19	12
16 November 1981	0	0

On 18 August 1979 and again in July 1980, numerous "floaters" were observed in Barkley Lake in the vicinity of the bed at CRM 67.0. These were dead *Corbicula* 35 - 40 mm in length. The shells were tightly closed with decomposing tissue producing gas to make them buoyant. Some were so recently dead that they had no unpleasant odor. Oxygen measurements revealed D.O. levels of about 5 mg/l, but temperatures were near 30°C. Sufficient monitoring was not conducted to determine if D.O. levels may have been significantly lower at night. For the past several years near anoxic conditions have been recorded during summer months at other locations in the deepest channels in both Barkley and Kentucky Lakes. The combination of low D.O. and high temperature may have contributed to the demise of the population.

SILTATION

Bickel (1966) reported annual spring mortalities of all age classes of *Corbicula* in the Ohio River at Louisville, Kentucky, during the month of March. He attributed those die-offs to suspended silt accompanying spring floods. Siltation in some of the channel regions of Kentucky and Barkley Lakes has reduced the habitat available to *Corbicula* as well as other mollusks. Where currents have been eliminated by altered hydrodynamics resulting from Kentucky and Barkley Dams, an extremely fine, soft, and sometimes flocculent sediment has accumulated which apparently does not support heavy shelled mollusks.

ACIDIC WATERS

Kat (1982) reported a low resistance to shell dissolution by acidic waters of *Corbicula* compared to unionid mussels. According to Kat, this difference results from the presence of conchionlin layers in the unionid shells. Without these layers in the *Corbicula* shell, once the periostracum wears off, usually in the region of the umbo, the shell dissolves rapidly in acidic waters. When a hole breaks through the shell Kat assumed that death would result from the invasion of microorganisms. Kat indicated that shell dissolution might be a major source of mortality for *Corbicula* over about 3 years old in Mosquito Creek, Florida, which had a pH of 5.6. In the Tennessee and Cumberland Rivers the pH is near neutral, and little shell dissolution has been observed.

BACTERIAL, VIRAL, AND PARASITIC INFECTIONS

On 9 May 1980, Tennessee Valley Authority biologists investigated a reported mussel kill in the Tennessee River in the vicinity of miles 407-413, Jackson County, Alabama (TVA 16 May 1980 memorandum from Robert T. Joyce to Gordon E. Hall). They found *Corbicula* bodies floating throughout the 8.8 km section of the river. A fisherman indicated that dead clams had been floating by for a week. Divers examined mussel beds, and none of the native unionid mussels appeared affected. The TVA biologists did not determine the cause of death, but they speculated that it was a form of bacterial or viral infection specific for *Corbicula*. They indicated that periodic die-offs of *Corbicula* are reported once or twice a year.

Al Scott (1980 personal communication) at the Auburn University Fisheries Laboratory examined recently dead *Corbicula* and concluded that 1) bacteria had not caused death, 2) histological sections indicated no parasites, and 3) electron microscopy revealed no viral inclusions.

In May and June 1980 many of the *Corbicula* from Barkley Lake CRM 67.0 were infested with *Chaetogaster limnaei*, a naidid oligochaete (Sickel and Lyles, 1981). *Chaetogaster* occurred in over 80% of the *Corbicula* with the highest intensity in one clam being 167 worms. By 15 August no more *Chaetogaster* could be found. The effect of *Chaetogaster* on *Corbicula* is uncertain. Eng (1976) first reported *Chaetogaster limnaei* in *Corbicula* from California and indicated that infestation was seasonal with the highest prevalence (87%) occurring from March through May. He noted no evidence of parasitism and reported a low intensity of only several worms per clam.

In the study by Sickel and Lyles (1981), the symptoms of disease observed in the dying clams, both those with and without *Chaetogaster*, included the following:

1. Loss of tissue mass, clams appeared emaciated.
2. Soft, watery tissue, lack of normal firmness, and greater tissue transparency.
3. Thin, transparent mantle had secreted rough nodules on inner shell surface.

Samples of dying *Corbicula* were collected in June 1980 from Barkley Lake (CRM 67.0) and sent to the Shellfish Disease Laboratory, National Marine Fisheries Service, Oxford, Maryland. The clams were examined by C. Austin Farley and Fred Kern (1980 personal communication). They reported much tissue necrosis and secondary bacterial decay. No indication of viral infection was found, and they reported no parasitism. The only unusual findings were large concretions of amorphous material in the intestinal tubule and gonads.

POLLUTION

Evidence of eutrophication in Kentucky and Barkley Lakes is seen as increasing areas of anaerobic water in the deep channel. The sources of nutrients contributing to this condition are diffuse. Contributing factors are probably housing developments, agricultural runoff, and municipal waste. This eutrophication and the associated anaerobic water have probably contributed to the demise of the *Corbicula* beds in Barkley Lake.

Pollution in other regions of the world has been detrimental to *Corbicula*. Chen (1976) reported that industrial pollution has eliminated *Corbicula fluminea* from many lakes and streams in Taiwan where the clam is used for food.

PREDATORS

The major predators of young and adult *Corbicula* are fish. Britton and Murphy (1977) reported shells up to 5 mm in length from a redear sunfish, *Lepomis microlophus*; 3 mm from a spotted sucker, *Minytrema melanops*; and 3-5 mm from a drum, *Aplodinotus grunniens*, from north Texas. Sickel *et al.* (1981) reported that drum, blue catfish, *Ictalurus furcatus*, and carp, *Cyprinus carpio*, in the Tennessee and Cumberland Rivers consumed large numbers of *Corbicula* as well as young mussels. Minckley *et al.* (1970) reported consumption of *Corbicula* by smallmouth and largemouth buffalofishes, *Ictiobus bubalus* and *I. niger*. In addition to drum, Dreier *et al.* (1981) indicated that bluegill, *Lepomis macrochirus*, and channel catfish, *Ictalurus punctatus*, regularly consumed *Corbicula*. They presented evidence suggesting that fish predation was a major cause of mortality and reduced clam density in Lake Sangchris, Illinois. Areas of gravel seemed to provide some protection for young clams from predation.

Although fish may play a minor role in regulating clam populations, it is difficult to believe that fish could eliminate a population of *Corbicula*. However, *Corbicula* may contribute significantly to the nutrition of mollusk-eating fish.

Other predators include birds, raccoons, crayfish and flatworms. Sanderson and Anderson (1981) reported that the gizzards of 36% of the hunter harvested waterfowl from Lake Sangchris contained *Corbicula* shells. They listed 13 species of ducks that ingested *Corbicula*. Taylor and Counts (1977) reported finding *Corbicula* shell fragments in Raccoon, *Procyon lotor*, scats along with other evidence that raccoons had been eating *Corbicula* on the banks of the Ohio River in West Virginia. In laboratory experiments, Covich et al. (1981) found that the crayfish, *Procambarus clarkii*, readily consumed *Corbicula* under 6 mm in length and *Cambarus bartonii* ate clams under 9 mm in length. Sinclair and Isom (1963) suggested that the flatworm, *Dugesia tigrina*, potentially could be a predator of *Corbicula* in Kentucky Lake. However, juvenile *Corbicula* offered to *D. tigrina* from Kentucky Lake by the author were never consumed. Another flatworm, *Macrostomum* sp., from the Tennessee River was observed to consume *Corbicula* larvae and juveniles under 0.25 mm in length.

INTERSPECIFIC COMPETITION

Although *Corbicula* frequently produces dense populations in newly invaded habitats, there is conflicting evidence regarding its ability to displace native unionid mussels with which it competes for space and food. Gardner *et al.* (1976) indicated a concurrent decline in unionid mussels during the rapid growth phase of *Corbicula* in the Altamaha River, Georgia, from 1971 through 1975. However, deteriorating water quality and over-harvest of unionids probably contributed to their decline. Sickel (1976) indicated that few *Corbicula* were found among dense populations of adult Unionidae in the Altamaha River, but that fewer juvenile unionids were found on sandbars where *Corbicula* was abundant. He concluded that *Corbicula* could not displace established adult mussels but might interfere with their reproductive success.

Fuller and Imlay (1976) reported abundant *Corbicula* among dead mussel shells in lower reaches of the Waccamaw River, South Carolina, which had been extensively altered by human activities. Upstream in undisturbed reaches of the river, they found a sparse population of *Corbicula* in areas heavily populated with mussels. They suggested that "*Corbicula* does not (and perhaps cannot) dominate indigenous bivalves in nearly or quite natural habitats, at least in slowly moving, soft-bottom Coastal Plain streams of the Atlantic drainage." Kraemer (1979) supported these observations in her discourse discribing how *Corbicula* was able to exploit habitats unfavorable to unionid mussels, but was not as successful in undisturbed areas favorable to mussels. Particularly, Kraemer stated that in chronically disturbed rivers such as the Arkansas River in which management practices including dredging and controlled discharge have reduced the coarse sediments favored by indigenous mussels, *Corbicula* has flourished while mussels declined. In the relatively undisturbed Buffalo River, Arkansas, *Corbicula* competes with a healthy indigenous mussel community with only moderate success. In this undisturbed river, Kraemer reported *Corbicula* locally abundant only in fine sediments normally not occupied by mussels.

In a conflicting report, Fuller and Richardson (1977) stated that *Corbicula* could be an active "amensalistic competitor" with mussels even in undisturbed areas. They reported finding mussels being "uprooted" by *Corbicula* in the Savannah River, Georgia and South Carolina. However, although the Savannah River is not as extensively managed as the Arkansas River, it is not an "undisturbed" river. Alterations to the river caused by pollution, agricultural and other human activities and somewhat controlled discharge may have stressed the indigenous mussels thus providing *Corbicula* a competitive advantage.

In the tailwaters of Kentucky Dam, Tennessee River, Kentucky, there is an extensive unionid mussel community in the gravel substrate, and *Corbicula* has coexisted with the mussels since the early 1960's (Williams, 1969). During periods of heavy commerical harvesting of mussels, *Corbicula* became the numerically dominant bivalve, constituting 99.4% of the community (Williams, 1969). Even though commerical harvesting by mussel brail continued to disrupt the mussel community, *Corbicula* declined after the massive mortality of 1977 (Sickel and Heyn, 1980).

GENETIC CHANGES

Demonstrating genetic changes in populations is not easy especially in a species which is reported to have little or no genetic variability (Smith *et al.*, 1979). However, Chitty (1977) believes that natural selection and the resultant genetic changes may play a major role in regulating numbers within a population.

Differences in size and growth rates of *Corbicula* in various populations have been considered to be evidence of the effects of different environments. Growth rates and maximum size vary geographically. Eng (1979) predicted a maximum length for *Corbicula* in the Delta-Mendota Canal, California, of 37.75 mm. Morton (1977) predicted a maximum length of 35 mm for *Corbicula* in Plover Cove, Hong Kong. The maximum size that Sickel (1979) found in the Altamaha River, Georgia, was 30 mm in 1974 and 35 mm in 1977. These lengths are similar and might be expected to be characteristic for the species. However, other populations show quite different shell lengths.

For about a decade prior to the summer of 1977, the Tennessee River in Kentucky commonly produced large *Corbicula* over 60 mm in length. They were so abundant and easy to catch on mussel brails or with long handled rakes that a prosperous fishbait industry developed. Commerical clammers received 2¢ per clam and wholesale bait dealers sold them for 4¢ each. In August 1977, essentially all of the large adult *Corbicula* in the Kentucky Dam tailwaters died from unknown causes (Sickel and Heyn, 1980). Since that time the population has been increasing in density, up to 1800/m^2 in 1983, but no individuals have been found in the main river greater than 12.3 mm in length (Table 2).

The evidence points to a shift in life history traits which can only be explained by a genetic change. This shift has resulted in a population with a high fecundity, rapid maturation, and short life span similar to a newly invading population.

INTRASPECIFIC COMPETITION

Recent visual observations with the aid of SCUBA have suggested yet another cause, and in certain cases perhaps the most plausible, for the occurrence of mass mortalities of *Corbicula*. A region of the Tennessee River in the vicinity of river mile 13.8 was being surveyed for unionid mussels. This region had been brailed extensively by commerical musselers for a number of years thereby reducing the unionid density, disturbing the substratum, and creating a habitat more favorable for invasion by *Corbicula*. The author observed the entire substratum along a 50 m transect to consist of living *Corbicula* among freshly dead *Corbicula* shells and a few scattered unionids. The bottom literally was creeping with *Corbicula*. One individual clam could not remain motionless for more than a few minutes because several neighbors would move, jockeying for better position, and climb over or dislodge it. This constant movement must require an unusually high energy output and, perhaps, contribute to a high mortality.

Table 2. Density, mean shell length and range of *Corbicula* in the Tennessee River downstream from Kentucky Dam.

Date	Number of Grabs	Density No./m^2	Mean Shell Length (mm)	Range (mm)
10/18/78	43	25	4.55	2.4-10.3
11/10/78	54	34	3.58	1.5-8.5
12/1/78	54	50	4.27	1.7-8.7
6/15/79	72	67	5.45	2.9-12.3
6/9/83	4	1825	5.35	2.4-12.0

The density in a l m^2 sample was 1600 live *Corbicula*, 3000 dead shells of *Corbicula*, and 3 unionid mussels. Over 99% of the *Corbicula* were 3 years old with an average length of 33.6 mm and a mean tissue dry weight of 656.8 mg/clam. This calculates to a dry weight biomass of 10,500 kg/ha. The greatest tissue dry weight biomass observed in the Altamaha River at the peak of the *Corbicula* invasion was 314 kg/ha (Sickel, 1979). Clearly, a biomass as large as that at Tennessee River mile 13.8 cannot be sustained, and a high mortality must ensue.

During July, August, and early September of 1984 and 1985, numerous dead bodies of *Corbicula* were seen floating down the Tennessee River. The primary source of the dead clams was the bed at mile 13.8. The occurrence of the mortality during late summer might suggest a temperature relationship. However, the temperature never exceeded 29°C which would not by itself stress the clams. A more complete explanation for the timing of the die-off is that the intraspecific competition is greatest during the summer when the high temperature causes high metabolic rates and a greater energy requirement, and the increased activity causes more frequent disturbance to neighbors and a higher energy output to remain in a competitive feeding position.

Another observation on this population suggests an explanation for the nearly single age distribution that has been seen numerous times. At the high density observed, and the high mobility of the adult clams, juveniles would be burried quickly and repeatedly by the adults and the feces and pseudofeces of the adults. The sediment between the shells consisted of these feces and pseudofeces. Since *Corbicula* only live 3 to 5 years, within the next year or two the mortality in this population will peak, reducing the density, and young clams will once again find a favorable habitat. These observations may explain the observed dynamics of *Corbicula* populations in certain regions where little interspecific competition exists and periodic overpopulation occurs.

CONCLUSIONS

Mortalities in which all age classes are affected are probably the result of toxic substances, excessive cold, high temperatures and low dissolved oxygen, or some other environmental insult. However, many of the mortalities that have been reported are not a direct result of some environmental change, but are a natural phenomenon of death in a dense population in which a large, overpopulated cohort reaches its age limit or exceeds the biomass capable of being sustained by the environment. The die-off generally occurs during the summer when metabolic rates are high and competition for space and food place excessive energy demands on the individuals. The result is high mortality made obvious by the many dead clam bodies floating past fishermen or drawn into water intake structures. One would not question a report of millions of dead adult mayflies. Similarly, it should be accepted that in dense *Corbicula* populations there will be periodic massive die-offs. These should be predictable once a population has been studied and its age structure and age limit have been determined. Predicting the timing and intensity of massive die-offs will allow suitable precautions to be taken to avoid problems with large numbers of decomposing clam bodies. However, one must not feel too complacent with such data because a genetic change under intense selection might alter the population age structure and life history.

If generalizations can be made to other species, gains will have been made toward understanding how populations are regulated in nature. However, *Corbicula* may be an extreme case in which mechanisms of selection are exaggerated because it is new to this continent and has yet to attain a balance with other species.

Even though this investigation is incomplete, it is of heuristic value if it stimulates further investigations or suggests different approaches for studies which might lead to a better understanding of *Corbicula* dynamics.

ACKNOWLEDGMENTS

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CONTROLLING *CORBICULA* (ASIATIC CLAMS) IN COMPLEX POWER PLANT AND INDUSTRIAL WATER SYSTEMS

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ABSTRACT

A plan for controlling Asiatic clams, *Corbicula* sp., was developed by an interdisciplinary team within TVA during the 1970's. This plan, which is now in place, has proven very effective in controlling Asiatic clams over the past three years. Basis for the plan include knowledge of the life history of *Corbicula*, including size of benthic veligers at spawning and timing of spawning events. A combination of straining with a 1/32-inch (0.8 mm) media, chemical injection, and general "housekeeping" has practically eliminated clam problems. Perhaps even this success could be enhanced and made more economical with more research on optimization/minimization of chemical concentration and selection of period(s) for application of controls.

Goss *et al*. (1979) reported preliminary experience of the Tennessee Valley Authority (TVA) in control of *Corbicula* in steam-electric generating plants up to that period, including some power generating systems that were just beginning or about to begin operation. Since 1979, TVA has had good experience controlling *Corbicula*, except where mechanical or operational problems were experienced that interrupted chlorination. The following "raw water" systems are the ones usually fouled in fossil and/or nuclear steam-electric generating plants: Condenser circulating water (CCW) system; raw service water (RSW) system; essential raw cooling water (ERCW) system; and the raw service water/high-pressure fire protection (RSW-HPFP) system (Goss *et al*., 1979).

The TVA is currently recommending the following methods for controlling Asiatic clams in its nuclear plants: All incoming water to the raw water systems should be strained. Straining is performed by automatic backwash type straining units located immediately upstream or downstream of the main pumping units of the system (i.e., at the source). Strainers have a 1/32-inch (0.8 mm) medium and are designed for periodic or continuous backwashing.

Chlorine is the only chemical currently approved for mollusc (macroinvertebrate) control (Federal Regulation 47[224]:52293, November 19, 1982) in steam-electric power generating plants. In order to eliminate the safety considerations necessary when using large storage tanks for gaseous chlorine, TVA has elected to use sodium hypochlorite that is generated onsite as needed.

METHODOLOGY

Chlorine is injected as close as is practical to the water system inlet. Secondary water sources (such as jockey pumps, normally open interconnections with other water systems, etc.) are also chlorinated. If the incoming water has already been chlorinated, no additional injection is necessary. System design must be considered in conjunction with plant chemical discharge limits in defining the exact location of chemical injection.

Except as otherwise noted, the chlorine level throughout the raw water systems and at the system discharge is maintained at a total available chlorine residual of 0.6 to 0.8 ppm during the entire clam spawing period. In actual practice an 0.6 ppm residual is desirable since 0.8 is the maximum concentration allowed by NPDES permit, and you don't want to exceed that concentration. The clam spawing period as defined here is that period of time when the system inlet temperature normally exceeds 60ºF (15.6ºC). It should be noted that this is a very conservative approach to clam control, but is warranted since costs of failure to control *Corbicula* fouling properly are extremely high. One system that is not normally chlorinated is the CCW system which effects the main cycle heat rejection. It should be remembered that the raw water systems which are chlorinated constitute only a small flow/volume in comparison with the CCW system and since the discharge of these systems is mixed with CCW before being discharged it can be shown by engineering calculations that the most stringent standard, 0.01 mg/L or less at the edge of the mixing zone, can be met without difficulty (Federal Regulation 47[224]:52293, November 19, 1982).

Provisions are made for periodic chlorine residual sampling near the discharge of normally-flowing raw water systems. Provisions are also made in both normally-flowing

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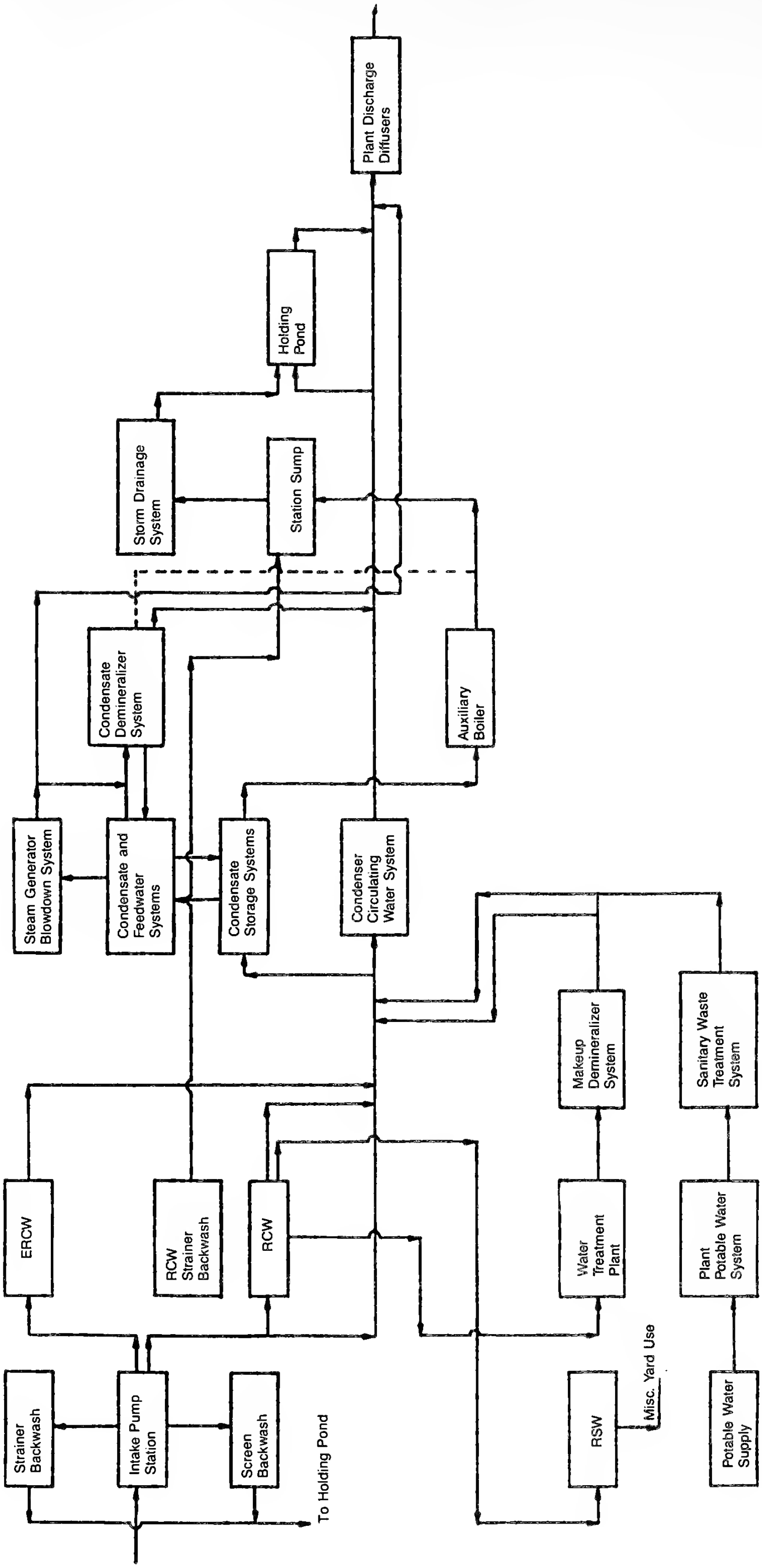

Fig. 1. Simplified water use diagram for a typical nuclear plant.

and stagnant water systems to sample residual levels periodically in undrained, normally-isolated system components which may have experienced occasional use during the clam spawning season. If an inadequate residual level is found in any isolated area, that area is opened for a period of time sufficient to allow replacement by chlorinated water.

Initially, sampling to ensure chlorine residual maintenance should be conducted on a weekly basis for those systems being chlorinated. A longer time interval may be found adequate after samples have been analyzed. Design provisions are made to flush isolated lines periodically in order to maintain chlorine residual levels.

RESULTS AND DISCUSSION

Goss *et al.* (1979) noted that initial fouling problems at a nuclear plant probably resulted from flooding the system at least two years prior to unit startup, which provided an environment for *Corbicula* growth. Therefore, TVA utilized the following methods to prevent primary colonization and fouling by *Corbicula*, even in temporary construction situations: Unchlorinated water is not allowed to lie stagnant in any raw water system at any time. Therefore, the systems are designed to allow drainage after initial testing (if practical). If a water system is going to be used regularly or if draining is not feasible, temporary provisions are made to inject some form of chlorine into the system in quantities sufficient to yield the required residuals. Filling of the system is accompanied by chlorine injection regardless of the inlet water temperature.

These measures during construction are applied to all raw water systems except the CCW system. The design permits temporary provisions for chlorinating the CCW system during the initial filling period. The system should be drained, cleaned, and refilled with chlorinated water prior to plant startup.

The following are exceptions to the standard control measures described above which are applicable to individual systems.

Essential Raw Cooling Water System (ERCW) - Areas of the system which are normally stagnant during normal operation are provided with small mini-flow lines which provide for sufficient flow through that part of the system to maintain the required chlorine residual (Fig. 1).

High Pressure Fire Protection System (HPFP) - Provisions should be made to flush the main supply line headers periodically.

Raw Service Water System (RSW) - The RSW system is continuously chlorinated during the entire clam spawning period only if the RSW system is interconnected with the HPFP system. Otherwise, chlorination for two 3-week periods, once at the beginning of the clam spawning period and again at the end of the clam spawning period, can be followed. Continuous chlorination during the entire clam spawning season may be required later if clam problems develop with this reduced chlorination schedule. These design provisions are not intended to imply that an automatic timer for chemical injections is recommended (Fig. 1).

Raw Cooling Water System (RCW) - The RCW system is chlorinated for two 3-week periods a year as described for RSW above. If the RCW system is supplied water by a closed cycle CCW system, the two 3-week periods should be established by the river temperature rather than the temperature in the CCW system. Continuous chlorination during the spawning period may be required if operating experience so dictates.

Condenser Circulating Water System (CCW) - The CCW systems have complete drainage capability for cleaning of the system if an excessive population of clams develops (Fig. 1). In addition, for closed cycle CCW systems, provisions are made to strain the incoming makeup water and ensure that it passes through the condenser prior to entering the cooling tower basin. Preliminary test results have shown that clams in the 1.5 mm size range cannot withstand the high temperatures (43ºC) found at main condenser discharges during the summer months. Directing the strained makeup water to the cooling tower discharge flume, rather than to the cooling tower basin, will quickly subject the incoming clam larvae to a lethal thermal stress (Isom, 1971 and 1976; Goss *et al.* 1979).

In response to NRC "Office of Inspection and Enforcement Bulletin 81-03," TVA conducted extensive inspections of safety-related raw water systems beginning in 1981. These inspections afford a meaningful comparison between incidents where these procedures were followed and where they were not followed. The results of these inspections are as follows:

Bellefonte Nuclear Plant is located at Tennessee River Mile (TRM) 391.5. Inspections of the ERCW system were conducted between April 1982 and January 1983 with eight major components and fourteen valves inspected. In addition, during September and October 1982, the 36-inch supply headers were drained, opened at intervals, and cleaned in conjunction with the cement mortar lining of these headers for control of corrosion. No evidence of Asiatic clams was found in any of these inspections.

Inspections of the combined RSW-HPFP system were conducted during November and December 1982. A total of eight valves were inspected with no evidence of Asiatic clams.

Watts Bar Nuclear Plant is located at TRM 528. Inspection of the ERCW system were performed in June and July 1981 and three components of the system were examined. In addition, during 1982 the supply headers were also drained, opened at intervals, examined, and cleaned for cement mortar lining to prevent corrosion. No evidence of Asiatic clams was found in any of these examinations.

In May 1981, approximately one-half of the fire protection nozzles at the station service transformer became clogged with small rocks and Asiatic clam shells. It was believed that this debris was left from the construction phase. A valve in the combined RSW-HPFP system was inspected for Asiatic clams in July 1981, but none were found. However, in December 1982 and again in January 1983, Asiatic clams were discovered in two different fire hose rack valves. Seven additional valves were inspected with no further indications of Asiatic clam infestation. The frequency of HPFP system flushing was increased from once each six months to once each three months. This occurrence is significant in that it demonstrates that Asiatic clams are, indeed, a threat at WBN and in that it illustrates the need to sample and flush normally stagnant systems.

Sequoyah Nuclear Plant is located at TRM 485. In May and July 1980, three major components of the ERWC system were examined and headers were flushed and examined for Asiatic clams. No Asiatic clams were discovered. Between February and April 1981, sections of piping were removed and inspected for corrosion products, no Asiatic clams were discovered. Then, in March 1982, while conducting a surveillance test of the system, a flow decrease from 100 to 31 percent of rated capacity to the containment spary heat exchanger was noted. The pipe was opened upstream of the manual inline strainer revealing approximately 15 gallons (57 L) of clam shells which were restricting the flow.

Under normal operating conditions, the 18-inch header supplying the heat exchanger is stagnant except for a 1-inch miniflow line around the heat exchanger. The miniflow line was found to be clogged. Combined with the fact that the ERCW was strained but not chlorinated the summer of 1981, except sporadically, this condition was conducive to clam growth. Subsequently, steps were taken to ensure flow through the miniflow line and chlorination by repairing the hypochlorite injection systems. Continuous chlorination as described above was practiced in 1982 with complete control of *Corbicula*.

In conclusion, a combination of straining and screening makeup water to 1/32-inch (0.8 mm), chlorine injections (0.6-0.8 ppm) during the spawning season, and improved "housekeeping" has practically eliminated Asiatic clam fouling problems in TVA power plants. We are still conducting research on optimization of chemical controls and selection of period(s) for application of controls.

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POWER STATION ENTRAINMENT OF *CORBICULA FLUMINEA* (MÜLLER) IN RELATION TO POPULATION DYNAMICS, REPRODUCTIVE CYCLE AND BIOTIC AND ABIOTIC VARIABLES[1]

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ABSTRACT

The passive downstream dispersal of specimens of the introduced Asian clam, *Corbicula fluminea*, was studied in the intake canal of a stream-electric power station on Lake Arlington, Texas, from 29 June 1981 through 6 December 1982. Downstream dispersal was monitored by a zooplankton net and clam trap periodically placed in the intake canal and by collection of clams from traveling screens in front of pump embayments. The population dynamics and reproductive cycle of the inlet canal *C. fluminea* population were monitored along with water quality parameters and phytoplankton densities.

The inlet canal *C. fluminea* population had a biannual pattern of reproduction, marked by incubation of developmental stages in the inner demibranchs from late March through early August leading to an "early" generation and again from late August through early November leading to a "late" generation. The growth rates of all generations were maximal during the warm summer months. Maximum densities were associated with recruitment of new generations. Mortality rates remained high throughout life leaving the majority of individuals as immatures (shell length (SL) < 5 mm). There was a distinct annual gonadal cycle in which periods of gonad maturation alternated with periods of larval incubation marked by gonad depletion.

Passive downstream dispersal on water currents was recorded in all size classes, but the majority were recently spawned juveniles (SL < 1 mm). Peak juvenile transport was associated with either reproductive periods or low winter water temperatures. Downstream dispersal of immature (SL = 1-7 mm) and adult clams (SL > 7 mm) occurred just prior to the advent of larval incubation. No correlations were found between passive downstream transport rates and phytoplankton densities or water quality parameters, suggesting that dispersal in this species is closely associated with the reproductive cycle, with the single exception of juvenile downstream dispersal induced by low temperatures.

Since its introduction to North America from Asia in the early 1900's *Corbicula fluminea* has become a biofouling pest species of major economic importance (McMahon, 1983). It has been reported to reduce flow in irrigation canals (Prokopovich and Hebert, 1965; Prokopovich, 1969; Eng, 1979) and underground pipes (Fitch, 1953; Ingram, 1959). *C. fluminea* also fouls the water lines and centrifugal pumps of water treatment plants and causes unpleasant taste and odor in drinking water (Ingram, 1959; Ray, 1962; Sinclair, 1964; Smith, *et al.*, 1979).

However, the most serious aspect of biofouling by this species is its ability to enter and foul the raw water systems of industrial facilities, including steam-electric and nuclear power plants where steam condensers, service water systems and auxillary water systems are occluded by accumulations of living clams and dead shells (McMahon, 1977; Goss and Cain, 1977; Goss, *et al.*, 1979; Smith, *et al.*, 1979). In nuclear power plants both primary and backup systems can be fouled simultaneously leading to major shut-downs for repairs (Henager, *et al.*, 1985). Incidents of *C. fluminea* biofouling at a number of nuclear power stations have caused the United States Nuclear Regulatory Commission (1981) to issue a

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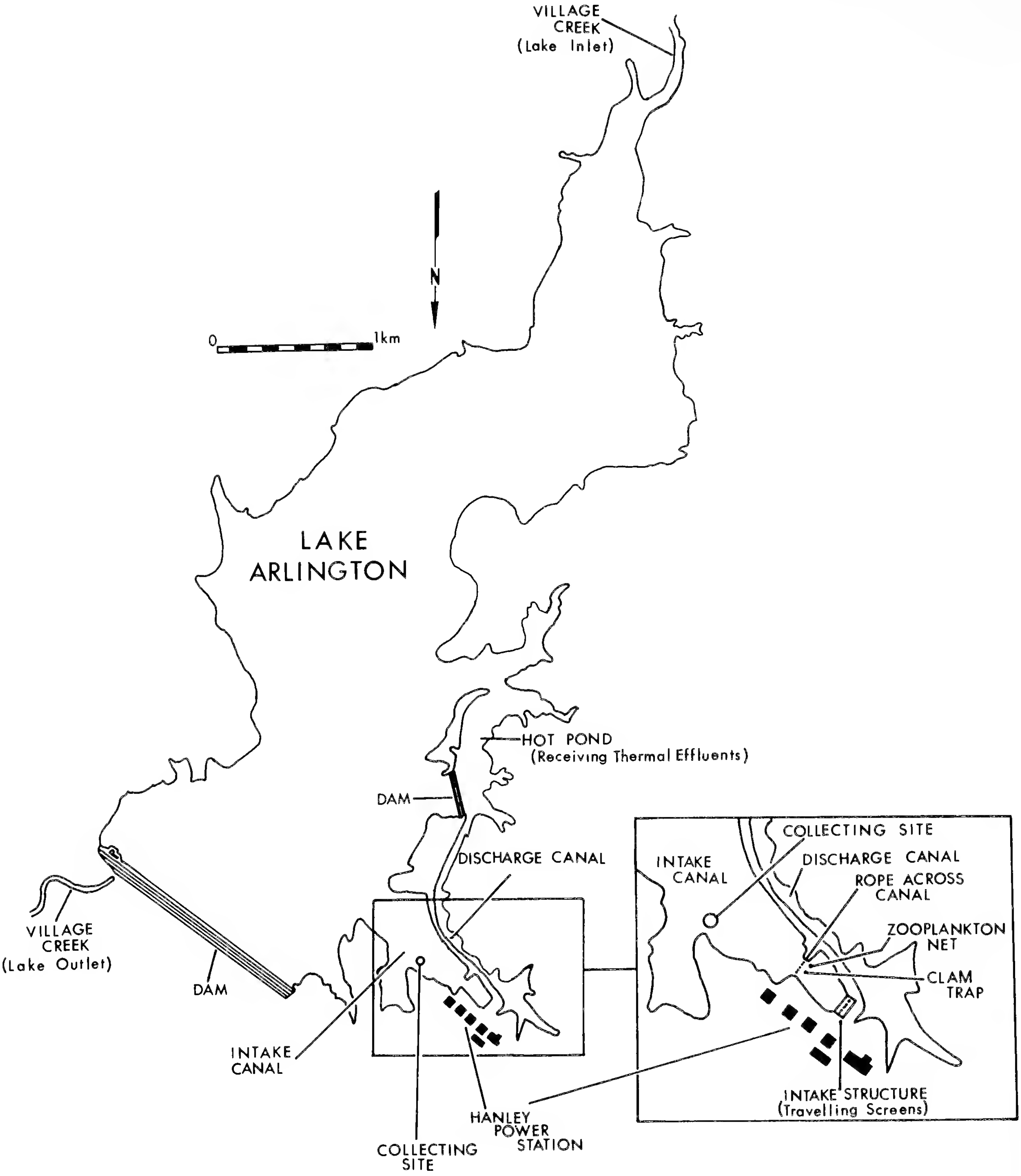

Fig. 1. Lake Arlington, Tarrant County, Texas. Small insert shows locations of collecting site, zooplankton net, clam trap and traveling screens in the intake inlet and intake canal of the Handley Steam-Electric Power Station.

bulletin instructing all US nuclear power stations to inspect their operations for fouling by *C. fluminea*.

The capacity of *C. fluminea* for biofouling appears to depend on its ability to be passively transported on intake water currents into these systems where they settle, grow and reproduce (McMahon, 1977; Goss and Cain, 1977; Goss, et al., 1979). The capacity for passive downstream dispersal is characteristic of natural populations of *C. fluminea* (Heinshon, 1958; Morton, 1977a; Aldridge and McMahon, 1978; Eng, 1979; Sickel, 1979; McMahon and Williams 1986a), accounting, in part, for its highly invasive nature (McMahon, 1982, 1983). Downstream dispersal in *C. fluminea* has recently been associated with its ability to produce mucus "draglines" from the exhalent siphon that act to buoy individuals in the water column (Prezant and Chalermwat, 1984).

Passive downstream dispersal appears to be uniquely characteristic of *C. fluminea*. It has not been reported to commonly occur in either unioniid or pisidiid species. In spite of its important implications to biofouling by this species, this singular mode of dispersal has received little attention with the exception of reports of seasonal variation in the densities of juvenile clams in the water column (Eng, 1979; Sickel, 1979). This report describes an extensive field investigation of the annual pattern of passive hydrological dispersal of juvenile, subadult and adult individuals of *C. fluminea* in the intake canal of a steam-electric power station in relation to the population dynamics and reproductive cycle of the source population, to phytoplankton density and to water quality parameters. Analysis of the results indicate the biological basis and adaptive significance of downstream dispersal in this species. The results of this study also provide data useful in the prediction of major episodes of impingement and subsequent biofouling by *C. fluminea* of industrial and power station raw water systems.

METHODS

A population of *C. fluminea*, composed entirely of the "white" shell morph of Hillis and Patton (1982) was quantitatively sampled bimonthly from 29 June 1981 through 6 December 1982. This population occurred in the intake inlet of the Handley Power Station of the Texas Electric Service Company on the northwest shore of Lake Arlington in Tarrant County, Texas. The power station drew water for its condenser and service water systems from the inlet (0.7 km long) through an 0.19 km long intake canal (Fig. 1). The Handley Power station consisted of five gas-fired, steam-electric generating units with a combined generating capacity of 1471 MW and a maximum effluent discharge rate of 4.7 (10^6) *l* day^{-1}.

The inlet *C. fluminea* population was sampled near the inlet's north shore, 2 km from its opening into the lake proper (Fig. 1). The substratum at this site was 20% gravel (particle diameter > 1.8 mm), 77.4% sand (0.1-1.8 mm) and 2.6% silt (< 0.1 mm) by dry weight and had an organic content of 3.5% of total dry weight (Williams, 1985).

The inlet population was quantitatively sampled with an Ekman dredge (sampling area = 0.052 m^2). Qualitative samples were also taken with a heavy steel box dredge with a 1 mm mesh collecting basket (for a description see Williams, 1985). This dredge was towed behind a jon boat with a 7.5 hp outboard motor. The box dredge bit deeply into the substratum and was capable of removing even large unionid bivalves such as *Quadrula quadrula* (Rafinesque) which burrow to much greater depths than *C. fluminea*. Clams were removed from the sediments by passing dredged material through a 1 mm mesh sieve.

Adult specimens of *C. fluminea* (shell length > 10 mm) transported passively on intake water currents were collected from two traveling screens located in front of pump embayments from which condenser and service water was drawn for the power station's no. 3 generating unit (maximum pumping rate = 1254 (10^6) *l* day^{-1}). The traveling screens had a mesh size of 1 cm, and functioned to remove any material potentially large enough to foul the steam condenser tubes. These screens remain stationary in the water column and are periodically rotated vertically past a high-powered water jet which propels lodged material (including clams) into a trough emptying into a large diameter outlet pipe that opened into the discharge canal (for a complete description of traveling screen operation see Bates, 1969). The traveling screens were rotated and cleaned of lodged debris at approximately 10:00 and 17:00 hrs each day. A steel bucket with a 1 cm x 2.5 cm diamond steel mesh bottom was placed in the outlet pipe to collect all clams washed from the screen at the 10:00 hr rotation on each collection date.

Juvenile clams carried in the water column were collected with an 0.5 mm mesh zooplankton net (50 cm diameter x 140 cm long). The zooplankton net was fitted with a current meter to record the volume of water passing through it. Clams carried along the bottom by currents were collected by a clam trap constructed of aluminum bar stock with a frontal opening 1 m wide by 0.5 m high. The clam trap was 1 m long, covered with 1 mm nylon mesh screen overlaid by a 5.0 mm wire mesh screen and fitted with a removable plastic jar at the back of the trap in which clams were collected (see, Williams, 1985, for a more complete description of the clam trap). Both the zooplankton net and clam trap were held in intake currents at the head of the power station's intake canal by attaching them to a rope secured across the canal (Fig. 1). The clam trap was weighted to remain on the substratum while the zooplankton net was maintained by a weighted lead line 30 cm above the substratum. At each collection the clam trap was submerged for 1-7 days and the zooplankton net for 0.8-3.3 hr.

At each collection ambient air temperature, surface water temperature and ph were recorded at the inlet collection site. Conductivity and dissolved oxygen (Hellige, Model 342-DO) were determined for water samples taken just above the substratum with a Kemmerer water sampler. Total water hardness was determined by EDTA titration on selected collection dates. Turbidity was measured by secchi disk. Daily power station water pumping rates through the intake canal were supplied by the Texas Electric Service Company.

At each collection phytoplankton cell density and chlorophyll concentrations were determined from water samples taken just above the substratum at the inlet collecting site. Three 0.5 *l* water samples were fixed and stained with 1 ml of Lugol's iodine. Within two days of collection a 5 ml subsample of each water sample was placed in a 2.54 cm diameter settlement chamber and allowed to stand overnight. The phytoplankton in 16 random 0.0625 mm^2 fields were counted at 400x under an inverted microscope (Olympus model IMT). Phytoplankton counts were divided into three major divisions: Chlorophyta; Cyanophyta; and Chrysophyta.

To determine chlorophyll contents, three 1 *l* water samples taken just above the substratum were filtered through a Whatman 934-AH glass microfiber filter with an effective retention size of 1.5 μm. The chorophyll of algae retained on the filter was extracted by grinding it in 90% acetone (by volume with H_20) and diluting the extract to a volume of 15 ml with 90% acetone. The absorption values of the extracted chlorophyll solution were then read at 630, 645, 665, and 750 nm before and after addition of 0.05 ml of 10% HC*l* to the cuvette sample (Parsons and Strickland, 1963). Trichromatic calculations based on absorption values before and after HC*l* addition gave the Chlorophyll *a,b,c* and phaeopigment concentrations (Strickland and Parsons, 1972).

The shells lengths (SL, the greatest anterior-posterior dimension across the valves) of each individual in the collections of the inlet population, from the traveling screens and from selected clam trap and zooplankton samples were measured to the nearest 0.1 mm. The SL of individuals $>$ 5 mm was measured with a dial caliper while that of those $<$ 5 mm was measured with an ocular micrometer in a binocular dissecting microscope.

For each inlet collection all individuals with an SL $>$ 5 mm were divided into 0.1 mm size classes, and the frequency of individuals in each size class expressed as a percentage fo the total sample size. These values were then plotted as frequency histograms for each collection against sampling date allowing direct visual separation of samples into separate generations characterized by distinct size groupings of different modal shell lengths and ranges of SL. Mean SL and a standard deviation were then computed for each generation in each population sample (Aldridge and McMahon, 1978). Individuals with an SL $<$ 5 mm were present in the collections of the inlet population throughout the sampling period. As these individuals proved to be impossible to assign to specific generations they were excluded from the analysis of population size distributions.

At each collection of the inlet *C. fluminea* population the reproductive condition of 10-40 mature individuals (SL $>$ 7.7 mm) was determined by opening the valves and examining the gonad for the presense of mature eggs and the inner demibranchs for incubated eggs, embryos, or juvenile clams.

RESULTS

Mean monthly power station intake water flow rates were 2545.8 (10^6) *l* day^{-1}. Flow rates were generally maximal in summer and minimal in late fall and early winter. Daily flow rates were much more variable than monthly averages and ranged from a high of 4623.5 (10^6) *l* day^{-1} on 29 June 1981 to a minimum of 760.9 (10^6) *l* day^{-1} on 16 November 1981 (Fig. 2A). Mean secchi depth was 0.9 m. indicating that inlet water was relatively turbid. Secchi depth values displayed a seasonal turbidity cycle in which turbity was greatest (low secchi depth values) during the fall, winter and

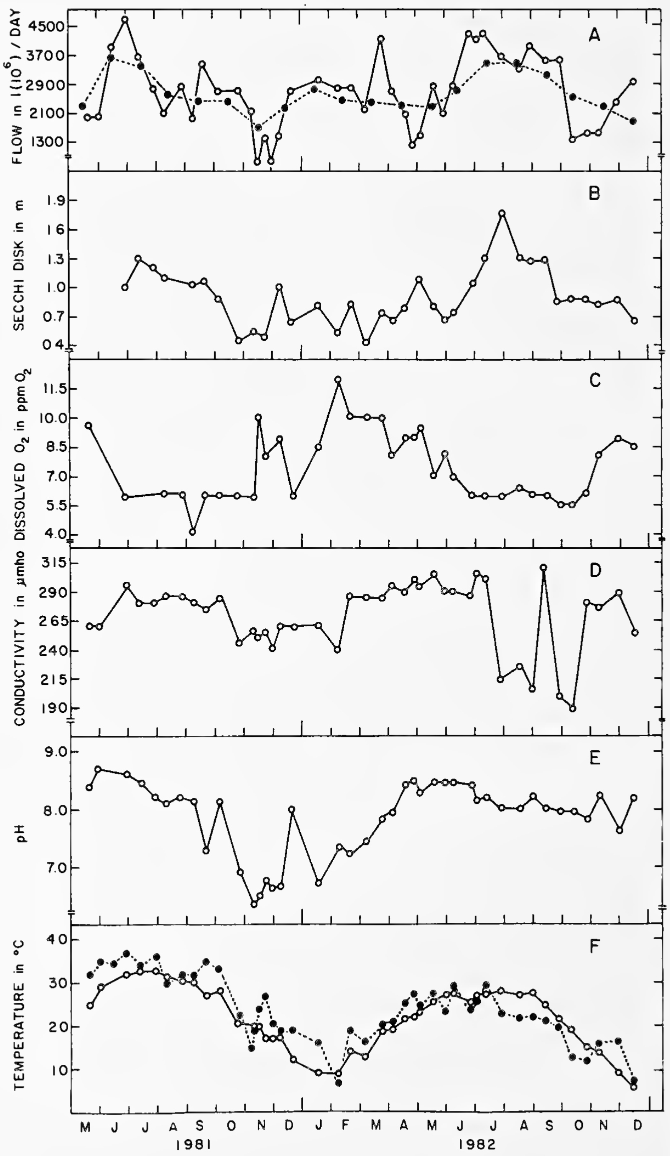

Fig. 2. Abiotic parameters recorded at the inlet *Corbicula fluminea* collecting site on Lake Arlington, Tarrant County, Texas, over the duration of the collecting period. **A.** Intake water flow pumping rates in 10^6 *l*/day. Open circles connected by solid lines are daily water flow rates, solid circles connected by dashed lines are monthly average pumping rates. **B.** Secchi disk depth readings in m. **C.** Dissolved oxygen concentrations in ppm O_2 (mg O_2/l). **D.** Conductivity in μmho/cm^2. **E.** Ambient pH values. **F.** Ambient air (solid circles connected by dashed lines) and surface water temperatures (open circles connected by solid lines) in °C.

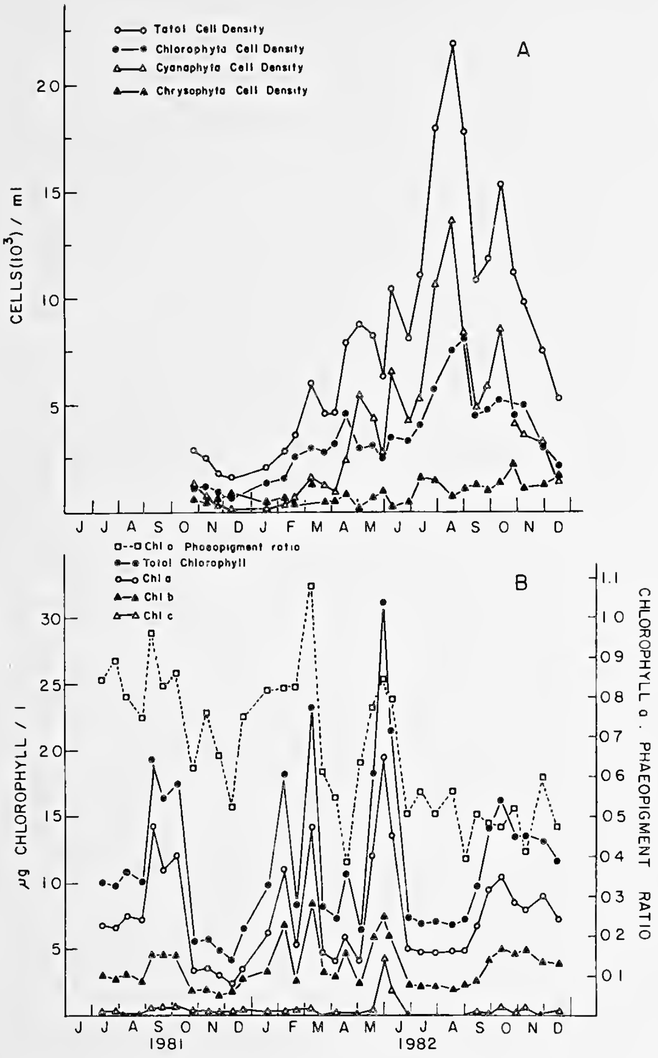

Fig. 3. Biotic parameters recorded at the inlet *Corbicula fluminea* collecting site on Lake Arlington, Tarrant County, Texas. The horizontal axis for both figures is months of the year over the collecting period. **A.** Annual variation in phytoplankton cell density. The vertical axis is phytoplankton cell density in cells (10^3) / ml for the total phytoplankton (open circles), chlorphytes (solid circles), cyanophytes (open triangles) and chrysophytes (solid triangles). **B.** Chlorophyll concentration and chlorophyll *a* : phaeopigment concentration ratios. The left vertical axis is chlorophyll concentration in μg/l for total chlorophyll (solid circles), chlorophyll *a* (open circles), chlorophyll *b* (solid triangles) and chlorophyll *c* (open triangles). The right vertical axis is the ratio of chlorophyll *a* concentration : phaeopigment concentration (open squares).

spring, and least during the summer (high secchi depth values) (Fig. 2B). Dissolved oxygen levels remained close to air saturation values indicating that the inlet *C. fluminea* population was not experiencing significant hypoxia (Fig. 2C). Mean conductivity over the collection period was 270 μmho cm^2 (Fig. 2D) and mean total hardness, 124.3 mg Ca l^{-1} which are both characteristic of waters with moderately high levels of dissolved minerals. Inlet waters were generally alkaline; ambient pH ranged from 6.36 to 8.72 and was less than 7.0 only during November 1981 and January 1982 (Fig. 2E). Ambient water temperature ranged from 6.7°C (7 December 1982) to 33.0°C (13 and 28 July 1981) over the collection period. Ambient air temperature was generally within a few °C of water temperature (Fig. 2F).

Phytoplankton cell densities were maximal in July and August and minimal in November and December (Fig. 3A). A maximum total phytoplankton cell density (21977 cells ml^{-1}) occurred on 18 August 1982, and a minimum (1605 cells ml^{-1}) on 8 December 1981 (Fig. 3A). Mean phytoplankton cell density over the entire study period was 8314 cells ml^{-1} (s.d. = ± 5377, s.e. = ± 1055, n = 27). Mean chlorophyte cell density was 3491 cells ml^{-1}, mean cyanophyte cell density, 3856 cells ml^{-1} and mean chrysophyte cell density, 2315 cells ml^{-1}. The cell densities of planktonic cyanophytes were greater than those of chlorophytes from May through October. The cell densities of chrysophtes were greater than that of cyanophytes from 23 November 1981 through 8 February 1982. Only on 23 November and 8 December 1981 did the cell densities of chrysophytes exceed those of chlorophytes (Fig. 3A).

Total phytoplankton chlorophyll concentration was depressed in mid-summer and in late autumn through early winter of both 1981 and 1982 (Fig. 3B). Maximum total chlorophyll concentrations occurred in early autumn and spring. This seasonal pattern in total chlorophyll concentration was reflected in the seasonal variation of the concentrations chlorophylls *a,b,* and *c* (Fig. 3B). Mean chlorophyll concentrations over the collection period were: Chlorophyll *a*, 7.607 μgl^{-1}; chlorophyll *b*, 0.438 μgl^{-1}; and chlorophyll *c*, 3.744 μgl^{-1}. With the exception of a single collection on 8 March 1982, phaeopigment concentration was always greater than that of chlorophyll *a* (chlorophyll *a* phaeopigment concentration ratio < 1) (Fig. 3B), indicating that a high proportion of the planktonic algal community was senescent throughout most of the year (Bastardo, 1980).

The inlet *C. fluminea* population displayed a biannual reproductive cycle characterized by the incubation of developmental stages in the inner demibranchs and the release of juvenile clams in the spring through mid-summer ("early" reproductive period) and again from late summer through early winter ("late" reproductive period) giving rise to distinct early and late generations (Fig. 4). Corresponding to the biannual reproductive cycle was a distinct variation in the percentage of adults with ripe gonads containing mature eggs. Gonads became depleted of mature eggs during incubation and juvenile release periods and ripened (characterized by higher percentages of individuals with gonads containing mature eggs) during non-incubatory periods. Thus, the highest percentages of individuals with ripe gonads were recorded from November through March and August through September, between the early (mid-March through mid-July) and late reproductive periods (mid-August through late November) when the lowest frequencies of individuals with ripe gonads were recorded (Fig. 4). Such data indicate that an annual cycle of gonad maturation and subsequent incubation of developmental stages occurs in the inlet *C. fluminea* population with the proportion of individuals with gonads containing large numbers of mature eggs approaching peak values just prior the onset of periods of ctenidial incubation of developmental stages and juvenile release, during which the number of adults in the population with ripe gonads markedly declines (Fig. 4). Decline of the number individuals with ripe gonads during incubatory periods suggests that incubation is associated with a suppression oogenesis in this species. Indeed, diversion of energy stores into gamete production and gonad maturation after the early reproductive period may be the fundamental cause of the characteristic mid-summer cessation of incubation and juvenile release reported for the majority of *C. fluminea* populations (McMahon, 1983).

The early and late reproductive periods give rise to corresponding "early" and "late" generations which appeared as distinct new size classes in the inlet population. The late reproductive period from 27 August through 12 November 1981, gave rise to a late generation (designated as L-81 in Fig. 4) which first appeared with a mean SL of 6.0 mm on 26 October 1981. Similarly the early reproductive period extending from 24 March 1982 through 18 August 1982 gave rise to an early generation (designated E-82 in Fig. 4) which first appeared in the inlet *C. fluminea* population with a mean SL of 5.2 mm on 31 May 1982. A second late reproductive period occurred from 18 August 1982 through 30 November 1982 giving rise to a second late generation (designed as L-82 in Fig. 4) first appearing in the collections with a mean SL of 5.5 mm on 12 October 1982. Other distinct size classes present in the collections of the inlet *C. fluminea* population represented the early and late generations resulting from reproductive periods that occurred prior to the initiation of sampling and included the E-81, L-80, E-80, L-79 and com-

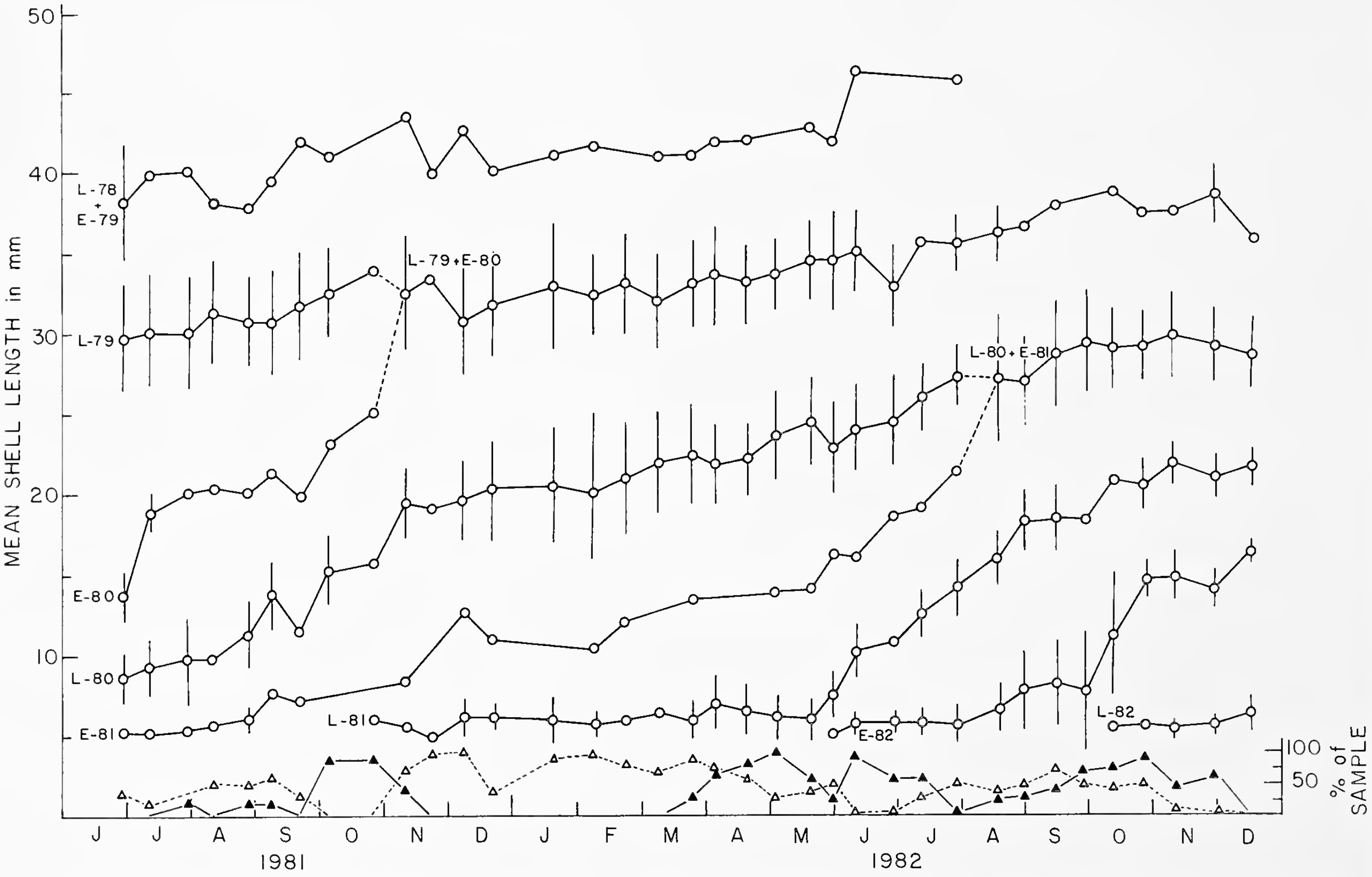

Fig. 4. Generation shell lengths and reproductive condition in the inlet *Corbicula fluminea* population in Lake Arlington, Tarrant County, Texas. The horizontal axis is months of the year over the collecting period. The left vertical axis is mean shell length (SL) in mm. The open circles connected by solid lines represent the mean SL of individual generations in each sample. The vertical bars about each mean indicate standard deviations. Individual generations are designated by the reproductive period which produced them [i.e., E-81, a generation resulting from the early (E) reproductive period in 1981 (81) or L-80, a generation resulting from the late reproductive period (L) in 1980 (80)]. L-78 + E-79 indicates the mean SL of combined generations produced from the late reproductive period of 1978 and the early reproductive period of 1979. The right vertical axis is the numbers of adult individuals in each sample incubating fertilized eggs, embryonic stages and juveniles in the inner demibranchs (solid triangles connected by solid lines) or with mature eggs in ripened gonads (open triangles connected by dashed lines) expressed as percentage of the total sample size.

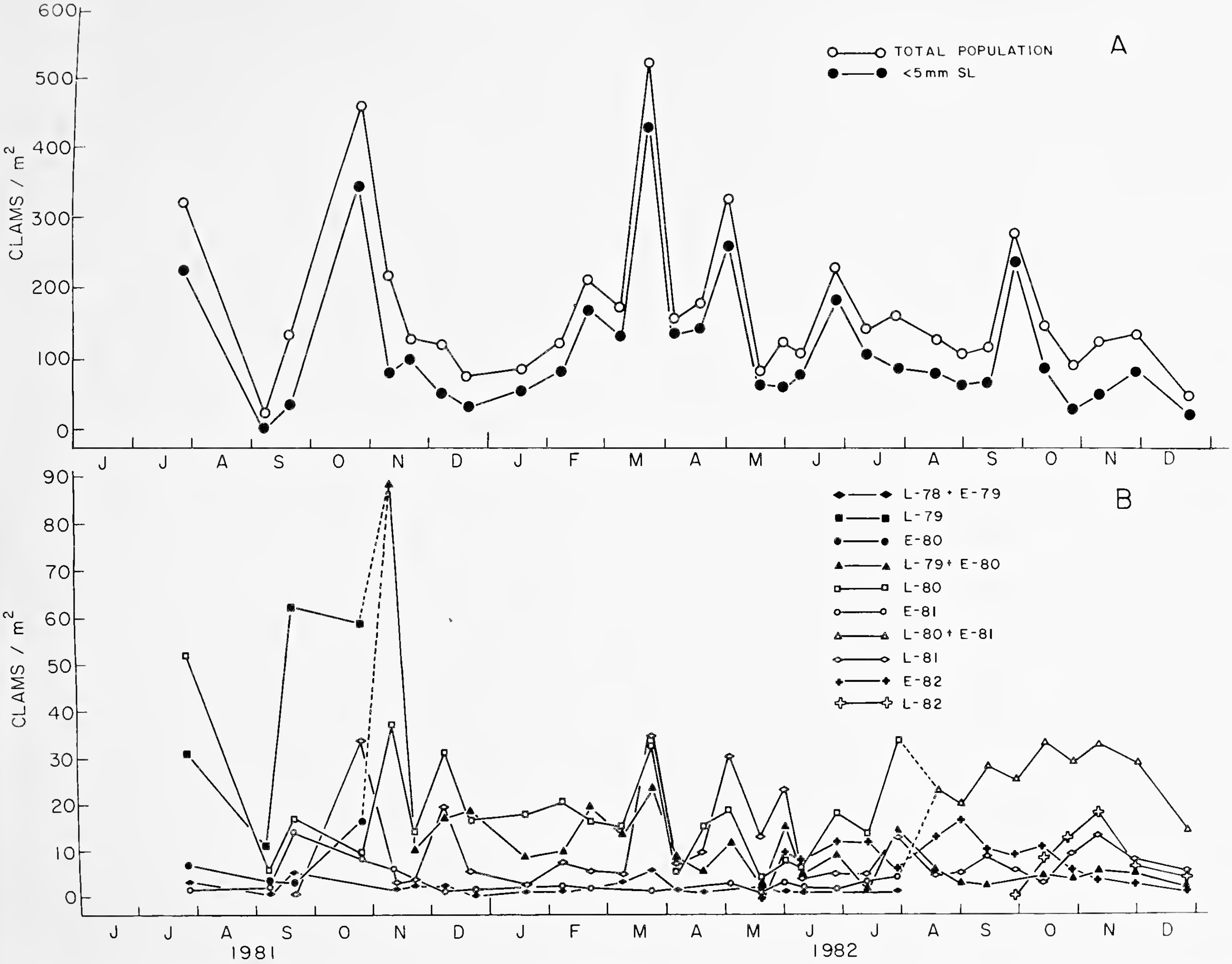

Fig. 5. Seasonal variation in the density of the inlet *Corbicula fluminea* population in Lake Arlington, Tarrant County, Texas. The horizontal axis for both figures is months of the year over the collection period and the vertical axis density in clams/m². **A.** Density of the total population (open circles) and of juvenile clams with shell lengths less than 5.0 mm (solid circles). **B.** Densities of specific generations. Densities of specific generations are designated by the reproductive period that gave rise to that generation (for further explanation see caption to Fig. 4) as follows: L-78 + E-79 (solid diamonds); L-79 (solid squares); E-80 (solid circles); L-79 + E-80 (solid triangles); L-80 (open squares); E-81 (open circles); L-80 + E-81 (open triangles); L-81 (open diamonds); E-82 (solid crosses); and L-82 (open crosses). The dashed lines represent points at which density estimates were intitiated for combined pairs of adjacent late and early generations.

bined L-78 + E-79 generation. These older generations were all present in the initial collections (Fig. 4).

Maximum growth rates for all generations were sustained from mid-May to early November when ambient water temperatures were above 15°C (Figs. 2F and 4). During the summer period of rapid growth the shell lengths of individuals of the E-81 generation became indistinguishable from the L-80 generation and, therefore, they were thereafter combined as a single size class into the L-80 + E-81 generation (Fig. 4). Similarly, the E-80 generation became indistinguishable from the L-79 generation during rapid summer growth in 1981 and were, thereafter combined into a single L-79 + E-80 generation which eventually disappeared from population samples in December 1982 (Fig. 4). A third grouped generation was present in the initial sample and was considered to represent the combined L-78 + E-79 generations. This group disappeared from the population samples in late July 1982. The presence of four annual pairs of late and early generations in the inlet *C. fluminea* population in both 1981 and 1982 strongly indicates that the maximum life-span of individuals in this population was approximately 3-3½ years (Fig. 4).

The mean total density of the inlet *C. fluminea* population was 168.2 clams m^{-2} (s.d. = ± 111.4, s.e. = ± 20.3, n = 31) over the study period. Peaks in total density were recorded on 28 July 1981 (320 clam m^{-2}), 26 October 1981 (426 clams m^{-2}), 3 May 1982 (320 clams m^{-2}), and 29 September 1982 (274 clams m^{-2}) (Fig. 5A). These density peaks were clearly associated with the recruitment of new individuals (SL <5 mm) to the population from early and late reproductive periods producing the E-81, L-81, E-82, and L-82 generations, respectively (Fig. 4). Another density peak occurred on 24 March 1982 (525 clams m^{-2}) (Fig. 5A). This peak was not associated with juvenile recruitment and most likely represented an extensive sampling error (ie., collection at a locally restricted site of exceptionally high juvenile clam density). The large decline in juvenile density following their recruitment to the population (Fig. 5A) reflects the high annual mortality rate of young clams in the inlet population.

After initial recruitment the densities of all generations in the inlet *C. fluminea* population declined steadily throughout the study period (Fig. 5B) suggesting that each generation is subject to a relatively constant mortality rate throughout its life span. During June and July 1982, there were four pairs of late and early generations in the population samples (Fig. 4), including the L-78 + E-79, L-79 + E-80, L-80 + E-81 and L-81 + E-82 generations. The densities of these pairs of generations were utilized to estimate annual mortality rates by expressing the difference in densiy between two adjacent yearly generation pairs as a percentage of the density of the most recent pair of early and late generations. These estimates of annual mortality rates for the inlet *C. fluminea* population were approximately 74% in the first year of life, 59% in the second and 93% in the third.

There was a distinct annual cycle of impingement of adult specimens of *C. fluminea* onto the powers station's traveling screens. Maximum impingement rates occurred in mid-April 1982 (127 clams day^{-1}), and in late July 1982 (105 clams day^{-1}) (Fig 6A), just prior to the onset of the early and late reproductive and incubatory periods, respectively (Fig. 4). There was no significant impingement of adult clams on the traveling screens during other times of the year (Fig. 6A).

The annual cycle of adult impingement on the traveling screens was reflected in the cycle of retention of smaller individuals (SL = 1-7 mm) in the clam trap. Clams were taken in the trap at low levels throughout the study period, indicating that some passive downstream transport was always occuring in these size classes. However, a distinct peak of maximum retention of individuals by the clam trap (161.6 clams day^{-1}; mean SL of trapped clams = 2.6 mm, s.d. = ± 0.75, n = 5857) occurred in early April 1982 (Fig. 6B). This peak of retention of subadult clams in the clam trap corresponded directly to the spring peak of adult clam impingement on the traveling screens (Fig. 6A) just prior to the initiation of the early reproductive and incubatory period (Fig. 4).

The density of juvenile *C. fluminea* (SL $<$ 2 mm) passively suspended in the water column as estimated from numbers taken in the zooplankton net was highly correlated with juvenile release by adult clams during reproductive periods. Peak juvenile densities in the water column were 760 clams 100 m^{-3} on 21 May 1981 and 211 clams 100 m^{-3} on 28 June 1982 during the early 1981 and 1982 reproductive periods, respectively (Fig. 6C). During the 1981

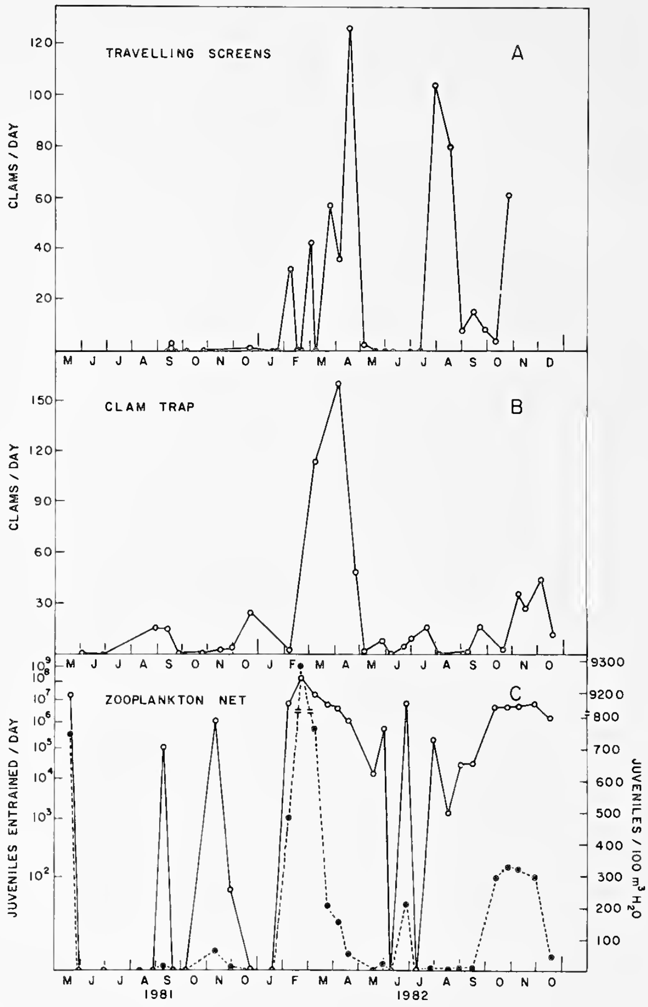

Fig. 6. Seasonal variation in the rates of passive downstream dispersal on water currents by juvenile, subadult and adult specimens of *Corbicula fluminea* in the intake canal of a power station on Lake Arlington, Tarrant County, Texas, as estimated from adult impingement on traveling screens, retention of subadults in a clam trap, and the density of juveniles suspended in the water column estimated by retention in a zooplankton net. The horizontal axis for all figures is months of the year over the collection period. **A.** Rate of impingement of adult individuals (shell length (SL) $>$ 10 mm) on two traveling screens in front of the intake embayments of the no. 3 generating unit in clams impinging the traveling screens per day (open circles). **B.** The rate of retention of subadult clams (SL = 1-7 mm) in a clam trap on the substratum of the intake canal in clams per day (open circles). **C.** The density of juvenile clams (SL $<$ 2.0 mm) suspended in the water column and the entrainment rate of juvenile clams into the power station's raw water systems as estimated from the retention of clams in a zooplankton net held 30 cm above the substratum of the intake canal. The left vertical axis is a logarithmic scale of the numbers of juvenile clams entrained through the power plant's raw water systems per day (open circles connected by solid lines). The right vertical axis is the density of juvenile clams suspended in intake canal waters in clams / 100 m^3 (solid circles connected by dashed lines).

and 1982 late reproductive periods peak juvenile densities in the water column were 77 clams 100 m^{-3} on 11 November 1981 and 332.8 clams 100 m^{-3} on 27 October 1982, respectively (Fig. 6C). Surprisingly, maximum suspension of juvenile clams in the water column (9154.4 clams 100 m^{-3}) occurred during a period of prolonged low ambient water temperature from January through February 1982 (mean water temperature = 10.5ºC) (Figs. 2F and 6C).

