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Proceedings, First International Corbicula Symposium
Texas Christian University
Fort Worth, Texas 76129 U.S.A.
October 13-15, 1977

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POPULATION DYNAMICS OF THE ASIATIC CLAM, *Corbicula fluminea* (MÜLLER), IN THE CONCRETE-LINED DELTA-MENDOTA CANAL OF CENTRAL CALIFORNIA

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ABSTRACT

Corbicula fluminea was studied in the Delta-Mendota Canal, California from September 1972 through November 1974. Clams inhabit thin incrustations on the concrete side-lining and disjunct sediment bars on the Canal bottom. Densities in the sediment bars typically are 10,000-20,000 clams/m^2. Two peaks (spring and late summer-fall) in spawning activity result in the appearance of two size classes annually. Larvae are brooded about one month and are released as pediveligers or juveniles. The side-lining incrustations are produced by the tube-building amphipod, *Corophium spinicorne*, and the colonial hydrozoan, *Cordylophora lacustris*, and are the principal habitat for recently set clams. The sediment bars are seasonally unstable and are an unfavorable habitat for larvae and small juveniles. These stages are initially recruited to the side-lining incrustations and secondarily recruited to the bottom as they reach lengths of 4-12 mm. Clams in bottom sediment bars attain lengths of over 40 mm and live at least into their fourth year. Growth of *C. fluminea* is restricted to the months between March and October when water temperatures are above 14°C. The high densities observed in the sediment bars appear to result, at least in part, from hydraulic accumulation.

This research was supported, in part, by U.S. Bureau of Reclamation contracts 14-06-200-6043A and 14-06-200-7762A to the California Academy of Sciences, San Francisco, California.

Key Words: *Corbicula fluminea*, Asiatic clam, Delta-Mendota Canal, California, recruitment, Sacramento-San Joaquin Delta, spawning, growth.

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INTRODUCTION

The Asiatic clam, *Corbicula fluminea* (Müller) (*C. manilensis* of recent authors) has successfully invaded western, southern and eastern United States during the last forty years (Sinclair, 1971). Evaluation of its eventual impact in both human and biological terms has been limited historically by ignorance of its biology. Published accounts typically rely heavily on biological studies of the genus in Asia (Sinclair and Isom 1963; Sinclair 1971) which may not be directly applicable to populations in the United States. Knowledge of the biology and population dynamics of the Asiatic clam in this country remains patchy and largely unknown.

Corbicula fluminea appears to thrive in highly modified or man-made habitats such as the large concrete-lined canals of central and southern California (Ingram, 1959; Hanna, 1966). The Delta-Mendota Canal (DMC), one of the larger canals in the U.S. Bureau of Reclamation's Central Valley (California) Project, has supported dense populations of *C. fluminea* since shortly after it began operation in 1951 (Prokopovich, 1968). These *Corbicula* populations, reaching 10,000 to 20,000 clams/m², were considered instrumental in the biodeposition of extensive sediment bars which reduced delivery capacity and required expensive dewatering and dredging operations (Prokopovich and Hebert, 1964; Prokopovich, 1969).

Previous data on *C. fluminea* in the DMC were collected incidental to geologic studies of DMC sediments during periodic winter dewaterings (Swain and Prokopovich, 1969; Prokopovich, 1970). These studies consistently indicated that the DMC was highly productive habitat for *C. fluminea,* although the high frequency of empty valves in sediments led Prokopovich (1970) to describe the canal as a "clam cemetery". Data limited to winter dewatering periods were inadequate to answer basic questions about the biology and population dynamics of these clams. Year round information was necessary to plan adequate procedures to minimize the fouling problems in future DMC operations.

This study was undertaken to provide that information. A dewatering and dredging operation during November-December 1972 enabled initiation of sampling in "cleaned" canal. The objectives were (1) to document the reinfestation of the DMC by *Corbicula* following the dredging operation; (2) to contribute to knowledge of *Corbicula* in the United States by examining aspects of its biology and population dynamics in the DMC; (3) to determine factors contributing to the high clam densities encountered in the DMC.

THE STUDY AREA

The DMC is located on the western side of the San Joaquin Valley and extends from the Sacramento-San Joaquin Delta near Tracy, California to Mendota Pool on the San Joaquin River about 48 km west of Fresno (Fig. 1). The DMC conveyance system includes an unlined intake channel, the Tracy Pumping Plant and the 182 km, mostly concrete-lined (153 km) canal. Water is lifted about 60 m by the pumping plant and delivered through three discharge tubes to the beginning of the concrete-lined section (km 5.6).

The canal is about 30.5 m wide at the top and 14.6 m at the bottom with a maximum water depth of about 5.5 m. It has a constant slope of 0.00005 (4.7 cm/km) and a designed capacity of 130 m³/sec. Mean velocity is 1.2 m/sec. Water level is controlled by 21 check structures which subdivide the DMC into pools (Swain and Prokopovich, 1969).

The immediate source of DMC water is the organically productive Sacramento-San Joaquin Delta. There are two primary components of Delta water at the canal intake (Ball and Lentz, 1973): 1. Sacramento River water, relatively low in total dissolved solids (TDS) and delivered via the Delta Cross Channel (Fig. 1), predominates during high tides; San Joaquin River water, relatively high in TDS and delivered via Grant Line Canal and Old River, is the major component during low tides. As a rule, excursion of Sacramento River water by high tides results in a decrease in dissolved solids of DMC water; whereas, excursion of San Joaquin River water at low tides increases TDS. Canal water thus consists of several masses of different

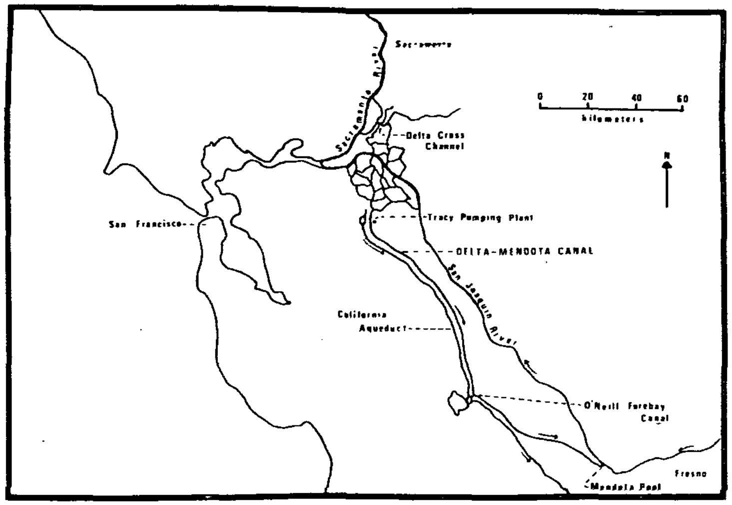

Figure 1. The Delta-Mendota Canal and associated water systems, Central California.

