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Gametogenesis in a Population of the Hard Clam, *Mercenaria mercenaria* (Linnaeus), in North Santee Bay, South Carolina[1]

by

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Abstract. Adult hard clams, *Mercenaria mercenaria* (Linnaeus, 1758), were sampled monthly between December 1977 and February 1979 and semi-monthly from March to June 1981, from subtidal populations in North Santee Bay, South Carolina. Gonad development was monitored using standard histological methods and resulting slides were examined with light microscopy at 100 and 400×. Observed gametogenic progression was best categorized by five stages or phases of development: inactive, ripe, spawning, partially spent, and spent. Both male and female clams displayed a complex progression of gametogenesis. Gonadal tissue was not uniformly dominated by clearly defined, distinct stages. Instead, gonads routinely exhibited several stages simultaneously and progressed through slow shifts in domination of stages in gonad tissue. Spawning in the population occurred continuously for six months (May to October) with at least two apparent peaks of spawning activity in the summer months.

INTRODUCTION

HARD CLAM, *Mercenaria mercenaria* (Linnaeus, 1758), landings in South Carolina have increased substantially in recent years. An estimated 6809 acres (2756 ha), or roughly 1% of South Carolina marsh-estuarine area of 746,445 acres (302,086 ha), contain clams in various commercial densities (ANDERSON *et al.*, 1978). As the demand on the fishery and subsequent pressure on the resource continue to grow, it becomes important to determine recruitment potential of the stocks. The documentation of gametogenesis in a fishery resource is the first logical step in estimations of population recruitment. Although data are scant on the reproductive cycle in hard clam populations of South Carolina, a number of studies on the gonadal development of clams from other areas have been described. LOOSANOFF (1937a, b) determined the seasonal gonadal changes of *M. mercenaria* from Long Island Sound and showed that temperature is an environmental factor regulating the gonadal cycle in hard clams. PORTER (1964) studied clams from Core Sound, North Carolina, and suggested that gonadal differences in populations could be caused by racial differences or by phenotypic responses to variable environmental factors. KECK *et al.* (1975) compared the gonadal cycles of *M. mercenaria* from Delaware Bay and Cape Henlopen for evidence of physiological races. They found that divergent developmental patterns did exist between the two areas. EVERSOLE *et al.* (1980) documented the gametogenic cycle of *M. mercenaria* seed from North Carolina planted in an estuary near Clark Sound, South Carolina. PLINE (1984) compared gametogenesis in two size classes of *M. mercenaria* in Georgia.

Differences in gonadal cycles between geographically separated populations are not limited to the hard clam (*Mercenaria mercenaria*) as shown by PFITZENMEYER (1962), ROPES & STICKNEY (1965), and SHAW (1962, 1965) for the soft clam, *Mya arenaria* (Linnaeus, 1758); HOLLAND & CHEW (1974) for the manila clam, *Venerupis japonica* (Deshayes); and JONES (1981) and THOMPSON *et al.* (1980) for the ocean quahog, *Arctica islandica* (Linnaeus, 1767).

Hard clam populations in South Carolina are subjected to environmental conditions that significantly differ from those characterizing the northeastern and Middle Atlantic states. Water temperatures are relatively moderate in winter (normally ≥10°C monthly means) and very warm in summer (≥28°C monthly means). This study was initiated to determine the natural cycle of gonadal development in native populations of South Carolina clams and to compare the results with those of previous studies on hard clam populations from other areas.