Values of juvenile density in the water column multiplied by daily intake water flow rates yielded juvenile clam entrainment rates through the Handley Power Station's raw water systems. Entraiment rates of juveniles on intake waters were relatively high throughout the study period (Fig. 6C). Peak levels of juvenile entrainment were clearly associated with the early and late reproductive seasons when large numbers of juveniles were suspended in the water column (Fig. 6C). However, maximum entrainment rates (2.5 (10^8) clams day^{-1}) occurred on 22 February (Fig. 6C) and were associated with maximal densities of juveniles in the water column during a period of low winter water temperatures (see above).

Least squares linear regression analysis was utilized to determine if any direct relationships exist between the various abiotic and biotic parameters recorded during the study (ie., water temperature, pH, conductivity, dissolved oxygen, turbidity, water flow rate, total algal cell concentration, total chlorophyll content, and chlorophyll *a*: phaeopigment ratio) and the rate of passive downstream transport of *C. fluminea* as represented separately by impingement of adults on the traveling screens, retention of subadults in the clam trap and suspension of juveniles in the water column (measured by retention in the zooplankton net). No significant linear relationships could be found between any of these parameters and passive downstream dispersal of adult, subadult and juvenile clams ($P > 0.05$). However, there appeared to be a tendency for adult clam impingement rates onto traveling screens to increase with decreasing chlorophyll *a*: phaeopigment ratio representative of increasingly senescent phytoplankton populations ($P < 0.1$, $r = -0.45$, $n = 19$), and for densities of juvenile clams in the water column to increase with declining oxygen concentration ($P < 0.1$, $r = -0.357$, $n = 30$).

DISCUSSION

The Lake Arlington inlet *C. fluminea* population had a life cycle characterized by a biannual pattern of reproduction. An "early" period of egg and developmental stage incubation and subsequent juvenile release extending from mid-spring to mid-summer was separated from a "late" reproductive period extending from late summer to early winter by a non-reproductive, non-incubatory period in mid-summer. Early generations from the early reproductive periods appeared in the population in May or June, grew to a mean SL ranging from 11 mm (E-82) to 16.5 mm (E-81) by the following December and, subsequently achieved a mean SL of 18.8 mm (E-81) to 18.9 mm (E-80) by the following June after one year of growth (Fig. 4). The late generations arising from late reproductive periods grew little through the winter and subsequently initiated rapid growth the following spring to reach a mean SL ranging from 19 mm (L-80) to 21 mm (L-81) after the first year of life (Fig. 4). Two year old clams in the Lake Arlington inlet population reached a mean SL of 35.7 mm (L-79 + E-80 generations) and in the third and terminal year of life a mean SL of 46.0 mm was attained (L-78 + E-79 generations) (Fig. 4).

A very similar pattern of life-cycle has been reported for a natural lotic population of *C. fluminea* in the Clear Fork of the Trinity River in north central Texas (McMahon and Williams, 1986b). Like the Lake Arlington population this population had two generations per year and a maximum life span of three years. The early generation reached a mean SL of 22.5 to 23.4 mm and the late generation, 20.6 to 24.3 mm in the first year of life. A mean SL of 35.6 mm was achieved after two years and individuals at the end of the third and terminal year of life reached a mean SL of 41.0 mm. Other detailed studies of the reproductive and life-cycles of *C. fluminea* populations also report two annual reproductive periods, attenuated life spans of 1.5 to 4 years and shell growth rates ranging from 16 mm to 33 mm in the first year of life in Texas (O'Kane, 1976; Aldridge and McMahon, 1978; McMahon and Williams, 1986b), central California (Heinsohn, 1958; Eng, 1979), Asia (Morton, 1977a) and Africa (Leveque, 1973). Thus, a biannual reproductive pattern, high growth rates and relatively short life spans appear to be characteristic of *C. fluminea* throughout its world-wide range. The minor difference in life-cycle, growth rates and life spans of geographically separated populations of *C. fluminea* may be attributable to environmentally induced ecophentypic variation. Certainly, as this species has been reported to have relatively variable generation growth rates and life spans from year to year within a single population (McMahon and Williams, 1986b), environmentally induced geographic variation in growth rates and life spans is not unexpected (see McMahon, 1983 and McMahon and Williams, 1986b for a review of growth rates in *C. fluminea*).

Surprisingly, the growth rates and life spans of the inlet *C. fluminea* population were quite different from those reported in an earlier study of another population of this species in the same lake carried out from late 1974 through the end of 1975 (Adridge and McMahon, 1978). In this earlier study both the early and late generations had shorter life spans (1.5-2 years) and much higher shell growth rates (mean SL = 30-33 mm in the first year of life). A possible explanation for these temporal differences in life cycle and growth rate may lie in a general decline in the phytoplankton production of Lake Arlington. Mean annual phytoplankton densities in Lake Arlington during 1971 were 18.3 (10^3) cells ml^{-1} (Carr, 1973). In 1979 they were 38.4 (10^3) cells ml^{-1} with a mean chlorophyll *a* concentration of 13.6 $\mu g\ l^{-1}$. (Peeler, 1980). During the present study (1981-1982) mean algal density declined to 8.3 (10^3) cells ml^{-1} and mean chlorophyll *a* concentration to 7.6 $\mu g\ l^{-1}$. These levels represent a 54% to 78% decline in mean phytoplankton density and a 44% decline in mean chlorophyll *a* concentration between the period during which Aldridge and McMahon (1978) completed their observations on *C. fluminea* in Lake Arlington and the sampling period of the present investigation. As phytoplankton appears to be a major food source for *C. fluminea* (Foe and Knight, 1985, 1986; Lauritsen, 1986), as it is for most lamellibranch bivalves (Owen, 1966), it is not unexpected that such a major decline in phytoplankton productivity would be associated with decreased growth rates and correspondingly increased life spans in this species. Certainly, it appears that variation in both physical factors as temperature and catastrophic climatic events (Horning and Keup, 1964; Bickel, 1966; White and White, 1977; White, 1979; Cherry, et al., 1980; Dreier and Tranquilli, 1981; McMahon and Williams, 1986b) and biotic factors such as the level of primary productivity may have significant impacts on the population dynamics of this species. Such environmentally induced ecophenotypic variations appear to account, in great part, for the geographic variations in growth rates, life spans and maximum shell lengths reported for *C. fluminea* in North America (McMahon, 1983).

The inlet *C. fluminea* population displayed a distinct seasonal alternation between gonad maturation and incubation of fertilized eggs, developmental stages and juvenile clams in the interlamellar spaces of the inner demibranchs. Gonads were observed to become depleted of mature eggs during incubatory periods and to produce mature eggs and ripen during non-incubatory periods (Fig. 4). In contrast, Eng (1979) and Kraemer, et al. (1986) have reported that mature eggs occurred throughout the year in the gonads of California and Arkansas populations of *C. fluminea*, while spermatogenesis occurred only during reproductive periods. This pattern was distinctly different from the Lake Arlington *C. fluminea* population in which the gonads of the majority of specimens became degenerate and appeared to be depleted of sperm and eggs during the latter portions of incubatory and juvenile release periods. A similar decline in gonad condition has been reported for an Asian lentic population of *C. fluminea* (Morton, 1977a). This inhibition of gametogenesis during incubatory periods may account for the marked midsummer cessation of incubation and juvenile release reported for the vast majority of *C. fluminea* populations (Heinsohn, 1958; Morton, 1977a; Aldridge and McMahon, 1978; Eng, 1979; Sickel, 1979; Dreier and Tranquilli, 1981; McMahon and Williams, 1986b). It is possible that incubation places considerable metabolic demands on adult clams, effectively diverting metabolites from incorporation into developing gametes. Such metabolic demands may be associated with the reduction of the filtering efficiency of the inner demibranches when they are distended with developing embryos, effectively reducing the assimilated energy available for gamate production. Alternately, Morton (1977b, 1982) has suggested that incubated embryonic stages may recieve nourishment from hypertrophied epithelial cells lining the interlameller spaces of the inner demibranch of adult *C. fluminea*. Such diversion of metabolites to incubated developmental stages could place a considerable pressure on the energy reserves of adult individuals preventing their utilization for gamete production during incubatory periods.

While the ability of *C. fluminea* to foul industrial water systems has been well documented (see McMahon, 1983, for a review of biofouling problems with *C. fluminea*), few attempts have been made to study the relationships between this species' biology and its nature as a biofouling pest species. Such studies are of great importance to the eventual development of rational and effective biofouling control procedures for *C. fluminea*. Two major biofouling problems occur with *C. fluminea* in the raw water systems of steam-electric and nuclear power stations. The first involves the passive transport of adults into turbine steam condensers where they lodge at slight constrictions in the condenser tube walls (McMahon, 1977). The second problem concerns the passive hydrological transport of juvenile and subadult clams on intake water currents into service and auxiliary raw water systems utilized for cooling and other purposes. Transported clams settle in low flow areas of these systems to grow, reproduce, accumulate and eventually occlude water flow to levels that seriously compromise system operations (Goss and Cain, 1977; Goss, *et a.*, 1979; Smith, *et al.*, 1979; Cherry, *et al.*, 1980; Henager, *et al.*, 1985).

Presently, the only effective control measures for service and auxillary water systems involve periodic chlorination to eliminate impinging juveniles and subadults (Sinclair and Isom, 1963; Goss and Cain, 1977; Goss, et al., 1979; Smith, et al., 1979; Mattice, *et al.*, 1982). Several reports have suggested that chlorination to control juvenile impingement of service water systems need ony be applied during high risk periods of juvenile impingement associated with the early and late reproductive periods whose onset and duration could be determined by monitoring the reproductive condition of adult clams in the source population and intake waters for the presence of newly released juveniles (Ingram, 1959; Cherry, *et al.*, 1980; Smith, *et al.*, 1979). The results of this study indicate that while high levels of juvenile transport on intake waters are certainly associated with reproductive periods, significantly high levels of entrainment also occurred in non-reproductive periods, particulay during periods of low winter water temperatures ($< 10^0$C) when the density of juveniles in the water column was 12-50 times greater than at any other time of the year (Fig. 6C). The reasons for high levels of juvenile suspension in the water column during low water temperatures are presently unknown. It may be associated with a low temperature inhibition of juvenile byssal thread formation (see Kraemer, 1979, for a description of the juvenile byssus in *C. fluminea*) or a reduced capacity for burrowing, either of which would greatly increase the susceptibility of juveniles to passively enter the water column. The level of entrainment of juvenile *C. fluminea* through the raw water systems of the Handley Power Station was quite remarkable, often surpassing 10^7 individuals day^{-1} (Fig. 6C). These high levels of downstream dispersal allowed the thermal effluent discharge canal of the power station to be recolonized at rates of 352 clam m^{-2} day^{-1} and 522 clams m^{-2} day^{-1} in the falls of 1981 and 1982, respectively, after the discharge canal population had been completely eliminated during the previous summers by lethally high ambient water temperatures (McMahon and Williams, 1986a).

As high levels of juvenile entrainment through power station raw water systems are not restricted to reproductive periods (Fig. 6C) and as immature clams (SL = 1-7 mm) are carried downstream continually on water currents as reflected by their retention in the clam trap throughout the year (Fig. 6B), chlorination procedures to control biofouling by *C. fluminea* will almost certainly have to be applied continuously throughout the year to be effective. If chlorination is not continuous small individuals suspended in the water column during non-reproductive periods may settle in service and auxillary water systems and rapidly grow to chlorination resistant sizes (Mattice, 1979; Mattice, et al., 1982) especially during the winter months when growth would be stimulated by the warmer water temperatures of service water systems (McMahon and Williams, 1986b).

Immature specimens of *C. fluminea* ranging in SL from 1 to 7 mm were retained in the clam trap which rested directly on the substratum. In contrast, only juvenile clams with a maximum SL of 2.0 mm were taken in the zooplankton net which was suspended 30 cm off the substratum. As no clams with an SL greater than 2.0 mm were taken in the zooplankton net, individuals with greater shell lengths do not appear to become suspended in the water column. Instead, they must be mainly transported downstream by being carried over the substratum surface by water currents ("rolling"). A recent study has inicated that specimens of *C. fluminea* with an SL much greater than 2.0 mm can enter the water column by producing a "dragline" composed of mucus threads from the exhalent siphon under laboratory conditions (Prezant and Chalermwat, 1984). However, no individuals with an SL greater than 2.0 mm were trapped in the water column of the intake canal even though many thousands of individuals were taken throughout the course of the study. Therefore, mucus draglines do not appear to function to suspend larger clams in the water column. Rather, they appear to be involved with transport of larger individuals over the surface of the substratum, even in the very high water current velocities of the intake canal. Certainly, as the vast majority of individuals of *C. fluminea* dispersed on water currents are juveniles, adult hydrological transport appears to be of little real significance to the downstream dispersal of this species.

There was an apparent tendency for the number of juvenile *C. fluminea* suspended in the water column to increase directly with decrease in dissolved oxygen concentration ($P < 0.1$). The O_2 consumption of adult *C. fluminea* is severely inhibited by even relatively minor levels of hypoxia (McMahon, 1979). If the metobolic rates of juvenile individuals are similarly depressed by hypoxic conditions, they may become stressed and unable to burrow and/or maintain a byssal connection to the substratum making them much more susceptible to passive hydrological transport.

Subadult and adult specimens of *C. fluminea* were maximally retained in the clam trap and traveling screens, respectively, in mid-April and late July just prior to the onset of the early and late reproductive periods (Fig. 6A and B). Adult individuals taken from the traveling screens appeared to be too dense to be carried in the water column. Instead, they appeared to be carried by intake water currents downstream over the substratum surface (unpublished observations). While there was an apparent tendency ($P < 0.1$) for adult impingement on the traveling screens to increase with increasing senescence of the phytoplankton community (associated with a decrease in food quality marked by chlorophyll *a*: phaeopigment ratios < 1), the pronounced increases in the numbers of clams impinging the travel screens and clam trap just prior to incubatory periods suggests the majority of this phenomenon is associated with the reproductive cycle. Certainly, it is tempting to speculate that the passive downstream transport of gravid individuals may represent a sort of pre-reproductive dispersal which would be of obvious adaptive significance to an invasive species such as *C. fluminea* which inhabits unstable aquatic environments (McMahon, 1983; McMahon and Williams, 1986a and b). However, this study and that of McMahon and Williams (1986a) indicate that adult downstream dispersal is of little consequence compared to the massive dispersal of juveniles in this species. Recently, it has been shown that adult clams impinging the traveling screens of the Handley Power Station prior to reproduction have reduced tissue weights, decreased tissue total organic content: nitrogen content ratios and decreased molar ratios of oxygen consumed: nitrogen excreted compared to individuals in the inlet source population, which indicated that dispersing adults were showing symptoms of reduced energy assimilation and starvation (Williams, 1985; Williams and McMahon, 1985). As such, dispersing adults appear to be in poor reproductive condition. Therefore, leaving the substratum to be carried downstream on water currents to microhabitats more favorable to the acquisition of food resources to support gamate production and embryo incubation may be a highly adaptive behavior in *C. fluminea*. Such a hypothesis is supported by the observation that adults only disperse in high numbers just prior to the onset of reproductive periods (Fig. 6C).

Power plant intake pump embayments behind traveling screens may harbor very dense populations of adult *C. fluminea* (McMahon, 1977; Dreier and Tranquilli, 1981; Harvey, 1981; Smithson, 1981). These populations appear to be the main source of adults impinging and fouling turbine steam condensers (McMahon, 1977; Smithson, 1981). If adults in these embayments are subject to the same seasonal patterns of passive downstream dispersal as those recorded for the Lake Arlington inlet *C. fluminea* population, then major episodes of steam condenser biofouling by *C. fluminea* will be most likely to occur just prior to the early and late reproductive periods, in early spring and mid-summer, respectively. In this regard, steam condenser biofouling control procedures involving either periodic removal (Goss and Cain, 1977; Goss, *et al.*, 1979; Smith, *et al.*, 1979; Harvey, 1981) or chemical treatment (Smithson, 1981) of embayment populations would be most effective if they were applied just prior to these major pre-reproductive episodes of passive adult downstream dispersal.

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CORBICULA IN ASIA - AN UPDATED SYNTHESIS

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ABSTRACT

A previous review of *Corbicula* in Asia (Morton, 1979b) came to the tentative conclusion that there are but two species. This resulted from analysis of early conchological assessments of the genus. This review is of contemporary conchological literature but relies principally on the researches of biologists who have collectively defined the species concerned. It is reasserted that two species are predominant.

C. fluminalis (Müller) occurs in estuaries and tolerates salinities of up to 50%. It is dioecious with a trend towards protogyny. Breeding occurs over a single winter season, when temperatures are low. Eggs are not incubated, fertilization being external; strangely, however, typical incubatory glands develop in the inner demibranchs and it seems possible that under certain extreme conditions eggs may be incubated. A single growth ring/annum is produced, the species reaching a maximum theoretical shell length in southern China of 54 mm and living for up to 10 years.

C. fluminea (Müller) is fresh water with only a limited tolerance of low (15%) salinities. This smaller species (a shell length of up to 35 mm in southern China) is dioecious with a high percentage of hermaphrodites in lentic waters but hermaphrodite with an equal % of females (no males) in lotic systems. Possibly other sexual strategies occur under extreme conditions. The species incubates fertilized eggs within the inner demibranchs. These are released as crawling pediveligers at a shell length of 220 μm. There are two peaks of reproduction, one in early, the other in late summer when temperatures are high. Two growth rings are thus produced/annum, the species living for approximately three years.

C. fluminea has been introduced into N. America.

In an earlier review of the status of *Corbicula* in Asia, the tentative conclusion was reached, despite the plethora of available species names, that but two highly variable, widely distributed, species occur (Morton, 1979b). Following research upon the biology, ecology, reproduction and morphology of representatives of these two species in Hong Kong (Morton, 1973; 1977a; 1982; 1983) it was concluded (Morton, 1982) that these could be correlated with the types of *Corbicula fluminea* and *C. fluminalis*, though since the latter species has never before been recorded from China, this judgement was qualified.

The earlier review concentrated, largely, on old conchological studies particular attention being paid to the works of Prashad (1924; 1928a; b; 1929; 1930). At that time there was very little biological information on the genus that would enable a more meaningful analysis to be made. New species of *Corbicula* are still being described (Ray, 1967; Temcharoen, 1971; Brandt, 1974; Djajasasmita, 1977b), despite the fact that there is already a ridiculous nomenclatorial load, and, it is further clear, there is immense variability in shell form, size and colour in representatives of *Corbicula*.

Recently, species of *Corbicula* have been introduced into areas outside the usual range (Asia) and the artificial but established range in N. America. These are France and Por-

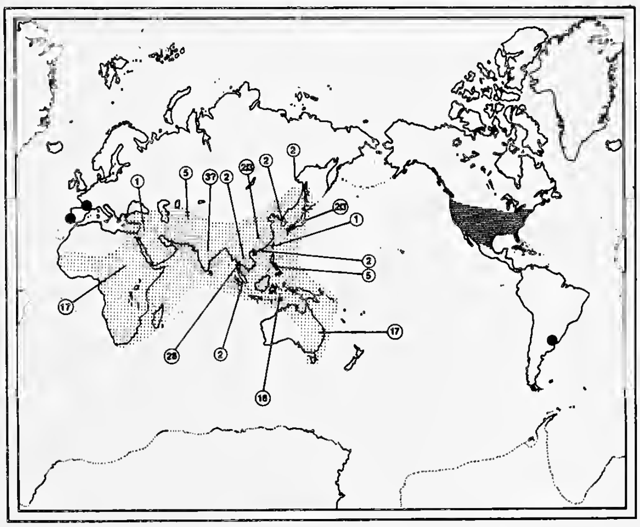


Fig. 1. The distribution of *Corbicula* in Africa and Asia. (after Zhadin, 1948; 1965) and in N. America (after Britton and Morton, 1982). Sites of recent introductions into Portugal, France and Argentina are also recorded. Figures in circles refer to the numbers of species of *Corbicula* presently recorded from various regions of Africa and Asia.

tugal (Mouthon, 1981) and Argentina (Ituarte, 1981). It seems very clear that *Corbicula* is going to be spread yet further. Where *Corbicula* has spread outside its native range, it has become an important biofouling pest, especially in N. America (Morton, 1979a). It may equally become a pest organism in newly occupied areas. It is thus necessary for responsible decisions to be made now with regard to the identity of the introduced species on the basis of reliable characters. The present taxonomic chaos that surrounds *Corbicula* in Asia results from the quest of conchologists to erect names for shells barely "different from", "somewhat similar to" or somehow "related to" other highly dubious "species". Here the taxonomic status of *Corbicula* in Asia is re-examined, principally on the characteristics of each species, other than the shell. The researches of modern biologists in Asia are discussed and form the basis for the decisions made here. However, I have also tried to ascribe names to what I believe to be the extant species based upon (to me) reasonable taxonomic criteria.

In light of the considerable biofouling problems that are ascribed to the introduced *Corbicula* in N. America, I also assess the biofouling potential of the species in its home range.

CORBICULA IN ASIA

TAXONOMY AND BASIC BIOLOGY

U.S.S.R.

This discussion of *Corbicula* in Asia commences with a review of those species occurring in the fresh waters of the U.S.S.R. It begins here for the single important reason that from this vast region, Zhadin (1965) records but two species, namely *C. fluminalis* (Müller 1774) and *C. fluminea* (Müller 1774). The former (apparently) has a middle Asian, the latter an east and southern Asian distribution. A point of anomaly with Morton (1977a; 1982), is that Zhadin records maximum shell lengths of 21mm (*C. fluminalis*) and 37mm (*C. fluminea*), whereas Morton records maximum theoretical lengths for these species of 54mm and 35mm respectively. However, Alimov (1974) has shown that the growth constant of the von Bertalanffy equation is functionally dependant upon prevailing environmental factors and that the maximum length of the adult animal increases with an increase in the sum of the effective habitat temperatures. Thus both species may have a highly variable form and attain different maximum sizes in the various components of their wide ranges.

Zhadin (1948) maps the range of *Corbicula*, demonstrating for both species an essentially Asian, tropical, distribution (Fig. 1). On the basis of Zhadin's researches Sinclair & Isom (1963) suggested that *C. fluminalis* might prevail in west Asia while *C. fluminea* might prevail in the south and east.

Mandryka (1981) records *C. japonica* Prime from brackish water lakes on the shore of the Sea of Japan; from two of these, populations of the bivalve were thought to be heterogenous with length/height relationships suggesting two morphological groupings. Perhaps, however, two species were coexisting here. Yaroslavtseva, Pavlenko & Fedoseeva (1981) also record *C. fluminea* from the U.S.S.R.

Issatullaev (1980) describes the Corbiculidae of Central Asia. *C. tibetensis* (Prashad) and *C. ferghanensis* (Kursalova and Starobogatov) are said to be ovoviviparous while *C. cor* (Lamarck), *C. purpurea* (Prime) and *C. fluminalis* are said to be oviparous.

AFRICA

Counts (1980) has examined the zoogeographic records of museums around the world for species of *Corbicula* collected in Africa. Seventeen species were recorded (including *C. fluminea*) as follows:

> *C. aegyptica* Bogart, *C. africana* Kiawis, *C. agrensis* Kurr, *C. artini* Pallary, *C. astartina* Martens, *C. australis* (Müller), *C. cummingtoni* Smith, *C. fischeri* Germain, *C. fluminea* (Müller), *C. kirkii* Prime, *C. lamarckiana* Prime, *C. oliphantensis* Craven, *C. pusilla* (Philippi), *C. radiata* Hanley, *C. sikarae* Ancey, *C. subradiata* Kurr, and *C. tanganyicensis* Crosse.

Records for *C. agrensis* and *C. australis* from Ghana and South Africa were considered doubtful as these species have an Indian and Australian distribution respectively. Most African species were confined between longitudes 26ºE and 34ºE and between elevations of 0 and 1500m.

Kenmuir (1980) records only *C. africana* Krass from Lake Kariba. Most significantly, Mandahl-Barth (1954) records that but two species occur in the White Nile, i.e., *C. africana* in the middle reaches of the river and *C. fluminalis* in most of its lower reaches.

ISRAEL

Tchernov (1975) reports that *C. fluminalis* is the only corbiculid found in the Sea of Galilee.

INDIA

Lomte (1971) records two species of *Corbicula* from the Marathwada region of India. Akhatar (1978) similarly records two species from Lahore, i.e., *C. striatella* Deshayes and *C. regularis*. Mudkhede and Nagabhushanam (1977) report upon the heat tolerance of *C. regularis* from Marathwada.

Ray (1967) records a new species of *Corbicula*, *C. krishnaea*, from Maharashtra, India.

LAOS

Temcharoen (1971) describes a new species of *Corbicula* - *C.crocea* - from Laos. It differs from all other species of this genus "by its reddish-yellowish colour" and is known from the type locality only.

CAMBODIA

Mizuno and Mori (1970) record *C. noetlingi* Martens and *C. petiti* Clessin from Lakes in Cambodia.

MALAYSIA

Berry (1974) sexed a sample of *C. malaccensis* from Malaysia and showed that of those individuals greater than 8mm shell length, 40 were hermaphrodites, 19 were female and two were male. Fertilized eggs are brooded in the inner demibranchs of both females and hermaphrodites and are released as juveniles. This author also records *C. javanica* from Malaysia.

THAILAND

Mizuno and Mori (1970) have made an ecological survey of Asian lakes and record the following species of *Corbicula* from Thailand: *C. noetlingi* von Martens, *C. siamensis* Prashad, *C. petiti* Clessin, *C. lamarckiana* Prime, *C. larnaudieri* Prime and *C. ligidiana* (= *C. lydigiana* Prime) from Thailand.

A major review of the Corbiculidae of Thailand by Brandt (1974) recorded the following 23 species, including *C. fluminea: C. arata* (Sowerby), *C. blandiana* Prime, *C. bocourti* (Morelet), *C. javanica* (Mousson), *C. lamarckiana* Prime, *C. lydigiana* Prime, *C. pisidiformis* Prime, *C. castanea* Morelet, *C. cyreniformis* Prime, *C. tenuis* Clessin, *C. fluminea* (Müller), *C. noetlingi* von Martens, *C. regia* Clessin, *C. gustaviana* von Martens, *C. moreletiana* Prime, *C. siamensis* Prashad, *C. erosa* Prime, *C. iravadica* Hanley & Theoblad, *C. baudoni* Morelet, *C. gubernatoria* Prime, *C. leviuscula* Prime, *C. solidula* Prime, *C. messageri* Bavay and Dautzenberg.

Not content with this, however, Brandt also describes 5 new species: *C. virescens, C. pingensis, C. occidentiformis, C. vokesi* and *C. heardi*. Virtually all of the earlier described species reported upon by Brandt can be allied to *C. fluminea* (Morton, 1979), many of them being so synonymised by Prashad (1928b) anyway.

INDONESIA

Djajasasmita (1975; 1977a) reviewed the species of *Corbicula* occurring throughout Indonesia. Of 35 previously described species, 16 were considered valid. These are:-

Sumatra: *C. gustaviana* von Martens, *C. moltkiana* Prime, *C. sumatrana* Clessin, *C. tobae* von Martens, *C. tumida* Deshayes.
Java: *C. javanica (*Mousson), *C. pulchella* (Mousson), *C. rivalis* (Philippi).
Borneo: *C. bitruncata* von Martens, *C. pullata* Philippi.
Celebes: *C. lindoensis* Bollinger, *C. loehensis* Kruimel, *C. matannensis* Sarasin and Sarasin, *C. subplanata* von Martens.
Timor: *C. australis* (Lamarck).
New Guinea: *C. debilis* (Gould).

A Philippine species, *C. squalida* Deshayes, was also added as a new record. Subsequently, Djajasasmita (1977b) described a new species (*C. lacunae*) from 21 specimens collected from two freshwater marshes in E. Java. The new species apparently shows 'relationship' with *C. loehensis* from Celebes.

Bentham-Jutting (1953) had earlier reviewed the Corbiculidae of Java and also recorded only *C. javanica, C. rivalis* and *C. pulchella* from this region.

U. S. Nat. Mus. 122429 Lea Coll.

Smithsonian Institution.

Plate 1. The holotype and label of *C. leana* Prime (USNM. 122429).

PHILIPPINES

Villadolid and Del Rosario (1930) report that *Corbicula manillensis* Philippi is the only corbiculid recorded from Laguna de Bay and its tributaries. This name is a junior synonym of *C. fluminea* (Morton, 1979). In Laguna de Bay the species attains a length of some 30mm, breeds from March through to July, incubates larvae in modified inner demibranchs and the population comprises approximately 4 size classes.

CHINA (PEOPLE'S REPUBLIC OF)

From China, Liu and Huang (1964) recorded *C. nitens* (Philippi) and *Corbicula* sp. from the San-Men-Hsia Reservoir of the Yellow River. Tchang, Li and Liu (1965) recorded *C. fluminea, C. aurea* (Heude), *C. largillierti* (Philippi) and *C. nitens* as occurring in Tung-ting Lake and its surrounding waters, Hunan Province. Tchang and Li (1965) record but *C. fluminea* and *C. largillierti* from Poyang Lake and its surrounding waters, Kiangsi Province. Chen (1979), however, only records *C. fluminea* from Lake Hwama, Hubei Province.

Liu, Zhang, Wang and Wang (1979) have reviewed the Corbiculidae from China and record the following species - *C. fluminea, C. largillierti* and *C. nitens*, the latter two having a restricted distribution, with *C. largillierti* endemic to the lakes of the Yangtze River.

Miller and McClure (1931) and Morton (1973) reported upon a species called *C. manilensis* from the Pearl River, southern China. This name, however, is but a junior synonym of *C. fluminea* (Morton, 1979b) and Morton (1982) has subsequently suggested that this species is, in fact, comparable with *C. fluminalis*, a species hitherto not recorded from the Chinese mainland.

HONG KONG

Morton (1977a; 1983), Brandt (1980) and Dudgeon

(1980; 1982) record only *C. fluminea* from Hong Kong, though as noted above *C. fluminalis* occurs in the Pearl River estuary close to Hong Kong.

TAIWAN

A major review of Taiwanese literature by Wu (1980) concludes that only *C. fluminea* occurs in Taiwan. The same author (Wu, 1979) provides morphometric data for this species. Similarly, Chen (1976) records that the common cultivated species in Taiwan is *C. fluminea* but is reported to be dioecious with external fertilization and planktonic larvae!

KOREA

Oyama (1943) reviewed the species of Korean *Corbicula*, recording 7 species but including, significantly, *C. fluminea* and *C. japonica*. The other five species were *C. suifunensis* Lindholm, *C. colorata* von Martens, *C. felnouilliana* Heude, *C. vicina* Heude and *C. papyracea* Heude.

Lee and Park (1974) further recorded *C. orientalis* Lamarck (considered by Johnson (1959) to be *C. japonica*) while Lee and Heo (1980) discuss *C.elatior* von Martens (a species which Oyama considered but a form of *C. japonica)*.

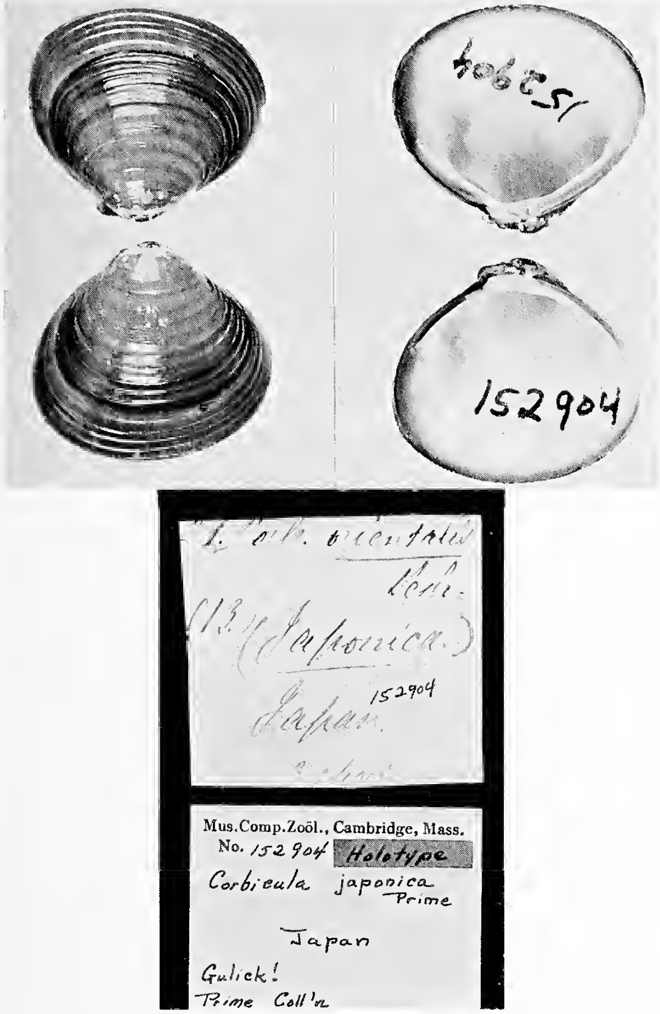
Lee and Chung (1980) believe the common 'marsh' clam of Korea to be *C. fluminea*. Thus, contemporary Korean authors seem to be reporting upon two species referrable to *C. fluminea* and *C. japonica*.

JAPAN

Perhaps the most authoritative accounts of *Corbicula* in Asia come from Japan where there is a long history of conchological and malacological research. Kuroda (1938) recorded 20 species from Japan but, significantly, concluded that all of these could be assigned to two species groups one generally found in saline waters, the other in freshwater. Kurashige (1945a;b) reports upon the distribution, ecology and shell shape of *C. felnouilliana* and *C. fluminea*. The most recent review of Japanese *Corbicula* by Habe (1977) concludes that there are 4 species, i.e., *C. japonica* Prime, *C. sandai* Reinhardt, *C. fluminea* Müller and *C. leana* Prime.

The holotype of *C. leana* is shown in Plate 1 and can

Plate 2. The holotypes and labels of *C. fluminea* Müller) and *C. fluviatilis* (Müller). (Universitetets Zoologiske Museum, Copenhagen).



1. Corb. orientalis
Lea.
(13.) (Japonica.)
Japan. 152904

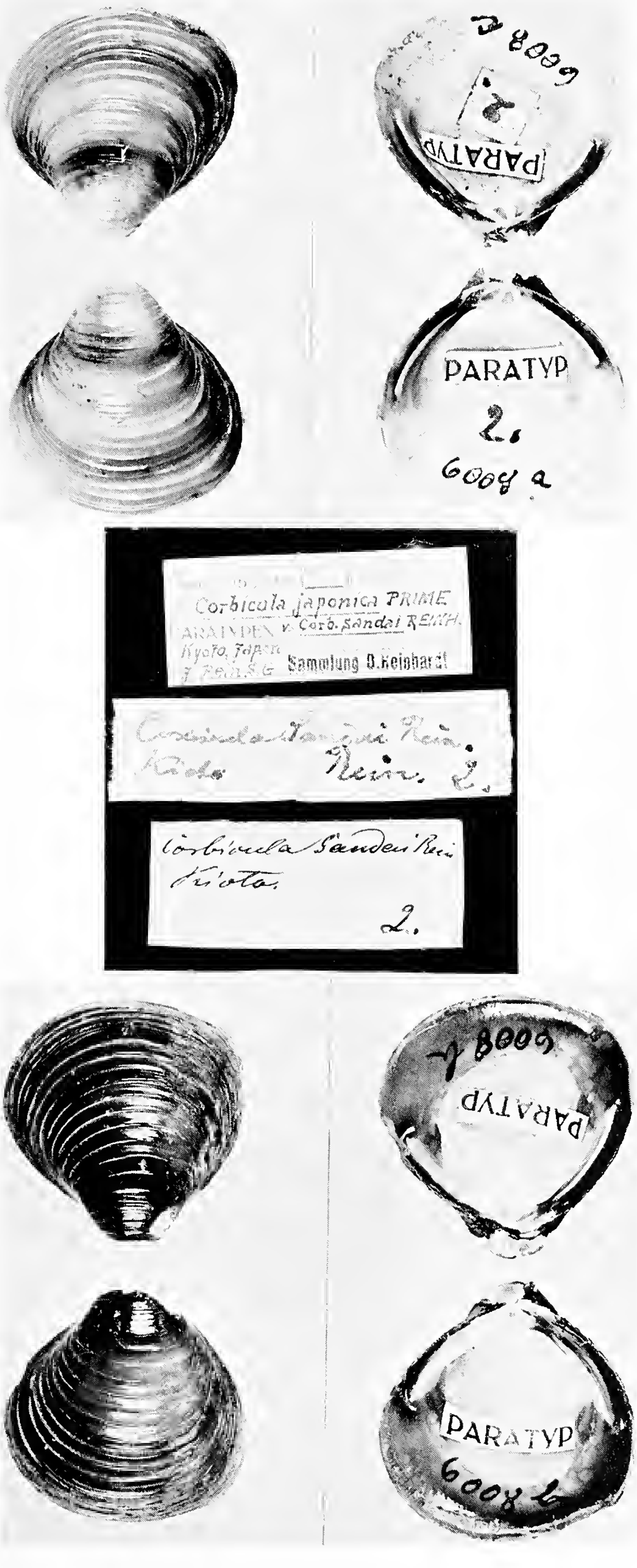
Mus.Comp.Zoöl., Cambridge, Mass.
No. 152904 Holotype
Corbicula japonica
Prime
Japan
Gulick!
Prime Coll'n

Plate 3. The holotype and label of *C. japonica* Prime (MCZ. 15904).

be compared with the holotypes of *C. fluminea* and *C. fluviatilis* (Plate 2) (the latter is by general consent (Prashad, 1929; Morton, 1979b) considered synonymous with *C. fluminea*). Bearing in mind that the type of *C. fluminea* is a juvenile, there can be little doubt that *C. leana* is virtually indistinguishable from *C. fluminea* (or *C. fluviatilis*). Indeed even Prashad (1924) who thought there were 69 valid species of *Corbicula* in Asia, considered *C. leana* to be an "insular form" of *C. fluminea*.

Plates 3 and 4 illustrate the holotype and paratype of *C. japonica* and *C. sandai* respectively (note that *C. sandai* was originally described as but a variety of *C. japonica*). When compared with the holotype of *C. fluminalis* (Plate 5) they are virtually indistinguishable, showing the same conical shell with narrow growth lines.

On conchological grounds therefore it is suggested that in Japan but two species occur; *C. fluminalis* (= *C. japonica*) and *C. fluminea* (= *C. leana*). It is, however, conceded that *C. sandai* may be either a lake morphological form of the otherwise brackish water *C. fluminalis* or a species endemic to the ancient Lake Biwa (Hayashi, 1972; Mori,



Corbicula japonica PRIME
ARAINDEN v. Corb. sandai REINH.
Kyoto, Japan
J Rein S.G Sammlung O.Reinhardt

Corbicula Sandai Rein.
Kioto Rein. 2.

Corbicula Sandai Rein
Kioto.
2.

Plate 4. The paratype and label of *C. sandai* Reinhardt (SMF. 6008).

Cyrena
C. fluminalis Müll.
Ch: 6. f. 320.
Moltk: 107. Ven. fluminalis

Cÿrena fuſcata. Lmck ?
Lmck, n:o 4,
var: Chemn. 6. f. 320.
Mus: Moltk. 101 Venus fluminalis

Plate 5. The holotype of *C. fluminalis* (Müller) (Universitetets Zoologiske Museum, Copenhagen).

JAPAN		SOUTHERN CHINA	
Corbicula japonica		*Corbicula fluminalis*	
Brackish waters	Asahina, 1941 Hayashi, 1956 Kado & Murata, 1974 Matsushima, 1980 Maru, 1981	Brackish waters	Miller & McClure, 1931 Morton, 1973; 1982
Dioecious	Utoh, 1981 Maru, 1981	Dioecious with a trend towards protogyny	Morton, 1982
Non incubatory	Asahina, 1941	Non incubatory	Morton, 1982
Winter breeding season	Utoh, 1981	Winter breeding season	Morton, 1982
Late summer breeding season	Maru, 1981		
Life span of 8-9 years	Utoh, 1981	Life span of up to 10 years	Morton, 1982
Growth rings: 1/annum	Utoh, 1981 Maru, 1981	Growth rings: 1/annum	Morton, 1973; 1982

JAPAN		SOUTHERN CHINA	
Corbicula leana		*Corbicula fluminea*	
Fresh water	Asahina, 1941 Matsushima, 1980 Kado & Murata, 1974	Fresh water	Morton, 1977a
Hermaphrodite	Fuziwara, 1979	Lentic waters: dioecious + hermaphrodite Lotic waters: female + hermaphrodite	Morton, 1983
Incubatory (inner demibranchs)	Fuziwara, 1977	Incubatory (inner demibranchs)	Morton, 1977a; b; c
Matures at 10mm	Fuziwara, 1977; 1979	Matures at 10mm (approx.)	Morton, 1977a
Breeding season:		Breeding season:	
May-August	Tamura, 1959	(2 peaks/annum):	
May-November	Ikematzu & Kammakura, 1975	April-October	Morton, 1977a
Summer	Ikematzu & Yamane, 1977		
early summer	Fuziwara, 1975; 1977; 1978		
April-October	Fuziwara, 1979		
May & July-September	Kaurajiri, 1948		
Larvae released as D-shaped crawling juveniles (200μm)	Fuziwara, 1977 Tamura, 1959	Larvae released as D-shaped crawling juveniles (200 μm)	Morton, 1977a
Growth rings: 2/annum	Fuziwara, 1978	Growth rings: 2/annum	Morton, 1977a
Life-span: ? *	Fuziwara, 1978	Life-span: 3 years	Morton, 1977a

*N.B. Fuji (1957) describes a population of *C. japonica* as comprising 3 age classes — was he *actually* investigating *C. leana*?

Table 1. A comparison of characterizing features of *C. japonica* and *C. leana* from Japan with *C. fluminalis* and *C. fluminea* from southern China.

1978), though Maru (1981), and Nakao (1982) also recorded this "species" from other lakes and lagoons in Japan and Itasaka, Sugita and Hori (1980) record it from the Seta River. Similarly, *C. japonica* is riverine but also occurs in lakes and lagoons (Gose, 1965; Fuji, 1979).

I have also reviewed the modern literature on Japanese *Corbicula* by biologists. It is significant that most contemporary Japanese scientists (e.g. Kado and Matsushima, 1976a; b) only refer to two species, namely *C. japonica* and *C. leana*, though some ecologists e.g. Hayashi

(1972), Mori (1978), Maru (1981) and Nakao (1982), also report on *C. sandai*. Biological data on these two species are compared in Table 1 with data on *C. fluminalis* and *C. fluminea* from southern China largely derived from Morton (1973; 1977a; 1982; 1983).

Thus, *C. japonica* (like *C. fluminalis* in the Pearl River, southern China) is a brackish water species with the ability to tolerate saline (70% sea water) conditions (Asahina, 1941; Kado and Murata, 1974; Matsushima, 1980). *C. leana* (like *C. fluminea*) on the other hand is essentially a fresh water species with a very much reduced capability of tolerating saline conditions up to 15% (Kado and Murata, 1974; Matsushima, 1980).

C. japonica apparently, even after up to 9 years growth rarely attains a shell length in excess of 30mm (Utoh, 1981), whereas *C. fluminalis* in China can attain a maximum shell length of 54mm. Such discrepancies are not critical, however, Alimov (1974), as pointed out earlier, having shown that growth is dependent upon temperature. Thus in higher latitudes *C. fluminalis* (and *C. japonica*) attains a smaller maximum size (Zhadin, 1965) than *C. fluminalis* in southern China (Morton, 1982). The same is true of *C. fluminea* in N. America (Britton and Morton, 1979).

C. fluminalis (Morton, 1982) and *C. japonica* (Utoh, 1981) live for over 8 years, possibly up to 10; they both produce 1 growth ring/annum, correlated with a single breeding season in the colder months of the year. Maru (1981) reports that in Lake Abashiri, *C. japonica* matures at a length of 15mm, three years after hatching. *C. fluminalis* and *C. japonica* are essentially dioecious, the former (Morton, 1982) possessing a small % of hermaphrodites as is typical of many fresh water, otherwise dioecious, bivalves, e.g., *Dreissena polymorpha* (Antheunisse, 1963), *Geloina* (Morton, 1985) and *Anodonta* (Dudgeon and Morton, 1983). In *C. fluminalis*, Morton (1982) has detected a trend towards protogyny so that a greater % of young animals are female, and a greater % of older individuals are male. Neither *C. fluminalis* nor *C. japonica* incubate larvae in the ctenidia, though Morton (1982) has shown that in *C. fluminalis*, ctenidial glands typical of those of the incubatory *C. fluminea* (Morton, 1977a; b; c) do develop, but for some as yet unknown reason. Possibly under extreme environmental conditions, larvae can be retained. It is (only) possibly significant that Miyazaki (1936) has suggested that *C. sandai* (from L. Biwa) is non-incubatory and yet produces non-swimming larvae. This anomaly has been commented upon before (Morton, 1979). Is it possible that in a lake environment *C. fluminalis* is incubatory? The problem of *C. sandai* has to be resolved, though this may be difficult as the "species" is apparently being replaced by *C. leana (C. fluminea)* with progressive eutrophication of Lake Biwa (Itasaka, Sugita, Okumura and Hori, 1980; Mori, 1978).

C. fluminea and *C. leana* similarly possess essentially the same characteristics. Both are smaller species, reaching in Hong Kong a maximum shell length of 35mm and in Japan between 26mm (Ikematsu and Yamane, 1977) and 40mm (Fuziwara, 1978). The species breeds in summer (Tamura, 1959; Ikematzu and Kammakura, 1975; Ikematzu and Yamane, 1977), typically in two peaks in early and late summer (Kaurajiri, 1948) though Fuziwara (1975; 1977; 1978; 1979) has shown that almost continuous breeding is possible when temperatures exceed 19ºC. It seems possible that temperature is critical in determining the length of the breeding season of this species there being minimum and maximum temperatures below and above which reproduction is possible. Morton (1977a) working on a reservoir population of this species suggested that it is a protandric hermaphrodite in contrast to other workers who considered it either dioecious (Lee and Chung, 1980) or a simultaneous hermaphrodite (Ikematsu and Yamane, 1977; Kraemer and Lott, 1977; Kraemer, 1978). This matter has now at least been partly resolved (Morton, 1983). In Hong Kong, the species is dioecious in lakes with a large (30%) percentage of hermaphrodites. Thus, since juvenile males attain maturity before juvenile females, gonad smears to determine sex would suggest protandry (Morton, 1977a). This is not so, however. In streams, no males occur in the population and the species can in these situations be described as hermaphrodite with an equal percentage of females. It seems possible that *C. fluminea* has an extremely variable sexuality, enabling it to survive a wide range of environmental conditions. This has been noted by both Morton (1983) and Ikematsu and Yamane (1977) and Fuziwara (1979) for *C. fluminea* and *C. leana* respectively. However, one thing is clear, *C. fluminea* (and *C. leana*) broods fertilized eggs in the inner demibranchs to a D stage crawling pediveliger. Such juveniles are released at a characteristic length of 200μm in both *C. fluminea* (Morton, 1977a) and *C. leana* (Fuziwara, 1977). Glands in the inner demibranchs possibly serve to nourish the juveniles; unreleased, dead juveniles result in the formation of cysts to encapsulate them (Morton, 1977c; Britton, Barcellona, LaGrone and Hagan, 1981). These in turn are autotomised from the gill. *C. fluminea* produces two growth rings/annum, reaches maturity at a shell length of approximately 10mm and lives for but up to 3 years. Age is not reported upon for *C. leana* in Japan, but Fuji (1957) working on *C. japonica* showed that the population of this species had three age classes. However, other workers (Utoh, 1981) have shown that *C. japonica* lives for 8 or 9 years. Is it possible that Fuji was in fact working on *C. leana*, the taxonomy of these species being at that time completely confused anyway? If so, then it is clear that *C. fluminea* and *C. leana* share almost identical characters.

Thus on biological grounds (as with conchological criteria) it is suggested that in Japan but two species of *Corbicula* occur, i.e., *C. fluminalis* and *C. fluminea*, which are equivalent to what are at present called *C. japonica* and *C. leana*. Much contemporary biological literature from Africa and Asia similarly indicates that two species are present throughout. These too can be allied to *C. fluminalis* and *C. fluminea*. Figure 1 indicates the numbers of species presently thought to occur in each country here discussed.

BIOFOULING OF *CORBICULA* IN ASIA

There are no records in the literature of *Corbicula* causing problems of biofouling in its natural range. To the contrary, in its introduced range of N. America, *Corbicula* is a serious pest, these problems being reviewed by Sinclair and Isom (1963) and Morton (1979a).

Two reasons, possibly, account for this. First, in its natural range, *Corbicula* will be subject to the natural checks of disease, parasitism and predation that maintain a population balance. Only in the introduced range, free of these constraints can the population balance be overturned such that the invasive species undergoes a population "explosion". Second, the major centres of urban population in Asia are at river mouths. Power stations erected here would not be invaded by *C. fluminalis* since this estuarine species does not possess the attributes necessary for fouling existence i.e., it is long-lived and dioecious with external fertilization. *C. fluminea* on the other hand though possessing all the advantages for fouling i.e., a short life span, rapid development, hermaphrodite and the release of brooded pediveligers is similarly excluded because of a low salinity tolerance. The widespread use of salt or estuarine waters for industrial cooling purposes thus effectively excludes *Corbicula fluminea* as a significant biofouling agent in Asia.

INTRODUCED *CORBICULA*

To date, species of *Corbicula* have been introduced into three significant areas (Fig. 1).

1. *North America*. Britton and Morton (1979; 1982) have shown that the species of *Corbicula* introduced into North America is *C. fluminea*. Previously called by a number of other names, e.g., *C. leana* and *C. manilensis* (both of which are considered junior synonyms of *C. fluminea*) (Morton, 1979b) this species matches in every respect the biological characters of *C. fluminea* (Table 1). It has become a very important biofouling pest throughout its range in North America.

2. *South America*. Counts (1980) records 20 species of *Corbicula* from South America, though generally speaking the continent is not within the range of *Corbicula* s.s. and the family is here represented by *Neocorbicula* Fischer, 1887 (Parodiz and Hennings, 1965). Ituarte (1981) has reported the introduction of species of *Corbicula* into Argentina. This author considers that two species have been introduced, namely *C. fluminea* and *C. leana*. It is here concluded that *C. leana* is no more than the Japanese "form" of *C. fluminea* thereby suggesting that either *C. fluminea* in Argentina exists as two morphological forms or that *C. fluminalis* as well as *C. fluminea* has been introduced. More research on *Corbicula* in the La Plata River is required. Native S. American *Corbicula* are not known to be biofouling pests, but the potential problems of the introduced species have yet to be determined.

3. *France and Portugal*. Mouthon (1981) reports that a species of *Corbicula* has recently been introduced into the estuaries of the Dordogne, France and the River Tagus in Portugal, accompanied by various species of *Pisidium*. Mouthon concludes that this species is *C. fluminalis*. The two populations exhibit physiological and morphological differences, however, and thus more research is required to demonstrate whether either or both *C. fluminea* and *C. fluminalis* have been introduced into either or both sites. In this area, *Corbicula* can be considered to be reoccupying its old range (Zhadin, 1948; 1965).

A careful watch should be maintained for other *Corbicula* introductions elsewhere.

CONCLUSIONS

This review reaches but one conclusion. Throughout the generic range, i.e., Africa and Asia, there are two predominat species of *Corbicula*. These can be named *C. fluminalis* (Müller, 1774) and *C. fluminea* (Müller, 1774). A vast array of other *Corbicula* species names have been erected by conchologists on shell characters alone. I consider all of these invalid until such time as each and every one of them can be shown to be biologically different from *C. fluminalis* or *C. fluminea* which are now distinguished by a range of good characters not based on the shell, a feature clearly extremely variable in both species.

Two areas requiring caution are identified. First, it seems possible that both species can occur in the same river system e.g., the White Nile, (Mandal-Barth, 1954); *C. fluminalis* at the mouth, *C. fluminea* at the head. Since both are capable of some degree of salt tolerance, the former more so than the latter, it seems clear that in the middle reaches, the two species may overlap. Investigation of this mixed population could lead to erroneous conclusions. Some anomalies already exist, e.g., Mandryka (1981) reports two morphological groupings for *C. japonica* in coastal lakes of the Sea of Japan. Fuji (1957) reported that *C. japonica* lives for but 3 years whereas contemporary authors (Utoh, 1981) report that this species lives for over 8 years.

Second, it is clear that *C. fluminea*, as in Hong Kong (Morton, 1977a; 1983), can occur in lentic and lotic systems where sexual strategies are different. Possibly, *C. fluminalis* can do likewise in which case river and lake populations of a long lived, dioecious winter breeding species of *Corbicula* need careful assessment.

Possibly the species concerned is *C. fluminalis*, or at least a morphological form of that species, or it may be an isolated endemic species, as are supposed to be *C. sandai* from L. Biwa (Japan) (Mori, 1978) and *C. largillierti* from the lakes of the Yangtze River, China (Liu, Zhang, Wang and Wang, 1979).

Such populations require urgent attention to test the 2 species model, here argued for *Corbicula* in Asia.

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ELECTROPHORETIC VARIATION IN NORTH AMERICAN *CORBICULA*

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ABSTRACT

An electrophoretic study of 16 populations of *Corbicula* has revealed genetic variation in all but two populations. This study used starch gel electrophoresis to analyze 14 enzymes encoded by 21 loci. There was a high degree of similarity between most populations at most loci. There were, however, some loci, notably CAT, where eastern and western populations had a different allele at greatest frequency. There were also unique alleles, present at relatively high frequencies, in single populations. These data suggest 1) the possibility of multiple introductions of *Corbicula* into this country and, 2) the existence of several genetic races within any given population. There is also evidence for two species of *Corbicula* in this country. These data have possible importance to the success of control measures.

Corbicula is of interest to population geneticists and systematists for several reasons. It is a relatively recent introduction to North America, the earliest recorded collections being 1924 in British Columbia (Counts, 1981) and in 1938 in Washington state (McMahon, 1982). *Corbicula* is now almost universally found throughout the major river systems south of 40^0 latitude. It has, then, in roughly 45 years migrated across the United States. In doing so, these clams have had to successfully conform to a large variety of environmental conditions. The assumption has been that both the initial introduction and the subsequent migrations represent founder events (Smith *et al.*, 1979). The genetic structure of populations immediately following the bottleneck induced by a founder event and the rate at which variation is reintroduced into such populations are both important to our overall understanding of colonization as well as population genetic theory. *Corbicula* is an ideal system for investigating the genetics of founder events, partly because the timing of its spread has been so well documented (McMahon, 1982).

We do not know the reproductive strategy employed by *Corbicula* in this country. Recently, based on histological evidence, Kraemer (1979), Kraemer and Lott (1978), and Morton (1982) have suggested that North American *Corbicula* are simultaneous hermaphrodites and at least potentially self-fertilizing. If true, this would be interesting since there have been very few studies of founder events involving self-fertilizing species. In any event, this clam has a high fecundity (Aldridge and McMahon, 1978) and can quickly establish itself in favorable habitats. It is a weed species (*sensu* Harlan, 1965) and a highly opportunistic organism. One objective of the study described in this paper was to explore the amount and pattern of genetic variation in populations of North American *Corbicula*.

A second major question that was addressed here concerns the number of species of *Corbicula* in North America. The conclusion of the First International *Corbicula* Symposium was that only one species had been introduced (Britton and Morton, 1979). This conclusion has recently been challenged based on both electrophoretic and morphological evidence (Hillis and Patton, 1982).

There have been three previous published electrophoretic studies of North American *Corbicula*. The first (Smith *et al.*, 1979) surveyed five populations in the U.S. as well as five Asian populations. They reported no variation within or among U.S. populations although they did find some variation in clams in Asia. Hillis and Patton (1982) surveyed populations from the Brazos River, Texas, and likewise found no variations within each species, although they suggested that two species were present. McLeod and Sailstad (1980) collected a single population from the Catawba River, NC, monthly for one year. They reported genetic variation in the population at three of the seven loci examined.

MATERIALS AND METHODS

Clams from 15 populations were examined using horizontal starch gel electrophoresis. The populations were as follows: TOL = Lake Erie (Toledo), Ohio; DAY = Great Miami River (Dayton), Ohio; CHA = Catawba River (Charlotte), NC; GTF = Wateree (Catawba) River (Great Falls), SC; SAN = Wateree (Catawba) River (Santee), SC; WIL = Lake Waccamaw (Wilmington), NC; PUG = Caloosahatchee River (Punta Gorda), FL; CAD = Little River (Cadiz), KY; DGL = DeGray Lake, AR; LOP = Lake of the

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Pines, TX; LFF = Lake Fairfield, TX; AUS = Colorado River (Austin), TX; DR-1, DR-2 = Pinto Creek (Del Rio), TX; VVA = Verde Valley, AZ; RVC = Sacramento River (Rio Vista), California. Sample size ranged from 18-43, depending mostly on survival during transit. There was no indication of differential survival rates between the two morphs. Individuals from the Charlotte, NC population were included on every gel for reference.

Clams (whole bodies) were homogenized in an equal volume of cold 0.5 M tris HC1, pH 7.1 buffer (Hornbach *et al.*, 1980) and the samples stored at -45C until run (usually not more than 24 hours). Twenty-one loci were resolved using the methods of Selander *et al.* (1971) and Ayala et al. (1972), except for octopine dehydrogenase. The stain for octopine dehydrogenase was 20ml 0.2 tris HC1, pH 8, 30 mg octopine, 2ml NAD, 2ml MTT, 0.5 ml PMS. The loci and buffer systems employed were as follows: discontinuous borate/tris-citrate buffer (Poulik, 1957), phosphoglucose isomerase (GI-1, -2), phosphoglucose mutase (PGM), octopine dehydrogenase (OCT-1, -2); tris-borate buffer, pH 9.4 (Ayala et al., 1972), malic enzyme (ME), glutamate oxaloacetate transaminase (GOT-1, -2), total protein (TP-1, -2, -3), leucine aminopeptidase (Lap -1, -2), 6-phosphoglucose dehydrogenase (6-PGDH); tris-maleate EDTA buffer (Selander et al., 1971), malate dehydrogenase (MDH-1, -2), isocitrate dehydrogenase (IDH-1, -2), catalase (CAT), xanthine dehydrogenase (XDH), x-glycerophosphate dehydrogenase (X-GPDH).

Estimate of genetic distance, D, (Nei, 1972; 1978) and a cluster analysis (unweighted pair group method, Sneath and Sokal, 1973), were calculated using the BIOSYS-1 computer program of Swofford and Selander, (1981).

RESULTS

The generally accepted methods of interpreting gels were followed in this study. The general methodology and assumptions involved in interpreting banding patterns on gels and distinguishing monomeric and dimeric proteins, as well as identifying homozygous and heterozygous individuals have been extensively discussed (Scandalios, 1969; Manwell and Baker, 1970; Tracey *et al.*, 1975; Crawford and Wilson, 1977).

Table 1. Allele frequencies at each of the polymorphic loci. Populations are listed in the same order as in Table 2 and abbreviations are explained in the methods section. The n at PGI-1 designates a null allele and indicates that the locus was not resolved.

		POPULATION															
Locus[1]	allele	TOL	DAY	CHA	GTF	SAN	WIL	PUG	CAD	DGL	LOP	LFF	AUS	RVC	DR-1	DR-2[2]	VVA[2]
PGM	a											0.10					
	b	1.00	0.30	1.00	1.00	1.00	1.00	1.00	1.00	1.00	1.00	0.90	1.00	1.00		0.57	1.00
	c		0.70												1.00	0.43	
LAP-1	a			0.07												0.24	
	b	1.00	1.00	0.93	1.00	1.00	1.00	1.00	1.00	1.00	1.00	1.00	1.00	0.52	1.00	0.76	1.00
	c													0.48			
LAP-2	a			0.05	0.05					0.10						0.78	
	b	1.00	1.00	0.95	0.95	1.00	1.00	1.00	1.00	0.90	1.00	1.00	1.00	1.00	1.00	0.12	1.00
GOT-l	a			0.05	0.10	0.11										0.09	
	b	1.00	1.00	0.95	0.90	0.89	1.00	1.00	1.00	1.00	1.00	1.00	1.00	1.00	1.00	0.91	0.16
	c																0.84
GOT-2	a	1.00	1.00	1.00	1.00	1.00	1.00	1.00	1.00	1.00	1.00	1.00	0.03	1.00	1.00	1.00	1.00
	b												0.97				
PGI-1	a															1.00	1.00
	b	1.00	1.00	1.00	0.97	1.00	1.00	1.00	1.00	1.00	1.00		1.00	1.00	1.00		
PGI-2	a	1.00	1.00	1.00	0.97	1.00	1.00	1.00	1.00	1.00	1.00		1.00	1.00	1.00	1.00	1.00
	b				0.03							1.00					
CAT	a	0.68	1.00	0.97	1.00	1.00	0.93	1.00	1.00		0.24				0.10		
	b	0.32		0.03			0.07			1.00	0.76	1.00	0.97	1.00	0.90	0.82	
	c												0.03			0.18	1.00
6-PGDH	a	1.00	1.00	1.00	1.00	1.00	1.00	1.00	1.00	1.00	1.00	1.00	1.00	0.38	1.00	1.00	1.00
	b													0.62			
ME	a															1.00	1.00
	b	1.00	1.00	1.00	1.00	1.00	1.00	1.00	1.00	1.00	1.00	1.00	1.00	0.97	1.00		
	c													0.03			
XDH	a	0.18															
	b	0.82	1.00	1.00	1.00	1.00	1.00	1.00	1.00	1.00	1.00	1.00	1.00	1.00	1.00	1.00	1.00

[1] Locus designations are PGM = phosphogulcomutase, LAP = leucine aminopeptidase, GOT = glutamate oxaloacetate transaminase, PGI = phosphoglucose isomerase, CAT = catalase, 6-PGDH = 6 phosphoglucose dehydrogenase, ME = malic enzyme (NADP-dependent malate dehydrogenase), XDH = xanthine dehydrogenase.

[2] These two populations are the purple morph. All other populations are the white morph.

Fig. 1. Geographic variation in allele frequencies at the catalase (CAT) locus in *Corbicula*. The CAT-*a* allele is predominant in the eastern population and the CAT-*b* allele is the major allele in the west.

Therefore it is not necessary to repeat those discussions here.

Zones of activity on a gel, which varied independently of other such zones of activity, were considered to be encoded by a single gene locus. The fastest anodally migrating zone of activity was arbitrarily designated as the first locus encoding a particular enzyme, the next fastest as the second locus, and so on. Within a zone of activity, the most anodal band was designated the *a* allele, the next fastest the *b* allele, and so on until all bands in that zone were identified.

The quaternary structure of the proteins examined in *Corbicula*, at least where it could be determined by banding patterns of heterozygotes, was what would be expected for those molecules. There were very few heterozygotes found and only a limited number of loci were heterozygous. Specifically, heterozygotes were only found at LAP-1, LAP-2, CAT, PGM and PGI-2 and the banding patterns for heterozygotes at each locus was consistent with what has been reported in the literature (Scandalios, 1969; Selander *et al.*, 1971; Ferguson, 1980). For example, PGM had the double banded pattern expected of a monomeric molecule. The only exception to the expected patterns was at CAT, where the heterozygotes were double banded although CAT has been shown in mice to be a tetramer (Hoffman and Grieshaber, 1976).

There were distinct morphological types examined in this study, corresponding to the white and purple forms of Hillis and Patton (1982) and Fontanier (1982). The purple form was found as a distinct population in Verde Valley, Arizona, and was sympatric with the white morph at Del Rio, TX. No microhabitat difference such as was reported by Hillis and Patton (1982) was observed in the Del Rio population. The other 13 populations were exclusively the white morph. The white morph is the form that has been considered *C. fluminea* and I will refer to it as such. A total of 21 loci (10 monomorphic and 11 polymorphic) were resolved in the purple morph. The PGI-1 locus was never resolved in specimens of the white *C. fluminea*. Because of this lack of activity, even when white morph specimens were run on the same gel as purple morph individuals which stained for PGI-1, the PGI-1 locus in the white morph was considered to be coded for by a null allele (Manwell and Baker, 1970; Ferguson, 1980). PGI-1 provided a marker between the two forms. There was also a fixed difference at ME, with the purple form being monomorphic for the ME-*a* allele and *C. fluminea* monomorphic for the ME-*b* allele. There was a frequency difference at PGM between the two morphs (Table 1).

Electrophoretic variation was present in every population except Cadiz, KY, and Punta Gorda, FL. The variant loci were not identical in all populations (Table 1). For example, all populations were monomorphic for the PGI-1*a* allele except Lake Fairfield which was fixed for PGI-2*b* allele. Most populations were monomorphic for GOT-*b*. Three Catawba (Wateree) River populations, however, had the GOT-1*a* allele at a frequency of about 0.1. The purple morph from Del Rio, TX, also had the GOT-1*a* allele. There was one locus, CAT, where the two major alleles were segregated geographically into eastern and western populations (Figure 1). The western populations mostly had the CAT-*b* allele, while the eastern populations had the CAT-*a* allele at greatest frequency.

There was, actually, very little variation in any single population. The percent of polymorphic loci (99% criterion) per population ranged from 0 to 19% in *C. fluminea* and up to 22.8% in the purple morph (Table 2). The percentage of polymorphic loci did not appear to be biased by sample size (Table 2). The mean number of individuals heterozygous at a locus (averaged over all loci) in a population was extremely low. Only five populations had any heterozygous individuals (Table 2), and heterozygosity in those varied from 0.13% to 0.37%. Heterozygosity at a particular locus (*h*) is defined as $h = 1 - \Sigma X_i^2$ where X_i is the frequency of the *i* th allele, and average heterozygosity (H, the value reported in this paper) is the mean of *h* over all loci in a population.

Table 2. Genetic variation in each population of *Corbicula* . Del Rio-1 is *C. fluminea*, Del Rio-2 and Verde Valley are the purple morph.

Population	N	% Poly-morphism[1]	% Hetero-zygosity	Mean number of alleles/ locus
Toledo	39	9.5	0.37	1.09
Dayton	20	4.8	0	1.05
Charlotte	29	19.0	0.13	1.19
Great Falls	20	14.3	0.25	1.14
Santee	18	4.8	0	1.05
Wilmington	40	4.8	0	1.05
Punta Gorda	38	0	0	1.00
Cadiz	20	0	0	1.00
DeGray Lake	20	4.8	0	1.05
Lake of Pines	19	4.8	0.25	1.05
Lake Fairfield	20	4.8	0	1.05
Austin	31	9.5	0	1.09
Rio Vista	40	14.3	0	1.14
Del Rio-1	30	4.8	0	1.05
Del Rio-2	43	22.7	0.25	1.23
Verde Valley	19	4.8	0	1.05

[1] 99% criterion

Nei's (1972; 1978) standard genetic distance is generally accepted as representing the average number of codon substitutions per gene, detected electrophortically, since two populations diverged (Ayala *et al.*, 1975; Nei, 1976; Thorpe, 1982). The genetic distance, D, between populations of *C. fluminea* (Table 3), indicate that these populations have diverged from each other to varying extents (range of D = 0.001 - 0.185). The *C. fluminea* populations are, however, closer to each other than to the two populations of the purple morph (Table 3). There is also a rough separation of the *C. fluminea* populations into two geographic groups; an eastern group and a west-southwest group. This relationship is evident in the dendrogram (Fig. 2) drawn from the genetic distance between populations.

DISCUSSION

In the first electrophoretic survey of *Corbicula*, Smith *et al.* (1979) found no variation in the U.S. populations but did see variation in Asian populations. I used somewhat different techniques and also surveyed for some different enzymes and did find low levels of electrophoretic variation in most U.S. populations. The different results are not necessarily surprising in that different chemical conditions, such as changes in pH, can influence protein mobility on an electrophoretic gel. Similarities on gels may not be real,

Table 3. Nei's Genetic distance between populations of *Corbicula*. Numbers at top of Table correspond to populations in the same order as at the left. Del Rio-2 and Verde Valley are populations of the purple morph.

Population	1	2	3	4	5	6	7	8	9	10	11	12	13	14
Dayton														
Toledo	0.030													
Charlotte	0.071	0.056												
Santee	0.089	0.073	0.060											
Wilmington	0.069	0.056	0.001	0.060										
Punta Gorda	0.069	0.056	0.001	0.060	0.001									
DeGray L.	0.123	0.072	0.047	0.113	0.049	0.049								
L. of Pines	0.071	0.028	0.034	0.081	0.035	0.035	0.009							
L. Fairfield	0.176	0.126	0.100	0.170	0.101	0.101	0.050	0.060						
Austin	0.173	0.121	0.094	0.163	0.095	0.095	0.046	0.055	0.098					
Del Rio-1	0.090	0.119	0.089	0.158	0.090	0.090	0.050	0.057	0.097	0.098				
Del Rio-2	0.185	0.143	0.224	0.131	0.230	0.230	0.180	0.150	0.244	0.240	0.220			
Great Falls	0.024	0.006	0.050	0.065	0.050	0.050	0.101	0.049	0.154	0.151	0.145	0.168		
Rio Vista	0.160	0.107	0.079	0.149	0.082	0.082	0.030	0.040	0.082	0.079	0.083	0.213	0.138	
Verde Valley	0.284	0.246	0.191	0.147	0.196	0.196	0.196	0.197	0.257	0.249	0.251	0.134	0.253	0.237

although differences almost always are so and thus electrophoresis tends to underestimate variation (Ayala, 1982). Differences in results between Smith *et al.* (1979) and this present study may also be a reflection of the number of loci sampled and also different number of populations sampled in the two studies.

