REPRODUCTIVE CYCLE OF MYA ARENARIA IN NEW ENGLAND

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Knowledge of the reproductive cycle in the soft-shell clam, *Mya arenaria* L., is essential to an understanding of larval production and ultimately of the abundance of this commercially important bivalve. By following the progress of gonad and gamete development in *Mya* throughout the year, the times and duration of spawning can be determined—information useful in the management of this fishery.

Although the literature contains numerous references to the times of spawning, information about gonadal changes in *Mya* is fragmentary or incomplete. We found the smear technique, used by Battle (1932), unreliable for determining gamete development because important details seen in the histological preparations were obscure in fresh, unstained smears. Coe and Turner (1938) described the development of juvenile *Mya* and gametogenesis from histological preparations. Unfortunately, their study indicated only the beginning of spawning and gave no data on its duration. In a preliminary report, Rogers (1959) described gonad development in Chesapeake Bay, Maryland, during the summer and fall. He observed a fall spawning period and ventured an opinion that a spring spawning also occurred, but he had not completed a full year of observations. Pfitzenmeyer (1962) also reported preliminary histological observations to support a conclusion that Maryland clams have two separate maturations.

Plankton studies by various investigators have revealed both annual and biannual periods of larval abundance. Both Stevenson (1907) and Stafford (1912) reported their observations of larvae as most numerous during a single period of time. Sullivan (1948) used the term "broods," possibly to describe successive large groups of larvae, but did not mention intervals between the groups when none were caught. Landers (1954) observed both an early-major and later-secondary larval occurrence. Between the two swarms, larvae disappeared for intervals of one to two months. Pfitzenmeyer (1962) observed an early-secondary and later-major larval occurrence. Larvae were not caught for intervals of three to four months between these biannual swarms.

Inferences about the frequency of spawning have also been made from observations of the first appearance of newly settled juveniles in the flats. Successive ripening and spawning periods during a single reproductive cycle were hypothesized by Belding (1930) to explain the "not uncommon" occurrence during any one year of "two distinct sets" in areas on the southern shores of Cape Cod. Pfitzenmeyer (1962) used special collectors in Chesapeake Bay and obtained two distinct sets of juvenile clams each year. A period of two to three months when none were caught separated the biannual settings.

