REPRODUCTION AND RECRUITMENT OF THE BRACKISH WATER CLAM *RANGIA CUNEATA* IN THE JAMES RIVER, VIRGINIA[1,2]

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ABSTRACT

Reproduction and recruitment of the brackish water clam *Rangia cuneata* were investigated in the James River, Va., from February 1970 to January 1972. Histological examinations of gonads were made, newly set clams were collected, and temperature and salinity measurements were taken from three populations living in different salinity regimes.

Gametogenesis began in April and ripe gonads were found from May to late November with no inactive period. From observations of set abundance, two periods of spawning were determined: one in early through midsummer, coinciding with the beginning of spawning as determined from gonadal examinations; and a second and longer period in late fall and early winter, with an increased percentage of partially spawned and spent clams. Gametogenesis ceased in December through March as residual gametes were cytolyzed. Sex was not detected during this last phase. More females than males were found in the upstream (lower salinity) populations. Temperature was important in initiating gametogenesis in the spring and midsummer. Spawning correlated best with changes in salinity to approximately 5 °/oo.

Over its estuarine range, salinity has a controlling effect on *Rangia* spawning and recruitment. Seasonal reduction in input of freshwater (increased seawater intrusion) is needed to induce spawning and recruitment in upstream populations. Best recruitment occurred to the middle of the habitat range which has an annual salinity change from fresh to 5°/oo.

A southern species of clam, *Rangia cuneata* (Gray) has in the last 15 yr extended its range into Chesapeake Bay estuaries (Hopkins and Andrews 1970). This clam occupies an otherwise "open niche" in the oligohaline region of these estuaries. Although species diversity is usually low, there may be large numbers of individuals of species adapted to this environment. In the upper James River estuary, *Rangia* accounts for nearly 95% of the benthic biomass.

Rangia is important both ecologically and commercially (Hopkins 1970). It provides a substantial food source for several species of fish and crabs (Darnell 1958), and waterfowl (Wass and Wright 1969). It is ecologically significant because it converts detritus into biomass that can be utilized by these organisms (Odum and Copeland 1969).

Not only is *R. cuneata* a species for which low salinity, 1-15°/oo, is optimal; it is also a species which evidently cannot maintain a population outside this range (Hopkins 1970). That *Rangia* thrives in a zone unfavorable for most animals indicates it has some unusual adaptations. Despite its abundance in favorable environments and long history on the Gulf Coast, this clam has received little attention.

The study reported here concerns the reproductive cycle and recruitment of *Rangia cuneata* in the James River. The major objectives were to: (a) study the gametogenic cycle of *Rangia* from histological sections; (b) determine differences in gametogenesis or spawning of clams over the species range in the estuary; (c) investigate, from analysis of field data, the influence of temperature and salinity on initiation of gametogenesis and spawning; (d) corroborate gametogenic findings by collecting newly set clams; and (e) determine the duration of the larval period and differences in set abundance in the estuary.

Fairbanks (1963) studied the spawning cycle of *Rangia* in Lake Pontchartrain, La., but it is known that physiologically different races of bivalves can occur at different latitudes (Loosanoff 1969). Cain

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(1973, 1974) reported on the laboratory spawning of *Rangia* and the combined effects of salinity and temperature on embryos and larvae.

The impending action (at the time the work was initiated) of discharge of waste heat into the *Rangia* community by the Virginia Electric and Power Company's (VEPCO) Nuclear Generating Station at Surry, Va., was a further impetus to the study of the reproductive cycle, especially those factors that initiate gametogenesis and spawning.

DESCRIPTIONS OF THE STUDY AREA

The study area in the James River is a transition region between freshwater and salt water. The area has a seasonably variable salinity that ranges between about 0 and 15‰, depending on the volume of freshwater input. In the spring, high river flow covers most of this region (except station A) with freshwater (Figure 1). Occasionally, in late summer and fall the study area may exhibit measurable salinity as far upstream as station C. The mean annual discharge of the James River is approximately 212 m^3/s (7,500 cfs).

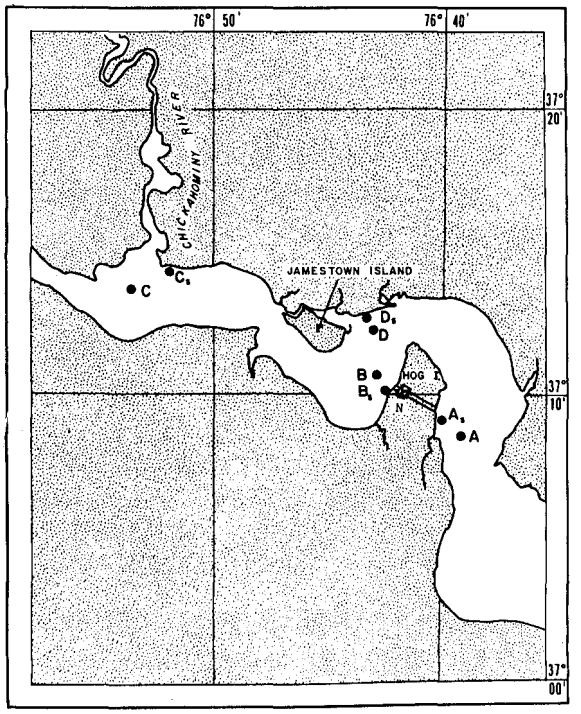

FIGURE 1.—Location of sampling stations for *Rangia cuneata* in the James River, Va. (N = nuclear generating station).

Field and hydraulic model studies of the James River estuary have shown a two-layer density flow pattern, in which the deep, more saline water has a net upstream flow and the surface, fresher water has a net downstream flow. The net sediment transport of the two-layer section averaged over many tidal cycles is upstream (Pritchard 1952). The transition section of the James River is characterized by high natural turbidity and sedimentation from the flocculation of river-borne sediments.

The distribution of bottom sediment types in the James River estuary has been studied by Nichols (1972). His survey indicates silt-clay substrates at stations A, B, C, and D and sand substrates at locations As, Bs, Cs, and Ds.

The distribution of *Rangia* in the James River was found to be approximately from nautical mile 25 to 55 above the river mouth (Figure 2). The downriver extent of its range overlaps the habitat of typical estuarine organisms such as the oyster; at the upriver limit *Rangia* is associated with completely freshwater forms such as freshwater mussels. In the oligohaline portion of its range it is typically associated with the polychaetes *Scolecolepides viridis* and *Laeonereis culveri;* the crustaceans *Cyathura polita, Corophium lacustre,* and *Gammarus* sp.; and the bivalves *Macoma balthica, Brachidontes recurvus,* and *Congeria leucophaeta.*

METHODS AND MATERIALS

The reproductive cycle was investigated by collecting clams at stations A, B, and C (Figure 1). Station A was near the downstream range of the clam. Station B was 18.5 km above station A. Station C was located (18.5 km above station B) near the mouth of the Chickahominy River in order to include part of the clam's range which seldom experiences salinity changes. All stations were located at approximately the same depth (3-4 m). The clams used in this study were collected from a predominantly silt-clay substrate. Although Tenore et al. (1968) indicated that such sediments were detrimental to *Rangia*, the clams at the various stations appeared to be thriving over the 2-yr study.

Beginning in February 1970 approximately 20 clams, 30-40 mm long, were collected at stations A and B using a modified oyster dredge. Attempts were made to collect clams at these stations every

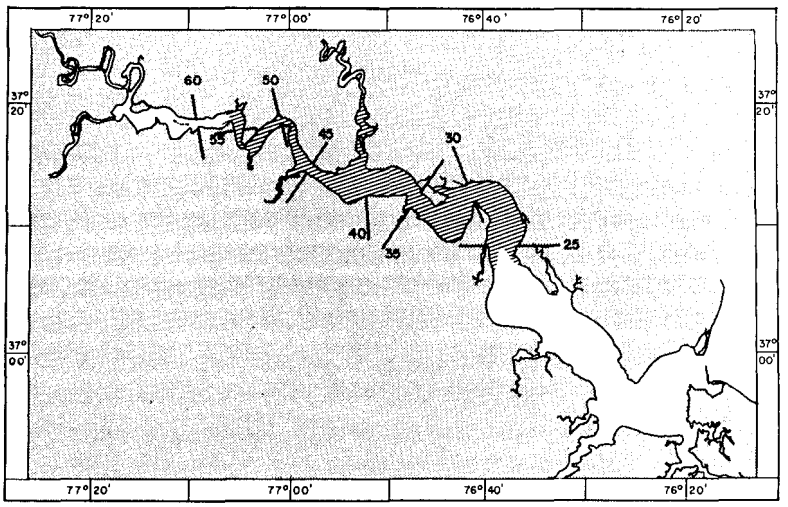

FIGURE 2.—The distribution of *Rangia cuneata* in the James River, Va. Segments are at 5-nautical mile intervals.