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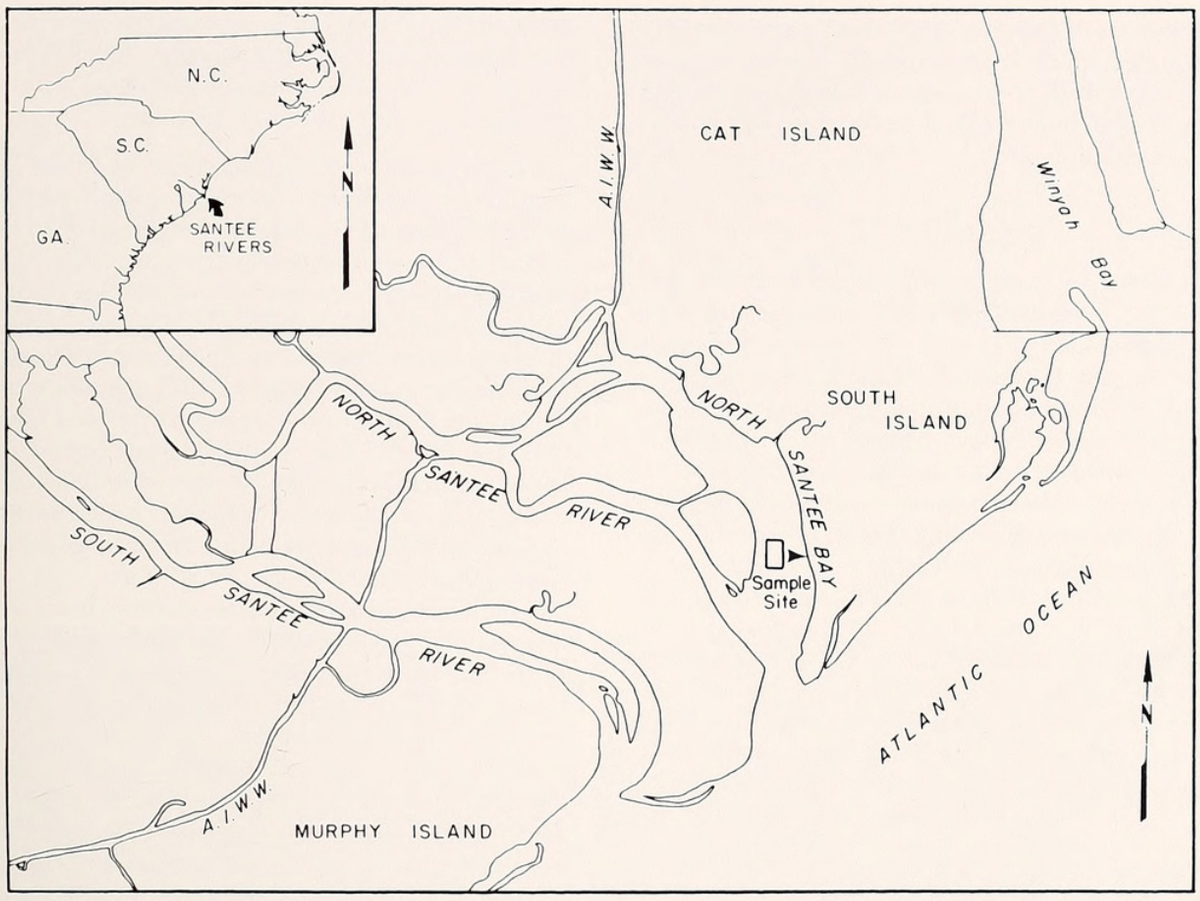


Figure 1

Sampling location in North Santee Bay, South Carolina.

MATERIALS AND METHODS

Twelve hard clams were collected monthly from December 1977 to February 1979 and biweekly from March to June 1981. All animals were from North Santee Bay, South Carolina (Figure 1). The bay is characterized by substrates of soft mud mixed with shell and an average depth of approximately 1–2 m at mean low water. The North Santee Bay was chosen as a study site because of its dense beds of hard clams and oysters (*Crassostrea virginica* Gmelin, 1791). ANDERSON *et al.* (1978) found the highest density hard clam populations in South Carolina in the North Santee delta system. Hard clams for this study were obtained with a 19-cm × 53-cm boxed-type oyster dredge. Hydrographic data were collected coincidentally with sampling and included measurements of air and water temperatures, and salinity. All clams were returned to the laboratory and stored under refrigeration at approximately 5°C. Tissue samples were always removed within 24 h of collection. Before dissection, shell lengths (anterior-posterior axis) were measured to the nearest millimeter with vernier calipers.

Whole clams were fixed in FAA (formalin-acetic acid-alcohol) for two to four weeks. Either a cross- or longitudinal section was cut through the mantle, gonad, and underlying digestive gland. Dissected tissues were then placed in FAA for 24 h and washed in running tap water for approximately 4 h. Tissues were prepared for sectioning by dehydration in alcohol, clearing in toluene, and infiltration in 57°C paraffin (PREECE, 1972). After proper embedding in paraffin, the tissues were sectioned at 7 μm on a rotary microtome. Sections were made at three areas of each tissue block, approximately 20 μm apart. All sections were stained with Gill's hematoxylin and counterstained with alcoholic eosin. The sections were examined with a light microscope and photomicrographs of various stages of gametogenesis were taken at 40, 75, and 185×.

Examination of slides made it quite evident that a gametogenic index had to be devised to organize or categorize the developmental stages in this study. The slides were examined first under low power (100×) to scan the entire gonadal area and under high power (400×) to assess each follicle. Often, two or more stages occurred simultaneously within each section; therefore, stage criteria decisions were based upon the condition of the majority of the section. In most cases 80% or more of the section represented no more than one stage. This technique was

particularly useful in staging the spawning and partially spent categories which were segregated on the basis of percent lumen filled with ovocytes and spermatocytes (representing spawning activity) and the number of mature gametes remaining.

RESULTS

Initial surveys of collected gonadal tissues indicated that only five readily identifiable stages of gametogenesis were apparent in the populations of South Carolina *Mercenaria mercenaria* sampled. PORTER (1964) and KECK *et al.* (1975) used 14 and 10 developmental stages, respectively, to describe the gametogenic cycle of *M. mercenaria.* EVERSOLE *et al.* (1980), however, also classified the gonads of *M. mercenaria* into five developmental stages. In contrast to the latter, the degree of spawning that we observed in this study made classifying the gonads into the single stage of "ripe and spawning" difficult. Staging gonads as early active and active was also difficult. This necessitated the formulation of an index suitable for the prolonged ripe and spawning period and reduced inactive period characterized by these hard clams. The five developmental stages (spent, inactive, ripe, spawning, and partially spent) established were distinguished by the following characteristics.