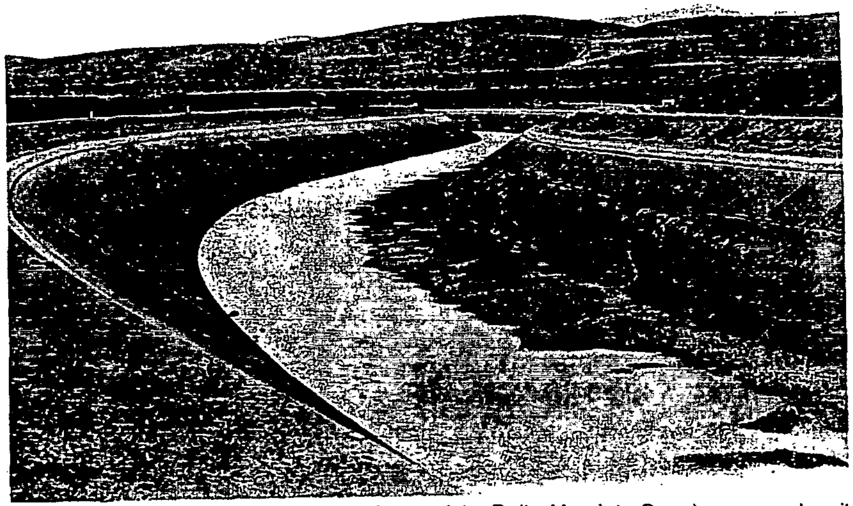

Figure 2. Typical sediment bar on the invert of the Delta-Mendota Canal as seen when it was dewatered.

salinity (and productivity) with a residence time of about 2.5 days (Anon., 1973).

Disjunct sediment bars (Fig. 2) occur on the canal bottom. These bars constitute the primary habitat for *Corbicula fluminea* in the DMC. Sediment composition is typically silt and clay (about 20% by weight), inorganic sand with some admixtures of shell fragments and peaty debris (about 50%) and gravel and clam valves (about 30%). Virtually all of the gravel-sized fraction is living and relict (empty valves) *C. fluminea* (Prokopovich, 1973).

Biological incrustations on the concrete side-lining (slopes) between km 5.6 and 32.0 (Fig. 3) provide another habitat for Asiatic clams on the canal. These incrustations, formed by the tube-building amphipod, *Corophium spinicorne* Stimpson, and the colonial hydrozoan, *Cordylophora lacustris* Allman, were usually less than 6 mm thick.

MATERIALS AND METHODS

Both the amphipod/hydrozoan incrustations on the concrete side-lining (seven stations) and the sediments on the bottom (nine stations) were sampled at four week intervals from January 1973 until the DMC was again dewatered in November 1974. Biweekly plankton samples were taken at three stations to corroborate data on the frequency and duration of reproductive activity. Table 1 locates the stations by kilometer from the source and identifies the type(s) of sample(s) collected at each.

Figure 3. Typical side-lining station (km 6.9) exposed during dewatering. Concrete panels are approximately 2.6 m square.

The engineering term "invert" will be used hearin to distinguish the concrete-lined bottom from the earth-lined bottom and the concrete-lined side slopes. Invert sample sites were selected because of the historical presence of sediment bars (Prokopovich, 1968) and the proximity of bridges from which sampling could be accomplished. A special grab was developed to sample the invert sediments. Essentially a modified Ekman grab with a 30 foot handle in detachable ten foot sections, it is closed hydraulically with a hand operated power pack generating 800 lbs/in^2 and samples a surface area of 400 cm.^{2}

Samples were taken along a transect at on bar width, the actual number of samples taken at each site varied among trips from 0-5. A specific spot along any transect was never sampled on two consecutive trips. Since clams are rarely found in anaerobic sediments encountered more than 5-10 cm below

Kilometer	Type(s) of Sample(s)	Kilometer	Type(s) of Sample(s)
0.1	P	31.2	S
5.6	S	59.2	B
6.9	S	81.3	B
9.1	S,B	103.5	B
12.0	S	125.0	B,P
17.1	S,B	167.7	B,P
22.5	S,B	177.2	B

Table 1. Location of stations (kilometers from DMC source at Old River) and type(s) of sample(s) taken at each. (S = side-lining incrustations, B = bottom of canal, P = plankton).

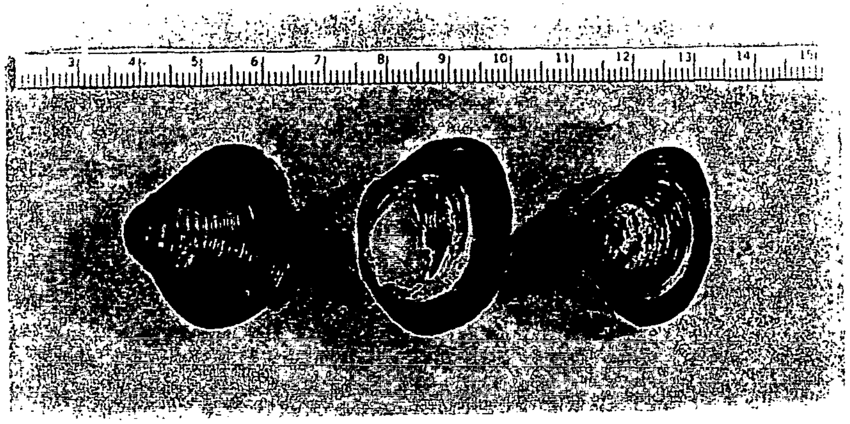

Figure 5. *Corbicula fluminea* from the Delta-Mendota Canal. Clam at left is typical of clams from earth-lined reaches. Clams in center and at right are from bottom sediments in concrete-lined reaches.

mm and are without umbonal erosion (Fig. 5). Both live clams and relict valves in the earth-lined reach are frequently incrusted by the freshwater entoproct, *Urnatella gracilis* Leidy.

Side-Lining Incrustation Populations

Corbicula fluminea was not present in the amphipod/hydrozoan incrustations when sampling began in January 1973; however, by fall and winter 1973-74, it had attained densities exceeding 21 clams/70 cm² sample (3000/m²) (Fig. 6). Populations declined during spring and by early summer 1974 ranged between 0.26 and 1.69 clams/70 cm² (37-241/m²). Clam density was rapidly increasing when the DMC was dewatered in November 1974 (Fig. 6).

The decline of these populations during spring appears to result from a combination of physical displacement and clam behavior. During winter, incrustations become loosely compacted and unstable. Extensive sloughing occurs locally. Deterioration of incrustations corresponds with a winter decline in the density of the colonial hydrozoan, *Cordylophora lacustris* (Eng, 1975). Seasonally reduced water velocity (Table 2) allows the accumulation and persistence of less compact incrustations. Subsequent increased pumping during late winter and spring removes the weakened incrustations and associated clams from the slopes.

The concrete slope underlying the incrustations is an impenetrable barrier to clams. Larger clams are more exposed and become increasingly vulnerable to displacement by water current. Attempts by growing clams to remain buried result in net downward movement with ultimate loss from side-lining populations. This downward movement may be accentuated in autumn as water temperature declines. Annandale *et al.* (1919) reported that at least one *Corbicula* species, *C. fluminalis*, burrows deeper into the substrate during the winter.