Variation was observed at different loci in different populations. For example, the XDH-*a* allele was found only in the Toledo population and was present there at a frequency of 0.18 (Table 1). There are two possible explanations to account for these apparently unique alleles. The first is that these alleles really exist in a number of populations at very low frequency and have only been detected where random drift has acted to increase the frequency of a particular allele. This hypothesis requires that the original bottleneck (introduction to the U.S.) was relatively large and non-restrictive. Genetic drift has been frequently cited as a mechanism to explain differences in gene frequencies between populations (Spiess, 1977; Beaumont, 1977; Beaumont, 1982; Lieb *et al.*, 1983). A second possibility is that these apparently unique alleles arose in the particular population in which they were found by mutations. Most of the populations surveyed had been established for less than 15 years when they were sampled. While it can be argued that the short period of time that the populations have been in existence necessitates a high *de novo* mutation rate for *Corbicula*, this is not the case. If one assumes a similar mutation rate for allozymes in *Corbicula* as has been observed in *Drosophila* (1.28x 10^{-6}, Voelker *et al.*, 1980), and makes reasonable assumption of genome size (10^4 genes), then the number of mutations per individual is equal to 0.026. Given both the fecundity and the large population sizes of which *Corbicula* is capable and the possibility of 0.026 mutations/individual, the detection of one new allele in a population which has been extant for 10-15 years (20-30 generations) does not seem unreasonable. Therefore, an abnormally high mutation rate is not necessary to account for the unique alleles. However, either relaxation of selection, such as that proposed by Carson (1975) in his

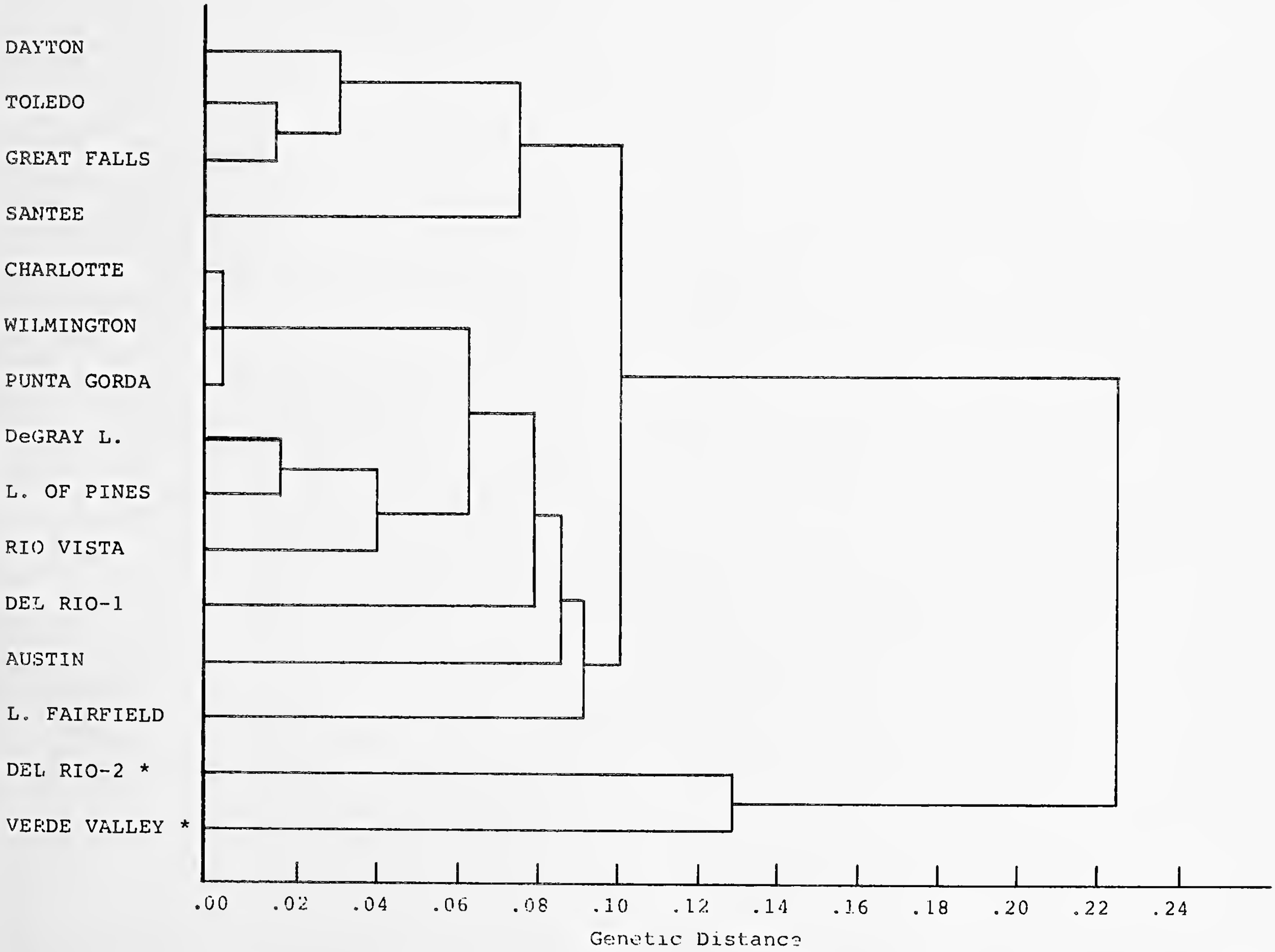

Fig. 2. Dendogram constructed from standard genetic distance estimates (Nei, 1972) using an unweighted pair-group method. Note that the purple morph populations (marked with an *) are distinct from the white morph populations.

founder flush-crash speciation theory or strong selection favoring the allele would seem to be important to allow the mutations to increase to the frequencies reported here (Table 1).

The pattern of variation (low to moderate polymorphism and little or no heterozygosity) is the same as been observed in facultative self-fertilizing species (Selander and Hudson, 1976; McLeod *et al.*, 1981). In these species a series of monomorphic races become established in a population with only infrequent cross-fertilization between races. These monomorphic races allow a population to maintain both genetic variability in case of an environmental perturbation and also gave large numbers of individuals that are highly adapted to the current conditions. Hybridization between races (reflected by the low level of heterozygosity) is both rare and a chance occurrence. Smith *et al.* (1979) suggested, and the data presented here also indicate, that *Corbicula* possesses generalist alleles that allow for wide phenotypic responses to environmental conditions. The fact that *Corbicula*, with a limited amount of genetic diversity, has been able to invade a number of different habitats should indicate that controlling the occurrence of this clam would be difficult. *Corbicula* would seem to be so phenotypically plastic that it can respond physiologically to many control measures. If the unique alleles do represent mutations then the potential ability of *Corbicula* to respond to control measures, as well as the potential to colonize new areas, increase. This is not meant to imply that mutations necessarily increase the homeostatic ability of *Corbicula*. As is frequently mentioned in textbooks, most mutations are deleterious (Dobzhansky *et al.* 1977). However, deleterious does not mean lethal but instead implies a reduction in fitness from an ideal genotype (Spiess, 1977). It is conceivable that a rare mutation would change the kinetic properties of a critical enzyme so that the enzyme could function in the new conditions presented by control efforts or a range extension and the animal would survive.

Control could potentially be even more difficult if the genetic variation reported here allows for differential response in a population to specific control measures. If having different alleles at a particular locus allow a few individuals to survive and continue the population, then the effect of control has been to select for a population resistant to that control measure. This resistance is what has occurred in insect populations treated with pesticides (Dobzhansky *et al.*, 1977). Correlations have been found between environmental components and allele frequencies at a specific locus in *Drosophila* (Steiner, 1979).

In the context of one theme of the symposium (control of *Corbicula*), the question of how many species of *Corbicula* exist in the U.S. is not entirely academic. There are, however, several problems which make answering that question difficult. One problem is the definition of a species when dealing with an organism that is capable of self-fertilization and apparently has a limited amount of outcrossing. The biological species concept (Mayr, 1970) depends on the ability or inability of organisms to interbreed. No truly satisfactory and accepted definition which can be applied to organisms such as *Corbicula* has been advanced. All attempts to distinguish species, whether they are based on comparative morphology, karyotype, interbreeding ability, behavioral or physiological differences, or electrophoretic similarity, have as a basic premise an assumption of underlying genetic differentiation. Electrophoresis has been shown to be efficacious in demonstrating genetic relationships and divergence (Ayala, 1972, 1982; Avise, 1974).

There are a number of studies which compare electrophoretic and morphological similarities between and among populations or species. As one might expect, in some studies isozymes and morphology are in close correspondence (Grudzien and Turner, 1983; Bryant, 1984), and in other studies there is no congruence (Gould *et al.*, 1974; Hornbach *et al.*, 1980). Examples of convergence in morphology, but distinctness in isozymes between species are known (McLeod *et al.*, 1980; Zimmerman and Nejtek, 1977). Enzyme electrophoresis differs from morphology in terms of providing systematic data. Morphological characters are often controlled by several to many genes and alleles at these loci may influence the phenotype in the same way so that a large number of genotypes can result in the same phenotype (Gottlieb, 1977). The phenotype in electrophoresis is represented by colored bands on a gel that indicate areas where an enzyme has catalyzed a particular reaction. Difference in mobility on gels are the result of changes in the gene coding for the polypeptide and so the mobility differences are a result of genetic differences (Ferguson, 1980). While it is true that electrophoresis has a number of limitations (see Ayala, 1982), the relationship between genotype and phenotype is reasonably straight-forward in electrophoresis especially when compared with morphology (Ferguson, 1980).

The presence of two species was suggested by Hillis and Patton (1982) based on both morphology and on the presence of fixed differences at six loci. The data presented in this study also suggests that there are two species present. Fixed differences were found at two loci (PGI-1 and ME) as well as major frequency difference at PGM. The enzymes considered here were not completely the same as those used by Hillis and Patton (1982) and so between their study and this one fixed differences have been found at eight loci. Nei's genetic distance (Table 3) indicates that the two populations of the purple morph were relatively closely related to each other ($\bar{D} = 0.135$) and were distinct from *C. fluminea* ($\bar{D} = 0.21$). While the presence of heterozygotes in some populations indicated that some outcrossing does occur, albeit infrequently, there were no heterozygotes in the Del Rio white morph population at PGI-1 or ME. There were heterozygotes within the purple morph population. If these were a single species it would not be unrealistic to expect to find hybrids in a sympatric population where heterozygotes do exist in one component of the population. There was information presented at the symposium by Britton, and Schofield and Britton (see paper in this volume) that indicates that the purple and white morphs have different juvenile growth rates, differential physiological responses to potassium and to sodium thiosulfate, and some segregation into habitats of different water quality. Hillis and Patton (1982) also found differences in shell length, width, height, and weight, as well as shell color and number of sulcations. Shell morphology, including color, is notoriously poor for delineating species in molluscs. In oysters, shell color, size, and individual shell dimensions are greatly influenced by local environmental factors (Galtsoff, 1964), and do not reflect electrophoretic relationship (Groue and Lester, 1982). However, the combination for morphologic, electrophoretic, physiological and ecological differences taken together seem substantial. It does seem pointless and even foolhardy to attach a species name to the purple morph. Since *Corbicula* is not endemic to the U.S., and was introduced from Asia, a much more thorough survey of Asian species is necessary before taxonomic relationships to Asian species can be established.

There are indications in the data that the east coast and Ohio Valley populations are distinct from the more western ones (Figs. 1 and 2). This suggests that the eastern populations have been isolated from the western ones and that most have probably orginated from other eastern populations. McMahon (1982) has suggested that east coast populations were founded from an Ohio River population (at Paducah, KY) via southern migration along the Mississippi River. It is possible that the Paducah population was formed from a California population (McMahon, 1982; Britton and Morton, 1982) and was isolated for a sufficiently long time to evolve the frequency differences now seen. It is equally possible that there were two separate introductions to this country; one on the west coast and a second into the Ohio River. Without a more complete survey of Asian populations it is impossible to choose between these two options. If the eastern populations do represent a second successful introduction then the presence of western population alleles at loci like CAT (Fig. 2) may represent recruitment from those populations through migration. It may also represent convergence through mutation and genetic drift.

There is, then, genetic variation in most populations of *Corbicula* examined in this study and, by extrapolation, in North America. There may also have been two successful introductions of *C. fluminea*, thus increasing the potential gene pool of U.S. *Corbicula*, as well as an introduction of a second species (possibly *C. fluminalis*?, Morton, 1977). The presence of genetic races in a population, as well as the existence of two species, increases the problem of controlling the occurrence of these organisms.

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A METHOD FOR EVALUATING THE SUBLETHAL IMPACT OF STRESS EMPLOYING *CORBICULA FLUMINEA*

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ABSTRACT

The feasibility of using the Asiatic clam, *Corbicula fluminea*, for monitoring point source discharges has been evaluated. Clams were transplanted into cages at several locations around the outfall of a proposed waste treatment plant in the Sacramento-San Joaquin Delta, California. Reproduction, shell growth, condition index (ratio of tissue weight to shell length), survival, and copper and zinc tissue concentration were evaluated for ten months. In addition, at one test site, the reproduction, growth, and condition index of a wild clam population was also determined. Comparison of sublethal parameters between the wild and caged clams demonstrated no significant difference ($P>0.10$).

Initiation of the operation of the proposed waste treatment facility was delayed; therefore, our study includes only predischarge data. However, in June, there was a strong settlement of the barnacle, *Balanus improvisus*, on the monitoring cages and clams. Barnacle fouling appeared to produce a clam stress gradient as we recorded a simultaneous decrease in clam reproduction, condition index ($P < 0.05$), and survival ($P < 0.05$), but not growth ($P > 0.1$), with increased fouling. The seasonal pattern in the estuary for *Corbicula's* copper and zinc tissue concentration was also determined. Metal concentration increased in the summer independent of both the clam's gut content and alterations in its biomass. In conclusion, we believe our technique may represent, with more work, a promising method for simultaneously monitoring alterations in clam tissue concentration and sublethal impacts.

The pollution of aquatic systems is of increasing concern. One aspect receiving considerable attention is the evaluation of toxic materials and their sublethal impact on aquatic invertebrates. A major problem is the development of methods for measuring alterations in the life history characteristics of aquatic organisms under field conditions. The Marine Mussel Watch (Goldberg *et al.*, 1978) and the Coastal Environmental Assessment Stations Program (Phelps and Galloway, 1980) were implemented to assess the impact of marine pollution using the bay mussel, *Mytilus edulis*, as a sentinel organism. The Marine Mussel Watch program attempts to identify areas with pollution problems by measuring alterations in tissue burden levels while the Coastal Environmental Assessment Stations Program attempts to develop methods for assessing the sublethal impact of these contaminants. Together, these programs appear to be making progress in identifying the impact of pollution on marine communities at the population level. Unfortunately, no comparable techniques are presently available for freshwater.

The objective of the present study was to begin the development of methods to ascertain the impact of pollution on freshwater communities by using the Asiatic clam, *Corbicula fluminea* (Müller). Specific objectives were to develop methods for simultaneously measuring alterations in *Corbicula* life history characteristics and tissue-burden levels. Cause and effect relationships may be more apparent if changes in both functions are measured simultaneously. In general, the methods employed in this study have been modelled after those of the Marine Mussel Watch and the Coastal Environmental Assessment Stations Program.

The freshwater clam was chosen as it appears a promising bioindicator candidate. First, as a filterfeeder, it is known to bioaccumulate both heavy metals and synthetic organic compounds (Burress and Chandler, 1976; Woodard, 1979; McCleneghan and Rectenwald, 1979; Leard *et al.*, 1980; Rodgers *et al.*, 1980; Cory and Dresler, 1981; Graney *et al.*, 1983; Hayes and Phillips, 1985). Second, although recently introduced, it has spread rapidly across the United States and is now an important benthic invertebrate in many major drainage basins. Consequently, the clam is easy to collect for study and alterations in its population dynamics may be of ecological significance. Third, the clam is relatively immobile and long-lived (often > 3 years, Eng, 1979) and, therefore, an excellent long-term water quality monitoring organism. Fourth, methods for spawning and culturing *Corbicula* in the laboratory are under development (Foe, 1983;

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Foe and Knight, 1985; 1986b). Considerable other basic physiological information, relative to other freshwater invertebrates, is also available (Mattice and Dye, 1975; McMahon, 1979a,b; Gainey, 1978a; Foe and Knight, 1986a). This information could be valuable in the future for interpreting monitoring observations. Finally, *Corbicula* has a salinity tolerance of 0 to, at least, $3\ ^{0}/_{00}$ (Gainey, 1978a,b). No other freshwater bioindicator candidate has this wide a salinity distribution. This trait is essential for evaluating toxicity in the upper portion of estuarine systems, often the area most heavily impacted by pollution (Förstner and Wittman, 1979).

METHODS AND MATERIALS

Location. The clams evaluated in the present study were collected in early February, 1981, from a clean, subtidal, sand beach off the main channel of the Sacramento River near Sherman Lake, California (Fig. 1). This population has been identified electrophoretically as Hillis and Patton's (1982) white *Corbicula* morph (McLeod, 1986). The clams were transferred to cages, which were suspended for ten months around the Contra Costa Sanitation District outfall located in New York Slough. Five stations (number 1 through 5) were established around the outfall in subtidal areas characterized by continuous water movement but minimal wave action. Temperature and salinity were recorded weekly at each site. Differences in temperature between stations were compared by Analysis of variance (ANOVA) and Duncan multiple range test.

Cages Units. Seven cages (66 clams/cage) were placed at each station. In March the cages containing clams for the growth evaluation were lost from station 4. The remainder of the cages lasted until December when all cages from station 3 were lost resulting in the termination of the experiment.

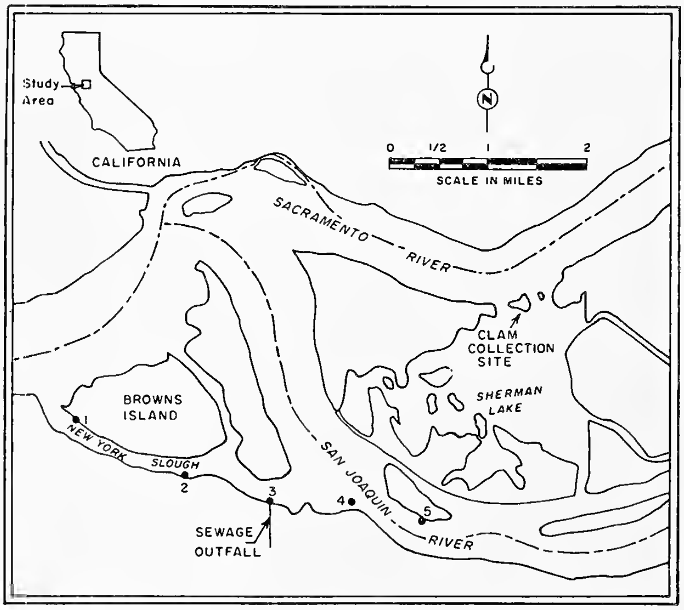

Fig. 1. Map of the Western Sacramento-San Joaquin Delta, California showing the monitoring stations (1-5), the waste outfill, and the clam collection site.

Cage units were constructed of plastic fluorescent light egg-crate-type panelling and from polyethylene screen with a 3 mm X 4 mm mesh (Fig. 2a,b). Cage sections were bound together with surgical rubber tubing and stainless steel bolts. Individual cage compartments measured 41mm X 41mm X 22mm and were each numbered to aid in identifying individual clams. During field exposure, each cage unit was secured about half a meter off the bottom in an upright position by metal rebar stakes driven into the substrate.

The cages were colonized during the study by several invertebrates including juvenile *Corbicula*, the barnacle *Balanus improvisus*, the amphipods *Corophium spinicorne* and *C. Stimpsone*, and the hydroid *Cordylophora lacustris.* These epizooites restricted water flow through the cages and, undoubtedly, competed with clams for suspended food. Fouling was minimized by cleaning the cages (but not the clams) monthly with a coarse nylon scrubbrush.

SUBLETHAL INDICES

1. *Reproduction.* Clam reproduction was estimated by a combination of laboratory and field experiments exploiting the fact that *Corbicula* incubates its young on its inner gill demibranchs (Eng, 1979). The development rate of the marsupial larvae was estimated by inducing adults to spawn in the laboratory by means of thermal shock (Loosanoff and Davis, 1963) and recording daily the percentage of adults with young on their gills. Simultaneously, replicate sets of petridishes placed on the aquarium bottom were monitored to determine when larvae first settled. The results of these experiments were used to establish the sampling frequency necessary for estimating field reproduction.

Field reproduction was determined by transplanting 400 clams (30 to 35 mm shell length) into four cages at each station. Previous work demonstrated that this size class has the highest fecundity (Foe and Knight, 1981). Ten individuals were collected weekly between 1 April and 30 November from each station and preserved in 5% Formalin for subsequent analysis. In addition, concurrent reproduction samples were taken from the wild population at station 5 to compare the reproduction of caged and natural clam populations. Cages were sampled sequentially to minimize clam disturbance.

Corbicula's reproductive output was estimated quantitatively only for the caged and wild clam population at station 5. Here, the number of incubated larvae in one randomly selected gill from each of the five clams was counted by extrusion onto a microscope slide followed by resuspension in 100 ml of saturated sugar solution. After vigorous agitation, a 5 ml subsample was drawn and passed through a 60-μm mesh screen. The larvae were enumerated using a dissecting microscope at 30 X power magnification. This process was repeated until either 100 young or the entire sample was processed. Repetitive larval counts of gill extracts with known numbers of larvae present demonstrated that the procedure had an accuracy of about 90%. To improve our estimate of *Corbicula*'s reproduction, an additional five clams were examined during periods of intense clam reproduction. Reproductive output was averaged for each week and

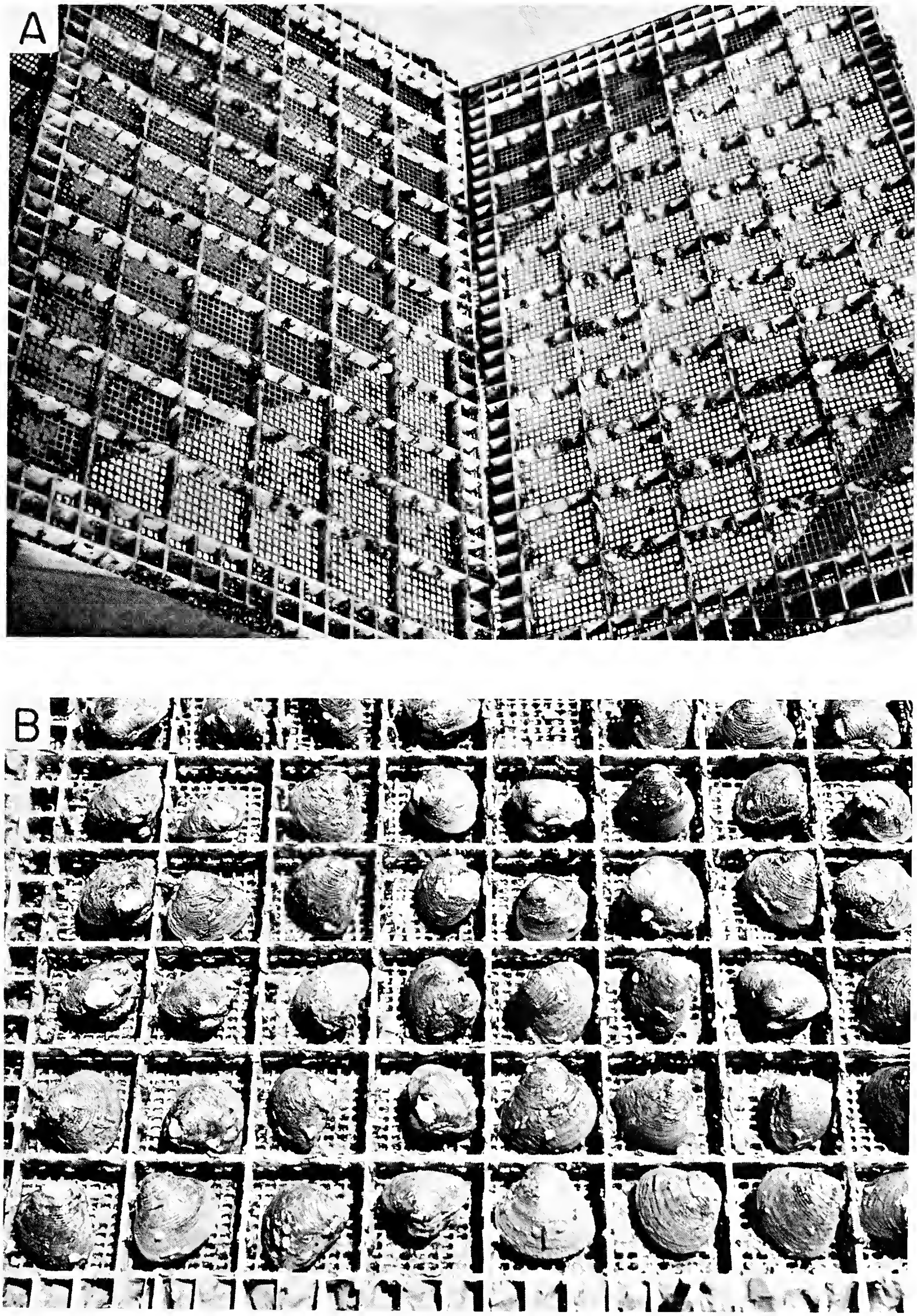

Fig. 2a. Cage before the addition of clams. **2B.** Cage with clams after several months of field exposure.

summed over the entire season to estimate the clam's annual fecundity.

At the remaining four sites, a more qualitative estimate of reproduction was employed because of the large effort involved in direct counts of marsupial young. These estimates were made by inspecting the gills from five animals weekly and assigning them a score from 1 to 5 based on a subjective estimate of the number of larvae present. Scores of 1, 2, 3, 4, and 5 represented 0-1000, 1000-10,000, 10,000-20,000, 20,000-30,000, 30,000-40,000 young per adult, respectively. These scores were averaged weekly for each station and summed over the entire season to estimate annual reproduction.

2. *Shell Growth.* Seventy-six individuals (2 clams in each 1 mm size class between 3 and 40 mm) were deployed in cages at each station and their shell growth determined every 60 days using vernier calipers. After ten months exposure, growth was averaged for clams in each initial 5 mm shell size class, and the difference in growth between stations compared using ANOVA and Duncan multiple range test.

At station 5, the growth of caged *Corbicula* was also compared with that of transplanted tethered individuals to ascertain the effect, if any, of caging on clam growth. Previous work (Foe and Knight, unpubl.) has demonstrated that the growth of tethered clams is not statistically different from that of the wild population. The tether method consisted of cementing a small plastic disk with an identifying number and a short length of 5 lb monofilament fishing line (20-30 mm) to each clam shell with fast-drying Duro Super glue® . The monofilament fishing lines were attached to a heavier nylon line with stainless steel fishing swivels, and the unit staked taut along the bottom. The method has the advantage of allowing the clams to burrow and move about naturally in the sediment. Also, the tether unit is easily retrieved for measurement of individual clam growth.

One hundred individuals (four in each 1 mm shell size class between 15 and 40 mm) were tethered, and their growth was measured every 60 days. Differences in growth between tethered and caged clams at station 5 was analyzed by a paired t-test using the recorded growth rate of each 5 mm shell length size class.

3. *Condition Index.* Condition index is defined as the ratio of dry tissue weight to shell length. A decrease in the ratio is indicative of a deterioration in health of the bivalve population (Bayne *et al.*, 1976). Condition indices were determined by transplanting at each station six groups of 25 animals (3 individuals in each 5 mm shell length size class between 3 and 40 mm) and randomly selecting one group every 60 days for analysis. In addition, twenty-five wild clams from station 5 were also collected on each occasion to compare their condition index with that of caged clams. Condition indices were calculated by measuring individual clam shell lengths with vernier calipers and determining ash free dry weight from the difference in clam tissue weight dried at 60°C and ashed at 480°C. For each group, log weight was regressed against log shell length. Differences in the slope and intercept of the regressions from each of the five stations were compared bimonthly using an analysis of covariance. If a difference was detected, then a pairwise comparison of the individual lines was conducted to determine which lines were different after correcting the overall significance level of the test with a Bonferroni adjustment (Neter and Wasserman, 1974). Lines which were not different were combined to calculate a common regression equation.

4. *Mortality.* Clam mortality was assessed every two months in the cages by recording the number of clams dying during

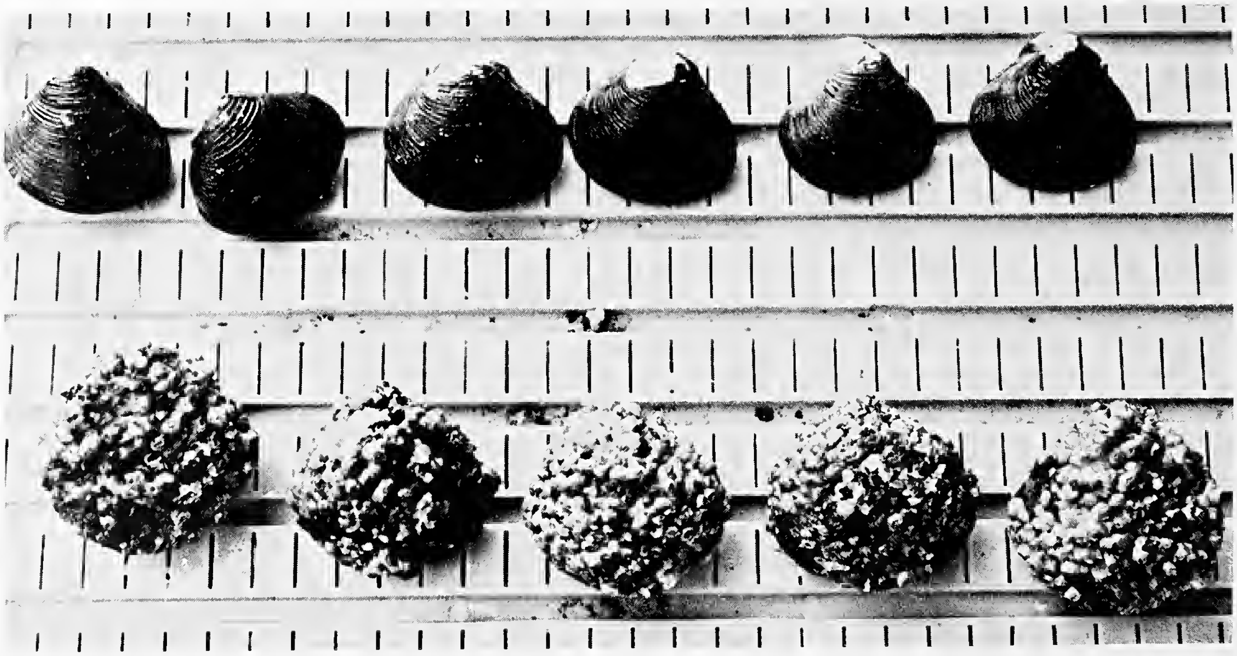

Fig. 3. Comparison of barnacle infestation on clams during August from station 1 (lower row) and station 5 (upper row).

the interval as determined from the number of empty shells or missing animals and dividing this by the number alive at the start of the period.

HEAVY METAL TISSUE CONCENTRATIONS

Field Procedures. Seasonal changes in copper and zinc tissue concentration were monitored by transplanting 160 clams (30 to 35 mm shell length) into cages at each station. In addition, at station 3, animals were attached to tethering units adjacent to the cages to determine if the metal content of clams buried in the sediment differed from those of clams held in cages in the water column. Twenty transplanted clams from each group were collected every 60 days and frozen at -20°C in acid-washed ziplock plastic bags for future analysis. Whenever possible, wild clams were also collected from station 3. Comparisons of metal concentration between wild and transplanted individuals provide an indication of how representative the metal content of transplanted clams are of the natural population. Finally, an additional 20 animals were harvested from the cages placed at station 3 in August and their stomach and intestinal tracts dissected out with stainless steel scalpel and forceps. Their tissue concentration was compared with that of ungutted caged clams to determine whether increases in metal concentration reflected an increase in the metal content in the animals' gut or an actual increase in clam tissue concentration.

LABORATORY PROCEDURES. Mean copper and zinc tissue concentration was determined bimonthly from 5 samples of 3 homogenized clams each using the procedures outlined in the California Marine Mussel Watch (Stephenson *et al.*, 1979). At least five procedural blanks were employed during each assay to detect contamination arising during the digestion or analysis phase. No detectable amount of either metal was ever reported for the blanks. Metal concentrations were determined by the flame method on a model 751 Instrumentation Laboratories atomic adsorption spectrophotometer and reported as μg metal/gm dry tissue weight (ppm). Differences between sample means were analyzed with ANOVA and Duncan multiple range test.

RESULTS AND DISCUSSION

To date, only background information on *Corbicula* sublethal indices and its heavy-metal concentration have been obtained for the New York Slough area. A delay in initiating the operation of the treatment plant provided us little opportunity to evaluate our monitoring method in a waste discharge. However, in June, the settlement of the barnacle, *Balanus improvisus*, provided an opportunity to evaluate our method in another stress gradient. Greatest barnacle recruitment occurred at station 1 and decreased rapidly eastward with no settlement at site 5 (Fig. 3). The juvenile barnacles were removed from the cages but left on the clams, as we did not wish to unduly disturb the test animals. However, by August, the barnacles had grown considerably and appeared to be stressing *Corbicula* by preventing the complete closure of the clam's valves. All barnacles were cleaned off the clams; however, it appeared that the barnacles had already stressed many *Corbicula*. Although this was not the kind of stress we had originally intended to measure, we reason that our sublethal indices should exhibit a response in any stress gradient. Therefore, we have analyzed, instead, *Corbicula*'s sublethal response to *Balanus* settlement.

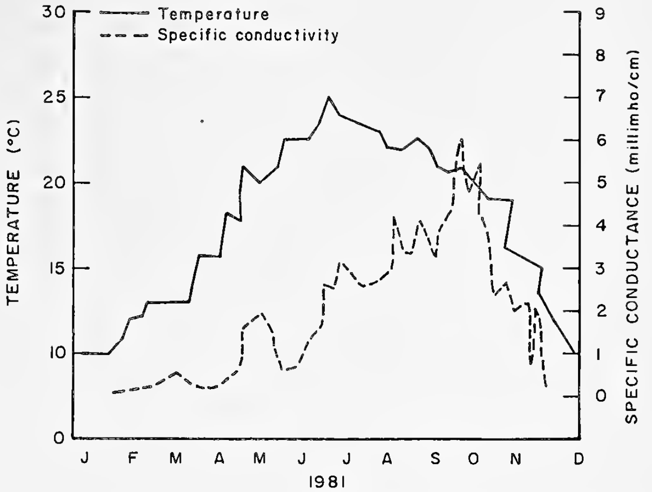

Fig. 4. Seasonal pattern of temperature (^{0}C) and specific conductance (millimho/cm) at station 5.

Ambient water temperature was similar at all five stations on each occasion measured (Fig. 4, $P>0.25$, ANOVA). Water temperature rose rapidly after January, peaked at 25^{0}C in July, and declined quickly in November and December. Electrical conductivity increased at the more seaward stations. However, the largest difference recorded between stations 1 and 5 was only 7%. At no time did any value exceed $3\ ^{0}/_{00}$ salinity, well within *Corbicula's* tolerance (Evans *et al.*, 1979).

SUBLETHAL INDICES

1. *Reproduction.* Laboratory experiments demonstrated that the development time from egg to pediveliger larva was between 3 and 8 days. The first eggs appeared in the gills on day 3 and were all released by day 11 (solid line, Fig. 5). This established an upper limit of eight days for maturation. The first pediveligers were observed settling in petri-dishes on the aquaria bottom on day 6 (broken line, figure 5). The differences in time between when eggs were first observed in the gill pouches and young on the aquaria bottom provided the lower estimate of 3 days for larval development. These laboratory estimates of *Corbicula*'s marsupial development rate were used to establish the seven day sampling periodicity used subsequently for collecting field reproduction samples.

The wild clam population at station 5 spawned twice in 1981 (Fig. 6). The first spawning occurred from mid-April to May and the second from August to September. Sixty percent of the larvae (36,521 larvae per adult) were produced in the first reproductive periods and forty percent in the second (24,660 larvae per adult). This was different from 1980 at station 5 when 38% of the fecundity occurred in the first

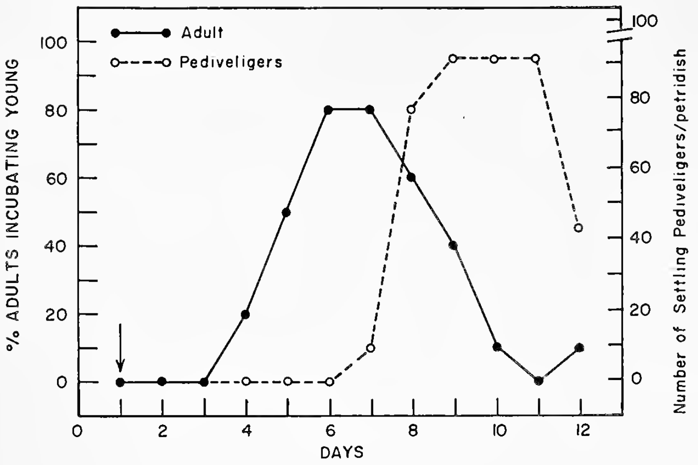

Fig. 5. Percentage of adult clams incubating young and the number of settled pediveliger larvae petri-dish^{-1} on consecutive days after thermal induction of spawning.

period and 62% occurred in the second (Foe and Knight, unpubl.). Also, total reproductive output was somewhat greater in 1980 at 74,810 larvae per adult (Foe and Knight, 1981). However, both fecundity estimates appear similar to those reported for *Corbicula* from north central Texas (Aldridge and McMahon, 1978).

Comparison of reproduction rates for wild and caged clams at station 5 (Fig. 6) demonstrate a greater overall reproduction output in the wild population. This was primarily due to a failure of the caged clams to spawn as intensively as the wild population during the second reproductive period. This is, tentatively, interpreted as being due to cage induced stress. Estimates of reproductive activity for clams from the remaining four stations indicated that spawning was also strong and similar at all sites during the first reproductive period (30,000-40,000 young adult $^{-1}$). However, clam reproduction appeared to decrease progessively at more westward stations in the estuary during the second spawning period. Fall reproduction was 0, 0, 5-12,000, 20-30,000 and 24,660 young per adult at sites 1, 2, 3, 4 and 5, respectively. The decrease in reproductive activity is attributed to the progressive increase in *Balanus* fouling.

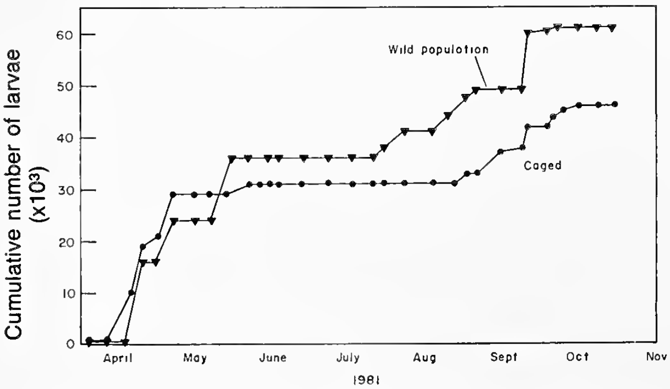

Fig. 6. Comparison of reproduction for caged and wild clams at station 5.

2. *Shell Growth*. Caged *Corbicula* began to grow in April, when the water temperature rose above 15°C, and continued through November. Growth was greatest for smaller clams and decreased as shell size increased. Shell formation appeared normal for clams of all size classes, except some individuals of a 15 to 20 mm shell length who exhibited an abnormally concave growth form. This deformation did not appear to affect their subsequent growth.

The growth of caged and tethered clams was compared at station 5 to determine the effect of caging on clam growth. Previous experiments have demonstrated that the growth of tethered clams is similar ($P>0.25$) to that of the surrounding wild population (Foe and Knight, unpublished). The growth of caged clams was slightly less than that of tethered ones, however, not significantly so ($P>0.1$, paired t-test). Previous experiments have demonstrated that the growth rate of small clams (4 to 9 mm shell length) is unaffected by caging (Foe and Knight, 1985). Therefore, it was concluded that holding *Corbicula* in cages did not significantly alter their growth pattern. So, we feel justified in presenting the growth rates derived from caged individuals as representative of the natural population.

Comparisons of growth between stations revealed a decrease at sites 1 and 2 in both August and October. This decrease is attributed to the *Balanus* infestation. However, the difference in growth was not significant when evaluated over the entire transplant period (7 February to 15 December, $P>0.1$, ANOVA). Therefore, an annual size-specific growth curve (Fig. 7) for *Corbicula* has been calculated for the Sacramento-San Joaquin Delta in 1981 by averaging the growth of all clams in each 1 mm shell size class using cage

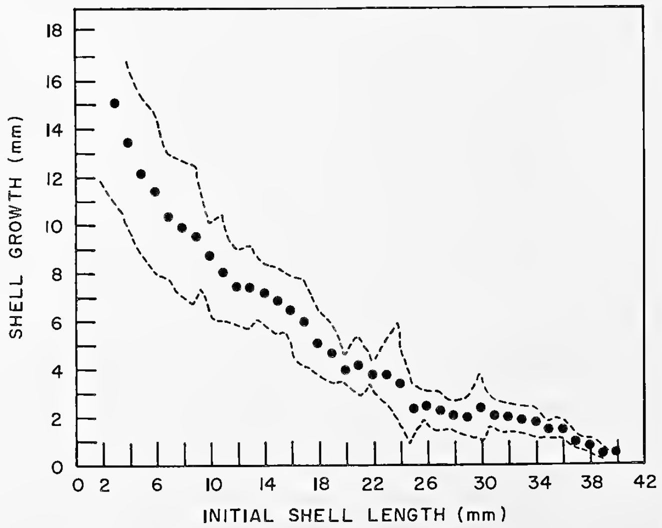

Fig. 7. Annual size-specific growth of *Corbicula* caged in the Western Sacramento-San Joaquin Delta, California during 1981. Data points are the mean of 5 to 10 clams; the dotted lines are ± standard deviation.

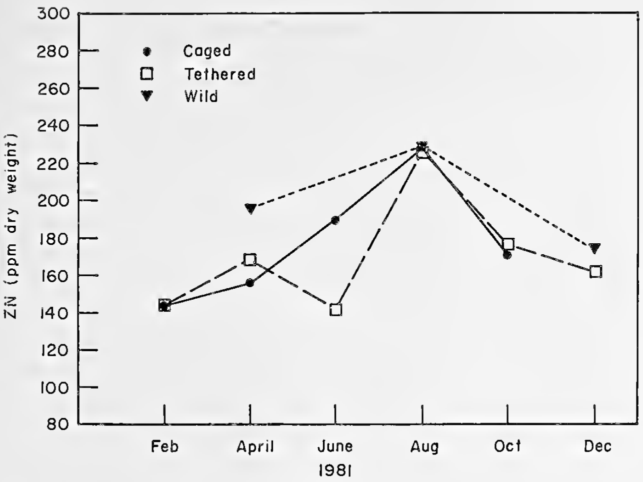

Fig. 8. Zinc concentration (µg mg⁻¹) for caged, tethered and wild clam populations at station 3.

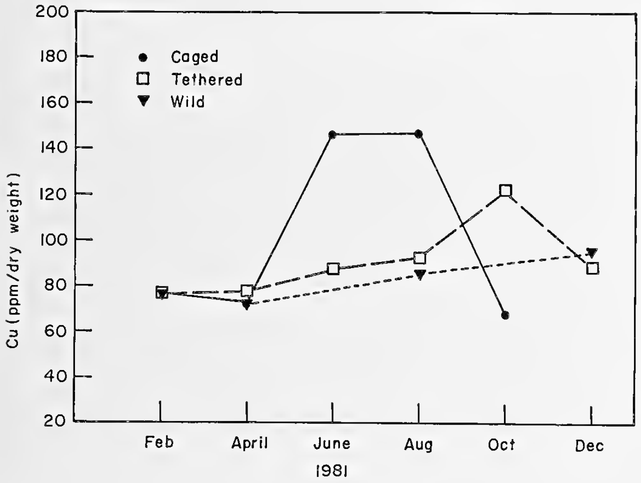

Fig. 9. Copper concentration (µg mg⁻¹) for caged, tethered and wild clam populations at station 3.

growth from stations 1, 2, and 5 and tether data from site 5 (the growth cages for station 3 were lost in November, and from station 4 in March). The resulting growth pattern is similar to that report for clams from the Sacramento-San Joaquin Delta during 1980 (Foe and Knight, 1981).

3. *Condition Index*. Comparison of the condition index regression equations for caged and wild clams at station 5 demonstrated that both had similar length-weight ratios ('b' regression coefficients) throughout the year (Table 1). This indicates that caging had little effect on *Corbicula's* condition index. However, the data does reveal a strong seasonal alteration in the weight of a 'standard' 30 mm clam at station 5 (Table 1). The decrease in weight appeared greatest during the second reproductive period (August through September). Decreases in clam weight were also recorded in December. We have noticed a similar phenomenon during other years and now tentatively attribute this to a lack of food during the winter months (Foe and Knight, 1985).

Comparison of the regression equations between stations revealed no significant difference in clam condition indices through June ($P > 0.1$, analysis of covariance, Table 1). However, in August there was a significant decrease in weight at the more westerly stations ($P < 0.05$). This decrease occurred simultaneous to the *Balanus* fouling, suggesting that the barnacles imposed the stress on *Corbicula*.

4. *Mortality*. Mortality through June averaged 1% (Table 2). Between August and October there was a significant increase in mortality at the more westward stations ($P < 0.05$, ANOVA) which corresponded with the gradient of *Balanus* fouling. Mortality decreased again in December after barnacle removal.

SUBLETHAL INDEX SUMMARY. The biological indices provide a coherent picture of *Corbicula* stress. All four indices decreased during barnacle fouling at the more heavily infested stations. Differences in condition index and mortality

Table 1. Summary of condition index regression equations for *Corbicula*'s ash-free dry weight (gms) regressed against shell length (mm) and predicted weight derived from those equations for a 'standard' 30 mm clam.

Month (1981)	Station	Regression equation[1]/ b	a	Predicted weight (mg)
April	1,2,3,4,5,5W[2]/	3.00	4.93	317
June	1,2,3,4,5,5W	2.66	4.93	280
August	1,2[3]/	2.91	4.83	294
	3,4	2.91	4.81	310
	5,5W	2.95	4.83	334
October	1,2	2.99	5.00	261
	3,4,5,5W	2.84	4.75	286
December	1	2.95	5.00	225
	2,3,4,5,5W	2.50	4.32	238

[1]/ log weight (gms) = b (log shell length (mm)) - a.

[2]/ Wild population at Station 5.

[3]/ Differences between stations in regression coefficients during the same sampling period indicate statistical differences in at least one of the regression values at the 5% level.

Table 2. Mortality (%) of caged *Corbicula* in New York Slough. Values are for the percentage of deaths occurring during the previous two month period.

Month (1981)	STATION 1	2	3	4	5
April	0.5	0.8	0.9	1.1	0.9
June	0.5	2.6	2.5	0.5	1.1
August	0.4	1.5	1.2	0.0	0.7
October	61.0	28.0	15.5	6.7	0.6
December	6.6	4.9	—	2.8	1.6

Table 3. Copper tissue concentrations (μg/gm) for caged *Corbicula* in New York Slough.

Month (1981)	STATIONS				
	1	2	3	4	5
February (pretransplant)	76.6 a[1,2]/ ± 19.0	76.6 a ± 19.0	76.6 a ± 19.0	76.6 a ± 19.0	76.6 a ± 19.0
April	78.4 a ± 15.2	77.5 a ± 7.3	75.3 a ± 9.0	85.5 a ± 13.6	94.5 a ± 6.9
June	81.5 a ± 6.4	145.9 b c ± 16.7	146.2 b c ± 15.0	239.9 d e ± 19.2	118.0 a b ± 14.0
August	114.4 a b ± 17.8	148.6 b c ± 17.3	146.7 b c ± 10.0	275.4 e ± 19.4	120.4 a b ± 18.6
October	103.3 a b ± 9.6	107.5 a b ± 24.2	67.7 a ± 4.4	172.8 d ± 14.8	150. a b ± 16.4
December	89.7 a ± 10.5	95.0 a ± 12.8	— —	219.2 d ± 40.0	66.4 a ± 7.1

Mean ± standard error.
Values with the same letter are not statistically different at the 5% level.

were significant ($P<0.05$, Tables 1 and 2). We believe this provides a good example of the clam's response in a stress gradient. In the future, fouling problems such as those encountered in this study can be avoided by cleaning both clams and cages.

METAL TISSUE CONCENTRATIONS

Comparison of metal concentrations in tethered, caged and wild clams- Zinc. Zinc tissue concentrations were always similar for caged and tethered clams at station 3 (Fig. 8). However, April zinc levels were greater in the wild population than in either set of transplanted clams ($P<0.05$, ANOVA). Thereafter, both wild and transplanted clams exhibited similar zinc concentrations. The differences between the April samples is interpreted as being due to the fact that transplanted clams initially had a lower zinc level and that the rate of metal uptake required between four and six months before the two concentrations could become equal. However, once similar, the metal dynamics of both groups remained the same. All three groups subsequently demonstrated a significant increase in zinc concentration in the summer and depuration in the fall and winter ($P<0.05$, ANOVA, Fig. 8). *Copper.* The copper concentration of the tethered and wild clam population was similar on all occasions (Fig. 9, $P>0.1$, ANOVA). In contrast, the copper concentration of the caged

Table 4. Zinc tissue concentrations (μg/gm) for caged *Corbicula* in New York Slough.

Month (1981)	STATIONS				
	1	2	3	4	5
February	143.4 a[1,2]/ ± 29.5	143.4 a ± 29.5	143.4 a ± 29.5	143.4 a ± 29.5	143.4 a ± 29.5
April	178.6 b c ± 13.1	171.6 b c ± 9.3	155.8 a b ± 6.9	159.9 a b ± 5.5	173.7 b c ± 10.1
June	152.8 a b ± 5.5	168.9 a b c ± 6.6	189.8 c d ± 11.5	221.2 e ± 17.4	134.9 a ± 10.1
August	232.5 e ± 13.3	194.7 c d ± 11.5	227.7 e ± 14.2	219.0 d e ± 9.9	200.2 c d e ± 14.8
October	169.2 a b c ± 2.9	194.2 c d ± 8.2	171.2 b c ± 4.6	159.1 a b ± 14.4	211.9 d e ± 9.8
December	186.9 c d ± 7.5	179.5 b c ± 9.1	— —	188.0 c d ± 19.9	179.6 b c ± 14.2

[1]/ Mean ± standard error.
[2]/ Values with the same letter are not statistically different at the 5% level (see text for details).

Table 5. Summary of reported copper and zinc tissue concentrations for *Corbicula*.

Tissue Concentration			
Zn[1]	Cu[1]	Location	Author
126[2] (72-288)	44[2] (18.6-81.0)	California inland rivers (1976-1978)	Woodward, 1979; McCleneghan and Rectenwald, 1979.
421 (313-522)	43.5 (33.5-108.2)	Glen Lyn Power Plant, New River, VA.	Cherry *et al*., 1980
173.7 (134-232.5)	94.5 (66.4-275.4)	New York Slough and San Joaquin River, CA.	Present study

[1] Median and range in ppm dry weight.

[2] Wet weight converted to dry weight (x6).

clams appeared higher in June and August than that of either the wild or tethered population. However, this difference was not significant ($P > 0.05$, ANOVA). In conclusion, therefore, comparisons of copper and zinc tissue concentrations between wild and transplanted clams seem to demonstrate that transplanted individuals can be employed to monitor metal concentrations of the natural population.

SEASONAL CLAM TISSUE CONCENTRATION IN NEW YORK SLOUGH

Copper and zinc tissue concentrations in caged clams along New York Slough and the San Joaquin River increased during the summer at all stations (Tables 3 and 4). Peak values often occurred in August. Copper concentration was significantly higher during the summer at stations 2, 3 and 4 (Table 3), whereas zinc was greater at station 1, 3, 4 and 5 (Table 4, all at $P < 0.05$, ANOVA).

After April, the copper concentration in clams at station 4 was significantly greater (Table 3) than that at any other site ($P < 0.05$, ANOVA). This result was unexpected, as there was no apparent source for the metal. We speculate that it may have eminated locally from the sediment.

Rapid fluctuations in biomass have been documented to produce an impression of a rapid fluctuation in metal tissue concentrations if the data is analyzed on a dry weight basis (Boyden, 1974; Strong and Luoma, 1981). *Corbicula*'s biomass did fluctuate significantly during the study both as a function of reproduction and the *Balanus* settlement (Table 1). However, all our conclusions concerning clam metal tissue concentrations remain the same when the data was reevaluated in terms of the total metal content of a standard 30 to 35 mm clam.

Flegal and Martin (1977) have cautioned that erroneously high metal tissue concentrations can result from including sediment bound metals in gut tissues. This could be particularly important for suspension-feeding bivalves such as *Corbicula*, which are known to ingest large amounts of inorganic material (Foe and Knight, 1985). Therefore, the metal concentrations of gutted and ungutted clams at station 3 were compared in August to determine whether the increase in clam metal concentration represented an actual increase in tissue concentration or a transient increase in ingested sediment-bound metal. The copper and zinc concentration of gutted clams was 152.4 ± 16.5 ppm and 216.4 ± 12.6 ppm. respectively (mean ± 1 standard error). These differences were not significantly different from those reported for ungutted clams ($P > 0.25$, student t-test, Tables 3 and 4). Therefore, the seasonal increase in clam metal concentration appears to represent an actual increase in tissue concentration.

No other metal tissue concentration data has been reported for an invertebrate from the Sacramento-San Joaquin Delta. However, Siegfried *et al*., (1980) has reported an increase in sediment metal concentrations during the summer in the same general area. The metal appeared to be bound to the silt and organic fractions of the sediment. The reported increase in *Corbicula*'s metal concentration may, therefore, represent the bioaccumulation of this metal into the filterfeeding portion of the food chain.

Finally, we have found no evidence of a deleterious sublethal impact on *Corbicula* of the high summer metal concentrations. However, our results are confounded by the simultaneous settlement of *Balanus* and by the loss of the growth cages at station 4.

The State of California monitored between 1976 and 1979 metal concentrations in selected fish and invertebrates from California's inland waters, but not from the Sacramento-San Joaquin Delta (Table 5). When available, *Corbicula* was employed as their benthic bioindicator species. Our zinc levels are somewhat higher but still comparable to those measured by the State (Table 5); however, our copper values are consistently greater than theirs. For example, at station 4 our copper concentrations ranged between 1 and 3.5 times greater than those reported by the state monitoring program. The high metal tissue concentrations in *Corbicula* may result either from the extensive industrial activity along the shores of the western delta or from the natural tendency of metals to concentrate in the freshwater portion of the estuary (Förstner and Wittman, 1979). Regardless, the headwaters of the Sacramento-San Joaquin Delta are one of the most productive areas of the entire estuary (Ball and Arthur, 1979) and the presence of high metal concentrations here in both the sediment and some fauna deserve additional study.

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A THERMAL ENERGY BUDGET FOR JUVENILE *CORBICULA FLUMINEA*

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ABSTRACT

A thermal energy budget was developed for immature *Corbicula fluminea* (Müller) at 16, 20, 24 and 30°C. Water filtration rate at these temperatures was 2.80, 3.85, 5.33, and 13.39 m*l*/mg dry wt/hr. Respiration rates were 0.39, 0.56, 0.71, and 0.85 $\mu l O_2$/mg dry wt/hr. Assimilation efficiency was 48, 51, 36, and 13%, and activity levels were 98.9, 90.1, 95.1, and 8.0%, respectively. These rates have been combined to form a scope for growth model which predicts optimal clam growth near 20°C, negative growth above 29°C, and high tissue growth at temperatures as low as 16°C. Growth was measured in the laboratory at two-degree increments between 16 and 32°C. Tissue growth at each temperature was 6.2, 6.8, 6.9, 5.8, 4.9, 3.0, 1.4, and -0.52 mg dry wt/month, respectively. All experimental animals died when evaluated at 32°C. These results are discussed in terms of our current knowledge about *Corbicula*'s thermal tolerance and life history.

The Asiatic clam, *Corbicula fluminea* (Müller), was first reported in the Pacific Northwest at the turn of the century (Burch, 1944; Counts, 1981a) and has since spread eastward, becoming a dominant benthic invertebrate (in biomass) in many of the major drainage basins in the United States (Mattice, 1979). This expansion is still in progress today with reports in 1980 of the successful colonization of additional rivers in Maryland, Pennsylvania, New Jersey and a section of Lake Erie along the Ohio Shoreline (Counts, 1981b; Trana, 1982; Clarke, 1981). In some locations, *Corbicula* now occurs in sufficient numbers to clog water transportation systems and power plant intakes and may even competitively exclude other benthic forms (Goss and Cain, 1975; McMahon, 1977; Prokopovich, 1969; Morton, 1979; Gardner *et al.*, 1976; Boozer and Murkes, 1979; Kraemer, 1979). As a result there is interest in predicting the ultimate geographic distribution of this pest organism.

Temperature is a major environmental factor that influences invertebrate physiology and is important in determining geographic distributions (Kinne, 1970). There have been several studies of *Corbicula*'s thermal tolerance (Mattice and Dye, 1975; Mattice, 1979; McMahon, 1979). However, no one has investigated the influence of temperature on *Corbicula*'s growth and attempted to explain the pattern in terms of the underlying physiological processes.

Energy budgets follow the flow of energy through organisms by measuring caloric intake and losses. If the net energetic balance is positive the animal will grow, if it is negative, it will be forced to utilize its own tissues in order to survive. Therefore, energy budgets represent an integration of all the physiological processes occurring in an organism and provide an indication of the "whole animal" response (Bayne *et al.*, 1976a).

The purpose of this study was to develop a laboratory thermal energy budget for *Corbicula*. We were particularly interested in determining the optimal temperature for growth and the extremes where stress occurs. Our results are discussed in terms of what is presently known about *Corbicula*'s thermal tolerance and employed to speculate about the clam's ultimate geographic distribution in the United States.

METHODS

The formula for a bivalve energy budget is (Crisp, 1971):

$$C = R + F + P \qquad (1)$$

upon rearrangement this reduces to

$$C - F = A = R + P \qquad (2)$$

or

$$P = A - R \qquad (3)$$

where C is the amount of energy ingested, R is the energy expended in metabolism, F the energy lost through urea and fecal production, A the caloric value of the food absorbed across the intestinal wall, and P the energy value of somatic and gametic tissue growth.

Equation (3) has been termed the "scope for growth" of an animal (Warren and Davis, 1967; Bayne *et al.*, 1976a) and represents an index of energy available for growth and reproduction. Immature clams were used in this study and, therefore, alterations in *Corbicula*'s energy balance only affect its capacity for somatic growth.

The various physiological parameters needed to calculate the energy budget were estimated as follows (Widdows, 1978):

C (cal/month) = filtration rate (m*l*/month) x activity level (%) x algal concentration (cells/

m*l*) x algal caloric content (cal/cell).

A (cal/month) = C (cal/month) x assimilation efficiency (%).

R (cal/month) = metabolic rate (m*l*0_2/month) x oxycaloric constant (4.86 cal/m*l*0_2).

P (cal/month) = tissue growth (mg/month) x caloric content of tissue (cal/mg).

Each of these rates was estimated as a function of temperature, converted to caloric equivalents per month, and combined to estimate *Corbicula*'s scope for growth at 16, 20, 24, and 30°C. The model was validated by comparing the predicted growth with actual measured laboratory tissue growth over a 30-day period.

Immature clams (8.0-11.0 mm shell length) were collected from a subtidal population at Sherman Island in the Sacramento River near Rio Vista, California. This population has been identified electrophoretically (McLeod, 1986) as the white *Corbicula* morph (Hillis and Patton, 1982). Clams employed in the growth, filtration and respiration evaluations were checked for reproductive activity at the end of the respective experiments. No evidence of reproduction was ever obtained. Shell lengths were determined to the nearest 0.1 mm with an ocular micrometer. Tissue weights were estimated from a log-log regression of shell length (mm) against ash-free dry weight (mg) of animals dried at 60°C and ashed at 450°C. The equation for this relationship was:

$$\log \text{weight} = 3.45 \log \text{length} - 2.24 \ (R^2 > 0.99) \quad (4)$$

Clams were collected during July and August at an ambient water temperature of 22°C and acclimated to the appropriate experimental temperature at the rate of 1°C per day. Once at the proper temperature, they were held an additional four days prior to use. Specimens for the growth and filtration experiments were fed during acclimation while those used in the respiration studies were not. Culture water was obtained from a nonchlorinated deep-well system with the general chemical composition listed in Foe and Knight (1986). The difference between means for each physiological rate measured was analyzed with analysis of variance and Newman-Keul mean separation tests.

FILTRATION

Filtration was measured in a static system consisting of a series of 30 m*l* glass funnels partially submerged in a water bath to control temperature (SE<0.08°C for each experiment, N = 9). The stem of each funnel was connected to an air supply to insure a gentle source of mixing. One animal was held per funnel in a small aluminum cup cemented to the inside wall. Clams were fed during the thermal acclimation period on a trialgal culture of *Chlamydomonas, Chlorella,* and *Ankistrodesmus* each at a concentration of 3 x 10^5 cells/m*l*. Filtration experiments were conducted in a similar culture at an initial algal concentration of 10^6 cells/m*l*. The procedure consisted of placing animals in the funnels and observing when they opened and commenced filtering. After an hour of continuous feeding, a water sample was drawn and the cell concentration determined with a hemacytometer. Filtration was calculated from the formula of Fox *et al.* (1937):

$$F = \frac{1n\, C_1 - 1n\, C_2}{W} \quad \frac{V}{T}$$

where F is the filtration rate (m*l*/mg-hr), C_1 the mean algal density of three control funnels maintained without clams after 60 minutes of continuous aeration (cells/m*l*), C_2 the algal density after 60 minutes of clam filtration (cells/m*l*), V the funnel water volume (m*l*), T 60 minutes, and W clam ash-free dry weight.

ASSIMILATION

Assimilation efficiency was determined by the Conover method (Conover, 1966):

$$A = \frac{(f - E)}{(1 - E)\,(f)} \quad x\ 100$$

where f is the ash-free dry weight ratio of phytoplankton prior to ingestion and E is a similar ratio for the feces. *Corbicula*'s fecel pellets were easily recognized among the pseudofecal material as compact string-like extrusions. They were collected from the bottom of the culture vessels every fourth day with a micropipette and filtered onto tared precombusted 0.45-μm size glass fiber filters. These were dried at 60°C and ashed at 450°C. Water samples were simultaneously taken from each treatment and processed in a similar fashion to estimate a valve for f. A bacterial control was conducted by holding feces an additional four days at 24°C in order to determine if microbial action significantly altered E. A paired one-tailed T-test indicated no significant decrease in this value ($p>0.25$, N = 6).

METABOLIC RATE

Oxygen consumption was measured with a Gilson differential respirometer. The procedure consisted of randomly selecting groups of four clams and placing them in sterilized sediment in the respirometer flasks for at least one hour to adjust to test conditions. Oxygen consumption was then determined at 10 minute intervals for three consecutive hours. A least squares regression was used to calculate the mean oxygen consumption rate for each set of one hour measurements. These values were averaged, corrected to standard temperature and pressure, and divided by the estimated weight of the animals to calculate each oxygen consumption replicate in $\mu l 0_2$/mg dry wt/hr.

GROWTH

Growth was evaluated at 2^0 increments between 16 and 32°C using 10 *l* aquaria. Water temperature was controlled to within 0.5°C with an American Instrument Company supersensitive relay system. Clams were held in these aquaria in small dishes without sediment. Previous experiments have demonstrated that the laboratory growth of *Corbicula* is independent of both flow and substrate (Foe, 1983). Water temperature, nitrate, nitrite, ammonia, pH and dissolved oxygen were monitored regularly. Hydrogen ion concentration was measured with a Corning model 610A pH meter, dissolved oxygen with a model 51B YSI oxygen probe, and nitrite and nitrate concentration with a DR-EL/1 Hach kit. Ammonia concentration was determined by the phenolhypo-chloride method of Solorzano (1969). The concentration of toxic unionized ammonia was calculated from pH and total ammonia (Armstrong *et al.*, 1978).

Clams were fed on a trialgal diet consisting of even proportions of *Ankistrodesmus*, *Chlorella*, and *Chlamydomonas* at a total concentration of 10^5 cell/m*l*. In previous feeding experiments with *Corbicula* this defined algal diet has been found to produce consistent, positive clam growth (Foe and Knight a, 1986). We assume for this experiment that this algal concentration represented an *ad libidum* food level for *Corbicula* as pseudofeces, which are thought to indicate a food saturated condition (Winter, 1969, 1978; Schulte, 1975), regularly formed at all temperatures and repeated microscopic examinations of the pseudofecal material demonstrated that all three algal species were present in about similar proportion. Stock cultures of *Ankistrodesmus* and *Chlorella* were purchased from the Carolina Biological Supply Company. *Chlamydomonas* was obtained from the University of Texas. All were grown as monocultures under greenhouse conditions in aerated bottles immersed in a temperature controlled water bath (20-25°C). *Ankistrodesmus* and *Chlorella* were cultured on Woods Hole media (Nichols, 1973) while *Chlamydomonas* was grown on Hunter's media (Starr, 1978).

The algal concentration in each clam growth treatment was restored daily to maintain a constant algal density. These concentrations were estimated by *in vivo* fluorescence with a model III Turner Fluorometer from a least square regression of algal fluorescence against cell number (Strickland and Parsons, 1969). Cell densities for each regression were determined with a hemacytometer. Repetitive microscopic examinations of the clam growth cultures demonstrated that all algal species were always present in similar proportions. There was no evidence of either a differential algal filtration rate by the clams or of differential algal settlement from the aquaria water column. Algal dry weight was estimated by filtering water of a known cell concentration through a tared 0.45 μm glass fiber filter (mean weight = 6×10^{-2}mg/10^6 cells,SE = 0.01, N = 6). A known amount of seston was scrapped from these filters, compacted into a pellet and oxidized in a Phillipson microbomb calorimeter (mean caloric value = 2.27 cal/mg, SE = 0.25, N = 6). From this the average caloric value of the trialgal culture was determined to be 1.36×10^{-2} cal/m*l* of water.

Clam shell and tissue growth was determined by numbering both valves of each individual with a Sharpie pen®. Shell length was determined to the nearest 0.1 mm at the beginning and end of the experiment with an ocular micrometer. Initial weights were estimated from the log-log regression of shell length (mm) against ash-free dry weight (mg) of animals collected at the beginning of the experiment (Eq. 4). Final organic weights were determined as the difference in weight of shelled animals dried at 60 and ashed at 450°C. Tissue growth was estimated from the difference between initial and final weight. Relative tissue growth was calculated by dividing the estimated tissue growth of each individual by its initial weight and multiplying by 100. The caloric value of the tissue was determined by gutting juvenile clams and drying the tissue at 60°C before oxidation in a Phillipson microbomb calorimeter. The mean caloric value was 5.14 cal/mg (SE = 0.41, N = 8).

ACTIVITY LEVELS

The proportion of time clams spend actively filtering is defined as their activity level. This figure was determined for each temperature by inspecting the growth treatments twice daily to establish the number of individuals open and with siphons extended. This posture is presumed to indicate active feeding.

RESULTS

FILTRATION

Filtration rates for *Corbicula* are presented in Table 1. Filtration was not statistically different at 16 and 20°C but increased rapidly thereafter with rising temperature ($p < 0.05$).

Several authors have reported filtration data for *Corbicula*. The values measured by Haines (1979), Prokopovich (1969) and Habel (1970) are lower than those reported in the present study. However, both Haines' and Prokopovich's rates may represent stressed animals as the authors report some mortality during experiments. In contrast, most of our values are comparable to those reported by Mattice (1979).

Table 1. Respiration, filtration, and assimilation rates for *Corbicula* as a function of temperature.

Temp	Metabolic Rate[1] ($\mu l O_2$/mg-hr)			Filtration Rate[1] (m*l*/mg-hr)			Assimilation[1] (%)		
(°C)	$\overline{X}$	SE	N	$\overline{X}$	SE	N	$\overline{X}$	SE	N
16	0.39 a	0.03	15	2.80 a	0.37	14	48 a	8.1	8
20	0.56 a b	0.03	16	3.85 a	0.41	12	51 a	6.5	7
24	0.71 b c	0.03	17	5.33 b	0.22	13	36 a	7.6	8
30	0.85 c	0.01	16	13.39 c	0.99	12	13 b	2.9	8

[1] Values with the same letter are not statistically different at the 5% level. (See text for statistical details.)

An important difference though, is that Mattice reports his rates to be greatest at 24°C while we found that *Corbicula*'s potential filtration rate increased steadily through 30°C. However, actual clam ingestion rates (filtration rate x activity level) decreased at the higher temperature in the growout experiment as activity levels fell faster than filtration rates rose.

ASSIMILATION

Assimilation rates for *Corbicula* are listed in Table 1. Assimilation was constant over a range of temperature from 16 to 24°C. However, the efficiency dropped significantly at 30°C ($p < 0.01$), which we interpret as the result of the clam entering a zone of thermal stress. Lauritsen (1986) reports similar assimilation values for *Corbicula* feeding on monoalgal diets of *Chlorella* (33%) and *Scenedesmus* (45.4%).

METABOLIC RATE

Metabolic rates (Table 1) increased with rising temperature as the Newman-Keul multiple comparison test revealed statistical differences between each nonadjacent pair. Q_{10} values for differences in the rate of oxygen consumption between 16-20, 20-24, and 24-30°C were 2.47, 1.81, and 1.35, respectively. The decrease in Q_{10} between 24 and 30°C may indicate the onset of thermal stress.

Reported literature respiration data for *Corbicula* indicate that our values are somewhat higher than previous estimates (Habel, 1970; McMahon, 1979). Some of this difference may be explained by the fact that other studies used larger animals and weight specific metabolism is known to be inversely proportional to body size (Zeuthen, 1947). It is interesting that McMahon's data indicates a decrease in metabolic rate at 30°C for both "acclimated" and "nonacclimated" individuals. This decrease may indicate thermal stress. Our rate data did not show a similar trend (Table 1), however, the Q_{10} data does suggest some thermal inhibition at the higher temperatures.

ACTIVITY LEVELS AND MORTALITY

Table 2 summarizes mortality and activity rates for the clam growth experiment. No mortalities were reported below 30°C while three clams died at this temperature and all animals died in two weeks at 32°C. Differences in activity were analyzed with a one-way ANOVA and a Duncan multiple range test. The results indicate no difference in activity below 28°C which suggests that *Corbicula* filters continuously at these tempertures. Activity falls at 28 and again at 30°C as clams spend a greater portion of their time in the closed mode ($P < 0.01$).

Table 2. Temperature dependent activity and mortality rates for *Corbicula*.

Temperature	Activity level (%)[1]			Mortality (%)
(°C)	$\bar{X}$	SE	N	$\bar{X}$
16	98.9 a	2.2	54	0
18	96.3 a	4.1	54	0
20	90.1 a	3.3	54	0
22	97.3 a	6.9	54	0
24	95.1 a	4.6	54	0
26	98.2 a	7.1	54	0
28	74.1 b	5.2	54	0
30	8.0 c	1.8	54	17
32	—	—	—	100

[1] Values with the same letter are not statistically different at the 1% level. (See text for statistical details.)

Table 3. The caloric value of the physiological rates used in the computation of *Corbicula* scope for growth* (Fig. 1).

Temp. (°C)	C (cal/mo)	A (cal/mo)	R (cal/mo)	A-R (cal/mo)	P (cal/mo)
16	74.83	35.92	3.77	32.15	31.87
20	93.65	47.76	5.40	42.36	35.47
24	136.89	43.79	6.84	36.95	25.19
30	28.95	3.76	8.13	-4.37	-2.67

*See the methods section for computational details.

ENERGY BUDGET

The laboratory rates for *Corbicula*'s filtration, assimilation, respiration, and activity levels have been converted to caloric equivalents per month in Table 3 and integrated into a scope for growth model (Eq. 3) in Fig. 1. The figure includes two curves. The area bounded by the upper dashed line and the abscissa is an estimate of *Corbicula*'s caloric intake (A). The area between the lower solid line and the X-axis is the energy expended in respiration (R). The stippled area between (A-R), represents the amount of energy available for *Corbicula*'s growth as a function of temperature.

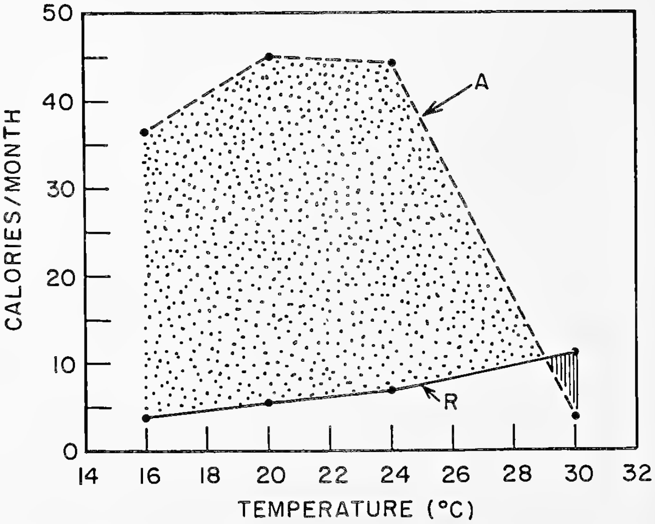

Fig. 1. Predicted scope for growth model for *Corbicula* at temperatures between 16°C and 30°C. Curve "A" is calculated from the number of calories assimilated at each temperature, and "R" from the number lost through respiration.