2 wk, but bad weather and boat failures occasionally delayed this to 3 wk. Beginning 22 September 1970 collections at station C commenced. Collections at all stations were terminated in January 1972.

In the laboratory these clams were measured, weighed, shucked, and the gonads dissected out and placed in a solution of alcohol, Formalin,[4] and acetic acid (AFA) for fixation. Gonad tissues were sectioned at 7-10 μm with a rotary microtome, stained with Delafield's hematoxylin, and counterstained with eosin. Gonad tissue stage of development was determined following the scheme of Ropes (1968) who categorized the seasonal gametogenic cycle of *Spisula solidissima* as: early active, late active, mature, partially spawned, or spent. Similar stages of development were first described by Ropes and Stickney (1965) for *Mya arenaria* and have subsequently been used for two other members of the family Mactridae; *Mulinia lateralis* (Calabrese 1970), and *Tresus capax* (Machell and De Martini 1971). The number of clams in each category, regardless of their sex, was recorded for each sample.

The sex ratio of clams from each station was calculated and a chi-square test used to establish goodness of fit to a 1:1 ratio.

During June 1970, clams collected at stations A and B were placed in four groups (5-10, 11-20, 21-30, and 41-50 mm). These clams were sectioned and stained to determine the size at which they contain reproductive products.

[4]Reference to trade names does not imply endorsement by the National Marine Fisheries Service, NOAA.

Set Collectors

Collectors used to determine the time and intensity of setting were placed at stations A, B, C, and D and inshore from these areas in shallow, sandy areas (Figure 1). These stations were designated as As, Bs, Cs, and Ds. Stations A, As, B, Bs, and Ds were examined from June 1970 and C, Cs, and D from September 1970, at approximately 2-wk intervals until January 1972.

The set collector was a plastic gallon jar with an 8.7 cm diameter mouth. The mouth was covered with a plastic 5 mm mesh to prevent the entry of predators. The jar rested on the bottom, fastened to a concrete block.

Water flowed across the mouth of the jar and suspended sediments, detritus, and metamorphosing clams settled to the bottom. In the field, the contents of the jar were washed through a 0.174 mm mesh screen. In the laboratory each sample was elutriated to remove most of the detritus (Coffin and Welch 1964). The material remaining after elutriation was examined for clams under a dissecting microscope. All bivalves were counted and some were measured. Set of bivalve species other than *Rangia* was also identified and counted.

Environmental Data

Water samples for salinity, dissolved oxygen, and temperature measurements were taken whenever biological collections were made. A Kemmerer bottle was used to obtain bottom water samples at the deep stations. Samples at shallow

stations were collected about 0.3 m below the surface. Temperature measurements were taken immediately with a stem thermometer. Bottom temperatures recorded at VEPCO instrument towers 1 and 6 (near stations A and B, respectively) were also used in this study. Salinity samples were analyzed in the laboratory with a Beckman RS7B induction salinometer. Dissolved oxygen samples were fixed immediately after collection and analyzed in the laboratory by a modified Winkler method.

Freshwater input was compiled from records taken at gauging stations on the James River near Richmond, the Appomattox River near Matoaca, and the Chickahominy River near Providence Forge. Combined, these three rivers are the major sources of freshwater for the James River in the study region.

RESULTS

Histological Study of the Reproductive Cycle

A histological basis for classifying the gonadal condition was used because the external appearance of gonads did not accurately reflect phase of development. The appearance of gonads of both sexes is superficially the same during each phase.

No evidence of gonadal parasitism was found in any of the tissue sections, nor were hermaphroditic individuals found.

There was little difference in the time of initiation of gametogenesis and ripening between the sexes so the number of males and females in each stage was combined for analyses. Figures 3 to 6 show the phases in the development of the female and male gonads.

Station A

The reproductive cycle of clams at station A (Figure 7) was more complex than at the other stations. From early February to late March 1970 most clams were in the spent phase, although a few male clams contained ripe sperm with sperm balls. In early April 1970, 40% of the sample were in the early active phase. By May, 40% were ripe, with 10% partially spawned. From May through September clams were found in all gonadal phases. Evidently some spawning and rematuration occurred during the summer months. In early October 1970, all clams examined were ripe. The volume of eggs and sperm at the second ripening was much greater than that in the early spring and summer. Partially spawned clams were numerous at the end of October and by mid-November 85% of the sample were partially spawned or spent. Throughout the rest of the winter most clams were in the spent stage, although some males retained sperm and slight gonadal activity was noted in some females.

The reproductive cycle for 1971 was basically the same as the previous year. In early June 1971, 65% of the clams were ripe. Spawning was indicated during the next 2-wk period because 60% were spent or partially spent. The fall spawning season was very similar to that of 1970, with 95% ripe by late September. Spawning was completed by early November and, again, some ripe males were observed during the winter.

Station B

Clams in the spent or inactive phase were found from February to early April 1970 (Figure 8). Some males still contained sperm in various stages of cytolysis. By late April 1970, half of those collected had begun gametogenesis, resulting in 80% being ripe by early June 1970. Clams remained in the ripe phase throughout the summer with some spawning occurring during July. During August there was a second development, resulting in all clams observed being ripe in early September 1970. Spawning commenced in early October and was completed by mid-November 1970. Immediately after spawning some clams were in the early active phase, but development did not proceed further during the winter.

The reproductive cycle for 1971 was similar to that of 1970. Gametogenesis commenced in early May. Fewer ripe clams were observed during the summer months than in 1970. The second cycle began in early July and by early September all clams were ripe. Spawning began in late October and was completed by late November. As found at station A, the second seasonal cycle for station B was more intensive; more ripe clams were found and their gonads contained far more sperm and eggs. Spawning was more intensive during the fall, with gonads progressing from ripe to spent in a month.

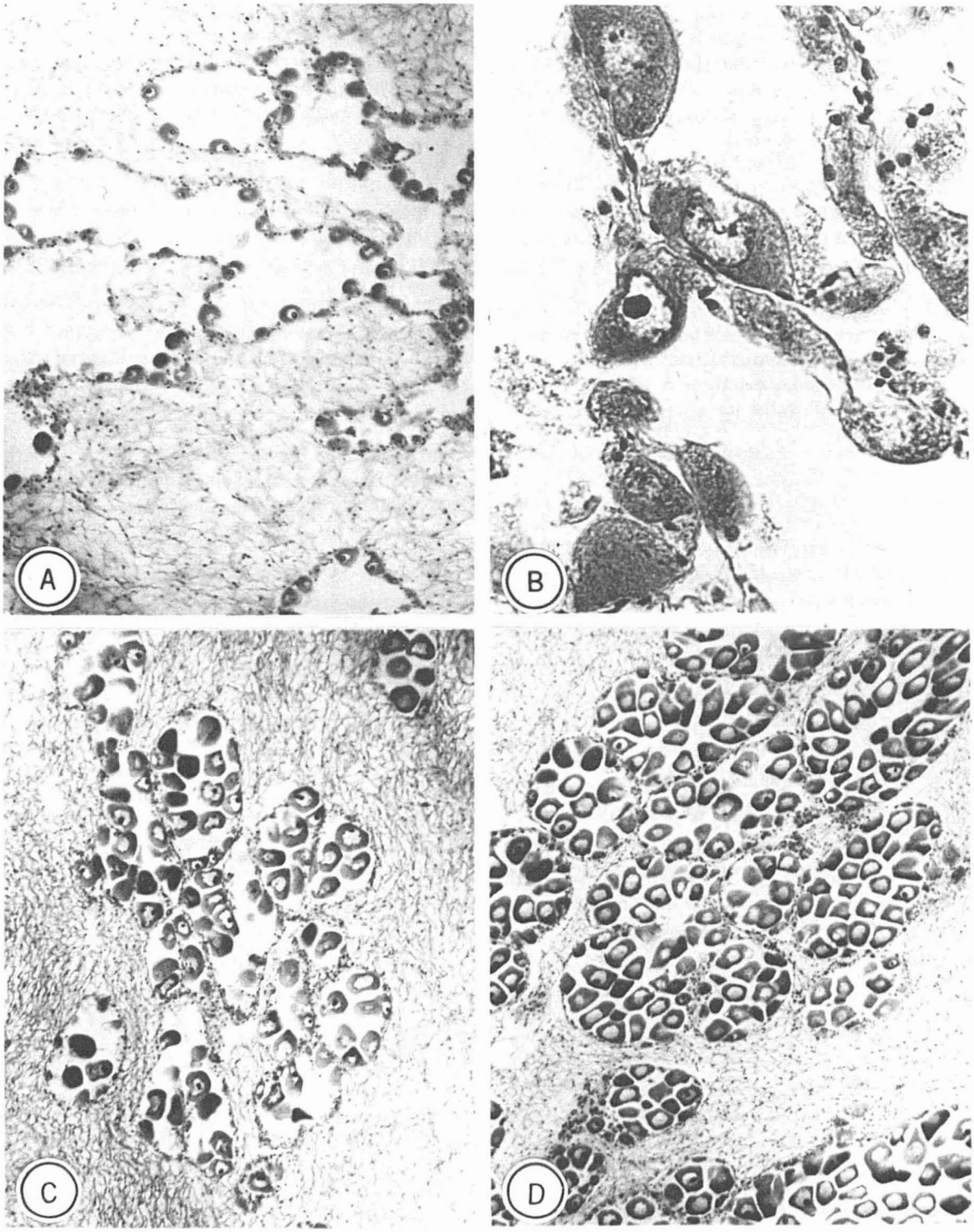

FIGURE 3.–A, section of *Rangia* ovary in the early active phase of oogenesis (× 120); B, ovary in early active phase (× 500); C, ovary in late active phase (× 120); D, ripe ovary (× 120).