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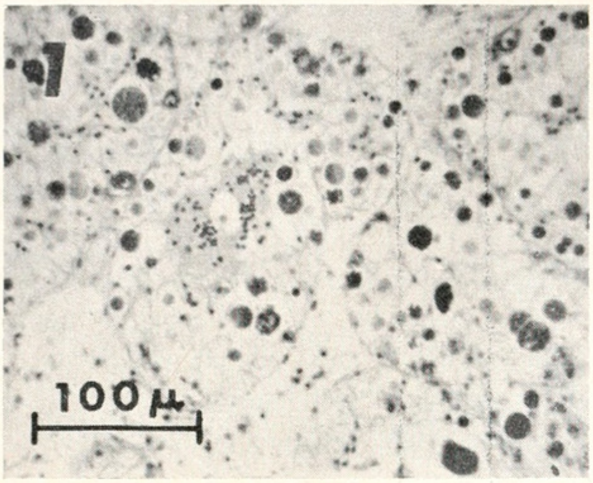
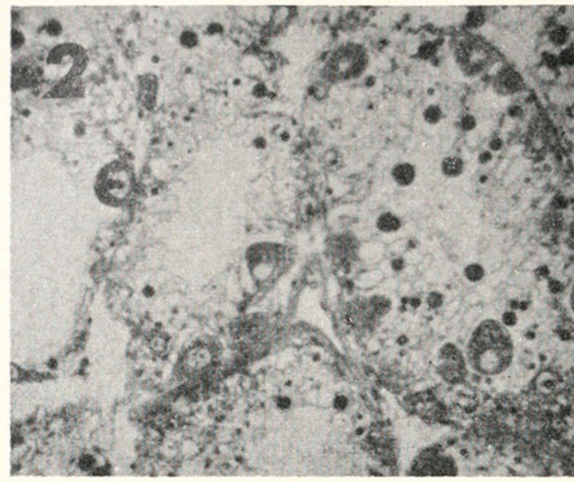
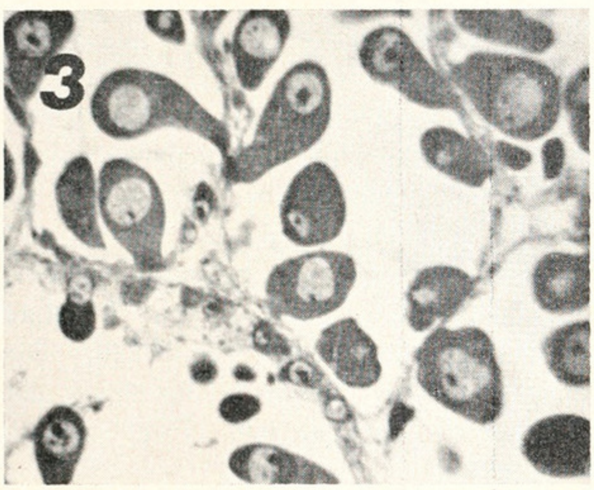
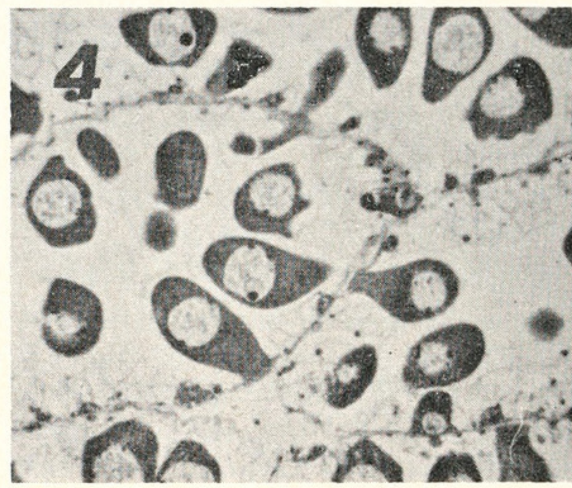








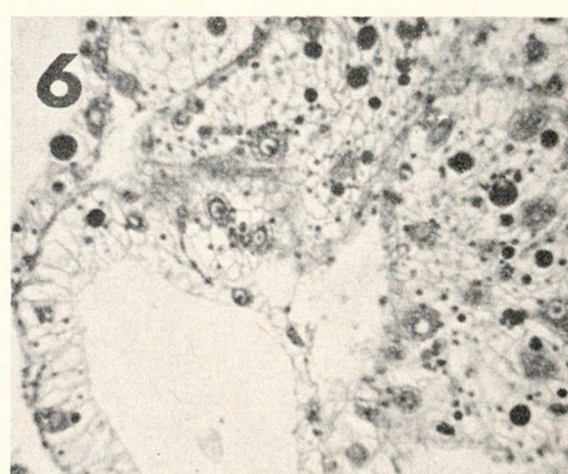


FIGURE 1. Section of gonad tissue from female clam, inactive phase of reproductive cycle. Note the small, dark phagocytes in the center of the alveolus, nutritive inclusions scattered within the follicle cells, and a large, round, almost completely cytolyzed ovocyte. To permit a comparison of cell size during maturation, all the photomicrographs were taken at the same magnification and a scale (100 μ) is provided.

FIGURE 2. Same, from female clam in active phase, showing early stages of ovogenesis.

FIGURE 3. Same, from female clam in active phase, showing later stages of ovogenesis.

Unfortunately, no certain conclusions about the nature of the reproductive cycle itself can be drawn from observations of either planktonic larvae, or newly metamorphosed set, since several seasonal peaks of abundance may appear from spawnings resulting from a single annual reproductive cycle. While observations of larval swarms can provide corroborative evidence, the annual frequency and duration of the reproductive cycle of clams can best be learned from periodic histological examinations of their gonad tissue. This paper presents the results of such studies made on clams from several New England areas.