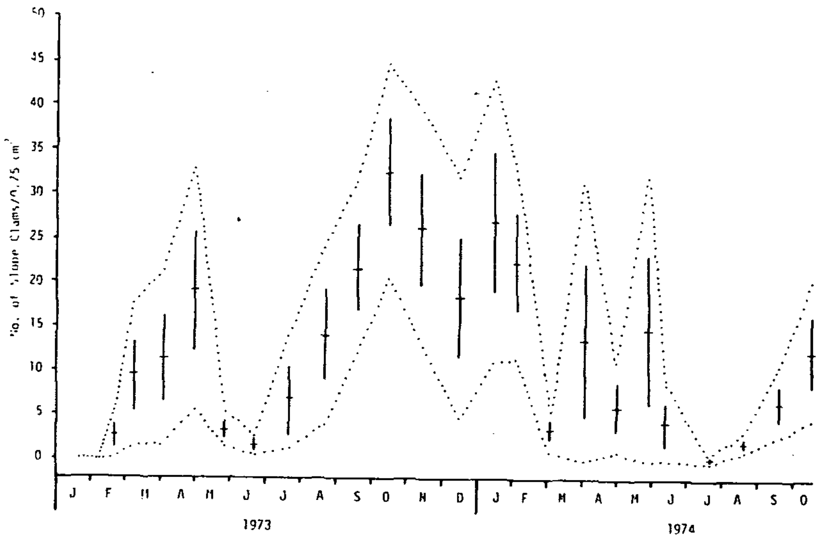

Figure 6. Density of *Corbicula fluminea* in amphipod/hydrozoan incrustations on the concrete-lined side slopes of the Delta-Mendota Canal. Horizontal lines are sample means. Vertical lines are standard errors of the means. Broken lines enclose 95% confidence limits.

Date	Water (m^3/sec) at head	Stations (km)						
		9.1	17.1	22.5	59.2	81.3	103.5	125.0
1973								
1/23	<1	-	-	-	-	-	-	3.3
2/21	1	-	-	-	-	-	-	3.3
3/19	11	3.3	4.9	0	2.1	1.8	5.8	3.3
4/12	23	3.3	5.2	0	2.4	2.1	5.8	3.0
4/30	119	2.1	2.4	0	1.8	0.6	5.5	3.7
5/28	113	0	2.4	0	0	0	4.6	3.7
6/25	133	0	0	0	0	0	4.6	2.7
7/23	133	0.6	0	0	0	0	0	3.3
8/20	133	3.3	0	0	0	0	0	tr
9/17	116	0	6.4	0	0	0	5.2	0
10/15	98	3.7	6.1	0	1.2	0	4.6	4.6
11/13	96	3.3	7.3	0	1.2	0	4.6	4.9
12/11	31	4.9	7.0	1.2	1.2	0	6.1	4.6
1974								
1/08	25	6.1	8.2	0	tr	0	5.2	4.9
2/05	71	6.4	8.2	0	1.2	0	5.5	4.9
3/05	133	3.3	5.8	0	0	0	5.5	3.7
4/02	85	tr	5.5	0	tr	0	3.7	4.3
4/30	98	0	5.2	0	0	0	4.0	3.3
5/28	134	0	4.6	0	0	0	4.0	2.7
6/25	134	0	4.3	0	1.2	0	5.8	1.8
7/23	132	0	4.6	0	tr	0	4.9	0
8/20	133	0	3.0	0	tr	0	4.6	0
9/17	95	0	4.6	0	0	0	5.2	2.7
10/15	125	0	5.2	0	0	0	3.7	3.0
11/15	0	-	-	-	-	-	-	-

Table 2. Seasonal changes in water delivery through the Delta-Mendota Canal and width (m) of sediment bars at established stations. tr = trace.

Invert Sediment Bar Populations

The density of *Corbicula fluminea* in invert sediment bars was variable (Table 3) ranging from 0 to 4248/400 cm^2 sample (131,200/m^2). Highest densities were at upstream locations where small clams predominated.

A pronounced variation in the size frequency distribution of *C. fluminea* occurs within the Canal. In November 1972 clams larger than about 15 mm were relatively uncommon between the Canal head (km 5.6) and km 24.0 but dominated downstream samples (Fig. 7). By contrast, clams less than 15 mm dominated samples upstream from km 24, but with the exception of km 125, were virtually absent from downstream sites.

An extensive sediment bar, covering the invert to depths of from 0.3-1.0 m between km 21 and km 24, roughly separated the reaches where small size classes predominated from those dominated by larger clams. The length-frequency distribution of clams at km 22.5 was intermediate between those at upstream and downstream sites (Fig. 7). The infrequency of smaller clams downstream suggests that clams are recruited from upstream by drift on or near the bottom and that the bar transecting the invert was an effective barrier to further downstream transport.

If this hypothesis were true then elimination of upstream "barrier" bars should allow recruitment of small clams throughout the Canal. Supportive evidence was obtained during the November 1974 dewatering. No "barrier" bars had developed during the two year period and small clams were present throughout the dewatered reaches (Fig. 7) while larger clams were again uncommon at upstream sites. The disappearance of clams from Pool 1 (km 5.6-19.2) before they reach 15-20 mm implies that the entire population, at least in this portion of the DMC, is transient. This possibility was not considered by earlier authors (Prokopovich, 1968, 1970; Swain and Prokopovich, 1969) who attributed the paucity of larger clams in the upper reaches to a mass mortality at about 10 mm. No evidence for size specific mortality was observed during this study; however, ample evidence for net downstream transport of clams and associated sediments was observed (Eng, 1977).

Reappearance of small clams at km 125 may be explained by recruitment through the O'Neill Forebay Canal which enters the DMC at km 111.5. This canal, which connects the DMC with O'Neill Forebay and the California Aqueduct system is the only juncture of the DMC with another water system between its source in the Sacramento-San Joaquin Delta and its terminus at Mendota Pool (Fig. 1).

The width of sediment bars at all stations fluctuated markedly during the study and each disappeared at least once during the first year after dewatering (Table 2). The stability of these bars was inversely related to the volume of water pumped through the Tracy Pumping Plant.

Downstream movement of clams and associated sediments may occur through bed-load transport. Bruun and Lackey (1962) describe bed-load transport as the intermittent sliding and rolling of coarse sand and gravel

Station	1973			1974		
	N	$\bar{x}$	$s_{\bar{x}}$	N	$\bar{x}$	$s_{\bar{x}}$
9.1 km	19	1624.89	425.0663	13	1778.15	814.6010
17.1 km	25	836.28	257.2287	39	522.10	111.2225
59.2 km	11	77.63	41.0966	8	71.37	35.5029
103.5 km	27	208.11	33.7743	40	502.97	59.9518
125.0 km	34	561.82	211.5523	34	492.29	63.2669

Table 3. Mean density (#/400 cm^2) of *Corbicula manilensis* in sediment bars on the invert of the Delta-Mendota Canal. N = number of samples.