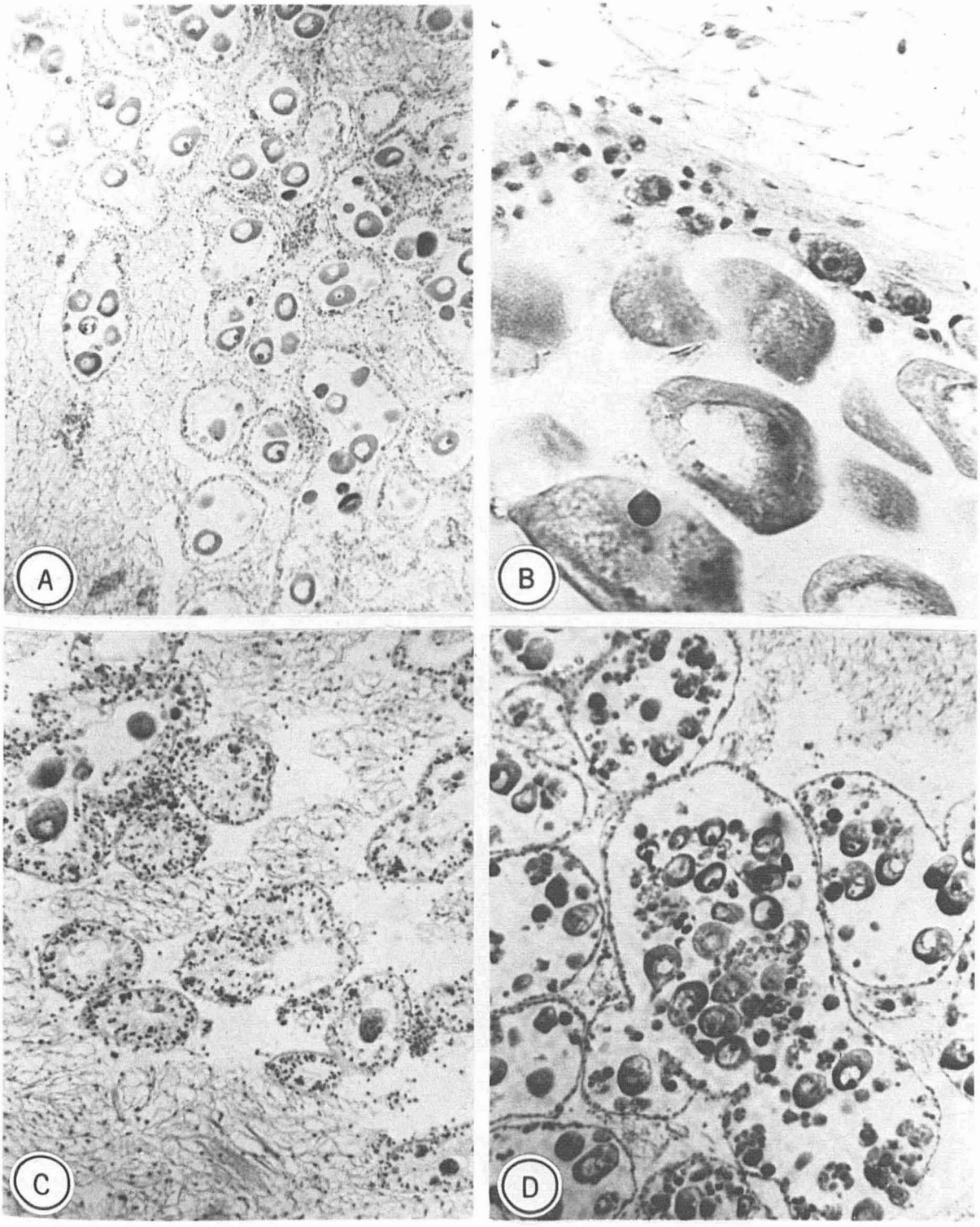

FIGURE 4.—A, *Rangia* ovary in the partially spawned phase (×120); B, partially spawned ovary (×500); C, spent ovary with few ova retained (×120); D, cytolysis of unspawned eggs (×120).

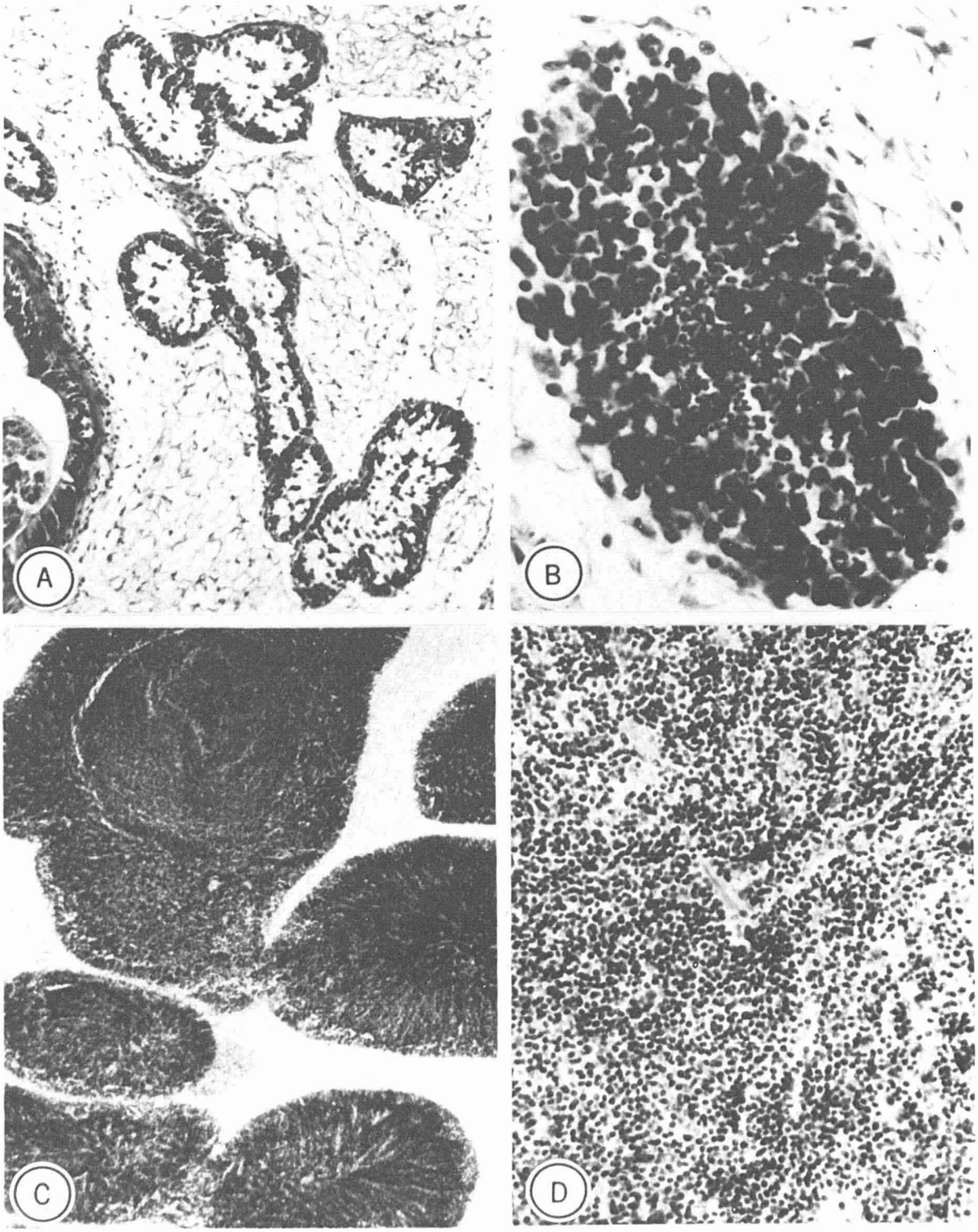

FIGURE 5.—A, Section of testis of *Rangia* in early active phase of spermatogenesis (× 120); B, testis in late active phase—note sperm in center (× 500); C, ripe male (× 120); D, ripe male (× 500).