Methods

Collections of clams were obtained periodically from the following New England areas north of Cape Cod. Plum Island Sound clam flats in Newbury, Massachusetts, were sampled twice each month from April, 1951, through February, 1953; flats near Boothbay Harbor, Maine, from February to November, 1961 (except April); and flats in Sorrento, Milbridge, Roque Bluffs, Cutler, Lubec, Pembroke, and Robbinston, Maine (collectively designated as eastern Maine in the text), each month from September, 1959, through December, 1960. The clams were dug from the middle of the intertidal zone in the eastern Maine and Boothbay Harbor areas, but throughout the whole intertidal zone in Plum Island Sound because the clams were not abundant. Miscellaneous collections were also obtained from Falmouth and Woods Hole, Massachusetts. These samples from areas on the south side of Cape Cod provided valuable supplementary data. Each sample included approximately 10 clams, $1\frac{1}{2}$ to 3 inches in shell length.

Within a few hours after field collections were made, the anterior third of the visceral mass of each clam was removed and preserved in Bouin's fixative. Standard techniques of dehydrating in alcohol, imbedding in paraffin, sectioning at 10 μ, and staining in Delafield's hematoxylin and eosin were used to prepare slides of the gonad tissues.

A microscopic examination was made to assign each specimen to a category which represented the gonad condition. The proportion of clams in each category, regardless of sex, was recorded for the individual samples. Although minor differences were observed, data on the clams from the seven eastern Maine sample areas, as well as the twice-a-month samples from Plum Island Sound, were combined each month to simplify presentation. Since the combined samples had no single collection date, a date midway between the first and last collection dates was chosen to represent each month's observation of gonad condition.

Categories of Gonad Condition

Female gonads

Except for certain pre-meiotic stages, ovocyte maturation occurs not in the ovaries, but after the eggs are shed (Raven, 1958). Therefore, tissues could not be classified according to the meiotic stages of the ovocytes. Instead, arbitrary

FIGURE 4. Same, from female clam in ripe phase. Note the amphinucleoli in the centrally located ovocyte.

FIGURE 5. Section of gonad tissue from female clam in partially spawned phase.

FIGURE 6. Section of gonad tissue from spent female clam. Note the small ovocytes at the periphery of the alveoli.

categories of development were distinguished by dividing the more or less continuous reproductive process into five phases. These are described below.

1. *Inactive phase*

At certain times of the year the rate of gonad activity becomes so low that changes in appearance of the gonad tissues in successive samples are imperceptible. Therefore, this state of relative quiescence is hereafter termed the inactive phase of the reproductive cycle. The term, however, is used for convenience and is not meant to imply that no activity at all is taking place. Small ovocytes occur at the periphery of alveoli (Fig. 1). A round nucleus in the ovocyte contains a conspicuous basophilic nucleolus and is encircled by an irregularly shaped cytoplasm. Vacuolated follicle cells that completely imbed the ovocytes sometimes fill the lumina of alveoli. Inclusions, apparently nutritive in function (Coe and Turner, 1938), frequency occur in the follicle cells. Small migratory cells sometimes appear between alveoli and within the lumina of alveoli. These migratory cells are probably phagocytic for they surround cytolyzed, unspent ovocytes.

2. *Active phase*

That part of ovogenesis which takes place within the gonad tissue and where definite quantitative and qualitative changes in the ovocytes are perceptible is designated as the active phase of the reproductive cycle. Enlarging ovocytes grow between the follicle cells toward the centers of alveoli during the early stages (Fig. 2). These ovocytes, which may be sub-conical, hemispherical or cylindrical in shape, are characteristically rounded at their apices and have broad cytoplasmic bases attaching them to the wall of the alveolus. The nuclei measure from 8 to 16 μ and average 13.3 μ in diameter.

Subsequent growth produces large, round ovocytes with constricted cytoplasmic bases (Fig. 3). The free ends of ovocytes extend beyond the basal membrane of follicle cells into the lumina of alveoli. The nuclei measure from 15 to 23 μ and average 19.2 μ in diameter. These ovocytes occur late in the active phase.

