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POPULATION DYNAMICS OF THE ASIATIC CLAM, *CORBICULA FLUMINEA* (MÜLLER) IN THE LOWER CONNECTICUT RIVER: ESTABLISHING A FOOTHOLD IN NEW ENGLAND

D. E. MORGAN, M. KESER, J. T. SWENARTON, AND J. F. FOERTCH
Millstone Environmental Lab, Dominion Nuclear Connecticut, Inc., Waterford, Connecticut 06385

ABSTRACT The founding population of *Corbicula fluminea* in the Lower Connecticut River, discovered in 1990, was studied for ten years (1991–2000). Seasonal abundance of six size classes was monitored near three electric power plants. *Corbicula* abundance varied seasonally as well as annually, but peaked in 1992. Winter survival of clams was positively correlated with the average winter water temperature and negatively correlated with frequency of daily mean water temperatures ≤1°C and with frequency of daily mean April spring freshet flows ≥1700 m^3/s. Higher winter survival at Middletown Station sites during most years, when compared with survival near Connecticut Yankee, was attributed to the influence of the Middletown Station thermal discharge. Thermal discharge did not support a permanent population at Connecticut Yankee because of temperature extremes during power plant operation in summer. Clam growth under ambient river temperatures began in May when water temperatures exceeded 10°C and ceased in December when temperatures fell below this threshold. Cooling water discharges altered this seasonal growth pattern; growth began in November, as temperatures fell below 35°C, and ceased in the summer, when discharge temperatures exceeded this upper thermal threshold. Reproduction occurred in the river when water temperatures were between 17°C and 28°C, typically from June to October. Peak spawning occurred in August. Discharge temperatures shifted clam reproduction back to spring (March to May). The key to *Corbicula*'s success in establishing a population in the Connecticut River is its ability to colonize refugia from winter temperature and spring freshet flow extremes that often cause high clam mortality.

KEY WORDS: Asiatic clams, *Corbicula fluminea,* thermal discharges, electric power plants, winter survival, thermal tolerance, reproduction, growth, invasive species

INTRODUCTION

The Asiatic clam (*Corbicula fluminea*) is a freshwater bivalve, native to southeast Asia, that is now common in Europe, Africa, the Pacific Islands, and North and South America. Early evidence of *Corbicula* in North America was empty shells collected in 1924 at a British Columbia site (Counts 1981) and at a Columbia River site in Washington, United States in 1938 (Burch 1944). Today, *Corbicula* is reported in 37 US states including, most recently, New York and Connecticut (McMahon 1983; Foehrenbach & Raeihle 1984; Morgan et al. 1992). The rapid spread and persistence of *Corbicula* throughout North America is related to its rapid growth rate, early onset of maturity, high fecundity, and its ability to tolerate a wide range of environmental conditions (Mattice & Dye 1976, Aldridge & McMahon 1978, Graney et al. 1980, McMahon & Williams 1986a, McMahon & Williams 1986b, McMahon 2002).

While *Corbicula* is considered an economically important food species in its native range (Chen 1990), it is recognized as a nuisance in North America (Ingram 1959, Sinclair 1964, Prokopovich 1969, McMahon 1977, McMahon 1983, Isom 1986). Its ability to clog water systems makes *Corbicula* a serious and costly problem for the electric generating industry (Goss & Cain 1975, Mattice 1979, Page et al. 1986). Thus, the discovery of Asiatic clams in water systems at Connecticut Yankee Nuclear Power Station (CY) on the Connecticut River in May 1990 (Morgan et al. 1992) received considerable attention. The range extension of *Corbicula* to the Connecticut River, the northernmost population in the eastern United States, was not expected because river temperatures frequently drop below 2°C, the minimum temperature tolerated by this clam (Mattice & Dye 1976). This study was initiated in 1991 as a condition of a Connecticut Department of Environmental Protection (CTDEP) permit to allow CY to continuously chlorinate its service water system to prevent *Corbicula* biofouling. Monitoring was later expanded upriver to the Middletown and South Meadow power plant sites. This study examines the abundance, growth, and reproductive phenology of *Corbicula* under ambient Connecticut River conditions and under thermal discharge conditions at the Connecticut Yankee and Middletown power plant sites.

SITE DESCRIPTION

The Connecticut River originates in northern New Hampshire near the Canadian border and flows south for 660 km, dropping 800 m in elevation by the time it reaches the mouth at Long Island Sound (LIS) (Merriman & Thorpe 1976 and Fig. 1). Annual average water flow, measured at Thompsonville CT (102 km from LIS), during the period 1991 to 2000 ranged from a low of 410 m^3/s in 1995 to a high of 735 m^3/s in 1996 (USGS 2002). Daily maximal rates usually occur in April, often exceeding 1700 m^3/s.

The focus of this study is the lower Connecticut River extending downstream from Hartford, Connecticut to a point 30 km above the mouth of the river (Fig. 1). The survey area extends over a 51 km section of river and encompasses three electrical power plant sites: South Meadow Station (SM), a 68.5 megawatt, solid waste-to-energy plant; Middletown Station (MS), an 856 megawatt oil fired power plant; and Connecticut Yankee (CY), a 582 megawatt nuclear power plant (Fig. 1). River width varies between ~400 m and 600 m over the study area. Depths at sampling sites were 1–6 m below mean low water. Semidiurnal tides affect river flow, bringing on average 425 m^3/s of additional flow to the lower Connecticut River in the vicinity of CY (Merriman & Thorpe 1976), causing periodic fluctuations in river height of ~1 m (NSI 1995, Rozsa 2001). The tidal influences are large in relation to natural flow during periods of low river discharge, and absent or nearly absent during freshet conditions (Boyd 1976, Rozsa 2001). The study areas at CY and farther north at MS and SM are above any seawater incursion. Daily average ambient water temperatures were similar for all three power plants and ranged between −1.7 and 30.6°C during the 10-year study period (Fig. 2). The river frequently freezes over during the winter in our study area, but the duration of ice cover varies from year to year. Discharge water temperatures at CY during plant operation were 8 to 12°C above ambient river temperatures at a maximum flow rate of 25 m^3/s.

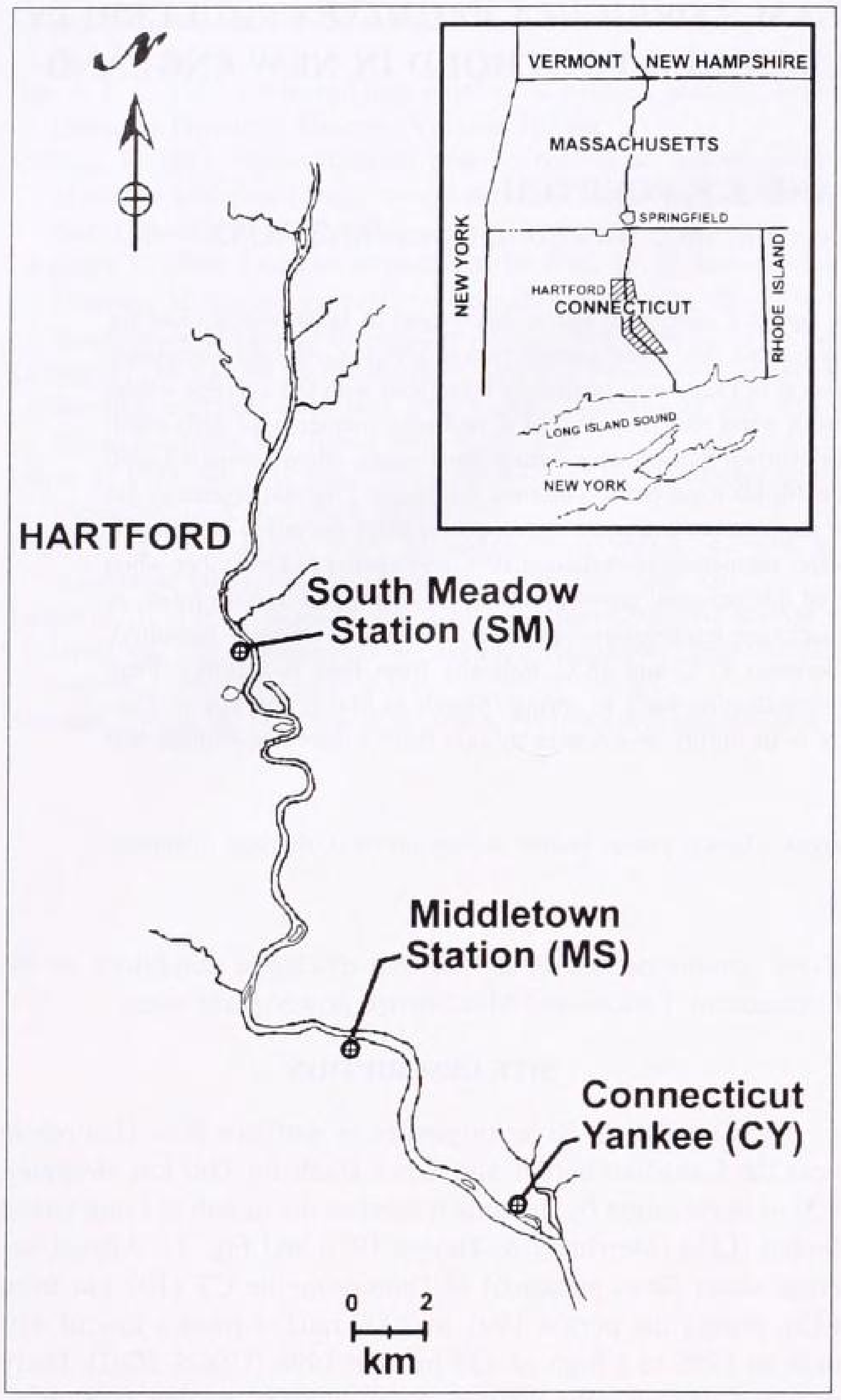


Figure 1. Location of Asiatic clam study area and sampling sites on the Connecticut River, showing the three electric power station sites (SM, MS, and CY).

The CY cooling water discharge flows through a man-made canal 1 km long before mixing with ambient Connecticut River waters. Connecticut Yankee ceased operation on July 22, 1996. At MS, the average sustained discharge temperatures from 1992–1994 ranged between 7 and 10°C above ambient river conditions with an average discharge of 3.6 m^3/s. At MS and SM, the cooling water is discharged directly to the river.