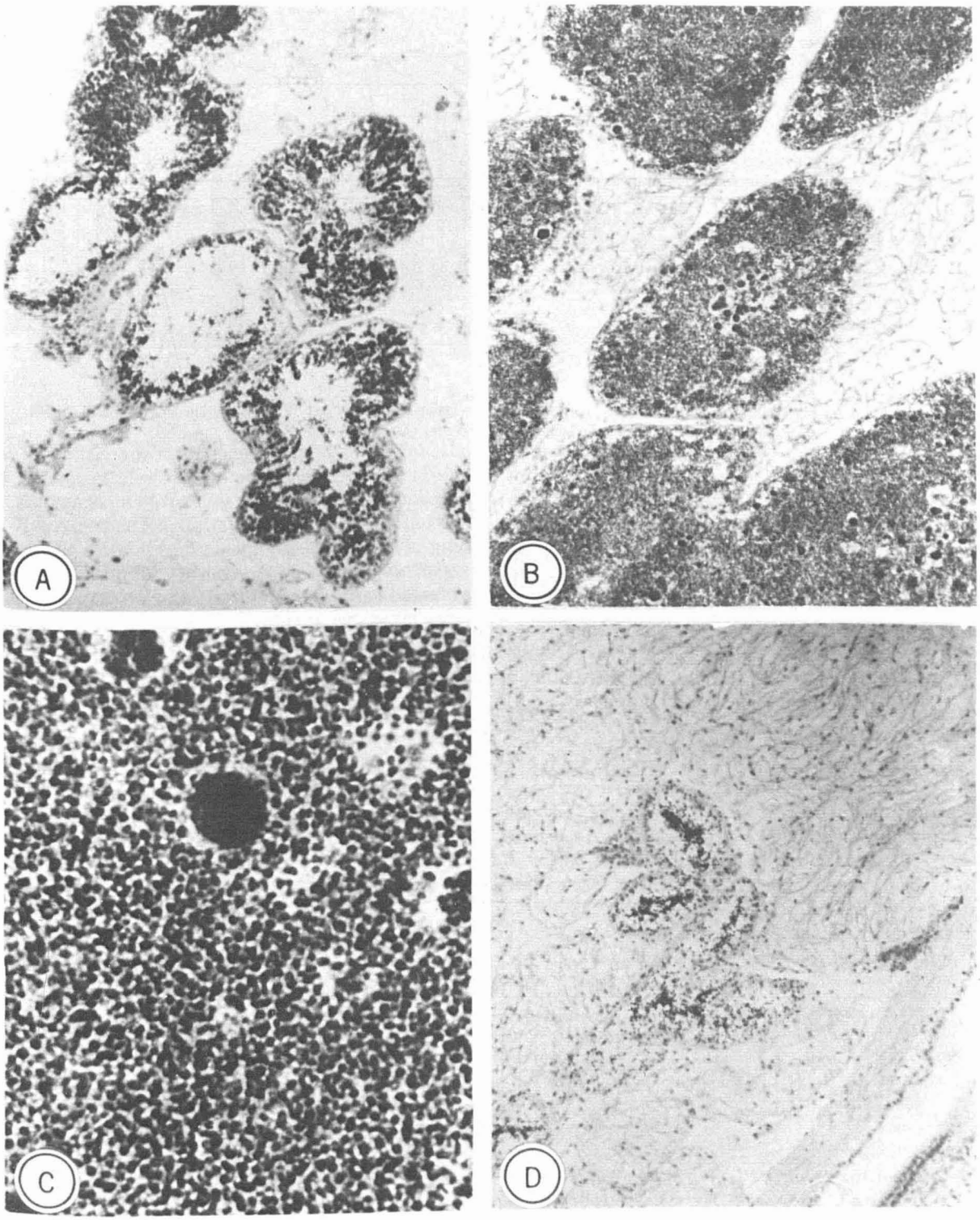

FIGURE 6.—A, Section of testis of *Rangia* in partially spawned phase (×120); B, testis with retained sperm and sperm balls (×120); C, testis with sperm balls (×500); D, spent testis with few sperm retained (×120).

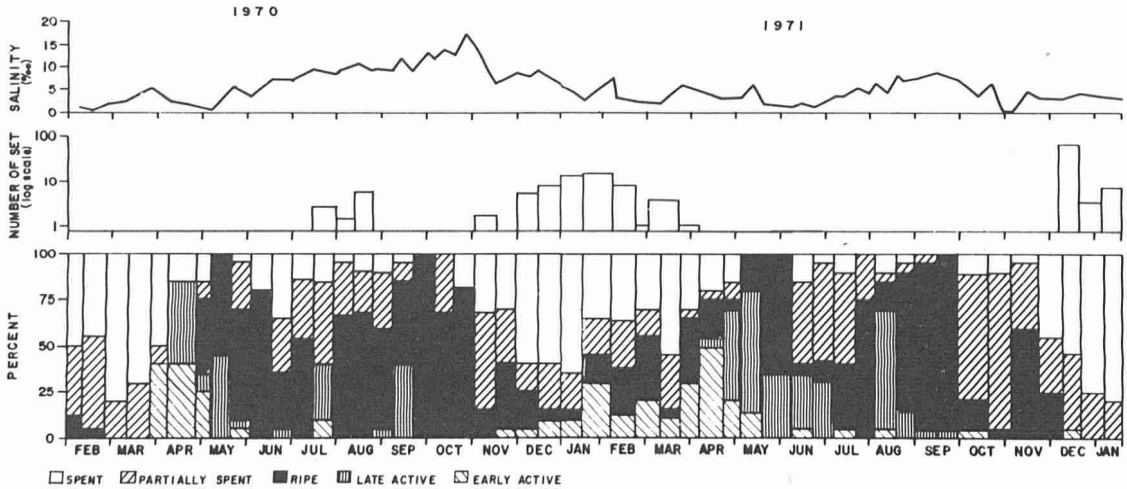

FIGURE 7.—Gonadal phases and setting of *Rangia* at station A in relation to salinity from 1970 to 1971. The length of each shaded area represents the percentage frequency of clams in each category.

Station C

The reproductive cycle at station C was similar to that at station B during 1970. However, earlier spawning was indicated by 88% of the clams being either partially spawned or spent in early October (Figure 9). Clams remained in the spent phase until early May 1971, when gametogenesis began. Few ripe clams were found at this upstream station during the late spring and summer. Clams in the early active phase were found during July and by the end of August all clams were ripe. From September to November 1971 clams were predominantly ripe, but there was no spawning. Cytolysis of the eggs began in November, resulting in a spawned-out appearance (Figure 4D). No spawning occurred at station C during 1971, in marked contrast to stations A and B where the fall spawning was intense.

Sex Ratio

The data were divided into summer-fall and winter-spring seasons, because many clams contained no discernible gonads during the winter

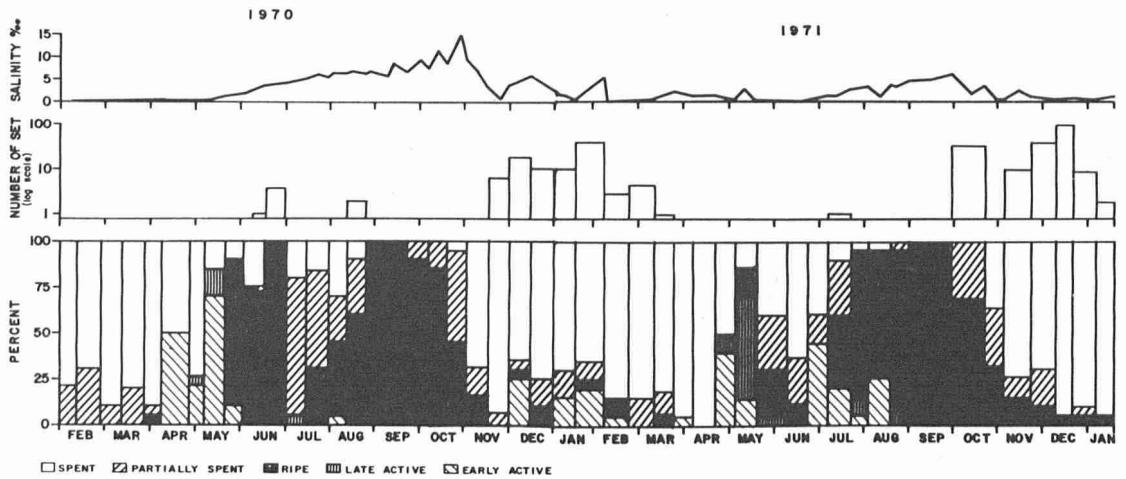

FIGURE 8.—Gonadal phases and setting of *Rangia* at station B in relation to salinity from 1970 to 1971. The length of each shaded area represents the percentage frequency of clams in each category.