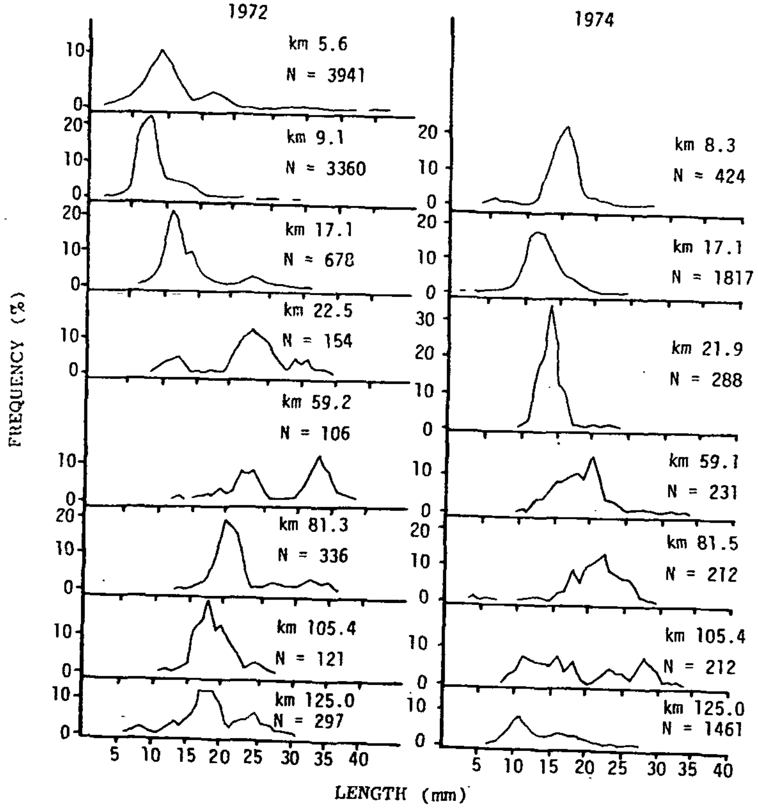

Figure 7. Length-frequency distribution of *Corbicula fluminea* from different invert sites during the 1972 and 1974 dewaterings of the Delta-Mendota Canal. km = distance in kilometers from the Canal source.

REPRODUCTION

Spawning activity of *Corbicula fluminea* in the DMC peaks biannually. Brooding occurs from mid-April through May and from mid-August through September (Fig. 9). In 1974 the frequency of sperm-bearing clams peaked prior to both spawning peaks; however, a third increase in sperm-bearing clam frequency (September-October) was not followed by increased spawning activity (Fig. 9). Ova at all stages of development are present from February through October (no data available for November-January). In the Sacramento-San Joaquin Delta, Heinsohn (1958) found *C. fluminea* bearing mature ova throughout the year. Since mature ova are apparently present year round, it is tempting to hypothesize that, under favorable conditions, spawning is dependent upon spermiogenesis and that seasonally declining conditions preclude late fall spawning in the DMC. Such a hypothesis should be testable. If it proves true, it may be possible to anticipate spawning by monitoring the frequency of sperm-bearing clams in a population. Such predictability might be useful in coordinating control operations.

All clams examined during the spring 1974 peak contained marsupial larvae. During the second peak only 20% were brooding (Fig. 9). Heinsohn (1958) reported spring and fall spawning efficiencies of 100% and 60% respectively. By contrast, Aldridge and McMahon (1976) reported reproductive activity of Texas populations to be greater during the second (fall) peak.

Heinsohn (1958) reported that the juvenile stage is reached before clams are released from the marsupium and suggested release of trochophores and veligers represents aborted broods. Sinclair and Isom (1963), on the other hand, found larvae released as 0.20-0.25 mm veligers which they described as free-living but functionally benthic. Sinclair (1971) later reported that larvae are released as planktonic early-veligers which become benthic within 48 hours. In DMC populations, the pediveliger stage is reached before release and it appears that both pediveligers and very early juveniles are released. For simplicity in the following discussion these two stages will be jointly termed "larvae". It appears that release may be accomplished at any one of several life history stages. Whether one stage may be designed as typical or if the stage depends on the vagaries of geography, season, climate, etc. remains to be determined. Alternately, the possibility that more than one *Corbicula* species has been introduced into the United States (J.P.E. Morrison, personal communication 1972; Morton, 1977) should be further investigated.

Whatever the initial free-living stage, it is commonly transported in the turbulent waters of rivers and canals (Sinclair and Isom, 1963). The initial appearance of "larvae" in DMC plankton (Fig. 9) indicates a marsupial existence of about one month. These "larvae" are 0.20-0.25 mm (the same as marsupial larvae). Occasional abnormal veligers less than 0.2 mm are observed and juveniles up to 2 mm may be collected in the turbulent waters near the canal head. Since larvae have not been reported from the plankton of lentic habitats and growth is not apparent for "larvae" in DMC plankton, I suspect that planktonic existence is not an absolute requirement for this species. An opportunistic planktonic habit would have significant advantages for dispersal and, at least in the DMC, allow colonization of habitats unavailable to larger juveniles and adults.

Biannual reproductive modes have also been reported for *Corbicula* populations in the Sacramento-San Joaquin Delta (Heinsohn, 1958), the Philippines (Villadolid and del Rosario, 1930), Texas (Aldridge and McMahon, 1976) and Hong Kong (Morton 1977). In Kentucky, however, populations have but a single annual reproductive period (Bickle, 1966).

Spawning in the DMC is limited to months (April-October) when water temperatures are above 16°C. Similar temperatures are required for spawning in Georgia (Gardner *et al.*, 1976). Early workers suggested that certain bivalve species required specific "critical" temperatures for spawning (Orton, 1926). More recent studies suggest that spawning can be triggered by a combination of factors in physiologically ripe bivalves and that critical temperatures are those which allow maturation of gonads (Fretter and Graham, 1964). Morton (1977) reported that both rising spring and falling autumn temperatures triggered reproductive activity in Hong Kong *C. fluminea*. *Corbicula fluminea* in the DMC begins spring reproductive activity as water temperatures rise, but the second spawning occurs while temperatures are at summer highs.

Corbicula spawns later in the northern part of its range where spring warming begins later (Table 4). California and Texas populations (biannual spawning periods) begin spawning in mid-April while Kentucky populations (single, mid-summer spawning) are still experiencing water temperatures well under 10°C (Bickle, 1966). While data from additional regions are required for confirmation, it appears that biannual spawnings may be expected provided thermal conditions are favorable.

Location	No. of Annual Spawnings	Spawning (presence of marsupial larvae	Veliger Release	First 1 mm Recruits	Reference
Delta-Mendota Canal, Calif.	2	April-May Aug-Sept	May-June Sept-Oct	June-July Oct-Nov	Eng 1977
Colorado River Aqueduct, Calif.	?	May-June	?	?	Pearson 1961
Altamaha River, Georgia	?	April-Nov	?	?	Gardner <u>et</u> <u>al</u> 1976
Lake Arlington, Texas	2	April-July Aug-Nov	?	?	Aldridge & McMahon 1976
Tennessee	?	?	July-Nov	?	Sinclair & Isom 1963
Ohio River, Kentucky	1	?	?	August	Bickle 1966

Table 4. Reproductive activity of *Corbicula* in the United States.