MATERIALS AND METHODS

This study was conducted between August 1991 and November 2000. Data at CY were collected during the entire study at four sampling sites located in the river near the power plant and one site in the discharge canal (CY discharge). The four CY river sites were similar in *Corbicula* abundance and the data from each were combined for data analysis (CY). Sampling was extended to three sites at MS in May 1992 and continued through November 1994; two sites were grouped for data analysis as river sites (MS), and the third, adjacent to the cooling water discharge (MS discharge), was analyzed separately. At SM, a single river site downstream of the cooling water discharge (minimal thermal influence) was sampled between August 1993 and November 1994.

In the first year of the study (1991), field sampling was conducted in August and November. For the remainder of the study period (1992–2000), field sampling was conducted three times each year, in May, August, and November. To collect *Corbicula*, five 0.1 m^2 bottom sediment samples were obtained at each sampling site using a weighted Peterson grab (Wildlife Supply Company, Buffalo, NY). Sample processing techniques were similar to those of Gardner et al. (1976). Grab samples were sieved in the field by passing the sample through a series of three screens (6.3, 2.0, and 1.0 mm mesh size). Clams and sediment retained on the 1-mm screen were subsampled in the field by placing a well-mixed 1-L sample in an elutriator (Magdych 1981) for 3 min at a water flow of 20–30 L/min. The overflow from the elutriator was collected on a 1-mm mesh sieve and sorted in the laboratory under a dissecting microscope (10×). Sediment and clams retained on the 6.3 and 2.0 mm screens were taken to the laboratory and washed through a series of five US Standard Testing Sieves (19.0, 12.5, 6.3, 3.4, and 2.0-mm mesh sizes). Size classes were determined based on the mesh size on which clams were retained. Clams

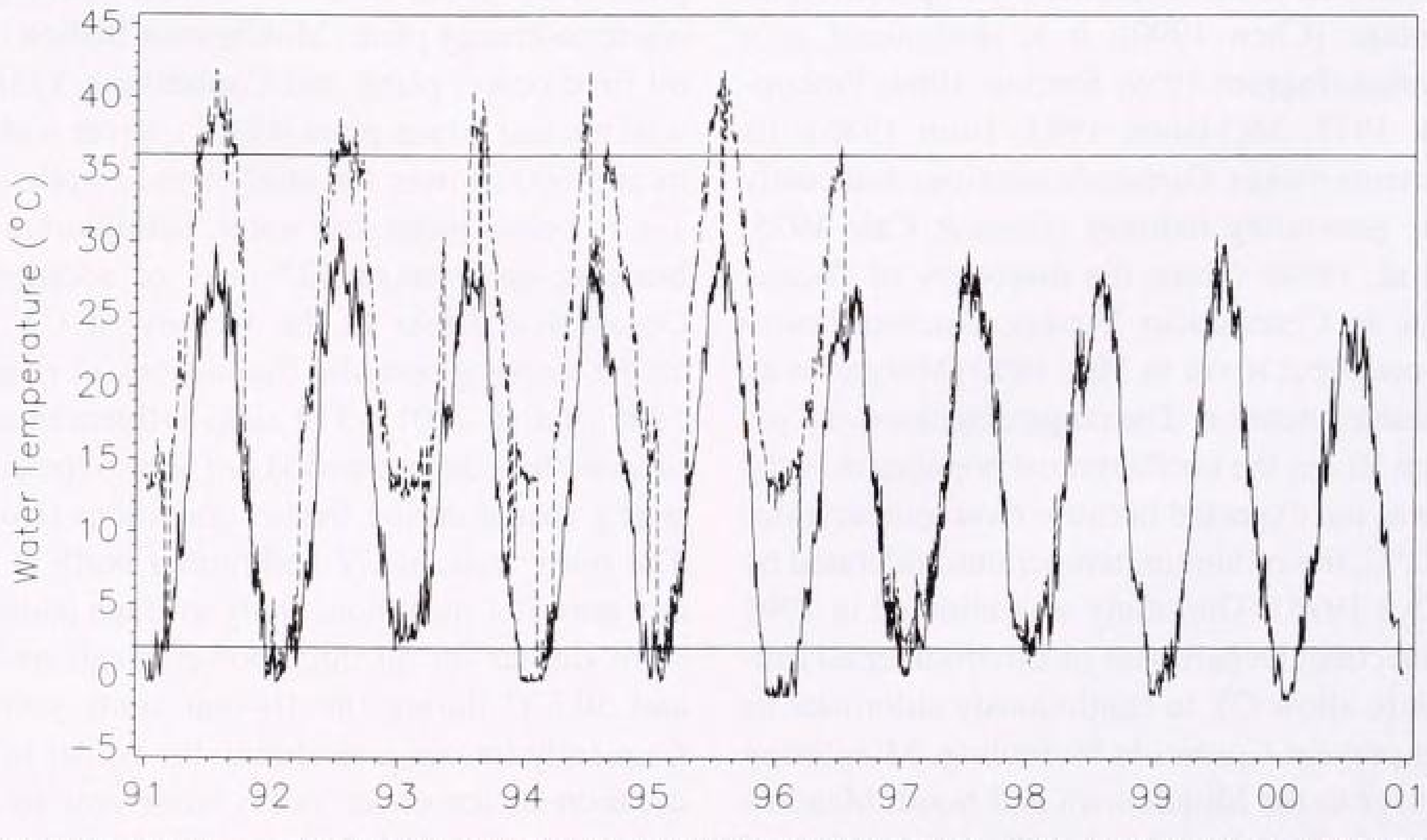
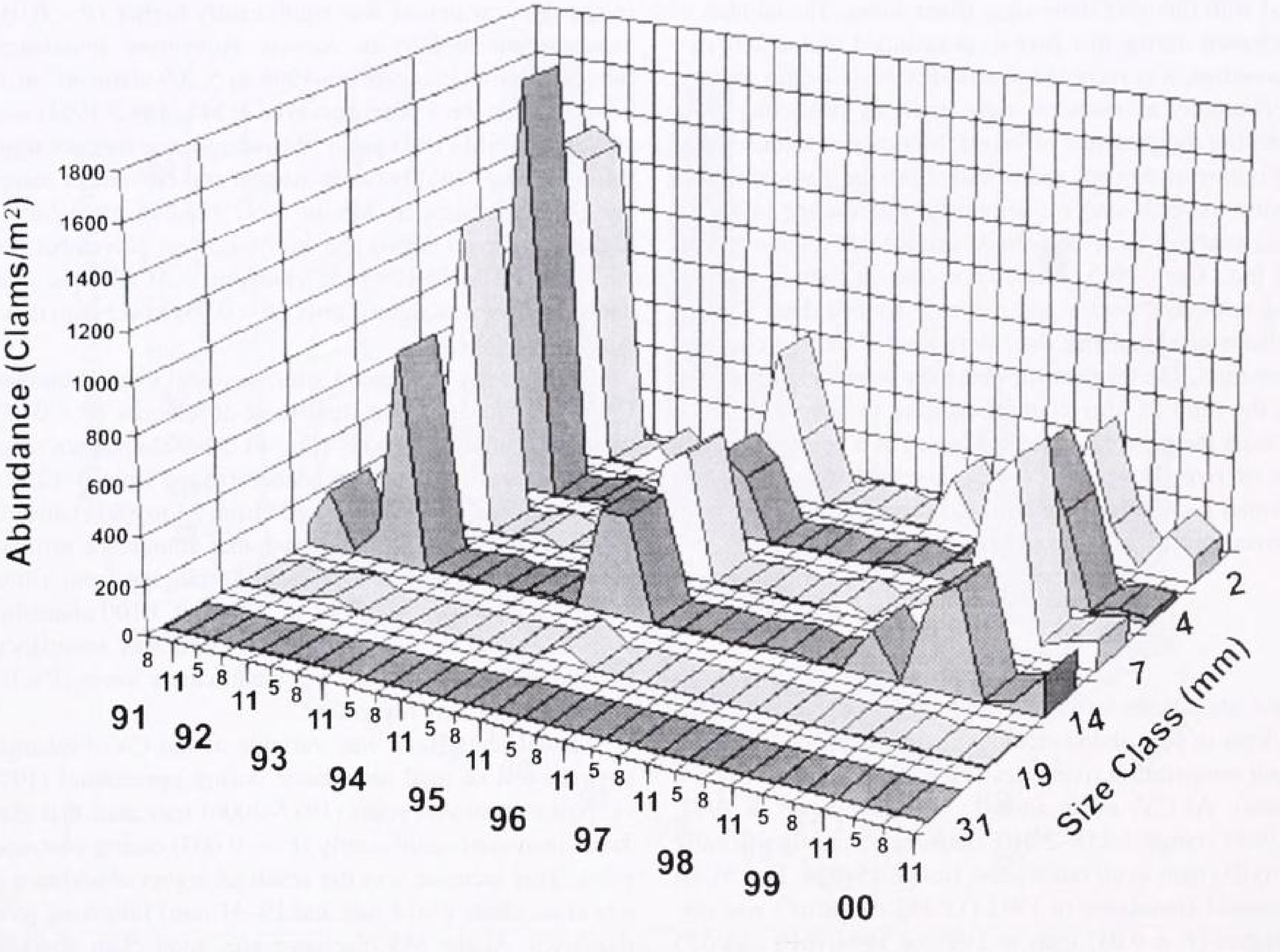


Figure 2. Intake (—) and discharge (- - - -) water temperatures at CY from January 1, 1991 to January 1, 2000. Horizontal reference lines represent upper and lower lethal temperature limits for *Corbicula fluminea*.