The onset of ovogenesis is difficult to determine with precision, as pronounced changes in staining reactions do not occur. However, the slight enlargement of many ovocytes, the more regular shape of their cytoplasm and protrusion toward the alveoli centers are visible indications of growth activities. Thereafter, the growth of ovocytes and tissue changes are more definite.

3. *Ripe phase*

In ripe clams, a very slender stalk may connect many of the largest ovocytes to the basal membrane (Fig. 4). Other ripe ovocytes appear as round cells in the lumina of alveoli, as if free of attachment to the basal membrane. The nuclei of these largest ovocytes contain amphinucleoli (Allen, 1953), each consisting of an almost transparent nucleolus and a small opaque nucleolinus. The amphinucleolus resembles a signet ring in some sections because the smaller nucleolinus occurs at the periphery of the nucleolus. The nuclei of ripe ovocytes measure from 20 to 31 μ and average 28.2 μ in diameter. These large ovocytes fill the lumina of alveoli and are usually more numerous than less developed ovocytes.

4. *Partially spawned phase*

In partially spawned clams, gonad tissues contain a few ripe ovocytes in some of the alveoli (Fig. 5). Small ovocytes are imbedded in follicle cells at the periphery of empty alveoli. Nutritive inclusions appear in many of the follicle cells. An absence of ripe ovocytes in many alveoli and the cessation of ovogenesis in all alveoli is indicative of the partially spawned condition.

5. *Spent phase*

Follicle cells form a thin layer covering the basal membrane of alveoli in some spent tissues, while in others they fill the alveoli (Fig. 6). Spent individuals can be distinguished from those in which no gametogenesis has taken place at all by the presence of a few unspent ovocytes in the early stages of cytolysis, which appear in the lumina of some alveoli as large, darkly stained bodies with obscure nuclei. Also, very numerous spherical droplets of lipoids and other products of cytolysis are characteristic of individuals which have completed a period of ovogenesis and have spawned (or, when conditions were not conducive for spawning, have resorbed their gametes).

Since the reproductive process is cyclic, the spent phase merges with and overlaps somewhat the inactive phase. Sharp distinction between the two is a convenience rather than a natural phenomenon.

Male gonads

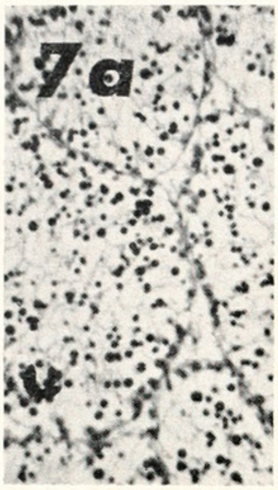
The criteria for the five corresponding categories of gonad condition in the male are presented below.