RECRUITMENT

Length-frequency distributions of *Corbicula fluminea* in the side-lining incrustations are primarily unimodal and skewed to the right with maximum length infrequently exceeding 12 mm (Fig. 10). Populations in invert sediment bars are, in contrast, polymodal with maximum length commonly over 30 mm (Fig. 11). Invert populations exhibit progressive increases in class modes and a biannual appearance of new size classes. The differences between length-frequencies of side-lining and invert populations are fundamentally related to the recruitment process of *C. fluminea* in the DMC.

Side-Lining Incrustations

Side-lining incrustations were exposed for nearly two months during dewatering and dredging operations in November and December 1972. As a result, no live clams were present in January 1973. In February 1973, 1-2 mm *Corbicula* appeared in the incrustations (Fig. 10) indiciating that small juveniles as well as larvae are recruited to this habitat. "Larvae" released in May-June (Fig. 9) appeared in samples as 1 mm juveniles about two months later (Figs. 10, 12); however, growth is retarded during late autumn and winter so only those "larvae" released early in the fall appear in benthic samples before spring.

Recruitment occurs during all months but May and/or June (Fig. 10) with two seasonal peaks (fall and spring) observed (Fig. 12). The fall peak results from continued recruitment of 1 mm clams and seasonally retarded growth. The spring peak parallels increased canal operation and includes recruitment of larvae and small juveniles which overwinter in the source area. The availability of potential late winter-early spring recruits is of major importance in the initial reinfestation of the canal following winter dewatering operations. Without this "recruitment reservoir" repopulation of the side-lining would be delayed several months until after spring reproduction. These recruits also provide replacements for clams displaced during winters when the DMC remains filled.

Planktonic larvae have been considered a liability to freshwater benthic organisms (Hynes, 1970, p 356). Of all freshwater bivalves, only *Corbicula* spp. and *Dreissena polymorpha* have larvae commonly reported as components of the plankton. These species are, however, noted for their rapid and successful colonization of new areas. Initial introduction is typically through the activities of man (Clark, 1952; Sinclair and Isom, 1963); however, once established in a new drainage, planktonic transport facilitates rapid dispersal through the system. As noted above, a planktonic stage appears facultative rather than obligatory in *C. fluminea*.

A second reproductive period occurring shortly before the end of the growing season may enhance invasion capabilities. In the USSR, September-spawned *Dreissena polymorpha* required more than eight months to attain the same stage reached by summer-spawned veligers in two weeks

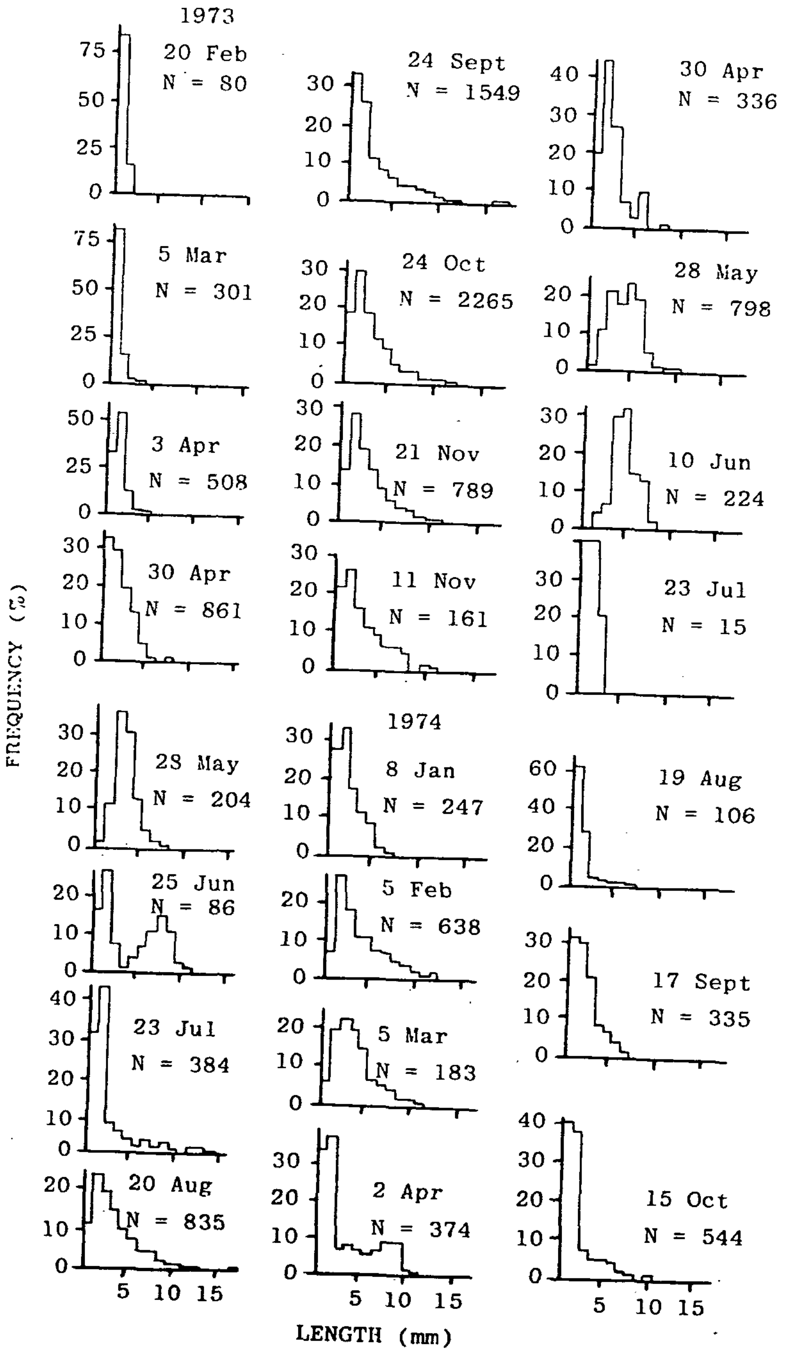

Figure 10. Seasonal length-frequency of *Corbicula fluminea* from the incrusted concrete side-lining of the Delta-Mendota Canal, 1973-74. Histograms represent the lumped samples collected on each date. No clams were present during January 1973.