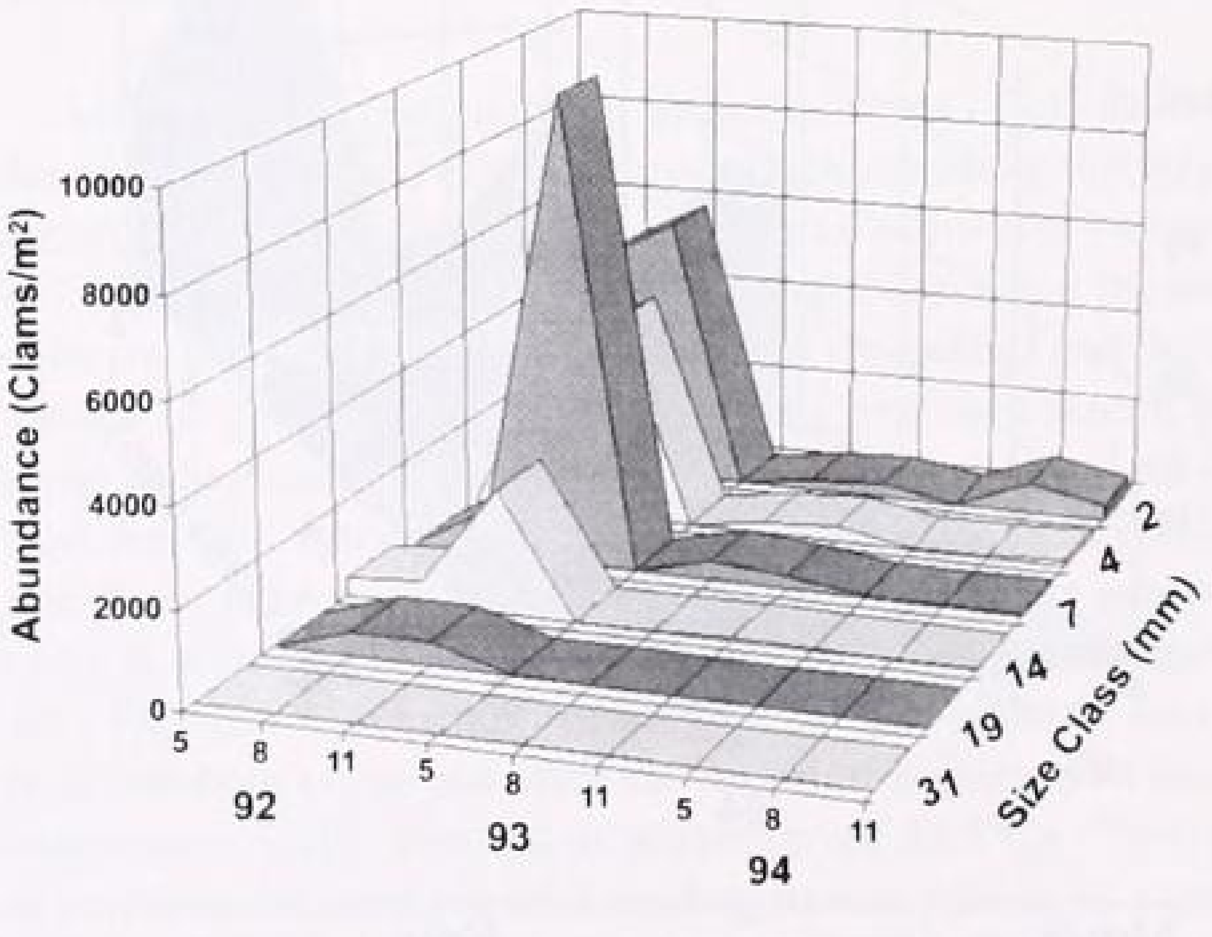
Month	Year									
	1991	1992	1993	1994	1995	1996	1997	1998	1999	2000
5	-	55 ±40	4.0 ±8.5	0	124 ±56	0	8.0 ±7.5	38 ±33	94 ±35	78 ±58
8	399 ±131	2,568 ±1,538	35 ±24	68 ±22	1,828 ±622	56 ±22	57 ±28	291 ±130	2,148 ±617	366 ±138
11	807 ±387	5,209 ±2,630	206 ±91	225 ±118	1,522 ±565	80 ±38	350 ±136	649 ±272	1,758 ±635	412 ±189
ANNUAL	-	**2,610 ±1,136**	**89 ±40**	**98 ±45**	**1,158 ±328**	**45 ±16**	**138 ±59**	**326 ±116**	**1,334 ±362**	**286 ±85**

Figure 3. Average abundance (# clams/m^2) of *Corbicula fluminea* by size class (graph) and total (table, ±95% CI) at CY river sites.

retained on the 1.0-mm sieve averaged 2.0 mm in shell length; on the 2.0-mm sieve, 4.1 mm; on the 3.4-mm sieve, 6.7 mm; on the 6.3-mm sieve, 14.1 mm; on the 12.5-mm sieve, 19.3 mm; and on the 19-mm sieve, 31.1 mm.

Individual clam growth was monitored monthly in 1993 and 1994 using shell length measurements to the nearest 0.1 mm. In the river near the CY plant intakes, marked clams maintained in lantern nets were used for monitoring growth. In the CY discharge canal, 12 clams collected randomly from lantern nets were measured monthly to assess growth.

Clam fecundity was determined monthly using techniques of Aldridge and McMahon (1978). Several hundred adult clams (>8.0 mm in shell length) were collected from the river in May/June of 1991 through 1994 and held in lantern nets placed at two locations, one in the river near CY plant intakes, the other in the CY discharge canal. Clams were collected monthly from river nets until winter, when no live clams remained in lantern nets. In the CY discharge canal, all clams were dead by June (when water temperatures at this site exceeded 37°C). In this study, data for fecundity in the discharge canal were collected from November 1992 to July 1993, and June and July fecundity data were at ambient river temperature due to a power plant shut down. Twelve clams were subsampled monthly from each net. In the laboratory, each clam was held under static conditions at 20°C for 24 h in a 100-ml



Month	Year		
	1992	1993	1994
5	758 ±688	43 ±36	138 ±68
8	10,413 ±7,233	878 ±451	786 ±577
11	23,275 ±5,494	928 ±339	533 ±295
ANNUAL	**11,482 ±4,416**	**616 ±227**	**555 ±253**

Figure 4. Average abundance (# clams/m^2) of *Corbicula fluminea* by size class (graph) and total (table, ±95% CI) at MS river sites.

beaker filled with filtered Connecticut River water. The number of juveniles released during this period, determined with a 10× dissecting microscope, was recorded as an index of spawning activity. Additional fecundity assessments were made by dissecting these clams and noting the presence of brood. Maturity of gametes was assessed by removing egg and sperm cells from the gonadal tissues and examining the cells under a compound microscope (400×).

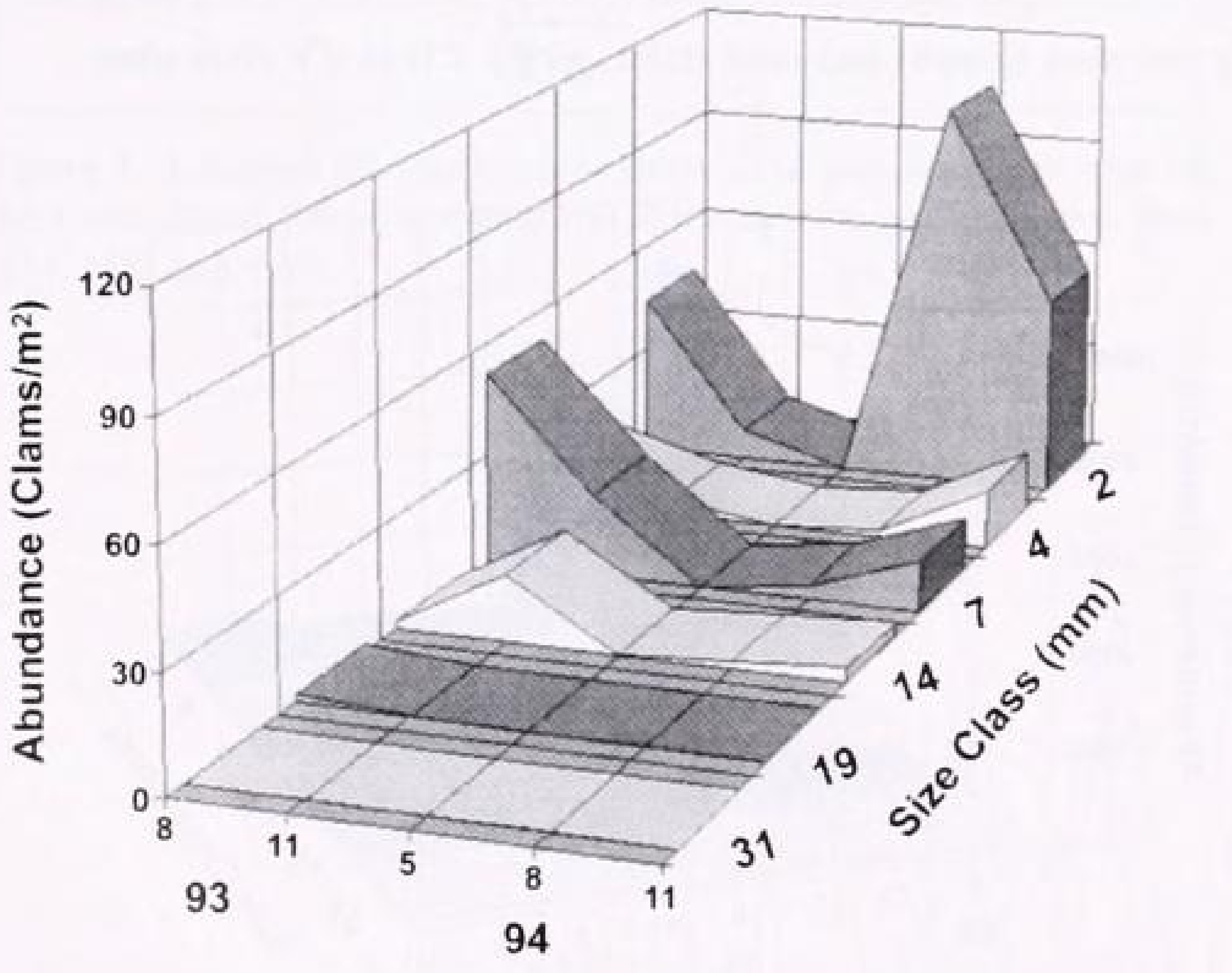
Statistical analyses were performed using SAS version 8 software (SAS Inc., Cary, NC). Abundance data in figures are presented using arithmetic means and non-transformed data. Statistical comparisons of abundance data were always carried out after log transformation. The relationships between winter clam survival (defined as the ratio of May clam abundance to November clam abundance from the previous year, expressed as a percentage) and temperature or river flow indices were assessed using the rank-order Spearman correlation. Growth and reproduction data were not transformed prior to statistical testing.