This model allows us to make several important predictions. First, optimal *Corbicula* growth for the "white" morph should occur around 20°C. This is the temperature where *Corbicula* has the greatest amount of net available energy. Second, the model predicts negative growth to occur at temperature above 29°C as more energy is being expended at this temperature than can be obtained by filtration. Third, the model predicts a high potential growth rate at temperatures as low as 16°C.

GROWTH

Water quality parameters were measured during the 30-day growth experiment. Test temperatures varied less than 0.2°C in each treatment. Dissolved oxygen was always close to saturation. Hydrogen-ion concentration appeared to be strongly influenced by the photosynthetic activity of the algae and rose and fell with the diel light cycle (values ranged between 8.3 and 8.8). Algal concentration ranged between 0.4 and 1.5 x 10^5 cells/m*l* with a mean concentration for each treatment of about 10^5 cells/m*l*. Nitrogen levels were always low. Nitrite and nitrate concentrations were undetectable. Mean total ammonia concentration ranged between 0.02 and 0.06 mg/*l*. The concentration of toxic unionized ammonia was consistently less than the 20 μg/*l* value which EPA considers safe (EPA, 1975).

Clam growth is summarized in Table 4. Growth was positive at temperatures below 30°C. Relative tissue growth was particularly high at the lower temperatures evaluated. For example, clams nearly tripled in weight during the month at 20°C. Differences in tissue growth were analyzed by a one-way ANOVA and a Duncan multiple range test. Tissue growth appears optimal between 18 and 20°C and thereafter decreases steadily with increasing temperature ($p<0.05$). Growth was negative at 30°C. Shell growth was analyzed in a similar fashion with like results. Shell growth was greatest between 18 and 20°C and decreased rapidly at higher temperatures ($p<0.01$). A slight amount of positive growth was recorded at 30°C. This suggests that the processes of shell and tissue growth may not occur simultaneously.

An advantage of using energy budgets is that the animal's caloric intake must balance its energy loss. The degree to which these do not balance is a measure of the errors included in the measurement of the various physiological parameters. Figure 2 includes a comparison between *Corbicula*'s predicted tissue growth derived from the scope for growth model, and actual laboratory growth. *Corbicula*'s predicted growth was always greater than that actually measured. However, the 95% laboratory growth confidence limits include the predicted scope for growth value at three or the four temperatures tested. This indicates that the various physiological rates used in the calculation of the scope for growth model are approximately correct. The data also substantiates, at least for immature *Corbicula*, the use of scope for growth (Widdows, 1978) to estimate instantaneous growth rates. We have no reasonable explanation for the large differences between the predicted and measured growth values for 24°C.

There are several hypotheses as to why the scope for growth model overestimates *Corbicula*'s actual growth. First, the model assumes no pseudofecal production. Observations show that *Corbicula* begins producing pseudofeces at algal densities between 10^5 and 10^6 cells/m*l*. Small amounts of pseudofeces were regularly seen intermixed with the fecal pellets and were carefully separated out before estimating assimilation. No attempt was made to calculate their caloric value and subtract this from the ingestion rate. Consequently, we may have overestimated the animals' net caloric intake. Second, respiration was estimated using starved animals. Therefore, our respiration values approximate the standard metabolism of Bayne *et al.* (1976b). Unpublished data (ours) demonstrates that *Corbicula*'s respiration almost doubles when phytoplankton is introduced into the respiration chamber. Presumably the increased metabolic costs are the result of filtration and digestion of the algae. The rates

Table 4. Laboratory growth of *Corbicula* as a function of temperature.

Temp.	Shell growth[1,2] (mm/moth)			Tissue growth[1,2] (mg/month)			Relative tissue growth
(°C)	$\overline{X}$	SE	N	$\overline{X}$	SE	N	(%)
16	1.38 a	0.05	18	6.2 a b c	0.20	18	164.7
18	1.73 b	0.06	18	6.8 a b	0.19	17	181.6
20	1.74 b	0.16	18	6.9 b	0.21	10	186.7
22	1.03 c	0.08	18	5.8 c	0.17	16	151.4
24	0.96 c d	0.09	18	4.9 d	0.30	11	125.6
26	0.91 d	0.08	18	3.0 e	0.25	13	74.6
28	0.70 e	0.10	18	1.4 f	0.24	15	39,5
30	0.153 f	0.04	15	-0.52 g	0.21	14	-17.8
32	—	—	—		—		—

[1] Values with the same letter are not statistically different for shell growth at the 1% level and tissue growth at 5% level.

[2] No growth is reported at 32°C as all animals in the treatment died during the experiment.

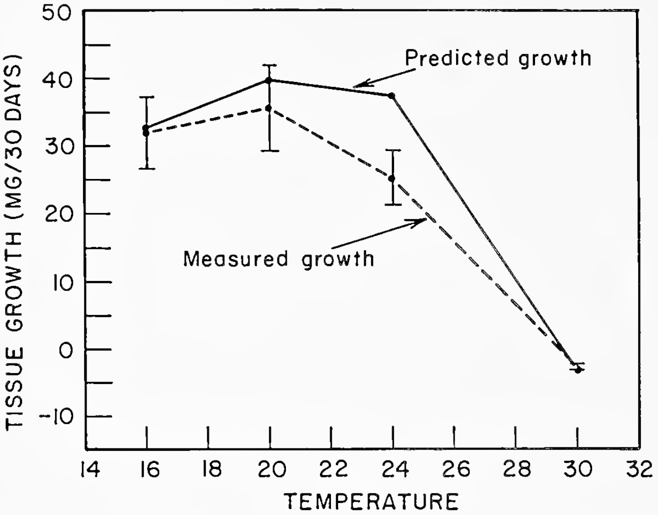

Fig. 2. Comparison of *Corbicula*'s predicted growth derived from the scope for growth model and actual measured laboratory growth. The vertical bars indicate the laboratory 95% growth confidence limits.

we report, therefore, may underestimate *Corbicula*'s actual daily metabolic costs. Finally we did not determine the amount of energy lost through ammonia production. The marine mussel *Mytilus edulis* is estimated to lose between 0.1 and 4% of its ingested energy as excreta (Bayne and Widdows, 1978; Widdows *et al.*, 1981).

Net production efficiency (K_2) is defined as the amount of energy an organism expends on growth and reproduction (P) divided by the amount assimilated (A). The parameter is a measure of the efficiency with which the ingested energy is utilized for growth and reproduction. K_2 values calculated from Table 3 for *Corbicula* at 16, 20 and 24°C are 88.7, 74.3 and 57.5%, respectively. These values are similar to those measured for an Asiatic clam population from Lake Arlington, Texas (66-77%; Aldridge and McMahon, 1978). As noted by these authors, *Corbicula*'s K_2 values are among the highest ever recorded for a freshwater mollusc. Such a high K_2 efficiency should confer an exploitative-type competitive advantage for *Corbicula* relative to other freshwater invertebrates. This energetic advantage may, in part, help explain how the recently introduced Asiatic clam so rapidly become a dominant benthic invertebrate in many American water systems.

Our laboratory clam growth data (Table 4) is difficult to compare with that of other researchers because of differences in animal size and season of measurement. However, our growth rates appear roughly comparable to the average summer growth rates of 1.60-2.50 mm/month reported for small clams in field studies by O'Kane (1976), Mattice (1979), and Eng (1979). We have also measured (in the laboratory) the shell and tissue growth of another group of somewhat smaller (5-8 mm shell length) clams fed on the same trialgal diet (Foe and Knight, 1986). Their shell and tissue growth was 0.39 ± 0.09 mm/month and 2.54 ± 0.75 mg/month (mean ± 1 standard error). The growth rate of the latter group of clams was similar to that of other individuals of the same size caged in the Sacramento-San Joaquin Delta (2.43 ± 0.18 mg/month). The reason for the large difference in growth rate between laboratory studies is not well understood. However, the slower growth of the smaller clams is undoubtedly, in part, due to the fact that *Corbicula*'s growth increases with body size until about 15-18 mm shell length (Foe and Knight, in preparation). Also, the two groups of clams were collected at different times and many, therefore, not have been in similar physiological condition. In other laboratory studies, we have obtained shell and tissue growth rates of 2.78 mm/month and 9.25 mg/month for 6-9 mm clams fed on algae from water collected from the Sacramento-San Joaquin Delta, spiked with nitrogen and phosphorus and incubated in a green house for 4 days to induce a phytoplankton bloom before being further enriched with 10^6 cells/m*l* *Ankistrodesmus* (Foe and Knight, 1985). The enhanced clam growth in this latter study appears to result primarily from the higher assimilation rate of estuarine diatoms (~95%). Unfortunately, this latter, more successful, culture method is not suitable for the present type of study in which a defined algal diet with known caloric value is needed. These reported variations in clam laboratory growth do not negate the conclusions of the present study. However, they do suggest that the various physiological rates which together determine a clam's energy budget may vary substantially with animal size, season, ration type, and previous environmental history. Also, obviously, our reported energy budget applies only for the "white" *Corbicula* morph. An interesting future research topic might be to ascertain how the energetics of the "purple" morph differ from that of the "white" one. Such information could be valuable for predicting how the two morphs will eventually partition their niche.

DISCUSSION

Temperature is a major environmental factor influencing the geographic distribution of aquatic invertebrates (Kinne, 1970). Low temperatures may set the northern limit of *Corbicula*'s distribution as clams were unable to survive winter temperatures below 0°C in the New River, Virginia in 1975, while in contrast, population density remained stable in an adjacent thermal outfall (Gainey *et al.*, 1980). This agrees well with laboratory studies which have shown that the ultimate lower incipient lethal temperature for *Corbicula* is 2°C (Mattice and Dye, 1975). By definition this is the lowest temperature to which clams can be acclimated without temperature related mortality.

Reproductive studies demonstrate that spawning is induced biannually as water temperature passes through 16°C (Eng, 1979; Heinsohn, 1958; Sickel, 1979). In northern states, reproduction may be delayed for several months or even reduced to a single period because of prolonged low winter temperatures (Eng, 1979). We propose that the 2°C lower incipient lethal temperature and the 16°C temperature dependent reproductive cycle may constitute the critical lower temperatures for *Corbicula*. Together they may define the northern range of the Asiatic clam.

Field observations suggest that *Corbicula*'s upper thermal limit lies between 29 and 35°C. This temperature range may determine the clam's southern distribution. Haines (1979) reported the complete mortality of animals transplanted into sewage treatment ponds at St. Croix, Virgin Islands when temperatures ranged between 25 and 35ºC. Busch (1974) observed high mortality in ponds where temperatures frequently exceeded 32ºC. Habel (1970) recorded almost complete mortality in catfish enclosures when the temperature rose to 35ºC. Mattice and Dye (1976) indicate that the upper incipient lethal laboratory temperature for *Corbicula* is 32ºC. Our scope for growth model predicts a somewhat low upper temperature limit as growth was negative above 29ºC. Our laboratory growth and mortality data (Tables 2 and 4) subsantiate this conclusion by showing adverse temperature effects at 30ºC.

Field studies indicate that *Corbicula* has a positive growth potential between 15 and 30ºC. However, it is difficult to predict the optimal growth temperature from these studies. For example, in northern California growth is inhibited in the winter at temperature below 14ºC and in the summer at temperatures above 25 and 30ºC (Heinshon, 1958; Eng, 1979). Unpublished data (ours) from California's Sacramento-San Joaquin Delta show that the growth of caged clams cease at temperatures below 15ºC while optimal growth occurs between 20 and 23ºC (the maximum recorded ambient water temperature). Sickle (1979) reports negligible growth below 15ºC in the Altahama River, Georgia. Maximal growth occurred somewhere between 18 and 28ºC. Mattice (1979) reported maximum growth at 24ºC for clams caged at the Glen Lynn thermal outfall in Tennessee. Our laboratory culture experiments demonstrate that *Corbicula*'s growth is maximal at 20ºC. Analysis of the scope for growth model reveals that this is not the result of the dominant performance of any one physiological process but rather results from small adjustments in each rate. As a result, *Corbicula* exhibits no evidence of a thermal compensatory adjustment enabling it to maintain a stable scope for growth over a wide thermal range as has been reported for several marine interidal invertebrates including the bivalve *Mytilus edulis* (Bayne *et al.*, 1976b). Laboratory growth experiments (Table 4) confirm a single narrow growth maximum between 18-20ºC. We conclude, therefore, that *Corbicula* is best adapted to grow in environments with ambient temperatures near 20ºC.

Finally, the laboratory based scope for growth model predicts a high potential growth rate at temperatures as low as 16ºC. This is in contradiction to field work (Heinsohn, 1958; Sickle, 1979; Eng, 1979) which has reported that growth ceases at this temperature. This contradiction implies that factors other than temperature may control *Corbicula*'s growth at least in the lower portion of its temperature range. This conclusion led us to investigate the effects of ration size on Asiatic clam growth. We have found that *Corbicula* is food limited during most of its growing season in California's rather eutrophic Sacramento-San Joaquin Delta (Foe and Knight, 1985). This result leads us to conclude that in most other systems the growth dynamics of *Corbicula* are also probably being determined to a large extent by the amount of available food and not by the ambient water temperature. Hence, we recommend that the optimal thermal growth conclusions of this study be applied to field situations with caution.

ACKNOWLEDGMENTS

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A REASSESSMENT OF GROWTH RATE, LIFE SPAN, LIFE CYCLES AND POPULATION DYNAMICS IN A NATURAL POPULATION AND FIELD CAGED INDIVIDUALS OF *CORBICULA FLUMINEA* (MÜLLER) (BIVALVIA: CORBICULACEA)[1]

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ABSTRACT

A population of *Corbicula fluminea* in the Clear Fork of the Trinity River, Tarrant County, Texas, was sampled bimonthly from 10 September 1980 through 20 December 1982. Growth rates of caged and free living marked individuals were also monitored. The population had a distinct biannual pattern of reproduction, incubation of eggs and embryonic stages occurring from late March through July and again from late August through November, giving rise to distinct "early" and "late" generations, respectively. Growth rates, life spans and reproductive patterns for individual generations were variable. The late generation was not successfully produced in the fall of 1982. Population density ranged from 305 to 16198 clams m^{-2}. The high reproductive capacity of the population allowed quick recovery of density after catastrophic population declines.

Shell growth of caged and freeliving marked individuals closely paralleled that of individual generations. Growth rates were maximal during the warmest periods of the year and were minimal during the colder winter months. Degrowth [decreases in shell length (SL)] occurred in larger individuals during the winter and catastrophic declines in population density. Growth rates of caged individuals were negatively correlated with size and positively correlated with temperature allowing the development of a growth rate model based on these two parameters. Maximum growth rates ranged from 5.4 mm SL 30 $days^{-1}$ to 0.8 mm SL 30 $days^{-1}$ for individuals with a SL of 5 mm and 30 mm, respectively.

The high growth rates, attenuated life spans, high fecundity, high proportion of immature individuals in the population, and ability to rapidly recover from catastrophic declines in density characteristic of the Clear Fork *C. fluminea* population are all life history traits associated with optimalization of reproduction and survival to maturity in highly unstable habitats. Such characteristics also account for this species' rapid spread through North American drainage systems and its nature as a biofouler of industrial raw water systems.

The growth, reproduction and life cycle of North American populations of the Asian freshwater bivalve, *Corbicula fluminea* (Müller), have been a matter of considerable confusion and controversy since the first reports of its introduction into the United States from Southeast Asia (Burch, 1944) (for reviews of the population dynamics of *C. fluminea* see Britton and Morton, 1979; McMahon, 1983). While the majority of investigators now agree that *C. fluminea* has two annual reproductive periods in which juveniles are released (mid-spring through mid-summer and late summer through early to late fall) in both North America (Aldridge and McMahon, 1978; Boozer and Mirkes, 1979; Eng, 1979; Dreier and Tranquilli, 1981; McMahon and Williams, 1986; Sickle, 1973, 1979; Williams and McMahon, 1986) and endemic Asian populations (Morton, 1977), there continues to be significant disagreement in the literature regarding this species' growth rate, population age structure and life span.

The earliest investigations of growth rates and life span in *C. fluminea* were based on size distributions of one time

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only population samples and/or on growth rings or annuli in the periostracum and/or mineral portions of the shell. These initial estimates appeared to be biased toward the previously known, relatively slow growth rates of unionid (Negus, 1966) and pisidiid bivalves (Avolizi, 1976, Hornback *et al.*, 1980, Way *et al.*, 1980, and references therein) and were often based on the erroneous assumption that *C. fluminea* had only one annual reproductive period. Later studies described a biannual reproductive pattern which produced two distinct generation size classes each year (Aldridge and McMahon, 1978; Britton *et al.*, 1979; Coldiron, 1975; Eng, 1979; Heinsohn, 1958; McMahon and Williams, 1986; Morton, 1977; Williams and McMahon, 1986). In addition, shell annuli numbers are not closely associated with age in *C. fluminea* (Dudgeon, 1980; Heard, 1964).

Utilization of size class-frequency and shell annuli data from single collections to interpret population dynamics based on the assumption of a single annual reproductive period led to initial estimates of the life span of *C. fluminea* that were often up to twice actual values and, therefore, to underestimations of shell growth rates (Diaz, 1974; Gardner, Ingram, *et al.*, 1976; Gunning and Suttkus, 1966; Hubright, 1966; *et al.*, 1964; Keup, *et al.*, 1963; Sickel, 1973; Sinclair and Isom, 1963). These early estimates of growth rates ranged from 2 mm to 12 mm in the first year of life. In contrast, studies recognizing that this species produced two distinct annual generations estimated growth rates to range from 16 mm to 30 mm in the first year of life (for a review of growth and reproduction in *C. flumina* see McMahon, 1983).

Some early published estimates also suggested that growth rates increased with size and age in *C. fluminea*, a very atypical pattern among molluscs (for a review of estimations of growth rate see Britton et al., 1979). Recent studies have indicated that *C. fluminea* both grows more rapidly and has a much shorter life span than previously suspected. These studies indicated that growth rate declined with increasing size and age and that maximum life span was approximately 1.5 to 4 years in North American (Aldridge and McMahon, 1978; Britton, *et al.*, 1979; Eng, 1979; Heinsohn, 1958; Williams and McMahon, 1986), Asian (Morton, 1977) and African populations (Leveque, 1973).

Reported growth rates of enclosed individuals of *C. fluminea* ranging from 2.0 mm / 30 days to 6.5 mm / 30 days, closely correspond to those determined by iterative population sampling. In addition, they have provided strong collaborative evidence that growth rate is negatively correlated with size and age in *C. fluminea* (Britton *et al.*, 1979; Buttner and Heidinger, 1980; Dreier and Tranquilli, 1981; Mattice, 1979; O'Kane, 1976).

In spite of the apparent general concensus in the recent literature on the population dynamics of *C. fluminea*, accounts of North American populations with reduced growth rates and life spans extended beyond three to four years still appear in the literature, particularly for populations in the southeastern United States (Mattice and Wright, 1985). Furthermore, even though *C. fluminea* appears to be most highly adapted for life in lotic habitats (Kraemer, 1979; McMahon, 1983; Morton, 1982), there have been no examinations of the population dynamics of this species in a lotic habitat. Nor have there been any concurrent estimations of growth rate from both the iterative analysis of population size-frequency data and from field enclosed individuals. In order to more rigorously reassess the population dynamics of this species in a natural lotic habitat, an intensive, two year study of growth, reproduction and life cycle was carried out on a river population of *C. fluminea* in North Central Texas. This study reports the results of the analysis of the age-size structure of iterative bimonthly population samples and densities of that population. In addition, concurrent determinations were made of the growth rates of marked, released, recaptured individuals and of individuals maintained in a field enclosure. The data from these studies allowed development of a simple model of individual growth rate in *C. fluminea* based on regression against shell length and ambient water temperature.

METHODS

Specimens of *C. fluminea* were collected bimonthly from 10 September 1980, to 20 December 1982, from a population in the Clear Fork of the Trinity River approximately one mile downstream from the outfall of Lake Benbrook, an artificial impoundment of the Clear Fork, in Tarrant County, Texas. The Clear Fork population consisted entirely of individuals of the "white shell morph" (characterized by white to light purple or light blue internal shell color and widely spaced shell sulcations) as described by Hillis and Patton (1982). The collection site was an area of the river approximately 12 m wide, 15 m long and 0.25-1.5 m in depth at normal river levels. The substratum was course limestone gravel mixed with larger limestone boulders, sand and silt. Generally the site was characterized by relatively moderate current flow (≈ 4 m / min) with the exception of isolated periods of high runoff.

Specimens were quantitatively sampled with an Ekman bottom dredge (sampling area = 0.19 m^2) forced by hand deeply into the substratum. Clams were removed from dredged material by sieving it through a 1.0 mm mesh. Sampling continued until a sample size of at least 100 individuals was taken. Average sample size over all collections was 341 individuals (s.d. = ± 261, range = 104-1243, n = 47). All individuals were returned to the laboratory within two hours of collection and immediately fixed in 12% (by volume with H_2O neutralized) formaldehyde. Large individuals (Length $\geq$ 8 mm) were maintained in water at 70°C for approximately 15 min to induce shell gaping prior to fixation.

The shell length (SL, hereafter referred to as "length", the greatest anterior-posterior dimension across the shell valves) of each individual in the sample was measured to the nearest 0.1 mm. The SL of larger individuals (SL $\geq$6 mm) was measured with a dial caliper and that of smaller individuals (SL $\leq$ 6 mm) with an eye piece micrometer at 10x under a binocular dissecting microscope.

The individuals in each sample were then divided into consecutive 0.2 mm size classes and each size class was expressed as a percentage of sample size. These values were then plotted as frequency histograms against sampling date over the entire collection period. Individuals in each sample were assigned to separate generations by visual separation of the size-frequency histograms into distinct size class groupings with separate modal SL values (after the method of Aldridge and McMahon, 1978). Mean SL, standard deviations and ranges were computed for each generation in each sample.

The reproductive condition of a subsample of 10 to 15 adult clams (SL $\geq$ 10 mm, Aldridge and McMahon, 1978) was assessed for each collection. The tissues of each individual in the subsample were excised and the inner demibranchs of both ctenidia (gills) examined under a binocular microscope for the presence of fertilized eggs, developmental stages and/or juveniles being incubated in their interlamellar cavities (for a discussion of reproduction in *C. fluminea* see Kraemer, 1977, 1978; Kraemer and Lott, 1977).

Throughout the collecting period, individually marked specimens of *C. fluminea* were maintained at the collecting site in an enclosure constructed of 5 mm mesh galvanized hardware cloth that was 45 cm long, 30 cm wide and 7 cm high. This cage was anchored directly on the substratum at a depth of 0.7 m by covering it with an arched cement tile that allowed water circulation through the top and sides of the cage. Water current velocity at the cage site was 9 m min^{-1}. On 10 September 1980 the cage was initially stocked with 66 individuals. The shell lengths of caged individuals were measured to the nearest 0.1 mm with a dial caliper and a permanent identifying number was scraped on the shell with a scapel blade. The SL of caged individuals which ranged from < 7.0 mm to > 40.0 mm, were selected to be representative of the SL range of the natural population. At every collection the SL of each caged individuals was measured to the nearest 0.1 mm with a dial caliper. Dead individuals were removed from the cages and new individuals were recruited to the cage periodically to maintain a size range representative of the natural population. The number of caged individuals remained at 44-70 throughout the sampling period. Mortality of caged individuals was low and generally never accounted for more than 10% of caged individuals between adjacent collections.

To determine the field growth rates of freeliving individuals, 994 clams were individually marked and their SL measured to the nearest 0.1 mm. These were released at the collecting site in an area (2m x 2m) immediately downstream from the cage on 10 September 1980. The area of release was sampled at each collection and the lengths of any recaptured individuals measured to the nearest 0.1 mm. After measurement captured individuals were returned to the collecting site. On 17 May 1981, and 26 May 1981, another 215 and 77 marked individuals were released at the collecting site, respectively. The sampling of released individuals continued until 13 September 1981.

Physical measurements of ambient air temperature, ambient water temperature, pH, conductivity and dissolved oxygen (utilizing a modified Winkler assay: Helliage, Model 342-DO) were determined at each collection. Total calcium and magnesium water hardness were determined by EDTA titration on 23 July, 1982, and 5 August, 1982. All collections were carried out between 1100 and 1500 hours, a period when ambient water temperatures, pH and dissolved oxygen values approach their daily maxima.

RESULTS

Dissolved oxygen concentration at the collection site remained close to air saturation levels (Fig. 1A). Mean dissolved 0_2 concentration was 6.8 mg $0_2 l^{-1}$ (s.d. = ± 2.7, n = 36) over the course of collection. With the exception of an unusually high value of 898 μmho cm^{-2} recorded on 1 October 1980, and an unusually low value of 119 μmho cm^{-2} on 5 August 1982, conductivity ranged from 200 to 450 μmho cm^{-2} (mean conductivity = 314.2 μmho cm^{-2}, s.d. = ± 103.4, n = 48)(Fig. 1B). Total water hardness was 102 mg Ca l^{-1} and calcium hardness, 82 mg Ca l^{-1}. Such conductivity and

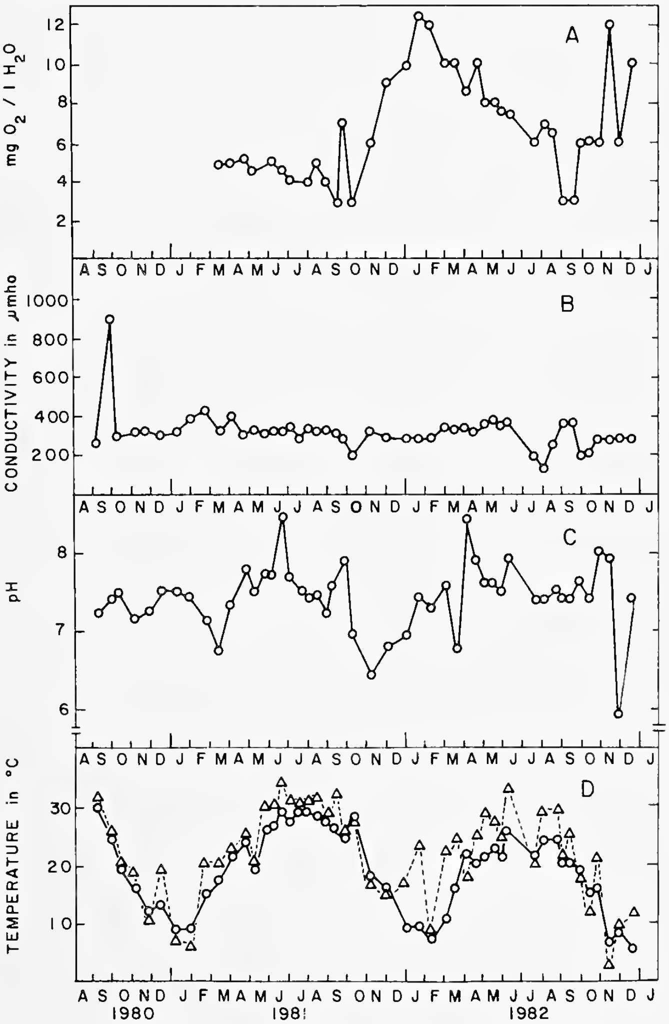

Fig. 1. Physical parameters at the *Corbicula fluminea* collecting site on the Clear Fork of the Trinity River, Texas. The horizontal axis is months of the year. **A** Dissolved oxygen concentration (mg $0_2/l$). **B.** Conductivity (μmho / m^2). **C.** pH. **D.** Ambient air (open triangles connected by dashed lines) and water temperatures (open circles, solid lines) in °C.

hardness values are characteristic of the moderately hard waters that generally occur in North Central Texas (Aldridge and McMahon, 1978; McMahon, 1975, 1976). Ambient pH ranged between 5.90 and 8.46. A pH of less than 7.0 was recorded on only 7 of 48 collections, indicating that the Clear Fork was generally alkaline (Fig. 1C). Ambient air temperature was more variable than water temperature, ranging from 2.6°C to 34.2°C (mean air temperature = 22.0°C, s.d. = ± 7.8, n = 48) (Fig. 1D). A minimum ambient water temperature of 4.8°C occurred on 20 December 1982, and a maximum of 29°C, on 7 June, 19 July and 2 August, 1981 (Fig. 1D). Mid-summer water temperatures in the Clear Fork of the Trinity River were significantly higher from June through August in 1981 (mean water temperature = 27.9°C, s.d. = ± 1.2, range = 26.2-29.0, n = 7) than in 1982 (mean water temperature = 24.0°C, s.d. = ± 1.6, range = 22.0-25.8, n = 4) (Fig. 1D).

In 1982 the Clear Fork *C. fluminea* population had two distinct reproductive periods during which fertilized eggs, developmental stages and juvenile individuals were incubated in the interlamellar spaces of the inner demibranches followed by the spawning of juveniles (Fig. 2). An "early" reproduc-

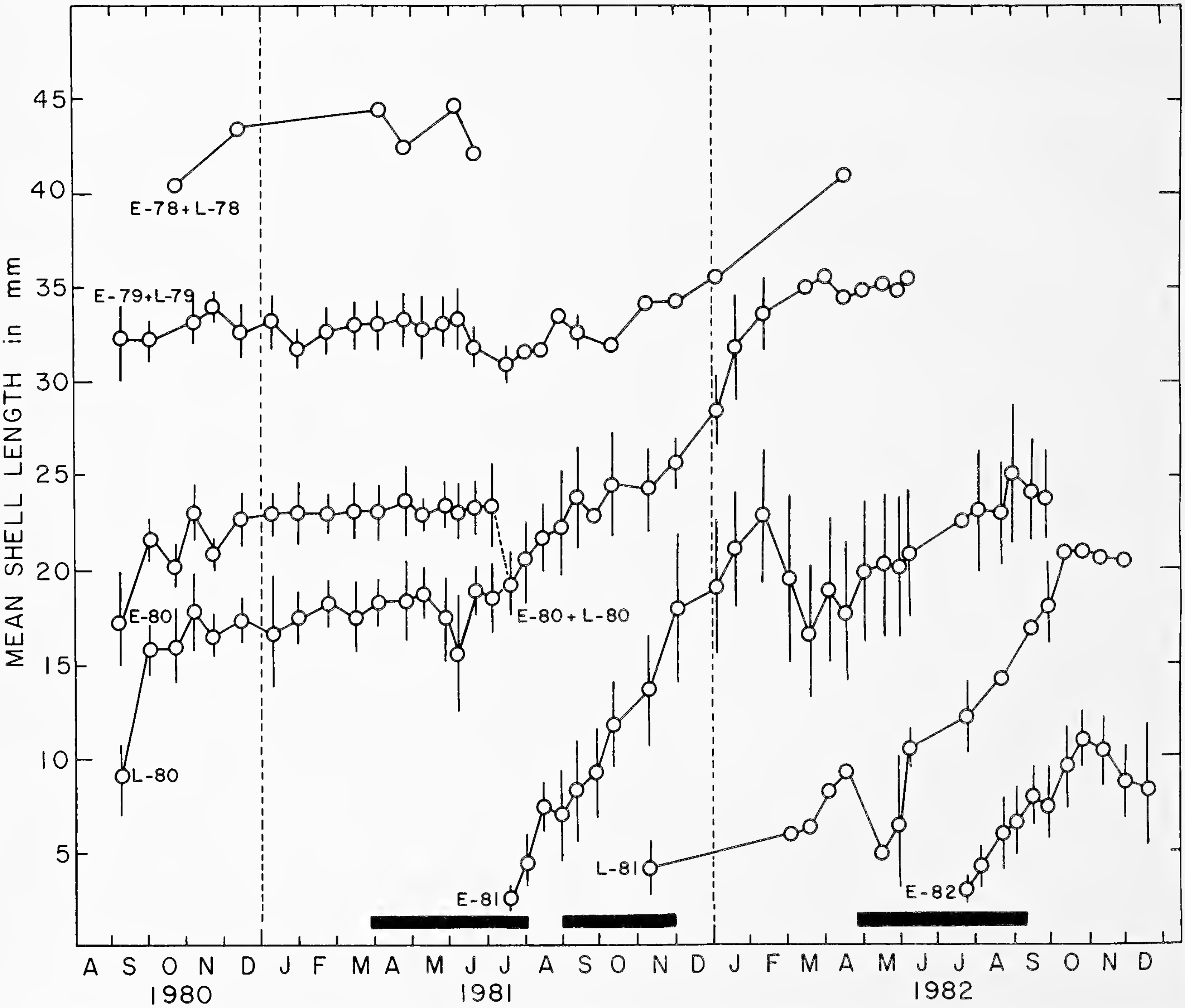

Fig. 2. Mean generation shell lengths (SL) in bimonthly samples of the Clear Fork *Corbicula fluminea* population. The horizontal axis is months of the year over the collection period. Open circles connected by solid lines represent the shell length of separate generations. Vertical bars are standard deviations. Points without standard deviation bars are means of samples with n ≤ 7. Specific generations are designated by time (E = early or L = late) and year of recruitment to the population, *ie.*, E-80 = a generation recruited from the early reproductive period of 1980, L-81 = a generation recruited from the late reproductive period of 1981. The solid bars above the horizontal axis indicate periods when adult individuals were observed to incubate fertilized eggs and developmental stages in the inner demibranchs.

tive period extended from late March through the end of July 1981, and the "late" reproductive period extended from the end of August through the end of November 1981. During 1982 the only significant reproductive effort observed was the "early" reproductive period from late April through early September (Fig. 2).

The early reproductive periods gave rise to early generations designated as either E-81 or E-82, which first appeared in the population as distinct size classes with a mean SL of 2.6 mm on 19 July 1981 and 3.0 mm on 23 July 1982, respectively (Fig. 2). The 1981 late reproductive period similarly gave rise to a late generation designated L-81, first appearing as distinct size grouping with a mean SL of 4.1 mm on 10 November 1981 (Fig. 2). The E-81 generation grew rapidly through the summer and fall, reaching a mean SL of 18.0 mm by December 1981. The E-82 generation grew more slowly, reaching a mean SL of only 8.6 mm by December 1982 (Fig. 2). The L-81 generation displayed only a small increase in mean SL during the winter of 1981-1982, but, subsequently grew rapidly through the following spring, summer and fall to reach a mean SL of 20.6 mm by December 1982. The E-81 generation disappeared from the collections at a mean SL of 23.8 mm on 30 September 1982, after 1.5 years of life (Fig. 2). In contrast, some individuals of generations spawned prior to 1981, appeared to survive for longer periods. These generations were represented by distinctly larger size classes in the samples and were designated as the E-80 and L-80 generations (Fig. 2). In January 1981 these generations had a mean length of 23.0 mm and 16.7 mm, respectively. They could no longer be separated as distinct size classes by July 1981, and were, therefore, combined into a single size class designated as the E-81 + L-81 generation. These combined generations reached a mean length of 28.5 mm by the January 1982, and disappeared from the samples as two year old individuals on 10 June 1982, after achieving a mean length of 35.6 mm (Fig. 2).

Initially, two other distinct size classes of larger clams appeared in the samples. One had a mean SL of 32.2 mm and represented the combined E-79 + L-79 generations. This group grew to a mean length of 41.0 mm by 19 April 1982, and then disappeared from subsequent samples after three years of life (Fig. 2). The largest distinct size grouping in the initial samples had a mean SL of 40.4 mm and represented the combined E-78 + L-78 generations (Fig. 2). This group reached a mean length of 42.2 mm on 21 June 1981, before disappearing from the samples after three years of life (Fig. 2).

Maximum density values in the Clear Fork *C. fluminea* population were clearly associated with the recruitment of new individuals from the early and late generations (Figs. 3A, D and E). For example, maximum density in 1981 was 9445 clams m^{-2} on 3 December. Of this value, 8714 clams m^{-2} or 92% were newly recruited individuals of the E-81 and L-81 generations (Figs. 3A and D). Similarly, the E-82 generation accounted for 15524 clams m^{-2} or 96% of the maximum density value of 16198 clams m^{-2} recorded on 27 August 1982 (Figs. 3A and E).

Annual mortality rates were relatively high in all age classes. Within the first year of life the density of the E-81 generation declined from a maximum of 8714 clams m^{-2} on 3 December 1981, to 96 clams m^{-2} on 3 December 1982, yielding an annual mortality rate of 98% (Fig. 3D). In the sample of 14 December 1980, the generation densities were as follows: 1.5 year old individuals of the E-80 + L-80 generations, 2250 clams m^{-2} (Fig. 5C); 2.5 year old individuals of the E-79 + L-79 generations, 693 clams m^{-2} (Fig. 5B); and

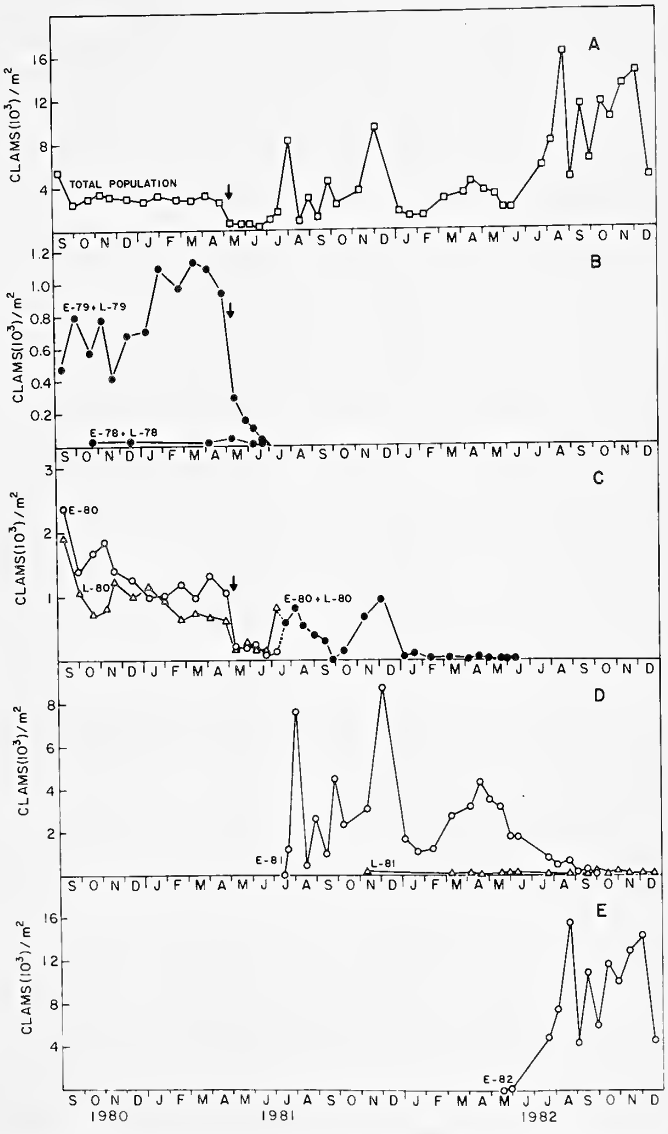

Fig. 3. Seasonal variation in the density of the Clear Fork *Corbicula fluminea* population. The horizontal axes for all figures are months of the year, and the vertical axes, population density in clams (10^3) / m^2. Densities of specific generations are indicated by time (E or L) and year of generation recruitment (see caption of Fig. 3 for further explanation). **A.** Density of the total population. **B.** Densities of the combined E-78 + L-78 generations and the combined E-79 + L-79 generations. **C.** Densities of the E-80 (open circles), L-80 (open triangles) and subsequently during collections of these generations combined (E-80 + L-80) (solid circles). **D.** Densities of the E-81 (open circles) and L-81 generations (open triangles). **E.** Density of the E-82 generation. The vertical arrow indicates the date of a hail storm and tornado associated with a catastrophic density decline.

3.5 year old individuals of the E-78 + L-78 generations, 19 clams m^{-2} (Fig. 3B). These data yield the following mortality rates: 69% in the second year of life (2250 - 693/2250 × 100); and 97% in the third year of life (693-19/693 × 100).

There were large year-to-year variations in the relative success of early and late generations. The density of the E-80 generation was nearly equal to that of L-80 in 1981, indicating nearly equal recruitment rates (Fig. 3C). In contrast, the density of the L-81 generation was only 2.7% that of the E-81 generation from early November 1981 through mid-June 1982, suggestive of extremely poor recruitment of the L-81 generation to the population (Fig. 3D). This trend towards poor recruitment of the late generation in the Clear Fork *C. fluminea* population culminated in 1982 when there was no recruitment of a late generation to the population (Fig. 3E).

A catastrophic density decline of the Clear Fork *C. fluminea* population occurred in the spring of 1981. Total density declined from 2655 clams m^{-2} on 26 April 1981, to 725 adult clams m^{-2} on 10 May 1981. Density subsequently declined to 305 clams m^{-2} by 21 June 1981 (Figs. 3A, B and C), yielding an 89% mortality over a 25 day period. This massive population decline was associated with an extensive hail storm and the passage of a tornado directly over the collection site on the night of 9 May 1981. The very large hail stones (diameter ≤ 4 cm) and cold rain appeared to have rapidly reduced water temperatures at the site. The following morning water temperature was 19°C, 4-5°C below normal temperatures for that period (26 April 1981 = 23.5°C; 26 May 1981 = 26.1°C) (Fig. 1D). This initial cold shock appeared to have induced a major, instantaneous mortality in the *C. fluminea* population. The decomposing clam tissues caused hypoxic conditions, resulting in a subsequent near elimination of both the remaining *C. fluminea* and fish populations for many miles downstream. During this period the E-78 + L-78 and E-79 + L-79 generations were completely eliminated from the population, while the densities of the E-80 and L-80 generations were severely reduced (Figs. 3B and C). In addition, recruitment of the E-81 generation was delayed by two to three weeks (Fig. 3D). In spite of this catastrophic reduction in density, subsequent recruitment of the E-81 and L-81 generations allowed recovery of the population to normal densities of approximately 4000 clams m^{-2} by the winter of 1981-1982 (Figs. 3A and D). During the spring of 1982 density reached 14,000 clams m^{-2}, following the highly successful recruitment of the E-82 generation (Figs 3A and E).

The shell growth rates of caged individuals appeared to closely parallel those of marked individuals released into the natural population when they were visually compared over the same time period (October 1980-August 1981) (Fig. 4). The equivalency of growth rates of caged and freeliving in-

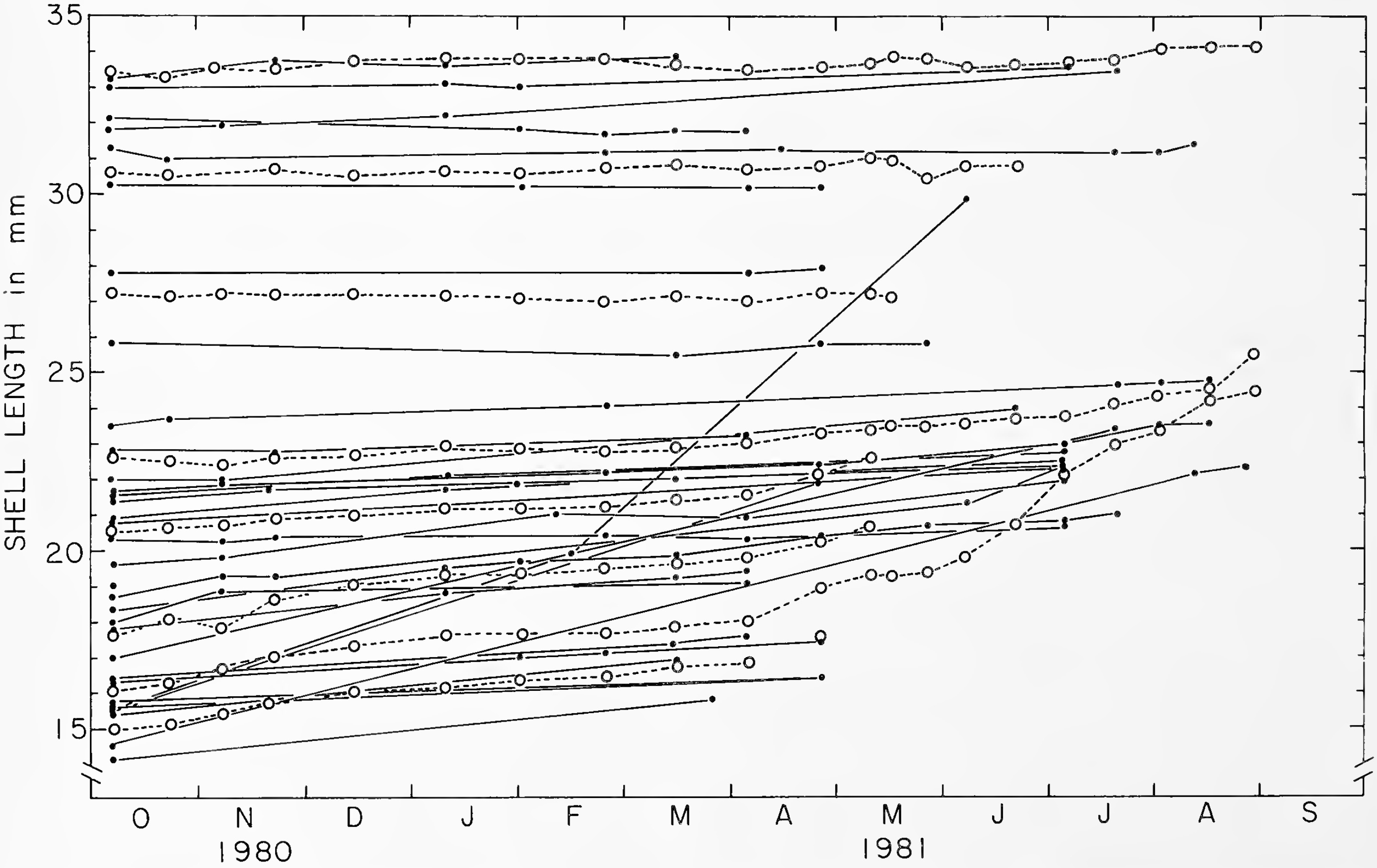

Fig. 4. Growth of selected individuals of *Corbicula fluminea* marked, released and recaptured in the field (solid circles connected by solid lines) compared with that of individuals maintained in field enclosures (open circles connected by dashed lines). The horizontal axis is months of the year, the vertical axis, shell length in mm.

dividuals indicated that the method of enclosure utilized did not inhibit shell growth as reported for other enclosure experiments with *C. fluminea* (Britton *et al.*, 1979).

The growth rates of caged clams had a strong negative linear correlation with SL. Forty six separate least squares linear regressions of the daily rate of increase in SL versus length were computed from the progressive change in the SL of caged individuals over sequential measurement periods (Table 1). Of these 46 growth rate regressions 36 were significant at $P \leq 0.1$ and 26 at $P \leq 0.001$ (Table 1). The relationship between growth rate and SL was not generally significant during winter periods of little or no observable growth when temperature fell below 11°C or during periods of environmental stress associated with population declines (Figs.

Table 1. Slopes (b), y intercepts (a), coefficients of determination (r), probability levels (P), and sample size (n) of linear regression equations relating daily growth rate to shell length (SL) [Growth Rate in mm SL/day = a + b (SL in mm)] over periods between adjacent collections at indicated average ambient water temperatures (°C).

Date		a	b	r	P	n	°C
22 Oct.,	1980	0.0003	-0.00001	-0.095	>0.20	66	22.0
7 Nov.,	1980	0.0048	-0.0001	-0.015	>0.20	65	20.3
22 Nov.,	1980	0.0310	-0.0010	-0.537	<0.001*	67	15.1
14 Dec.,	1980	0.0322	-0.0011	-0.935	<0.001*	67	12.3
10 Jan.,	1981	0.0160	-0.0004	-0.682	<0.001*	67	11.0
1 Feb.,	1981	0.0046	-0.0001	-0.461	<0.001*	67	9.0
25 Feb.,	1981	0.0024	-0.00001	-0.313	<0.01*	67	12.0
15 March,	1981	0.0221	-0.0007	-0.526	<0.001*	67	16.0
5 Apr.,	1981	0.0236	-0.0008	-0.526	<0.001*	67	19.0
26 Apr.,	1981	0.0690	-0.0021	-0.816	<0.001*	66	22.3
10 May,	1981	0.2212	-0.0082	-0.394	<0.001*	66	21.3
16 May,	1981	-0.0085	0.0004	-0.152	>0.20	24	19.5
26 May,	1981	0.0091	-0.0006	-0.213	<0.05*	99	23.1
7 June,	1981	0.0675	-0.0003	-0.492	<0.001*	49	26.2
21 June,	1981	0.0482	-0.0015	-0.371	<0.005*	55	27.6
5 July,	1981	0.1058	-0.0033	-0.467	<0.002*	44	28.0
19 July,	1981	0.0888	-0.0025	-0.447	<0.002*	45	28.0
2 Aug.,	1981	0.1984	-0.0065	-0.293	<0.05*	53	29.0
16 Aug.,	1981	0.0965	-0.0029	-0.535	<0.001*	51	28.6
30 Aug.,	1981	0.0814	-0.0024	-0.607	<0.001*	49	27.6
13 Sept.,	1981	0.0870	-0.0024	-0.619	<0.001*	49	26.5
27 Sept.,	1981	0.1335	-0.0042	-0.885	<0.001*	65	25.3
12 Oct.,	1981	0.1041	-0.0032	-0.735	<0.001*	63	25.3
10 Nov.,	1981	0.0458	-0.0012	-0.602	<0.001*	68	22.0
3 Dec.,	1981	0.0319	-0.0009	-0.743	<0.001*	68	17.0
5 Jan.,	1982	0.0128	-0.0003	-0.648	<0.001*	66	12.5
21 Jan.,	1982	0.0013	0.00002	0.024	>0.50	65	9.2
12 Feb.,	1982	-0.0005	0.00007	0.169	>0.10	64	8.2
3 Mar.,	1982	0.0020	-0.00006	-0.209	<0.10*	65	8.8
5 Apr.,	1982	0.0082	-0.0003	-0.447	<0.001*	64	16.9
19 Apr.,	1982	0.0295	-0.0008	-0.647	<0.001*	64	19.0
3 May,	1982	0.0154	-0.0003	-0.306	<0.02*	64	20.5
18 May,	1982	0.0702	-0.0018	-0.708	<0.001*	64	21.8
31 May,	1982	0.0952	-0.0025	-0.751	<0.001*	64	21.8
10 June,	1982	0.0740	-0.0020	-0.646	<0.001*	63	23.4
23 July,	1982	0.1665	-0.0053	-0.700	<0.001*	24	23.9
5 Aug.,	1982	0.0677	-0.0021	-0.337	>0.10	22	23.0
27 Aug.,	1982	0.0047	0.0003	0.006	>0.50	69	24.0
3 Sept.,	1982	0.0788	-0.0029	-0.385	<0.002*	62	22.0
17 Sept.,	1982	0.1007	-0.0036	-0.543	<0.001*	56	19.9
30 Sept.,	1982	0.0802	-0.0032	-0.717	<0.001*	49	19.4
15 Oct.,	1982	0.1226	-0.0046	-0.781	<0.001*	57	16.9
29 Oct.,	1982	0.0757	-0.0028	-0.655	<0.001*	53	15.2
15 Nov.,	1982	0.0271	-0.0006	-0.090	>0.20	53	10.9
30 Nov.,	1982	0.0108	-0.0004	-0.223	>0.10	53	7.1
20 Dec.,	1982	0.0028	-0.0001	-0.036	>0.50	53	6.4

*Indicates a significant linear relationship between shell length in mm and shell growth rate in mm SL/day at $P \leq 0.1$.

3A, B and E) as occurred on 16 May 1981, and 27 August 1982 (Figs. 2 and 5).

Sequential regressions of shell growth rate versus SL of caged animals (Table 1) were utilized to estimate the growth rates of standard size individuals with shell lengths of 5, 10, 20 and 30 mm over the entire collection period (Fig. 5). Such determinations indicated that growth was maximal in all size classes from late April through late October. Growth rate subsequently declined in November and essentially ceased in mid-winter (Fig. 5). This annual growth cycle of caged individuals was also reflected in the growth of individual generations in the natural population (Fig. 2). The shell growth rate of smaller caged individuals was always greater than that of larger clams (Fig. 5). Similarly, in the natural population the mean SL of younger generations composed of smaller individuals increased at a greater rate through time than that of older generations consisting of larger individuals (Fig. 2). Maximum estimated shell growth rates of standard size individuals were: 5 mm SL = 0.181 mm day^{-1}or 5.40 mm 30 $days^{-1}$; 10 mm SL = 0.139 mm SL day^{-1} or 4.17 mm SL 30 $days^{-1}$; 20 mm SL = 0.069 mm SL day^{-1} or 2.07 mm SL 30 $days^{-1}$; and 30 mm SL = 0.025 mm SL day^{-1} or 0.75 mm SL 30 $days^{-1}$ (Fig. 5). No substantial growth was recorded in individuals over 40 mm SL throughout the study period. Moreover, during periods of both environmental stress (marked by major declines in population density) and over-

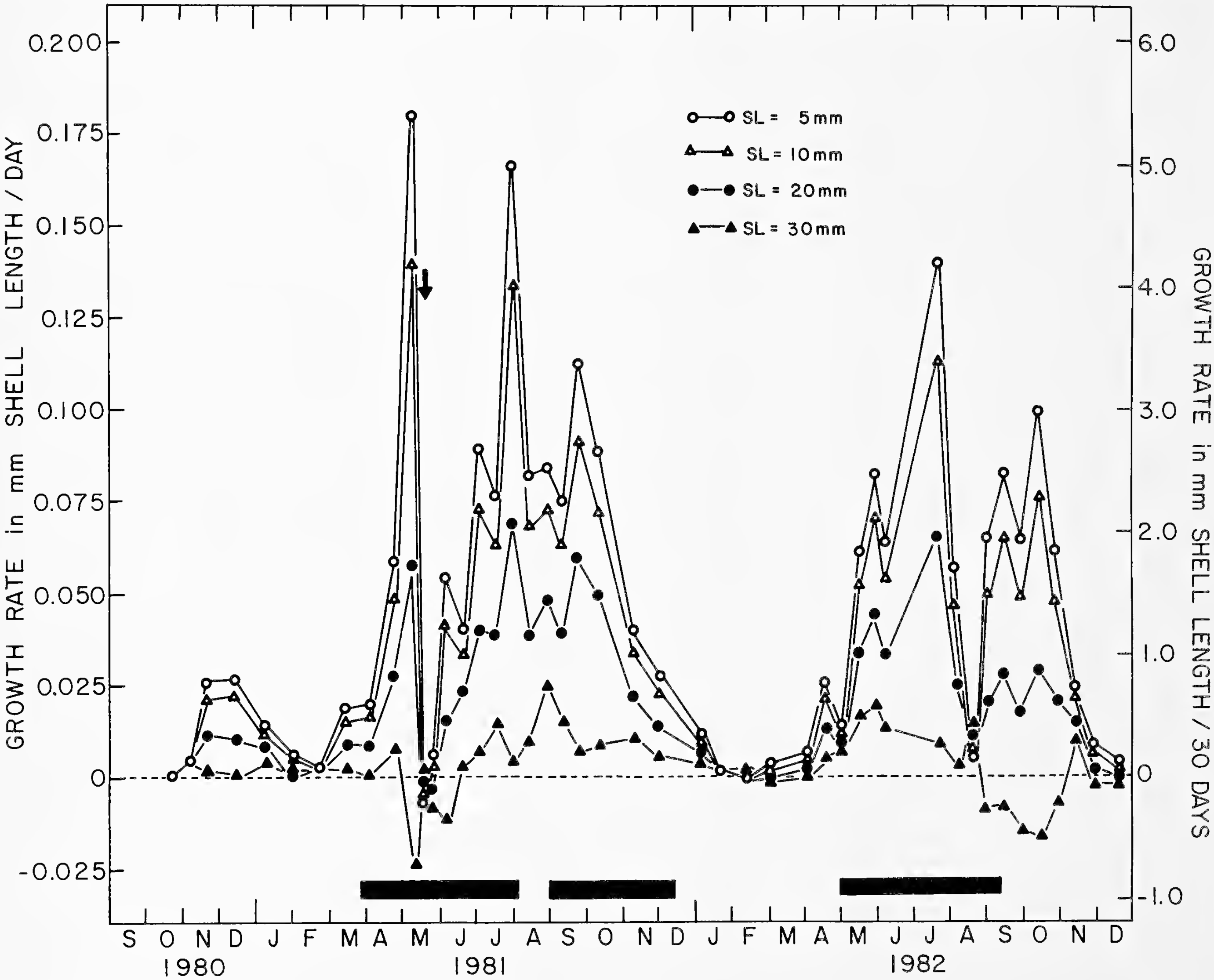

Fig. 5. Shell growth rates of standard sized individuals of *Corbicula fluminea* as estimated from least squares linear regressions of growth rates versus shell length (SL) computed from individuals maintained in an enclosure in the Clear Fork of the Trinity River, Texas. The horizontal axis is months of the year. The left and right vertical axes are shell growth rate in mm additional SL / day and mm SL / 30 days, respectively. The solid bars above the horizontal axis indicate the duration of reproductive and spawning periods. The solid vertical arrow indicates the date of a catastrophic reduction in population density associated with a hail storm and tornado. Note that this reduction in density was associated with a distinct, short-term cessation of growth.

wintering the SL of larger caged individuals (SL > 20 mm) decreased, yielding the negative growth rate estimates for larger size classes from the growth rate regressions computed for these periods (Table 1, Fig. 5).

The annual cycle of shell growth in caged individuals of *C. fluminea* was closely related to field ambient water temperature, increasing with increasing temperature (Figs. 1D and 5). Linear least squares regressions of the common logarithms of daily shell growth rate values (predicted from the growth rate regressions in Table 1) versus ambient water temperature for standard size individuals were found to be significant ($P < 0.1$) in specimens $\leq$ 30 mm SL. These regressions for standard individuals with an SL of 5 mm, 10 mm, 20 mm, 30 mm and 40 mm are as follows:

5 mm SL, Log_{10} mm SL $\mathrm{day}^{-1} = -3.152 + 0.077$ (°C), $n = 44$, $r = 0.624$, $P < 0.001$;

10 mm SL, Log_{10} mm SL $\mathrm{day}^{-1} = -3.032 + 0.069$ (°C), $n = 44$, $r = 0.658$, $P < 0.001$;

20 mm SL, Log_{10} mm SL $\mathrm{day}^{-1} = -3.249 + 0.068$ (°C), $n = 44$, $r = 0.697$, $P < 0.001$;

30 mm SL, Log_{10} mm SL $\mathrm{day}^{-1} = -3.345 + 0.041$ (°C), $n = 33$, $r = 0.333$, $P < 0.1$; and

40 mm SL, Log_{10} mm SL $\mathrm{day}^{-1} = -3.800 + 0.050$ (°C), $n = 10$, $r = 0.310$, $P > 0.2$.

These regression equations were then utilized to predict the growth rates of standard individuals of 5, 10 and 20 mm SL over the normal ambient water temperature range occurring at the Clear Fork collecting site (4.8°C - 29°C) (Fig. 6). For all three standard individuals growth rate increased exponentially above 15°C, and was greatly inhibited below that temperature (Fig. 6). When these growth rate regressions are plotted on a $\log_{10}$ scale against ambient water temperature it became apparent that relatively high levels of growth were only sustained by individuals with an SL $\leq$ 20 mm, while those of clams > 30 mm SL were greatly depressed at all temperatures. Indeed, the growth rates of individuals > 40 mm SL were detectable only above 15°C (Fig. 7).

Since the growth of caged specimens was the same as that of marked freeliving individuals (Fig. 4) it was also assumed to be equivalent to that clams in the natural population. This assumption was tested by comparing the increase in the mean SL of individual generations through time with that predicted from sequential regressions of the shell growth rate of caged individuals versus SL (Table 1). Generation growth rates were predicted from these regression equations by utilizing the mean SL of generations with relatively high field densities in January 1981 (E-81, L-80, and E-80) and 1982 (E-82, L-81, E-81 and E-80 + L-80) as an initial SL value and iteratively estimating increases in SL between successive collection dates over an annual growth cycle from the appropriate sequential growth rate regression equations. This predicted annual growth pattern was then compared visually to that estimated from the mean SL of generation size classes in sequential population samples (Figs. 8A and B). In nearly all cases the annual pattern of increase in SL predicted by the growth rate regression equations almost exactly coincided with the actual annual increase in SL of specific generations (Figs. 8A and B). The exceptions were the L-81 and combined E-80 + L-80 generations in 1982 (Fig. 8B). These two generations had relatively low densities (Fig. 3C); therefore, differences between predicted and observed shell growth patterns may have resulted from random field sampling errors in the determination of both initial and subsequent mean lengths of these generations.

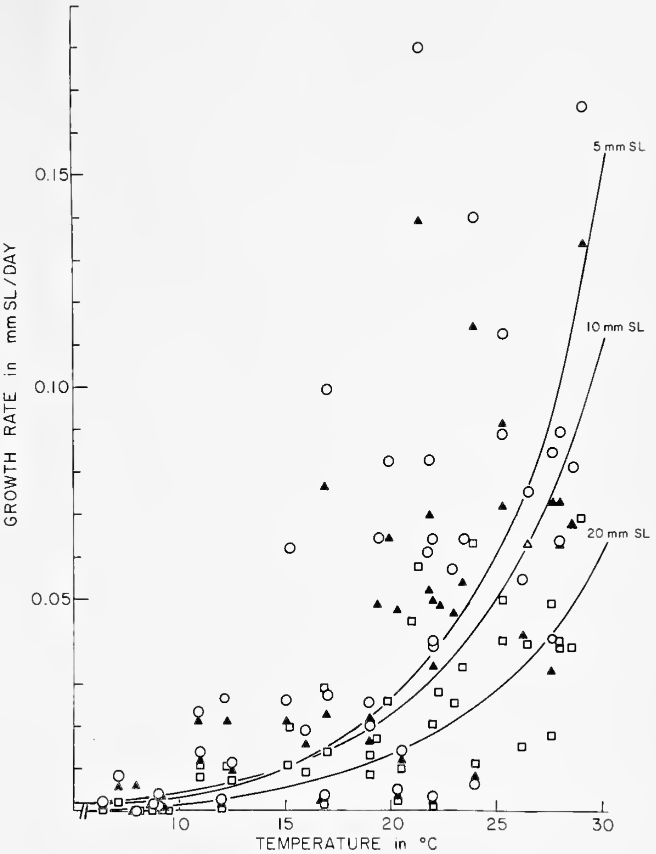

Fig. 6. Effect of ambient water temperature on the shell growth rate of standard individuals of *Corbicula fluminea* in the Clear Fork of the Trinity River, Texas. The horizontal axis is ambient water temperature in °C. The vertical axis is shell growth rate (mm additional shell length / day) estimated for individuals with standard lengths of 5 mm (open circles), 10 mm (solid triangles) and 20 mm (open squares) from regressions of growth rate versus shell length of caged specimens (SL) (Table 1). The solid lines represent best fits of least squares linear regression equations of the common logarithm of estimated shell growth rates versus ambient water temperature for standard individuals as follows: 5 mm SL, $\log_{10}$ mm SL $\mathrm{day}^{-1} = -3.152 + 0.077$ (°C); 10 mm SL, $\log_{10}$ mm $\mathrm{day}^{-1} = -3.032 + 0.069$ (°C); and 20 mm SL, $\log_{10}$ mm $\mathrm{day}^{-1} = -3.249 + .068$ (°C).

In order to incorporate both the effects of ambient water temperature and size into a more general model of shell growth in *C. fluminea* the per day growth rates of standard individuals of 5 mm, 10 mm, 20 mm, 30 mm and 40 mm SL were computed from the sequential growth rate versus SL linear regression equations for each collection date (Table 1). These estimated growth rate values were then transformed

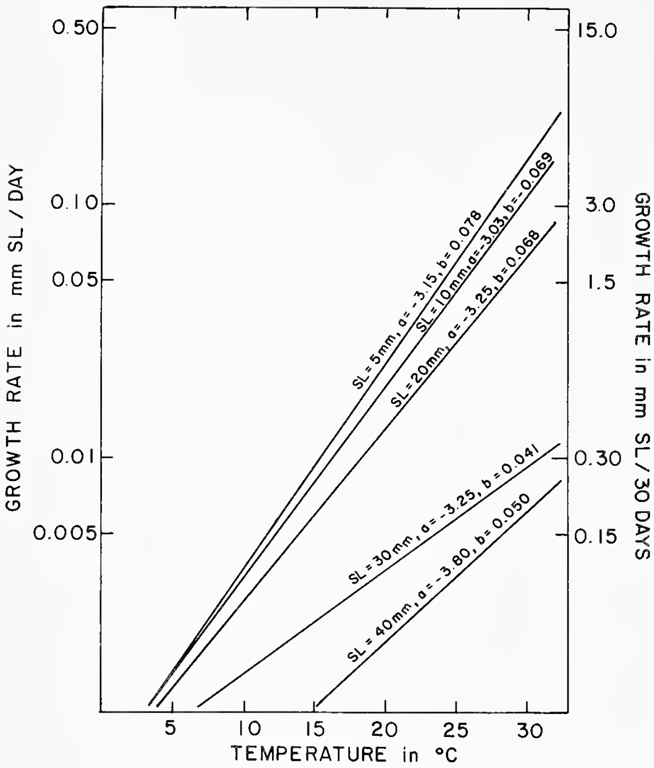

Fig. 7. Least squares fits of shell growth rate versus ambient water temperature of individuals of *Corbicula fluminea* held in field enclosures in the Clear Fork of the Trinity River, Texas. The horizontal axis is field ambient water temperature (°C). The left and right vertical axes are logarithmic scales of shell growth rate as mm of additional shell length per day (mm SL / day) and mm SL / 30 days, respectively. The solid lines represent best fits of least squares linear regressions of the common logarithm of shell growth rate in mm SL / day versus ambient water temperature [$\log_{10}$ mm SL / day = a + b(°C)], for individuals with a standard shell lengths of 5 mm, 10 mm, 20 mm, 30 mm and 40 mm. Regression parameters "a" (intercept) and "b" (slope) are indicated above the appropriate regression line.

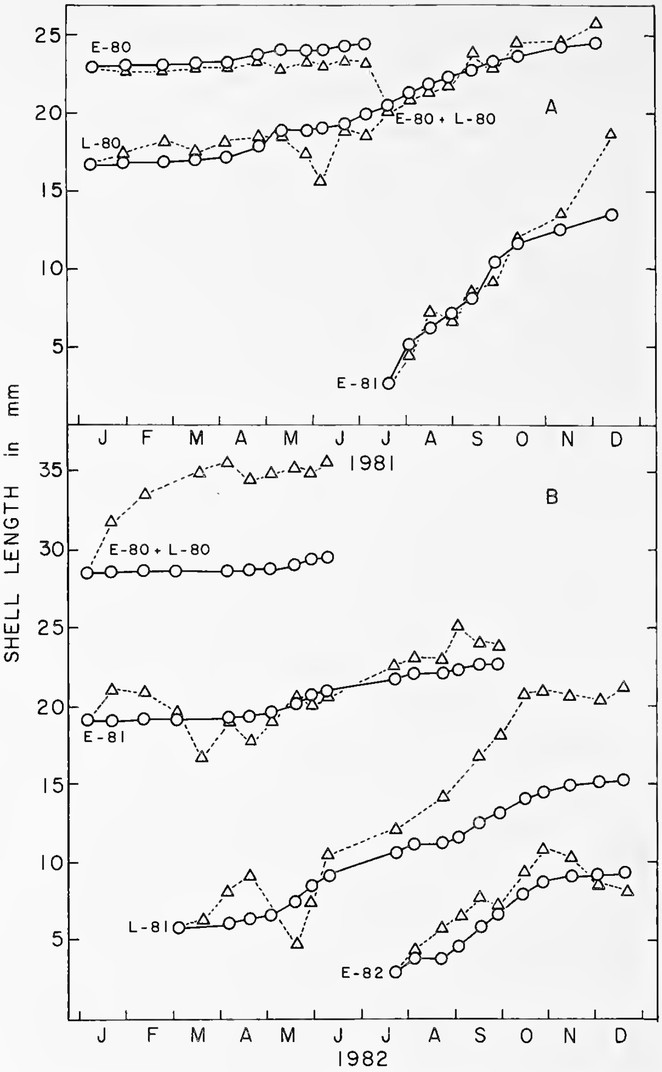

Fig. 8. Comparisons of the increase in the mean shell length (SL) of individual generations of the Clear Fork *Corbicula fluminea* population as estimated independently by the visual analysis of size-frequency distributions of bimonthly samples and by computation from corresponding regressions of shell growth rate versus shell length derived from the growth of individuals held in a field enclosure (Table 1). **A.** Comparisons of the increase in the mean SL of specific generations estimated from sample size frequency analysis and individual growth in a field enclosure during 1981. **B.** Comparisons of the increase in mean SL of specific generations estimated from sample size-frequency analysis and individual growth in a field enclosure during 1982. For both figures the horizontal axis is months of the year and the vertical axis, SL in mm. The open triangles connected by dashed lines are the mean SL of specific generations estimated from distinct size-frequency groupings in field collections. The open circles connected by solid lines are the increase in shell SL of the same generations independently predicted by starting at the same initial SL as that of a specific generation size-frequency grouping in the earliest January sample and estimating subsequent SL increases from sequential least squares linear regressions of the shell growth rate of field enclosed specimens versus SL (Table 1).

into common logarithms and fitted to a least squares multiple linear regression versus both SL and average ambient water temperature between sequential SL measurements of caged individuals. This model incorporates both the negative linear relationship between shell growth rate and size, and the positive exponential relationship between shell growth rate and temperature. However, it cannot predict the decrease in SL that occurred in larger specimens (SL $<$ 30 mm) during the colder winter months. As shell degrowth occurred at very low rates over relatively short durations, the inability of the model to predict it appears to be of little real significance. This multiple linear model of shell growth rate for the Clear Fork *C. fluminea* population is:

$$\text{Log}_{10}\ \text{mm SL day}^{-1} = -2.621 - 0.034\,(\text{mm SL}) + 0.065\,(^{0}\text{C}),$$
$$r = 0.691,\ n = 174,\ P < 0.001.$$

Best fits of this model at temperatures spanning the normal ambient range (5°-30°C) over shell lengths ranging from 5 mm to 40 mm (Fig. 9A) and for standard individuals ranging in SL from 5 mm to 40 mm over an ambient

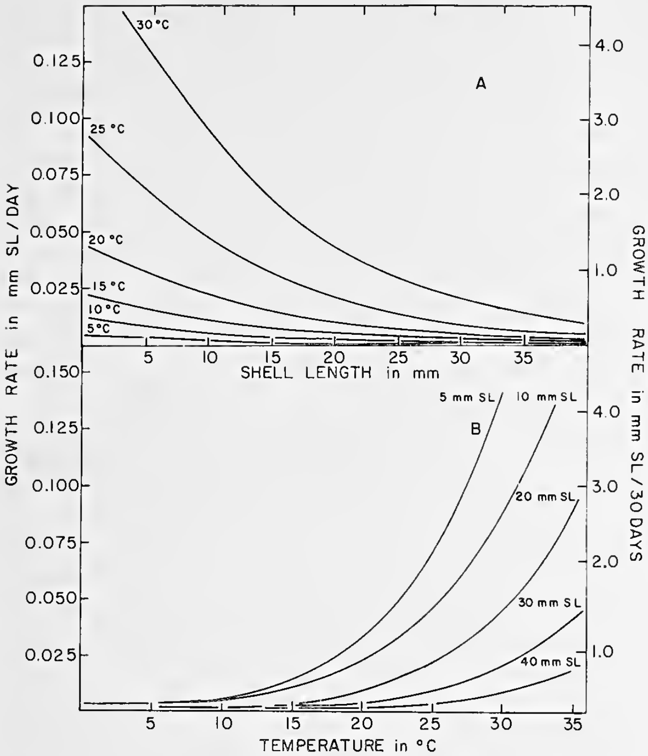

Fig. 9. Least squares fits of multiple linear regression model of the shell growth rate of *Corbicula fluminea* in relation to individual shell length (SL) and ambient water temperature (°C) based on the growth rates of individuals held in a field enclosure in the Clear Fork of the Trinity River, Texas. The shell growth rate model utilized was: Log$_{10}$ shell growth rate as additional mm SL day^{-1} = -2.621 - 0.0342 (mm SL) + 0.0645 (°C); $r = 0.69$; $n = 174$; and $P < 0.0001$. For both figures the left and right axes are shell growth rates in additional mm SL / day and mm SL / 30 days, respectively. **A.** Least square best fits of the shell growth rate at natural ambient water temperatures over a range of SL extending from < 5 mm to > 35 mm. The horizontal axis is SL in mm. The solid lines represent best fits of the above regression equation at ambient water temperataures of 5°C, 10°C, 15°C, 20°C, 25°C and 30°C. **B.** Least squares best fits of the shell growth rate of standard sized individuals over a temperature range of < 5°C to > 30°C. The horizontal axis is ambient water temperature in °C. The solid lines represent best fits of the above growth rate model for standard individuals with shell lengths of 5 mm, 10 mm, 20 mm, 30 mm, and 40 mm.

temperature range of 0°C to 35°C (Fig. 9B) clearly demonstrate the stimulatory effects of increasing ambient temperature and inhibitory effects of increasing size on the shell growth rates of *C. fluminea*. Such curves allow rapid visual estimation of shell growth rate at any particular size-temperature combination within the normal range of SL and ambient water temperatures encountered in North American *C. fluminea* populations.