Spent (Figures 2, 3): Follicles are nearly empty, and a thin band of spermatocytes or few small ovocytes may occur along the follicle wall. Few large undischarged ovocytes or spermatozoa and some spermatids are found free in the lumen of some follicles. Usually follicles are extended but may occasionally be compressed in shape or size. Undifferentiated cells may be present in a few follicles.

Inactive: Gonads are in a state of quiescence, and follicles are either absent or very few in number. A few follicles contained numerous undifferentiated cells, but no recognizable primary or secondary gametogonia are present.

Ripe (Figures 4, 5): Follicles are extended and full of darkly staining ova or spermatozoa with their tails pointing toward the center of the lumen. Large ovocytes have been freed from the follicle wall into the lumen, with the nucleus apparent in most cells and the nucleolus apparent in some. Some attached spermatocytes and ovocytes are located along the follicle wall. Spermatids, staining lighter than the spermatocytes or spermatozoa, lie in a layer or in groups outside the central core of the spermatozoa.

Spawning (Figures 6, 7): Generally large expanded follicles still contain many mature ova in the lumen or dense bands of ripe spermatozoa surrounding a partially empty lumen. Around the periphery of the follicles may be many spermatids, spermatocytes, or ovocytes still attached to the follicle wall.

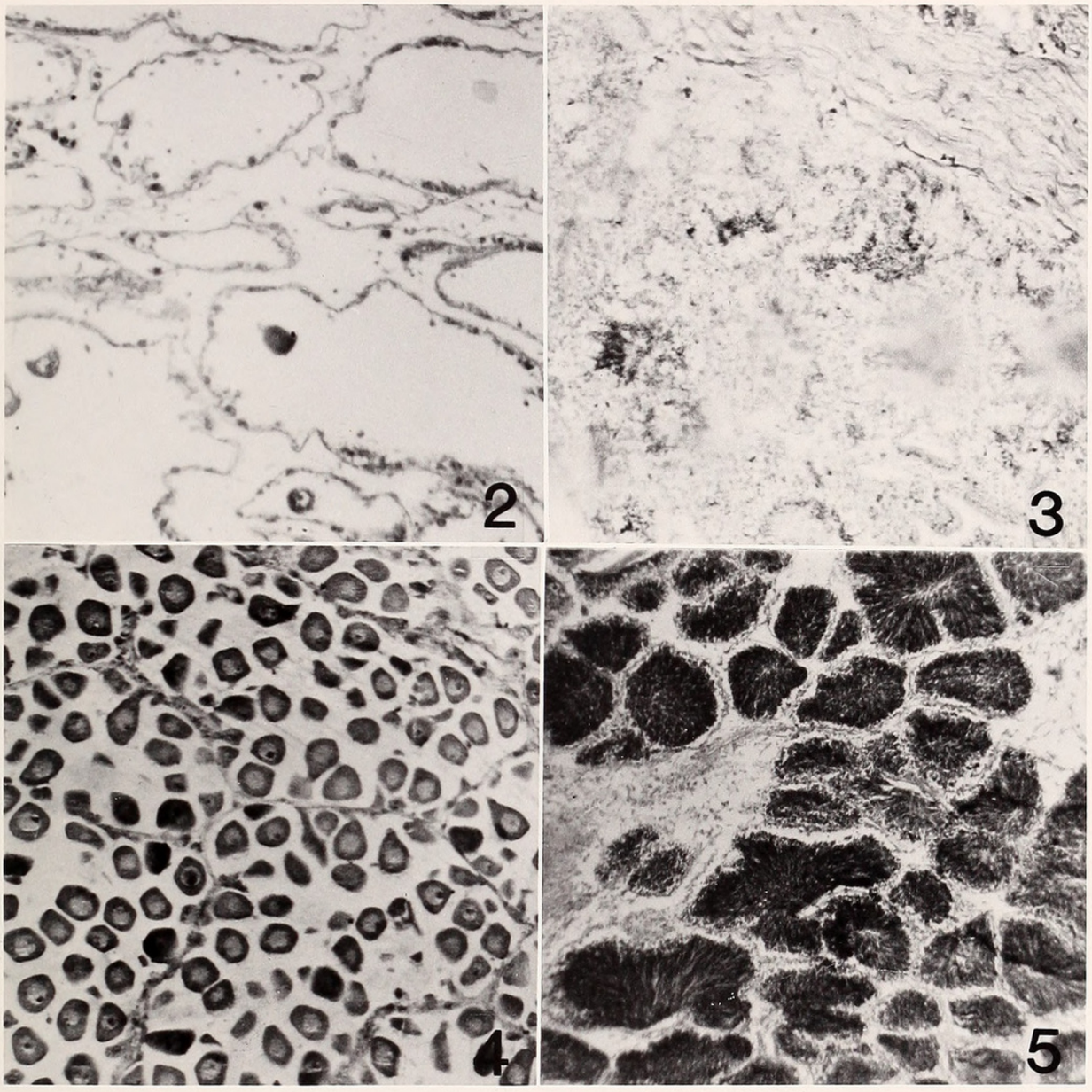
Partially spent (Figures 8, 9): Most follicles are empty of spermatozoa or of large ovocytes but generaly have a thin band of spermatocytes or small ovocytes along the follicle wall. Other follicles are still dense with spermatozoa or ripe ova scattered in the lumen.