RESULTS

Abundance

Corbicula abundance exhibited high intra- and inter-annual variability. Year to year abundance fluctuations were considerable at all ambient temperature river sites (Figs. 3, 4, 5; note different vertical scales). At CY, mean annual clam abundance in 1992, 1995, and 1999 (range 1,158–2,610 clams/m^2) was significantly higher ($P < 0.05$) than in all other years (range 45–326; Fig. 3). At MS, mean annual abundance in 1992 (11,482 clams/m^2) was significantly higher ($P < 0.05$) than in 1993 or 1994 (616 and 555 clams/m^2, respectively; Fig. 4). At SM, mean annual abundance was low, with 82 clams/m^2 in 1993 and 67 clams/m^2 in 1994 (Fig. 5).

Of ambient temperature river sites, seasonal abundance at CY over a 10-year period was significantly higher ($P < 0.05$) in November than in May or August. November abundance at CY ranged from 80 clams/m^2 in 1996 to 5,209 clams/m^2 in 1992. By contrast, over the 3 years surveyed at MS (1992–1994) and 2 years surveyed at SM (1993 and 1994), abundance was not significantly different ($P > 0.05$) between August and November samples. November abundance at MS in 1992 (23,275 clams/m^2) was the highest observed during the study. Lowest November abundance occurred at SM in 1993 (52 clams/m^2). At all sites, clam abundance in May was significantly ($P < 0.05$) lower than that in either August or November.



Month	Year	
	1993	1994
5	-	0
8	112 ±30	114 ±103
11	52 ±21	88 ±75
ANNUAL	**82 ±27**	**67 ±43**

Figure 5. Average abundance (# clams/m^2) of *Corbicula fluminea* by size class (graph) and total (table, ±95% CI) at SM.

Of thermally influenced sites, seasonal clam abundance in the CY discharge canal had significant differences ($P < 0.05$) among the three sampling periods (Fig. 6). May abundance ranged from 0–92 clams/m^2. August abundance ranged from 0–12,174 clams/m^2. November abundance ranged from 24 to 880 clams/m^2. At the MS discharge, August and November abundance estimates were not significantly different ($P > 0.05$), ranging from a low of 322 clams/m^2 in November 1993 to a high of 7,100 clams/m^2 in November 1992 (Fig. 7). As with river sites, May abundance at both CY and MS discharge sites was significantly lower ($P < 0.05$) than that in August and November.

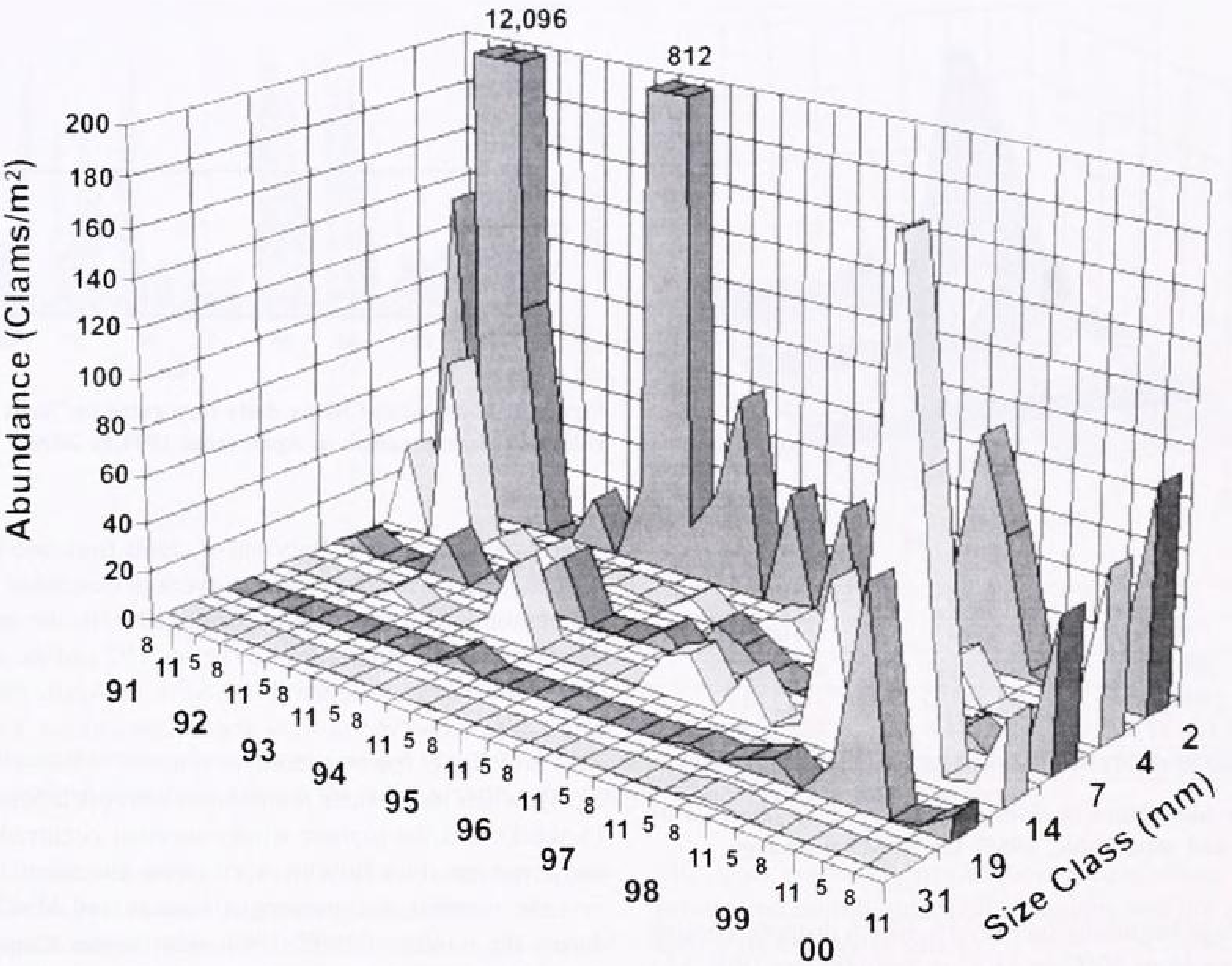
Annual abundance was variable at the CY discharge site. A pooled t-test of total abundance during operational (1991–1996) vs. post-operational years (1997–2000) indicated that clam abundance increased significantly ($P = 0.007$) during post-operational years. This increase was the result of higher abundance of larger size class clams (7–14 mm and 19–31 mm) following power plant shutdown. At the MS discharge site, total clam abundance was significantly higher ($P < 0.05$) in 1992 (3,322 clams/m^2) than in 1993 and 1994 (496 and 549 clams/m^2, respectively; Fig. 7). Clam abundance was not significantly different ($P > 0.05$) between the river and discharge sites at MS, except for the largest clams (31 mm size-class), which were most abundant at the MS discharge site. In fact, the largest clam measured during the entire study (37.6 mm) was collected at MS in August 1992.

Winter Survival

Declines in clam abundance from November of one year to May of the next were used to determine winter survival; values at CY ranged from 0% in 1994 and 1996 to 55% in 1995 (Fig. 3). The effects of winter water temperatures and peak river flows on clam winter survival were examined using Spearman-ranked correlation (Table 1). The severity of winter water temperatures, as indicated by the number of days with average water temperature ≤2°C, was not significantly correlated ($r_s = -0.65$, $P = 0.081$) with clam winter survival. The number of days, however, ≤1°C was negatively correlated ($r_s = -0.73$, $P = 0.040$) with winter survival, and average December through April water temperature was positively correlated ($r_s = +0.87$, $P = 0.004$). Highest average monthly flow in the Connecticut River typically occurs in April (Fig. 8). Accordingly, the number of days each year exceeding 1,700 m^3/s in April was used as an index of spring freshet severity. This index was negatively correlated with winter clam survival ($r_s = -0.91$, $P = 0.002$). Data from 1993 were omitted from this analysis because a single storm in March caused total mortality of clams at our sampling sites.

Growth

Corbicula growth rates under ambient river conditions exhibited seasonal cycles, and growth of marked clams was size-



Month	Year									
	1991	1992	1993	1994	1995	1996	1997	1998	1999	2000
5	-	2 ±5.0	32 ±22	0	24 ±29	8.0 ±5.1	92 ±62	20 ±22	76 ±37	4 ±10
8	34 ±58	12,174 ±30,269	0	60 ±54	38 ±50	48 ±75	6 ±15	62 ±83	243 ±172	30 ±35
11	178 ±181	96 ±121	42 ±26	880 ±1254	90 ±187	44 ±70	24 ±6.3	212 ±227	210 ±73	268 ±181
ANNUAL	-	**4,091 ±8,454**	**25 ±14**	**313 ±397**	**51 ±53**	**33 ±28**	**41 ±27**	**98 ±78**	**173 ±63**	**101 ±83**

Figure 6. Average abundance (# clams/m^2) of *Corbicula fluminea* by size class (graph) and total (table, ±95% CI) at CY discharge.