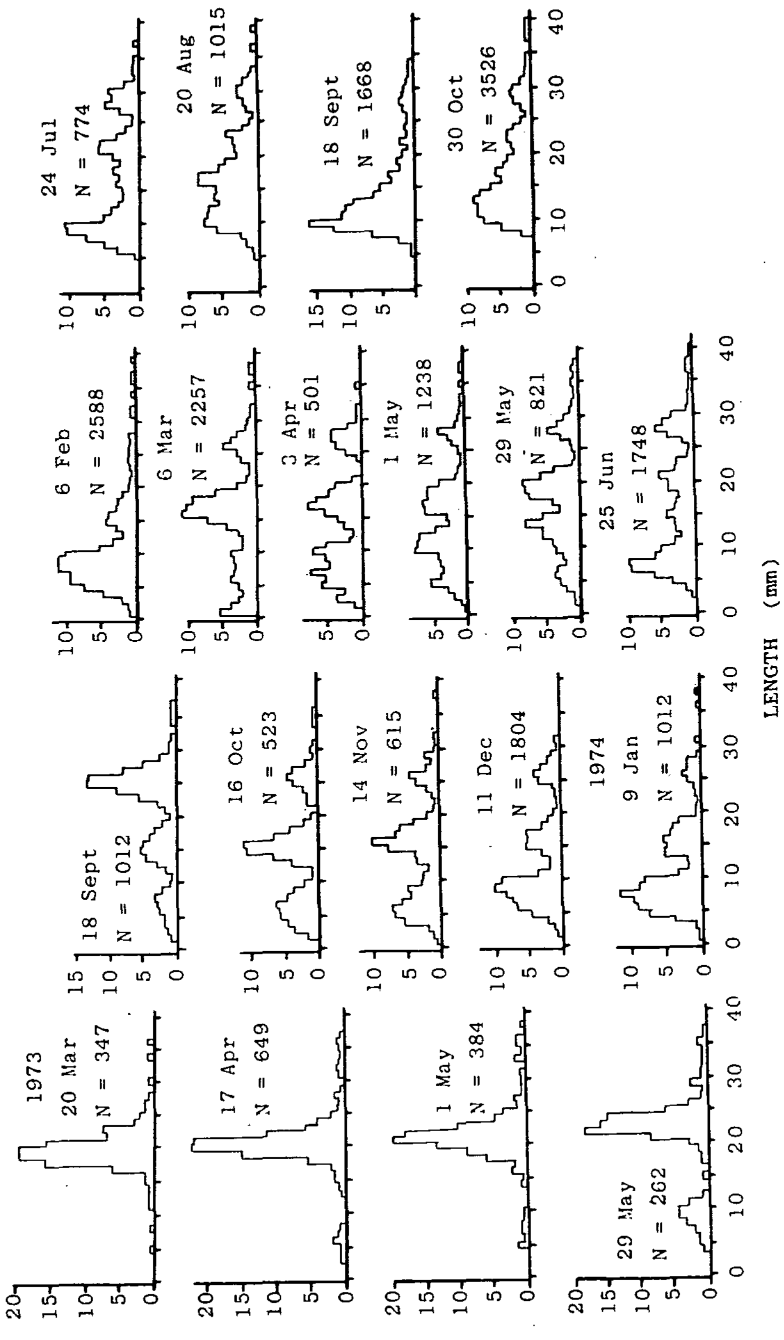

Figure 11. Seasonal length-frequency of *Corbicula fluminea* in invert sediments at km 103.5 of the Delta-Mendota Canal, 1973-74. (Note seasonal progression of class modes). No sediment bar was present during June, July and August 1973.

(Kirpichenko, 1964). While not so extreme, the development of fall-spawned *Corbicula fluminea* in the DMC is delayed several months. Delayed growth and development extend the time that these bivalves can be transported in the plankton and thereby increase the opportunity for coloniza-

Invert Sediment Bars

Direct recruitment of "larvae" to invert sediments is of minor importance. Principal recruits are advanced juveniles (4-10 mm). Two recruitment classes appear annually (Figs. 10, 11). Spring-spawned ("a" class) clams are recruited during late summer about 4-5 months after spawning. Recruitment of late summer/fall-spawned ("b" class) clams begins in October at upstream stations and in January and February at downstream sites (Fig. 8). Recruitment of both classes lasts several months with some overlap. Greatest density occurred during the winter 1973-74 for the 1973 "a" class and during the following spring and summer for 1973 "b" clams. For each age class, peak densities generally occur sequentially later at downstream stations (Fig. 8) suggesting recruitment from an upstream source.

The low frequency of 1 mm clams in the invert sediments (Fig. 12) indicates poor success in "larval" recruitment. During late spring and summer when the mean daily pumping rate through the Tracy Pumping Plant is above 3000 ft³/sec (85 m³/sec), 1 mm clams are virtually absent in invert samples although side-lining populations are simultaneously receiving heavy recruitment (Fig. 12). Only during late fall and winter, when water deliveries are at minimum levels and pump operation is low and intermittent, are 1 mm clams significantly represented in samples. Even then, the inverse relationship between 1 mm clam densities in the side-lining incrustations and in invert sediments (Fig. 12) suggests these clams are displaced from the slopes rather than recruited as "larvae"

Several factors may account for the virtual absence of 1 mm clams in invert

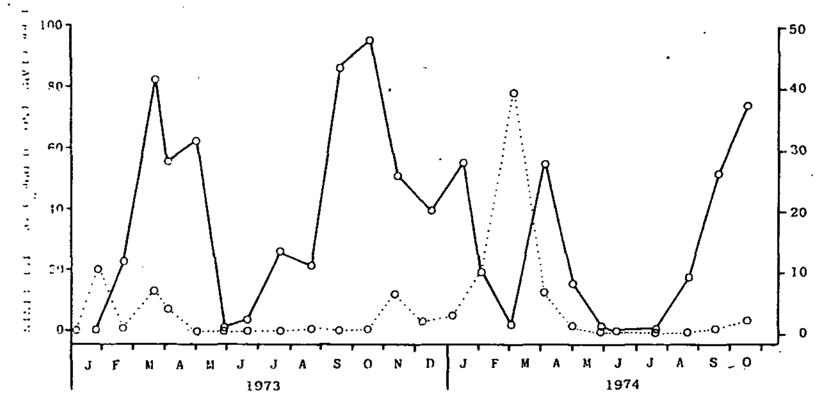

Figure 12. Seasonal frequency (No./0.09 m²) of 1 mm *Corbicula fluminea* in the Delta-Mendota Canal. O—O side-lining incrustation density, O••O invert sediment bar density.

sediments during periods of sustained high water velocity: (1) Hydraulics may prevent the settlement of "larvae". (2) Invert sediments are unstable and transient at this time. The fragile "larvae" may be crushed among larger clams or against the concrete lining as sediments are transported through the DMC (3) "Larvae" settling interstitially among layers of large clams may be suffocated by silt, feces and pseudofeces. (4) Filter-feeding by larger clams in high density situations may actually result in "predation" upon the "larvae". The feeding activity of dense populations (1025/m^2) of the estuarine bivalve, *Scrobicula plana* (da Costa) was believed responsible for the poor settlement success of spat in Gwendraeth Estuary, South Wales (Green 1957). MacKenzie (personal communication, 1977) notes that larvae of the American Oyster, *Crassostrea virginica* Gmelin, when drawn into the inhalent siphons of adults, are expelled entrapped in loosely compacted pseudofeces. Such entrapment of "larval" *Corbicula fluminea* in the dense clam populations of the DMC would increase the likelihood of interstitial suffocation.

Recruitment of advanced juveniles to invert sediments necessitates prior growth at some other site. Since recruitment occurs sequentially later downstream, this site must be upstream near the head of the canal or in the Sacramento-San Joaquin Delta.