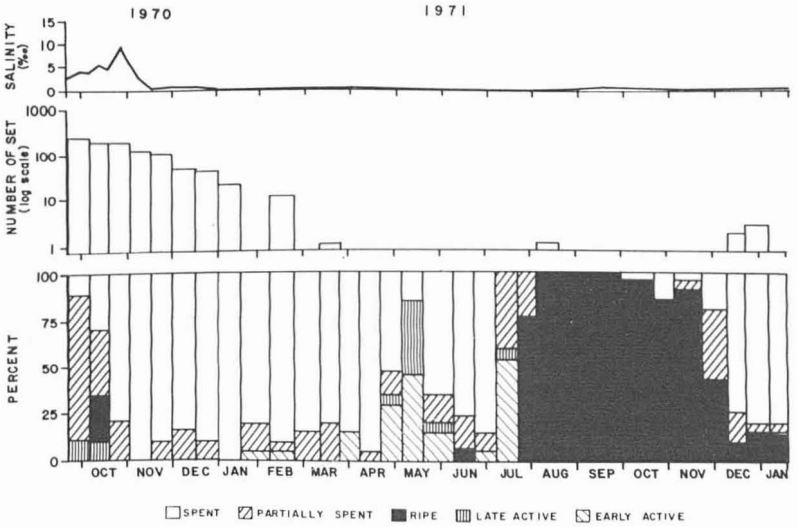

FIGURE 9.–Gonadal phases and setting of *Rangia* at station C in relation to salinity from 1970 to 1971. The length of each shaded area represents the percentage frequency of clams in each category.

and early spring. During summer and fall the gonads of most clams could be recognized (Table 1). The ratio of females to males at station A was not significantly different from 1:1. Females predominated at stations B, D, and C during the summer and fall months of 1970 and 1971. When the clams of non-determinable sex are added to the male group, there are still significantly more females.

Of the clams collected in late June 1970 at station A, none measuring 5-10 mm contained gonads. In the second group 50% showed signs of gametogenesis and had recognizable sex products; 70% of the third group had discernible gonads; and most clams in the fourth group contained gonads. Most small clams were males, but too few were examined to test the significance of sex ratios.

Larval Setting

The number of *Rangia* clams setting at each station is shown in Figures 7 to 14. This number does not provide an estimate of survival because predators were excluded by the screen cover. The number of set clams at both deep and shallow stations by season is shown in Table 2. At stations A and As a small number (< 7) set during late July and August 1970. In December 1970 through March 1971 set clams were common but not very abundant at these two downriver stations. Only one setting period (29 individuals) was recorded during the summer months at station As. Larvae began setting again during the third week of December 1971 with 70 at station A. Collectors at both stations continued receiving set until sampling was terminated on 18 January 1972.

Setting at stations B and Bs was sporadic during the spring and summer of 1970, with no more than four clams in any jar. Setting began at station B in mid-November 1970 and continued there until late March 1971. A maximum of 42 individuals was collected on 8 February 1971. Set clams were found on only one sampling date during the next summer. Setting in the fall began in late October 1971, with very large numbers during late November and early December.

Setting at station D was similar to that at station B except more individuals were found during the fall and winter of 1970-71. One hundred eighty-five were collected in the station D bottle in mid-December 1971.

Only data beginning in September 1970 were available from station C. As noted in the tissue sections, spawning had commenced earlier. Setting from early September 1970 to March 1971 was very heavy, with 257 clams collected at this station

TABLE 1.–The ratio of females to males and the number of clams with non-determinable (ND) gonads at each station. Summer and fall seasons were tested with the ND clams added to the male group.

	Station A			Station B			Station D			Station C		
Seasons	F	ND	M	F	ND	M	F	ND	M	F	ND	M
Summer and fall 1970	140	0	153ns	209	3	57**				166	9	70**
Winter and spring	61	53	83	46	128	35	13	44	13	29	118	66
Summer and fall 1971	127	7	102ns	178	22	34**	41	5	11**	138	38	54**

ns = not significant.
** = highly significant.

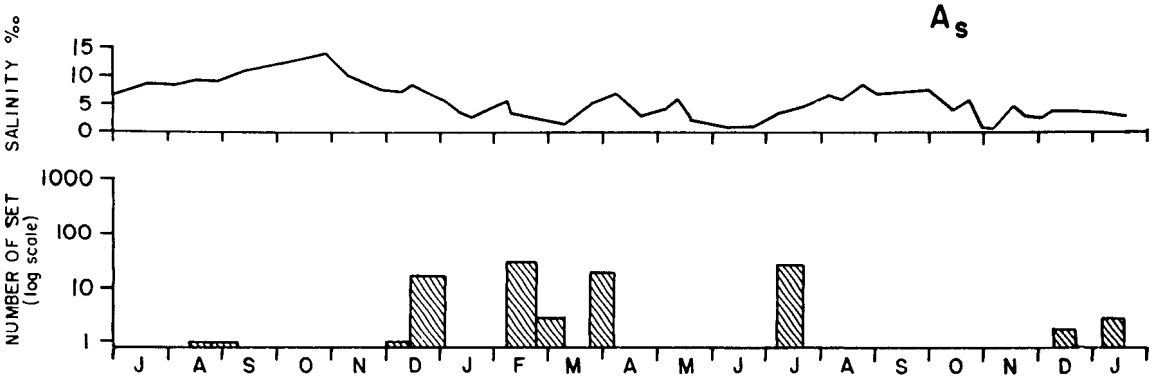

FIGURE 10.—Number of *Rangia* set and salinity at station A_S from July 1970 to January 1972.

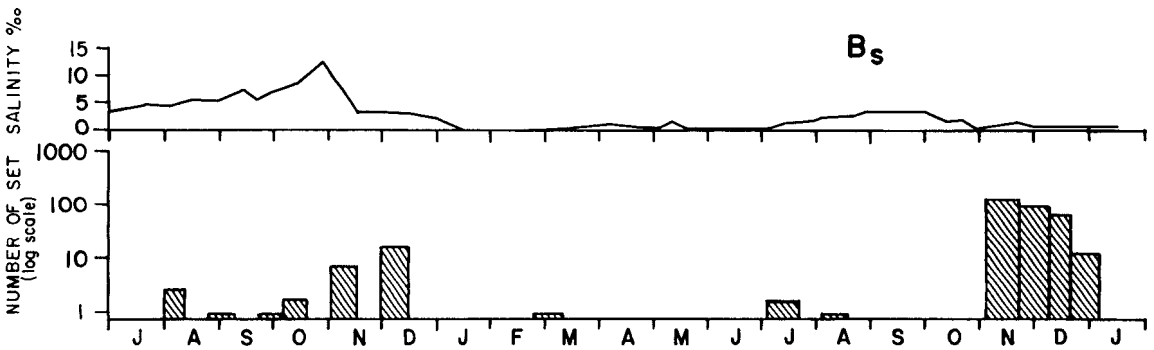

FIGURE 11.—Number of *Rangia* set and salinity at station B_S from July 1970 to January 1972.

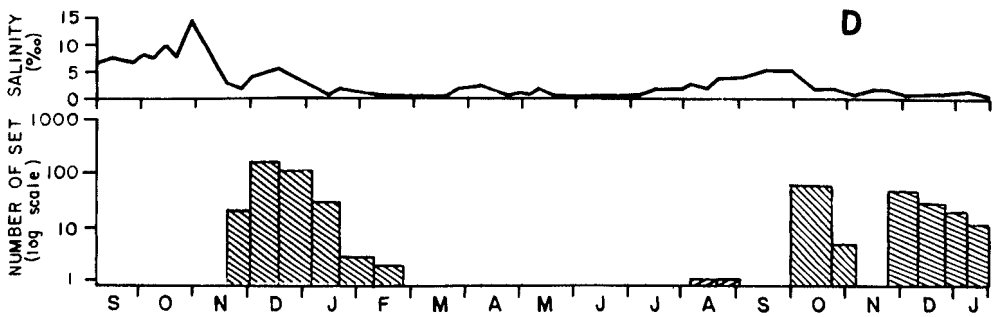

FIGURE 12.—Number of *Rangia* set at station D in relation to salinity for September 1970 to January 1972.