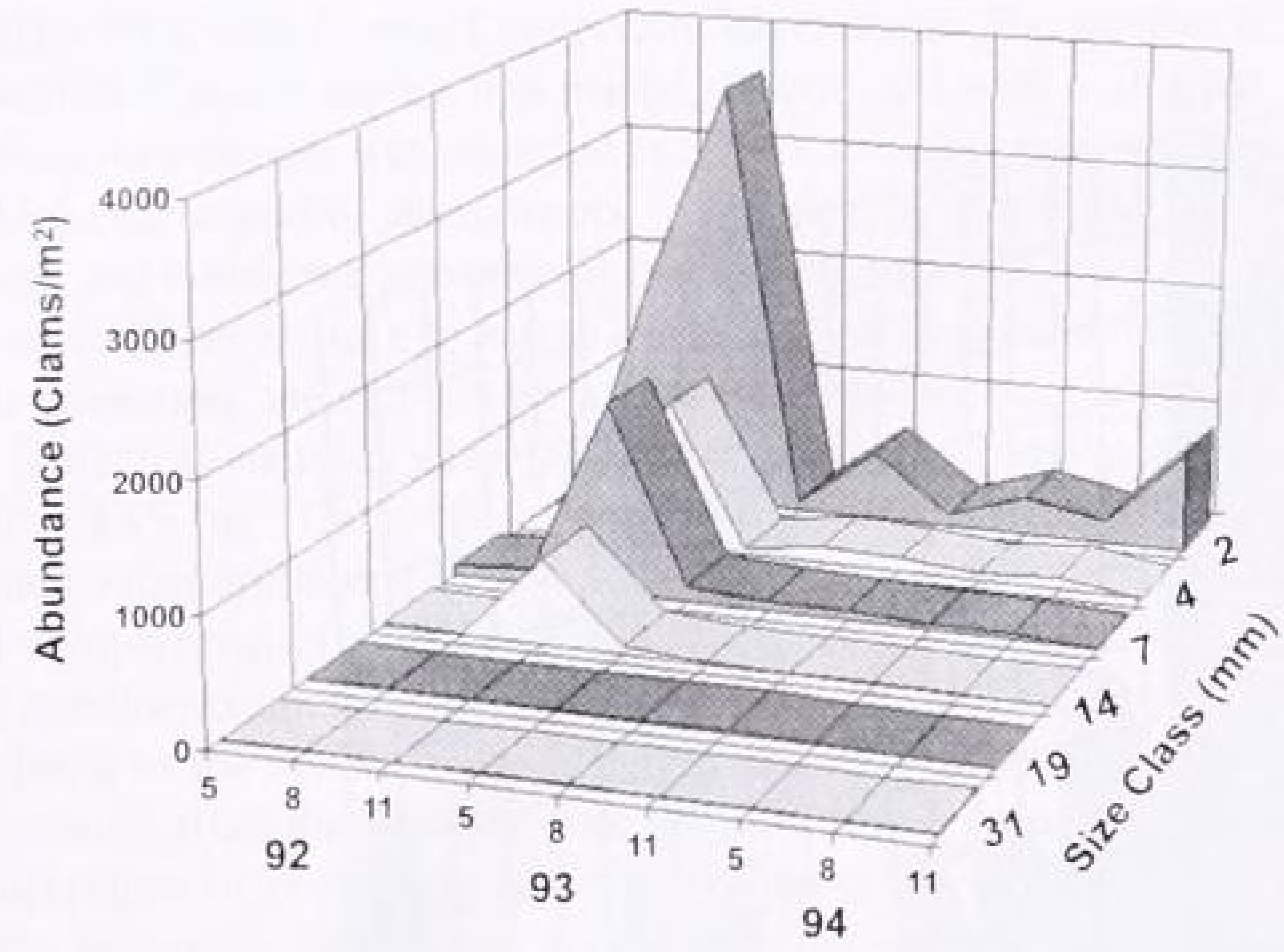
dependent (Figs. 9 and 10). In 1993, clams with an initial shell length of ~14.5 mm had a higher growth rate (0.54 mm/wk) from June to October than those starting at ~17.5 mm (0.41 mm/wk), and ~21.7 mm (0.35 mm/wk). A similar size-dependent relationship was also observed in the 1994 study; clams with an initial length of ~12 mm grew fastest from June to October (0.51 mm/wk), followed by ~20 mm (0.32 mm/wk) and ~30 mm (0.14 mm/wk) clams. Growth rates were significantly different ($P < 0.05$) among the three size classes through August. In September through December, however, mean monthly growth rates for all size classes were generally low and not significantly different from each other.

Clam growth rates in the CY discharge canal from November 1992 to February 1993 were ≤0.18 mm/wk, when water temperatures were 13–19°C, 10–12°C above ambient river temperatures (Table 2). As these clams were not marked, negative growth rates could occur as a result of mortality of large individuals. Growth rates were as high as 0.27 mm/wk from March to May when water temperatures ranged from 13–27°C. Maximum growth rates at this site occurred during June (0.38 mm/wk) and July (0.33 mm/wk), when canal temperatures were similar to those at ambient river conditions because of a power plant outage. All clams died after the power plant restarted and discharge water temperatures exceeded 37°C (July).

Reproduction

Microscopic examination of gametic tissues of clams held under ambient river and CY discharge conditions show that eggs and sperm were continually present as long as clams were alive (Fig. 11). For clams held at ambient river temperatures, the presence of embryos and veligers in the demibranchs (brooding) and the active release of juveniles occurred primarily over a 4-month period (June to September). By October, only one clam out of 48 examined was still spawning. The maximum number of juveniles released per clam per day typically occurred in August across all 4 years in which reproduction was monitored (2,862 juveniles/clam/day; Fig. 12). This pattern of juvenile release allowed maximum recruitment to occur just after the period of maximum river water temperature (July, with a 4-year average of 27.5°C). The number of juveniles released per adult in August was positively correlated with the size of the clam ($r_s = 0.77$; $P < 0.01$; Fig. 13).

The reproductive cycle of *Corbicula* in the CY discharge canal was seasonally shifted (Fig. 11). Brooding and releasing of juveniles first occurred in November 1992 when discharge temperatures averaged 18.3°C, and ceased from December through February when temperatures averaged <14°C. Spawning began again in March and increased through April when discharge temperatures averaged 17°C. The sharp decrease in May was the result of



Month	Year		
	1992	1993	1994
5	200 ±122	326 ±141	448 ±277
8	2,666 ±836	840 ±450	340 ±116
11	7,100 ±1,896	322 ±69	860 ±931
ANNUAL	**3,322 ±1,721**	**496 ±186**	**549 ±283**

Figure 7. Average abundance (# clams/m^2) of *Corbicula fluminea* by size class (graph) and total (table, ±95% CI) at MS discharge.

a power plant outage beginning on May 15, which dropped cooling water temperatures from 30°C to 18°C in a single day (Fig. 14). Spawning activity recovered and peaked in June and July as the plant outage continued, similar to the pattern observed at ambient river temperatures (17–27°C). On July 21, 1993 the power plant restarted and temperatures increased to >35°C in 4 days. By August 18, 1993 all clams held in the CY discharge were dead.

DISCUSSION

Corbicula fluminea was first documented in the Connecticut River in May 1990 (Morgan et al. 1992), the first report of this nonindigenous clam in New England waters. Before this discovery, *Corbicula* was not expected to colonize the Connecticut River because water temperatures routinely fall below 2°C for prolonged periods. It is commonly accepted among researchers that the lower lethal temperature limit for *Corbicula* is ~2°C (Horning & Keup 1964, Bickel 1966, Mattice & Dye 1976, Rodgers et al. 1979, Cherry et al. 1980).

Corbicula abundance varied seasonally as well as annually, but clearly peaked in 1992. Survival of clams from one year to the next is positively correlated with the average December to April water temperatures and negatively correlated with the number of days the river water temperature was below 1°C and the number of days that river flows exceeded 1700 m^3/s in April. For example, no clams were observed in May at our Connecticut Yankee sampling sites following the two coldest winters (1993–1994 and 1995–1996), when river water temperatures dropped below 2°C for 12–15 weeks and the highest winter survival occurred in 1995 when daily average river flow in April never exceeded 1700 m^3/s.

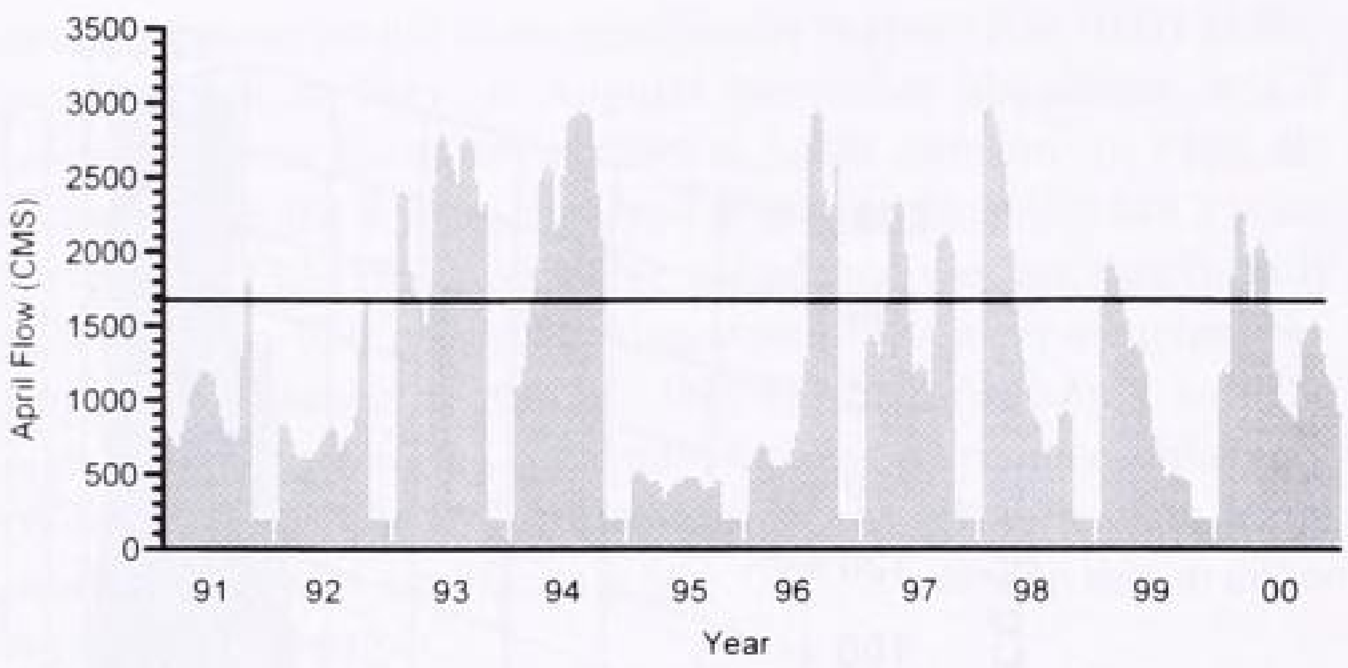


Figure 8. Connecticut River daily flow rates (m^3/s) at the Thompsonville, CT gaging station in April from 1991 to 2000.

Low survival at Connecticut Yankee and Middletown Station during the winter of 1992–1993, when water temperature did not drop below 2°C, was attributed to winter storm Joshua (March 13, 1993). This storm produced low water levels (1–2′ below normal) and left shoal areas, specifically our sampling areas, exposed to air temperatures as low as −8°C, freezing sediment and clams (NUSCO 1994).