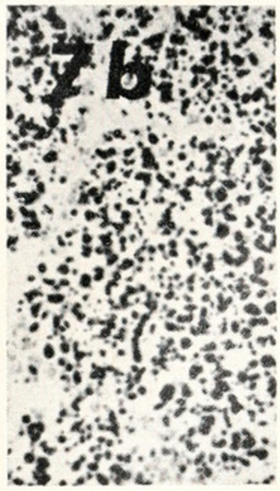
1. *Inactive phase*

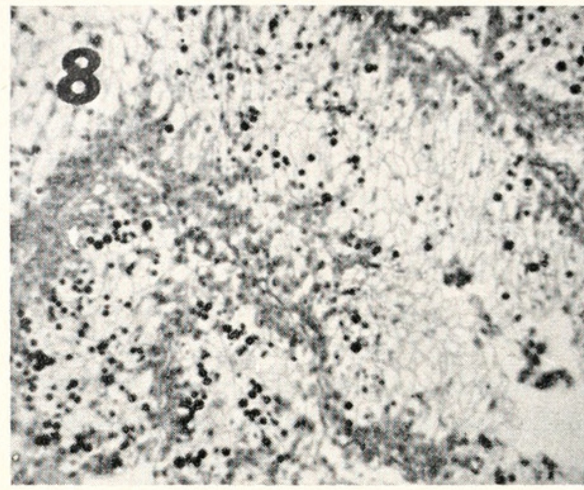
During the inactive phase, the male tissues frequently contain the products of an aberrant meiotic activity, which Coe and Turner (1938) have called "atypical spermatogenesis." Pycnotic cells (Fig. 7a) and multinucleated, non-pycnotic cysts (Fig. 7b) appear in the follicle cells. Many tissues contain both types although one usually predominates over the other. Both types of inclusions disappear during normal spermatogenesis, but reappear before it ceases, as do the nutritive granules seen in female tissues. Follicle cells fill the alveoli, surround the aberrant cells, and imbed the few spermatogonia and primary spermatocytes at the periphery of alveoli.

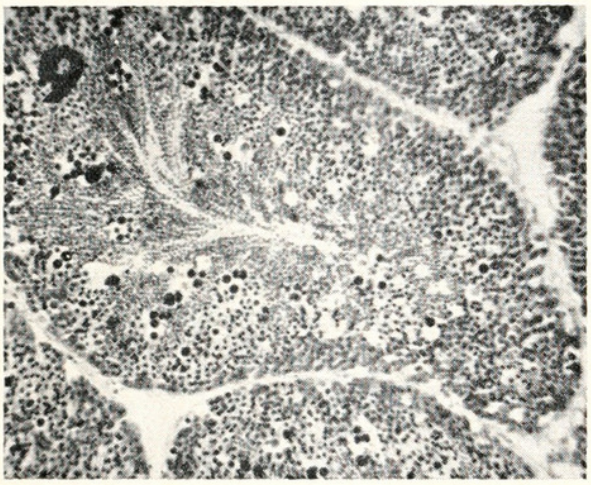
2. *Active phase*

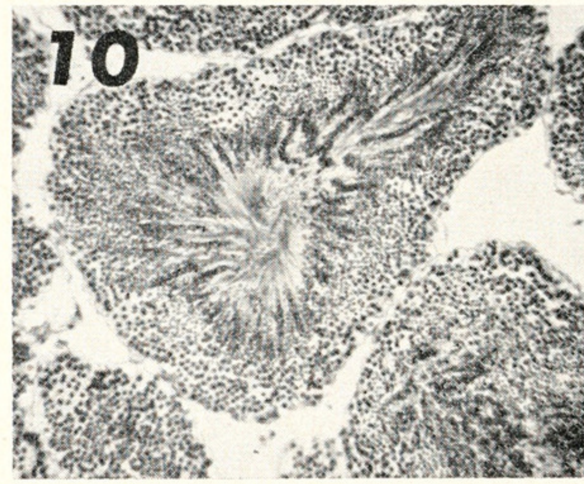
The active phase of the reproductive cycle in the male includes the entire process of spermatogenesis, unlike that in the female where only pre-meiotic stages are included. At the onset of the active phase, tissue sections contain proliferating primary spermatocytes at the basal membrane of the alveoli (Fig. 8). These small and uniformly sized cells, very similar in appearance to the earliest ovocytes, force their way between follicle cells and toward the centers of alveoli. Early stages of meiosis occur in the spermatogenic cells near the basal membrane, whereas the