The progression of gametogenesis in female clams as reflected by this study was not characterized by clearly defined, distinct stages. Instead, the gonads often exhibited several stages simultaneously and progression of the sexual cycle occurred in a gradual but complex manner. Figure 11 illustrates this progression in oogenesis throughout the study period. Approximately 80% of the female gonads examined from late December 1977 samples were spent. Gonads with partly discharged ovocytes and others with follicles filled with ripe ova in the largest part of the lumen appeared in February and continued until May. By the end of May, as the water temperature increased to 22°C, all females examined were ripe and normal oval-shaped ovocytes had reached a size of 65–70 μm.

Indications of spawning were evident in late June (water temperature, 26°C) with a distinct decrease in the number of ripe ova and an increase of gonads with partially spent lumen. This spawning condition continued through October showing a gradual shift from a ripe appearance to a partially spent condition. LOOSANOFF (1937b) suggested that the spawning of an individual hard clam is not completed in one attempt but is extended for a certain period of time, depending upon the individual and ecological peculiarities. Some follicles with few undischarged ovocytes free in the lumen were characteristic of all of the females examined in November. This completely spent condition was not evident in December when ripe ova reappeared in half of the gonads examined. The percentage increase in ripe females in December, January, and February could indicate that active gametogenesis occurred immediately after the spawning. The new ovocytes at this time varied considerably in size and averaged 55–60 μm. In most cases, the ova were oval in shape with the nucleus clearly apparent.

Samples taken biweekly, March through June 1981, are combined into monthly means in Figures 10–12. Most female gonads (Figure 11) were marked with a spawning or partially spent condition. The number of large unspawned ova found in the ovaries of these clams varied greatly with individuals. In some cases, almost all the ova were discharged with only a few ripe ovocytes remaining (Figure 8). In most, however, a comparatively large number of ova were retained (Figure 6). Ovocytes at this time averaged 55–60 μm in size. Some small ovocytes were observed in March but these were relatively sparse. Ovocytes greater than 68 μm in size had increased in number by May and June, but the majority of the ova were still between 55 and 60 μm.

Male clams reiterated the complex progression of gametogenesis exhibited by the females. Figure 12 illustrates, by percent of sample population in various sexual stages, this progression of the male sexual cycle. In Feb-



Explanation of Figures 2 to 5

Figure 2. Spent stage of oogenesis (×40).

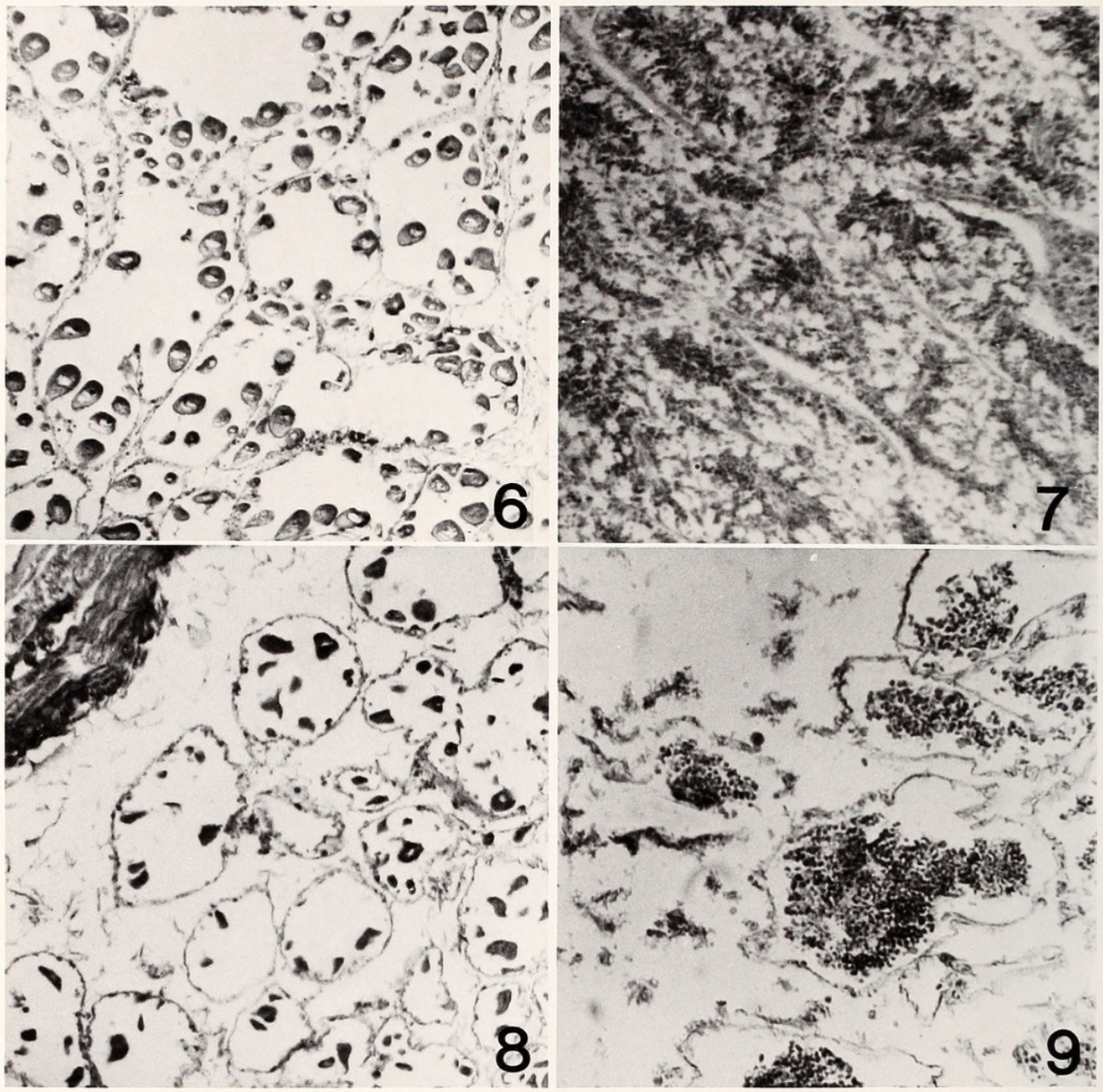
Figure 3. Spent stage of spermatogenesis (×75).