Higher winter survival at Middletown Station sites, when compared with those around Connecticut Yankee, was attributed to the influence of the Middletown Station thermal discharge. River water temperatures seldom dropped below 2°C in the Middletown Station discharge mixing zone (NUSCO 1994). Other overwintering populations likely exist in the river in refugia provided by other industrial thermal discharges or in areas of the river receiving regular influxes of groundwater that maintains a temperature of 9.0 ± 2°C (R. Lewis, State of Connecticut Geologist; pers. comm.). Graney et al. (1980) and Kreiser and Mitton (1995) suggest that warm water refugia such as these were assisting the Asiatic clam in expanding its geographical range northward.

Clam densities in the Connecticut Yankee discharge canal were

TABLE 1.

Spearman correlations coefficient (r_s) for percentage winter survival of *Corbicula fluminea* at CY versus indices of winter temperatures and Connecticut River flow.

Variable	r_s	Prob >|r|	n[a]	Mean	Std Error	Min.	Max.
Percentage Survival[b]	—	—	8	12.7%	6.23%	0%	54.9%
Ave. Winter Temp.[c]	+0.87	0.004	8	2.93	0.37	1.32	4.86
No. Days ≤1°C	−0.73	0.040	8	54.9	8.75	17	93
No. Days ≤2°C	−0.65	0.081	8	70.6	8.12	28	103
Flow ≥1700 m^3/s[d]	−0.91	0.002	8	6.4	1.54	0	13

[a] 1993 data were omitted because of the mortality caused by the March storm Joshua (see text).

[b] % Survival = (May abundance/prior November abundance) × 100.

[c] Average Winter Temperature = the annual December to April mean daily Connecticut River temperature at CY.

[d] Number of days in April when the Connecticut River flow equaled or exceeded 1700 m^3/s.

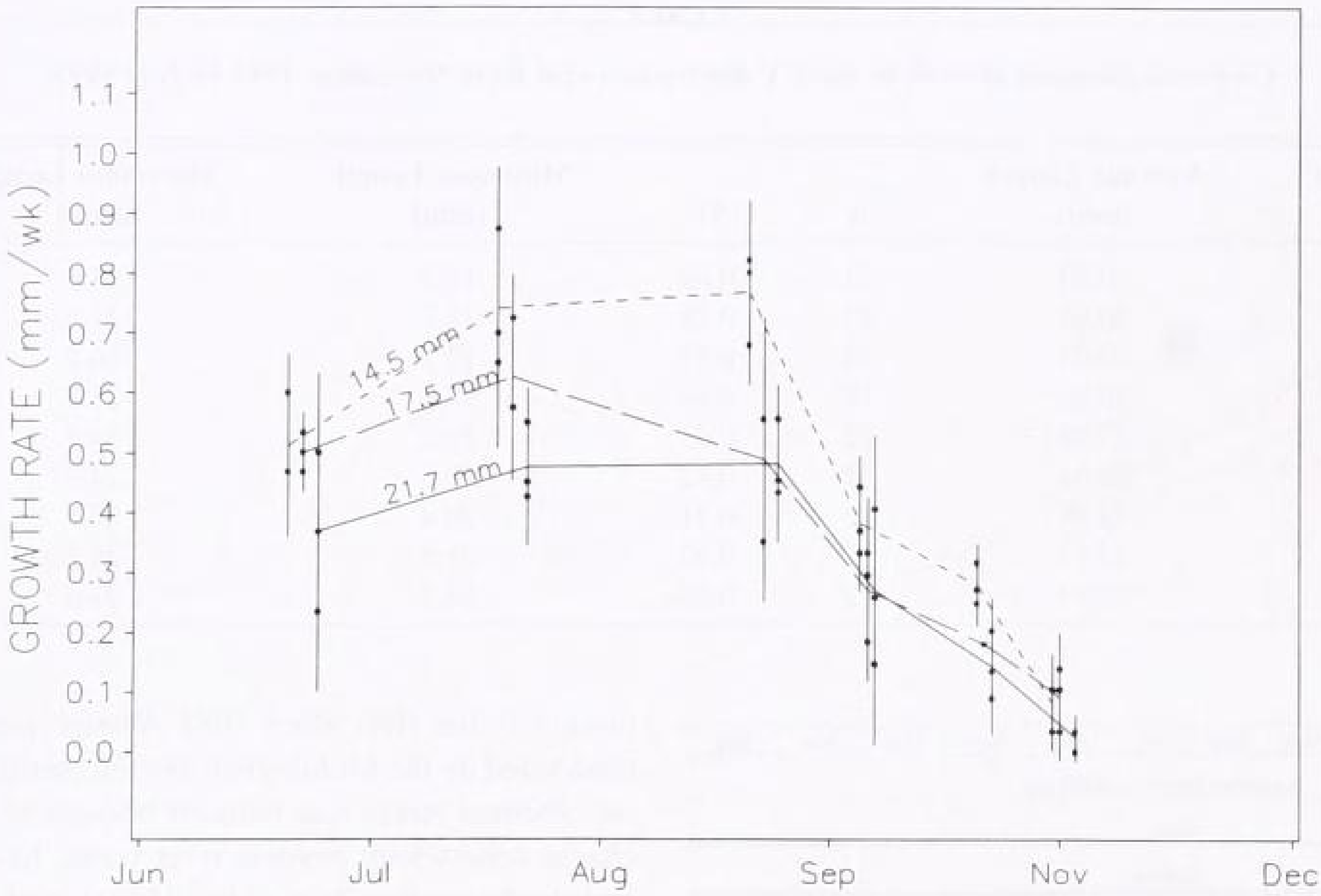


Figure 9. ***Corbicula fluminea*** **growth rates (mm/wk) in 1993 for marked clams within initial size classes based on shell length. Vertical bars represent two standard deviations around the mean growth rates for three individuals in each size class.**

most variable. Large numbers of small (2 mm) clams that apparently survived passage through the power plant cooling water system characterized transient populations in the canal. A permanent population, however, was not established during power plant operation because summer water temperatures often exceeded 37°C, the upper lethal temperature limit for *Corbicula* in our study. McMahon and Williams (1986b) reported similar findings for *Corbicula* living in the thermal discharge of the Handley Power Station in Texas. Following Connecticut Yankee closing in 1996, size range of clams collected in the discharge canal has increased with shell lengths now ranging from 2–19 mm. These results indicate not only that clams are successfully over-wintering in the canal under ambient river temperatures, but also surviving for >1 year. The canal essentially has become a cove where circulation is dependent on semidiurnal tidal exchange, and not vulnerable to high spring freshet water flows.

Clam abundance in the Middletown Station discharge area also fluctuated, but was consistently higher than abundance at CY discharge during the same period. Similar to the CY discharge, the population near the MS discharge was dominated by clams 2 mm in size. In contrast, however, to the CY discharge, clams of all size classes, including those in the 31 mm class, were regularly collected at the MS discharge. The presence of larger size clams suggests that this area provided a more stable refugium. The 37-mm clam collected at this site in 1992, along with growth rates observed during our study, suggests that *Corbicula* has been

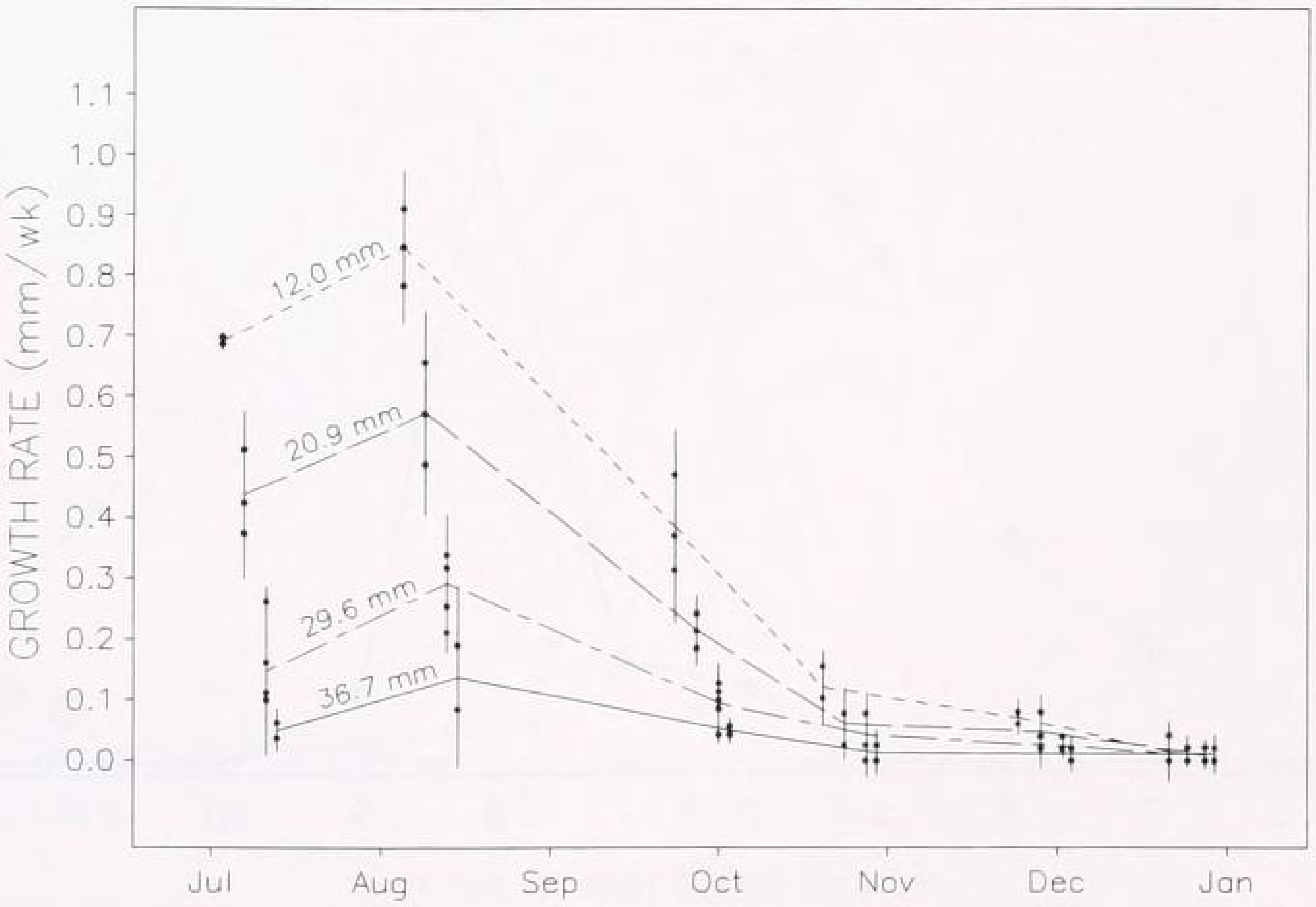


Figure 10. ***Corbicula fluminea*** **growth rates (mm/wk) in 1994 for marked clams within initial size classes based on shell length. Vertical bars represent two standard deviations around the mean growth rates for two to five individuals in each size class.**

TABLE 2.