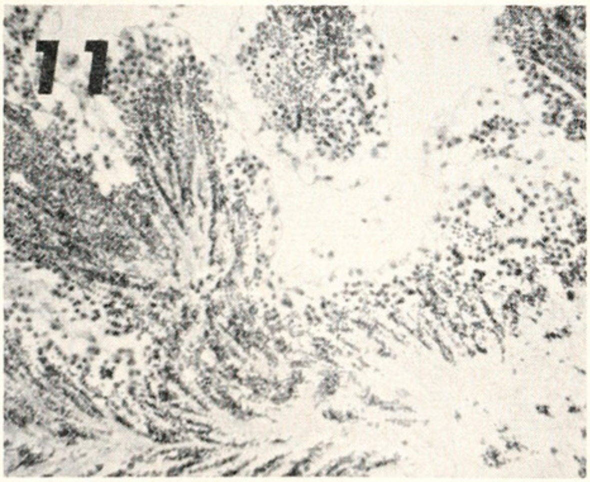












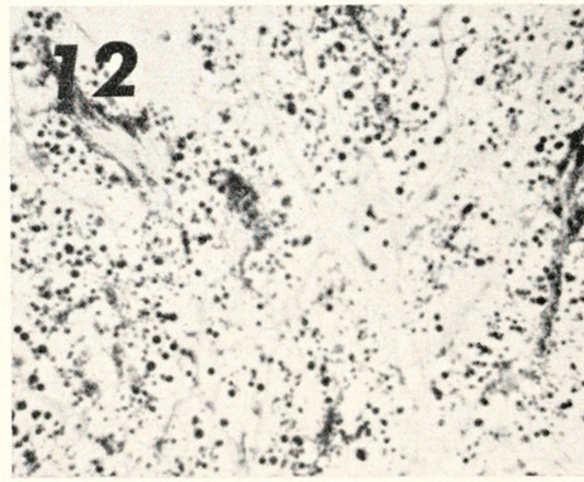


FIGURE 7a. Section of gonad tissue from male clam in inactive phase of reproductive cycle. Inactive phase of spermatogenesis in male soft-shell clams. Note the round, pycnotic cells, products of atypical spermatogenesis.

FIGURE 7b. Same, showing the cysts of multinucleated, non-pycnotic cells, also products of atypical spermatogenesis.

FIGURE 8. Section of gonad tissue from male clam in active phase of reproductive cycle, showing early stages of spermatogenesis.

FIGURE 9. Same, showing later stages of spermatogenesis. Late, active phase of spermatogenesis.

later spermatids occur at the centers of alveoli (Fig. 9). A very thin-walled membrane surrounds each spermatid. Meiotically active cells between the periphery of the alveoli and their centers eventually obliterate the follicle cells. A large number of spermatids produce a distinct mass in the centers of alveoli.

3. *Ripe phase*

Ripe male tissues contain masses of spermatozoa, arranged in more or less radial columns with their tails oriented toward the center. In fully ripe specimens these spermatozoa may nearly fill the lumina of the alveoli (Fig. 10).

4. *Partially spawned phase*

Partially spawned male tissues contain relatively few spermatogonia at the basal membrane (Fig. 11). Follicle cells occur between the basal membrane and groups of cells undergoing spermatogenesis. A scattering of pycnotic cells occur within the follicle cells. Spermatozoa still occupy a substantial portion of the central alveolar area.

5. *Spent phase*

Spent male tissues contain no or very few spermatozoa in the central alveolar area (Fig. 12). Numerous follicle cells with multinucleated, non-pycnotic cysts and pycnotic cells from atypical spermatogenic activities surround small groups of spermatozoa. Spent tissues lack cells in the active phase of spermatogenesis.

Geographic Variations in the Reproductive Cycle

Eastern Maine

Clams in the inactive phase were encountered throughout the year in eastern Maine, but were least numerous during June (Fig. 13). All were in this condition from September through December in 1959 and 1960. By January, 1960, some had begun gametogenesis. Clams in the active phase became more numerous each month after January, until May, after which fewer individuals were in this condition, and were absent from the August samples. Clams in the active phase were obtained to some extent for a period of about seven months.

Ripe clams were first observed in the middle of May, but none showed indications of having spawned. In June about half of the clams were ripe and some were partially spawned. Partially spawned clams were more numerous in July and by August about 75% of the clams had completely spawned and had returned to the inactive condition. The spawning period, then, extended from early June to about the middle of August, a period of 2½ months.

Minor exceptions to the reproductive cycle described above were observed in clams from two eastern Maine areas where gametogenesis began earlier than in the

FIGURE 10. Section of gonad tissue from ripe male clam. Note the columns of spermatozoa.

FIGURE 11. Section of gonad tissue from male clam in partially spawned phase.