Figure 4. Ripe female (×75).

Figure 5. Ripe male (×40).

ruary, gonads in 85% of the males examined were ripe, with most follicles containing mature spermatozoa in the lumen. A decline in the percentage of ripe males occurred in March when approximately half of the gonads examined were ripe while all of the others were spawning. In April, all male gonads were ripe with follicles packed with darkly stained spermatozoa with their tails oriented inwards toward the center of the lumen. A mature condition continued in the majority of the males through October with only a small percentage in a spawning or partially spent condition. By November when water temperatures were approximately 18°C, all male gonads examined had discharged their gametes and were in a generally spent condition. Males exhibiting extended follicles filled with ripe spermatozoa were apparent again in December, and a high percentage of ripe males remained through February.

Water temperatures recorded during the study were not significantly different from typical South Carolina coastal conditions. Water temperatures ranged from a low of 5.3°C in February 1978 to a high of 30.2°C in August 1978. Ambient water temperatures recorded at sample collection



Explanation of Figures 6 to 9

Figure 6. Spawning female, with many ova retained (×75).

Figure 7. Spawning male, with many sperm retained (×40).

Figure 8. Partially spent female (×75).

Figure 9. Partially spent male (×185).

are presented in Figure 10. Available salinity records indicate a salinity range of 24.0 to 34.0‰ over the collection period.

The seasonal variation of the gonadal cycle is presented in Table 1. Data are presented as percentage of individuals in each developmental stage per season. The table indicates that during the winter of 1977–1978 clams were undergoing all stages of gametogenesis, although a high percentage (36%) were ripe. The largest percentage (27%) of inactive clams were observed during this season. By the summer, ripe gonads were present in 69% of the population examined. All other clams were spawning or partially spent. The fall season of 1978 was characterized by the greatest percentage of spent individuals. Follicles containing ripe gametes were apparent in most clams examined during the winter of 1978–1979. The spring and early summer of 1981 were represented by a high proportion of ripe clams, reiterating the observations of 1978.

DISCUSSION

Temperature is a major environmental factor regulating gametogenesis in a variety of marine bivalves (Loosanoff, 1937a, b; Giese, 1959; Ansell, 1961; Galtsoff, 1964;