Corbicula fluminea growth in the CY discharge canal from November 1992 to July 1993.

Date	Growth Week	Average Length (mm)	n	SE	Minimum Length (mm)	Maximum Length (mm)	Growth Rate (mm/wk)
11/10/92	0	20.20	12	0.69	15.3	24.0	
12/22/92	6	20.04	12	0.38	18.1	21.5	−0.026
01/26/93	11	20.97	12	0.59	17.7	26.5	0.185
02/23/93	15	20.89	12	0.48	18.6	23.8	−0.019
03/23/93	19	21.96	12	0.43	19.2	24.4	0.267
04/29/93	24	23.04	12	0.42	20.6	24.9	0.205
05/18/93	27	22.57	12	0.31	20.4	24.1	−0.172
06/24/93	32	24.57	11	0.40	21.5	26.1	0.378
07/22/93	36	25.89	12	0.39	24.2	27.6	0.330

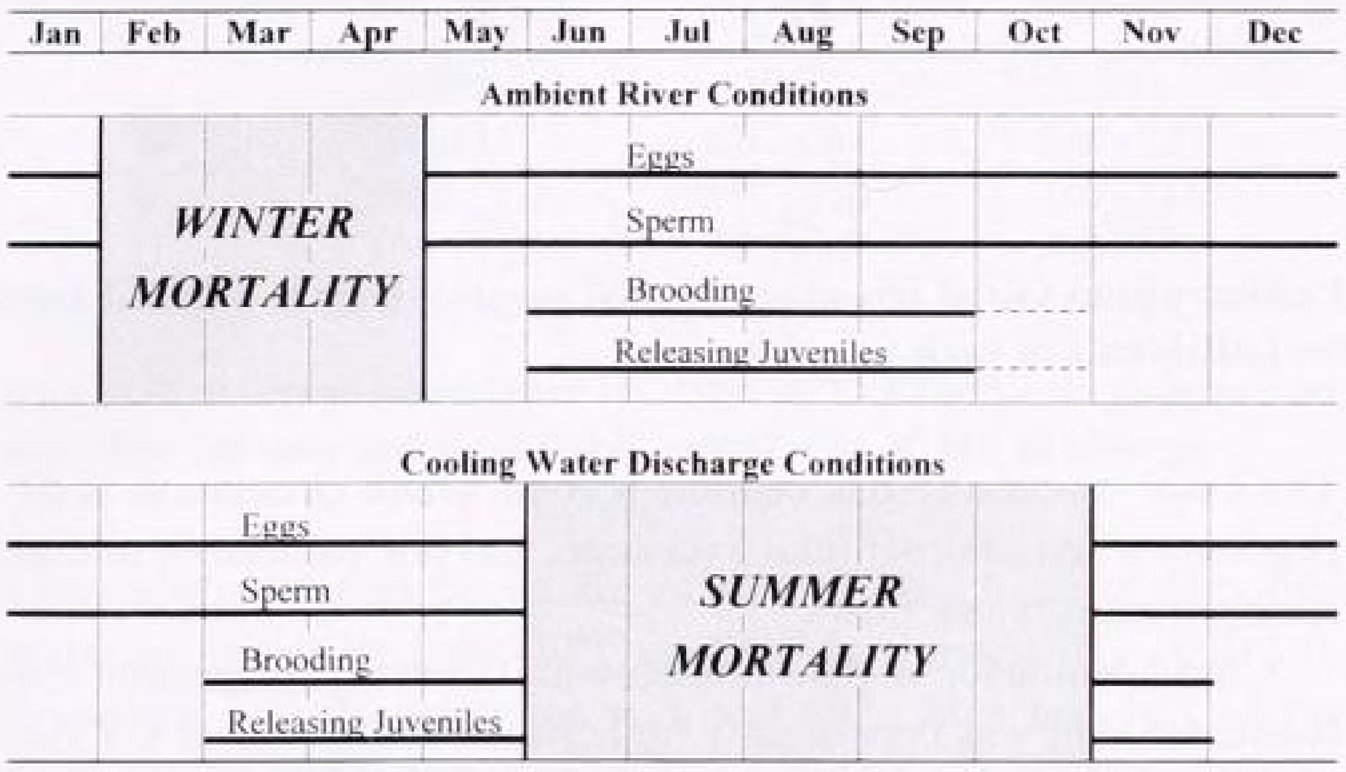


Figure 11. Summarization of the 1991 to 1994 annual reproductive cycle of *Corbicula fluminea* under ambient Connecticut River conditions and the thermally elevated conditions of the CY cooling water discharge.

present in the river since 1988. Winter water temperatures were moderated by the Middletown Station thermal discharge, and summer thermal stress was reduced because of rapid dilution of discharge waters with ambient river water. In addition, the MS thermal discharge flow was only ~15% that of CY.

Corbicula growth in the Connecticut River under ambient water temperatures is consistent with reports by other researchers in North American (Morton 1977, Britton et al. 1979, Eng 1979, Mattice 1979, McMahon 1983, Welch & Joy 1984, Joy 1985, Mattice & Wright 1986, McMahon & Williams 1986b, Doherty et al. 1990, French & Schloesser 1991), and was primarily influenced by water temperature. Growth began in May when water temperatures rose above 10°C and continued until December when water temperatures dropped below this threshold. Other researchers reported 9–15°C to be the lower temperature threshold for growth of *Corbicula fluminea* in their studies (Hall 1984, Mattice & Wright 1986, McMahon & Williams 1986a, French & Schloesser 1991).

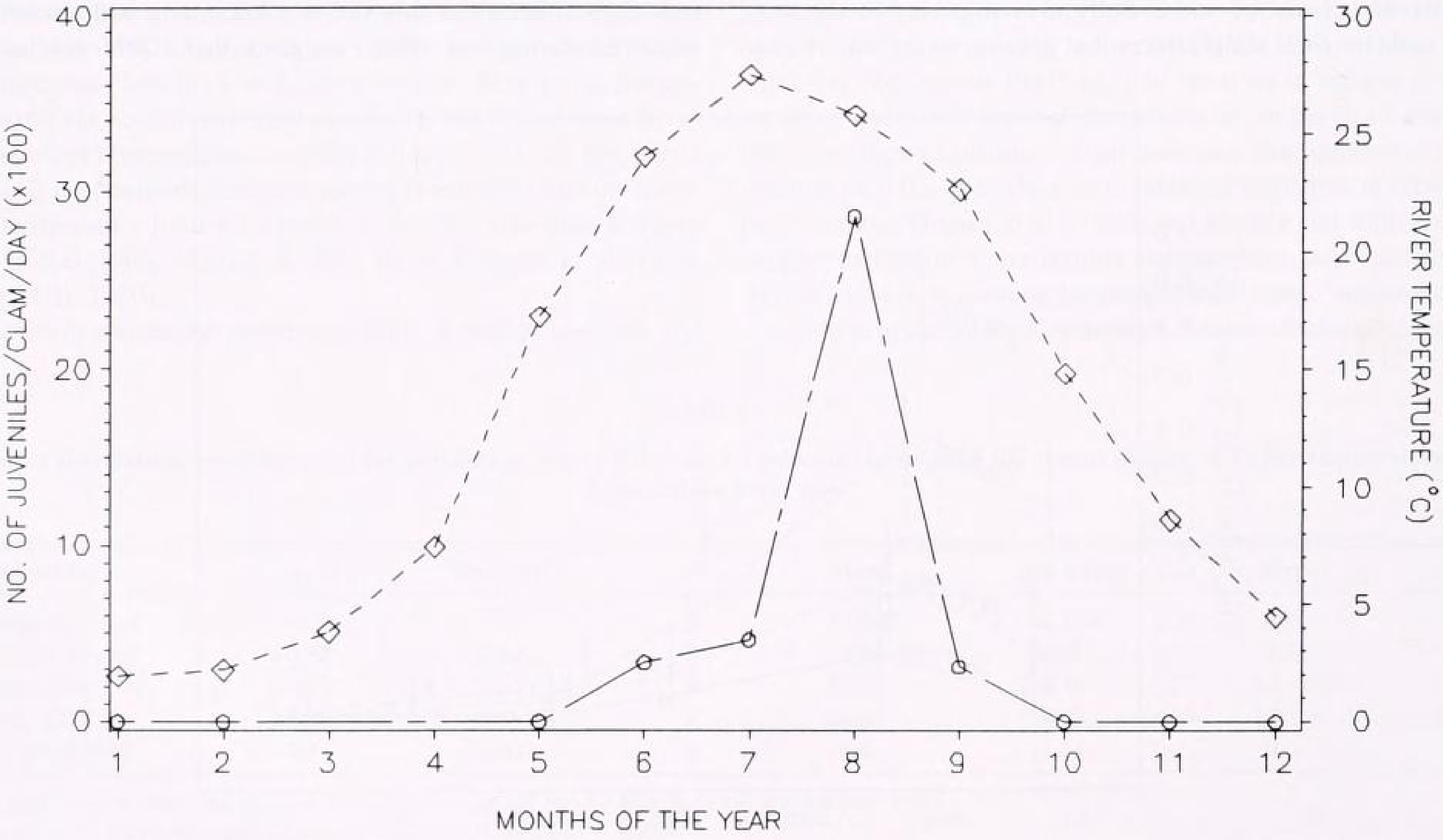


Figure 12. *Corbicula fluminea* fecundity (–○–) and water temperature (- - ◇ - -) for clams held in ambient temperature Connecticut River water from 1991–1994.