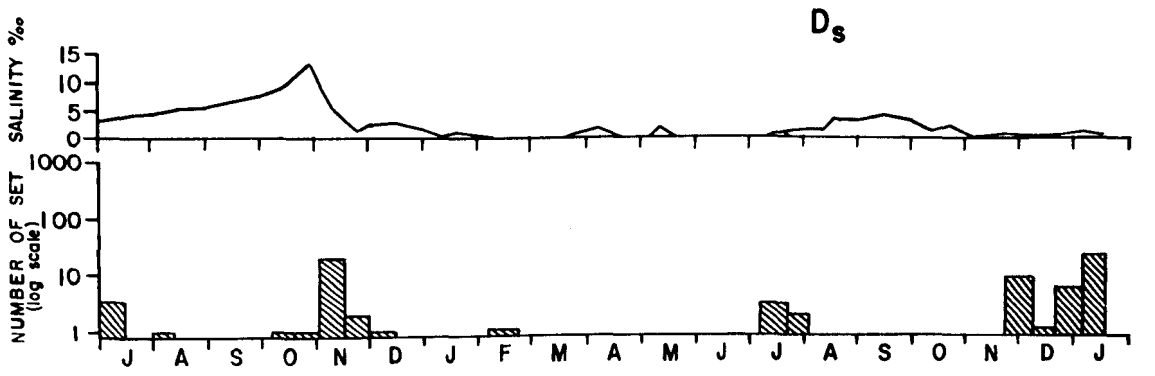

FIGURE 13.–Number of *Rangia* set and salinity at station D_S from July 1970 to January 1972.

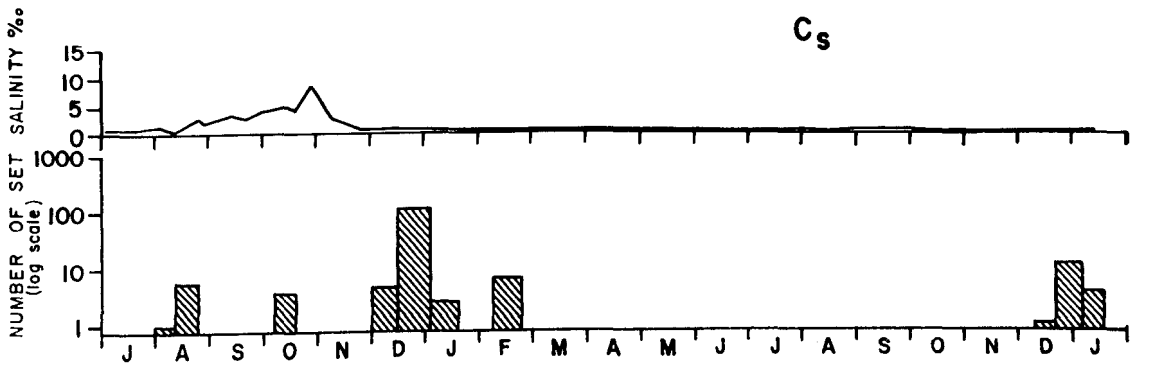

FIGURE 14.–Number of *Rangia* set and salinity at station C_S from July 1970 to January 1972.

TABLE 2.–Average number of *Rangia* set (per collector) at both deep and shallow stations by season.

Season	Station A	B	D	C
Summer (1970)	0.7	0.7	0.7	–
Fall-winter	3.6	6.1	25.5	74.3
Summer (1971)	1.6	0.2	0.4	0.1
Fall-winter	6.2	44.9	15.4	2.5

by early October 1970. This was the highest number collected at any time or place during the study. No set was collected at stations C or Cs from late March to late December 1971. The fall setting was very small with only 5 collected at station C and 18 at station Cs during December 1971 and January 1972.

Rangia set ranged in length from 230 to 500 μm, but averaged about 300 μm. Larger individuals were generally collected at the shallow stations but may have been members of an earlier set washed in by wave action.

The setting patterns of the other bivalves are presented in Figure 15. Station A received more set of all three species than the other stations because of its proximity to their adult populations. *Brachidontes recurvus* and *Macoma mitchelli* were collected farther upriver than *M. balthica*. The first two species were common at stations A, B, and D. *Brachidontes recurvus* and *M. mitchelli* are evidently more tolerant of low salinities as they were the only set found during the low salinity conditions of fall 1971. All three species have a nearly year long spawning season with minor spring peaks and a major peak in the fall.

The three most common organisms found on the bottles were *Rhithropanopeus harrisii*, *Callinectes sapidus*, and the blenny, *Chasmodes bosquianus*. These three potential set predators were typically found at stations A, B, and D during the fall and winter months. During high salinity periods, *R. harrisii* was found at station C.

Hydrographic Data

Freshwater input levels were usually high in late winter and spring, declining to low levels in late summer and fall (Figure 16). Flow during the

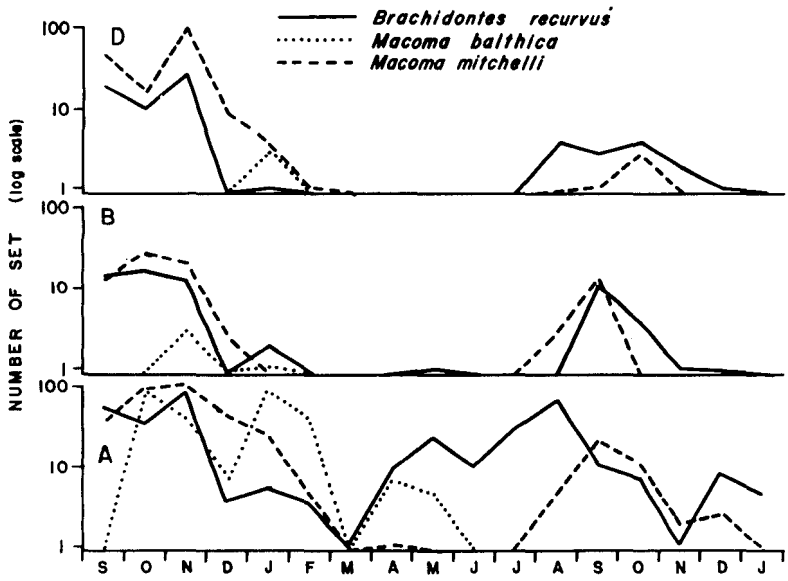

FIGURE 15.—Setting patterns of other bivalves at stations A, B, and D from September 1970 to January 1972. Data combined at deep and shallow stations.

fall of 1970 was very low, with about 28.32 m^3/s (1,000 cfs) input in September and October. This low input allowed measurable-salinity water to extend as far upstream as mile 45. Input was high and variable during the winter and early spring of 1971. The peak for the 2-yr period of 2,747 m^3/s (97,000 cfs) was recorded on 1 June 1971. The summer input was fairly low but quite variable and river flow during September and October was considerably higher than the previous fall. The salinity was rarely measurable at station B throughout the fall and winter months of 1971.

The annual temperature pattern for station B (Figure 17) is representative of the study area. Within relatively narrow limits, all deep stations exhibited similar temperature profiles. Lowest temperatures were measured during late January and early February, followed by a relatively smooth increase to a maximum of 29°C during early August. A period of stable high temperatures was recorded from June through September.

Dissolved oxygen concentrations in this region

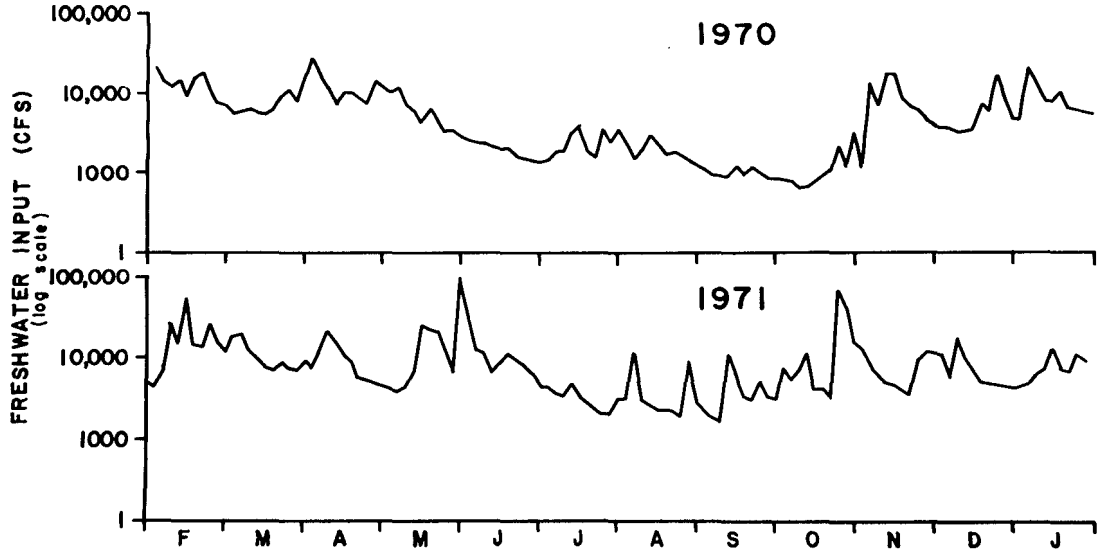

FIGURE 16.—Freshwater input into the James River at 4-day intervals. The data include input from the Appomattox and Chickahominy Rivers.