DISCUSSION

The growth rate of caged individuals of *C. fluminea* was equivalent to that of marked freeliving individuals and, therefore, to that of the natural population (Fig. 4). Since the growth rates estimated from sequential growth rate regression equations of caged individuals correspond closely to concurrent generation growth rate estimates based on the size-frequency analysis of sequential population samples (Fig. 8), such analysis appears to be a reliable methodology to estimate the growth rates and life spans of *C. fluminea* populations. Size-frequency analysis of repetitive population samples has been utilized to evaluate the growth and life cycle of a number of *C. fluminea* populations (Aldridge and McMahon, 1978; Eng, 1979; Heinsohn, 1958; Leveque, 1973; McMahon and Williams, 1986; Morton, 1977; Williams, 1985; Williams and McMahon, 1986). These studies have indicated that *C. fluminea* populations have two reproductive and spawning periods per year and a variable life span as short as 1.5 years (Aldridge and McMahon, 1978; Heinsohn, 1958), but never extending beyond three (Leveque, 1973; Morton, 1977; McMahon and Williams, 1986; Williams, 1985; Williams and McMahon, 1986) or four years (Eng, 1979). In the past, such analyses have been questioned because the interpretation of shell size-class frequency distributions could reflect the biases of individual investigators. However, this study has demonstrated that the directly measured growth of caged individuals is essentially equivalent to that estimated for distinct generation cohorts from seqential sample size-frequency analysis. Therefore, the latter should now be accepted as a reasonably accurate methodology for the analysis of population growth and age structure in this species.

The life cycle, life span and population dynamics of the Clear Fork *C. fluminea* population displayed a remarkable year-to-year variation. Individuals representing four different biannual reproductive and spawning periods (the E-78 + L-78, E-79 + L-79, E-80 + L-80, and E-81 + L-81 generations) were present in the 1981 samples, indicative of a life span of slightly greater than three years. Yet, the 1982 samples had representatives of only three biannual reproductive periods (the E-80 + L-80, E-81 + L-81, and E-82 generations) (Fig. 2), indicative of a 1.5 to 2.5 year life span. In addition, while there were distinct early and late reproductive periods in 1980 and 1981 only the early reproductive and spawning period was successful in 1982.

Generation growth rates in the Clear Fork population were also highly variable from year to year. The E-81 generation reached mean SL of 17.9 mm by December 1981, while the E-82 generation achieved a mean SL of only 10.3 mm by that time (Fig. 2). Differences in ambient water temperature may account for this growth rate variation. Summer (June - end of August) ambient water temperatures averaged 4°C lower in 1982 (24.0°C) than in 1981 (27.9°C). The growth rate model described in the Results predicts that the growth of individuals with an SL of 5-15 mm would be 78% greater in the warmer temperatures of 1981 than in 1982 (Figs. 9A and B). In December the mean SL of the E-81 generation was 74% larger than that of the E-82 after the first summer and fall of growth (Fig. 2), suggesting that the observed difference in growth rate was wholely attributable to interannual temperature differences. Indeed, the reduced growth of the

E-82 generation prevented it from reaching sexual maturity (SL > 10 mm, Aldridge and McMahon, 1978) in time to participate in the late reproductive and spawning period of 1982. As older generations were extinct by this time (Fig. 3), no effective late reproductive and spawning period occurred. Therefore, differences in ambient water temperature appear to have accounted for most of the observed interannual variation in life cycle and reproduction of the Clear Fork *C. fluminea* population. Temperature variation may also partially account for the geographic, ecophentypic variations reported in the growth, reproduction and population dynamics of this species in North America and Asia (see McMahon, 1983 and papers published in this symposium for a review of growth and life cycle in *C. fluminea*).

Certainly, the high levels of environmentally induced, year-to-year variation in the life-history parameters of the Clear Fork *C. fluminea* population, may reflect the even greater levels of variation reported for geographically separated populations in North America. Such interpopulation and intrapopulation variation could be partially responsible for the apparent confusion regarding this species' growth, reproduction and life cycle. However, this study along with those of Aldridge and McMahon (1978), Britton *et al.* (1979), O'Kane (1976) and Williams and McMahon (1986) all indicate that *C. fluminea* populations in Texan freshwaters have maximum life spans of two to three years and a biannual reproductive pattern. Data for Texan populations closely corresponds to that of Heinsohn (1958) and Eng (1979) for Californian populations and those of Morton (1977) and Leveque (1973) for native Asian and African populations, respectively.

The maximum growth rates of caged individuals in the Clear Fork population (5 mm SL = 5.4 mm SL 30 days^{-1} to 30 mm SL = 0.75 mm SL 30 days^{-1}) fall well within those reported for other enclosure experiments with *C. fluminea*. Growth rate estimates for caged specimens with a SL < 10 mm have ranged from 2.0 to 2.5 mm 30 days^{-1} (Mattice, 1979; O'Kane, 1976) to 6.5 mm 30 days^{-1} (Dreier, 1977; Dreier and Tranquilli, 1981). For larger specimens (SL > 10 mm), reduced growth rates have been reported (Britton, *et al.*, 1979; Buttner and Heidinger, 1980) which were similar to those recorded in this study.

The growth rate of caged individuals in the Clear Fork had a highly significant negative linear relationship with SL (Table 1). Negative correlations between growth rate and size have been reported a number of times for *C. fluminea* (Britton, *et al.*, 1979; Dreier and Tranquilli, 1981; Joy, 1985, O'Kane, 1976; Mattice, 1979; Mattice and Wright, 1985; Pool and Tilly, 1977). The majority of these studies have suggested that the relationship between growth rate and size is linear while Britton *et al.*, (1979) indicated that an exponential model may be more appropriate. While exponential models are generally appropriate to descirbe the relationship between growth and size in this species they cannot predict the negative growth rates (measured decrease in SL) observed to occur in larger caged specimens during the winter or periods of environmental stress (Fig. 5). In order to account for such negative growth 48 separate linear models of growth rate versus SL have been presented, each associated with a specific set of environmental temperature conditions (Table 1).

Of the environmental factors that affected the growth rate of the Clear Fork *C. fluminea* population temperature was, by far, the most important. Our data and that of others (Britton *et al.*, 1979; Buttner and Heidinger, 1980; Dreier and Tranquilli, 1981; Mattice, 1979; Mattice and Wright, 1985; O'Kane, 1976; Pool and Tilly, 1977), indicate that increasing temperature stimulates growth in this species. Therefore, no universal model of growth in *C. fluminea* can be valid unless it incorporates both size and temperature effects, as does the model presented herein (Figs. 9A and B). As our growth rate model incorporates both size and temperature effects it may allow biologists and engineers concerned with control of this species to predict the time required for impinging juveniles to reach sizes that occlude heat exchangers in service and auxiliary water systems.

The high capacity for growth of *C. fluminea* may be associated with its unusually high filtration rates compared to other freshwater species. Filtration rates for *C. fluminea* are estimated to range from 250 ml clam^{-1} hr^{-1} to > 1000 ml clam^{-1} hr^{-1} (Buttner and Heidinger, 1982; Foe and Knight, 1986; Mattice, 1979). Such high ingestion rates are associated with elevated assimilation efficiencies (Foe and Knight, 1986; Lauritsen, 1986) and net production efficiencies (> 70%, Lauritsen, 1986, Aldridge and McMahon, 1978) in this species, supporting rapid tissue growth.

Unlike reports from Asia, Africa and the Western United States which all suggest that *C. fluminea* populations have roughly similar growth rates and life spans, United States populations east of the Mississippi River have been reported to have lower growth rates and longer life spans of 5 to 8 years (Gardner *et al.*, 1976; Keup *et al.*, 1963; Mattice, 1979; Mattice and Wright, 1985; Sickel, 1973; Sinclair and Isom, 1963). While some of these estimates may have resulted from assuming one generation per year for this species, others are based on the growth of caged individuals (Mattice, 1979; Mattice and Wright, 1985). The growth rate model developed by Mattice and Wright (1985) predicts a life span of at least 6 years to reach an SL equivalent to the largest individuals in the population. However, this study and others have demonstrated high levels of interannual, intrapopulation variation in the growth rates of *C. fluminea* populations (Mattice and Wright, 1985; Williams and McMahon, 1986). Large interannual variations in growth are associated with phytoplankton availability (Williams and McMahon, 1986) or with differences in temperature regime (this study). McMahon (1983) suggested that maximum size is directly correlated with growth rate in this species. Therefore, the presence of very large specimens in a population may not be indicative of individuals with long life spans but rather, of generations previously experiencing exceptionally good conditions for growth. This is the case in the Clear Fork *C. fluminea* population where individuals of the E-78 + L-78 generation attained lengths > 45 mm at the end of a three year life span, while members of the E-79 + L-79 generation did not have shell lengths much in excess of 35 mm in their third and terminal year of life (Fig. 2). Indeed, when growth is computed from our model over the exceptionally low annual temperature cycle that occurred in 1982 (Fig. 1D), an early generation would require 8 years to reach an SL of 30 mm, while only four years would be required to reach that size over the warmer temperature cycle of 1981 (Fig. 1D). At the even warmer temperatures recorded for a *C. fluminea* population in Lake Arlington, Texas, from March, 1981 to March, 1982 (Williams and McMahon, 1986), our growth model predicts only three years to reach an SL of 30 mm. The summer of 1980, prior to our initial collections of the Clear Fork population, had been among the warmest on record in Texas, with maximum daily ambient air and water temperatures averaging 32ºC from June through August 1980 (National Oceanic and Atmospheric Administration, 1980). Water temperatures in this range exponentially increase the growth rate of *C. fluminea* and stimulate new growth in larger specimens (SL > 30 mm) (Figs. 6 and 9). Therefore, the very warm water temperatures of 1980 may have allowed two and three year old individuals to grow rapidly to the very large sizes observed in our initial collections (Fig. 2). Indeed, continual monitoring through the spring of 1986 has indicated that although a three year life span has been maintained in the Clear Fork population, such large size classes have not reoccurred since 1981 (McMahon, unpublished observations). As such, at least in Texas, exceptionally large individuals in *C. fluminea* populations may result from environmental conditions that support elevated growth rates in specific generations, but do not result from extended life spans.

There is biochemical evidence that *C. fluminea* populations east of the Mississippi River have gene pools distinct from those west of the Mississippi River (McLeod, 1986). Therefore, these populations may represent genetically distinct "physiological races" characterized by longer life spans than reported for this species throughout the rest of its world-wide range (McMahon, 1983). However, such populations should be subjected to long-term concurrent studies of both population age-size structure variations and individual growth rates in field enclosures before the general acceptence of extended life spans (> 6 years) for this species in the southeastern United States. Recently, specimens of *C. fluminea* were reported to grow from a mean SL of 13 mm to 26 mm when held in an enclosure in the Kanawha River, West Virginia, for 38 weeks (Joy, 1985). This growth rate is very similar to those recorded for the E-81 and L-81 generations in the Clear Fork population. Such new data strongly suggest that the growth and life span of *C. fluminea* populations in the eastern United States are well within the ranges recorded for this species in other geographical areas of its range.

In the Clear Fork population the majority of growth occurred above 15ºC. Similarly, a 14ºC limit for growth was reported for a *C. fluminea* population in the Delta Mendota Canal, California (Eng, 1979). This is also the approximate temperature at which reproductive activity is initiated in both the Clear Fork and other populations (13º-19ºC) (Aldridge and McMahon, 1978; Dreier and Tranquilli, 1981; Eng, 1979; Morton, 1977; Williams and McMahon, 1986). In addition, the filtration rate of *C. fluminea* is reduced by > 50% below 20ºC (Mattice, 1979). Therefore, fundamental physiological and metabolic changes must occur which allow this species to switch from a slow growing, non-reproductive, rather inactive state, to a fast growing, reproductive, highly active state as temperatures rise above 15º-18ºC.

Temperatures above 24º-25ºC are reported to inhibit growth in laboratory acclimated specimens of *C. fluminea* (Foe and Knight, 1986; Mattice 1979; Mattice and Wright, 1985) and to reduce filtration rate (Mattice, 1979) and ventilation and oxygen consumption rates (McMahon, 1979a). It was somewhat surprising then that no suppression of growth rate was observed in caged individuals in the Clear Fork population at temperatures up to 30ºC (Figs. 6 and 7). Indeed, other studies indicate that population growth rates are maintained in *C. fluminea* at field water temperatures as high as 33ºC (Aldridge and McMahon 1978; Williams and McMahon, 1986). A recent study of a steam-electric power plant thermal discharge *C. fluminea* population reported no inhibition of growth at temperatures approaching 36ºC, the apparent long-term upper lethal limit of this species (McMahon and Williams, 1986). Further, oxygen consumption rates were not suppressed at temperatures as high as 33ºC in specimens of *C. fluminea* experiencing those temperatures in the field (Williams, 1985). The conflicting data from laboratory acclimated and field-conditioned individuals suggest that this species is capable of long-term (seasonal) physiological temperature compensation under ambient field conditions, not revealed in shorter-term laboratory temperature acclimation experiments.

There were distinct declines in the growth rate of caged individuals in May 1981 and June 1982, associated with periods of catastrophic reductions in population densites (Fig. 3). During these and overwintering periods larger individuals exhibited shell "degrowth", characterized by a directly measured slow decrease in SL. Bivalves are reported to buffer hydrogen ion produced during anaerobic respiration with carbonate released from dissolution of the shell. Therefore, long-term anaerobiosis leads to a reduction in shell mineral content (Akberali *et al.*, 1983; Goddard and Martin, 1966). During overwintering periods and periods of environmental stress *C. fluminea* may close its valves and become partially or completely anaerobic, leading to shell dissolution, erosion of the shell edge and degrowth. Exposure of *C. fluminea* to environmental stress causes changes in the internal shell microstructure (Prezant and Chalermwat, 1983). Dissolution of the shell in specimens exhibiting degrowth was evidenced by the presence of greater amounts of uncalcified shell maxtrix and periostracum at the shell edge.

This study also provided an opportunity to observe the recovery of a *C. fluminea* population after a catastrophic density decline. Major declines of population density in this species have been associated with reproduction (Ingram, 1959), low winter water temperatures (< 2ºC) (Bickel, 1966; Cherry *et al.*, 1980; Dreier and Tranquilli, 1981; Horning and Keup, 1964; Mattice and Dye, 1976; Rodgers *et al.*, 1979), and exposure to air by receding water levels (McMahon, 1979b; White, 1979; White and White, 1977). *C. fluminea* can rapidly reestablish populations after severe density reductions. A population in the New River, Virginia, recovered to 1000 clams m^{-2} within five months of nearly complete extermination by low winter water temperatures (Rodgers *et al.*, 1979). Similarly, irrigation canal populations of *C. fluminea* have been reported to recover to extremely high densities within one year of canal dewatering and nearly complete removal of resident adult populations (Eng, 1979; Prokopovich, 1969; Prokopivch and Hebert, 1965). In the Clear Fork population density declined from 2655 clams m^{-2} on 26 April 1981, to 305 clams m^{-2} on 21 June 1981 (Fig. 3A). Reproduction by the relatively few surviving adults allowed recovery of 1980 density levels through recruitment of the E-81 and L-81 generations by the spring of 1982 (Figs. 3A and D). Reproduction by these two generations and subsequent recruitment of the resulting E-82 generation increased population density to 12000 clams m^{-2} by the winter of 1982 (Figs. 3A and E). This astonishing capacity for rapid population recovery is associated with the high fecundity of *C. fluminea*, reported to average 68,678 juveniles per adult in Texas populations (Aldridge and McMahon, 1978). The high reproductive capacity, high growth rate, small size at maturity (SL < 10 mm, Aldridge and McMahon, 1978), and attenuated life span (Aldridge and McMahon, 1978; Eng, 1979; Heinsohn, 1958; Leveque, 1973; Mattice and Wright, 1985; Morton, 1977; Williams and McMahon, 1986; this study) of *C. fluminea* appear to be adaptations that optimize the production and survival to maturity of offspring in highly unstable environments where such life history traits favor rapid population growth and expansion and, therefore, are of high selective value (Stearns, 1976, 1977; for a review of life history traits in *C. fluminea* see McMahon, 1983). It is the exceptional ability of *C. fluminea* to successfully invade and survive in highly disturbed habitats that not only accounts for its rapid spread in North American fresh waters (McMahon, 1982), but, also for its ability to invade, survive, grow and reproduce in industrial raw water cooling and service water systems.

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ASPECTS OF GROWTH OF *CORBICULA FLUMINEA*

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ABSTRACT

Studies of caged Asiatic clams (*Corbicula fluminea*) in Watts Bar Reservoir (Clinch River, Tennessee) indicate that interaction of intrinsic and extrinsic factors affects the rate of increase in shell length (SL). Measurements of marked and unmarked clams were made at two sites differing by about 5°C in both 1976 and 1977, and at lower temperature sites in 1978 and early 1979. The growth season in Watts Bar began in April and continued through October. From November through March growth virtually ceased. Increase in SL was an inverse linear function of initial SL; i.e., small clams grew faster than large ones. Rate of shell length increase differed between the two sites. Growth rates also varied during the growth season. A comparison of these rates for each site during the year indicated that temperature plays a major role in growth rate determination. Type of algae and food (seston concentration) were not correlated with growth rate. A decline in growth rate in spring, at about the time of peak reproduction, indicates that intrinsic factors are also important. Nevertheless both laboratory and field studies suggest that the temperature for optimum growth occurs in the mid-twenty °C range. Because of this relationship between growth and temperature, estimates of both growth and life span may vary depending on the natural annual temperature regime. For example, life span of *Corbicula* in the Clinch River System is more than four years and could be as long as six (or more) years, which is substantially longer than for populations in some locations. Such differences could influence decisions regarding initiation of control procedures at industrial facilities.

*Corbicula fluminea** has become the primary focus of macrofouling control for industrial facilities sited on freshwater bodies in the United States (Mattice, 1983). With the recent report of *Corbicula fluminea* in Lake Erie (Clarke, 1981), this species has now achieved expansion into all of the major drainage basins in the United States. This has taken place in roughly 40 years, an invasion that appears unprecedented for aquatic invertebrates. Although no comprehensive list of industries impacted by this expansion has compiled, a large variety of facilities have been specifically mentioned. It is probably safe to say that a majority of the industries in *Corbicula*'s geographic range that require supplies of raw water have had problems with *Corbicula* fouling. The expense of fouling incidents has varied greatly, but has at least reached the multimillion dollar level in some cases (pers. comm., Robert West, Arkansas Power Co., Little Rock, Ark.). It is clear that some method of controlling fouling of *Corbicula* is sorely needed to prevent increasing societal costs of generation and manufacturing.

At present, cost effective control of *Corbicula* fouling requires information about when the clams reproduce and how fast they grow. Despite the burgeoning interest in control of *Corbicula* fouling, the only procedure that has proven universally effective has been physical removal (Mattice, 1983). Thus, it is important to know when to schedule clam removal to prevent the clams from reaching a size large enough to occlude water lines or condenser tubes. Reproduction and rate of growth play important roles in determining these schedules.

This study examined growth of *Corbicula* in a river/reservoir system known to present *Corbicula* fouling to industrial facilities (Sinclair and Isom, 1963; Goss and Cain,

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*We have chosen to use the species name *fluminea* here because of evidence (Smith *et al*., 1979) that clams from the population we studied are not different from those in Texas that Morton (1979) has described as *Corbicula fluminea*. However, some controversy does exist regarding the proper name (Sinclair and Isom, 1963) suggesting the need for further comprehensive study.

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1976; Goss *et al.*, 1979). Comparisons between and within years at sites differing in water quality were made to determine intrinsic and extrinsic factors that affect growth of the clams. Only data summaries are reported here; the complete data set is included in Mattice and Wright, (1985).

SITE DESCRIPTION

Growth of *Corbicula fluminea*, was investigated from 1975 to 1979 in the intake and discharge areas of the Kingston Steam Plant, a coal-fired electricity generating station near Kingston, Tennessee (84°31'W, 35°54'N). Intake source water varied seasonally depending on relative flows of the Emory, Clinch, and Tennessee Rivers. Flows of the latter two rivers depended on operation of upstream dams. However, the three sites where clams were held (Fig. 1) were dominated by through-plant water flow (3671 m^3 per minute when all nine units are operating) so that water qualities at all sites could be assumed to be similar except for changes induced by plant operation. These changes included a discharge-to-intake water temperature differential of 7.5 to 8.0°C and intermittent application of chlorine ranging from 499 to 2722 kg per day depending on time of year. Chlorination is conducted 5 days/week with each unit receiving application for 30 minutes to control condenser fouling. Chlorine is measured daily at the discharge of each unit during chlorination to ensure that limits of 0.5 mg/l total residual and 0.2 mg/l free residual chlorine are not exceeded; no chlorine can be detected (amperometric titration) more than 3-15 meters beyond the combined discharge of all units (personal communication, Alex Riddings, Public Safety Office, Kingston Steam Plant, Kingston, Tenn.).

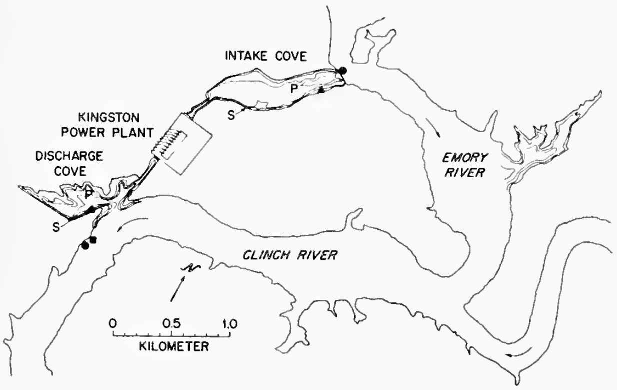

Fig. 1. Schematic diagram of the study site indicating the locations of cages (■ = study of winter growth of small clams, ◄ = all other growth studies), Tennessee Valley Authority temperature probes (●), and phytoplankton (P) and seston (S) sample sites.

MATERIALS AND METHODS

Clams used in these studies were collected from areas near the Kingston Steam Plant using a venturi suction sampler (Mattice and Bosworth, 1979). After transport of the samples to the laboratory, clams were separated from the substrate and acclimated in a flowing water system to within +/-2°C of the intake or discharge temperatures at $\leq$ 1°C per day. Clams greater than 9.0 mm (maximum shell length) were marked with a number using a small dental grinder; clams smaller than 9.0 mm were not marked. Clams in the laboratory were fed a mixture of ground trout chow (Ralston Purina Co., St. Louis, Mo.) and Staple Flake food for Tropical Fish (Hartz Mountain Corporation, Harrison, N.J.) twice a day except on weekends. Clams maintained on this regimen did grow. Once acclimated, the shell length (SL) of each clam was measured with a dial caliper to the nearest 0.1 mm, and clams were transferred to field cages (described below) weighted to rest on the substrate at water depths of about 3 m. At various intervals thereafter, the cages were brought to the surface and the shell lengths of the clams remeasured. Individual clams were not out of water for more than one-half minute at a time during any of these procedures.

Three types of cages were used in these studies. Clams greater than 15 mm SL were held in 0.5 x 0.5 x 0.33 m cages of ~4 mm mesh Vexar plastic netting attached to a redwood frame. Clams less than 15 mm SL were generally held in 2 liter cages made of covered plastic tubs. Each of these covered tubs had four holes (2.5 x 2.5 cm) in the sides and one larger hole in the top covered with 1 mm mesh nitex screening to permit flow of water and food into the cage. The screened tubs were held inside the larger cages described above. The third type of cage was used only for studies of winter growth of small (3.0-6.5 mm SL) clams. These cages consisted of an envelope (~8 x 15 cm) of 1 mm mesh stainless steel screen held together with staples. Cages were attached to a weighted line.

Several water quality parameters were also measured at various times during these studies. Water temperatures were measured daily either as continuous recordings at the cage sites (Ryan recording thermometer, Ryan Instruments, Inc., Kirkland, WA 98033) or at hourly intervals (Tennessee Valley Authority temperature recorders). See Figure 1 for positions relative to cage positions. Mean daily temperatures were estimated by eye from the 30-day strip charts after the recordings were retrieved from the Ryan recording thermometer. Hourly temperatures were averaged from the TVA data. In some cases, interconversions between temperature readings were made to supply missing data (Mattice and Wright, 1985). Phytoplankton complement and relative composition were estimated by examining water samples taken with a 2 liter Kemmerer bottle and filtered through a plankton net. Samples were collected monthly from October 1975 through November 1976 except for the months of April, July, and September. From October 1975 through May 1976, samples were filtered through a relatively coarse (80 μm) mesh Wisconsin-type plankton net. From June 1976 through November 1976, samples were filtered through a 10 μm mesh synthetic net. At each station on each date, two samples were filtered, one near the surface and one near the bottom of the water column. Algal identity and relative composition were determined microscopically. On numerous occasions seston concentration was measured in one or both coves by filtering 1 liter of water through a tared Whatman GF/C glass fiber

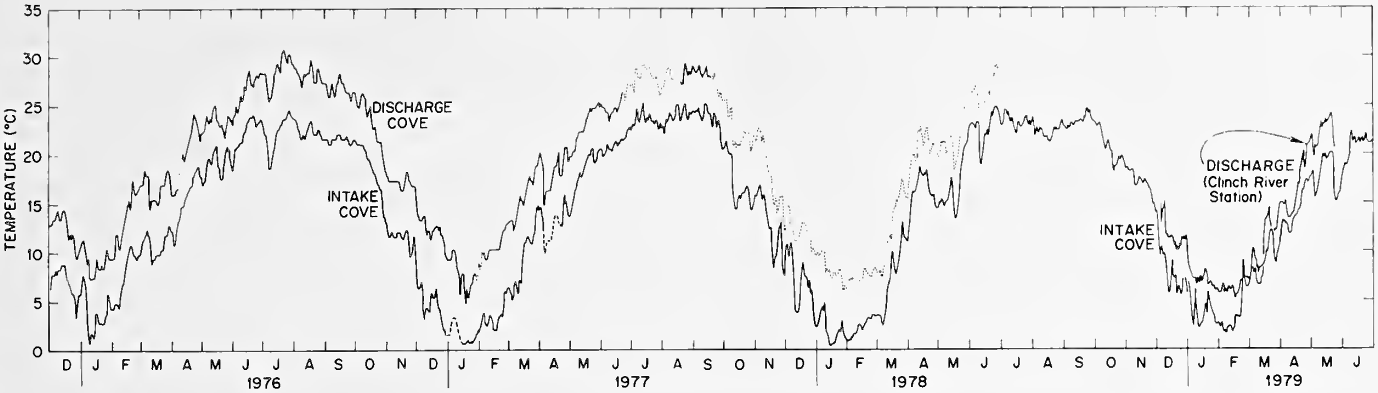

Fig. 2. Intake and discharge water temperatures (°C) during cage growth studies in 1976-1979. Dotted lines indicate periods when temperature in the discharge was estimated based on data from TVA's closest temperature probe with a correction factor applied.

filter ($\sim$0.45 μm equivalent pore size). Following drying for 12-24 h at 105°C the filter was reweighed using a balance accurate to 10^{-4}g to obtain seston concentration (mg/1).

Coincident with these field studies, a short-term laboratory study was conducted to examine growth of ten *Corbicula* at each of several temperatures in the laboratory. Clams were collected and acclimated as above to temperatures of 15, 20, 25, and 30°C and marked individually. The clams (four size groups) were taken placed on stainless steel screening in 195-1 flow-through aquaria. The influent water of each aquarium contained a mixture of ground and slurried flakefood and trout chow from a head tank. The slurry of food was added to the head tank twice per day and the flow from the head tank was controlled by a metering pump to produce a calculated maximum seston concentration of 6 mg/l (measured as above) in each aquarium. Between food additions to the head tank, the concentration available to the clams varied from 2-7 mg/l. Seston was kept in suspension in the head tank and aquaria by air bubblers. At weekly intervals, all clams were remeasured and growth estimated as the difference between final shell length (FSL) and initial shell length (ISL).

Several samples of clams in the 15 to 40 mm SL size range that had been fixed in 12% neutral formalin after collection for other purposes were examined for presence of incubating young. The adult clams were opened and the inner demibranch removed to a petri dish. The demibranch was teased apart with needles and examined at 30x using a dissecting microscope. Numbers of incubating young per clam were counted according to the following categories: 0, 1-19, 20-99 and >100.

Various factors were examined as determinants of growth. Effect of initial clam size on growth was determined by linear regression. Length data were not log transformed because variance did not appear related to size. In addition, growth rates for most intervals and years were fit better by the linear model than by an exponential model (see Mattice and Wright, 1985). Based on these results, growth rate comparisons between sites and between years were made by F-test comparisons of linear regressions of shell length increase on initial shell length (ISL). Examination of effect of temperature and seston on growth of clams in the field was based on comparison of growth by a standard-size clam during the various intervals between measurements. Before conducting these analyses we examined the growth rate data for serial correlation by regressing growth rate in each interval (except the first) on growth rate in the previous interval for the summer of 1977. Regressions for clams held in the discharge (r^2 = 0.078; p = 0.47) and intake r^2 = 0.073; p = 0.46) were not significant so we assumed that growth rate in each interval was independent of that in the other intervals. A 20 mm SL clam was chosen to be the "standard" clam, because growth at this size was relatively rapid and would thus easily demonstrate seasonal differences, and because use of this size did not involve extrapolation from measured size groups.

A typical life cycle was estimated by assuming that mean release of young occurred on April 21 and in late

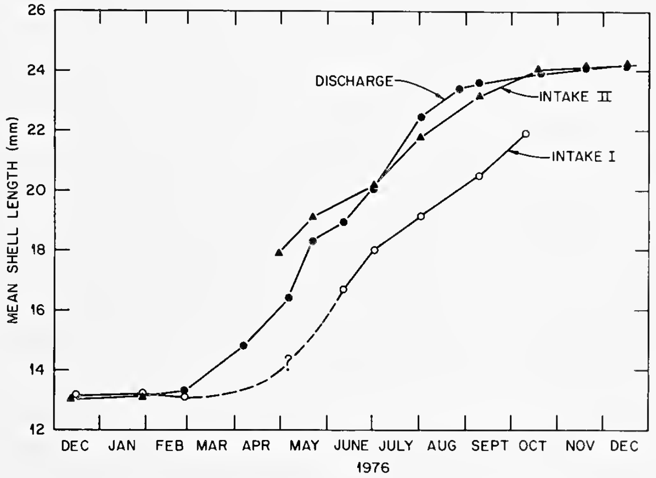

Fig. 3. Comparison of mean shell lengths of clams held in cages in the intake and discharage areas of the Kingston Steam Plant during 1976. Intake cage I was lost between March and June so a new cage (Intake II) was positioned in April. The dotted line is a hypothetical construction of clam growth in Intake I during the period between actual measurements.

August, that release size was 0.2 mm SL, and that growth to the mean maximum size found in the natural population in the discharge area would approximate that which occurred in 1977. The April 21 date was chosen based on reproductive data presented below, on the appearance of recruits in the cages, and on earlier reports (Heinsohn, 1958; Isom, 1971; Aldridge, 1976; Aldridge and McMahon, 1978) relating appearance of young to water temperature. The late August date was chosen by back-calculation from the size of recruits, which could not have been from the spring generation, in the field growth cages. For each subsequent interval the change in SL for the appropriate size of clam was calculated from the linear regression of increase in SL on initial shell length (ISL) for that interval. (Equations may be found in Mattice and Wright, 1985, Appendix D.) This increase in SL was then added to the initial SL to obtain the initial SL for the next interval. This procedure was continued until the growth curve became asymptotic and the time for this occurrence was then chosen to indicate the mean length of life. Determination of the asymptote is somewhat arbitrary, but comparison of the plot with a standard Walford (1946) plot helps provide support.

RESULTS AND DISCUSSION*

FIELD WATER TEMPERATURES

Water temperatures at the cage sites followed a typical yearly cycle (Fig. 2) for the period of all studies. Diurnal temperature variation was small (≤ 1°C) except during periods of rapid temperature change in spring and fall (≤ 2°C). The discharge temperature at the cage site averaged about 5°C higher than that in the intake, the difference tending to be largest at the winter and summer extremes.

FIELD STUDIES - SEASONAL PATTERN OF GROWTH

Growth (mean shell length increase) of *Corbicula fluminea* from December 1975 through December 1976 was distinctly seasonal (Fig. 3). The clams (ISL ranged from 10.7-16.4 mm) did not grow significantly in either the discharge or intake cages from December 5, 1975, through February 25, 1976. Water temperatures during this period did not exceed 16.0°C (m = 10.9°C) or 10.5°C (m = 7.5°C) in the discharge and intake, respectively. Discharge clams had grown significantly by the next time shell lengths were measured on April 6. Water temperatures during this period ranged from 16-18°C (m = 16.5°C). The first intake cage was lost between February 25 and June 11, but clams in the second cage did grow in the period from April 29 to May 21, suggesting that the hypothesized relation (Fig. 3) is not unreasonable. Growth of clams in the intake and discharge continued at a fairly rapid rate from April through September or October, then rapidly decreased. Significant shell length increases were not observed in November or December when temperatures averaged 14.8°C in the discharge and 8.9°C in the intake.

Table 1. Mean growth (mm) of clams[1] held in the intake and discharge areas of Kingston Steam Plant during winter and early spring, 1978-1979.

	INTAKE			DISCHARGE		
Date	Water Temp. (°C)	Number of Clams	Mean Growth[2] (mm)	Water Temp. (°C)	Number of Clams	Mean Growth[2] (mm)
11/21/78	16.5	18	—	—	—	—
12/1/78	—	—	—	18.9	30	—
1/11/79	2.4	18	0.12*	5.9	22	0.23
1/26/79	2.4	14	0.01	5.1	21	0.02*
2/16/79	1.0	14	0.00	4.6	16	0.00
3/9/79	8.4	14	0.01	6.8	9	0.07*
3/30/79	10.2	12	0.05*	14.6	5	0.26*
4/27/79	16.1	8	0.09	20.4	1	—

[1] Initial shell lengths ranged from 4.2 to 9.1 mm.
[2] Since previous measurement.
*Significantly different from zero (t test, p = 0.05).

Absence of winter growth also applied to clams in the 4 to 9 mm SL range (Table 1). Growth was essentially nil in the intake for the whole period from November 21 through April 27, 1979, and in the discharge for the period from January 11 through March 9, 1979 (Table 1). When growth did occur, in a statistical sense, discharge clams grew more than those in the intake. Biologically significant growth appears limited to a 7 to 9 month period in the Clinch River system.

Despite the appearance of the growth curves in Figure 3, growth, expressed as mean shell length (SL) increase per day, of *Corbicula* was not constant over the summer months (March through August 1976) in either the intake or discharge (Fig. 4). In both areas, growth increased

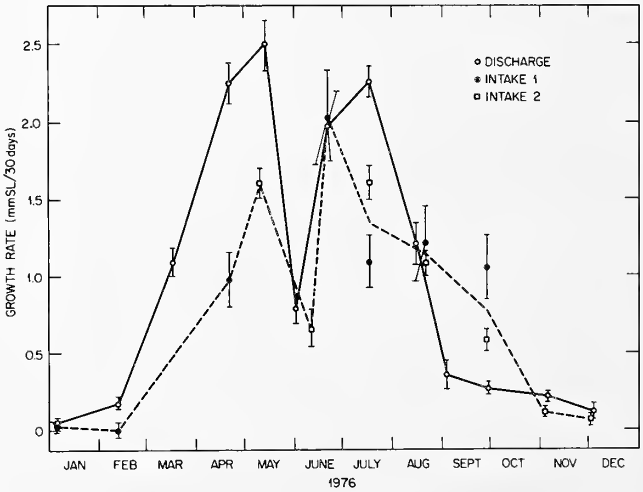

Fig. 4. Mean growth rates (and 95% confidence limits) of clams in the intake and discharge areas of Kingston Steam Plant during various periods of 1976. Growth rate for a period is plotted at the midpoint of that period.

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*Summary data are presented here; the complete data set is included in Mattice and Wright (1985).

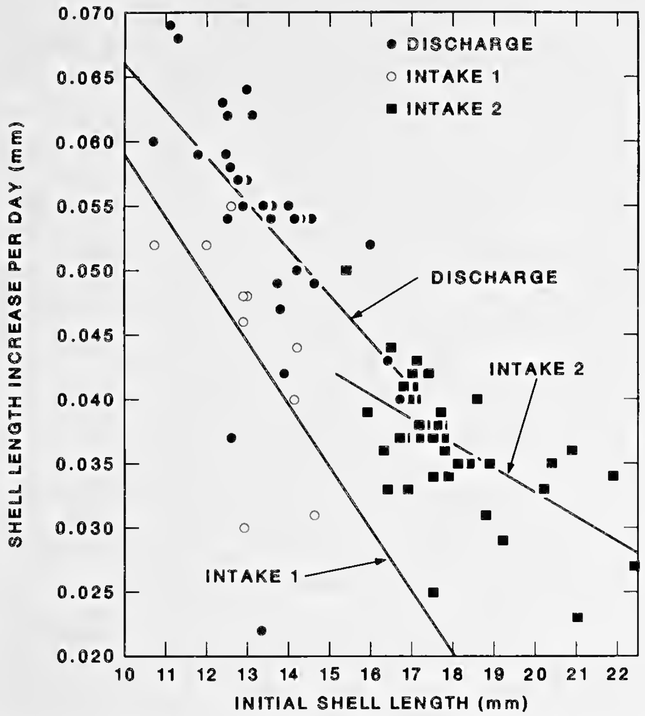

Fig. 5. Relation between shell length increase and initial shell length for clams held in the intake and discharge areas in 1976. The Intake I and Discharge results are for the period February 25 through October 18, while those for Intake II are for the period April 19 through November 19.

to a peak in May then dropped radically in early June before again increasing in late June. A second peak in growth in late June or July was again followed by a decline. Growth rates in the discharge generally exceeded those in the intake except during June and late August through September. Because of the relationship between ISL and growth (see below), caution must be used in comparing the above rates between intervals, as they ignore the fact that the clams grew progressively larger over the period of measurement.

FIELD STUDIES - RELATIONSHIP BETWEEN GROWTH AND INITIAL CLAM SIZE

Growth of *Corbicula* in 1976 was negatively correlated with ISL (Fig. 5). The correlation coefficents (r^2) for each group were 0.29, 0.41, and 0.37 for clams in cages Discharge, Intake I, and Intake II, respectively. Each of the r^2 values was significantly different from zero (F test, $p < 0.05$) despite the relatively small range of initial shell lengths for each group. Direct comparison of growth in all three groups was obviated by the unequal periods of measurements, however, Intake I and Discharge data were collected over the same period (February 25 to October 18, 1976). Growth in the discharge area generally exceeded that in the intake area in 1976 (F test; $p < 0.05$). The relationship between growth and ISL indicates that valid comparisons of growth between areas or over time must be carried out for clams of similar size.

Clam growth in 1977 was also inversely related to ISL (Fig. 6). Both linear and exponential models were examined for fit to the relationship between SL and ISL. Based on comparison or r^2 and p values and residual sums of squares, the linear model provided a better fit both for the whole period the clams were in the field and for a great majority of the indivdual observation periods (Mattice and Wright, 1985). For reasons sited in Mattice and Wright (1985), data for clams in the 5 mm ISL size class were not included in the analysis. This did not affect the choice of the linear model.Coefficients of correlation for clams 10 mm SL and larger were 0.96 and 0.83 for intake and discharge clams, respectively. Britton et al. (1979) reported that an exponential model provided a better fit to their data, but this conclusion was probably influenced by inclusion of data for unequal time intervals and different initiation dates in the analysis. McMahon (this volume), on the other hand, found that a linear model provided the best fit for growth of the clams that he studied and data reported by Dreier and Tranquilli (1981) also appear to support choice of a linear model.

FIELD STUDIES - GROWTH COMPARISONS BETWEEN SITES AND YEARS

In 1977, clams in the intake grew more rapidly than clams in the discharge, except for the largest clams (Fig. 6). The intercepts and slopes are significantly different ($p < 0.001$); F test). The relationship between growth rate in mm SL/day (G) and initial shell length in mm (ISL) was $G = -0.0013\ ISL + 0.064$ for the intake clams and $G = -0.0011$

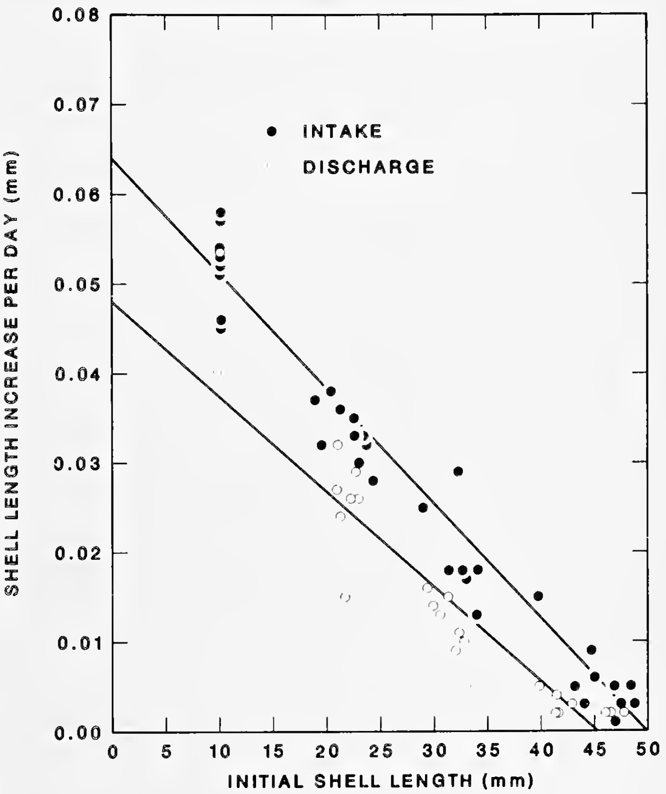

Fig. 6. Growth rates of clams held in the intake (●) and discharge (O) areas of the Kingston Steam Plant in 1977 as a function of initial size. Clams were held from April 21 to November 23, 1977. Solid lines are least squares fits to data for all clams excluding the 5 mm SL size group. Dashed lines are least squares fit to data for all clams.

ISL + 0.049 for the discharge clams. The relationship between growth in the intake and discharge (intake $<$ discharge) is the opposite of that found in 1976. This will be discussed later, but it is clear that clam growth can differ between sites.

Rate of SL increase per day also can differ between years at the same site (Fig. 7). The total interval over which growth was compared, differed somewhat between 1977 (April 21-October 4 or 166 days) and 1978 (April 4-September 27 or 175 days), but the longer time in 1978, all within the growth period for the clams, would tend to increase the 1978 growth rate in comparison to that for 1977. Nevertheless, growth in the intake in 1977 exceeded that in 1978 (F test; $p < 0.05$). The relationship between growth rate (G) and initial shell length (ISL) for 1977 was $G = -0.0016 \text{ ISL} + 0.079$ ($r^2 = 0.96$) and for 1978 was $G = 0.0016 \text{ ISL} + 0.070$ ($r^2 = 0.93$). The slopes did not differ significantly (F test; $p = 0.50$), but the intercepts were significantly different ($p < 0.05$).

The growth rates determined in our studies are well within the range of those reported by other investigators. *Corbicula* near the Kingston Steam Plant grow significantly faster than two populations in Hong Kong (Morton, 1977), at about the same rate as those in Lake Benbrook, Texas (O'Kane, 1976; Britton et al., 1979), and substantially slower than those in Lake Arlington, Texas (Aldridge, 1976; Aldridge and McMahon, 1978). The reasons for these differences are unknown.

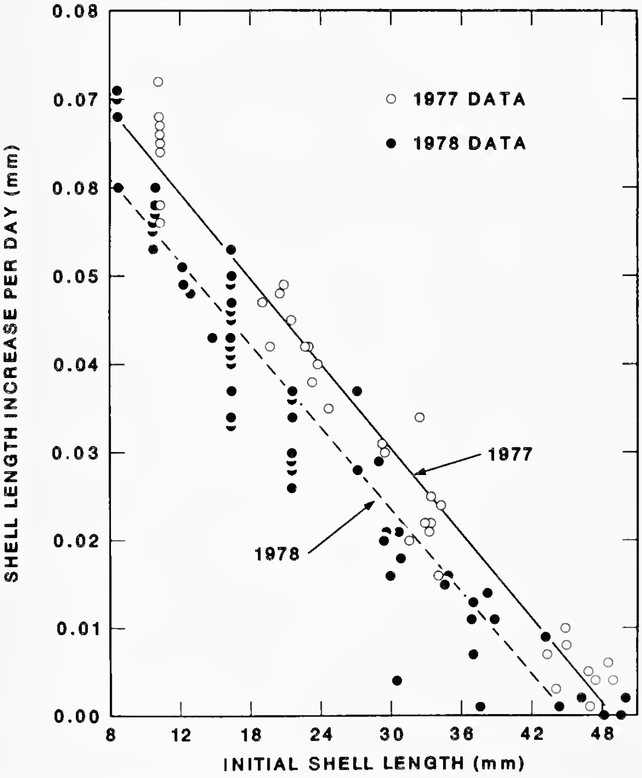

Fig. 7. Growth rates as a function of initial shell lengths of clams held in the intake of the Kingston Steam Plant in 1977 (O) and 1978 (●). The smaller groups of clams were not individually marked, and thus were assigned the mean initial shell length for the groups.

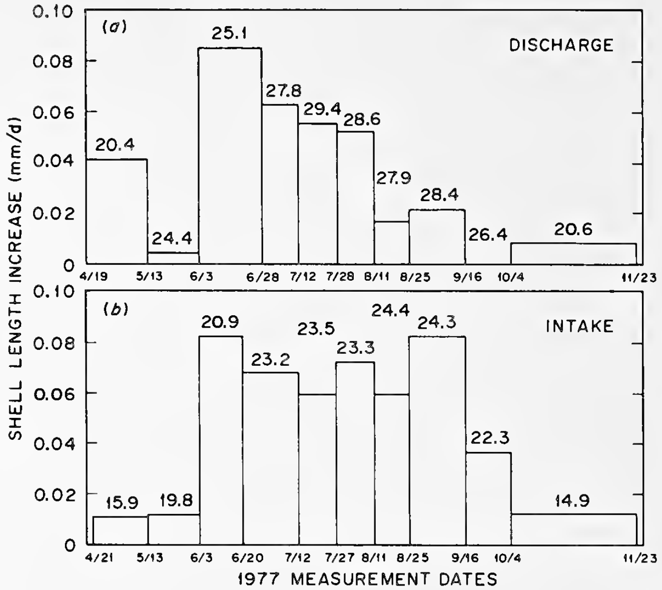

Fig. 8. Growth rates for a "standard" 20 mm SL during various intervals from April through November 1977, in the intake (a) and discharge (b) of the Kingston Steam Plant. Mean temperature ($^{\circ}C$) for each interval is shown above the growth rate for that interval.

FIELD STUDIES - GROWTH DURING SUCCESSIVE INTERVALS

Growth of clams in 1977, normalized for initial size, was not constant during the yearly growth period (Figures 8a and 8b). Normalization was achieved by calculating growth of a 20 mm SL clam for each period from a regression of growth for the period on size at the beginning of the period (for equations see Mattice and Wright, 1985). In the discharge, growth in the first period was at about the median rate for all periods. This was followed by a distinct decrease for the May 13 and June 3 period. Growth in the discharge then rose to its maximum which included most of the month of June. Mean temperature during this period was $25.1^{\circ}C$. Growth from July through November declined roughly linearly through a period of increasing then decreasing temperature. In the intake, growth from April to June was low, followed immediately by growth at the maximal rate observed for the year. Growth was then relatively constant through late August. Temperatures also were relatively constant during this period. A second period of maximal growth occurred during the August 25 to September 16 period, after which growth declined rapidly as the temperature also declined. Growth in the discharge was higher than in the intake from mid-April through late June, but this relationship was reversed for the rest of the growth period. The higher growth in the intake during this latter (and longer) period accounted for the higher overall growth of intake clams over the whole time the clams were in the field.

RELATIONSHIP BETWEEN FOOD AVAILABILITY AND GROWTH

We examined both algal type and seston concentration as potential causes of some of the differences that we observed in growth rates. Davis and Guillard (1958) found that growth of larvae of the oyster, *Crassostrea virginica* declined when they were fed high concentrations of the algae, *Monochrysus*, but the relationship of seston concentration or algal type and growth of clams has not been examined. However, a number of investigators have demonstrated effects of algal concentration or types on filtration, the primary food gathering mechanism of most bivalves.

Diatoms were the dominant phytoplankton in samples collected in the intake and discharge areas of Kingston Steam Plant between October 7, 1975, and November 9, 1976. A total of 48 genera were identified (Mattice and Wright, 1985), but diatoms always constituted 95% or more of the phytoplankton in terms of both cell number and cell volume. The change in mesh size of nets used before and after the June sampling period did not affect conclusions with regard to dominant classes or genera (Mattice and Wright, 1985). Percent distribution of the genera of Bacillariophyceae and Chrysophyceae was quite uniform throughout the year. *Melosira* was the most prominent genus, making up greater than 90% of total cell number except in May, when *Asterionella* and *Fragilaria* each accounted for 5 to 10% of total cell number, and on June 24, when *Melosira* accounted for about 50% of the total number and *Asterionella, Fragilaria, Stephanodiscus,* and *Synedra* made up about 45% of total number.

The other phytoplankton taxa were represented by more species in summer than winter, but were never dominant. Chlorophycean diversity was high especially in summer, but at no time did the total come to more than about 3% of the total of all phytoplankton, Cyanophyceae, Dinophyceae, and Euglenophyceae combined never accounted for as much as 2% of total numbers, and generally were found sparingly. Phytoplankton were present sparsely in January, February, and March, but had increased greatly by May in both intake and discharge samples. Intake and discharge samples were generally similar except on February 10 and March 16. On the former date, only empty frustules of *Melosira* and *Fragilaria* were found in the discharge although cells in the intake samples appeared viable. On March 16, numbers of both genera and cells of phytoplankton in the discharge were substantially lower than in the intake.

Although the phytoplankton populations in the study area were diverse, it is unlikely that changes in the algal complement could account for any differences observed in growth of *Corbicula*. Diatoms were dominant throughout the year. All the dominant genera are large, which may have affected the maximum filtration rate of the clams (Morton, 1971), but it seems doubtful that the variation in size that does occur would be responsible for seasonal effects. Furthermore, concentrations of potentially toxic phytoplankton such as *Gymnodinium veneficum* (Ballatine and Morton, 1956), *Chlorella* (Davids, 1964), and *Ceratium hirundinella* (Stanczykowska et *al.*, 1976), which have been shown to inhibit bivalve filtration, either were not present or were rare. Thus, it seems unlikely that the type of algae in the seston had any effect on *Corbicula* growth.

Seston concentration did vary significantly during the year, ranging from about 7 to 23 mg/l from March to October in 1977 and 1978 (Figure 9). Seston levels in the intake and discharge frequently were not measured on the same date. On dates where comparable data were taken, seston levels in the discharge were slightly lower, but we assumed that this difference was too small to be significant. We therefore combined the data from the two areas for seasonal comparisons. In 1977, concentration rose from early March to a peak in mid-April, then declined through about mid-May before rising to the seasonal maximum in early June. Seston dropped to the lowest seasonal concentration in early July, then, except for one low value in late August, remained between 15 and 20 mg/1 through mid-October. For most of 1978, seston concentrations were lower than in 1977 (Figure 9). The major differences were the lack of a May-June peak in seston concentration in 1978 and the sustained low concentrations in August and early September. By late September concentrations rose rapidly to reach 1977 levels in mid-October.

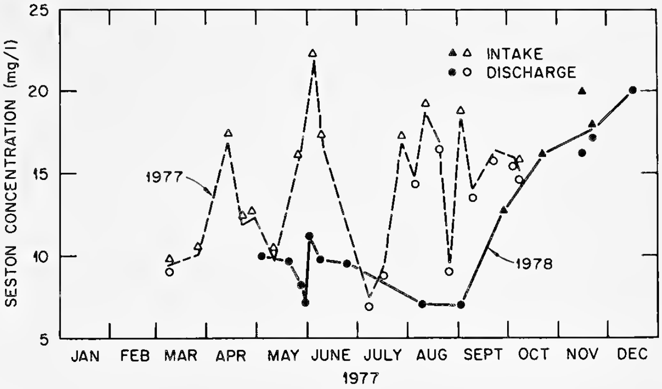

Fig. 9. Seston concentrations measured in the intake and discharge of the Kingston Steam Plant from March through October 1977 and May through November in 1978. Line connects values for consecutive dates in each year regardless of site.

Growth differences at the intake and discharge sites (1 each) for periods within 1977 (Figure 8) did not correlate with seston concentration. This type of analysis is permitted, because growth in successive intervals was not correlated (see Materials and Methods). Correlation coefficients (r^2) for the relationship between mean seston concentration and growth rate for each interval were 0.041 ($N = 9$; $p = 0.61$) and 0.001 ($N = 9$; $p = 0.98$) for intake and discharge areas, respectively. In addition, correlation coefficients were not significantly increased by assuming that growth in an interval was related to food availability in the prior interval ($r^2 =$ 0.04 and 0.02 for intake and discharge areas, respectively). Unless seston concentration was completely independent of the amount of usable food available to *Corbicula*, food supply did not appear to be related to growth for this year. Thus, we conclude that changes in seston concentration were not responsible for the differences in growth that we observed.

This conclusion seems counterintuitive. Mattice (1979) has shown that filtration rate (volume of water pumped/time) of *Corbicula* is not related to seston concentration over the range from 7 to 24 mg/l. This would suggest that the higher the seston concentration the more food that *Corbicula* could remove from the water to support growth. There are obvious limits to this expectation as indicated by results of earlier workers (Loosanoff and Engle, 1947; Morton, 1971; Thompson and Bayne, 1974), who found that much higher concentrations of inert particles or monoalgal cultures caused decreases in filtration rate of mussels, oysters, and the zebra clam, *Dreissena polymorpha*. However, filtration is only the first step in the feeding process, sorting and ciliamediated transport to the mouth also being necessary for ingestion. During normal feeding large particles are rejected prior to reaching the mouth and ejected from the mantle cavity as pseudofeces. At high concentrations of seston, ingestion declines and may actually cease even though filtration continues. We have no hard data to indicate whether this might cause the lack of correlation between seston concentration and growth, but substantial amount of pseudofeces were produced by *Corbicula* during field studies of filtration (Mattice, 1979; Mattice and Wright, unpublished data). Further possibilities are that growth of *Corbicula* in the Clinch River system is dependent on the presence of the smaller algal species or that a factor other than food, e.g., calcium, is the limiting factor in growth. Clearly, further studies of relationships between nutrition and growth are needed.

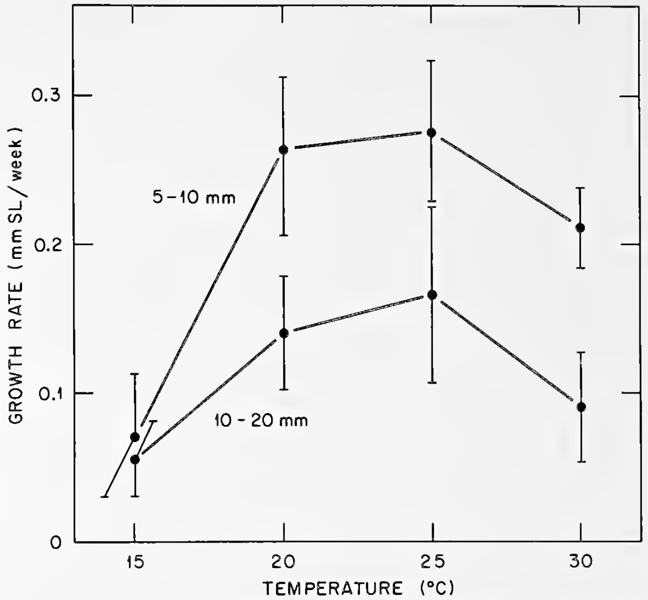

Fig. 10. Growth rates and 95% confidence intervals for clams with initial shell lengths of 5-10 mm and 10-20 mm at 15, 20, 25, and 30°C. Optimum growth temperature appears to be about 25°C.

EFFECTS OF TEMPERATURE ON GROWTH

We examined the relationship between temperature and *Corbicula* growth in the laboratory. As in the field studies, growth rates of clams in the laboratory varied with initial size of the clams. All but 4 of the 130 clams examined grew over the four week period but growth of clams >20 mm ISL appeared to be limited by total nutritional intake and these data

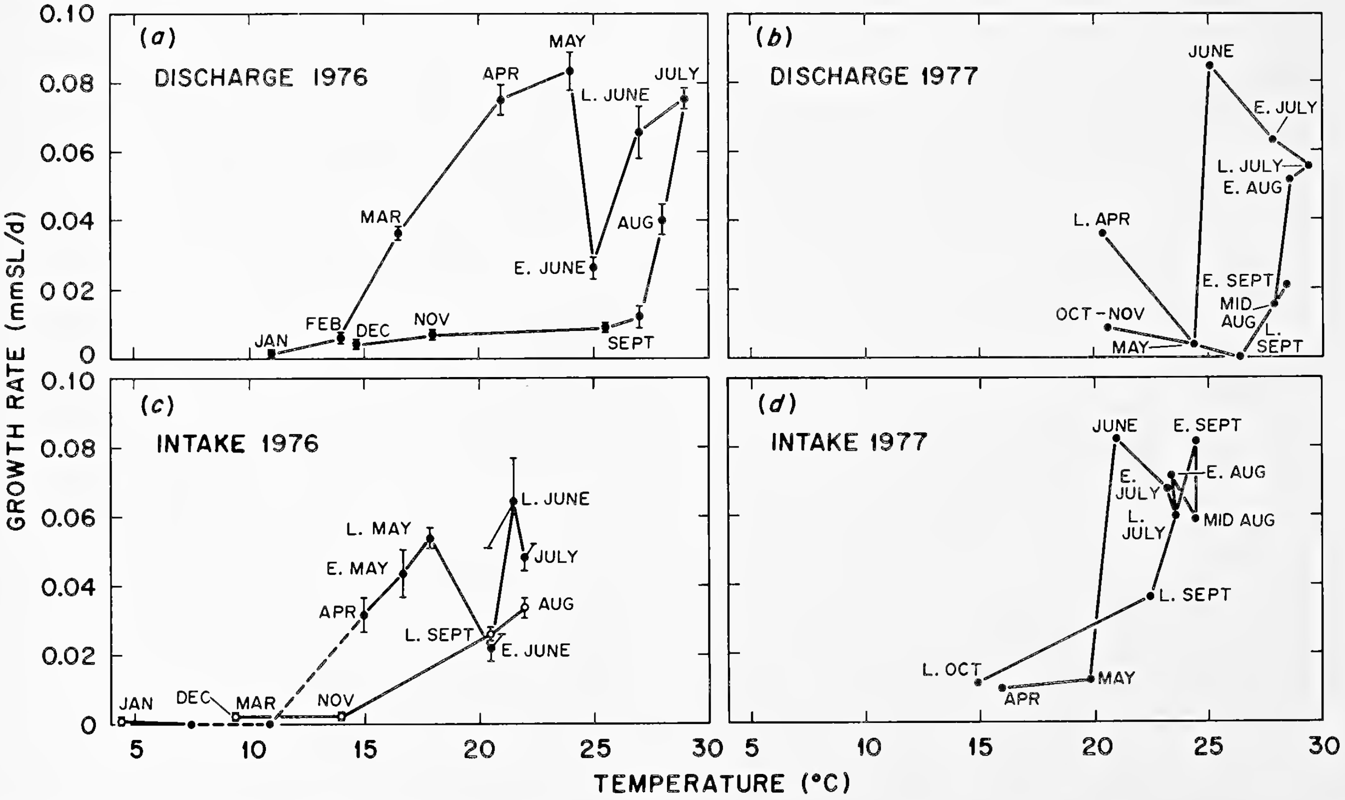

Fig. 11. Growth rates of clams during each interval in 1976 and 1977 in the discharge (a) and intake (b) areas plotted against the mean temperature of the interval.

are not presented here (see Mattice and Wright, 1985). Growth rates of clams in the two smaller size groups followed the usual relationship found between physiological rates and temperature (Fig. 10). Growth rates of clams was low at 15°C. Growth rates increased with temperature through about 25°C, then decreased at 30°C. Optimum growth temperature appears to be about 25°C, although rates at 20°C and 30°C were not significantly lower. Extrapolation from these data to lower temperatures suggested 11 to 12°C as a lower threshold for growth, which is within the range (8 to 16°C) found during our various field studies.

We also considered the relationship between temperature and growth rate using field data collected in 1976 and 1977 (Fig. 11a-d). The validity of this type of evaluation is based on the lack of correlation between growth rates of clams during consecutive sampling periods. Our logic is somewhat circular, but it appears that the relationship between growth rate and temperature in the field is similar in form to that found in the laboratory (growth rate is highest at water temperatures about 25°C) except during May and early June and during the late summer-autumn period after occurrence of the highest water temperatures in both the intake and discharge areas. A similar relationship was found when data from Aldridge (1976) were plotted in this way suggesting that these periods are important for understanding the seasonal shifts in growth of *Corbicula*. The mid-20°C optimum for growth, which is supported by both laboratory and field data on growth, may reflect optima for filter feeding (Mattice, 1979) and/or oxygen consumption (McMahon and Aldridge, 1976).

CLAM REPRODUCTION

Growth rates appear to decline during the period of incubation. The small percentage of adults incubating young and the predominance of tanned shells of the young on May 26, 1977, followed by the total absence of young in the adults collected June 1 suggest the end of a spring incubation period (Table 2). A similar situation (declining occurrence of incubating young) is also indicated for the period from September 27 through November 21 even though samples were taken in two areas and on two different years. Although further work is required for confirmation, these data suggest a bimodal reproductive period with peaks in release of young occurring before late May and sometime between early June and late September (probably closer to the latter) such as has been found for *Corbicula* populations in some other areas (Heinsohn, 1958; Coldiron, 1975; Aldridge and McMahon, 1978). Growth rates of clams during both 1977 and 1978 appear to decline at about the same time as the spring peak of larval release, but the coincidence of the late summer growth decline and peak of larval release is not clear. Decline at the time of incubation is not unexpected because the gills become distended as the larval clams grow and water flow is likely inhibited.

Table 2. Occurrence of young *Corbicula* in the incubatory gills of adults.

			Percent of Clams Containing Indicated Number of Larvae in Single Gill			
Date[a]	Area[b]	Number of Clams	< 100	20-99	1-19	0
5/26/77	D	18	—	6	22[c]	72
6/1/77	D	25	—	—	—	100
9/27/77	D	15	33[d]	7[c]	13[c]	47
10/11/77	I	5	40[c]	—	—	60
10/19/77	I	5	20[c]	—	—	80
10/19/77	D	14	—	—	—	100
10/20/78	I	11	—	—	9[c]	91
11/21/78	I	12	—	—	—	100

[a] In day order, regardless of year collected.
[b] D = discharge area; I = intake area.
[c] Shells of most young tanned (= older stages).
[d] Shells of most young clear (= younger stages).

LONGEVITY AND MAXIMUM SIZE

Corbicula in the Clinch River system appear to have life spans that can approach six or more years, but almost certainly exceed four years (Figure 12). The smoothed curves obscure seasonal shifts in growth (Figure 8), but are convenient. The equation used to estimate growth over each 12 month period was FSL = 13.86 + 0.71ISL, where FSL = final shell length and ISL = initial shell length, both in millimeters. This relationship was derived from measured growth of clams ranging from 4.8 to 48.4 mm SL that were observed in the intake in 1977 between April 21 and November 23. This interval encompasses the total growth period in the intake cove. Equations derived for shorter intervals (Mattice and Wright, 1985) were used to estimate growth during the first growing season for both spring and fall generations. Year to year shifts are not considered since only data from one year were used

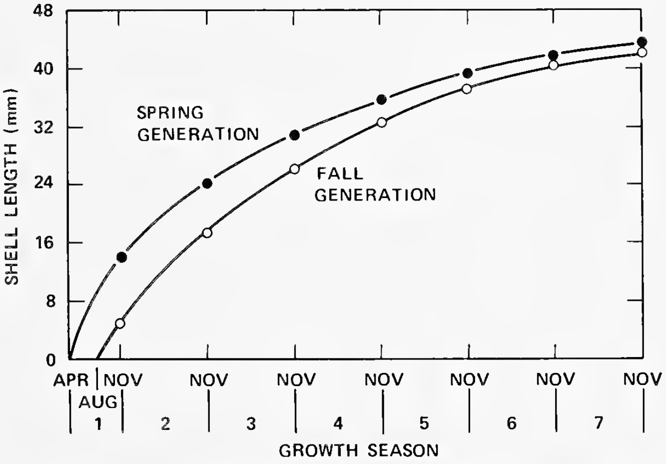

Fig. 12. Hypothetical mean growth over time of *Corbicula* from release (~0.2 mm) through death. The growth curve is based on data collected in the intake of the Kingston Steam Plant in 1977 and assumes April 21 and late August release dates. Growth season refers to growth within a 12 month period except for the first growth season. Not shown are the cessations of growth during each winter period.

to generate the curve. Regardless, it seems unlikely that the conclusions would be invalidated.

Life spans reported for populations of *Corbicula* have ranged from 14-17 months (Aldridge and McMahon, 1978) to 5-7 years (Sinclair and Isom, 1963). Britton *et al.* (1979) presented arguments regarding interpretation of length-frequency distributions and concluded that the typical life cycle of *Corbicula fluminea* was three or fewer years. They attributed the longer estimates to the failure of earlier investigators to recognize that young clams were released during two rather distinct periods each year. Their argument is compelling, but the same criticism does not apply to our results or to those of Dreier and Tranquilli (1981), both of which support life cycle estimates of four or more years. Cage studies (Dreier and Tranquilli, 1981; this study) are subject to the criticism of confinement or cage effect, but Britton *et al.* (1979) showed that such criticism was largely unwarranted even for their cages which had smaller and fewer openings and thus would have inhibited water flow substantially more than in our study and that of Dreier and Tranquilli (1981). Further substantiation for our longer (≥4 years) estimate of longevity is evidenced by the fact that only one of the ten clams of ≥40 mm SL in our cages died during the period from April 21, 1977, to September 27, 1978. Even if we assume the minimum times to reach the 40 mm size class from Aldridge and McMahon (1978) or Britton *et al.* (1979), our conclusions regarding longevity based on the subsequent 1.4 years survivorship would differ from theirs. We agree that the three- or fewer-year life cycle estimate is reasonable for the populations they studied, but not for those in Illinois (Dreier and Tranquilli, 1981), Tennessee, and perhaps California (Eng, 1979). It appears that there is no typical *C. fluminea* life cycle, though reasons for this are yet obscure.

Plasticity also appears to characterize maximum adult size of different populations. The von Bertalanffy (1938) growth model appears to provide a good fit to data on *Corbicula* populations (Morton, 1973 and 1977; Alimov, 1974). This is true for our growth data as well (displayed as a Walford plot in Figure 13) and provides an estimate of maximum theoretical shell length of 47.6 mm. As stated by Britton and Morton (1979), however, maximum theoretical length appears to vary from population to population, a conclusion that is supported by observed maximal lengths ranging from 25 mm (Lauritsen, 1982) to the 75-mm behemoth that Billy Isom (Tennessee Valley Authority, Muscle Shoals, Ala.) displayed at this Symposium. Analysis using a Walford (1946) plot may prove to be of limited use even within a single population because in the early 1970s it was not unusual to find clams in the 50- to 60-mm size range (maximum size ~65 mm) in the discharge area near the site of our cage studies (Mattice and Wright, unpublished observations). Perhaps these larger clams are characteristic of an earlier stage of population development, because clams >50-mm SL have become rare in our collections. Again, however, the variability of response of *Corbicula* in different environments is obvious, a characteristic that would appear to allow the clam to exploit a broad range of environments and spread as rapidly as it has through the United States.

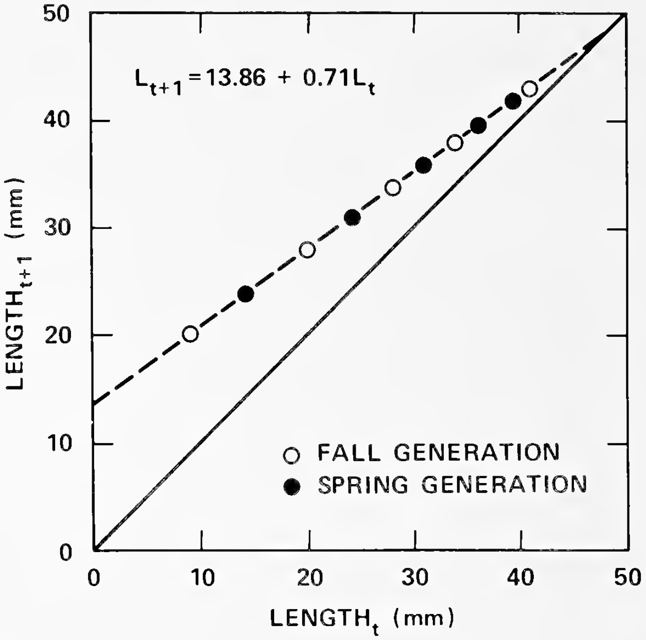

Fig. 13. A Walford plot for *Corbicula fluminea* based on data presented in Figure 12. Shell length on April 21 for one year (L_{t+1}) was plotted as a function of shell length on the same date as a year before (L_t). Initial size for young at the time of release was assumed to be 0.2 mm. The maximum theoretical length was calculated as 47.6 mm SL.

This plasticity does not augur well for development of standardized schedules of *Corbicula* control at industrial facilities. Most fouling occurs after the clams, which have entered the plant as larvae or young, grow to fouling size. In Tennessee, control would appear to be effectively applied once per year because clams would not be likely to grow to fouling size in the interim. However, at least in some areas of Texas fouling could be a problem unless control strategies are applied twice per year. Further investigation of the intrinsic and extrinsic factors that control clam growth will be required to determine control startegies at specific industrial sites.