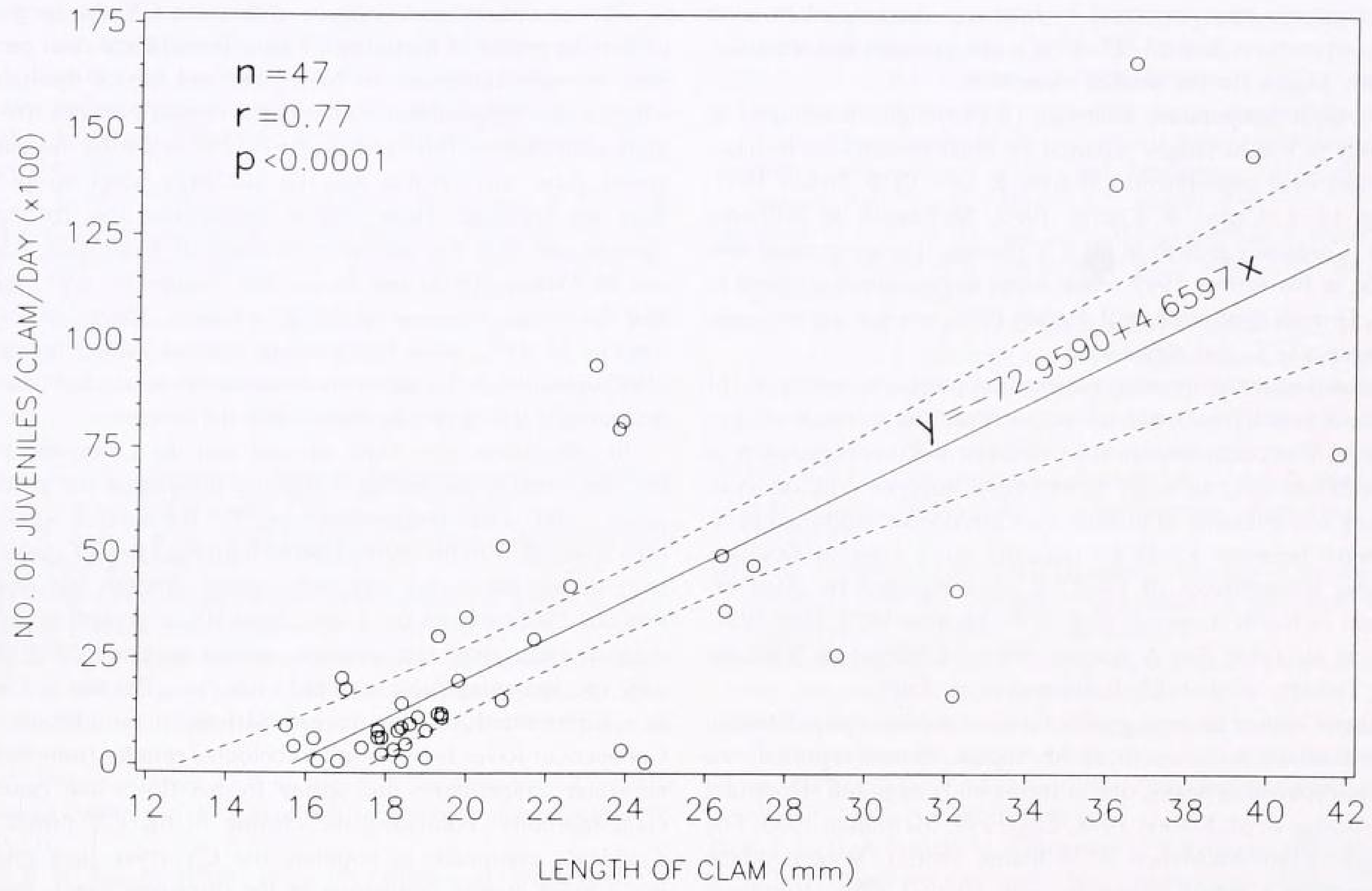


Figure 13. Linear regression with 95% CI on mean predicted values for the number of juveniles released per day in relation to shell length (mm) of the spawning *Corbicula fluminea* during the peak spawning month of August in the mainstem Connecticut River.

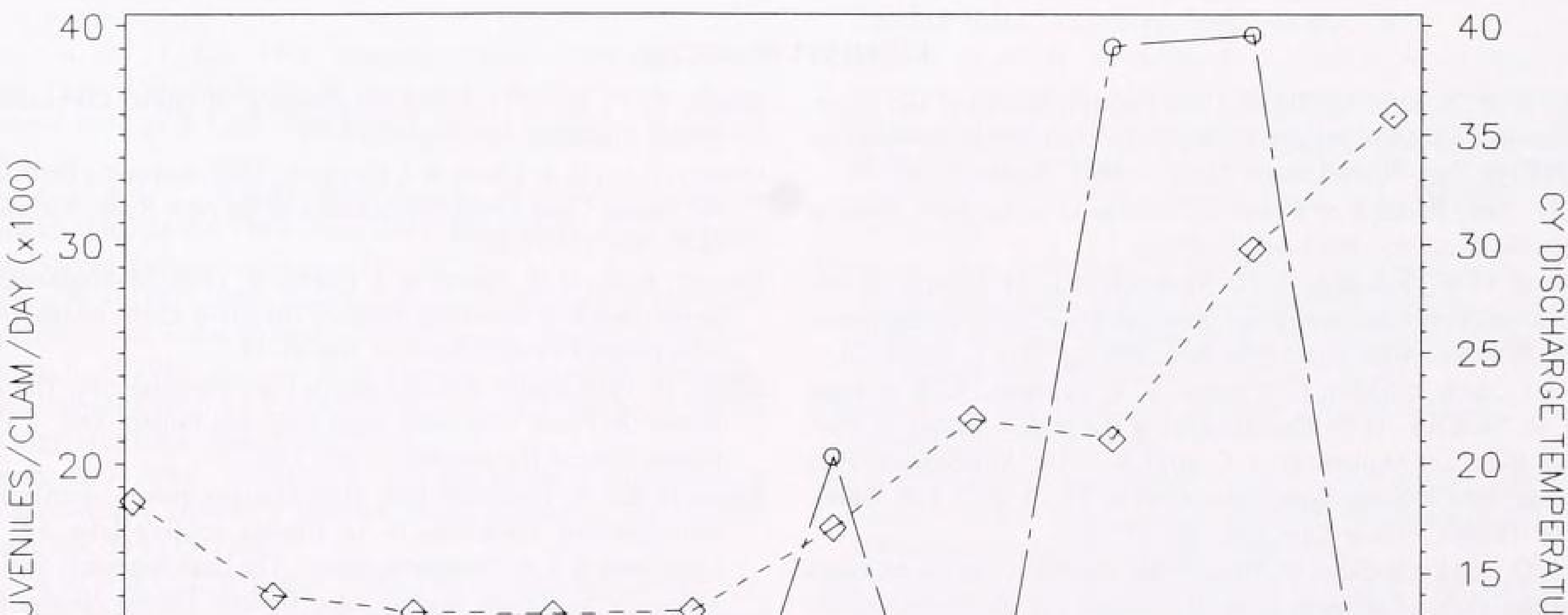


Figure 14. *Corbicula fluminea* fecundity (–○–) and water temperature (- - ◇ - -) for clams held in the discharge canal at CY from November 1992 to August 1993.

Highest growth rates occurred in July and August, when river water temperatures peaked (25–30°C), and growth rates were significantly higher for the smaller clam sizes.

The upper temperature tolerance of *Corbicula* determined in this study is within ranges reported by other researchers in laboratory and field experiments (Mattice & Dye 1976, Dreier 1977, Mattice 1979, Cairns & Cherry 1983, McMahon & Williams 1986a). *Corbicula* growth in the CY thermal discharge canal was initiated in November 1992 when water temperatures dropped to <35°C. Growth continued until August 1993, when water temperatures were >37°C and clams died.

Seasonal water temperatures also control reproductive cycles of the Connecticut River *Corbicula* population. The presence of eggs and sperm was continuous in the Connecticut River population of this species as long as water temperatures supported its survival. Brooding and releasing of juveniles occurred when water temperatures were between 17–28°C, typically from June to October. Spawning temperatures of 14–27°C were reported by other researchers in North America (Eng 1979, Mattice 1979, Hall 1984, Cherry et al. 1986, Foe & Knight 1986; McMahon & Williams 1986a; Doherty et al. 1987; Rajagopal et al. 2000).

A single annual spawning peak for the *Corbicula* population in the Connecticut River occurred in August. Others reported two *Corbicula* spawning peaks, one in spring and one in fall (Heinsohn 1958, Aldrige & McMahon 1978, Eng 1979, McMahon 1983, Foe & Knight 1986, McMahon & Williams 1986a). Several others have reported a single spawning peak (Bickel 1966, Hornback 1992, Mouthon 2001). The presence of a single reproductive peak in the Connecticut River population may be related to longer periods of cold-water conditions, more severe spring flooding, and the quantity and quality of available food.

The altered thermal regimen within the CY discharge canal shifted the period of reproduction from the ambient river period of June through September to November and March through May when water temperatures in the canal ranged between 16–30°C. Spawning during July and August 1993 occurred because the power plant was off-line and the discharge water temperatures were not elevated. These results demonstrate that thermal discharges can alter the reproduction cycle of *Corbicula*. Aldridge and McMahon (1978) and Dreier and Tranquilli (1981) reported that *Corbicula fluminea* spawning activities stopped at temperatures of 30–34°C, most likely due to thermal stress. Graney et al. (1980) speculated that elevated temperatures in thermal discharges may extend the spawning season into the winter.

In conclusion, this study showed that the Connecticut River has supported a fluctuating *Corbicula* population for at least 10 years. Cold water temperatures (<2°C) for several weeks, and high water flow in the spring caused high mortality of clams in the river during the winter and early spring. Growth and reproduction for *Corbicula* in the Connecticut River peaked in July and August when river temperatures ranged between 24–30°C and only one spawning peak occurred each year. The key to *Corbicula*'s unexpected success in establishing a population in the Connecticut River is its ability to colonize refugia from cold winter water temperatures and spring freshet flows that cause high clam mortality. Following the closing of the CY power plant, *Corbicula* continued to populate the CY river sites establishing a more mature population in the discharge canal. Based on our observations of *Corbicula* in the Connecticut River, we expect that this species will continue to successfully colonize other rivers and lakes in New England, where similar winter refugia exist.

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