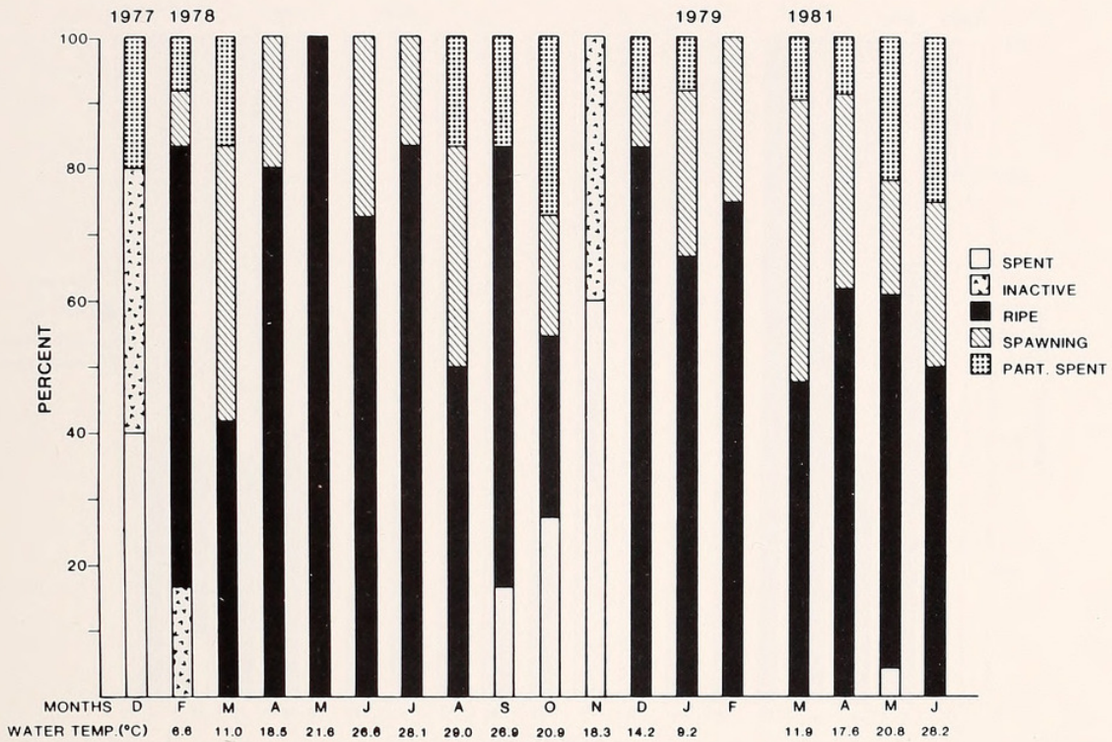


Figure 10

Stages of gonad development in *Mercenaria mercenaria* from North Santee Bay, South Carolina. Shaded areas represent percent frequency of clams in each stage from December 1977 to February 1979 (see legend). March to June 1981 data represent composites of biweekly samples. Temperatures are ambient recorded water temperatures at time of sampling.

PORTER, 1964; KECK *et al.*, 1975; EVERSOLE *et al.*, 1980; PLINE, 1984). The seasonal temperature differences that exist between Long Island Sound, Delaware Bay, Georgia, and North and South Carolina coastal waters would naturally lead to differences in their respective bivalve population reproductive cycles. Local environmental conditions can also influence and confound gametogenesis in bivalves. CARRIKER (1961) showed that depth of water

Table 1

Seasonal variation (as percentiles) in developmental stages of gonads from a hard clam, *Mercenaria mercenaria*, population in North Santee Bay, South Carolina.

Seasons	Number examined	Stage				
		Spent	Inactive	Ripe	Spawning	Partially spent
Winter (1977–1978) Dec.–Feb.	22	18	27	36	5	14
Spring Mar.–May	34			74	21	6
Summer Jun.–Aug.	35			69	26	6
Fall Sep.–Nov.	33	33	12	30	9	15
Winter (1978–1979) Dec.–Feb.	36			75	19	6
Spring/Summer (1981) Mar.–Jun.	90	1		56	29	14

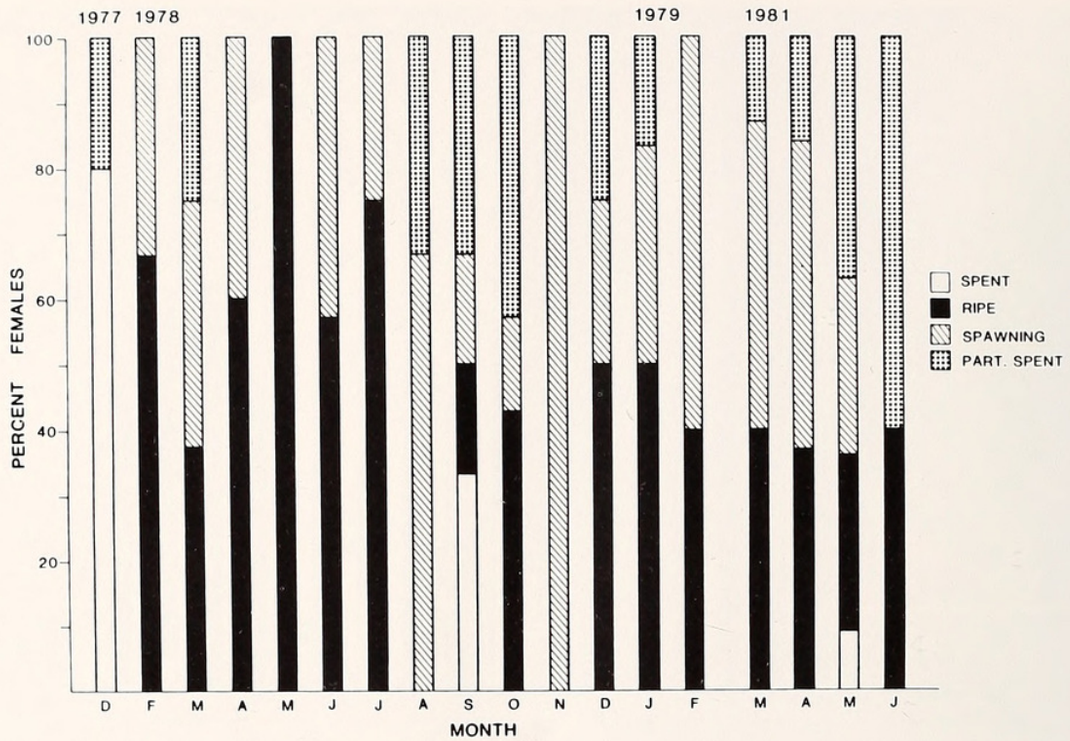


Figure 11

Stages of gonad development in female *Mercenaria mercenaria* from North Santee Bay, South Carolina, between December 1977 and June 1981. Shaded areas represent percent frequency of each stage of development for each month (see legend).