SUMMARY

Growth in shell length (SL) of *Corbicula fluminea* varies during periods within a year and between years and is related to both intrinsic and extrinsic factors. During the periods of the year when ambient water temperature is low, clams do not grow. The threshold for growth seems to be about 11-12°C; the range of estimates from the different studies suggest that some other environmental factor such as food supply may play modifying role. As temperatures begin to rise in spring, growth begins and for most periods is linearly related to clam size: smaller clams grow faster than larger clams. Growth rate appears to increase as temperature increases until May or early June when there is a rapid decline in growth, apparently related to the peak period of incubation of the Spring generation of young clams. This decline seems likely to be related to both shifts in energy use and inhibition of water flow for feeding by the young clams in the inner, incubatory, half of the gill. Growth rate then increases again, the level of growth attained being consistent with a hyperbolic relation between growth and temperature, with a temperature about 25ºC being the optimal growth temperature. Food (measured as seston concentration) does not appear to be related to growth, but it is doubtful that this conclusion is generally applicable to all environments where *Corbicula* is found. Growth from mid to late June through mid-August or early September appears to follow temperature, again suggesting a 25ºC optimal growth temperature. However, growth rate in the subsequent period, which also includes the second yearly peak of incubation and release of young, is substantially less than would be expected based on temperature. Growth continues at a low rate through October or November, depending on temperature, then essentially ceases for the winter period (temperatures less than 11 or 12ºC). Growth rate also varies from year to year at the same site, but the reason is less clear.

The life span of *Corbicula* in the Clinch River system is more than four years and could be as long as 6 + years. Differences between observations of life span and maximum size of *Corbicula* in populations as widely dispersed as Hong Kong, Tennessee, Texas and Illinois suggest that *Corbicula* has a plastic rather than a predetermined physiology, which allows populations to efficiently exploit a wide range of environmental conditions. This plasticity is undoubtedly responsible for the rapid and unprecedented spread of *Corbicula* in the United States and its success in infesting industrial facilities of all kinds.

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CORBICULA IN PUBLIC RECREATION WATERS OF TEXAS: HABITAT SPECTRUM AND CLAM-HUMAN INTERACTIONS

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ABSTRACT

Examination of water bodies associated with Texas State Parks and other selected recreational areas revealed presence of *Corbicula* in 41 of 92 surveyed sites. Absence of *Corbicula* is related to presence of salt or brackish waters, extreme winter temperatures, periodic water shortages in small streams and lakes, and undefined ecological of historical factors which have delayed invasion into certain waters. Prime microhabitats for *Corbicula* in Texas include sandy-bottomed streams in eastern Texas, loose-gravel-bottomed pools in the Texas Hill Country, and moderate-energy reservoir lake shores. Construction of recreational facilities may either enhance or reduce the local habitat for *Corbicula*. No harmful effects of *Corbicula* upon park facilities were discovered.

The Asiatic clam, *Corbicula fluminea* (Müller, 1774), has spread over most of the United States (McMahon, 1982) following its initial introduction into the northwestern United States in the early twentieth century (Burch, 1944; Counts, 1981). The first Texas populations were discovered near El Paso in 1964 (Metcalf, 1966), followed by reports from the lower Rio Grande by 1969 (Murray, 1971). East Texa populations probably invaded from Louisiana (Britton, 1982; McMahon, 1982). By the late 1970's *Corbicula* had been found in most of Texas except the Brazos River (Britton and Murphy, 1977). Fontanier (1982) later documented the appearance and spread of *Corbicula* in the Brazos River. The most up-to-date distribution map for *Corbicula* in Texas can be found in Britton (1982).

Two phenotypes of *Corbicula* have been found in Texas waters: the white morph and the purple morph. Proper taxonomic treatment of these two forms is unclear at this time. Fontanier (1982) found both forms at the same locality, but these forms do not appear to be inter-breeding as revealed by allozyme studies (Hillis and Patton, 1982). Previous studies have revealed color variation in *Corbicula* due to genetic, ontogenetic and environmental factors (Sinclair and Isom, 1963). In this report, Asiatic clam populations in Texas would be referred to by generic name only. All *Corbicula* observed in this study are referable to the white morph.

Corbicula has been the focus of many studies due to its economic importance when it blocks condensors of electrical generating plants (Mattice, 1979). Other economic effects of *Corbicula* have been discussed (Sinclair and Isom, 1963). *Corbicula* is also significant as a food item for fish (Minckley *et al.*, 1970), utilization as a clarifying agent in sewage treatment ponds (Dinges, 1976; Haines, 1979) and as a bio-assay organism in pollution studies (Clark *et al.*, 1979). *Corbicula* has been implicated in the decline of native freshwater mussels (Gardner *et al.*, 1976) especially in heavily managed waterways (Kraemer, 1979).

Apparently, no discussion of the relationship between *Corbicula* and outdoor human recreational facilities has appeared in the vast literature on *Corbicula* (see Mattice *et al.*, 1979). The outdoor recreation industry has grown steadily in the past few decades, coincidentally or not, during the same time period as the expansion of *Corbicula*. The purpose of this study was to investigate the occurrence of *Corbicula* in public recreational waters of Texas in order to determine human impact upon this clam and any effects of the clams upon humans. Concurrently, optimum microhabitats for *Corbicula* in Texas could be characterized.

METHODS AND MATERIALS

For this survey, various bodies of water were sampled from June 1978 to March 1983. Most sites were sampled more than once. Particular effort was made to visit localities during low flow and low lake level periods. Bottom sampling was accomplished manually as well as utilizing an 8mm mesh net and an Ekman dredge (utilized from bridges, piers and boats). Water line accumulations and flood debris piles were

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examined if no living *Corbicula* were found in initial surveys. If shells were located in these latter sites, sampling for live clams was continued. Peripheral localities were sampled upstream and downstream or on adjacent lake shores as appropriate.

Texas State Parks with water bodies were visited for sampling. Several other public recreational areas were investigated and those which produced significant data concerning *Corbicula* are discussed below. Particular attention was given to areas with direct clam-human interaction. Notes on microhabitat of viable populations of *Corbicula* were recorded. Operational personnel of Texas Parks and Wildlife Department were questioned regarding the impact of *Corbicula* upon park operations. References to mud, sand, gravel, etc. refer to standard geological size classifications.

RESULTS

STATE PARK SYSTEM SURVEY

The Texas State Park system presently consists of 116 units which are located from the Pineywoods Region of east Texas westward to the Chihuahuan Desert of El Paso and from the High Plains and canyons of the Panhandle southward to the subtropical alluvial plain of the Rio Grande delta region. Elevational limits range from sea level along the Gulf of Mexico to a maximum of 2180 m in Franklin Mountains State Park. Area of park units varies from 6638 hectares for Palo Duro Canyon State Park in the Panhandle to .0024 hectares for Action State Park.

A total of 92 units were judged to have surface water present (2 parks were counted twice because of separate water systems of different classifications). Notes on microhabitats containing *Corbicula* were taken in order to characterize the preferred habitat in Texas. Presence/absence of *Corbicula* was related to type of freshwater habitat, east Texas vs. west Texas, status of park (open vs. closed to public) and type of park facilities.

Initially, the 94 park units with surface water were subdivided as to occurrence of fresh, brackish and salt water (Table 1). *Corbicula* was absent from all brackish and saltwater bodies and those freshwater bodies occurring in parks which also have saltwater. The freshwater systems in these coastal parks are generally small ponds which periodically dessicate and have very limited inflow streams, if any, which provide additional colonization routes. Of those parks with only freshwater present, exactly 50 percent contained populations of *Corbicula*.

Table 1. Relative occurrence of *Corbicula* in state park units of Texas subdivided as to class of water present. Probability value is measure of odds of obtaining observed distribution by chance.

	Corbicula		
Water Class	Present	Absent	Total
Freshwater only	41	41	82
Fresh and saltwater	0	4	4
Brackish water only	0	6	6
Saltwater only	0	2	2
Total	41	53	94

$x^2(3) = 10.64$; $p = .014$

Table 2. Relative occurrence of *Corbicula* in state park units of Texas subdivided as to type of freshwater present.

	Corbicula		
Water Class	Present	Absent	Total
Isolated	0	5	5
Enclosed lake	3	12	15
Reservoir	17	10	27
Stream	21	18	39
Total	41	45	86

$x^2(3) = 12.286$; $p = .006$.

The 86 parks with freshwater (including 4 also with saltwater) were characterized as follows: 1) isolated water system within a park, 2) small lake enclosed by the park, 3) park on reservoir, and 4) units with a stream along the edge or through the park (Table 2). *Corbicula* was found to be absent from parks with isolated water systems (ponds likely to dessicate) and rare in parks with enclosed lakes (which typically are fed by intermittent or small spring-fed streams). *Corbicula* was found most often in reservoirs and streams which have abundant colonization opportunities.

In order to determine geographical variations in *Corbicula* occurrence, these same 86 parks were divided into those in the eastern and western halves of Texas (Table 3). The eastern parks receive more precipitation and are almost all on the Coastal Plain. Western parks include a few coastal

Table 3. Relative occurrence of *Corbicula* in state park units of Texas with freshwater subdivided into eastern and western Texas.

	Corbicula		
Location	Present	Absent	Total
Eastern	26	23	49
Western	15	22	37
Total	41	45	86

$x^2(1) = 1.325$; $p = .25$

Table 4. Relative occurrence of *Corbicula* in state park units of Texas with freshwater subdivided into open and closed parks.

	Corbicula		
Park	Present	Absent	Total
Open	30	36	66
Closed	11	9	20
Total	41	45	86

$x^2(1) = 0.56$; $p = .454$

plain sites, but most units are in piedmont, hilly, upland plains and mountainous areas. The eastern half of Texas exhibits a greater dependability of water flow due to greater annual average precipitation and more even distribution throughout the year. No significant difference existed in percentage presence of *Corbicula* between eastern and western parks.

Further analyses of *Corbicula* distribution patterns were made to determine the correlation, if any, of public utilization of water bodies and presence of *Corbicula* (Table 4). The 86 park units were first divided into sites open to the public and those still closed pending planning and development procedures. *Corbicula* was just as likely to be present in closed parks as open parks.

The 66 open parks were characterized as to presence of fishing as a recreational resource. *Corbicula* was more likely to be present (slightly short of significance) in parks with fishing activities than ones without such facilities (Table 5). The 50 parks with fishing were then divided into those with and without boat ramps (Table 6). The presence of a boat ramp appeared to be irrelevant to the occurrence of *Corbicula*.

Table 5. Relative occurrence of *Corbicula* in open state park units of Texas with freshwater subdivided into parks with and without fishing facilities.

	Corbicula		
Facility	Present	Abent	Total
Fishing	26	24	50
No Fishing	4	12	16
Total	30	36	66

$x^2_{(1)} = 3.564$; $p = .06$

Table 6. Relative occurrence of *Corbicula* in open state park units of Texas with freshwater fishing facilities subdivided as to occurrence of boat ramp.

	Corbicula		
Boat Ramp	Present	Absent	Total
Present	15	14	29
Absent	11	10	21
Total	26	24	50

$x^2_{(1)} = .002$; $p = .963$

ECOLOGICAL PREFERENCES

In Texas *Corbicula* is restricted to non-saline waters. *Corbicula* is more abundant in waterbodies with a substantial fraction of sand with moving water.

In larger reservoirs optimal microhabitat appears to be a moderate-energy shore. Not only is the substrate likely to be of a coarse nature, but the oxygen level is presumed high and accumulation of metabolites is not likely. *Corbicula* has been found in non-stagnant cat-tail marsh along the margins of Cedar Creek Reservoir, Henderson County. At Twin Buttes Reservoir (Concho River), near San Angelo, *Corbicula* was abundant in sandy substrata that typify this reservoir. However, *Corbicula* also occurs in gravelly mud and rock riprap on the face of the dam where wave action was moderate (Twin Buttes Reservoir; Brady Reservoir on Brady Creek). In the Rio Grande immediately below Anzalduas Dam, *Corbicula* is found among and under small boulders (20-25 cm diameter) present in midstream areas and in sand banks along the shore.

Reservoirs with mud bottoms are not conducive to development of dense populations of *Corbicula*. Dead shells were found uncommonly in Lewisville Lake, Denton County; these shells are believed to be from low density populations in flowing creeks which drain into the reservoir. However, *Corbicula* was abundant in small-gravel substratum in the stream (Elm Fork Trinity River) immediately below the dam.

One clearly defined optimal microhabitat in the Central Texas Hill Country is among gravel (up to 100 mm in length) scattered in shallow pools below riffles (Fig. 1). Occurrence of *Corbicula* in such areas was observed at Guadalupe River State Park and South Llano State Park. Such substrates occur at depths between 10 cm and 1.5 m. *Corbicula* occurred on a packed clay/rock bottom at the same level as larger non-attached gravel rocks, but these clams had not burrowed into the substratum. Clams are not buffeted because they are within the boundary layer created by the larger gravel rocks where the current pressure is minimal. Limited number of small clams (6-8 mm) are present. *Corbicula* is found among small gravel in potholes of the limestone bottom of Onion Creek, McKinney Falls State Park.

River reaches below dams are also "favored" areas. Tremendous bars composed of live *Corbicula* are exposed during the fall months in the Colorado River in Travis County. Warm season flows are maintained because of demands for irrigation water downstream rice farmers. When demand for irrigation water diminishes in autumn, water flow is greatly reduced unless heavy rainfall occurs upstream. Large expanses of riverbottom consisting of hydraulic accumulations (see Eng, 1979) of *Corbicula* are exposed. Death occurs quickly with smaller clams expiring before the larger clams.

One of the major causes of mortality in *Corbicula* in

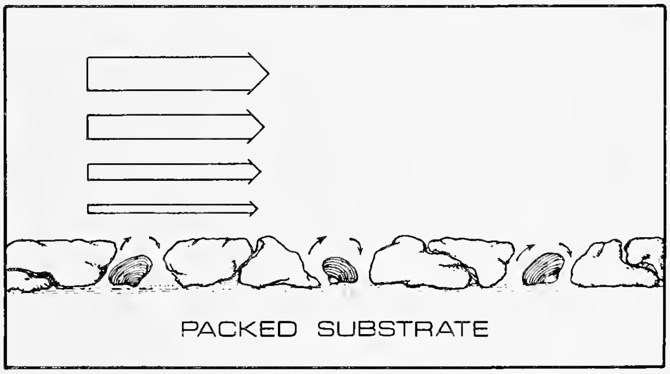

Fig. 1. Occurrence of *Corbicula* in gravel-bottomed pools of rivers in Hill Country of central Texas. Size of arrows directly correlated with relative water velocity.

many areas of Texas is alteration in water depth and current, both increased and decreased, due to natural and anthropogenic causes. Numerous clams were present in pools below riffles in Guadalupe River State Park, Comal Co., on 23 July 1978. A torrential flood with river rises of 15-18 m on 1-2 August resulted in massive flood damage (Schroeder *et al.*, 1979). Examination of these pools on 9 August 1978 revealed no living *Corbicula*. Subsequently, *Corbicula* has recolonized these areas. *Corbicula* in the sand banks below Anzalduas Dam, particularly the smaller ones, die from overheating following water level fall, even if they can reach water-saturated sand below the surface.

CLAM-HUMAN INTERACTIONS

The effect of human activities upon *Corbicula* was observed at Huntsville State Park, in eastern Texas in December 1977. Shells were present in most parts of the lake, but articulated shells were much less common in the swimming area (4.9 pairs/sq. m.) than in a nearby, otherwise similar, portion of shallow lake (25.2 pairs/sq. m.).

The distribution of *Corbicula* in an artificial impoundment (Lake Long) in Austin was investigated. A small area on Lake Long has been developed for picnic sites and swimming. Natural bottom of this lake is black clay, but a small area has been enhanced for swimming by placement of sand. Examination of the clay bottom portion (40 m beach length x 10 m distance from beach) of the lake edge revealed no *Corbicula*, while the sandy beach area supported a thriving population. A more intensive survey utilizing detailed hand sampling was conducted on 31 July 1981. Numbers of clams per square meter were recorded at intervals of 0.2 m depth (Fig. 2). Very small clams (2-5 mm) were found only under and attached to small gravel (up to 8 cm length). An average of 1.1 young clams were found attached to each piece of gravel (22 rocks per square meter).

Only seven state parks obtain water directly from surface sources. Of these seven parks, six contain *Corbicula* in the relevant body of water; the seventh park is located in the Panhandle in the large area of western Texas in which *Corbicula* has yet to be discovered. None of the six parks have reported any problems associated with *Corbicula*. A typical water procurement system utilizes a 3-inch intake pipe with a one-eighth inch mesh screen. Water is pumped into a settling basin where it is chlorinated, filtered and rechlorinated.

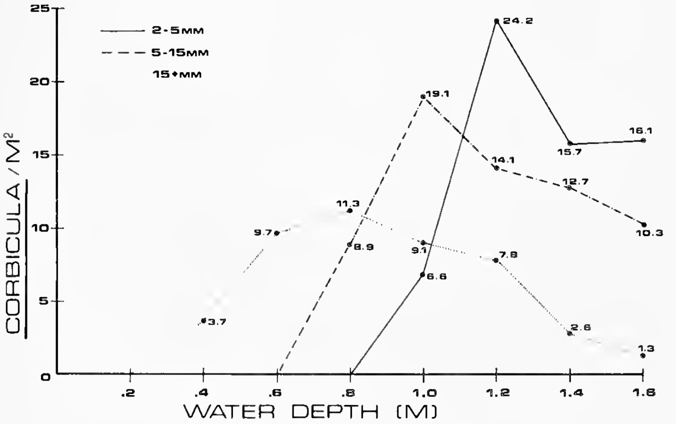

Fig. 2. Depth distribution of size classes of *Corbicula* at Lake Long, Austin, Texas. Numbers of data points indicate number of *Corbicula* per square meter.

DISCUSSION

This survey revealed that *Corbicula* was present in less than half the freshwater sites surveyed in the Texas Park system. Several parks which contain aquatic habitats suitable for *Corbicula* revealed no individuals. Some of these "absent" results may be due to sampling error at sites where individuals of *Corbicula* were too sparse or localized to detect. However, some of the "absent" results may reflect the highly dynamic nature of *Corbicula* populations in Texas. Following attainment of high densities, *Corbicula* populations often crash; some of these population declines may progress to local extirpation. The absence of *Corbicula* from irrigation water storage reservoirs at long distances from the Rio Grande coupled with the occurrence of populations in reservoirs close to the Rio Grande indicates a dispersal distance limit in silt-filled irrigation canals (Neck and Metcalf, in press). *Corbicula* shells from eastern Texas tend to be smaller than those from other portions of Texas with alkaline waters (indicating a shorter life span).

Unopened parks tend to be environmentally similar to those open parks which support populations of *Corbicula*. New parks tend to be on large reservoirs or streams with 13 of the 20 new sites located in eastern Texas. Only two of these new sites have an isolated system or an enclosed lake. Additionally, many of these new parks are located on lakes or streams which have other points of public access.

Corbicula is not a problem in park water systems because few ever arrive in the settling basin, and these individuals may be killed by the initial chlorination treatment. Sinclair and Isom (1963) discussed the success of chlorination in controlling *Corbicula* in an industrial water supply. Ingram (1959) recounted problems with *Corbicula* in underground canals and pumping stations in agricultural and municipal water supply systems, but did not report any occurrences in municipal water distribution systems. Such occurrences are known for aquatic snails and other species of clams as reviewed by Ingram (1956).

Certain operational techniques in various state parks may impact *Corbicula* populations. The water level of Lake Raven in Huntsville State Park is lowered each winter to control aquatic vegetation with chemical sprays. The winter drawdown of Lake Raven also functions as a management technique to control *Corbicula*, but this effect is entirely fortuitous. Such a lowering (in the cooler months) will cause mortality of most individuals in the shallow margins of the lake. The susceptibility of *Corbicula* to water level declines results from reduced migratory abilities (White, 1979) and intolerance to aerial exposure (McMahon, 1979).

There are three major microhabitat classifications which appear to be optimal for *Corbicula* in Texas. Areas of sandy or rock-bottomed streams of intermediate flow probably represent the "best" habitat for *Corbicula.* Greater numbers of *Corbicula* on sand than silt was observed in Florida populations (Gottfried and Osborne, 1982). Another prime microhabitat occurs among loose gravel substrata in shallow pools between riffles in streams of the Texas Hill Country in the central part of the state west of the Balcones Fault Zone (Fig. 1). In such locations, *Corbicula* is actually an epifaunal bivalve. The third favored microhabitat is a moderate energy lakeshore where wave action is sufficient to remove most or all silt and clay particles, but not strong enough to allow frequent disturbance of the substratum. These three classification types must contain non-saline, relatively unpolluted water in the warmer portion of the state.

The absence of *Corbicula* from brackish and saltwater habitats probably is due to physiological stress (Gainey, 1978a;b) which appears to be inversely proportional to period of acclimation (Evans *et al.*, 1979). Fontanier (1982) reported *Corbicula* in the Brazos River no further downstream than Farm Road 1462, Brazoria County. Absence of *Corbicula* from coastal rivers under tidal influence has been noted in Mississippi (Hartfield and Cooper, 1983). However, *Corbicula* occurs in tidal portions of the Potomac River, Maryland (Dresler and Cory, 1980). Valves of *Corbicula* found on Gulf beaches in Texas (O'Kane *et al.*, 1977) undoubtedly represent river drift material that has been redeposited in the surf zone. Britton (1982) was unaware of any records of live *Corbicula* from Texas tidewaters.

Absence of *Corbicula* from areas of Texas which experience the most severe winter weather may not be totally due to temperature effects, although *Corbicula* is not tolerant of long-term subfreezing conditions (Horning and Keup, 1964). The Panhandle and western Texas lack permanent streams due to reduced precipitation levels. Chances for introduction may be somewhat reduced, but the absence of *Corbicula* in Lake Theo (Caprock Canyons State Park, Briscoe Co.), contrasts with the occurrence of introduced populations of the bullfrog, *Rana catesbeiana* (Neck, 1980) and the extralimital unionid, *Anodonta grandis* (Neck, 1982), in this lake.

Since size of an individual indicates length of growth period and/or rate of growth, size of *Corbicula* valves also indicates suitability of habitat. The largest valves recovered during this study were 52.9 mm long and were from Llano Grande Lake, Hidalgo County. Britton (1982) reported a specimen from Benbrook Lake with a length of 60 mm.

Environmental reasons for the size-class/depth patterns observed at Lake Long are manifold. While the shallower water has a sandy bottom as opposed to a more mixed sandy clay substratum at greater depths, an area of shallow water with a similar mixed sand/clay substratum revealed no clams. Human activity patterns in the beach area both inadvertently disturb and deliberately remove clams. Clams in shallow water are continually buried by trampling action of humans and a substantial number are removed, particularly by adolescent humans. Substratum is significant in that the gravel rocks are important, and possibly essential, for survival of recently metamorphosed *Corbicula* in this area.

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THE ASIATIC CLAM IN LAKE ERIE

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In 1981 and 1982, the thermal plume areas of four power plants along the southern shore of Lake Erie were sampled for *Corbicula fluminea*. *Corbicula* were found in only two of those four locations: the thermal plumes of the Toledo Edison Acme and Bay Shore Generating Stations. Both power plants are coal-fired with once-through condenser cooling systems. Acme is located in Toledo on the Maumee River. Bay Shore is located east of Toledo on the southern shore of Maumee Bay.

The two power plants at which no *Corbicula* were found are the Toledo Edison Davis-Besse Nuclear Power Station located near the mouth of the Toussaint River and the Cleveland Electric Illuminating Company Eastlake Power Plant on the Central Basin east of Cleveland. Davis-Besse has a closed-cycle natural draft cooling tower, and hence no significant thermal plume. Eastlake has a once-through condenser cooling system and a large thermal plume.

In 1982, specimen length varied from 4 mm to 35 mm. The majority of the specimens were collected from the Bay Shore thermal plume. The substrates in which the clams were found were predominately clay and muck.

The 1981 and 1982 findings were consistent in indicating that *Corbicula* have not spread beyond the confines of the thermal plumes of the Acme and Bay Shore Generating Stations.

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BIOLOGICAL BASIS OF BEHAVIOR IN *CORBICULA FLUMINEA*, I. FUNCTIONAL MORPHOLOGY OF SOME TROPHIC ACTIVITIES

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ABSTRACT

Understanding the functional morphology of trophic activity of *Corbicula fluminea* (Müller) provides a useful basis upon which to design appropriate control protocols for the clams. Accordingly, this paper reports results of pertinent research by the author. Characteristic, rapid locomotion is accounted for at least in part by (1) the unusual (for a freshwater bivalved mollusk) structural autonomy of the adductor muscles and the "suturing" of the mantle lobes so as to provide a pallial foramen for those muscles; and (2) the recently discovered, conjoined statocysts near the pedal ganglion. Agile locomotion of juvenile clams is produced by (1) precocious differentiation of the statocysts; (2) well developed retractor muscles; and (3) telescoping "laminae" of the juvenile foot, all recently interpreted with videotaping and scanning electron microscopy (SEM). Putative sensory cilia discovered on the lip of the excurrent siphon help account for the extreme sensitivity of that tissue to mechanical stimuli. Location and interpretation of the paired sense organs, the osphradia, on the ventral surface of the visceral ganglion above the dorsal shelf of the excurrent chamber, indicate function different from that of gastropod osphradia, perhaps a light sensor function—and certainly needing further study.

As a consequence of the First *Corbicula* Symposium in 1977 (Britton, ed., 1979), consensus was reached that *Corbicula fluminea* Müller is hermaphroditic (Britton and Morton, 1979; Kraemer, 1979a), and that its young are shed into the environment primarily as juveniles (Kraemer, 1979a). It was also reported there that the juveniles develop a byssal thread that is used as an anchor to the substratum, and is thereby associated with rapid downstream disbursement and local establishment of the young clams (Kraemer, 1979a). In the literature reviewed for the preparation of this paper little further work on the functional morphology of *C. fluminea* other than that by the present author was to be found (Britton and Morton, 1982). During the interim since 1977 some investigators have been concerned with careful analysis of the taxonomic position of *C. fluminea* (e.g. McCleod, 1983), with life history and distribution of *C. fluminea* (Counts, 1981,1983; McMahon, 1982; Hall, 1983), with some physiological traits of *C. fluminea* (McMahon, 1982; McCleod, 1983) and with diagnostic shell microarchitecture (Counts and Prezant, 1979; Prezant and Chalermwat, 1983).

Primary focus in the Second International *Corbicula* Symposium, held in Little Rock, Arkansas, in 1983, was on the currently researched level of understanding of *C. fluminea* as a serious macrofouling organism in U.S. rivers, and on presently available technical means for bringing the clams under control. In that context it is appropriate to review results of research since 1977 which further elucidate the biological characteristics of *C. fluminea*. With thorough biological evaluation, technical protocols for control of the clams can be rigorously evaluated and the future role of *C. fluminea* can be assessed.

In this paper results of recent studies on the functional morphology of some trophic activities of *C. fluminea* (e.g. locomotion, siphoning) are reviewed and evaluated as a basis for estimating the likely efficacy of control procedures for the clams.

MATERIALS AND METHODS

Three-dimensional visualization of the microarchitecture of tissues and organs involved in trophic activities of *C. fluminea* was done by means of analysis of several thousand serial sections of whole clams. Ultrastructure study of some structures (e.g. motor and sensory cilia) was done with scanning electron microscopy (SEM). Developmental sequencing and the function of certain embryonic structures (e.g. the juvenile foot) was determined with the aid of a Panasonic Videocamera attached to an AO-Microstar compound microscope. Additional details regarding materials and methods used are included in the subsequent article (Kraemer *et al.*, 1985).

RESULTS

FUNCTIONAL MORPHOLOGY OF LOCOMOTION

Many workers have observed the remarkable rapidity with which *C. fluminea* spreads through great expanses of

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river bottoms in the United States. It was found, for example, that *C. fluminea* had not only spread through more than 240 miles of the Arkansas River in less than 10 years, but that it had become by far the most abundant species in the benthos (Kraemer, 1975,1977). It seemed evident that many juvenile clams were transported downstream, perhaps attached to sand grains by means of their byssal thread. Recently Prezant and Chalermwat (1984) have presented evidence from which they argue that *C. fluminea* may achieve downstream distribution by drifting attached to mucus strands. The very active movements of *C. fluminea* may account for some aspects of its distribution patterns, especially upstream. Unlike the indigenous river mussels (Unionacea) that exhibit slow, ponderous foot movement, *C. fluminea* has a foot regularly engaged in rapid backward and forward, and side-to-side movement. Locomotion by a large mussel is seldom more than 20 cm/hr, while the much smaller *C. fluminea* has been clocked at up to 250 cm/hr (Kraemer, 1977). Pyramidal shape of the shell valves of the clam and the unhampered movement of the adductor muscles have been shown to allow for more autonomous movement of the shell valves than is possbile for mussels.

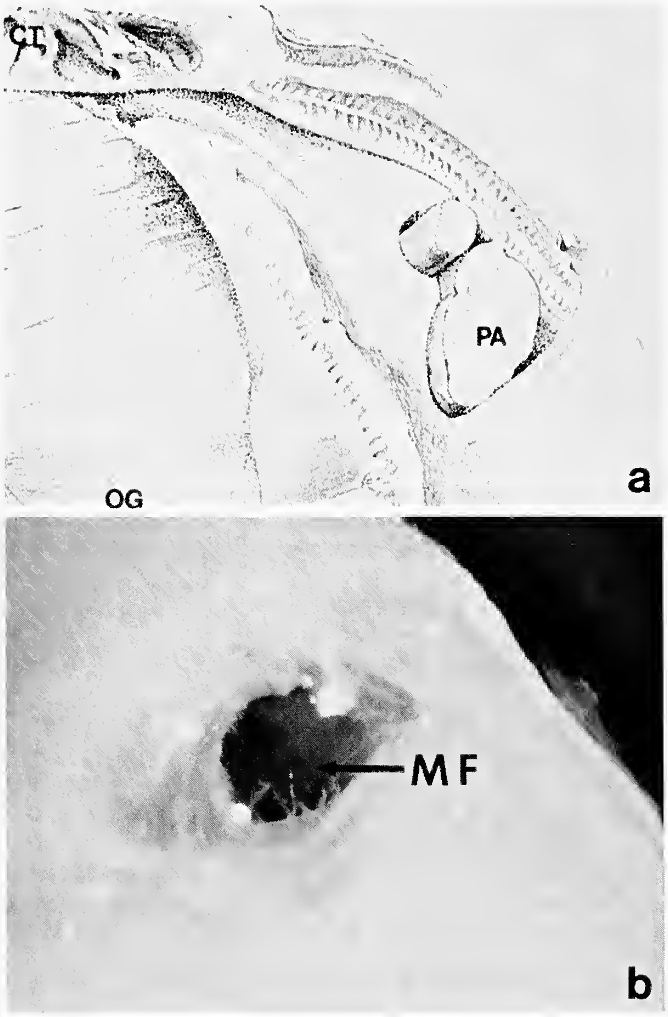

Fig. 1 a. Drawing of posterior region of *C. fluminea* from a specimen that was relaxed in Nembutal. The left shell valve was removed and the left mantle lobe was reflected to show underlying tissues, such as outer gill. The fusion of the mantle lobes not only reduces the pedal gape, but also creates a foramen around the posterior adductor muscle, etc. Horizontal field width = 33 mm. **b.** Photomicrograph of posterior region of relaxed specimen that was preserved and removed from the shell valves. The posterior adductor muscle has fallen out, leaving a foramen clearly visible in the mantle lobes. Horizontal field width = 6.5 mm. CT, cardinal tooth; MF, mantle foramen; OG, outer gill; PA, posterior adductor muscle.

In dissecting carefully preserved specimens of *C. fluminea* it was repeatedly observed that adductor muscles of the clam and especially the posterior adductor muscle, would simply fall out of the mantle when the muscle was separated from shell valves. A hole or "pallial foramen" thereby became visible (Fig. 1a,b). Frontal sections made from this region of the clam reveal a peculiar histological "suturing" of the right and left mantle lobes in the region of the pallial foramen (see Kraemer, 1977).

Corbicula fluminea, unlike any other bivalve similary studied, has a pair of statocysts (putative balance organs) located just above the pedal ganglion in the midventral portion of the visceral mass, and which are conjoined by a slender, hollow tube (Fig. 2a) (Kraemer, 1978). In contrast, the slow-moving, indigenous mussels have a pair of statocysts, each of which is slung by its own statocyst nerve from the cislateral cerebral ganglion, and each is thus widely separated from the other (Kraemer, 1978, 1984). It seems likely that the conjoined statocysts provide a neurological basis for the clam's rapid foot movements. While these are the first conjoined statocysts to be found for any bivalved mollusk, it seems probable that such statocysts will also be found in other bivalves exhibiting similar locomotion.

Juvenile locomotion. Recent studies have revealed that juvenile *C. fluminea* have well differentiated, disproportionately large statocysts, even though the young clams measure less than 200 μm in length at this stage. Further, it has been found (Kraemer, 1984; Kraemer and Galloway, in press) that the juvenile foot has accordion-like laminae along its length which facilitate rapid, agile movement, allowing the young clam to crawl under surface water film or over minute bits of detritus suspended in the water (Fig. 2b,c). These findings provide a morphological basis for repeated observations (West, personal communication) of young *C. fluminea* "floating" in the water column.

SIPHON MOVEMENTS

Siphons of several species of *Corbicula* have been found to be taxonomically distinctive (Britton and Morton, 1979,1982). Siphons of *C. fluminea*, like those of many of its indigenous relatives, the freshwater pill clams (*Pisidium*) and fingernail clams (*Sphaerium*), are slender, muscular, fused tubes. The siphons are extremely mobile, and are not particularly sensitive to light (as are the siphons of the mussels, Unionacea). The siphons are especially responsive to tactile stimuli or to movements of the water column, however. Recent studies using scanning electron microscopy (SEM)

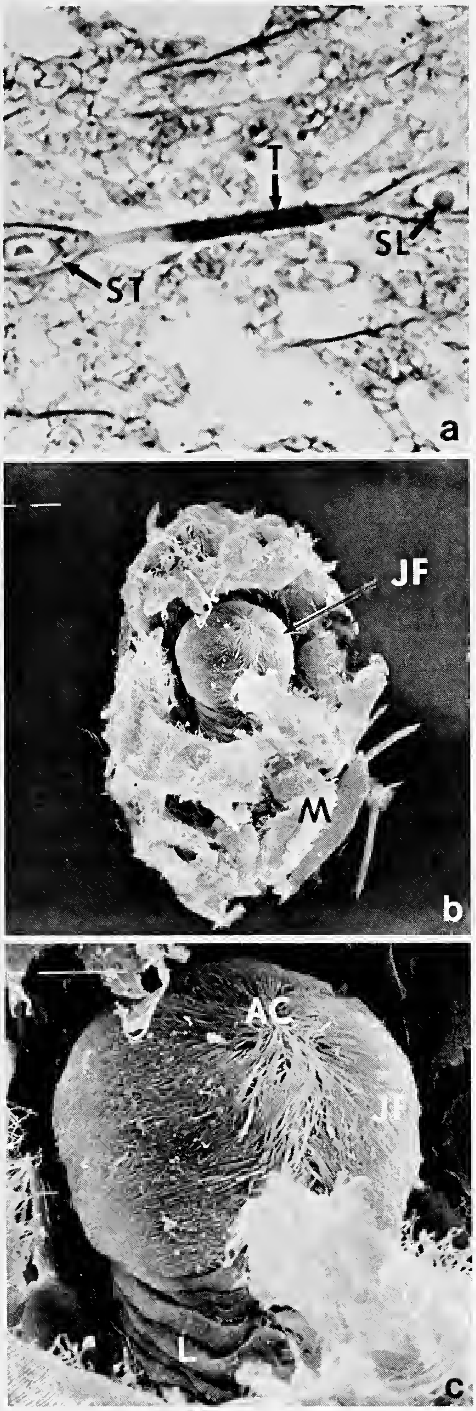

Fig. 2 a. Photomicrograph of cross-section of *C. fluminea* in region of pedal ganglion, showing unusual conjoined statocysts above the pedal ganglion. (from Kraemer, 1978) Horizontal field width = 3.2 mm. **b.** Scanning electron micrograph of juvenile *C. fluminea* taken from ovisac of marsupial gill in adult specimen. Note conspicous laminae of the large foot of the young clam. Horizontal field width = 225 µm. **c.** Scanning electron micrograph showing detail of distal end of foot in juvenile clam. Note the conspicuous laminae and the apical cilia. Horizontal field width = 73 µm. AC. apical cilia; JF, juvenile foot; L, lamina; M, mantle; SL, statolith; ST, statocyst; T, hollow tube which joins the statocysts.

made possible the comparative study of several kinds of effector cilia on the gills, gonopore lips and labial palps of *C. fluminea*. It was thus possible to evaluate newly discovered, minute clumps of cilia on the distal lips of the excurrent siphon of *C. fluminea*, as putative sensory cilia (Kraemer, 1983). The latter may very well constitute mechanoreceptors which account for the extreme tactile sensitivity of the siphonal lips (Fig. 3). Other authors seem to have found similar organelles with comparable function in some echinoderms (Whitfield and Emson, 1983).

OSPHRADIA: CHEMICAL OR PHYSICAL SENSORS IN *C. FLUMINEA*?

The osphradium occurs in the roof of the incurrent siphon of gastropod mollusks, where its function as a chemoreceptor or mechanoreceptor has been experimentally implicated. However, previous studies of (marine and estuarine) bivalve osphradia have been inconclusive as to location, orientation or function of the organ. Analysis of transverse and sagittal serial sections of *C. fluminea* reveal that the organ is paired, and that it is adjacent to the ventral surface of the large visceral ganglion. The osphradium of *C. fluminea* is extensively innervated by neuronal fibers from the dorsally situated, visceral ganglion. Ventrally, many delicate, unmyelinated fibers of the osphradia innervate a patch of modified epithelium on the roof of the excurrent canal (see Kraemer, 1981).

Recent studies of mollusk osphradia ultrastructure (Haszprunar, 1983) indicate that: (1) findings of the microarchitecture of osphradia in *C. fluminea* appear to be within the norm for bivalves; and (2) that function of these well differentiated sense organs in *C. fluminea* and in bivalves as a whole, is much in need of further study. It has been suggested (Kraemer, 1981) that their innervation, microarchitecture and location may even indicate a pineal body-like, light sensor function for the osphradia of *C. fluminea*.

SUMMARY AND DISCUSSION

Functional morphological studies of *C. fluminea* reveal that: (1) Rapid locomotion of the clams is aided by suturing of the mantle lobes around the adductor (especially posterior) muscles, which allows for more effective adduction of the heavy shell valves. (2) Locomotion is further aided by conjoined statocysts, the first such statocysts found in any mollusk species. Organization of the statocysts is peculiarly and necessarily implicated in their back-and-forth, side-to-side foot movements. (3) Recently discovered horizontal laminae of the foot of juvenile clams facilitate the agile, rapid extensions, turnings and withdrawals of the foot in young clams. (4) Videomicroscopy has recently allowed clear visualization of the proportionately large, well differentiated statocysts of juvenile *C. fluminea* and shows that the statocysts may function as sensors implicated in the complex movements of the clams. (5) The mobile, fused siphons of *C. fluminea* are equipped with patches of recently discovered, putative sensory cilia, which seem to provide the morphological basis for

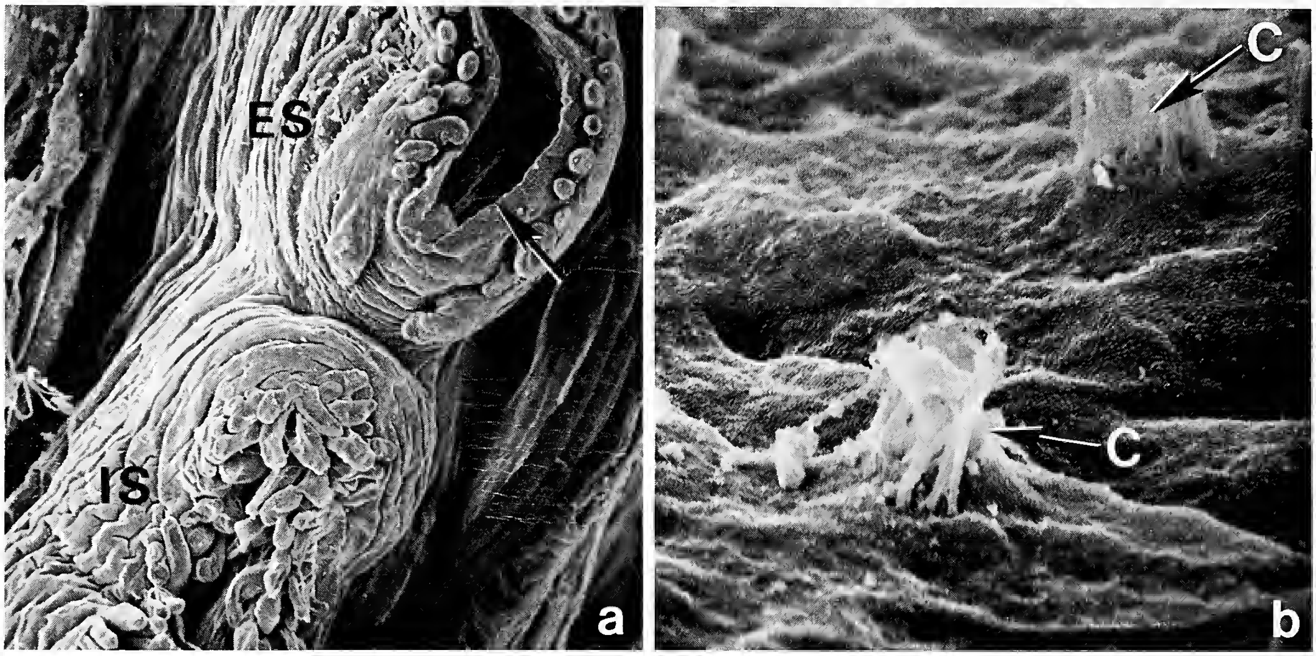

Fig. 3 a. Scanning electron micrograph of siphons of *C. fluminea*. Arrow indicates lip of excurrent siphon upon which the very small ciliary tufts shown in b were seen. Horizontal field width = 9.4 mm. **b.** Scanning electron micrograph of surface of lip of excurrent siphon, showing isolated ciliary tufts of putative sensory function. (after Kraemer, 1981). Horizontal field width = 55 μm. ES, excurrent siphon; C, ciliary tuft; IS, incurrent siphon.

the tactile sensitivity of the siphonal edges. (6) Histological and neuroanatomical details of the osphradia of *C. fluminea* offer a new view of possible physical or chemical sensory function for these sense organs, not only in *C. fluminea* but in other bivalves as well.

It seems plausible to argue that the foregoing information on the functional morphological basis of certain trophic activities of *C. fluminea* provides useful background for evaluating the *C. fluminea* populations in U.S. rivers, and the available means for their control. An immediate effect of the rapid spread and establishment of a great biomass of *C. fluminea* in managed U.S. rivers called attention of investigators to the apparent replacement of the indigenous freshwater mussel fauna in those stream bottoms by an "invasive" species. How had the swift faunal exchange taken place? Decline of the great U.S. mussel fauna has been considered at length (Clarke, 1970).

Was *C. fluminea* "taking over" the river bottoms as a superior competitor? It was argued that ecological "crunch" in those rivers created a far different interspecific contact than that due to true competition (Wiens, 1977). Evidence accumulated that *C. fluminea* was far more apt to attain a large biomass in benthos of "managed" rivers (e.g. dredged, dammed) than in less disturbed streams. In the latter sites, Asian clams could live along with mussels, but without the evident success of the mussels (Kraemer, 1979b). It was argued further that the great size range of *C. fluminea*, unusual for a freshwater benthic species, allows it: (1) to establish large populations of small, reproductively active clams, that equal the size of freshwater gastropods, insects and many crustaceans, *and* (2) to establish populations of large (reproductively active) benthic animals which approach the size of freshwater mussels (Kraemer and Gordon, 1980). These authors suggested that *C. fluminea* may be meeting criteria for "the size range of success" in establishing its significant presence in U.S. rivers (Kraemer and Gordon, 1980).

Why have the indigenous relatives of *C. fluminea,* the pill clams (*Pisidium*) and the fingernail clams (e.g. *Sphaerium*), not exploited damaged river bottom habitat with runaway biomass as *C. fluminea* has? *C. fluminea* certainly has a much heavier shell, a longer life span and a much greater size range. Important cues to the effectiveness of the trophic activities of *C. fluminea* are cited in functional morphological characteristics reported in this paper. Of equal or greater importance, however, are comparable considerations of the functional morphology of reproduction and development of *C. fluminea* which are analyzed in the paper following this one (Kraemer *et al.*, 1985).

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BIOLOGICAL BASIS OF BEHAVIOR IN *CORBICULA FLUMINEA*, II. FUNCTIONAL MORPHOLOGY OF REPRODUCTION AND DEVELOPMENT AND REVIEW OF EVIDENCE FOR SELF-FERTILIZATION

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ABSTRACT

Results reported in this study of the functional morphology or reproduction and development are based on findings from northwest Arkansas populations of *Corbicula fluminea* (Müller). A captive population of the clams was maintained by AP&L personnel in the intake bays of the Arkansas Nuclear One facility of the Arkansas Power and Light Company on Lake Dardanelle, an impoundment of the Arkansas River at Russellville, Arkansas. The captive population and other "natural" populations of *C. fluminea* in the Buffalo River and White River in Northwest Arkansas, and the Llano River in Llano County, Texas, were subjected to long term study. Serially sectioned *C. fluminea* at various stages of development, fresh-tissue dissections and scanning electron microscopy (SEM) were used in this study. Results include (1) verification of the proto-oogamous development of the reproductive system in *C. fluminea* and determination of the role of early innervation of the gonopores and development of follicular "ganglia" which accompany later stages of spermatogenesis; (2) verification of the developmental sequence in oogenesis and the sequential, changing appearance of the oogenic follicles in the visceral mass; (3) determination of characteristics of the biflagellate sperm of *C. fluminea* as well as evidence that three "kinds" of sperm are not polymorphic sperm but are quite likely several stages in spermiogenesis; (4) additional evidence of intrafollicular, self-fertilization of eggs in the visceral mass of *C. fluminea*, from sightings of intrafollicular embryos in fixed and in fresh tissues; (5) delineation of the entire developmental sequence in *C. fluminea*, along with evidence that the embryonic stages most frequently shed into the environment are the early to late juveniles.

Early reports in the United States regarding reproduction and life history of *Corbicula fluminea* (Müller) asserted a hermaphroditic habit and spawn of various developmental stages, especially the trochophore (Sinclair and Isom, 1963; Sinclair, 1971). These assertions were based largely on bibliographic evaluations assembled by earlier workers in the face of dramatic, sudden change in the malacofauna of U.S. rivers. While the 1977 *Corbicula* Symposium had produced consensus that *C. fluminea* is probably a hermaphrodite, definitive supporting evidence was not available. Consequently, later study by Kraemer and Lott (1977) and by Kraemer (1978) on histological differentiation of the reproductive tissues and related nervous tissue (Kraemer, 1983a, 1984) were apparently the first in the U.S. to report anatomical details of the reproductive process in *C. fluminea*.

In this paper we review results of our continuing study of the biological basis of reproduction in *C. fluminea*. A number of our findings stem from studies done with the support of the Arkansas Power and Light Company, whose personnel have maintained a captive population of *C. fluminea* at the Arkansas Nuclear One site at Russellville, Arkansas on the Arkansas River, since 1981. Since a costly "clam clog" at the site in September, 1980, AP&L has maintained a substantial logistical and administrative interest in the reproductive cycling of *C. fluminea*.

MATERIALS AND METHODS

Histological serial sections of approximately 6 animals each in the size ranges 2mm, 4mm, 8mm, and 20mm of *C. fluminea*, made as described elsewhere (Kraemer and Lott, 1977; Kraemer, 1978; 1979b) were used to work out the three dimensional structure and to describe: (1) the anatomical site and histological context within which differentiation of the gonadal follicles occurs; (2) intrafollicular development sequence of oogenic and spermatogenic follicles; (3) development and later innervation of the paired gonopores; (4) appearance and differentiation of the follicular "ganglia;" (5)

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histological evidence of intrafollicular fertilization and cross-fertilization; (6) mode of passage of gametes and (evidently self-fertilized) embryos from the gonopores into the anterior chambers of the inner gills.

Living specimens were obtained from several "wild" populations in the Buffalo River and the White River of northwest Arkansas, from the Llano River in Llano, Texas. Living clams were obtained also from some captive populations maintained in the intake bays at Arkansas Nuclear One, a facility of Arkansas Power & Light Company located at Russellville, Arkansas near Lake Dardanelle on the Arkansas River. Collections of living material from Russellville were made at monthly, bimonthly and (during reproductive seasons) at weekly and daily intervals. Fresh tissue dissections were made to determine: (1) the extent of growth of the oogenic follicles; (2) state of intrafollicular development of oogenic follicles; (3) presence or absence of spermatogenic follicles (which appear peripherally and mostly near the surface of the visceral mass); (4) kinds of spermatogenic cells present in the follicles; (5) kinds of sperm and sperm motility; (6) presence, developmental stages, numbers and distribution of embryos within the gills; (7) presence of embryos and their developmental stage, within the follicular chambers of the visceral mass. Results of the foregoing studies are reviewed in this paper and will be discussed in detail elsewhere (Kraemer and Galloway, 1986; Kraemer and Swanson, in prep.).

All stages of embryonic development and many stages of oogenic and spermatogenic development were monitored with a Panasonic VHS Minivision, Color Video Camera, mounted on an AO 110 Microstar microscope with phase optics.

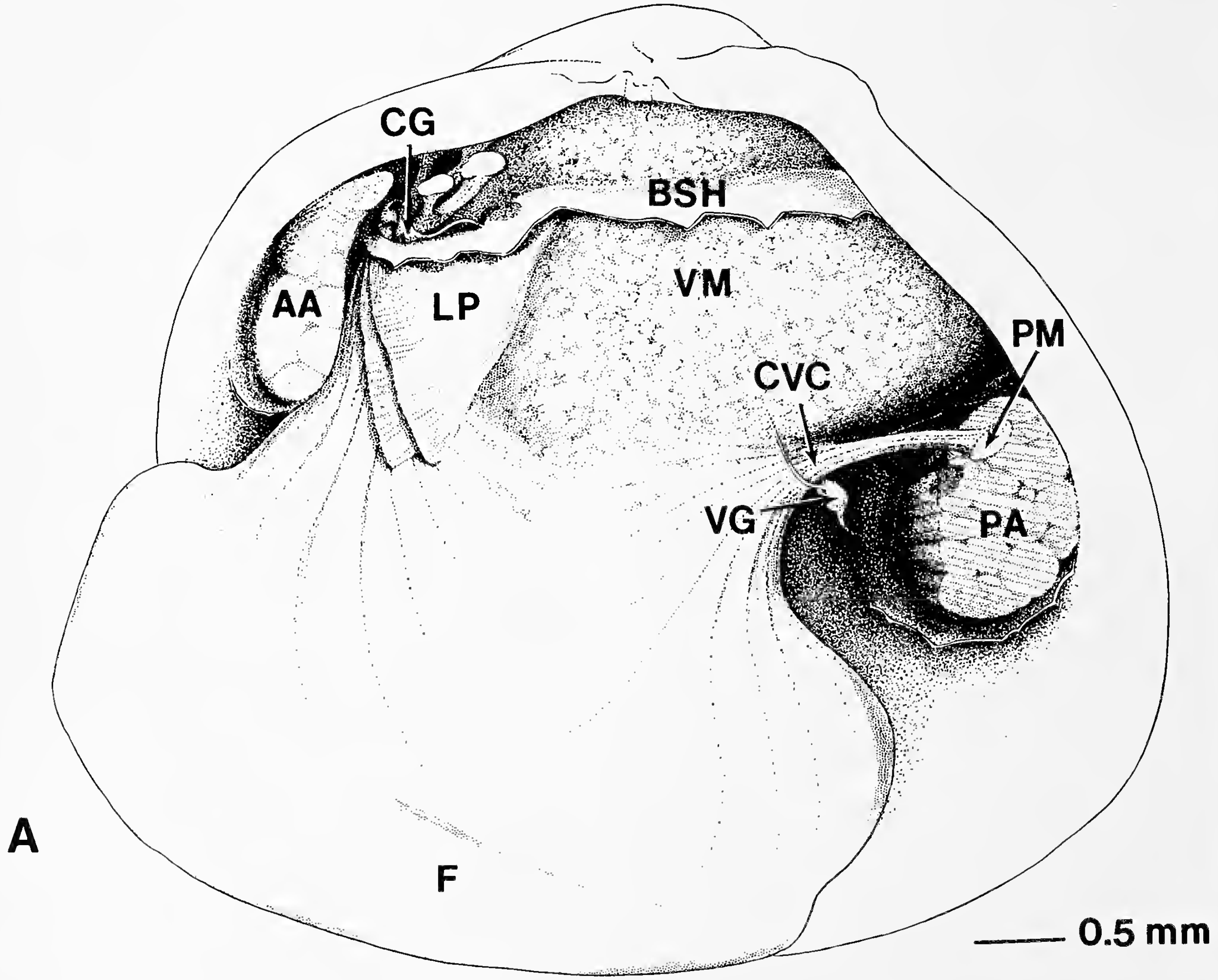

Fig. 1. Drawing of *Corbicula fluminea*, left valve removed and portion of left mantle lobe reflected to show location of main nerve ganglia and main connective nerves. AA, anterior adductor muscle; BSH, branchia shelf; CG, cerebral ganglion; CVC, cerbrovisceral connective; F, foot; LP, labial palp; PA, posterior adductor muscle; PM, pedal muscle; VG, visceral ganglion; VM, visceral mass.

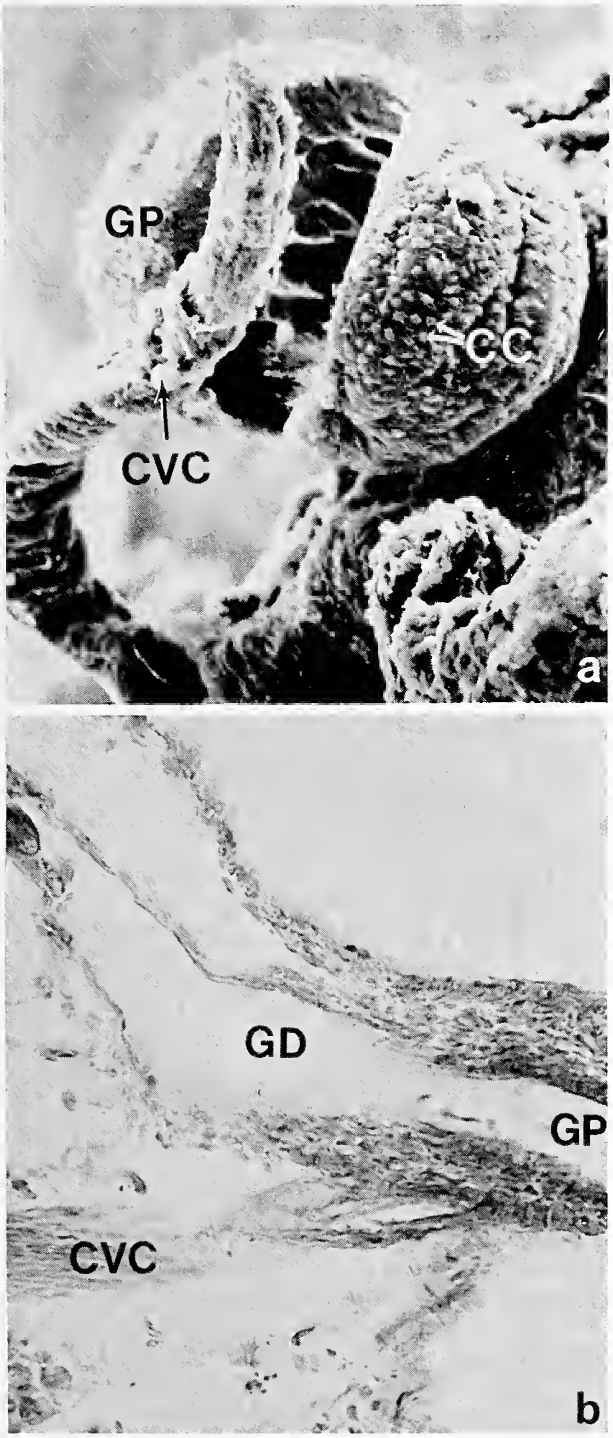

Fig. 2. a. Scanning electron micrograph showing gonopore of *Corbicula fluminea*. GP, lip of gonopore; CVC piece of cerebrovisceral connective; CC, ciliary cluster, peculiar to the gonopore lips. Horizontal field width = 373 μm. **b.** Photomicrograph of sagittal section of posterodorsal, lateral region of visceral mass, showing a gonopore and some of its innervation by means of fibers from the cerebrovisceral connective nerve. CVC, cerebrovisceral connective; GD, gonoduct; GP, gonopore. (From Kraemer, 1978). Horizontal field width = 663 μm.

Details of spermatogenesis, spermiogenesis and embryogenesis were elucidated with preparation of tissues as described elsewhere (Kraemer, 1983b) for viewing with an ISI-60 Scanning Electron Microscope (SEM) at 30 Kv and a working distance of 15 nm.

RESULTS

DEVELOPMENT AND INNERVATION OF THE GONOPORES. When young clams attain a length of 3-4 mm, serial sections reveal that, before there is any histological indication of gonad development, there are a pair of well-differentiated gonopores. The gonopores are located, one on either side of the posterior dorsal surface of the visceral mass, where the latter forms a juncture with the kidneys. This is also the site where large cerebrovisceral nerve connectives emanate from the visceral mass to course posteriorly and join the prominent, fused visceral ganglion of the clam's central nervous system (Kraemer, 1978) (Fig. 1).

The gonopores exhibit conspicuous lips composed of tall, ciliated columnar epithelium. The cilia are large, evidently effector organelles that manifest a peculiar clumped array (Kraemer, 1983b) (Fig. 2a). Only when oogenesis is initiated in young clams, do the cerebrovisceral connectives "sprout" nerve fibers that innervate the epithelium of the gonopore lips, (Fig. 2b) (Kraemer, 1978). Function of this highly innervated gonopore suface is not understood, but certainly merits further investigation because of several likely roles the gonopore opening may play in fertilization or embryogenesis.

PROTO-OOGAMY, OOGENESIS AND DEVELOPMENT OF OOGENIC FOLLICLES. It was initially assumed that *C. fluminea* was protandrous. Basis for this assumption rested on the finding that hermaphroditic bivalved mollusks tend to be protandrous (Fretter and Graham, 1964) and secondly that the indigenous, thin-shelled relatives of *C. fluminea*, the fingernail clams (*Sphaerium*) and the pill clams (*Pisidium*) were protandrous (Heard, 1977). Nevertheless, the first histological indication of gonadal development in *C. fluminea* occurs when oogenic follicles differentiate next to the basement membranes of the mucosa of the gut wall or of the digestive glands, (Kraemer, 1978). As slender tubes in close association with digestive tissues, the initial oogenic follicles enlarge, branch and ramify through the stroma of the visceral mass. The stroma itself undergoes substantial change from a loose collagenous tissue to a compact cellular tissue. Epithelium of the digestive glands also changes from low cuboidal to tall columnar epithelium (Kraemer, 1978).

As the oogenic follicles enlarge and increase in number, their contents undergo conspicuous histological change as well. At first the young oogenic follicles contain small oocytes of various sizes attached to the inner surface of the follicular membranes. The oocytes then enlarge and come to occlude the lumen of the oogenic follicles. Next the enlarged oocytes appear stalked and elongate. Finally the oogenic follicles appear quite empty of oocytes but may contain occasional embryos (discussed further below), as the mature oocytes are evidently discharged, (Kraemer, 1978).

The foregoing developmental sequence was worked

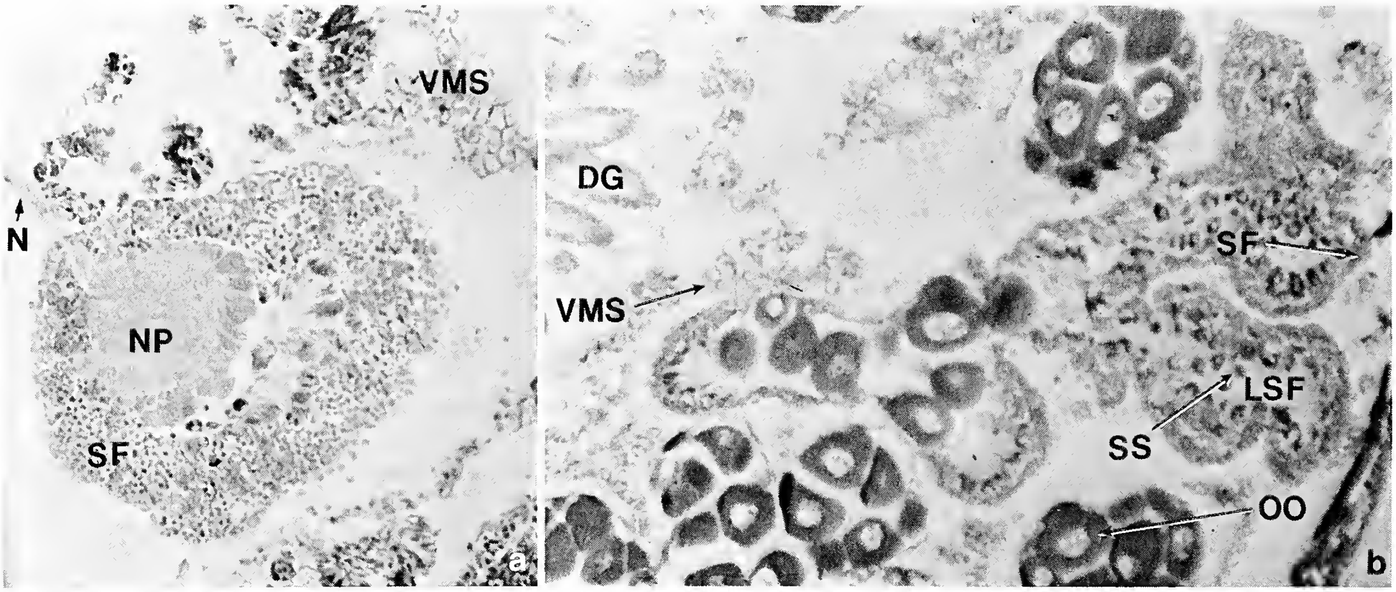

Fig. 3. a. Photomicrograph of section of visceral mass of *C. fluminea* showing "follicular ganglion" such as appear late in oogenic development at regions of confluence with spermatogenic follicles. N, nerve which attaches to follicular ganglion to either the pedal ganglion or one of the cerebral ganglia; NP, apparent neuropile; SF, spermatogenic cells in spermatogenic follicle; VMS, visceral mass stroma. (After Kraemer, 1978). Horizontal field width = 414 μm. **b.** Similar section of visceral mass, showing confluence of well developed oogenic and spermatogenic follicles. DG, digestive gland; LSF, lumen of seminiferous follice; OO, oocyte; SF, seminiferous follicle; SS, sperm sphere (comprised of mature sperm; VMS, visceral mass stroma. Horizontal width = 1968 μm.

Fig. 4. Scanning electron micrograph of mature sperm of *C. fluminea* showing most of its biflagellate tail. BT, biflagellate tail; SH, sperm head. Horizontal field width = 32 μm.

out from study of thousands of serial sections of young clams (Kraemer, 1978). In extensive study of hundreds of fresh tissue dissections since 1981, however, it has been possible for us to verify all of these stages in oogenesis as a seasonal sequence of oogenesis as well, with the exception of the initial follicle appearance. Evidently, once *C. fluminea* has achieved sexual maturity, although there is much seasonal growth and resorption of oogenic follicles, some oogenic follicles are present at all seasons of the year.

DEVELOPMENT OF THE SPERMATOGENIC FOLLICLES, FOLLICULAR GANGLIA, SPERMATOGENESIS, SPERMIOGENESIS AND SPERM MOTILITY. Only when oogenic follicles are well differentiated and when oogenesis within these follicles is advanced do spermatogenic follicles appear. The foregoing sequence is true not only developmentally but seasonally in the life history of *C. fluminea*. Spermatogenic follicles appear peripheral to the oogenic follicles. At the confluence of oogenic and spermatogenic follicles, in at least four paired locations in the visceral mass, clusters of what appear to be neuronal cell bodies appear during the reproductive maturation of the young clams. The cell bodies surround a feltwork of evident nerve fibers. Each of these structures, designated "follicular ganglia" (Kraemer, 1978, 1979b; 1984), is clearly (Fig. 3a) innervated by a nerve from either the cislateral cerebral ganglion or the pedal ganglion. The follicular space surrounding each "follicular ganglion" is typically filled with spheres of mature sperm, some oocytes, and occasionally what appear to be embryos (Fig 3b,5a). The foregoing observations have been made repeatedly in studies of serial sections of *C. fluminea*. It is the intrafollicular location of both the "follicular ganglia" and their proximity to the intrafollicular embryos which allow the conclusion that the "ganglia" may orchestrate sperm maturation and intrafollicular, self-fertilization as well.

Certain details of spermatogenesis, including spermiogenesis, have been worked out (Kraemer, 1983b; Kraemer and Swanson, in prep.). Mature sperm are all biflagellate, large cells. Their tapering heads cluster in spheres in the follicular lumen or in flattened spheres against the follicular wall. What initially appears to be polyspermy in

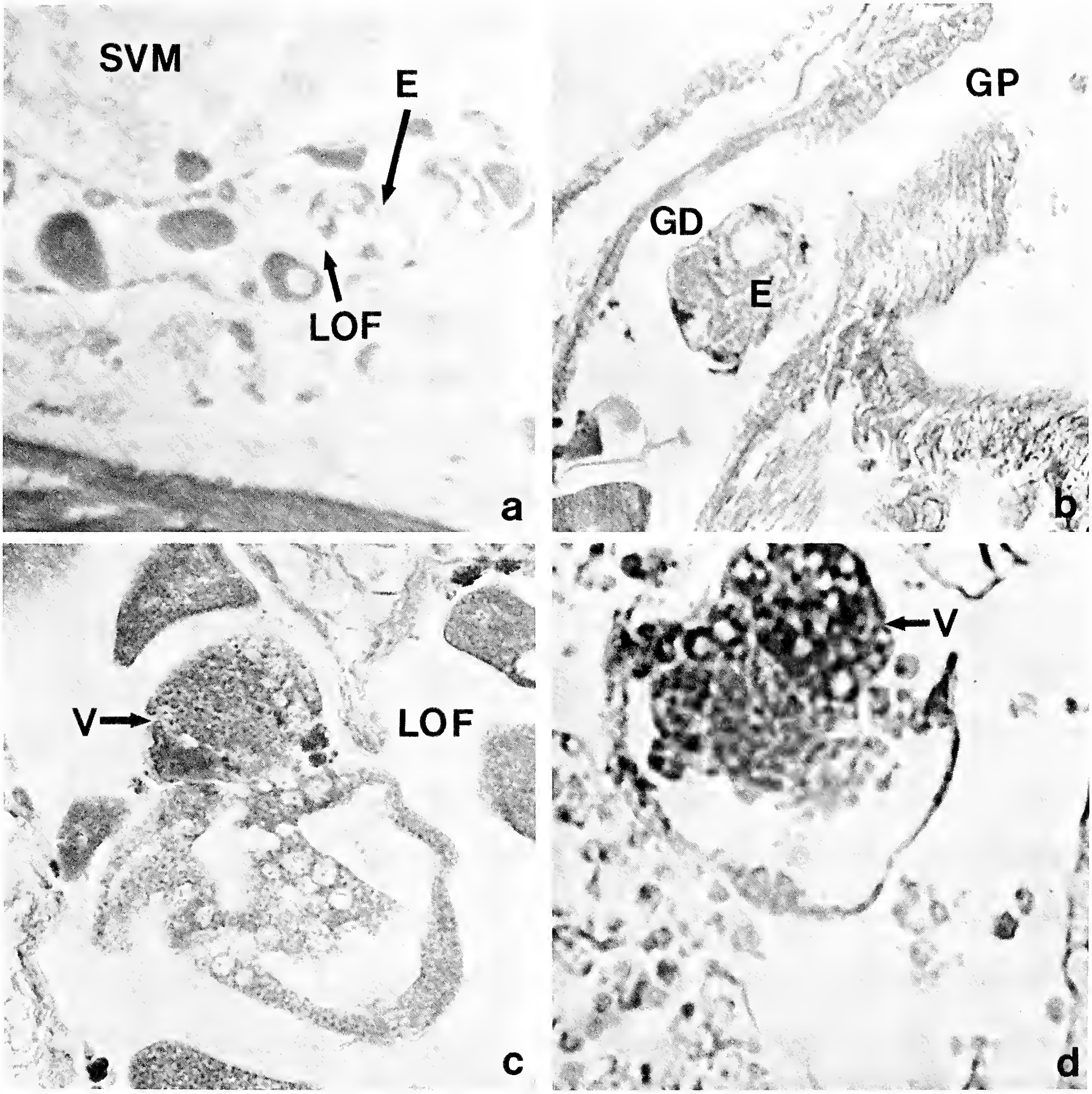

Fig. 5. a. Photomicrograph of mature gametogenic follicle of *C. fluminea*, showing presence of evidently self-fertilized embryos. Horizontal field width = 750 μm. **b.** Section of gonoduct, showing evidently self-fertilized embryo in the duct. Horizontal field width = 490 μm. **c.** Section of gametogenic follicle containing section of evidently self-fertilized embryo in veliger stage. Horizontal field width = 183 μm. **d.** Section of marsupial gill also showing section of veliger, evidently the result of cross-fertilization. Horizontal field width = 258 μm. E, embryo; GD, gonoduct; GP, gonopore; LOF, lumen of gametogenic follicle; LOG, lumen of marsupial gill; SVM, stroma of visceral mass; V, velum.

our studies of *C. fluminea*, now is found to be different stages of spermiogenesis. Both light microscopy of living sperm and SEM studies have allowed us to conclude a spermiogenic sequence in *C. fluminea* from "round-headed" to "wide-headed" to "slender-headed" (mature) sperm, all of which are biflagellate (Kraemer, 1983c; Kraemer and Swanson, in prep.). These are the first biflagellate sperm known to be reported for any bivalved mollusk, (Fig. 4).

Motile sperm are not commonly observed. In fresh tissue dissections, the "wide-headed" sperm often exhibit a characteristic, "twitching" movement in which one of the flagella trails at an acute angle from the sperm cell, and the other flagellum produces locomotor waves of varying amplitude which begin at the flagellum base and move to its distal tip, thereby producing the twitching movement of the large sperm head. Rarely are rapidly swimming, mature sperm seen in fresh preparations of living spermatogenic follicles. Mature sperm cells may readily separate from their spherical clumps, aided by water currents and by the lashing independent movements of one of the sperm cell's two flagella.

While our cumulative data indicate that oogenesis continues throughout the year, though it slows in January and February, our data also indicate (Kraemer and Galloway, 1986) that spermatogenesis is seasonal and responsive to water temperature change. After 7-10 days of water temperature between 17-19ºC in April, spermatogenic follicles become numerous in the visceral mass, and they are well developed, containing many spheres of mature sperm. Spermatogenesis will continue through the spring and summer, though in a fairly rhythmic pattern of approximately three week intervals, until the water temperature reaches 32-34ºC. In late fall (usually early November) spermatogenic follicles are much reduced in size, number and spermatogenic activity, once the water temperature has fallen and remains below 17ºC.

CROSS FERTILIZATION. On several occasions peculiar mucous strands have been observed in our laboratory (in shallow water, mid-summer), trailing from the siphons of one clam in a population to the siphons of another. When examined under the microscope, the mucous strands have been found to contain many, "twitching" sperm. It is hypothesized that the connecting mucous strands may effect cross-fertilization in these hermaphroditic animals. Some support for the foregoing contention lies in the fact that a senior malacologist from western China reports (Brian Morton, personal comm.) that commercial cultivators of *Corbicula* have known for years that within several weeks after such mucous strands appear in their clam cultures, young clams will appear in those cultures!