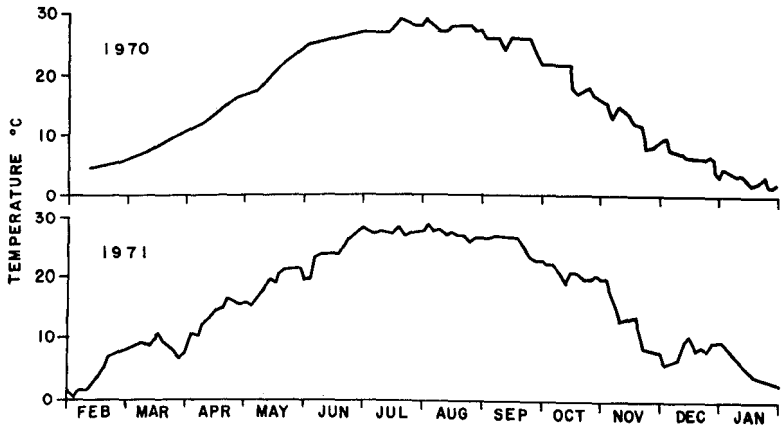

FIGURE 17.—Bottom water temperature at station B in the James River, Va. Values taken from VEPCO instrument tower (#6) and bottom water samples.

showed the normal seasonal variation, with the highest concentrations in the early part of the year during the low-water-temperature period. Low values (6-8 mg/liter) were recorded for deep stations during the summer months.

Relationship of the Reproductive Cycle to Environmental Data

At station A, gametogenesis started when the water temperature was near 10°C in the spring of 1970 (Figure 7). Ripe clams were first observed when the water temperature was 16°C and spawning was first noted when the salinity was between 3 and 5‰. Gametogenesis and spawning occurred through the summer period of high salinities and high temperatures. The fall spawning started at the highest salinities of the year with a definite major spawning after the salinity dropped 10‰ (Figure 7). The temperature during the fall spawning was 13°-15°C. Set first appeared the second week in November and occurred throughout the winter months. Fall and winter sets generally were accompanied by temperatures below 10°C and occasionally to 1°C. Gametogenesis was in progress again by the time the water temperature reached 15°C. No set clams were collected during the summer of 1971, although the histological sections showed all stages of development. Salinities and temperatures approximated those of the previous year, although salinity was more variable. Renewed gametogenesis coincided with the highest temperature of the summer and rising salinities. Some spawning took place with the declining salinity, but the major spawning occurred near 5‰.

Gametogenesis at station B started almost 2 wk later than at station A in the spring of 1970, with the temperature above 13°C (Figure 8). Ripe clams were similarly noted nearly 3 wk later than at station A. The salinity during the summer months was near 5‰ and gradually rising. There was little agreement between spawning times as noted in the histological sections and setting in the collectors during the summer. The progression of gonads in the fall from ripe to spent was clearer and more defined at station B than at station A. Spawning commenced when the salinity reached the yearly high and peaked when the salinity fell rapidly from 15 to 1‰. Setting took place 2 wk later and continued into the winter. Temperatures during spawning ranged from 22° to 12°C. Fewer clams were in the ripe phase throughout the summer of 1971 when the water was nearly fresh. More clams became ripe as the salinity increased, but few set were collected all summer at this station. Fall spawning commenced at 22°C and 6‰ and continued until the salinity reached approximately zero and the temperature dropped to 17°C. Some set were collected immediately after salinity decline and setting continued into January 1972.

Spawning was completed at station C by the end of October 1970, after salinity had fluctuated from 0 to 5‰ for the previous 2 mo. Setting began at temperatures above 25°C and continued throughout the winter at low water temperatures and low salinities (Figure 9). The salinity at station C remained below 1‰ until the termination of the study in January 1972. There was very little spawning and setting at station C during the low salinity period even though gametogenesis took place normally.

DISCUSSION

The histological examination of gonads indicates several generalizations about the reproductive cycle of *R. cuneata*. Gametogenesis began in early April and continued throughout the summer months. Ripe gametes were observed from May to late November. A slight spawning peak was noted during the summer, but a major spawn occurred in the fall. This was probably not a second cycle because gametogenesis in most cases had not terminated during the summer; instead, it appeared to be a continuation of gamete development at an increased rate.

The gametogenic cycle of *Rangia* in high and low salinities was basically the same. Temperature appeared to be the more important stimulus in initiating gametogenesis in the spring and summer. A temperature of approximately 15°C coincided with initiation of gametogenesis at all stations. Gametogenesis in clams from freshwater occurred at a slower rate during the spring and summer with more clams in the spent phase than at the other localities.

The reproductive cycle as determined in this study is similar to that reported for *Rangia* in other geographic areas. Fairbanks (1963) indicated that in Lake Pontchartrain, La., ripe clams could be found during March, April, May, and in the late summer and fall. A prolonged spawning season would seem reasonable as the rise in water temperature to 15°C in the spring is nearly 2 mo earlier at that location than in the James River. In addition, the drop in water temperature to 15°C in the fall is later. He also indicated a postspawning recovery phase during midsummer. The very high temperature (near 33°C) during the summer may have inhibited gametogenesis, but in the James River population a renewed surge occurred at the high midsummer temperatures of 28°-29°C. Tenore (1970) studying the macrobenthos of the Pamlico River, N.C., found *Rangia* containing mature gametes only in the fall. This observation was probably based on visual inspection of the viscera. The spring and summer ripening may have been missed because the gonads are not nearly as distended and colored as in the fall ripening. Pfitzenmeyer and Drobeck (1964) collected *Rangia* in August and September from the Potomac River. Clams at this time contained mature gametes, indicating that spawning was imminent.

The correlation of the environmental data to gonadal conditions suggests that temperature and salinity are important factors in spawning. Salinity, however, was more important than temperature. Clams upstream at station C spawned in fall 1970 following a 5°/∞ rise in salinity, but failed to spawn in 1971 when the salinity remained low. Spawning at station B was apparently related to salinity decreases. The correlation of salinity to spawning was not as clear at station A. The salinity variation at this station was very large over a tidal cycle and may have prevented complete synchrony of spawning.

Cain (1973) found that a salinity change was necessary for *Rangia* spawning in the laboratory. Spawning was accomplished by placing ripe clams from low salinities (< 1°/∞) into 5°/∞, 28°C flowing water. Evidently clams in upstream areas require a rise in salinity to spawn, while downstream populations require a reduction in salinity from the 10 to 15°/∞ levels at which they live.

There is little additional evidence in the literature on the importance of salinity to *Rangia* spawning. Fairbanks (1963) could not induce spawning. Chanley (1965) induced spawning at 15 °/∞ by rapidly increasing the water temperature 7°C and adding sperm stripped from a ripe male. However, spawning was poor and he did not study the survival of the eggs. Such strong stimuli may cause premature release of immature eggs, with subsequent poor fertilization and survival. The only data suggesting the importance of salinity to *Rangia* spawning is that from the Bureau of Sport Fisheries and Wildlife (1965) in connection with a study on the food habits of ducks in Back Bay, Va., and Currituck Sound, N.C. These two bodies of water normally have a salinity of less than 1°/∞. During that study, a storm forced ocean water into the bay and raised the salinity to about 4.5°/∞. This intrusion of salt water must have caused spawning and successful setting since the following year nearly 9% of the diet of dabbling and diving ducks consisted of small *Rangia*, an amount estimated to be 83,000 lb (dry weight) for the year. During the previous 3 yr no *Rangia* were consumed by these ducks.

Two periods of setting occurred in the James River. The first was in early and midsummer, which coincided with the beginning of spawning as inferred from tissue sections. The second period was much longer, with a greater number of collected set, and took place in the late fall and winter, coinciding with the increased percentage

of partially spawned and spent clams, as identified by histological preparations. The second peak of spawning appeared to be the major one for the normal reproductive period (Table 1). Fairbanks (1963) found set (>0.375 μm) from October to April. A longer and more intense setting period was found in the area with the more variable salinity. Tenore (1970) collected set in bottom grabs only during the fall and winter months. The spring and summer spawning was either so light in these areas that no set were found or an abundance of predators at this time quickly consumed the sparse set.