and local circulation patterns can, together with temperature, greatly influence the onset of spawning activity in hard clams. ANSELL *et al.* (1964) showed that thermal effluents produced marked temporal alterations in hard clam gametogenesis.

EVERSOLE *et al.* (1980) indicated that *Mercenaria mercenaria* had a prolonged spawning period with two breeding peaks per year in Clark Sound, South Carolina. Hard clams from Wassaw Sound, Georgia, exhibited a true bimodal cycle with two distinct periods of gametogenesis and two spawning periods (PLINE, 1984). PORTER (1964) found a similar pattern in North Carolina. This bimodal pattern, however, was not found in hard clam populations in Delaware Bay (KECK *et al.*, 1975) or in Long Island Sound (LOOSANOFF, 1937b). A similar pattern of changing reproductive strategies along a latitudinal gradient has been noted for *Mya arenaria* (PFITZENMEYER, 1962; ROPES & STICKNEY, 1965; SHAW, 1962, 1965). EVERSOLE *et al.* (1980) suggested that breeding seasons of *M. mercenaria* change with respect to latitude, becoming prolonged and containing more synchronized polymodal breeding patterns with decreasing latitude. This phenomenon has been observed in other temperate marine invertebrates (GIESE, 1959).

Spawning in this study was apparent only by declines in the percent lumen filled with ripe gametes. Spawning apparently is a long, rather continuous process beginning in April or May and continuing to September or October. EVERSOLE *et al.* (1980), PORTER (1964), KECK *et al.* (1975), and PLINE (1984) found similar protracted spawning seasons. KECK *et al.* (1975) noted that the rate of temperature change probably provides a stronger spawning stimulus than absolute temperature. PLINE (1984) noted that the rapid rise and fluctuation of the water temperatures over the intertidal hard clam beds in Wassaw Sound was probably the factor that induced spawning as early as March. Normal spawning temperatures are slightly different in the areas mentioned above: 27–30°C in North Carolina (PORTER, 1964), 25–27°C in Delaware (KECK *et al.*, 1975), 23–25°C in Long Island (LOOSANOFF, 1937b), above 20–23°C in Clark Sound (EVERSOLE *et al.*, 1980), 22–26°C in Wassaw Sound (PLINE, 1984), and above 20°C in North Santee Bay (present study).

The period of inactivity and/or early active gametogenesis could be rapid because of the moderate winter water temperatures in South Carolina, thus making it difficult to observe and document this stage of gametogenesis. PLINE (1984) observed a low percentage of recuperative (inactive) clams which he attributed to the short duration of this phase. EVERSOLE *et al.* (1980) indicated that undifferentiated (inactive) clam gonads and gonads showing early stages of gametogenesis occurred more frequently among smaller size classes of hard clams. This might also explain the low percentage of inactive and early active