SELF FERTILIZATION. As noted above, serial sections of *C. fluminea* earlier revealed that some of the gametogenic follicles contained young embryos (Kraemer, 1978). While embryos have been found within oogenic follicles, they are characteristically seen within follicles near the "follicular ganglia" described above (Fig. 5a,c). Embryos have also been seen in the gonoduct and in the region of the gonopore (Fig. 5b). Some of the intrafollicular embryos appearing in serial sections of the visceral mass prove to be veligers (Fig. 5b) indistinguishable from veligers which appear in serial sections of marsupial gills (Fig. 5d). It seems quite parsimonious to reason that embryos have been found within the gametogenic follicles in the visceral mass because they have been produced there as a consequence of self fertilization.

Recently, the opportunity to make hundreds of fresh tissue dissections of the visceral mass of *C. fluminea* has led to the discovery in at least four instances of large numbers of young embryos within the gametogenic follicles of the visceral mass (Kraemer and Galloway, 1986). The dissections were made with care to assure that no contamination of the visceral mass with marsupial gill tissue had occurred. It was thereby possible to ascertain that several clams thus dissected did indeed house hundreds of blastula-like embryos within the follicles of the visceral mass (Fig. 6a). These were often surrounded by sperm (Fig 6a,S). All of the aforementioned clams were identified during the fall reproductive pulse, after spermatogenesis had apparently ceased.

During the 1983 Second International *Corbicula* Symposium Kennedy (Kennedy, *et al.*, in press) reported on a very painstaking effort to rear *C. fluminea* isolates, in order to determine the likelihood of self fertilization. Results of this careful work were mixed. Self fertilization does seem highly likely to occur in *C. fluminea* however, for the following reasons: (1) young embryos have been repeatedly found in the visceral mass in serial sections of the clams (Kraemer, 1978, 1984); (2) the embryos have invariably been located within the gametogenic follicles or within the gonoduct; (3) intrafollicular embryos have often been seen in the region of the "follicular ganglia" where sperm and eggs are in close proximity; (4) since spermatogenic and oogenic follicles are contiguous in *C. fluminea*, the mature gametes have ready access to each other, a situation which obtains in other molluscan bivalves known to self fertilize (Fretter and Graham, 1964); (5) young embryos have been found within the visceral mass on several occasions in our fresh tissue dissections, when precautions have been taken to avoid contamination with gill tissue; (6) the instances of self fertilization seem to occur primarily during the fall reproductive pulse when falling water temperature seems to effect a "closing down" of spermatogenesis in most members of a clam population; (7) it seems that the fall pulse is more likely to be associated with "clam clogs" than is the spring pulse, according to some members of the nuclear power industry (Bob West, personal comm.). Such an observation may be due to the unusual spate of young clams generated in the fall pulse, both as a consequence of self fertilization and of cross fertilization; and (8) though rearing of isolate clams by other workers has not produced definitive results, it has developed some indication that self fertilization probably occurs in *C. fluminea*. In summary, we are convinced that self fertilization is a regular occurrence in *C. fluminea* although the process may be limited to a period late in the fall reproductive pulse.

REVIEW OF EMBRYOGENESIS. Unlike its indigenous relatives (the pill clams, *Pisidium*, and the fingernail clams, *Sphaerium*, etc.) that show repression both of the

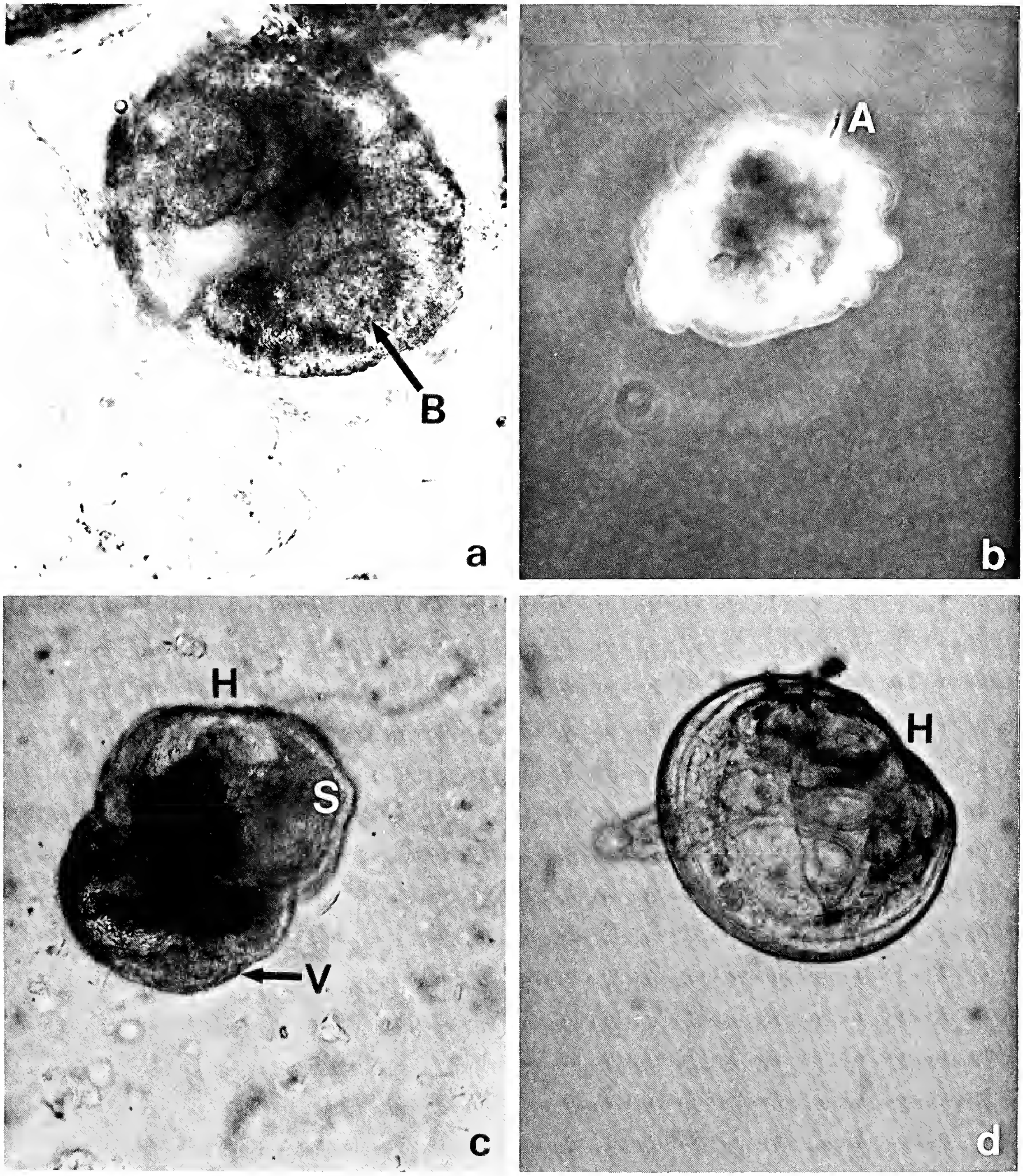

Fig. 6. a. Photomicrograph of a living blastula, taken from a gametogenic follicle in the visceral mass of an adult specimen of *C. fluminea*, and thus evidently self fertilized. Note the many sperm surrounding the blastula. Horizontal field width = 268 μm. **b.** Living trochopore, taken from the marsupial gill. Horizontal field width = 435 μm. **c.** Living veliger, taken from the marsupial gill. Horizontal field width = 310 μm. **d.** Living, straight-hinged juvenile, taken from the marsupial gill. Horizontal field width = 360 μm. A, apical ciliary tuft; B, blastocoel; H, straight hinge; S. larval shell valve; V, velum.

numbers of embryos developed and of the developmental stages which appear, *C. fluminea* characteristically produces thousands of juvenile clams during each reproductive pulse. In our laboratory we have determined that fertilization (cross fertilization and self fertilization) is followed by cleavage which produces a distinct blastula. After the blastula stage (Fig. 6a) a gastrula with pyramidal shape and a conspicuous blastopore near the vegetal pole, develops. Still within the parent's tissues, the gastrula develops into a barrel-shaped trochophore, replete with apical ciliary tuft, (Fig. 6b). In fresh tissue dissections, the trochopore larvae found in the gills exhibit varied behavior, swimming in circular or longitudinal paths, but always with apical cilia "forward".

Within the marsupial gills, metamorphosis of the trochophore into a veliger larva takes place, as a cilia-covered, flange-like membrane extends laterally from the surface of the larva, posterior to the apical ciliary tuft. Next, rudimentary valves of the clam appear, gradually enlarging to enclose more and more of the veliger. The velum and apical ciliary tuft remain conspicuously apparent, however (Fig. 6c). Still within the marsupial gill, the veliger develops into a pediveliger. With the apical ciliary tuft still "anterior", a mass of tissue just posterior to the velum begins to grow and differentiate, finally producing the small, increasingly active foot of the pediveliger.

Next, both the apical ciliary tuft and the velum disappear, and the juvenile stage is established as the foot grows, lengthens, changes its contour (Fig. 6d). At this stage the conjoined statocysts described earlier (Kraemer, 1984) are also well differentiated and the gills enlarge their ciliary surface. The gut now exhibits a long, algae-filled loop and a twirling crystalline style, as the young clam is busily feeding. Our data indicate that it is chiefly in the juvenile stage that *C. fluminea* is spawned, typically when the shell valves have reached a length of about 200 μm. The foregoing information is treated in detail elsewhere (Kraemer and Galloway, 1986).

SUMMARY AND DISCUSSION

We have reviewed findings from our continuing study of the biological basis of reproduction in *C. fluminea*. We have reported on oogenesis (1) that well defined gonopores constitute the first histological sign of development of reproductive structures in the young clam; (2) that the gonopores become innervated only when gonadal development begins; (3) that oogenesis occurs first and in association with basement membranes of gut wall or digestive glands; (4) that oogenesis is accompanied by changes in the visceral stroma and in the digestive gland epithelium; (5) that oogenesis, once initiated in the young clam, probably continues throughout the life of the clam, though more sluggishly in January and February; (6) that development of the oogenic follicles follows a predictable developmental and seasonal sequence.

Concerning spermatogenesis we have reported that: (1) spermatogensis occurs only after oogenesis is well advanced; (2) spermatogenesis occurs at intervals during the year, and is evidently quite susceptible to water temperature change; (3) spermatogenesis occurs in follicles which develop peripheral to the oogenic follicles; (4) at the confluence of oogenic and spermatogenic follicles, "follicular ganglia" appear which may affect maturation of sperm and/or self fertilization; (5) spermiogenesis involves development of a sequence of "round-headed," "wide-headed" and "slender headed" sperm, rather than polyspermy; and (6) all sperm in *C. fluminea* are biflagellate sperm, the only molluscan biflagellate sperm known to us.

Concerning fertilization we have reported that: (1) cross fertilization may be the norm in *C. fluminea*, as repeated observations of movement of spheres of mature sperm and a number of observations of sperm-laded mucous strands connecting siphons of neighboring clams, suggest apparent mechanisms by means of which cross fertilization takes place; (2) self fertilization, we are convinced, also takes place in *C. fluminea*, though perhaps on a less regular basis, perhaps primarily in the fall and in association with seasonal temperature drop; (3) self fertilization is evident from our serial section study which has repeatedly located embryos within the gametogenic follicles of the visceral mass, and from finding on at least four carefully controlled occasions, during fresh tissue dissections of the visceral mass, numerous young embryos within the visceral mass (Fig. 6a).

We have noted contrasting reproductive features of *C. fluminea* and its indigenous freshwater relatives, the pill clams and fingernail clams, and have reported that: (1) unlike the latter, *C. fluminea* does not exhibit extensive repression of embryo development and repression of developmental stages to produce relatively few, large, mature young; (2) on the contrary, *C. fluminea* not only produces from hundreds to thousands of tiny, 200 μm long, juvenile clams during each reproductive pulse, but also each of the juvenile clams has progressed rapidly through clearly evident blastula, gastrula, trochophore, veliger and pediveliger stages, before reaching juvenile status. It has been reported elsewhere (Kraemer, 1979a) that byssus development in *C. fluminea* is a post-spawning feature to aid the young clam as a holdfast for the substratum. The pill clams and fingernail clams, in contrast, develop a "placental" byssus that serves as a holdfast for the embryo within the marsupial gill (Mackie, 1979).

A continuing puzzle from our findings lies in the fact that there are some reproductive differences between the indigenous pill clams and fingernail clams and *C. fluminea* which are very striking: (1) protandry for the former, protooogamy for *C. fluminea*; and (2) uniflagellate sperm for the former, biflagellate sperm for *C. fluminea*. Other differences between the indigenous and the introduced clams seem to be those of timing of embryonic events— timing which allows a very different life style for the two kinds of clams.

In the indigenous pill clams and fingernail clams, development bypasses the trochophore, veliger and the pediveliger stages, all of which are evident in *C. fluminea*. In the indigenous pill clams and fingernail clams, byssus appearance is early, in *C. fluminea* it is late, as noted above. In the indigenous clams few young are produced with each brood, some of which attain nearly parental size and even undergo sexual maturation while still in the parental gill. Way, *et al.* (1980) examined comparative life history tactics of a sphaeriid clam, *Musculium partumeium* (Say) from a permanent and from a temporary pond and found significant intraspecific life history variations between the two clam populations. Interspecific variation in life history tactics has also been evaluated, by Stearns (1976, 1977).

It has been suggested elsewhere (Kraemer and Galloway, 1986) that *C. fluminea* may be able to vary its life history tactics from those of the indigenous clams by employing alternative timing of developmental events. Such a change in life history timing has been characterized at length by Gould (1977) as heterochrony. By speeding differentiation of many, many embryos, and by retaining a series of developmental stages which are repressed in the indigenous clams, *C. fluminea* can greatly increase its reproductive potential. By retarding its byssal development until after spawning in the juvenile stage, the byssus of *C. fluminea* can perform a substantially different function than is manifested by the "placental" byssus of the indigenous clams. Indeed it may well be that the *C. fluminea* presence in U. S. river systems is largely due to the evident heterochrony which, our studies have revealed, exists between the indigenous, thin shelled fingernail clams and pill clams, and the introduced Asian clam *Corbicula fluminea*.

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UNSOLVED PROBLEMS AND PROMISING APPROACHES IN THE STUDY OF *CORBICULA*

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ABSTRACT

Research on the introduction of *Corbicula* to the United States and subsequent biofouling problems has been fragmented by the need for immediate answers in special situations. The problems should be examined in the more general context of other introduced species problems and species outbreaks.

It is clear that basic research on *Corbicula* is badly hampered by confusion in systematics of the genus. Shell data alone are inadequate for species determination until allozyme and anatomical data establish the limits to taxa. Once limits are known, we can determine the number of species in the U.S., their distributions, and their affinities to Asian taxa. Topotype populations in Asia must be compared to U.S. *Corbicula* sp(p). Then, past conflicting research on life history, reproduction, historical distribution patterns, and physiology can be properly interpreted and extended. Finally, physiological and life history data can be applied to formulate general and local control strategies.

Examples of the use of allozyme data to solve problems in systematics and zoogeography, leading to clarification of physiological and life-history bases of species outbreaks, are presented. These include the cases of the polychaete *Capitella capitata,* the bivalve *Teredo bartschi,* and the gastropod *Crepidula fornicata,* in addition to *Corbicula*. Data available as of 1984 indicate that *Corbicula* consists of two species in North America.

Local control strategies depend upon knowledge of natural environments, reservoir populations, and the artificial environment of industrial plants. The importance of local biologists' knowledge of population dynamics in proposing cost-efficient solutions is obvious. Insufficient information on larval physiology and behavior still hampers biologists in formulating the best possible solutions.

Data that plant operators should accummulate and make available to biologists include exact location of living clams vs. shells, effectiveness studies of mechanical devices to eliminate clams, and data to be acquired whenever clams are removed from a plant, such as number and sizes. Finally, biologists can only present useful solutions if they are aware of economic and engineering aspects of potential control strategies.

Many kinds of professional scientists and engineers have had to deal with *Corbicula* as a biofouling agent. This group includes managers and government regulators, as well as general in-house and consulting biologists and chemists, and academic specialists in ecology or malacology. My remarks are intended to communicate with these people on several levels about the kinds of data needed to understand *Corbicula* in the U.S. I hope to illustrate to those eager for immediate answers the need for some research into fundamental questions such as systematics and ecology of natural populations.

I first present a hierarchy of interrelated questions that must be answered, optimally by coordinated research efforts of many types of scientists, in order to find optimal control strategies. I show how answers to some of these general questions have worked to bring understanding of other cases of introduced species and/or population outbreaks. Then I discuss site-specific data needed to adapt general strategies to local control problems.

METHODS

Most of this paper involves general discussion of the

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Table 1. Ecological and Reproductive Characteristics of Some *Corbicula*.

SPECIES	HABITAT	WHERE STUDIED	LIFE HISTORY	SEXUALITY
C. fluminea fide Morton, 1982	Streams	S. China	Breeds twice a year. Broods young to 200 μm. Lives 3 years.	Dioecious + hermaphrodites?
C. cf *fluminea*	Streams, impoundments	N. America	Same as above. Some reported to release veligers.	Simultaneous hermaphrodite; may self-fertilize
C. cf *fluminalis* fide Morton, 1982	Upper estuary	Pearl River, Canton area	Spawns annually; cool waters. May live 10 years.	Most are dioecious.
C. leana fide Fuziwara, 1975, 1979	Streams	Japan	Ovoviviparous; spawns twice a year; warm water.	Hermaphrodite

literature. The literature on *Corbicula* is not exhaustively reviewed; this is not a review paper *per se*. Literature on other introduced species problems and on related subjects are discussed in the context of *Corbicula*.

UNSOLVED PROBLEMS

SYSTEMATICS AND BIOLOGY

The literature of North American *Corbicula* is filled with taxonomic confusion. Although the name *Corbicula fluminea* (Müller) was used in the 1960's (e.g., Hubricht, 1963), *C. manilensis* Philippi was used frequently during the 1960's and 1970's (e.g., McMahon, 1977). *Corbicula leana* Prime, *C. fluminalis* Müller, and *C. sinensis* (e.g., Gunning and Suttkus, 1966; Gifford, 1974) have also been used to refer to the introduced *Corbicula* in North America. While some workers suggest that there is more than one species in North America (e.g., Hillis and Patton, 1982), others, recognizing taxonomic confusion, have attempted to standardize the usage of *C. fluminea* as the single species in North America (Britton, 1979; Britton and Morton, 1979).

These are not merely academic issues. The species question is critical to control issues especially as we consider more sophisticated and less environmentally-damaging chemical treatments, and treatments based on population dynamics and reproductive biology. Each species is unique in its range, habitat, physiology, life history, and mode of reproduction. The potential for spread to new waters may be species-specific. While the systematics even in its native Asia is by no means resolved, we do know that there are several species with differences in habitat. For example, *Corbicula fluminea* is said to prefer lotic environments (streams), and *C.* cf *fluminalis* of Morton (1982) prefers lentic upper estuaries. The species also differ in tolerance to saltwater. Table 1 summarizes some of the major ecological and reproductive differences between Asian species sometimes thought to have been species introduced to North America, as described in the literature.

There are relatively few shell characters to separate the species, and limits to intraspecific shell variation are poorly understood. Geographic variation in physiology, sex determination, and reproduction are undefined. There are references in the literature to a single species (*C. fluminea*) possessing different sexual strategies (e.g., protandry, protogyny, separate sexes) in different parts of its range (Morton, 1982). Morton uses evidence from other taxa such as Sphaeriacea (Mackie, 1973) and Unionacea (Bloomer, 1939) to support his claim that *C. fluminea* is protandric and a simultaneous hermaphrodite in different parts of its range. These other taxa, however, do not have both protandry and simultaneous hermaphroditism within a single species. In the Bloomer paper, one species was an asynchronous hermaphrodite; two others in a different genus had separate sexes. Evidence for *Corbicula* is circular, since we do not know from genetic or anatomical evidence if the different allopatric forms with supposedly different sexual strategies are the same species. In most cases in the Mollusca where a species was once thought to have more than one form of sexuality or reproduction, we now know sibling species were involved (e.g., Gallardo, 1977). In fact, in the mollusks, there are no documented cases showing protandry and protogyny in the same species. The data presented by Morton (1982) really suggest alternating sexuality, an asynchronous development of eggs and sperm, in a hermaphroditic species in Asia (see Hoagland, 1984b, for definitions of terms describing sexuality in mollusks). Even if it is shown that sex determination or reproduction is plastic in one species, we cannot extend such attributes to other species.

Those interested in control of *Corbicula* can proceed most efficiently by knowing, first of all, how many species there are and their distribution(s), both in North America and in Asia, and possibly also in South America. Historical patterns of introduction and spread can be clarified, and attributes of introduced populations can be compared with native populations. Then one can place the existing literature on physiology and reproduction in its proper context. Otherwise, past work, especially that done in Asia, is of little use. Since physiological factors such as limits to temperature, salinity, heavy metals, and oxygen are used in control strategies, the variance between and within species, and any adaptive changes between American populations and their Asian relatives, are significant.

The best data available for American *Corbicula* systematics are detailed anatomy (e.g., Kraemer, 1977, 1978, 1983; Kraemer and Lott, 1977), embryology (Kraemer *et al.*, 1985), and lately, electrophoretic analysis of allozymes. Although Smith *et al.* (1979) demonstrated genetic uniformity in 5 populations from California to S. Carolina suggesting one genetically impoverished species in North America, Hillis and Patton (1982) had different results. They demonstrated quite convincingly that there are two non-interbreeding stocks of *Corbicula* living at times sympatrically in Texas, fixed for alternate alleles at 6 of 26 genetic loci, yet both expressing genetic uniformity (lack of heterozygosity). Shell color, sculpture, shape parameters, and ecological differences sorted out perfectly with the two genetic types. Hence, they concluded there are two species of *Corbicula* in Texas, a "white" and a "purple" one. Their data are strengthened by those of McLeod (1986), who reports additional electrophoretic differences. Schofield and Britton (paper presented at the 2nd International *Corbicula* symposium) show some very suggestive physiological differences and microhabitat differences, correlated with the two shell types. The data suggest that a relatively rare purple species may exist that can extend into low pH, high calcium waters closed to the white species. The white taxon tends to live in sediments of smaller grain size than the purple taxon (Hillis and Patton, 1982).

The finding of more than one species through electrophoretic techniques has allowed the establishment of limits to ecological and phenotypic variation in other taxonomic groups. Chambers (1978) detected two sympatric species of the freshwater snail *Goniobasis* electrophoretically, one preferring vegetation and one preferring rocks. Grassle and Grassle (1976) could sort major reproductive differences and otherwise-overlooked morphological differences in 6 species of the pollution-indicating polychaete species complex *Capitella capitata,* once the species were determined electrophoretically. This work has forced re-evaluation of applied ecological studies, because each member of the species complex has its own life history and physiological tolerances. Yet many biologists still do not attempt to identify *Capitella* to the species level.

Other examples of electrophoretic separation of species followed by morphological delimiting of taxa are in the freshwater unionid clam group. Davis (1983) was able to sort the genus *Uniomerus* into three species electrophoretically, and once this was done, seeming confusion in shell phenotype variation was resolved and the species can now be identified morphologically. *Elliptio lanceolata* likewise has been found to be a complex of at least 6 species that sort electrophoretically and in terms of shell phenotype (Davis, 1984). Coney (in prep.) has found some important anatomical differences between *E. lanceolata*-group species as well. In slight variation of this sequence of scientific progress, I recognized sibling species of the marine gastropod *Crepidula* by noting major differences in larval development, and confirmed that these differences represented unique taxa by electrophoretic analysis of allozymes (Hoagland, 1984a).

A discussion of the uses of allozymes in systematics can be found in Ayala (1976, 1983). Use of electrophoretic techniques to identify allozyme variation provides discrete phenotypic characters that are often easily correlated with their genetic counterparts. On the other hand, complex phenotypic characters such as growth and reproductive patterns involve the interaction of many separate gene loci. Electrophoretic studies provide as many specific characters as loci can be resolved. Usually 20-30 consistently scorable loci can be achieved for mollusks with the common starch-gel technology, and more with more elaborate procedures. Starch-gel electrophoresis is conservative for systematic work at the genus level in that some closely migrating enzyme forms (allelomorphs) cannot be resolved as different. Therefore, genetic differences between closely-related taxa are usually underestimated.

If the species under investigation can be bred, the genetic basis of an allozyme pattern can be determined directly (e.g., Lassen, 1979). If not, it can usually be inferred from studies of other closely-related taxa and from the molecular structure of the particular enzyme. One value of electrophoresis is that the data so derived are independent of other data sets, and provide strong corroboration of taxonomic decisions based on other types of data, when the data sets converge (Davis, 1983).

It is easy to control for non-genetic aspects to enzyme patterns by avoiding use of food-containing organs, and by doing control studies of a known species of a particular genus. Controls can be done for age, sex, season, and food. Several populations of the known species from different environments can be electrophoresed. In reality, such control experiments have been done for many organisms, and environmental induction of allozymes has been found to be a rare exception rather than the rule (e.g., Livingstone, 1981). Problems have occurred only in a few cases, particularly with food-induced allozymes of non-specific digestive enzymes such as esterases (Oxford, 1975). Yet the genetic basis for esterase patterns has also been demonstrated (Saul *et.al.,* 1978). Environmentally-induced enzyme patterns would not be expected to correlate with characters such as shell sculpture, shell shape, or resistance to toxicants, nor would they be stable over time and space, as was found for *Corbicula* by Hillis and Patton (1982) and McLeod (1986). Therefore, the pattern observed by Hillis and Patton in which electrophoretic patterns at several loci consistently matched a set of shell phenotypic characters, with no intermediates, in a 3-meter^2 area where water quality and food availability are relatively uniform, makes implausible the argument that all these differences could be due to where the clams were living.

The electrophoretic characters are far more resistant to environmental change (i.e., have higher heritability) than are morphological shell characters such as color and distance between sulcations. While both of these shell characters undoubtedly have genetic components, they also have large environmental components. For example, the purple pigment highlights in the white taxon can be reduced or eliminated by stressing the animal (Prezant and Chalermwat, 1984). Experiments that are designed to test the hypothesis that the purple and white taxa are ecophenotypes must take the heritability of the traits used in testing the theory into account. It is more likely that an individual genetically competent to produce a purple shell can be stressed so as to lose the purple pigment, than it is for a white individual to suddenly begin to produce purple pigment when placed in a new environment. Switches in phenotypic expression of a shell trait do not address the question of whether or not the animals belong to the same gene pool.

The biological species concept states that two populations are separate species if they do not share a common gene pool. The only direct tests are to try to find evidence of interbreeding; e.g., to look for allozyme patterns demonstrating reproductive isolation of sympatric populations. The finding of fixed alternate alleles at several loci including Krebs cycle enzymes in mobile aquatic mollusks such as *Corbicula* living in a single creek or water system is indeed a conclusive demonstration of genetic (reproductive) isolation, assuming the electrophoretic data are sound. This type of finding has confirmed the species status of 5 often-sympatric sibling species of the gastropod *Littorina* in the British Isles (Wilkins and O'Regan, 1980). Experimental cross-breeding of individuals could also be attempted, but is ambiguous because animals sometimes have natural barriers to reproduction that can be circumvented in the lab.

Immediate work ahead is to delineate complete ranges of the two electrophoretically-delineated taxa. So far, the purple taxon is positively identified from Texas, Arizona, and California. Areas that need to be examined include Oklahoma, New Mexico, and Mexico. The electrophoretic data must be correlated with complete comparative anatomical, shell morphological, and reproductive characters such as presence of brooded larvae. Then, past work on physiology, ecology, and life history in the U.S. and Asia must be evaluated and assigned to the correct taxon, based on studies of topotypes in Asia. Characters such as shell pigment or globosity cannot be used alone to delineate species, but once species are defined on the basis of multiple data bases, these characters may be useful in species identification, especially in the field. Until species assignment is sure, conservative researchers will identify their data according to whether the purple or white taxon was studied, to avoid accidentally confounding the data for more than one species and to allow others to compare data on similar populations.

Positive indentification will require collection and comparative study of topotype material in Asia. This is because originally, most Asian taxa were described by shell characters alone, and the Asian names must be given biological reality in terms of assignment of the proper mode of sexuality, reproduction, and anatomical pattern. American researchers will certainly be cooperating in the future with their counterparts in Asia and in southern Europe and South America where *Corbicula* also exists, first to correlate species identifications and then to compare data on the biology and control of *Corbicula* species.

The allozyme studies themselves can be used to understand population structure and genetic variability of the introduced populations. Such information provides clues as to the reproductive mode of the populations. For example, polymorphism yet low individual heterozygosity as found by McLeod (1986) suggests that self-fertilization occurs at least some of the time in North American *Corbicula*. Recent anatomical and embryological work with the white taxon of *Corbicula* support the possibility of both cross- and self-fertilization. If self-fertilization is common in North American comparative anatomy of the purple taxon, relative to the white taxon, to find if it too might have the capability of self-fertilization. If self-fertilization is common in North America *Corbicula*, the development of genetic races with their own physiological characteristics is at least possible. This could make control more site-specific. The definitive experiment on self-fertilization, isolation of juveniles that eventually mature and produce offspring, has yet to be done.

Comparison of intra- and interspecific variation also provides information on adaptability of *Corbicula*. Studies of the shipworm *Teredo bartschi* introduced from Florida to New Jersey and Connecticut showed that the species was naturally highly monomorphic and that introduced populations were even more so, due to founder effects and bottle-necking. Parallel physiological studies revealed that, despite low enzyme variability, the native and introduced populations had broad physiological tolerances (Hoagland, 1983). I also found low polymorphism in the native and introduced populations of the marine gastropod *Crepidula fornicata* (Hoagland, 1984a). Other workers have found low genetic variability in a variety of invertebrate species that retain high powers of migration and are frequently introduced to new areas (Price and Jain, 1981; Selander and Hudson, 1976; Selander and Kaufman, 1975).

It is interesting that the work done so far on genetics of *Corbicula* also indicates low genetic variability at the population level (Smith *et al.*, 1979; McLeod and Sailstad, 1980; Mcleod, 1986). These findings violate the common wisdom that genetic variability of allozymes should be high to allow adaptation to a wide variety of habitats. In fact, restricted genetic variability with concommitant high phenotypic variability may be characteristic of organisms that are capable of being successful introduced species (Price and Jain, 1981). On the other hand, McLeod (1986) finds evidence of accumulation of new mutations in American *Corbicula*. Nevo, *et al.* (1977) have shown genetically-based thermal adaptation in marine fouling organisms living in thermal effluents. An important new line of research is in enzyme kinetics, especially thermal properties, of the forms of enzymes discovered in environmentally-distinct populations of *Corbicula*. Such work has been done in fishes (Powers *et al.*, 1979) and other organisms. The correlation of electrophoretic results with physiology and environmental parameters will increase our understanding of the potential for *Corbicula* to spread to both warmer and colder waters.

One confusing aspect of *Corbicula* life history is the report that the clam releases pediveliger larvae in many localities, but that veligers are released at other times and places (e.g. Aldridge and McMahon, 1978). Sickel (pers. comm.) reports that clams from the Little River released pediveligers in the lab, while those from the Tennessee River released veligers. Growth patterns of adults were also different. It is very unusual for a single species of mollusk to release different stages of larve. It could be that early release of veligers is an abnormality due to the stress of transport to the laboratory, yet reports suggest that the veligers are healthy. The question certainly requires more careful investigation, since stage and size of released larvae determine their ability to enter water systems. Planktonic larvae are highly unusual in riverine environments.

LOCAL POPULATIONS AND CONTROL

Assuming that the species of *Corbicula* and its general biological features are known as discussed in the above section, local factors of importance to control require on-site research. One must understand the local "natural" environment, in a river, lake, or impoundment, as well as the man-made environment. The river is the reservoir for future invasions. If *Corbicula* is also at high density in the natural river or if re-invasion is easy, any ameliorating action taken will be temporary. If the artificial environment has a much higher density than the river itself, one might ask why. What is it about plant design, especially water velocity, that provides an ideal habitat? A comparison of existing and new environmental data such as water chemistry, flow rates, sedimentation, and substratum for local man-made and natural areas with and without *Corbicula* is in order. Graney *et al.* (1980), for example, analyzed the influence of substratum and temperature on population dynamics of *Corbicula* near a plant, but such information correlating plant activities and the natural population dynamics is rare. The physical constraints on settlement and survival of pediveligers and post-metamorphosed juveniles are still not defined. Seasonal patterns of settlement, growth, and migration in the natural area are particularly important to correlate with control activities.

Corbicula in the United States does occur in many types of waters in terms of chemical composition, physical properties, and temperature regimes. In fact, one important piece of research would be to pick a geographical area and systematically collate existing information on water properties (and variations therein) where *Corbicula* exists and where it does not, but is expected, zoogeographically. Such work has begun, starting with the more general problem of water quality inside and outside the range of *Corbicula*, as reported elsewhere in this volume (Counts, 1986).

An example of this approach, where natural and outbreak populations of a nuisance organism were compared, is a study of hookworm in India. It was found that in West Bengal, two species of hookworm were endemic and a high proportion of people were infected, yet worm burden (density of hookworm in people) was low. Comparison with other areas with high worm burden suggested that social and agricultural habits played a role. Conversion of land to growing non-edible products such as mulberry had the potential to turn a mild disease into an outbreak situation because people would then have greater contact with the disease (Schad, 1971; Schad *et al.*, 1975). Analysis only of outbreak areas is insufficient to pick out essential differences in ecology that cause the outbreak. Similar reasoning suggests that we should study carefully the places where *Corbicula* was introduced, then died back. A disease organism as was suggested in a preliminary, inconclusive report by Sickel and Lyles (1981) or a change in water quality are possible findings with implications for local control. Few parasitologists or invertebrate pathologists have been involved in *Corbicula* research.

It would seem to be valuable also to compare local populations of *Corbicula* in North America with those in Asia that are natural and are not nuisance populations, to see how the natural populations are regulated. However, the Asian populations are usually reduced by heavy human predation. This solution does not seem to be possible in North America, as American Asians seem no longer attracted to this food source! I observed *Corbicula* in Lake Er Hai, Yunnan Province, People's Republic of China, to be very abundant from the lake shore to water of at least 10 meters, despite heavy fishing with nets and shoreline gathering. Mounds of shells were the result of years of human predation. *Corbicula* was only one of three mollusks consumed on regular basis; one other remained extremely abundant in the lake as well. The balance of invertebrates in the lake that would exist without interference by man could not be determined. Whether *Corbicula* is controlled in Asia by some disease, natural predator, or human predators in unknown. There is little hope that a simple introduction of another Asian invertebrate, a predator, to the United States would bring *Corbicula* under control. It would quite possibly create more problems, as has happened with many other introductions of predators, such as introduction of predatory snails in Hawaii, which have destroyed the native fauna.

Several kinds of data are needed for understanding *Corbicula* inside the man-made environment. First of all, exactly where are the clams living, and where are only dead shells accumulating? What are the water velocities in the affected areas, relative to lab-determined values for settlement and growth of *Corbicula*? What other fouling exists, e.g., slime and accumulation of silt? What food for *Corbicula* exists? One would expect that *Corbicula* has catholic taste, but local nutritional studies should be done to identify food organisms. If screens, traps, backflushing, or other physical means of control have been used, their effectiveness should be compared quantitatively to the situation before control was attempted. Records should be kept on the numbers of shells, number alive, size distribution, and time of year each time physical removals are done. These data should be given to biologists along with cost/benefit analysis on options the biologists feel are available for control.

A coordination of in-house biological work with plant management decisions can sometimes be facilitated by outside expertise. Such expertise can also effectively focus areas of research. It is necessary to combine general off-site laboratory studies such as flume studies or physiological and genetic analyses with on-site work on local population and environmental parameters. Whether on- or off-site, biologists need enough engineering and economic information to make reasonable suggestions for control of *Corbicula*. Optimally, biologists should work with experts in plant design to minimize clam habitats in new and redesigned plants. Scientists should broaden their literature searches to include works on other introduced and/or nuisance species. Finally it is essential that our work be published rather than buried in private or governmental reports, a fate too common in environmental biology.

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BIOLOGY OF *CORBICULA* IN CATFISH REARING PONDS

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ABSTRACT

Corbicula were stocked with channel catfish, *Ictalurus punctatus*, in two of four 0.06 ha ponds. In 1977 clams were placed in cages suspended in the water of two ponds at 828 and 1010 kg/ha. In 1979 clams were stocked on the substratum of two ponds at 1717 and 1222 kg/ha. In both years two similar ponds received no clams and served as control ponds. All ponds were mechanically circulated and stocked with 300 channel catfish fingerlings in 1977. None of the ponds were circulated in 1979 and each pond received 302 catfish fingerlings. *Corbicula* survived and reproduced in both 1977 and 1979, but survival and reproduction were insufficiet to maintain stock density. The clam had no significant ($P > 0.05$) beneficial or detrimental effect on catfish survival, growth or feed conversion, but was associated with improved water quality. Level of dissolved oxygen, rate of net production, and rate of net respiration were greater and turbidity was lower in ponds with *Corbicula*. Significant ($P < 0.05$) improvement of water quality occurred only in 1977. At densities stocked, *Corbicula* had a variable effect on total abundance, relative abundance, and diversity of plankton. I conclude that *Corbicula*, which is commonly viewed as a nuisance, may be an unrealized asset. The clam has potential as an aquaculture organism and biological filter.

The Asiatic clam, *Corbicula fluminea*, (Müller) is widely established throughout the United States (Clarke, 1981; Counts, 1981; Nichols and Domermuth, 1981; McMahon, 1982; and Scott-Wasilk *et al.*, 1983). Although the clam is tolerant of a wide variety of habitats it has been studied most intensively in large lakes and reservoirs (Dreier and Tranquilli, 1980; Sickel *et al.*, 1981) and flowing waters (Sinclair and Isom, 1963; Sickel, 1976, 1979). Few studies have examined the biology of *Corbicula* in small bodies of water (Carlton, 1973) and with the exception of Chen (1976) in Taiwan, growth studies by Buttner and Heidinger (1980) in southern Illinois, and unpublished theses by Habel (1970) and Busch (1974) none have examined the biology of *Corbicula* in aquaculture systems. I investigated the biology of *Corbicula* in channel catfish, *Ictalurus punctatus*, rearing ponds and examined effects of the clam on pond biota and water quality.

MATERIALS AND METHODS

Between 1 June and 20 September 1977 and between 1 July and 4 October 1979 *Corbicula* were stocked with channel catfish in two of four 0.06 ha ponds. In 1977 water in all ponds was mechanically circulated at approximately 86 *l*/sec; in 1979 none of the ponds were circulated. Number of clams stocked (Table 1) was determined by availability and filtration rate, which averaged 347 ml/h/clam (Buttner and Heidinger, 1981). Clam density was always sufficient to filter one volume of pond water (~530 m^3) each week (once every 168 h). In 1977 *Corbicula* were placed in cages suspended in the water of ponds 1 and 16 at 828 and 1010 kg/ha, respectively. In 1979 clams were stocked directly on the substratum of ponds 1 and 16 at 1717 and 1222 kg/ha, respectively. In 1977 additional clams were introduced; on 4 September 93.6 kg were obtained and stocked in cage D in pond 16 (Table 1). In both years ponds 2 and 17 received no clams and served as controls. On 17 April 1977 each of the four ponds were stocked with 300 channel catfish fingerlings that weighed approximately 49 g each and on 2 May 1979 each pond received 302 channal catfish that weighed approximately 60 g each. Catfish were fed Purina Trout Chow #6 at 2% of their body weight daily, six days per week. Feeding rates were adjusted weekly and all ponds received equal quantities of feed.

Corbicula survival, distribution, and reproductive success were monitored. *Corbicula* survival was determined by weighing all clams retrieved from cages between 28 September and 8 October 1977, except for cage D added to pond 16 on 4 September 1977. Five 2000 g samples of clams were collected from cage D, the proportion of live clams determined, and percentage survival computed. Between 7-9 October 1979 clam survival was determined by sampling the area stocked with clams. Clam distribution was not random so the sampling effort was weighted and areas of greatest clam density received more effort. Total area sampled in pond

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Table 1. *Corbicula* stock, harvest, and survival data for clams in 0.06 ha channel catfish rearing ponds in 1977 and 1979.

Year	Pond no.	Stock date	Weight stocked (kg.)	Turn[a] over (hrs.)	Harvest date	Weight harvested (kg.)	Survival (%)	Turn[a] over (hrs.)
1977	1	1-2 June	Cage		28 Sept.	Cage		
			A 21.9			A 7.0	32.0	
			B 23.3			B 9.5	40.8	
			C 4.5			C 2.3	51.1	
			Total 49.7	60		Total 18.8	Avg. 37.8	158
	16		Cage			Cage		
			A 24.4			A 6.4	26.2	
			B 16.3			B 5.4	33.1	
			C 19.6			C 9.1	45.7	
			Subtotal 60.6	49		Subtotal 20.1	Avg. 34.5	141
		4 Sept.	D 93.6			D 83.4	89.1	
						Total 104.3		28
1979[b]	1	27 June-	103.0	29	7-9 Oct.	82.9	80.5	36
	16	1 July	73.3	41		56.1	76.5	77

[a] Approximate time required by clams to filter water volume of each pond at stock and harvest densities.

[b] In 1979 all clams were stocked directly on the substratum. At harvest all *Corbicula* from 16.2% and 9.0% of the area with clams in ponds 1 and 16, respectively, were collected and used to compute harvest weight and percentage survival.

1 was 33.6 m² (16.2% of the area with clams) and in pond 16 was 10.5 m² (9.0% of the area with clams).

Distribution of *Corbicula* on the substratum was determined in 1979. Effect of water temperature, clam distribution as number/m² and clam depth in the substratum on clam survival were examined.

Reproductive success of *Corbicula* was determined by periodic sampling of the substratum and water for immature clams and by the presence of young-of-the-year clams at time of catfish harvest.

Effect of *Corbicula* on catfish survival, growth and feed conversion (weight of feed presented to catfish divided by weight gain of catfish) was determined at harvest.

Dissolved oxygen (D.O.), diurnal production and nocturnal respiration rates, water temperature, pH, turbidity, alkalinity and level of nitrogenous wastes were monitored throughout the study to describe the environmental situation and to determine if presence of *Corbicula* affected water quality. D.O., water temperature and pH were monitored daily just below the surface and at 1.0 m depth at dawn and dusk in 1977. In 1979 D.O. and water temperature at surface, 0.5 m and 1.0 m were measured 3 times per week at 0700-0900 and 1600-1800; pH was determined weekly from a single sample collected at 0.5 m. Reported values are the average of all depths sampled. Sampling frequency increased if D.O. fell below 3.0 mg/l. Net production and respiration rates were

Table 2. Channel catfish stock, survival, and growth data for ponds 1, 2, 16 and 17 in 1977 and 1979.

Year	Food fed per pond (kg)	Pond number	Clams present	No. catfish stocked	No. catfish harvested	Survival (%)	Aver. wt. stocked (g)	Aver. wt. harvested (g)	Feed conversion	Yield (kg /ha)
1977	111	1	Yes	300	288	96.0	49.0	387.8	1.14	1861
		2	No	300	266	88.7	49.0	394.1	1.21	1747
		16	Yes	300	296	98.7	49.0	366.2	1.18	1807
		17	No	300	288	96.0	49.0	395.0	1.11	1896
1979	113	1	Yes	302	293	97.0	60.0	342.2	1.37	1671
		2	No	302	296	98.0	60.0	345.8	1.34	1706
		16	Yes	302	295	97.7	60.0	345.4	1.34	1968
		17	No	302	296	98.0	60.0	388.2	1.16	1915

computed from level of D.O. observed at dawn and at dusk. Turbidity, alkalinity and nitrogenous wastes (total ammonia-nitrogen, TAN; nitrite-nitrogen, NO_2-N; and nitrate-nitrogen, NO_3-N) were measured weekly in both years by a single water sample collected at 0.5 m. A polarographic meter was used to measure D.O. and temperature; pH was determined with a pH meter, turbidity with a turbidimeter, TAN by colorimetry in 1977 and by an ion specific electrode in 1977 and 1979, NO_2-N and NO_3-N colorimetrically, and alkalinity potentiometrically.

Plankton were quantitatively sampled each week. Phytoplankton were collected with an integrated column sampler (Buttner, 1981), preserved in Lugols solution (20 ml KI, 10 g I, 20 ml glacial acetic acid, and 200 ml distilled water), identified to the generic level and counted as plants of each genus (Vollenweider, 1969). Zooplankton were collected by vertical tow from substratum to surface with a plankton net (a 35 μm mesh in 1977 and a 140 μm mesh in 1979). Zooplankton were preserved in 70% ethanol, identified to the species level, and counted. Plankton diversity was computed using the formula developed by Gleason (1922) and modified by Margalef (1958):

$$H = \frac{S - 1}{Ln(N)}$$

where H is taxa diversity, S is number of taxa, and Ln(N) is the natural log of the total number of plankton. Effect of *Corbicula* on plankton abundance, composition, and diversity was examined statistically.

All statistical analyses were conducted with the Statistical Analysis System computer package (SAS Institute, 1979). Effects of *Corbicula* on channel catfish were examined by ANOVA. Effects of *Corbicula* on plankton and water quality were examined by multiple regression analyses with the linear and quadratic effect of water temperature and week sampled as covariates.

Table 3. Summary of descriptive water quality parameters measured in 1977 and 1979.

Parameter	Minimum value	Maximum value
Alkalinity (mg/l $CaCO_3$)	58	130
Turbidity (JTU)	13	122
pH		
Dawn	7.06	8.58
Dusk	7.24	8.94
Temperature (C)		
Dawn	15.0	31.5
Dusk	17.6	34.0
Oxygen (mg/l)		
Dawn	1.09	9.59
Dusk	1.47	13.22

RESULTS

Corbicula survived and reproduced in the catfish rearing ponds, both when suspended in the water and when stocked on the substratum. Survival of clams suspended in circulated ponds was poor and averaged 36.0% (excluding

Table 4. Average dissolved oxygen (D.O.), net diurnal production and net nocturnal respiration rates, and turbidity for four 0.06 ha channel catfish rearing ponds with and without *Corbicula* in 1977 and 1979. Numbers in parentheses are standard deviations.

Year	*Corbicula*[a] present	No. days dawn D.O. below 3.0	D.O.		Net diurnal O_2 produced ($g/m^2/h$)	Net nocturnal O_2 consumed ($g/m^2/h$)	Turbidity (JTU)
			dawn (mg/l)	dusk (mg/l)			
1977 1 June- 20 Sept.)	Yes	7	5.29^x (1.31)	7.33^x (1.92)	0.148^x (0.099)	0.201^x (0.127)	60.4^x (27.0)
	No	13	4.81 (1.34)	6.30 (1.73)	0.110 (0.077)	0.144 (0.089)	79.4 (17.9)
Sample size [b]		448	448	444	444	444	64
1979 1 July- 4 Oct.)	Yes	16	4.31 (1.54)	6.80 (1.97)	0.301 (0.165)	0.166 (0.106)	59.5 (17.0)
	No	21	3.99 (1.53)	6.35 (2.40)	0.291 (0.177)	0.153 (0.101)	66.6 (28.8)
Sample size [b,c]		148	148	108	108	59	52

[a] *Corbicula* stocked in ponds 1 and 16 on 1-2 June 1977 and 27 June- 1 July 1979. Clams were absent from ponds 2 and 17.
[b] Unless stated otherwise sample size is the sum of an equal number of observations for ponds with and without *Corbicula*.
[c] In 1979 sample size for net nocturnal oxygen consumption was 30 and 29 for ponds with and without *Corbicula*, respectively.
[x] Indicates a significant ($P < 0.05$) difference between ponds with and without *Corbicula*.

cage D). Clam survival on the substratum averaged 78.8% (Table 1).

The presence of many immature clams, approximately 0.20 mm in shell length (SL), identified from preserved zooplankton samples collected in 1979 indicate *Corbicula* were fertile and spawned successfully in the catfish rearing ponds. Several clams less than 10 mm SL (minimum size stocked) were collected when ponds were drained. The presence of these clams confirms that some recruitment of *Corbicula* occurred in the catfish rearing ponds.

Table 5. Average level of nitrogenous wastes for 0.06 ha channel catfish rearing ponds with and without *Corbicula* in 1977 and 1979. Numbers in parentheses are standard deviations.

Year	*Corbicula*[a] present	Total ammonia NH_{3+4}-N (mg/l)	Nitrite NO_2-N (mg/l)	Nitrate NO_3-N (mg/l)
1977 (1 June-20 Sept.)	Yes	0.233[x] (0.200)	0.070 (0.059)	0.645 (0.536)
	No	0.060 (0.055)	0.072 (0.051)	0.591 (0.482)
Sample size[b,c]		27	64	64
1979 (1 July-4 Oct.)	Yes	0.772 (0.500)	0.042[x] (0.027)	0.592 (0.402)
	No	1.175 (0.936)	0.029 (0.011)	0.492 (0.212)
Sample size [b]		44	52	52

[a] *Corbicula* stocked in ponds 1 and 16 on 1-2 June 1977 and 27 June-1 July 1979. Clams were absent from ponds 2 and 17.

[b] Unless stated otherwise sample size is the sum of an equal number of observations for ponds with and without *Corbicula*.

[c] Sample size for total ammonia in 1977 was 14 and 13 for ponds with and without *Corbicula*, respectively.

[x] Indicates a significant ($P < 0.05$) difference between ponds with and without *Corbicula*.

Corbicula usually clumped together, both when placed in the cages and when stocked on the substratum. In cages *Corbicula* formed dense masses of many clams. On the substratum clams frequently clumped together in tight masses of 5 to 20 clams/50 cm² or in loose clusters of 50 to 100 clams/3000 cm². Clams were usually found in the substratum rather than upon it. An inverse relationship ($P<0.05$) was observed between clam size and depth in the substratum; smaller clams were located deeper in the substratum. Most clams were collected from the upper 5 cm of the substratum.

Channel catfish survival, growth, and feed conversion were not affected ($P>0.05$) by the presence of *Corbicula* (Table 2). Catfish survival for all ponds summed averaged 96.3% (S.D. = 3.2%) and average weight of catfish at harvest was 371 g (S.D. = 23 g). Catfish feed conversion (weight of feed presented to catfish divided by weight gain of catfish) averaged 1.23 (S.D. = 0.10).

Water quality parameters were monitored primarily to describe the system in which the clam was studied (Table 3), but the presence of *Corbicula* did influence water quality (Tables 4 and 5). Circulation of ponds in 1977 increased turbidity, broke up thermal stratification, and increased average temperature of the water by 2 to 4°C.

In 1977 D.O. was significantly ($P<0.05$) greater in ponds with *Corbicula* stocked in cages suspended in the water of circulated ponds than in ponds without the clam (Table 4). In 1979 the presence of *Corbicula* stocked upon the substratum of uncirculated ponds had no significant ($P>0.05$) effect on D.O. (Table 4). Incidence of D.O. at or below critical

Table 6. Total abundance of phytoplankton and zooplankton and average phytoplankton generic and zooplankton species diversity in 0.06 ha channel catfish rearing ponds with and without *Corbicula* in 1977 and 1979. Numbers in parentheses are standard deviations.

Year	*Corbicula*[a] present	Sample size	Phytoplankton abundance (No./l×10⁶)	Phytoplankton generic diversity	Zooplankton abundance (No./l×10²)	Zooplankton species diversity
1977 (1 June-20 Sept.)	Yes	32	14.9[x] (13.4)	2.4 (0.5)	23.4[x] (27.1)	2.3 (0.5)
	No	32	9.6 (5.8)	2.5 (0.5)	10.8 (6.0)	2.4 (0.6)
1979 (1 July-4 Oct.)	Yes	30	31.4 (37.3)	2.6[x] (0.5)	4.6 (3.0)	2.4[x] (0.5)
	No	30	31.8 (48.6)	2.9 (0.5)	3.6 (1.9)	2.0 (0.5)

[a] *Corbicula* stocked in ponds 1 and 16 on 1-2 June 1977 and 27 June-1 July 1979. Clams were absent from ponds 2 and 17.

[x] Indicates a significant ($P < 0.05$) difference between ponds with and without *Corbicula*.

levels (3.0 mg/l ~ 40% saturation) at dawn was less frequent in ponds with *Corbicula* than in ponds without the clam (Table 4). The reduction in frequency of critical oxygen levels at dawn in the presence of *Corbicula* was significant ($P<0.05$) only in 1977.

Average rates of net diurnal production and net nocturnal respiration were computed (Table 4). Net diurnal production and net nocturnal respiration rates, as determined by changes in D.O., were greater in ponds with *Corbicula*, but the differences were significant ($P<0.05$) only in 1977.

Turbidity was reduced in ponds with *Corbicula* (Table 4). Observed reduction in turbidity was significant ($P<0.05$) only in 1977.

Levels of nitrogenous wastes were occasionally greater in ponds with *Corbicula* than in ponds without the clam (Table 5). TAN was significantly ($P<0.05$) greater in ponds with *Corbicula* in 1977, but not in 1979. NO_2 -N levels were similar in all ponds in 1977, but significantly greater ($P<0.05$) in ponds with *Corbicula* only in 1979. Presence of *Corbicula* was not associated ($P>0.05$) with changes in level of NO_3 -N.

Seventy-one genera of phytoplankton and 69 species of zooplankton were collected and identified. Phytoplankton abundance ranged from 2.6×10^6 to 2.7×10^8 plants per liter and zooplankton numbers ranged from 76 to 1.2×10^4 per liter. Phytoplankton populations were dominated by green algae, but blue-green algae and diatoms occasionally became abundant. In 1977 zooplankton populations were dominated by rotifers and cladocerans; in 1979 calanoid copepods and cladocerans dominated. Phytoplankton generic and zooplankton species diversity ranged from 2.4 to 2.9.

Presence of *Corbicula* was correlated with changes in plankton abundance, composition, and diversity (Table 6). In 1977 *Corbicula* was associated with significantly ($P<0.05$) greater numbers of phytoplankton and zooplankton, but in 1979 no significant ($P>0.05$) difference in plankton abundance was observed between ponds with and without *Corbicula*. Presence of *Corbicula* was not correlated ($P>0.05$) with changes in composition of phytoplankton, and the only significant ($P<0.05$) effect on composition of zooplankton was an apparent increase in proportion of cyclopoid copepods in ponds with *Corbicula* in 1979. In 1979 phytoplankton generic diversity was significantly ($P<0.05$) lower and zooplankton species diversity was significantly ($P<0.05$) higher in ponds with *Corbicula*; in 1977 plankton diversity was smaller in all ponds.

DISCUSSION

SURVIVAL, GROWTH AND REPRODUCTIVE SUCCESS OF *CORBICULA*

Survival of *Corbicula* stocked at 828 and 1010 kg/ha in cages suspended in the water of mechanically circulated 0.06 ha channel catfish rearing ponds averaged 36%. Survival of clams stocked at 1222 and 1717 kg/ha on the substratum of uncirculated ponds averaged 79%. These values are superior to the 2% survival observed by Habel (1970) for *Corbicula* stocked at 6880 to 40,860 kg/ha in cages and on the substratum of 0.0007 ha catfish rearing pools. The 79% survival rate exceeds the 62% observed by Busch (1974) for clams stocked on the substratum, but the 36% survival rate is lower than the 88% observed by Busch (1974) for clams suspended in the water. Busch used the same system and approximate clam density as Habel (1970). Apparently *Corbicula* can survive in channel catfish rearing systems, but substantial mortality occurs.

I attribute *Corbicula* mortality to high temperatures (>33ºC), reduced ability to uptake oxygen at intermediate temperatures (25 to 30ºC), and relatively poor tolerance to low levels of oxygen. Mattice and Dye (1976) and Mattice (1979) found *Corbicula* survived indefinitely at 32ºC, while a 30 min. exposure at 33ºC produced mortalities. Mortality increased with temperature until 100% mortality occurred after a 30 min. exposure at 43ºC. Cherry *et al.*, (1980) observed temperature induced mortalities at 36ºC. McMahon and Aldridge (1976) found oxygen uptake increases to 25ºC, but decreases greatly between 25 to 30ºC. Above 30ºC oxygen uptake increases slightly until thermal stress becomes fatal. Compared with other freshwater mollusks *Corbicula* is considerably less tolerant to low levels of oxygen (McMahon, 1979). Oxygen uptake rate of clams at 70% oxygen saturation is 1/2 their rate at 100% saturation (McMahon and Aldridge, 1976). In my study water temperatures in excess of 33ºC commonly occurred in the summer between 1200 and 1800 h and contributed to *Corbicula* mortality. Temperatures above 25ºC were frequently associated with reduced levels of D.O. (≤40% saturation) at dawn in channel catfish rearing ponds and probably contributed to clam mortalities.

Since some *Corbicula* survived in channel catfish rearing ponds at least some of the clams were capable of withstanding or avoiding stressful temperatures and low oxygen. Caged clams could not avoid stressful temperatures and the dense clumps of *Corbicula* in cages also restricted water flow and promoted a localized area of reduced oxygen that contributed to the high rate of clam mortality observed. *Corbicula* stocked on the substratum were distributed in less dense clusters than clams in cages and frequently burrowed to a depth of 2 to 5 cm, which was 1 to 2ºC cooler than the water immediately above it. Superior clam survival observed in 1979 (uncirculated ponds) was probably due to water temperatures 2 to 4ºC cooler than those in circulated ponds (1977) and because the uncaged clams were able to disperse and avoid localized oxygen depletions. It is possible that *Corbicula* from the extreme southern United States may be more tolerant of conditions in channel catfish rearing ponds than were clams from southern Illinois.

Growth of *Corbicula* in catfish rearing ponds was previously reported (Buttner and Heidinger, 1980). Summer and fall growth rates were similar to rates observed by other investigators (O'Kane, 1976; Sickel, 1976; Britton *et al.*, 1979; Dreier and Tranquilli, 1980). Winter growth rates were not comparable with values reported from other studies conducted in the deep south where water temperatures in winter often exceed the average 3.0ºC observed by Buttner and Heidinger (1980).

Corbicula reproduced in catfish rearing ponds, but recruitment was insufficient to maintain stocking densities. Collection of several 8-10 mm SL and many 0.20 mm SL *Corbicula* in the late summer and early fall document the occurrence of at least two spawns. Late summer or early fall spawn of *Corbicula* in 0.0007 ha catfish rearing pools was also reported by Busch (1974) in Alabama.

Although *Corbicula* spawns continually, biannual spawning peaks exist that are correlated with water temperature (Heinsohn, 1958; Sickel, 1976; Eng, 1979; Mattice, 1979). Spawning is inhibited by temperatures less than 12-16°C or greater than 24-26°C (Heinsohn, 1958; Britton *et al.*, 1979; Eng, 1979). Temperatures above 32°C prohibit spawning (Aldridge and McMahon, 1978). Optimum spawning temperature is between 22 and 24°C (Britton *et al.*, 1979; Dreier and Tranquilli, 1980). Temperatures suitable for spawning occurred immediately after clam introduction in June and at the end of August or in early September. However, throughout most of the study period temperatures commonly exceeded the 26°C known to inhibit *Corbicula* spawning.

Recruitment of spawned *Corbicula* was poor and few clams survived to 8-10 mm SL. High water temperatures (commonly >26 C) and low D.O. (frequently ≤40% saturation) inhibited spawning and may have killed immature clams. Predation by crayfish, *Orconectes immunis*, possibly reduced abundance of juvenile clams. Other crayfish species, *Procambarus clarkii* and *Cambarus bartoni*, prey on juvenile *Corbicula* (Auerbach and Reichle, 1980; Covich *et al.*, 1981). Ingestion of juvenile *Corbicula* by channel catfish was not documented, although more than 50 gut samples were examined. Busch (1974) also found channel catfish predation upon *Corbicula* in 0.0007 ha pools negligible.

EFFECT OF *CORBICULA* ON CHANNEL CATFISH.

Channel catfish survival, growth and feed conversion compared favorably with values reported for commercial operations (Tiemeier and Deyoe, 1973; Gray, 1978; Piper *et al.*, 1982). Although *Corbicula* had no observable effect on catfish, its presence was correlated with improved water quality. Since catfish survival, growth and feed conversion depend upon the environmental situation (Thurston et al., 1979; Allen and Kinney 1981; Piper *et al.*, 1982), they may be enhanced only if *Corbicula* promotes water quality.

EFFECT OF *CORBICULA* ON WATER QUALITY

Corbicula reduced the biological oxygen demand by cropping detritus, bacteria, and phytoplankton. *Corbicula* cropping of the phytoplankton possibly stimulated production and respiration by promoting an active vigorous algal population. Busch (1974) found *Corbicula* stocked in excess of 6850 kg/ha decreased the incidence of critically low D.O. at dawn, but had no consistent effect on average D.O. at dawn.

Photosynthesis was promoted by turbidity reduction, which increased the depth of the euphotic zone. The limited reduction of turbidity associated with *Corbicula* (Table 4) was most likely due to pond circulation in 1977, to the activity of the abundant crayfish, *Orconectes immunis*, and to the relatively low density of clams stocked. Densities of *Corbicula* greater than 6800 kg/ha apparently are more effective in reducing turbidty than the lower densities used in my study (Habel, 1970; Busch, 1974; Haines, 1979).

Nitrogenous wastes were occasionally higher in ponds with *Corbicula* than in ponds without the clam; significant effects were observed in 1977 for TAN and in 1979 for NO_2-N. However, the increased level of nitrogenous wastes is likely independent of the clam. In laboratory studies that I conducted with *Corbicula* isolated in 50 ml of pond water for 24 h, no buildup of TAN was observed. Further, the only substantial source of nitrogenous waste unique to ponds with *Corbicula* was decaying clam tissue. Given the weight and composition of putrefying clam tissue the maximum daily increase in TAN would be approximately 0.0006 mg/l. This amount is insufficient, by an order of 2 to 3 magnitudes, to account for differences observed between ponds with and without *Corbicula*. At no time did nitrogenous wastes in any of the ponds attain toxic levels (Colt and Armstrong, 1981).

EFFECTS OF *CORBICULA* ON PLANKTON

Plankton populations were monitored each week by a single sample obtained from each pond. Samples so collected contain much inherent variability (Verduin 1959; Wetzel, 1975). However, the sampling regime would permit documentation of trends and differences between ponds with and without *Corbicula*. Unfortunately another variable existed, planktivorous fish. The fish, mainly gizzard shad, *Dorosoma cepedianum*, and sunfish, *Lepomis* spp., were accidently introduced into most experimental ponds through the water supply. Contaminant fishes were planktophagic and could reduce total abundance, alter composition and affect diversity of plankton populations. Effects of these fish on plankton populations were examined statistically. Weight of contaminant fish and abundance of plankton, both zooplankton and phytoplankton, was positively correlated (ANOVA, $P<0.05$) in 1977. In 1979 a significant (ANOVA, $P<0.05$) negative correlation existed between weight of introduced fish and abundance of zooplankton. Plankton most dramatically affected were the crustaceans.

Total abundance, composition, and diversity of plankton were similar to values previously reported for eutrophic waters (Pennak, 1946; Margalef, 1958; Meyer and McCormick, 1971; Wetzel, 1975). Phytoplankton abundance was greater in 1979 than in 1977, probably due to the absence of mechanical circulation which resuspended silt and maintained increased turbidity in 1977. Green algae and blue-green algae dominated the phytoplankton populations in all ponds as they normally do in fertile waters during the summer (Phillips and Whitford, 1959; Ewing and Dorris, 1970; Boyd, 1973). Zooplankton samples were dominated by rotifers and cladocerans in 1977, but not in 1979. This is probably an artifact related to differences in sampling technique. A 35 μm mesh net that retained rotifers was used in 1977 but the 140 μm mesh net used in 1979 permitted passage of rotifers.

Although invertebrates and fish have suppressed numbers of plankton (Pennington, 1941; Dunseth, 1977; Porter, 1973; Zaret, 1980), *Corbicula* did not consistently alter plankton abundance or composition. Algal populations were not reduced by *Corbicula*, probably due to the low number of clams stocked, low turnover rate (ponds water volume filtered once every 2 to 7 days) and the relatively rapid doubling time of algae. In 1977 the statistically significant ($P < 0.05$) increase in plankton abundance observed in ponds with *Corbicula* and the significant ($P < 0.05$) increase in abundance of cyclopoid copepods in 1979 were probably independent of the presence of *Corbicula*. Contaminant fish and aquatic insects (Notonectidae) were present in all ponds, particularly those with *Corbicula* in 1979. These organisms prey on zooplankton and can reduce their abundance and change the composition of plankton (Brooks and Dodson, 1965; Brooks, 1968; Applegate and Mullan, 1969; Zaret, 1980).

The reason for the significant decrease in phytoplankton generic diversity and increase in zooplankton species diversity observed in 1979 for ponds with *Corbicula* is unknown. Perhaps the greater density and increased survival of *Corbicula* and the large number of zooplankton present eliminated or reduced certain green algae and diatoms. Increased zooplankton species diversity may be related to the absence of contaminant fish in pond 16 and presence of relatively large numbers of contaminant fish in pond 1 (ponds 2 and 17 had approximately the same type and number of contaminant fish). Such a difference would promote the development of additional niches and increase diversity.

CONCLUSION

Corbicula has been viewed commonly as a nuisance or problem species. However, the attributes that promote this characterization indicate it may be an unrealized asset. *Corbicula* has potential as an aquaculture organism and biological filter in fish rearing ponds (Buttner, submitted). The clam grows rapidly, is low on food chain, effectively removes suspended materials, is tolerant of a wide variety of environmental conditions, does not compete with channel catfish, and possibly promotes superior water quality. Commercial markets of *Corbicula* as a bait, in the aquarium trade, as a food for domesticated animals, and for human consumption already exist (Fox, 1971; Chen, 1976; Sickel *et al.*, 1981; Britton and Sickel, 1982).

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ASSIMILATION OF RADIOLABELED ALGAE BY *CORBICULA*

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ABSTRACT

Despite its abundance in many aquatic systems, little is known about the feeding ecology of the Asiatic clam, *Corbicula fluminea*. Because *Corbicula* is now found in several coastal North Carolina rivers that have periodic summer blue-green cyanobacterial blooms, this study compared the potential for the clams to use ^{14}C labeled cultures of the filmentous blue-green *Anabaena oscillarioides* with that of the green algae *Chlorella vulgaris* and *Ankistrodesmus* sp. Although there were significant differences in the use of the algal foods by the clams, assimilation and net production efficiencies of clams fed the blue-green were not significantly different from efficiencies of the two green algae. The significance was a result of the lower assimilation of *Ankistrodesmus* (47%, compared to 58% for *Anabaena* and 56% for *Chlorella*). Also, net production efficiencies were significantly higher for *Ankistrodesmus* (78%) than for the other foods (61% for *Anabaena* and 59% for *Chlorella*). Any potential harm from blue-green "blooms" to populations of *Corbicula* is likely due to clogging of clam gills, causing most of the potential food material to be rejected as pseudofeces, and the reduction in dissolved oxygen concentrations in bottom waters as dead algae sink to the bottom and decay.

To date, little is known of the physiology of feeding in *Corbicula fluminea* (Müller), although previous work indicates that the clam can filter a wide range of particle sizes (Wallace *et al.*, 1977) at fairly high rates (e.g., Mattice, 1979). In particular, knowledge is lacking on the utilization of different food sources by the clams. This kind of information is needed to develop *Corbicula* aquaculture techniques, as well as to assess the impact of variations in food quality and quantity on the growth of these clams in more natural habitats.

C. fluminea has invaded most of the large coastal rivers of North Carolina within the past 5-8 years. Several of these rivers (such as the Chowan River in the Northeast) have become eutrophic, with periodic summer blooms of blue-green cyanobacteria. The abundance of blue-greens in eutrophic waters suggest that they do not readily enter food chains (Porter and Orcutt, 1980); the reasons for this are unclear and may be a combination of nutritional inadequacy, toxicity, unmanagability, and/or buoyancy of the algae.

The work reported here is a preliminary attempt to assess differences between food sources for *Corbicula* and in particular to compare blue-green to green algae. This has been done in the laboratory by measuring assimilation and net production efficiencies of *Corbicula* fed monocultures of algae that have been labeled with ^{14}C. This method has also facilitated comparison of filtration rates of the different algae, which included the filamentous blue-green cyanobacterium *Anabaena oscillarioides*, the small, sphaerical, unicellular green alga *Chlorella vulgaris*, and the sickle-shaped unicellular green alga *Ankistrodesmus* sp.

MATERIALS AND METHODS

Algal species used in feeding experiments were maintained in continuous culture at 20°C, with constant light provided by cool white fluorescent lamps. Cultures were gently agitated with a stirring bar and plate, and were bubbled with air to maintain a constant pH. Algal growth media and glassware were autoclaved before use and efforts were made to keep bacterial contamination at a minimum. The green algae *Ankistrodesmus* sp. and *Chlorella vulgaris* (obtained from Carolina Biological Supply, Burlington, North Carolina) were grown with a modified ASM media (Lauritsen and Mozley, 1983), while the nitrogen-fixing blue-green *Anabaena oscillarioides* (isolated from the Chowan River, North Carolina) was grown with Chu-10 media (Chu, 1942) containing no nitrogen.

Aliquots of each algal species were inoculated with 2.5 μ Ci of ^{14}C sodium bicarbonate 6-18 hr before feeding experiments, then placed in cool white light. After light incubation, green algal cultures were then centrifuged and algal cells resuspended in filtered (Whatman GF/C glass fiber filters) lake water. Cell volume and density of resuspended cultures was determined with a Coulter Counter Model T_{AII} with a 100μ aperture.

Collections of live *Corbicula* were made in Lake Waccamaw (Columbus Co., North Carolina) and the Chowan River near Winton, N. C. The clams were maintained in aerated aquaria at 20°C for at least a week prior to feeding experiments, and during holding were fed mixed cultures of

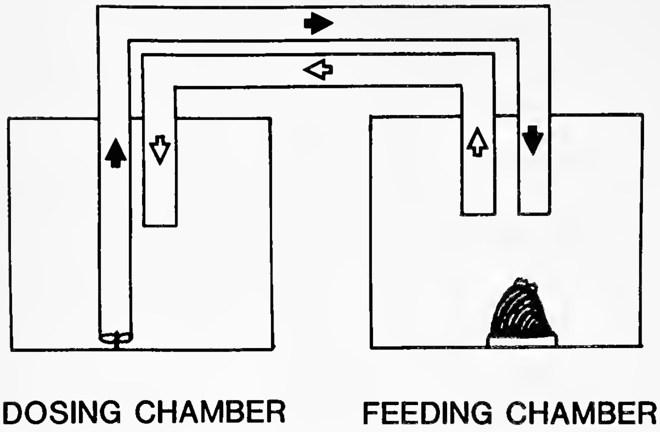

Fig. 1. Schematic of continuous-flow system for feeding experiments. Algae are added to dosing chamber, then circulate to the feeding chamber, where the clam filters out the algae.

Ankistrodesmus, Scenedesmus and *Chlorella*. Clams were always fed 36-48 hours before feeding experiments were begun, then 24 hours before the start of feeding experiments clams of similar sizes were isolated in beakers of filtered lake water to empty their guts. The range in shell length of *Corbicula* used in experiments was 20-23.3 mm.

Individual clams were placed in feeding chambers with 1.5 *l* of circulating, filtered lake water 1 hour before exposure to labeled algae to allow them to acclimate. A schematic of a feeding chamber is illustrated in Figure 1; they were a modification of a design by Peirson (1983) and Riisgard and Mohlenberg (1979). Specific volumes (1 mm³) of labeled food were added to the dosing reservoirs of the chambers and the clams were allowed to feed for 1 hour. Clams were then removed and the contents of the feeding chambers were filtered through 4.25 Whatman GF/C filters and radioassayed. Eight clams were tested for each algal food.