While direct recruitment of juvenial clams from the Delta source waters cannot be excluded, I believe that the amphipod/hydrozoan incrusted side-lining near the upper end of the DMC is the primary source of new recruits to the invert. Recruitment to the side-lining incrustations occurs as larvae or very small juveniles — stages which are virtually absent from the invert. Moreover, the size at which clams disappear from these incrustations corresponds to the size at which they appear on the invert. Length-frequency curves of slope populations are approximate inverse complements to those for populations at upstream (initial recruitment sites) stations (Fig. 13). Finally, maximum invert densities commonly occur as side-lining populations are declining.

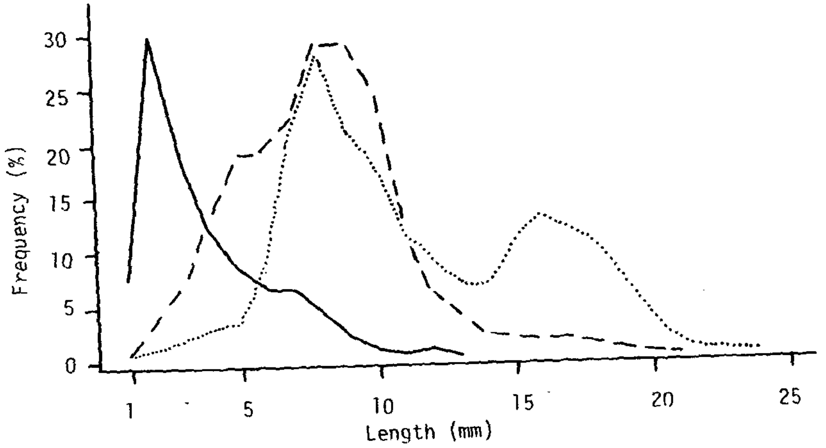

Figure 13. Typical length-frequency curves of clams from the side-lining and invert in the incrusted reaches (km 5.6-32.0) of the Delta-Mendota Canal. (Note that side-lining and invert curves are approximately inverse complements of each other). Clams from side-lining stations at km 5.6 and 6.9 (lumped), 2/5/74 (———). Clams from invert sediments at 9.1, 2/5/74 (••••••) and 3/5/74 (— — —).

The Incrusted Side-Lining — A Nursery Area for *Corbicula fluminea*

The thin slope incrustations provide an ideal habitat for recently set clams. However, the nature of these incrustations, located on a steeply sloping concrete base subjected to swift water currents, limits the size of clams which may utilize it. Most juveniles are displaced by the time they reach 4-10 mm. Since these displaced clams have developed relatively robust valves, delayed recruitment to the invert enhances the probability of their survival in the crowded, transient, invert sediments.

It is a biological axiom that utilization of alternate habitats by different life history stages minimizes intraspecific competition. Often habitat shifts are associated with metamorphosis. Common examples are caterpillar larvae of lepidopteran insects, aquatic larvae of many other insects, planktonic larvae of many benthic marine fishes and invertebrates, and amphibian tadpoles. Many species without great morphological changes undergo major migrations which allow the juveniles to grow in habitats far from those frequented by the adults. Anadromous and catadromous fish are well-known examples. Penaeid shrimp larvae are transported inshore by ocean currents and the juveniles develop in estuaries before migrating offshore to complete maturation (Kutkuhn, 1966). Such estuarine "nurseries" are also well-known for a variety of pelagic fishes (McHugh, 1966).

Unlike the obligate habitat segregation mentioned above, the utilization of the side-lining incrustations as nurseries by *Corbicula fluminea* in the DMC is fortuitous. It is, however, of paramount importance to the population dynamics of this species in the canal. Since the success of direct recruitment and/or survival of "larvae" in the invert sediments is poor, the maintenance of these populations is dependent on the recruitment of advanced juveniles. While the side-lining incrustations may not be the exclusive source of these juveniles, it is by all appearances the major contributor. The amphipod/hydrozoan incrusted concrete side-slopes are an unusual and perhaps unique habitat resulting from man's alternation of the natural environment. The systematic recruitment of advanced juveniles able to survive the crowded and transient conditions on the invert is probably the single most important factor in the maintenance of high populations of *C. fluminea* in the DMC.

SIZE AND AGE

Corbicula fluminea populations in the DMC include several size classes.

in invert samples three to four months after recruitment to the side-lining suggests that this estimate is reasonable.

Growth data for clams from invert sediments were summarized by developing Ford-Walford plots (Ford, 1933; Walford, 1946) to which regression lines were fitted using the least squares method. This line is described by the equation

$$L_{t+1} = L_t(k) + L_\infty(1\text{-}k),$$

where L_t = mean length at the beginning of the growing season, L_{t+1} = mean length at the end of the growing season, L_∞ = theoretical maximum (asymptotic) mean length and k = Ford's growth coefficient (Ricker, 1975).

Annual growth data for 1974 were generally lower than for 1973; however, there was no significant difference between the respective regression coefficients ($t = 1.633$, d.f. $= 15$, $p < 0.1$); hence, the data were pooled for subsequent analysis. The fitted line for the pooled growth data (Fig. 15) is described by the equation

$$L_\infty = 0.68\, L_t + 12.02 \quad (r = 0.9566).$$

The Ford-Walford plot has been used to predict L_∞ for molluscs (Hancock, 1965; Morton, 1977). L_∞ can be determined graphically as the point where the fitted line intercepts the 45° line (ie. where $L_t = L_{t+1}$ (Fig. 15). Alternately when both [L_∞(1-k)] and [k] have been determined, L_∞ can be easily calculated. The predicted asymptotic mean length for *Corbicula fluminea* in the DMC is about 37.6 mm (Fig. 15). Knight (1968) argues, convincingly, that L_∞ obtained in this manner is not a true estimate of the maximum length attained by the population and suggests that L_l be considered simply a descriptive summary of that data. Morton (1977) has suggested that L_∞ may be valuable as a descriptive parameter in comparing U.S. *Corbicula* populations.

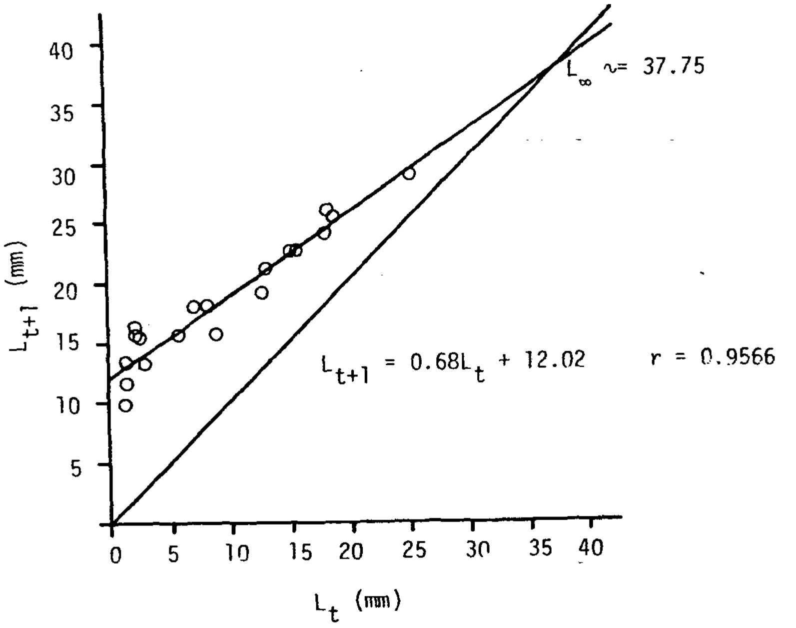

Figure 15. Ford-Walford plot of pooled growth data for *Corbicula fluminea* in the Delta-Mendota Canal, 1973-74. Regression lines were fitted by least squares. L_t = length at beginning of growing season. L_{t+1} = length at end of growing season. The hypothetical maximum mean length (L_∞) is shown by the intersection of the regression line with the 45° line.