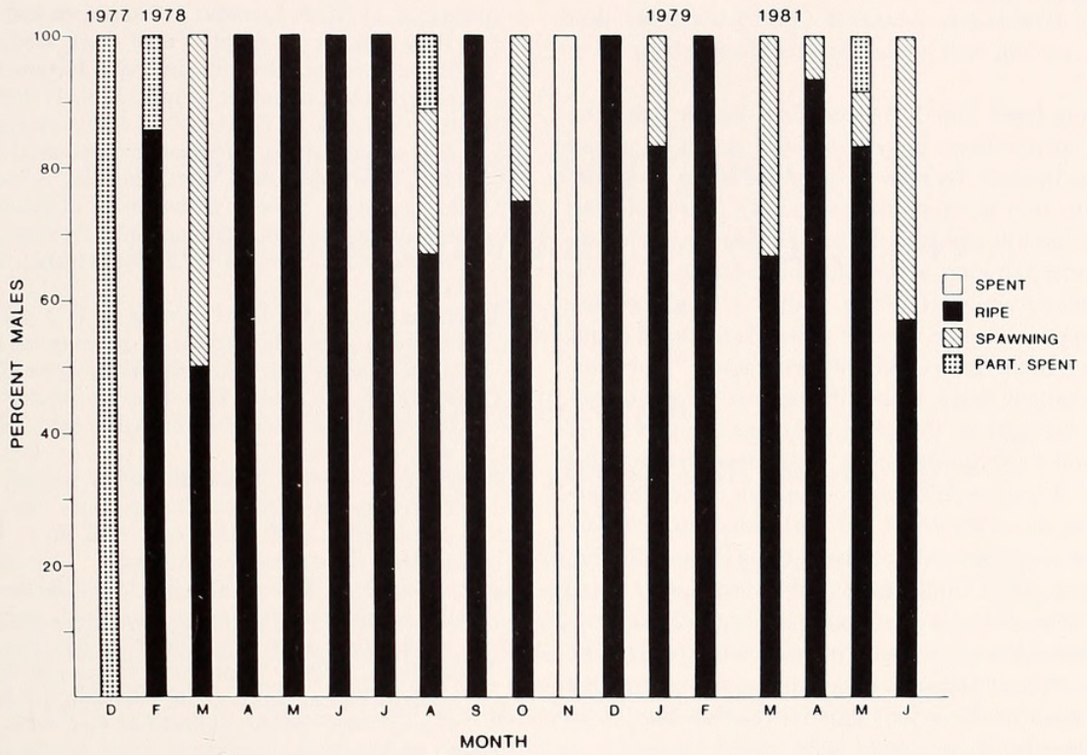


Figure 12

Stages of gonad development in male *Mercenaria mercenaria* from North Santee Bay, South Carolina, between December 1977 and June 1981. Shaded areas represent percent frequency of each stage of development for each month (see legend).

stages observed in the present study which used, for the most part, specimens in the large chowder size class (>75 mm SL). KECK *et al.* (1975) found no case where it was impossible to determine sex, indicating a paucity of inactive specimens in their survey. LOOSANOFF (1937b) did not report any undifferentiated gonads for Long Island male clams and mentions the presence of undifferentiated cells along the inner walls of the ovarian follicles only immediately after spawning. PLINE (1984), comparing littlenecks (38–68 mm SL) to chowders (>78 mm SL), indicated that there was evidence that chowders ripen more quickly than littlenecks. He also observed that chowders had longer and more extensive spawning periods and a shorter redevelopment period than littlenecks.

Active gametogenesis also appears to continue after spawning since so many ripe gonads were found in December and January. LOOSANOFF (1937b) reported major redevelopment immediately after spawning in Long Island waters, and observed many ripe gonads in December and January. PORTER (1964) reported that at least 50% of his clams retained a ripe appearance through the fall and winter. EVERSOLE *et al.* (1980) reported an increase in the number of ripe and spawning clams in December, March, and April collections, and suggested that this indicated that regeneration occurred after fall spawning and continued into spring.

EVERSOLE *et al.* (1980) observed differences in shell length between sexes in a young population of *Mercenaria mercenaria*. Females appeared larger than males and males were larger than undifferentiated clams. However, they speculated that as clams in a cohort continued to grow and entered subsequent breeding periods, these size differences should become less apparent. ANSELL (1961) found no significant size difference between male and female clams. There was no evidence of a size-sex relationship among the North Santee Bay chowders examined. Shell lengths ranged from 54 to 109 mm with approximately equal numbers of males and females in all size classes.

Ova, approximately 55–60 μm in diameter, were observed in the follicles of female clams during most of the sampling period. Although this dimension appeared to be the average size of the ovocytes, smaller and less numerous ovocytes (25–30 μm) appeared in small numbers during late winter and early spring. Occasionally, during the summer, large ova reaching the previously reported (LOOSANOFF & DAVIS, 1963) maximum size of 70–73 μm were seen. LOOSANOFF (1937b) found large ovocytes measuring 55–60 μm in almost every gonad studied. He indicated that they represented cells of previously developed gonad tissue. PLINE (1984) also noticed large ovocytes (50–60 μm), which he suggested were residual egg cells from previous ovogenic cycles, in gonads that were in an early

active phase. BRICELJ & MALOUF (1980) indicated that mature ovocytes can vary widely in size, from about 50 to 97 μm.

Hard clams from North Santee Bay, South Carolina exhibited no progression of well-defined stages of gonad development. Instead, there were gradual shifts in gametogenesis with two or more stages usually present in the same gonad simultaneously. PLINE (1984) found many male littlenecks showing a considerable overlap of developmental phases among follicles within a single gonad. There also appeared to be no time at which the hard clams in the North Santee Bay population were truly "inactive." Samples contained some clams in various stages of gametogenesis throughout the year, although the percent of the population undergoing active gametogenesis changed significantly. This condition is not unique to South Carolina adult clams. LOOSANOFF (1937b) found no undifferentiated gonads in hard clams from Long Island Sound, and KECK *et al.* (1975) and PLINE (1984) found only small percentages of hard clams in a recuperative phase in Delaware Bay and Wassaw Sound, Georgia, respectively. The occurrence of morphologically ripe sperm and ova throughout most of the year in North Santee Bay is an interesting feature of the sexual behavior of local *Mercenaria mercenaria*. LOOSANOFF (1937b) commented that the sexual cycle of the hard clam was not in phase with other bivalve mollusks in Long Island Sound. Results from this study substantiate the suggestion that *M. mercenaria* exhibits an unusual cycle of gonadal development. In South Carolina the cycle is further confounded by an extremely long spawning season and abbreviated periods of early active gametogenesis.

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