Clams removed from the feeding chambers were placed in aerated 1 *l* side-arm Erlenmeyer flasks with 500 ml of filtered lake water. Flask sidearms were connected to impinger traps containing 25 ml of a mixture of ethylene glycol monomethyl ether and ethanolamine to trap $^{14}CO_2$ (Peirson, 1983). Feces were collected daily by filtering the flask water through Whatman GF/C filters and radioassaying each day's sample separately. After two days, the clams were removed from the flasks and frozen. The water in the filter flasks was acidified with 1 ml of conc HC*l*, then aerated for 30 min with the impinger traps still attached to drive off any remaining $^{14}CO_2$. Aliquots of the flask water were then assayed to determine the amount of ^{14}C in soluble form. One ml of methanol was added to samples of the mixture in the CO_2 traps before radioassay to facilitate mixing of this liquid with the scintillation cocktail.

Frozen clam tissue and liquor was removed from shells, macerated, and placed in scintillation vials. Wet tissue weight was determined, then a mixture of Scintigest and water were added according to manufacturer's instructions. Tissues were then digested 12-24 hr in a 50°C water bath.

To measure ^{14}C incorporation in clam shells, individual shells were placed in side-arm Erlenmeyer flasks containing 100 ml of 10% HC*l*. The flasks were aerated and CO_2 impinger traps were attached to the sidearms to collect any $^{14}CO_2$ evolved during disintegration of the shells. Samples of the trap liquid were counted for radioactivity after addition of menthanol and scintillation cocktail.

All samples were counted on a Beckman LS 700 liquid scintillation counter, using a toluene ^{14}C external standard.

In radiotracer experiments, carbon assimilation is determined by adding the radioactivity retained in the animal (without gut contents) to the complete metabolic losses (respiration) of tracer during the experimental period. Animals were held in respiration chambers for a 2-day period after feeding experiments so that unassimilated material would be voided while at the same time measuring $^{14}C_2$ evolved. Because the clams did not filter out all of the labeled algal cells after 1 hr in the feeding chambers, assimilation was determined from the percentage of tracer ingested:

$$\%\text{ Assim. Eff.} = \frac{^{14}\text{C in tissues} + {}^{14}\text{C respired}}{^{14}\text{C ingested}}$$

Net production efficiency (energy available for growth and reproduction, e.g., Russell-Hunter, 1972) for clams fed each algal species were determined as:

$$\%\text{ Net Prod. Eff.} = \frac{^{14}\text{C in tissues}}{^{14}\text{C tissues} + {}^{14}\text{C respired}}$$

The following equation was used to determine filtration rate for individual clams (Coughlan 1969):

$$\text{filtration rate} = \frac{\text{volume (ml)}}{\text{time}} \log_e \left(\frac{\text{initial conc}}{\text{final conc}}\right)$$

The concentration ratio was determined as the total amount of algal radioactivity dosed divided by the algal radioactivity that remained in the chamber at the end of the feeding period. Because the water in feeding chambers was continuously circulating, algal settling was assumed to be negligible.

The F_{max} test (Sokal and Rohlf, 1981) was used to test for homogeneity of variances of assimilation efficiencies, net production efficiencies, and filtration rates. Assimilation and net production efficiencies were arcsine transformed, then analysis of variance tests were performed to determine if there were significant differences between treatments (algal species). Analysis of variance was calculated on untransformed filtration rates.

RESULTS

No significant difference was found in variances of assimilation and net production efficiencies, so standard errors of retransformed means for these efficiencies are expressed as the square root of the retransformed mean square error of the ANOVA for each (Table 1). There was a significant difference ($F = 4.66$, $P < .05$) between transformed assimilation efficiencies of the different algae, due to the significantly lower assimilation of *Ankistrodesmus* (47%) compared to *Anabaena* (58%) and *Chlorella* (56%) ($F = 9.19$, p

Table 1. Mean carbon assimilation (^{14}C utilized, as a % of what was ingested, or A/I) and net production efficiencies (represents the energy available for growth and reproduction as a % of what was assimilated, or P/A), and mean filtration rates (in ml·h^{-1}, with standard errors in parenthesis) for *Corbicula fluminea* fed equivalent volumes of ^{14}C labeled algae.

	A/I %	P/A %	Filtration Rate (ml·h^{-1})
Anabaena	57.7	61.4	587.4 (90.1)
Ankistrodesmus	47.4	78.2	765.6 (18.2)
Chlorella	56.3	59.4	770.0 (37.1)
SE	3.01	9.63	

Table 2. Mean percentage of total radioactivity filtered by *Corbicula* found in each kind of sample, with standard errors indicated in parenthesis. No label was recovered in clam shells.

	FECES	DO^{14}C	$^{14}CO_2$	TISSUES
Anabaena	12.37	30.09	21.14	36.38
	(2.19)	(31.5)	(3.58)	(5.36)
Ankistrodesmus	17.70	34.86	10.64	36.77
	(4.07)	(3.03)	(2.74)	(4.32)
Chlorella	37.08	6.68	22.70	33.52
	(3.86)	(1.38)	(.97)	(2.94)

$< .01$).

Net production efficiencies were also significantly different ($F = 4.55$, $p < .05$) between algal species. But while assimilation of *Ankistrodesmus* was low compared to the other algae, mean net production efficiency was significantly higher (78%) than *Anabaena* (61%) and *Chlorella* (59%) ($F = 9.02$, $p < .01$, Table 1). The high net production values of *Ankistrodesmus* were due to the lower percentage of assimilated carbon respired as $^{14}CO_2$ (Table 2).

A large proportion of feces were produced by clams fed *Chlorella* (Table 2), and microscopic examination indicated that the feces were composed primarily of clumps of green cells. A smaller proportion of intact cells of *Ankistrodesmus* were observed in clam feces, while no *Anabaena* filaments were found in feces. However, *Anabaena* was the only algal food that caused *Corbicula* to produce pseudofeces, or clumps of filaments that would be ejected before they were ingested.

Filtration rates were fairly constant over all algal food treatments, with means ranging from 709-770 ml·h^{-1} (Table 1), resulting in no significant difference between them ($F = 1.03$, $p > .25$).

DISCUSSION

Most feeding studies of bivalve molluscs have been done under laboratory conditions, and the advantages of this method include the ability to control and manipulate specific variables such as temperature, food quantity and quality. There are, however, certain disadvantages which must be taken into consideration when interpreting their results and applying them to natural systems. For example, bivalves can be very sensitive to disturbances and test conditions, resulting in significant deviations in important physiological functions. This is evidenced by the wide fluctuations in filtration rates reported for *Corbicula fluminea*: 20-150 ml·h^{-1} (Prokopovich, 1969); a mean of 11 ml·h^{-1} (Habel, 1970); a mean of 816 ml·h^{-1} (Auerbach *et al*., 1977); 500-600 ml·h^{-1} (Mattice, 1979). Although Mattice (1979) mentions that feeding rate in *Corbicula* can be affected by food "quality", I found very similar filtration rates for each algae used, indicating that the clams were not selecting against any algal food on the basis of "taste". Filtration rates of *Corbicula* are thus much higher than other freshwater bivalves such as *Dreissena polymorpha* (Stanczykowska *et al*., 1976; Walz, 1978) and *Sphaerium striatinum* (Hornbach *et al*., 1984).

Assimilation efficiencies are a measure of how much energy is utilized as a proportion of what is ingested. About half of the ^{14}C ingested by clams fed each of the three algal foods was expelled as wastes (feces and dissolved organic ^{14}C; Table 2), and so assimilation efficiencies were fairly similar. Other researchers (e.g., Peirson, 1983) have noted that *Chlorella* is not well assimilated by filter-feeding bivalves and have concluded that the thick cell wall effectively prevents lysing of the cells. This is probably the case with *Corbicula* as well, since the feces consisted primarily of mucus-bound clumps of cells. To a lesser extent the same also seems to hold true for the other green alga, *Ankistrodesmus*. It may be that freshwater bivalves are not particularly efficient at utilizing what they filter from the water; assimilation efficiencies for the freshwater mussel *Dreissena polymorpha* average about 40% (Stanczykowska *et al*., 1975; Walz, 1978). The important difference with *Corbicula* is that because filtration rates are so much higher, the total amount of material assimilated over any given time will be much higher.

Net production efficiencies are a measure of energy available for growth and reproduction, determined as a percentage of assimilation. The results from my laboratory experiments are similar to values calculated from carbon budgets of population of *Corbicula* in Lake Arlington, Texas (mean of 71%, Aldredge and McMahon, 1979). Such high net production efficiencies have been reported only for one other freshwater bivalve (60-80% for *Pisidium conventus*, Holopainen and Hanski, 1979). These high net production efficiencies are possible because *Corbicula*, a relatively sedentary organism, expends little energy on respiration (e.g., McMahon, 1979).

Growth rates of *C. fluminea* are usually much higher than rates reported for other freshwater bivalves (e.g., Hornbach *et al*., 1980; Negus, 1966). Filtration rates and net production efficiencies reported here indicate that the clams are able to remove a relatively large proportion of potential food material from the water, and are very efficient at utilizing what food is assimilated, thereby providing the energy needed for these rapid growth rates.

Any substantial differences in utilization of different kinds of algal would indicate that the diet could affect *in situ* growth rate of the clams (or otherwise be detrimental—cf. Introduction). *Corbicula* appears to show no substantial difference in its ability to utilize the blue-green *Anabaena* or the two green algae *Chlorella* and *Ankistrodesmus*. However, dense assemblages of blue-greens such as the filamentous *Anabaena* or clump-forming species such as *Microcystis*, which develop during nuisance blooms in summer, may have a negative impact on *Corbicula* by clogging their gills and causing most of the potential food they filter to be rejected as pseudofeces. But since many blue-greens float on or near the water surface, they may remain relatively "unavailable" to the clams in deeper water. *In situ* experiments would be needed to determine the actual effects of blue-green blooms on clam filtration.

Perhaps the most significant impact of blue-green blooms is in lowering dissolved oxygen concentrations near the sediment surface as dying algae sink to the bottom and decay. *Corbicula* is intolerant of low oxygen conditions (McMahon, 1979), so that blue-green blooms could wipe out existing populations of the clams (I have observed this in at least one large coastal river in North Carolina) and/or prevent the clams from becoming established.

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ADAPTATIONS OF PISIDIIDAE (HETERODONTA: CORBICULACEA) TO FRESHWATER HABITATS

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ABSTRACT

The Pisidiidae have representatives in virtually all types of freshwater habitats, from temporary ponds and roadside ditches to deep, cold profundal zones of oligotrophic and eutrophic lakes. A review of the studies reported to date suggests that there are peculiarities in the structure, composition and morphology of the shell, and in the anatomy of the gills, siphons and byssal apparatus, as well as in the physiologies and ecologies of many species that have made the Pisidiidae one of the most common and widely distributed groups of freshwater invertebrates in all parts of the world.

At present, 39 living species belonging to five genera of freshwater corbiculacean clams are recognized in North America. *Corbicula* and *Eupera* are monospecific in North America with *C. fluminea* (Müller) and *E. cubensis* (Prime) the only species reported to date (Britton and Morton, 1979; Mackie and Huggins, 1976). The greatest number of species are in the genus *Pisidium* (26). *Sphaerium* has 8 species and *Musculium* has 4.

Out of 62 states, provinces and territories in North America, *Pisidium casertanum* (Poli) occurs in 61 and is the most cosmopolitan of all corbiculacean clams (Mackie, 1981). *Corbicula* is found in 35 and *Eupera* in 7 states, provinces and territories (McMahon, 1982; Mackie, 1981). The rarest species is *Pisidium ultramontanum* Prime (Mackie, 1981).

All corbiculacean clams are ovoviviparous and relatively small in size. The largest species is *C. fluminea* reaching 6 cm in length (Britton and Morton, 1979). The smallest species is *Pisidium punctatum* Sterki (usually less than 1.5 mm long). Most pisidiids have shell lengths less than 8 mm; only *Sphaerium simile* (Say) and *Musculium transversum* (Say) grow as large as 2 cm in shell length (Mackie and Huggins, 1983).

ADAPTATIONS IN SHELL STRUCTURE AND SHAPE

The shell of *Corbicula* is thick and heavy. Pisidiids have relatively thin shells. Aragonite crystals, present in all corbiculacean clams, is laid down in a complex crossed-lamellar structure (Mackie, 1978). The laminated sheets of aragonite that characterize the nacre of Unionidae is absent in corbiculacean clams. The complex crossed-lamellar structure is considered to be an adaptation to high resistance to abrasion (Carter, 1980).

The effect of environment on shell shape and the relation between fecundity and shell shape are well documented. By transferring *Sphaerium corneum* (Linnaeus) from organically enriched water to clean water or by experimentally increasing the dissolved oxygen content of the water, Thiel (1926) was able to demonstrate a change in roundness or thickness of the shells. Since this change was also accompanied by an increase in natality, Thiel (1926) suggested that the clean water with lower food production was a less favorable environment for *S. corneum* and consequently the survival of the population required more effective reproduction. The higher number of embryos was suggested to need more room and to cause change in the direction of growth. Similar relationships between shell thickness (width) and number of embryos was demonstrated by Holopainen and Kuiper (1982) for *P. casertanum* and Mackie and Flippance (1983a) for *Sphaerium rhomboideum* (Say).

Changes in shell size (as well as weight and calcium content) have also been shown to be related to other environmental variables. Mackie and Flippance (1983b), using canonical correlation analyses on species collected from 53 habitats with total alkalinity ranging from 0 to 280 mg $CaCO_3L^-$, showed that a decrease in acid-neutralizing capacity relative to the noncarbonate anion content was accompanied by short but heavily calcified shells in *Pisidium variabile* Prime, *P. casertanum, S. simile* and *S. striatinum* (Lamarck). Waters with increasing acid-neutralizing capacity relative to calcium hardness are accompanied by longer shells with increases in tissue calcium relative to total weight in *Musculium securis* (Prime) and *Pisidium compressum* Prime. All six species of pisidiids that were analyzed for canonical correlations showed more than one significant canonical variate, suggesting that acid deposition would not be a factor in their disappearance from water with pH greater than 5.50 (Mackie and Flippance, 1983b).

Of the 13 species of pisidiids collected from the 53 habitats, Mackie and Flippance (1983c) were able to derive correlation coefficients between calcium content of the

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whole individual and pH, total alkalinity, total hardness and calcium hardness of the water for only seven species (the sample size being too small for the remaining six species). Significant correlations ($P < 0.05$) were found for only five of the seven species. Two species (*Sphaerium rhomboideum* (Say) and *S. simile*) showed negative correlations, while three (*P. casertanum, P. compressum,* and *S. striatinum*) showed positive correlations between calcium content of individuals and environmental calcium content. Numerous other studies also demonstrated strong correlations between environmental calcium content and molluscan (including pisidiids) calcium content (Russell-Hunter *et al.*, 1967; Lee and Wilson, 1969, 1974; Burky *et al*, 1979), distribution (Boycott, 1936; Macan, 1950; McKillop and Harrison, 1972), abundance (Dussart, 1976, 1979a; Williams, 1970a,b), physiology (Harrison, 1968; Hunter and Lull, 1977), and life history (Dussart, 1979b; Thomas *et al.*, 1974), to mention only a few.

Russell-Hunter *et al.* (1981) describe an irregular distribution of four shell types in gastropods with respect to water characteristics: (i) a direct relationship between the amount of shell calcification and water hardness, (ii) a constant ratio of shell calcium to whole animal dry weight throughout growth in a wide range of calcium concentrations, (iii) a positive relationship between shell mass and trophic conditions, and (iv) no relationship between the amount of shell calcium, organic carbon or nitrogen, and the water characteristics. A similar distribution of shell types is evident in Pisidiidae (Mackie and Flippance, 1983c), with even a fifth type, an inverse relationship between shell calcification and dissolved calcium, as reported by Burky *et al.* (1979) for *Sphaerium striatinum*.

Although many significant ($P < 0.05$) correlations were found by relating size, weight and calcium content of pisidiids to the "buffer variables" (i.e. pH, alkalinity, total hardness, calcium hardness) of the water, these correlations do not necessarily imply cause/effect relationships. Indeed, it was indicated earlier that reproduction may cause changes in shape. Nevertheless, the studies do show that the changes in size, weight and calcium content can be related to an environmental variable or set of environmental variables and these changes may be of adaptive significance. As an adaptation, changes in calcium content are easier to explain than changes in size and weight of pisidiids. Particularly easy to explain are positive correlations between calcium contents of pisidiids and of the environment. Decreases in shell calcium content are usually accompanied by increases in carbon content (Burkey *et al.*, 1979). Analyses of shell carbon content in species from acidified lakes indicate very large proportions of organic matter (probably conchiolin) in relation to calcium carbonate content (Table 1) suggesting that high organic content in shells may be an adaptation to resist erosion from acidified waters. Burky *et al.* (1979) discusses the adaptive significance of the inverse relationship between the amount of shell $CaCO_3$ and shell organic carbon and nitrogen in pisidiid clams; they concluded that this inverse relationship is convincing evidence that pisidiid shells are consistently built from some base level adaptive need of mechanical protection. Burky *et al.*, (1979) also suggested that pisidiid clams have a common strategy for shell secretion which is under genetic control. If this is true then the thick periostracum of *P. casertanum* in acidifying lakes may be merely reflecting the erosion of calcareous components, leaving only the periostracum which is more resistant to the corrosive effects of hydrogen ions. In this event, the inverse relationship between the amount of organic material and calcium contents in the shell may be a demonstration of the corrosive effects of hydrogen ions on shell calcification, rather than a thickening of the periostracum as an adaptation to resist shell erosion. Nevertheless, *P. casertanum* has a thicker periostracum than most other species of Pisidiidae, as Figure 1 in Mackie (1978) strongly indicates, and would explain the relative success of this species in corrosive environments. Correlations between organic content of the shell and pH, and trophic status of the environment are also present in unionids (Agrell, 1949; Singer, 1981).

Table 1. Calcium carbonate and carbon content of shells in common species of Pisidiidae in the study area. The species are arranged in order of decreasing calcium carbonate content.

Species	Shell $CaCO_3$ as % of total dry wt. ±95% C.I.	μg C mg^{-1} shell ±95% C.I.
Sphaerium striatinum	92.2 ± 1.69	5.33 ± 0.68
Sphaerium simile	90.7 ± 2.53	ND[2]
Pisidium compressum	90.3 ± 2.53	ND
Musculium securis	80.0 ± 3.21	8.32 ± 1.57
Pisidium casertanum	65.8 ± 1.66	10.18 ± 2.77

[1] C.I. = Confidence Interval

[2] ND = Not determined for species in waters with > 45 mg $CaCO_3$ L^{-1} total alkalinity.

Another interesting mechanism in Pisidiidae for resisting the corrosive effects of hydrogen ions is by changes in the morphology of the shell. Mackie and Flippance (1983b) showed by canonical correlations that in lake acidification (i.e. decreasing alkalinity) the calcium content of *P. casertanum* and *Sphaerium striatinum* decrease, but a high density of $CaCO_3$ is maintained in the shell by forming shorter (therefore more compact) shells. Hence, the protection offered by the shell can be maintained in low-alkalinity waters. The canonical correlation analyses also indicated that long, thin shells, which would provide less protection in acidifying waters than short, thick shells, are formed only in waters with increasing alkalinity relative to calcium hardness, as in *M. securis*.

Other species (e.g. *M. securis*) show no relationship in the calcium contents between the animal and environment (Mackie and Flippance, 1983c). These species appear to rely on calcium in allochthonous organic material (e.g. leaves of trees) rather than on bedrock supplies (i.e. limestone) which probably characterize the calcium content of most watersheds (Mackie and Flippance, 1983d). This adaptation to organically-derived calcium may also explain why most species of *Musculium* are found in woodland pools.

ADAPTATIONS IN SOFT ANATOMY

CTENIDIA. In *Corbicula* the two pair of ctenidia are well-developed, but in pisidiids the outer demibranches are reduced to small lobes or are absent. As in most freshwater bivalves, the inner gills of corbiculaceans function as marsupia. However, the larvae of *Corbicula* are released at an earlier developmental stage (i.e. veligers) than are the larvae of pisidiids. In pisidiids the trochophore and veliger stages are passed in the egg and the young are released as miniature adults. Also, the larvae of pisidiids are incubated in brood sacs (Mackie *et al.*, 1974a) whereas the larvae of *Corbicula* are incubated in the water tubes of the inner gill (Sinclair and Isom 1961).

The incubation of larvae within brood sacs until the young are capable of an independent existence has considerable survival value (for the population and species). Mackie (1979a) and McKee and Mackie (1980) demonstrated that extra-marsupial larvae survive longer periods of desiccation than do parents. The resistance of extra-marsupial larvae to desiccation (and/or the protection offered by the parent's shell) is an important adaptation for dispersal by aerial transport on waterfowl (Mackie, 1979a) and for survival of dry periods in ephemeral ponds (McKee and Mackie, 1980).

Brooding of larvae also has survival value in toxic environments. Ninety-six hour exposure of *Pisidium equilaterale* Prime, gravid with extra-marsupial larvae, down to pH 2.5 killed the parents but the larvae showed little mortality (Mackie *et al.*, 1983).

SIPHONS. The siphons of *Corbicula* are relatively complex compared to those of Pisidiidae. Although the anal and branchial siphons are merely modifications of the mantle lobes (Kraemer, 1977), they are ornamented with papillae, tentacles and pigment (Sinclair and Isom, 1963). The siphons in Pisidiidae are simple tubes and the branchial siphon is reduced to a mere slit in the mantle in *Pisidium* sp and is absent in *Neopisidium*.

The size and development of siphons in Pisidiidae are related to the size of the animal; the siphons are smallest and most poorly developed in *Pisidium* sp. which have smaller average shell lengths (4mm) than *Eupera* or *Musculium* (avg. length = 7 mm; the siphons are fused along their length for only the basal half) and *Sphaerium* (avg. length = 9 mm; the siphons are fused for almost their entire length). When fully extended, the siphons may be 50-100% of the animal's shell length.

The short, often slit-like sipons of *Pisidium* spp. appears to have some adaptive significance. Since most *Pisidium* spp. are small and live in the surficial layers of sediments (Meier-Brook, 1969) their siphons, even when fully extended, would rarely penetrate the mud-water interface. Hence, most of the water that is filtered by *Pisidium* is derived from the interstitial spaces of the sediments. Indeed long siphons in these situations would probably be cumbersome and impede or restrict water flow into the mantle cavity. The longer siphons in *Eupera, Musculium* and *Sphaerium* spp would therefore imply more of an epifaunal habit. An epifaunal habit has often been described for *Eupera* (Heard, 1965), *Musculium* (Boozer and Mirkes, 1979; McKee and Mackie, 1981) and *Sphaerium* (Hynes, 1972), although infaunal habits are also well known (Gale 1971, 1973).

BYSSUS. The only corbiculaceans with a functional byssus in adults are *Corbicula* (Sinclair and Isom, 1963) and *Eupera* (Heard, 1977). A byssal gland is present in larvae of *Musculium* and *Sphaerium corneum* and *S. occidentale* (Mackie *et al.*, 1974b; Heard, 1977) but all other species of *Sphaerium* and *Pisidium* lack a byssal gland in all life stages. In those species that have a functional larval byssus, the byssal stalk arises in the foot of the larvae (prodissoconch) and inserts on a small bulb attached to the descending lamella of the inner gill (Mackie *et al.*, 1974b). Heard (1977) suggests that the byssus functions to prevent precocious birth (i.e. abortion) until the larval gonads are sexually mature. However, the gonads of *Musculium* species mature during adult life (Mackie *et al.*, 1976), so this function seems doubtful. Yonge (1962) considers the presence of a byssal apparatus in the adult as representing the persistence of a post-larval organ (i.e. the animals possessing it are in this respect neotenous). Boozer and Mirkes (1979) suggested that *M. partumeium* (Say) has a functional byssus during adult life, but could not substantiate it. The threads observed by Boozer and Mirkes (1979) were probably mucous strings since the byssal gland is absent in adults (Mackie *et al.*, 1974b and unpublished data).

PHYSIOLOGICAL ADAPTATIONS

Respiratory adaptations of corbiculacean clams to temperature and oxygen content is well documented (Burky and Burky, 1976; McMahon, 1979; McKee and Mackie, 1983). All corbiculaceans appear to have poor respiratory adaptations to high temperature. Only *Corbicula* has so far been reported to have poor respiratory adaptation to hypoxia (McMahon and Aldridge, 1976; Aldridge, 1976; Aldridge and McMahon, 1978; McMahon, 1979), although Habel (1970) and Busch (1974) in less thorough studies report tolerance of *C. fluminea* to hypoxic conditions. Most pisidiids are more tolerant of hypoxia and are better regulators of oxygen consumption than are *C. fluminea* and appear to be able to adapt to hypoxia at some stage in their life cycles. All species of *Musculium* are commonly found in nearly anoxic pond waters; *Pisidium idahoense* Roper can survive hypoxia for at least two weeks (Juday, 1908); *Pisidium casertanum* inhabits nearly anoxic substrata in the summer (Berg and Jonasson, 1965; Mackie, 1979b); both *Musculium securis* and *Sphaerium occidentale* can survive anaerobic environments but *M. securis* is a facultative anaerobe and *S. occidentale* is an obligate aerobe during estivation (McKee and Mackie, 1983), while *C. fluminea* is largely excluded from reducing substrata.

Pisidiidae also appear to be more efficient at oxygen uptake during hypoxia than *C. fluminea* (McMahon, 1979). Berg *et al.* (1962) reported good regulation of oxygen uptake in *P. casertanum*. Alimov (1965), Burky and Burky (1976) and McKee and Mackie (1983) reported efficient oxygen uptake in *Sphaerium corneum, Pisidium walkeri* Sterki and *M. securis* and *S. occidentale*, respectively, although they attributed variations in respiration to variations in temperature.

Pisidiids exhibit both the over-compensation and "reverse" acclimation patterns described by Precht *et al.*, (1973). In *P. walkeri* (Burky and Burky, 1976) and *M. securis* (McKee and Mackie, 1983), the over-wintering generation displays over-compensation (decreasing respiration as temperature rises) in the spring at 10 and 20ºC. Reverse compensation is apparent in *S. corneum* since respiration rates at 20ºC decrease from summer to fall (Alimov, 1965). Both patterns occur in the annual life cycle of *S. occidentale* (McKee and Mackie, 1983).

In ephemeral habitats, respiratory adaptations are related to the specific life histories of the pisidiids. Oxygen uptake rates at field temperature and Q_{10} values are low in both *S. occidentale* and *M. securis* during hibernation and estivation, indicating respiratory stability and energy conservation (McKee and Mackie, 1983). These rates and respiratory coefficients peak in spring during maximum growth and reproduction. However, respiration in *M. securis* is more independent of temperature than in *S. occidentale*, reflecting the requirement of *M. securis* to complete growth and reproduction more quickly. During estivation, *M. securis* is a facultative anaerobe while *S. occidentale* is an obligate aerobe. Arousal from estivation, as indicated by oxygen uptake, is delayed when clams are introduced to pond water. This adaptation inhibits a premature resumption of activity and decreases the likelihood of desiccation (McKee and Mackie, 1983). Similar adaptations have been reported in some unionid bivalves (Dance, 1958; Dietz, 1974).

Although McMahon (1979) regards *C. fluminea* as relatively intolerant of high summer ambient temperatures, corbiculids appear able to tolerate higher temperatures than pisidiids. *Corbicula* is most common in the southern United States where ambient water temperatures above 30ºC occur frequently, but pisidiids are least common there and are most common in northern United States and Canada where ambient water temperatures usually do not exceed 30ºC. *Corbicula fluminea* can tolerate short-term exposure to 43ºC (after acclimating at 30ºC) (Mattice and Dye, 1976) but most pisidiids seem to perish quickly at 30ºC. Nevertheless growth and reproduction in both groups are severely impaired above 25-30ºC.

Being relatively poorly adapted to hypoxia and extreme temperatures, *C. fluminea* has remained physiologically closely allied to its estuarine ancestors (McMahon, 1979). Such physiological prerequisites are restricting *C. fluminea* to relatively large bodies of temperature-stable and well oxygenated flowing fresh water conditions (McMahon, 1979). Most pisidiids, on the other hand, appear to be less restricted by their respiratory physiology and should remain competitive in the majority of North American freshwater habitats. This has been confirmed by at least one study (Boozer and Mirkes, 1979).

ECOLOGICAL ADAPTATIONS

Some of the most interesting adaptations of pisidiids to temporary and permanent aquatic habitats have been elucidated through studies of growth dynamics and reproductive habits. By regressing larval shell length on parent shell length, Mackie (1976b) was able to compare larval growth rates in relation to that of parents. He found that species with slow larval growth rates are usually semelparous and univoltine. These species can be iteroparous by precocious birth of larvae and multivoltine by accelerated growth of semelparous individuals. Species that live one year and have rapid larval growth rates are usually iteroparous because larvae grow faster than parents and (or) there is precocious birth of larvae.

Studies of growth dynamics in two permanent pond populations of *S. rhomboideum* showed that width has a positive allometric relationship with length and height of the shell (Mackie and Flippance, 1983a). This results in an increase in interior shell volume that is significantly correlated with the increase in space required by developing larvae. An iteroparous reproductive strategy has been shown to be dependent upon both a positive allometric relationship between larval and parent shell lengths and birth of a cohort during or immediately before an active growing period. If birth of the cohort occurs immediately before a dormant period, semelparity will occur, no matter what type of allometric relationship is obtained between larval and adult shell lengths (Mackie and Flippance, 1983a).

Studies of species (e.g. *S. occidentale, M. securis, M. partumeium*) from temporary ponds to date show that all of them have the potential for iteroparous reproduction (Mackie, 1979b; Way *et al.*, 1980; McKee and Mackie, 1981). In some instances, semelparity is exhibited but only because the ponds dry up before a second litter is produced (Mackie *et al.*, 1978). In temporary ponds, where there may be high mortality during the dry season, an iteroparus reproductive strategy that produces many young in as short as time as possible by a single generation will perpetuate the population (and species) more effectively than a semelparous reproductive strategy.

For populations with a one year life span, semelparity could be considered to be a "luxury" that is afforded only to species that have low mortalities in a harsh environment (because the species is very tolerant to a wide range of environmental stresses). In this case the population can be maintained by several different parental generations with one reproduction each (i.e. semelparity) rather than by a single parent generation with several reproductive periods in its one year life span (i.e. iteroparity). Hence *P. casertanum*, a very cosmopolitan and tolerant species (Clarke, 1979) appears to have adopted a semelparous strategy (Thut, 1969; Mackie, 1979b; Burky *et al.*, 1981). Species less tolerant (e.g. *P. variable*) will adopt an iteroparous strategy when the environment imposes physiological limits on growth, reproduction, and maintenance functions (Way and Wissing, 1982).

For species that live for more than one year, very different reproductive strategies are observed. For example, *Pisidium conventus* inhabits only the deep, cold, profundal zones of oligotrophic lakes (or littoral zones of subarctic lakes) and has a three year life span. The profundal zones of oligotrophic lakes have relatively constant environmental conditions, including temperature, and in essence lack seasons. *Pisidium conventus* Clessin grows very slowly and produces such few offspring in each litter that it must reproduce 4-5 times in its lifetime in order to maintain the population density (Holopainen, 1979). Hence, an iteroparous reproductive strategy is characteristic of this oligotrophic species. However, *P. casertanum* (that lives for more than one year) is able to adopt either strategy. This versatility in reproduction strategy (inpart related to life span) is able to afford *P. casertanum* a very cosmopolitan distribution.

These data suggest that all species are potentially iteroparous and semelparity occurs only if a species' life span is suddenly truncated. However, this has been shown to be not the case for *M. securis*; Mackie *et al.* (1976) transplanted *M. securis* from a temporary pond into a permanent pond and a river and in all cases, the semelparous population from the temporary pond remained semelparous in the permanent habitats, even though their life spans were extended by two to three months. Hence, semelparity in this case appears to be an evolved (i.e. genetic) life history trait. For gastropods, Calow (1978) associates the semelparous state with reproductive recklessness and the iteroparous state with restraint on the part of the parent; semelparity is considered to have evolved in association with adaptations that ensure a greater chance of survival of the offspring. Calow (1978) should be consulted for an excellent discussion of theories on life-cycle strategies in gastropods.

Other life history traits also show some adaptive value. For example, pisidiids may display synchronous (e.g. *M. securis, M. partumeium, P. variable, P. compressum*) or asynchronous (e.g. *S. rhomboideum*) reproduction. Pisidiids which inhabit temperate, ephemeral ponds are synchronous in their reproductive patterns and respond to uncertainty in the length of time water remains in the pond (Way *et al.*, 1980; Hornbach, Way, *et al.*, 1980; McKee and Mackie, 1981; Way and Wissing, 1982). By being synchronous in their reproductive peiods, *P. variable* and *P. compressum* respond to habitat optima set by seasonality and the effects of local fluctuations in habitat features can be reduced by extending their reproductive period over several months (Way and Wissing, 1982).

In other pisidiids (e.g. *S. rhomboideum*) reproductive parents and newborn are present throughout most of the year (Mackie and Flippance, 1983e). This type of asynchronous reproduction ensures that the reproductive effort of an organism is not entirely lost during periods of environmental fluctuations. Several alternative adaptations to varying degrees of environmental uncertainty are discussed by Southwood (1977).

Many attempts (e.g. Mackie *et al.*, 1978; Holopainen and Hanski, 1979; Kraemer, 1979; Way *et al.*, 1980; Hornbach *et al.*, 1980, 1982; McKee and Mackie, 1981) have been made to predict corbiculacean life history from life history features according to r, k, and stochastic theories (Stearns 1976, 1977, 1980). However, many intraspecific variations in pisidiids cannot be explained by these theories (Way and Wissing, 1982; Mackie and Flippance, 1983e). The mix of reproductive strategies within a species may merely indicate that the variations in life history patterns (i.e. traits without coadaption) is more a function of local environmental impositions than of evolved (genetic) life history strategies (i.e. coadapted traits). Often environmental stability is defined on the basis of life history patterns; rather, life history should be predictable on the basis of environmental stability, as originally implied by McArthur and Wilson (1967). Calow (1978) discusses the possible consequences of "r" and "k" selection on gastropod life cycles.

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GROWTH, LIFE CYCLE, UPPER THERMAL LIMIT AND DOWNSTREAM COLONIZATION RATES IN A NATURAL POPULATION OF THE FRESHWATER BIVALVE MOLLUSC, *CORBICULA FLUMINEA* (MÜLLER) RECEIVING THERMAL EFFLUENTS[1]

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ABSTRACT

Quantitative bimonthly to monthly samples of *Corbicula fluminea* were collected from March 1981, through December 1982, from a power station's discharge canal receiving thermal effluents. Population density peaks occurred in the spring and fall. Maximum density was 21930 clams/m^2. The population was completely eliminated at summer water temperatures > 36°C, the apparent absolute upper lethal limit of this species. The population became reestablished in the fall by passive hydrological transport of juveniles through the plant's steam condensers from an endemic intake population. Recolonization occurred only after temperatures fell below 30°C, suggesting that higher temperatures may inhibit successful settlement by young individuals. Recolonization was rapid, ranging from 319 clams m^{-2} day^{-1} in 1981 to 522 clams m^{-2} day^{-1} in 1982. Spawning occurred in late spring and again in early summer leading to "early" and "late" generations, respectively. Both the early and late generations continued to grow until the upper lethal limit was reached in July. The early generation was thermally eliminated in the summer, but became reestablished in the discharge canal the following fall, disappearing from the population due to thermal elimination the following spring. Both generations survived less than one year and never exceeded a shell length of 18 mm. The high capacity of *C. fluminea* for rapid downstream dispersal and colonization is an adaptation to unstable, disturbed, lotic habitats and, in large part, is responsible for this species' spread through North American drainage systems. The relatively low upper thermal limit (36°C) of *C. fluminea* and the apparent inability of juveniles to successfully settle at temperatures > 30°C have important implications for the control of this species in industrial raw water systems.

The introduced, Asian freshwater bivalve, *Corbicula fluminea* (Müller), is reported to occur in the heated effluent canals of electrical power stations (Cherry, *et al.*, 1980; Dreier 1977; Dreier and Tranqilli, 1981; Eckbald, 1975; Rodgers, *et al.*, 1977, 1979; Thomas and MacKenthum, 1964). In discharge canals mid-summer ambient water temperatures can surpass the upper lethal limits of resident *C. fluminea* populations (Dreier, 1977; Dreier and Tranquilli, 1981). While long-term upper lethal temperature limits of *C. fluminea* have been determined in controlled laboratory studies (Mattice and Dye, 1976), and anecdotally estimated from populations in outdoor pools (Busch, 1974; Greer and Ziebell, 1972; Habel, 1970; Haines, 1979), no rigorous attempt has been made to determine the absolute upper lethal temperature limit for a population of this species in its preferred natural lotic habitat (McMahon, 1983). As power station discharge canals closely approximate the preferred riverine habitat of *C. fluminea* (Kraemer, 1979; McMahon, 1982, 1983), they provide a unique opportunity to assess this species' temperature tolerance limits under natural conditions. Such canals also allow the assessment of the rate of passive, current mediated, downstream dispersal and colonization by juveniles of this species after resident clam populations are thermally eliminated in mid-summer.

Information regarding field thermal tolerance limits and juvenile downstream colonization rates are of obvious

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significance to the future development of biofouling control measures for this species (for review of biofouling by *C. fluminea* see Goss, *et al.*, 1979; McMahon, 1977, 1983). This paper describes an investigation of a natural population of *C. fluminea* inhabiting the thermal effluent canal of a gas-fired steam-electric power station in north central Texas in which field estimations of upper thermal limits and downstream recolonization rates were determined from bimonthly to monthly samples over a 22 month period from 1981 to 1982.

MATERIALS AND METHODS

Over a period extending from 25 March 1981, through 17 December 1982, specimens of *C. fluminea* were quantitatively sampled from a population in the thermal discharge canal of the Handley Power Station of the Texas Electric Service Company on Lake Arlington, Tarrant County, Texas. This population was composed entirely of the "white" morphotype of *C. fluminea* (Hillis and Patton, 1982). The sampling site was approximately 200 m downstream from the opening of the effluent discharge pipe. Lake Arlington was formed from an artificial impoundment of Village Creek, a tributary of the West Fork of the Trinity River. At capacity it has a surface area of 920.7 ha and a volume of 56 x 10^6 m^3 H_2O (Dowell and Breeding, 1966). The Handley Power Station has five gas-fired generating units with a maximum output of 1471 MW. The discharge canal is approximately 15 m wide, 3-4 m deep and 1.5 km long (For a map of Lake Arlington and the discharge canal see Williams and McMahon, 1986). Maximum heated effluent discharge rate was 4716.1 x 10^6 *l* day^{-1}.

Specimens of *C. fluminea* were collected bimonthly to monthly from a substratum of clay and gravel with an Eckman Dredge (sampling area = 0.19 m^2). The dredge was mounted on the end of streel pole which allowed it to be forced deeply into the substratum. Dredged material was passed through a 1 mm mesh sieve and all individuals of *C. fluminea* removed. Sampling continued until at least 100 individuals were taken (sample size range = 100-1586). The sieve retained all individuals with shell lengths greater than 0.9 mm. Living specimens were immediately fixed in 12% neutralized formaldehyde (by volume). At each collection ambient air and water temperatures, pH, conductivity, and dissolved oxygen concentration were recorded. Water hardness values were also determined on selected collection dates by EDTA titration (Hach, Model HAC-DT Water Hardness Test Kit). Daily records of mean and maximum discharge ambient water temperature and effluent discharge rate were obtained from the Texas Electric Service Company.

After return to the laboratory the shell lengths (SL, the greatest anterior-posterior dimension across the shell valves) of each individual in the collection were measured to the nearest 0.1 mm. The shell lengths of larger individuals (SL $>$ 6.0 mm) were measured with a dial caliper while those of smaller individuals (SL $<$ 6.0 mm) were measured with an ocular micrometer mounted in a dissecting microscope under 10X magnification. For each collection the number of individuals in each 0.2 mm size class were expressed as a percentage of the total sample size and plotted as frequency histograms in sets corresponding to collection dates. Visual examination of size class distribution across sequential collections allowed each sample to be divided into separate generations characterized by distinctly different shell length distributions (after the method of Aldridge and McMahon, 1978). A mean SL, standard deviation, and range of SL were then computed for each generation in each sample.

RESULTS

The mean conductivity of discharge water during the collection period was 274 μmho cm^{-2} (s.d. = ± 35.1, s.e. = ±5.9, range = 190-320, n = 35). Mean water hardness was 102 mg Ca l^{-1} (s.d. = ± 19.5, range = 83-122, n = 3). Both values are indicative of moderately hard waters. Mean pH (computed from H^+ concentrations) was 7.78 (s.d. = ± 0.56, s.e. = ± 0.10, range = 6.69-8.52, n = 35) which is characteristic of relatively alkaline habitats. Mean ambient dissolved 0_2 concentration was 7.6 mg 0_2 l^{-1} (s.d. = ± 0.4, range = 5.5-12, n = 29). The mean difference between discharge water ambient 0_2 concentration and that at full air saturation was -0.7 mg 0_2 l^{-1} (s.d. = ± 1.6, s.e. = ± 0.3, range = ± -3.5-1.9, n = 29) indicating that the resident *C. fluminea* population was rarely if ever exposed to biologically significant levels of hypoxia.

Mean ambient air temperature at collection was 22.4°C (s.d. = ± 7.7, s.e. = ± 1.3, n = 35). Air temperature reached a maximum of 36°C on 28 July 1981, and a minimum of 6.7°C on 8 February 1982. Mean ambient discharge water temperature at the time of collection was 26.7°C (s.d. = ± 8.7, s.e. = ± 1.4, n = 35). A peak discharge water temperature of 40.8°C occurred on 29 June 1981, and a minimum temperature of 10.5°C on 8 February 1982 (Fig. 1). Daily mean discharge water temperatures (monitored continuously by the Texas Electric Service Company) were averaged over sequential three day periods (Figs. 1 and 2). The mean of these three day average discharge temperatures over the sampling period was 25.3°C (s.d. = ± 8.1, s.e. = ± 0.6, n = 196). A maximum three day average temperature of 39.0°C was recorded on 13-15 August 1982, and a minimum of 11.3°C on 16-18 January 1982 (Figs. 1 and 2). The mean daily maximum discharge water temperature (computed as sequential three day averages) over the sampling period was 27.1°C (s.d. = ± 8.5, s.e. = ±0.6, n = 195). The highest three day average maximum temperature recorded was 41.7°C on 13-15 August 1982. A minimum temperature of 12.4°C was recorded on 13-15 January 1982, 16-18 January 1982, and 7-9 February 1982 (Fig. 2).

The monthly mean of daily discharge flow rates averaged 2545.8 x 10^6 *l* day^{-1} (s.d. = ± 558.9 x 10^6, s.e. = ± 119.2 x 10^6, n = 22). The maximum mean monthly discharge rate of 3628.6 x 10^6 *l* day^{-1} occurred in June 1981, while a minimal monthly mean discharge rate of 1649.4 x 10^6 *l* day^{-1} occurred during November 1981 (Table 1). An absolute maximum discharge rate of 4623.5 x 10^6 *l* day^{-1} was recorded on 8 June 1981, 24, 25, and 26 July 1982, and 27 and 30 August 1982. There was no water discharged on 2 December 1981. The mean of the monthly averages of discharge current flow rate over the course of the study was 3.9 m min^{-1} (s.d. = ± 0.9, s.e. = ± 0.2, n = 22). Maximum and minimum average monthly discharge currents were 5.6 m min^{-1} and 2.5 m min^{-1} in June 1981, and November 1981, respectively (Table 1).

The means and standard deviations of shell length (SL) for each generation in each sample are displayed in Figure 1. Two generations per year occurred in the Handley Power Station discharge canal. An "early" generation resulting from a spring reproductive period appeared in the late spring and early summer of each year of collection and is designated in Figure 1 as either E-81 which first appeared as a distinct size class with a mean SL of 3.6 mm on 20 May 1981, or as E-82 which first appeared in the samples on 7 July 1982 with a mean SL of 5.1 mm. A second, or "late" generation resulting from a second, late summer reproductive period ap-

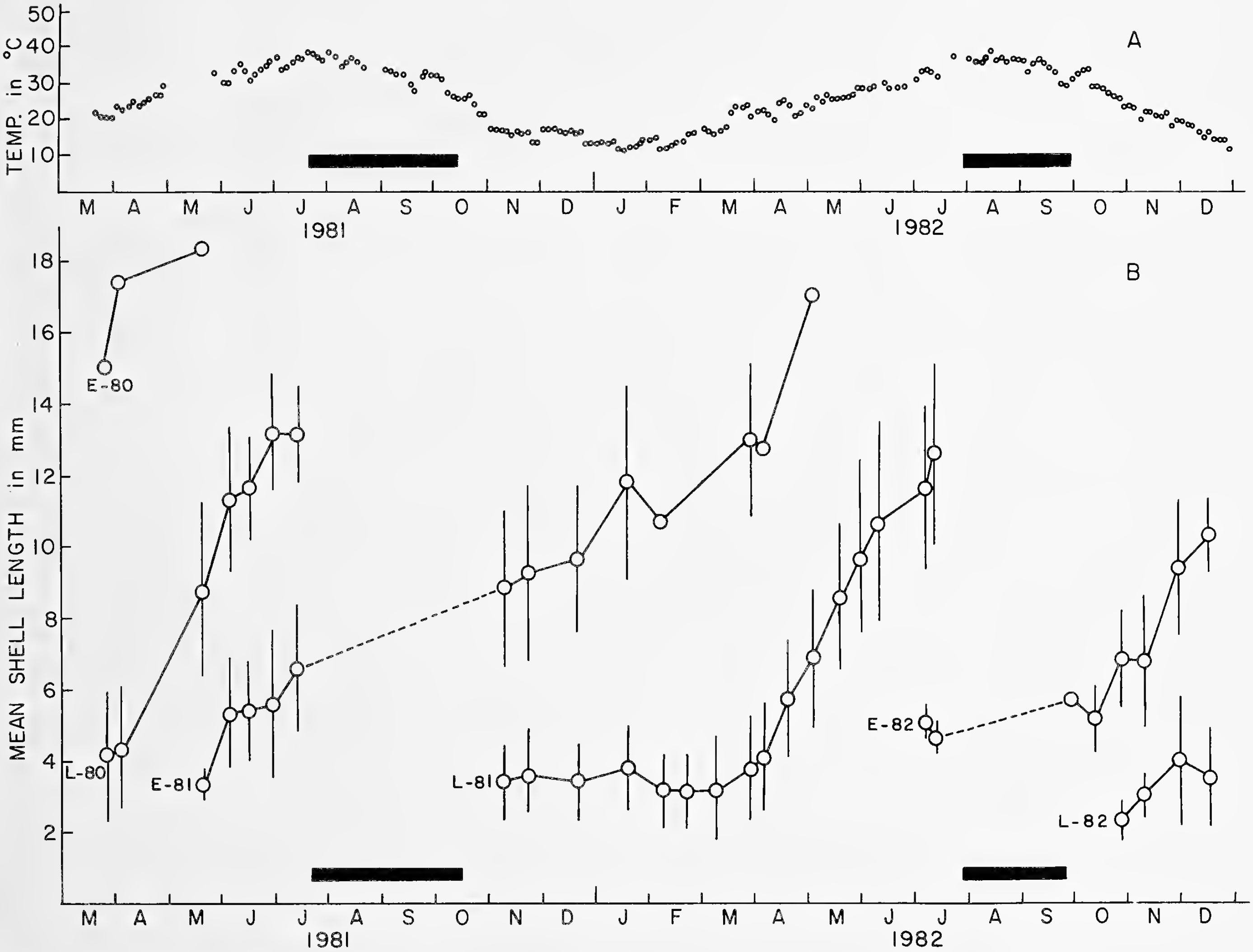

Fig. 1. Generation mean shell lengths of the *Corbicula fluminea* population in a power station's thermal effluent discharge canal on Lake Arlington, Texas. The horizontal axis for both figures is months over the collection period. **A.** Variation in the ambient water temperature of the discharge canal over the collection period. Vertical axis is ambient water temperature in °C, open circles are three day averages of mean daily discharge water temperatures and solid horizontal bars indicate periods when the *C. fluminea* population was thermally eliminated from the discharge canal. **B.** Generation mean shell lengths for consecutive samples of the discharge *C. fluminea* population. The horizontal axis is mean shell length in millimeters, open circles are the mean shell lengths of each generation in each consecutive population sample over the collecting period, and the vertical bars about each mean are standard deviations. Generation shell length means without standard deviation bars represent sample sizes of less than six individuals. Circles connected by solid lines indicate the change in mean shell lengths through time of specific generations identified by the reproductive period that gave rise to that generation (*i.e.* E-81 indicates the generation produced during the early reproductive period of 1981 and L-82, that produced during the late reproductive period in 1982). The dashed line connects the mean shell lengths of the E-81 and E-82 generations across periods during which all individuals were thermally eliminated from the population. The solid horizontal bars indicate periods when the *C. fluminea* population was thermally eliminated from the discharge canal.

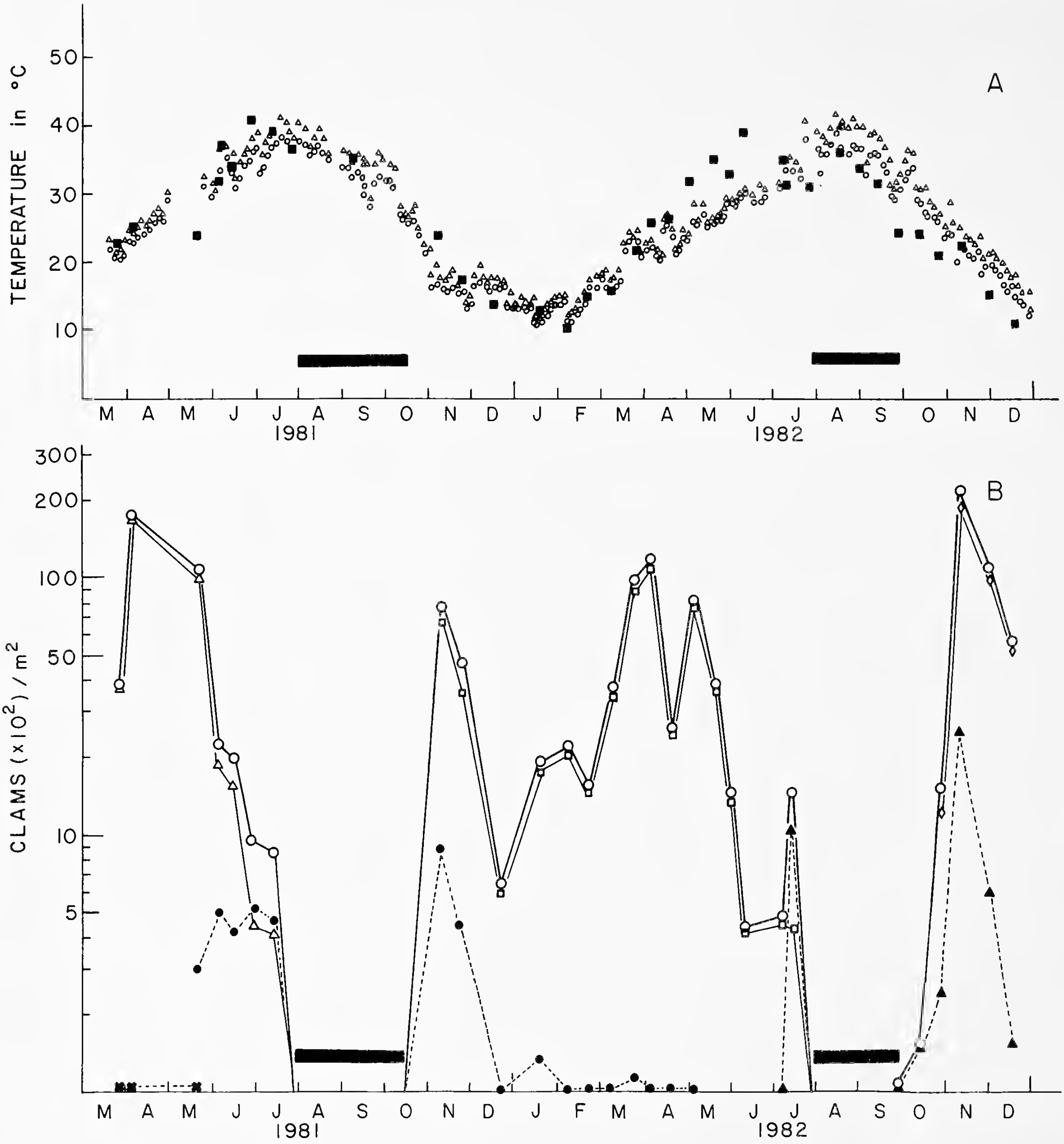

Fig. 2. Seasonal variations in the density of a *Corbicula fluminea* population in relation to ambient water temperature in the thermal effluent discharge canal of a power station on Lake Arlington, Texas. The horizontal axis for both figures is months of the year over the collecting period. **A.** Seasonal variation in ambient water temperature. Vertical axis is ambient water temperature in °C, open circles are averages of mean daily water temperatures for consecutive three day periods, open triangles are averages of daily maximum water temperatures for consecutive three day periods, solid squares are ambient water temperatures measured at the collection site at the time of collection, and solid horizontal bars indicate periods when all individuals of *C. fluminea* were thermally eliminated from the discharge canal. **B.** Seasonal variations in the densities of the total *C. fluminea* population and individual generations over the course of the collection period. The vertical axis is density in hundreds of clams/m² on a logarithmic scale. Open circles connected by solid lines are the density of the total population. The densities of individual generations are indicated as follows: E-80 (resulting from the early reproductive period of 1980), exes connected by dashed lines; L-80 (resulting from the late reproductive period of 1980), open triangles connected by solid lines; E-81, solid circles connected by dashed lines; L-81, open squares connected by solid lines; E-82, solid triangles connected by dashed lines; L-82 open diamonds connected by solid lines. The solid horizontal bars represent periods when all individuals of *C. fluminea* were thermally eliminated from the population.

Table 1. Monthly values of mean water discharge rate, standard deviation, standard error, range and mean current flow rate in the heated effluent discharge canal of the Handley Steam Electric Power Station, Tarrant County, Texas.

Month	Mean Monthly Discharge Rate lx10^6/day	Standard Deviation lx10^6/day	Standard Error lx10^6/day	Range lx10^6/day	Days Recorded	Mean Monthly Flow Rate m/min
Mar., 1981	1899.0	±572.4	±102.8	59.1-2434.8	31	2.9
Apr., 1981	1859.8	±533.5	±97.4	759.4-2926.1	30	2.9
May, 1981	2251.7	±885.4	±159.0	781.3-3519.4	31	3.5
Jun., 1981	3628.6	±736.3	±134.4	2032.0-4623.5	30	5.6
Jul., 1981	3375.4	±608.5	±109.3	2075.2-4259.0	31	5.2
Aug., 1981	2598.2	±816.1	±151.5	352.5-4432.7	29	4.0
Sep., 1981	2424.7	±549.9	±100.4	1253.0-3425.8	30	3.7
Oct., 1981	2411.5	±545.7	±98.0	1253.0-3425.8	31	3.7
Nov., 1981	1649.4	±935.7	±170.8	60.6-3324.2	30	2.5
Dec., 1981	2248.3	±844.9	±151.7	0.0-4201.8	31	3.5
Jan., 1982	2752.8	±1049.8	±188.6	1293.9-4601.5	31	4.2
Feb., 1982	2462.8	±675.8	±127.7	1321.7-3483.9	28	3.8
Mar., 1982	2419.8	±780.1	±140.1	821.5-4201.6	31	3.7
Apr., 1982	2308.3	±774.8	±141.5	1312.6-3595.8	30	3.6
May, 1982	2256.8	±517.8	±93.0	1331.1-2882.7	31	3.5
Jun., 1982	2714.5	±781.1	±142.6	1334.4-4220.2	30	4.2
Jul., 1982	3448.9	±879.1	±157.9	1500.1-4623.5	31	5.3
Aug., 1982	3462.4	±884.0	±158.8	2075.2-4623.5	31	5.3
Sep., 1982	3164.0	±707.2	±128.3	2056.7-4242.0	30	4.9
Oct., 1982	2538.0	±826.7	±148.5	1352.9-3618.7	31	3.9
Nov., 1982	2246.2	±827.2	±148.6	58.9-3310.9	30	3.5
Dec., 1982	1886.6	±867.8	±155.9	58.9-3326.2	31	2.9

peared in early autumn and is designated in Fig. 1 as either L-81, first occurring in the samples on 9 November 1981, at a mean SL of 3.4 mm or as L-82, first occurring on 27 October 1982, with a mean SL of 2.3 mm (Fig. 1). Also occurring during the early portions of the sampling period were the E-80 and L-80 generations which resulted from respective spring and fall reproductive periods in 1980 (Fig. 1).

During both 1981 and 1982 two annual peaks of density occurred in the discharge canal *C. fluminea* population, the first in early April (16938 clams/m^2 on 3 April 1981, and 11889 clams/m^2 on 5 April 1982) and a second in mid-fall (7656 clams/m^2 on 9 November 1981, and 21930 clams/m^2 on 10 November 1982). These spring and fall density maxima were associated with the appearance and rapid accumulation of new individuals of the "early" and "late" generations, respectively (Fig. 2) (Williams and McMahon, 1986).

The densities of all generations declined rapidly in both years of the study in June and early July as water temperatures rose above 30°C (Fig. 2). All living individuals were eliminated from the discharge canal by the end of July in both 1981 and 1982 (Fig. 2). This mid-summer extinction of all living clams was associated with a rise in daily, average, ambient water temperature above 36°C and with daily water temperature maxima generally greater than 40°C (Fig. 2). Following this apparent mid-summer thermal extinction, no living individuals of *C. fluminea* were taken in the discharge canal until 9 November 1981 or 29 September 1982 (Fig. 2). This elimination of the *Corbicula* population from the discharge canal appeared to be entirely temperature dependent as daily discharge volume and flow rates (which could possibly carry individuals downstream away from the population) remained near mid-summer levels in the fall when the population displayed a rapid increase in density in both 1981 and 1982 (Table 1, Fig. 2).

In the fall of both 1981 and 1982 recolonization of the discharge canal by *C. fluminea* was extremely rapid and presumably resulted from the passive downstream transport of juvenile and young clams from a viable population occuring in the power station's intake canal and its associated lake inlet (Williams and McMahon, 1986; for a discussion of passive dispersal of juvenile *C. fluminea* on water currents see McMahon, 1982, 1983 and references therein). This permanent inlet canal population was a source of juvenile and young individuals which were entrained through the power station's steam condensers and carried into the discharge canal with condenser effluents (Williams and McMahon, 1986). As such, the rate of reestablishment of the discharge canal popoulation could provide an estimate of the downstream colonization rate of *C. fluminea* by passive hydrological transport. On 15 October 1981, no living clams occurred in the discharge canal, while on 9 November 1981, population density had reached a maximum of 7656 clams/m^2 yielding a downstream colonization rate of 319 clams m^{-2} day^{-1}. Correspondingly, only 6 clams/m^2 were recorded on 29 September 1982, density thereafter rose to a maximum of 21930 clams/m^2, yielding a downstream colonization rate of 522 clams m^{-2} day^{-1}. As the approximate substratum surface area of the discharge canal was 6.75 x 10^4 m^2, downstream dispersal rates in the entire canal can be estimated as 2.15 x 10^7 clams/day and 3.52 x 10^7 clams/day in the falls of 1981 and 1982, respectively. These high dispersal rates are associated with the fall reproductive period and release of large numbers of juveniles of the late generation (L-81 in 1981 and L-82 in 1982, Fig. 1) which accounted for the vast majority of recolonizing individuals (Fig. 2). After fall recolonization the shell length distribution of the early generations (E-81 and E-82) increased in size throughout the winter and reached a maximum of 17-18 mm before disappearing from the population in the following spring (Fig. 1). The late generations (L-80 and L-81) grew very little during the winter. Rapid growth occurred the following spring, the late generations reaching a maximum mean SL of 12 to 15 mm just before thermal extinction in mid-summer. Therefore, both the spring and fall generations have highly attenuated life cycles, each generally surviving one year or less in the discharge canal (Fig. 1). The analysis of generation growth patterns is complicated by continual immigration of individuals from intake populations into the discharge canal (Williams and McMahon, 1986). As such, the growth rates of small individuals (< 10 mm SL) in the discharge canal essentially reflect those of the population in the lake proper (see the data of Williams and McMahon, 1986). However, as larger specimens of *C. fluminea* (< 15 mm SL), not subject to passive hydrological dispersal (see below), maintained high growth rates in the discharge canal up to the point of thermal extinction it appears that temperatures approaching the upper lethal limit do no inhibit growth in this species (Fig. 1).

Only relatively small individuals of *C. fluminea* occurred in the discharge canal population. No living specimens with an SL of greater than 18.3 mm occurred among the 9868 individuals taken over the collection period. As both the intake canal (Williams and McMahon, 1986) and intake embayments behind the traveling screens (McMahon, 1977) harbor populations of *C. fluminea* with individuals ranging in SL from 1 mm to 40 mm and as individuals with SL's > 20 mm routinely occur in the discharge side of the condensers (McMahon, 1977) the lack of large living specimens in the discharge canal appears to indicate that there may be a maximum size in this species for successful passive hydrological dispersal and downstream settlement (Table 1).

In both 1981 and 1982, individuals of the late generations (L-80 and L-81) did not recolonize the discharge canal after thermal extinction even though individuals of these generations occurred in relatively high densities in upstream areas of both the intake canal and intake embayments and were of an SL range that would readily allow them to pass through the tubes of the power station's steam condensers (McMahon, 1977). As these generations did not reappear in the collections after thermal elimination (Figs. 1 and 2) they may have grown beyond a size at which successful downstream resettlement could normally occur in lotic habitats, even though the passive hydrological transport of similar sized individuals has been reported (Williams and McMahon, 1986; McMahon, 1977; Prezant and Chalermwat, 1984). As the maximum sizes of recolonizing individuals in the falls of 1981 and 1982, were 14.3 mm and 12.8 mm, respectively, and as no individuals of the previous years late generation were recovered after thermal elimination it appears that only individuals of *C. fluminea* of less than 15 mm SL or one year in age are able to successfully disperse to and colonize downstream habitats.

DISCUSSION

The *C. fluminea* population disappeared from the discharge canal of the Handley Power Station after average ambient water temperatures rose above 36°C in both 1981 and 1982 (Fig. 2), suggesting that the absolute upper lethal limit of this species lies very near that temperature. While *C. fluminea* can tolerate short-term (acute) exposures as high as 43°-47°C (Mattice, 1979; Mattice and Dye, 1976; Isom, *et al.*, 1978; McMahon, 1979), it is far less tolerant of long-term (> 24 h) exposures to elevated temperatures (Mattice and Dye, 1976). Our field estimate of upper lethal limit at 36°C corresponds well with the long-term (96 hour exposure) maximum upper lethal limit of 34°C reported in a laboratory study of individuals of *C. fluminea* acclimated to 32°C (Mattice, 1979; Mattice and Dye, 1976). Other laboratory determinations of tolerance of extended exposure to high temperatures place the upper lethal limit of *C. fluminea* between 33.5°C and 38.0°C (Cherry, *et al.*, 1980; Habel, 1970; Mudkhede and Nagabhushanam, 1977). In artificial outdoor ponds *C. fluminea* is reported to have a somewhat lower long-term temperature tolerance, reported upper lethal limits ranging from 30°-35°C (Busch, 1973; Greer and Ziebell, 1972; Habel, 1970; Haines, 1979). However, such estimates may be confounded by exposure of experimental individuals to severe hypoxic stress in artificial standing water habitats (Busch, 1974; Habel, 1970; McMahon, 1979).

Another *C. fluminea* population in a discharge canal receiving heated effluents has also been reported to have been eliminated when mid-summer water temperatures reached 40°C (Dreier, 1977; Dreier and Tranquilli, 1981). Such data have lead to suggestions that the introduction of heated discharge water into intake areas either by backflashing through steam condensers (Goss, *et al.*, 1979; Mattice, 1979; Mattice, *et al.*, 1982) or by recirculation of heated effluents from discharge canals into intake structures (Mattice, 1979; Mattice, *et al.*, 1982) could raise water temperatures to levels which would eradicate *Corbicula* populations and, therefore, eliminate the major sources of juvenile and small clams impinging a power station's raw water systems.

Periodic recycling or backflushing of thermal effluents through steam condensers into intake areas may not be a feasible eradication procedure for *C. fluminea* as this species can withstand short-term exposures (15-30 min) to temperatures ranging from 43-45°C (Mattice and Dye, 1976; Isom, *et al.*, 1978; McMahon, 1979). Such temperatures are rarely achieved in the thermal effluents of most power stations (Figs. 1 and 2, Dreier and Tranquilli, 1981; Bird, 1976; McMahon, 1975, 1976a; Cherry *et al.*, 1980; Gibbons and Sharitz, 1974; Esch and McFarlane, 1976). Indeed, the mixing of backflushed heated effluents with cooler intake waters would probably reduce their temperatures well below lethal levels.

While short-term temperature shock appears impractical as a control measure for *Corbicula*, the results of our observations indicate that longer-term recycling of thermal effluents into intake areas during warmer summer months may have promise as a control methodology. Summer water temperatures in Texas lakes and reservoirs (and presumably in other aquatic habitats in the southern United States) routinely reach or surpass 30° to 32°C (see the data of Aldridge and McMahon, 1978; McMahon, 1975, 1976a, 1976b; Bird, 1976; Tommey, 1976). Long-term recirculation of thermal effluents into intake areas during these periods could allow maintenance of intake water temperatures above the field upper lethal limit of 36°C eliminating *C. fluminea* populations from intake canals, embayments and other structures within 14 days (Figs. 1 and 2).

In the summers of 1981 and 1982 the *C. fluminea* population in the Handley Power Station's discharge canal was reestablished (presumably by individuals hydrologically transported through the steam condensers from resident intake populations) in late September (1982) or early October (1981). In both of these years reestablishment of the population did not occur until average ambient water temperatures in the discharge canal had fallen below approximately 30°C (Figs. 1 and 2), a temperature approximately 6°C below the apparent upper lethal limit. Clams remained absent from the canal during the periods when water temperatures ranged from 30-36°C (September through early October) even though entrainment of young individuals through steam condensers into the discharge canal remained at relatively high levels (> 10^7 juveniles/day, see the data of Williams and McMahon, 1986). The inability of juvenile *C. fluminea* to become successfully established in the substratum at temperatures above 30°C is somewhat surprising as this species has been reported to survive summer temperatures above 30°C in natural populations (Aldridge and McMahon, 1978; Dreier and Tranquilli, 1981; Williams and McMahon, 1986). It is tempting to hypothesize that at temperatures above 30°C small individuals of *C. fluminea* may be incapable of successfully producing or anchoring themselves to the substratum with the larval mucilagenous byssal thread (Kraemer, 1979; Sinclair and Isom, 1963) and, therefore, would be incapable of successful settlement at these temperatures. Indeed, sharp declines in the density of the *C. fluminea* population in the Handley Power Station's discharge canal occurred in both 1981 and 1982, as spring ambient water temperatures rose above 30°C (Fig. 2), indicating not only an inhibition of settlement by newly released juveniles, but also the possible hydrological removal of individuals that had become established in the substratum the previous fall. The possibility that temperatures greater than 30°C can inhibit successful settlement of juvenile *Corbicula* has very important implications to the development of control measures for this species in industrial facilities utilizing large quantities of raw water. Certainly, the effects of temperature on byssus formation and successful establishment in the substratum by juvenile *C. fluminea* warrants further study.

High sublethal temperatures appeared to have little or no effects on the generation growth rates of the *C. fluminea* population in the Handley Power Station's discharge canal. Instead, growth rates remained constant or increased as the upper thermal limit of 36°C was approached (Fig. 1). Examination of other published growth rate data for *C. fluminea* also seems to indicate a lack of high temperature inhibition of growth (Aldridge and McMahon, 1978; McMahon and Williams, 1986; Pool and Tilly, 1977). Rather, increasing temperatures appear to have direct stimulatory effects on growth rate (McMahon and Williams, 1986), including evidence for stimulated growth rates in populations receiving thermal effluents (Mattice, 1979; Dreier and Tranquilli, 1981).

Juvenile (SL = 0.2 mm) and young specimens (SL < 5.0 mm) of *C. fluminea* are passively transported in large numbers on water currents (Goss and Cain, 1977; Goss *et al.*, 1979; Sickel, 1979; Sinclair, 1964; Sinclair and Isom, 1963). Entrainment of the Handley Power Station's raw water systems by such hydrologically transported specimens has been reported to reach levels on the order of 10^8 clams/day (Williams and McMahon, 1986). Such passive downstream dispersal has been claimed to be responsible for the rapid spread of this species in North American drainage systems (McMahon, 1982, 1983). Recently, it has been suggested that such hydrological transport is associated with the ability of *C. fluminea* to produce mucus draglines from the exhalent siphon that increase it's susceptibility to passive suspension in the water column (Prezant and Chalermwat, 1984). Certainly, passive hydrological transport accounted for the extremely rapid reestablishment, after thermal elimination, of the Handley Power Station's discharge canal population of *C. fluminea* as fall temperatures returned to favorable (< 30°C) levels (Fig. 2). The reestablishment of the discharge canal population was extremely rapid, densities increasing from 0 to 7656 clams/m^2 in 25 days in 1981 and from 6.4 to 21930 clams/m^2 in 42 days in 1982 (Fig. 2) yielding colonization rates of 319 clams m^{-2} day^{-1} and 522 clams m^{-2} day^{-1}, respectively. A similar mid-summer thermal extinction and fall reestablishment of a discharge canal *C. fluminea* population has been reported for an electrical power station on Lake Sangchris, Illinois. This population's density increased from 3 clams/m^2 (below 1 m in depth) on 12 August, 1975 (after water temperatures had reached 40°C) to 430 clams/m^2 in February, 1976 (Dreier, 1977; Dreier and Tranquilli, 1981) yielding a recolonization rate of 2.5 clams m^{-2} day^{-1}. After a mid-winter extinction of a *C. fluminea* population occurred in the New River, Virginia, when water temperatures fell below 2°C clam densities recovered from 0.0 clams/m^2 in early April to 1000 clams/m^2 in late September, (Cherry *et al.*, 1980; Rodgers, *et al.*, 1979) yielding a recolonization rate of 5.5 clams m^{-2} day^{-1}. As the vast majority of individuals in this reestablished population were immature (SL < 7.5 mm) (Cherry, *et al.*, 1980; Rodgers, *et al.*, 1979), it must be assumed that they were passively carried downstream on water currents from a viable upstream population.

The results of this study indicate that only individuals with an SL of less than 15 mm became reestablished in the

Handley Power Station's discharge canal after thermal extinction. The vast majority of these individuals were juveniles of the most recent late generation with an SL less than 5 mm (Figs. 1 and 2). Similarly, a portion of the New River in Virginia was recolonized by individuals of *C. fluminea* less than 13.5 mm SL following a mid-winter extinction of the endemic population (see above) (Cherry, *et al.*, 1980; Rodgers, *et al.*, 1979), indicating that successful downstream dispersal and colonization is essentially limited to smaller, mostly immature specimens. While larger adult specimens are also subject to passive hydrological transport (Williams and McMahon, 1986), their numbers are so small in relation to passively transported juvenile and immature specimens as to be of no real significance to the passive downstream dispersal of this species.

The extensive capacity of juvenile *C. fluminea* for passive hydrological transport is not only associated with its ability to invade and foul industrial raw water systems (Goss, *et al.*, 1979), but may also be primarily responsible for this species' remarkably rapid disersal in, and colonization of the downstream portions of the major North American drainage systems in which it has become established (McMahon, 1982, 1983). The great capacity of *C. fluminea* for dispersal along with its reduced age and size at maturity, high growth rates, elevated fecundity, short generation times, abbreviated life cycles and hermaphroditic reproductive schesis make this species highly adapted for reproduction and survival in disturbed, highly variable, lotic freshwater habitats, particularly those subjected to human interference (McMahon, 1982, 1983). These characteristics, in large measure, also account for the nature of *C. fluminea* as a pest species in North America.

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