Sex Ratio

There are at least two possible explanations for the unusual sex ratios in *Rangia*. *Rangia* may be protandric with a higher ratio of females to males in the older stages. If so, the clams at stations B, D, and C would have had to be older than those at station A; however, there were no consistent differences in the lengths of the clams at the various stations. This does not preclude the possibility that the ages of clams at the stations are different, but masked by varying growth rates resulting from substrate effects or nutrient levels.

The second possibility is that the environmental conditions upriver differ enough from those downriver at station A to affect the sex ratios. Changes in environmental factors could affect either juveniles or adults during the undifferentiated period. There is no proof of this type of sex alteration. None of the other mactrids studied, *M. lateralis*, *S. solidissima*, or *T. capax* have been found to have a ratio other than 1:1.

Relationship of Larval Studies to Setting

Cain (1973), on the basis of laboratory results, indicated that best survival and growth of larvae would be expected in the summer. Higher temperatures and generally high salinities are expected to provide for rapid growth to setting. But setting is very poor in summer (Table 1). A number of factors may account for this: clams are in all stages of gametogenesis, the gonads of ripe clams are not as full, and even though the stimulus to spawn may exist there is probably poor synchrony of spawning.

In the James River, fall and winter were the times of greatest setting activity. Fall spawning occurred as the temperature dropped from 29° to 15°C. This temperature range would provide good survival of eggs to straight-hinge larvae, but the larvae are exposed to declining fall temperatures. Larvae at low temperatures (and low salinity) should survive well, but grow slowly. Consequently, set in the late fall and winter come from a fall spawning after the delay in growth and metamorphosis expected from low temperatures. Some set in the jars could have come from previously set, slow-growing clams washed in by turbulence. This set, which is fairly active, tends to crawl over the bottom by use of the muscular foot and therefore is affected by currents (Carriker 1961).

Distribution and Recruitment of *Rangia* in the James River

Rangia extends to nautical mile 60 in the James River. In the upper reaches of its distribution it has been in freshwater for the last 4 or 5 yr. Since the embryos and early straight-hinge larvae cannot tolerate freshwater (Cain 1973) and a salinity rise is needed to induce spawning, there must be little recruitment to this population. No set or small clams have been found in this area, which raises the similar question of how *Rangia* spread into this region initially. The upriver population consisted of clams ranging in length from 53 to 63 mm in the spring of 1971. Using the von Bertalanffy growth curve constructed for *Rangia* by Wolfe and Petteway (1968), these clams were estimated to be from 5 to 7 yr old. The water records for the James River basin were analyzed from 1963 to 1966 (Anonymous 1966, 1970b). These records show yearly lows in the late summer and fall when the input dropped below 22.66 m^3/s (800 cfs), and in 1966 the input dropped to an average of 13.59 m^3/s (480 cfs) during the first half of September. These very low flow periods allowed measurable-salinity water to extend 63.5 miles upstream in December 1965 (Brehmer and Haltiwanger 1966).

To reach these upstream areas larvae must be transported in the more saline bottom water which has a net upstream movement (Pritchard 1952; Nichols 1972). Although the mechanism of such transport has not been deduced for *Rangia*, work done on the eastern oyster may indicate some possible mechanisms. Wood and Hargis (1971), who studied the lower James estuary, found a definite upstream transport of oyster larvae and

also of small coal particles. They indicated that the larvae move upstream by selectively swimming in more saline water associated with the flood tide. They further indicated that Korringa's (1952) idea of passive transport could not be denied, as the coal particles also had a net upstream motion. *Rangia* could be carried into upstream areas both by selective swimming or by passive transport under low flow conditions, and a series of dry years would allow set to progressively move upriver. Set from one year should be able to spawn the next year and certainly within 2 yr. Gonads occurred in clams 14 mm long, a length easily reached by the end of the first year (Fairbanks 1963; Wolfe and Petteway 1968). Rapid early growth and a relatively short larval life (above 20°C) should allow for the fast spread of set into areas uninhabited by adults. As *Rangia* has an 8-yr average life span (Fairbanks 1963) and a maximum life of 14 yr (Wolfe and Petteway 1968), recruitment to the population could occur at fairly long intervals. The Virginia Division of Water Resources (Anonymous 1970a) statistically predicts that low flows of less than 1,000 cfs for 7 days will occur at 5-yr intervals. This situation could allow minimum recruitment to maintain the upstream population, assuming good survival of set and adults in this region.

The downstream extent of *Rangia* could be determined by the adults approaching their high-salinity limit. This may not be the case as the larvae can survive higher salinities than normally occur at the downstream limit—and the adults may also do so. The downstream extent likely represents a multifactor barrier involving biological competition for space and food, and increased predation of the set.

Recruitment to the downstream population was at a low level but more regular, with more set collected in the summer months than at the upstream stations (Table 1). Probably the best recruitment would be expected in the population at station B near the lower middle of the habitat range. The fall set there was high and fairly consistent over the 2-yr period. Averaged over many years, this segment would likely receive more set, as this part of the estuary usually has an annual salinity change from fresh to 5‰.

General Discussion

The adults can utilize the high levels of detritus in this oligohaline sector (Darnell 1958) and convert it into growth and reproductive materials. *Rangia* is ripe for at least 7 mo of the year so it can spawn whenever favorable changes in salinity allow successful reproduction. Although adults are euryhaline, embryos are much more sensitive. Spawning at a salinity near 5‰ allows for the survival of the sensitive stages to the more eurytopic later larval stages. The increased tolerance of the larvae permits good survival during its more stressful pelagic existence.

The planktonic existence of *Rangia* larvae is greatly extended by low temperatures. Thorson (1946) indicated that prolonged low temperatures exposed larvae to increased mortality from disease, starvation, predation, dispersion, and environmental stress. *Rangia* larvae evidently are well adapted to a prolonged exposure because many set were collected during the coldest months. This increase in dispersal may allow *Rangia* to consume the unexploited resources of the species-poor environment in low salinity. Increased dispersal may also provide genetic interchange between populations distributed over a relatively extended habitat in the estuary. Pfitzenmeyer and Drobeck (1964) found the rate of increase of *Rangia* over a 4-yr period in the Potomac River to be very great. Pfitzenmeyer (1970) also recorded this clam in the upper Chesapeake Bay when its numbers increased from 0 to 10,000 per square meter in 2 yr.

Spawning of *Rangia* apparently is controlled by salinity change. The mechanism of this control, however, has not been examined. The exogenous factor of salinity may activate an endogenous control system of osmoregulation and serve as a signal to induce synchronous spawning of the population. The concept of "critical salinity" reviewed by Khlebovich (1969) appears operative for *Rangia* which spawns near 5‰. Khlebovich concluded that the salinity range of 5-8‰ is a faunal boundary defining the distribution of marine and freshwater species. Characteristic differences in physiological performances (adaptation, growth, activity and, especially, osmoregulation) are revealed at this salinity range.

The latitudinal distribution of *Rangia* is important because of its spread northward in the last decade. In the present study, gametogenesis and spawning were observed to occur over a wide range of temperatures. Although larval growth was best at high temperatures, survival and growth apparently take place even at low temperatures. Consequently, it appears that the

northward limit of *Rangia* is not controlled by low temperature effects on reproduction or larval tolerance. Reports on populations in upper Chesapeake Bay (Gallagher and Wells 1969; Pfitzenmeyer 1970) infer large adult mortalities from low temperature and low salinity. The only mortality of adults (freshly gaped clams) in this study was seen in the dredge hauls during the winter and early spring. Long periods of low temperature and freshwater may combine to increase the mortality of adults and thereby limit the northward range.

The possibility that widely separated populations may belong to different physiological races cannot be excluded (Loosanoff 1969). Populations of marine animals exposed to different environments within their geographical range may have different physiological properties (Sastry 1970), suggesting that more research should be conducted on the tolerances of embryos, larvae, and adults from different geographical areas.

The key to the welfare of a *Rangia* population over its normal distribution is probably not the physiology of the adult individual but successful reproduction and recruitment. Adults may live for years in habitats where reproduction is impossible. Spawning will not occur unless salinity changes, up from low salinity or down from high salinity. If spawning does occur, embryos and early larvae will have poor survival unless salinity is between 2 and 10‰ (Cain 1973). Once the larvae have developed past the swimming stage and settled to the bottom as juvenile clams, salinity is probably not as critical (except in combination with low temperatures).

The influence of salinity on reproduction and recruitment indicate that some changes in its environment may restrict the distribution of *Rangia* in the estuary. *Rangia*'s estuarine distribution is maintained by changes in salinity related to variations in the freshwater input. Any overall reduction in freshwater input or reductions in the seasonal variations of salinity will limit its range. These characteristics of this species should be considered before dams are constructed, freshwater is diverted for other uses, or other changes in the hydrography of the estuary are approved.

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