Growth of *C. fluminea* in the DMC (Table 5) is less than reported from other areas where comparable data are available. Elsewhere in central California, this species reaches a mean length of about 12 mm during the first growing season and adds an additional 15 mm during the second year (Heinsohn, 1958). Villadolid and del Rosario (1930) reported the mean length of *C. manilensis* after one and two seasons' growth as about 13 mm and 20-26 mm, respectively. Aldridge and McMahon (1977) found that in certain Texas populations, spring-spawned classes reach lengths of about 29 mm by winter and fall classes grow to about 31 mm by the next summer (11 months). In Kentucky class size ranges similar to those of DMC populations were reached by the end of the first season even though spawning occurred in the summer (Bickle 1966) more than two months later.

Much published data on size/age relationships of *Corbicula* in the United States have been based on limited temporal sampling (frequently from a single collecting trip) and size classes were presumed annual (Keup *et al.*, 1963; Ingram *et al.*, 1964; Gunning and Suttkus, 1966; Thomerson and Myer, 1970). Such presumptions, in light of this and other recent studies (Aldridge and McMahon, 1976) demonstrating that two persistent size classes may appear annually, are inadequate. Additional life-history data will be required to determine their validity.

DISCUSSION AND CONCLUSIONS

In the Delta-Mendota Canal, dense *Corbicula fluminea* populations inhabit both thin biological incrustations restricted to the concrete side-lining in the upstream 5-30 km and disjunct sediment bars distributed on the canal bottom throughout the concrete-lined reaches. The high densities attained by these populations are related to a complex of biological and physical factors. The physical location of the DMC intake in the southern Sacramento-San Joaquin Delta apparently creates a situation similar to that observed in streams below lakes and reservoirs where, for short distances (usually only a few km) below the outflow, the density of filter-feeding benthic invertebrates is greatly increased presumably because of an enhanced food supply (Hynes 1970, pp. 256-259). Not only does *C. fluminea* benefit directly from increased nutrients, but incrustations on the side-lining created by dense populations of *Corophium spinicorne* and *Cordylophora lacustris* provide a habitat which is secondarily invaded by larval and early juvenile clams.

The thin (1-10 mm) incrustations and steep concrete-lined side-slopes limit the size of clams which can persist in this habitat. As they grow to 4-12 mm, clams become increasingly vulnerable to displacement by water current. Furthermore, attempts to remain buried as they grow result in a net down-slope movement to the invert. Displacement of larger clams from the side-slopes provides space for subsequent recruitment, reduces competition and thus enhances survival of those remaining. Displaced clams are recruited to the invert sediments.

While such a supplementary habitat could benefit clam populations in any locality, it is of critical importance in the DMC where direct recruitment and/or survival of larvae in the invert sediments is negligible. These densely populated and unstable sediments are an unfavorable habitat not only for larvae but also for the fragile early juveniles. As clams mature valves become thicker and more robust. The amphipod-hydrozoan incrustations in the DMC provide a "nursery" area where *C. fluminea* can develop to robust juveniles capable of surviving the crowded, abrasive conditions on the invert. Initial recruitment of these juveniles to the invert occurs in the incrusted reaches. Recruitment to downstream locations occurs primarily through hydraulic transport of juveniles and adults along the invert.

Truly planktonic *Corbicula fluminea* larvae may occur in some localities; however, in DMC populations the pediveliger or juvenile stage is attained before release from the adult marsupium is accomplished. Both pediveligers and small juveniles (< 2 mm) are transported in the turbulent DMC waters. Since these stages are functionally benthic, fortuitous transport in the water column provides an additional and effective means of dispersal.

Although spawning occurs primarily in two seasonal peaks and is limited to April-October, "planktonic" stages are recruited throughout winter and early spring. Winter-spring recruits are the product of late season spawning. Seasonally low temperatures retard growth and development during late autumn and winter and, thereby, greatly extend the period of vulnerability to planktonic transport. Larvae and juveniles in the source waters constitute a "recruitment reservoir" which is of major importance in the initial repopulation of side-lining incrustations after the periodic winter dewaterings of the DMC. A second, late season, spawning period also occurs in Texas and may be typical throughout the southern range of this species.

Reproduction appears to be limited to seasons when water temperature is above 13-16°C. Abbreviated warm water periods may limit the northward range expansion of *C. fluminea*.

The DMC supports dense populations of *Corbicula fluminea;* however, growth of these clams is less than that reported in other areas. Analysis of length-frequency distributions reveals that, at least in California and Texas, two size classes occur annually. Thus, caution should be exercised in assigning age class designations for size classes of *C. fluminea* populations in localities where supportive population data is lacking.

Corbicula fluminea populations in the DMC are strongly affected by water current. While flowing water enhances the total volume of nutrients available to benthic communities and is a vehicle for recruitment, it also has considerable negative impact. Under heavy flow conditions sediment bars become unstable and entire clam beds are transported downstream. Aside from physical abrasion during transport, it is probable that periodic disturbances impede growth. High velocity flows may prevent "settlement" of "larvae" or may dislodge juveniles before they are large enough to survive in the unstable invert sediments.

All things considered, the DMC is probably not the ideal clam habitat suggested by the exceptionally high population densities observed. These densities are perceived as the results of (1) a unique habitat (amphipod/hydrozoan incrustations on the concrete side-lining) which allows rapid growth under enhanced conditions for early life-history stages that are unable to survive in the invert sediments; (2) recruitment of robust late juveniles displaced from these incrustations to invert sediments in the incrusted reaches and (3) subsequent hydraulic recruitment to downstream locations. The exceptional *Corbicula fluminea* densities in the DMC appear more the product of hydraulic accumulation than biological activity. Indeed, it appears that *in situ* reproduction of *C. fluminea* contributes very little to DMC populations.

ACKNOWLEDGEMENTS

This paper is based on portions of a PhD dissertation at the University of California, Davis, 1977. The field studies were undertaken while I was Research Biologist at the California Academy of Sciences. I wish to thank staff of both the Academy and U.S. Bureau of Reclamation for assistance in collecting and logistics. I additionally wish to thank Dr. M. A. Miller, Zoology Department, University of California, Davis, who critically reviewed portions of this manuscript.

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