FIGURE 12. Section of gonad tissue from spent male clam. Note the occurrence of both types of atypical spermatogenesis.

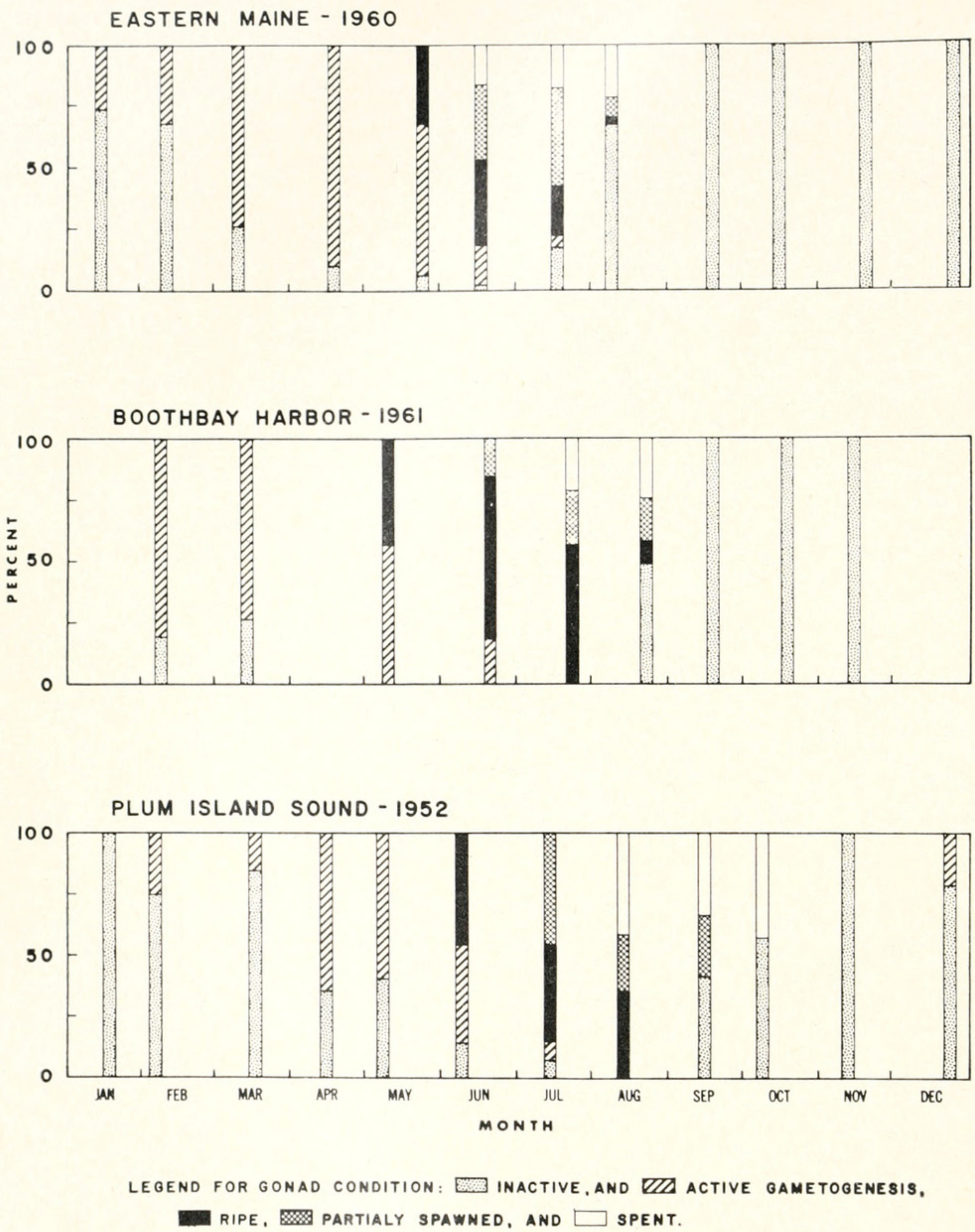


FIGURE 13. Gonad conditions of *Mya arenaria* from New England. The length of each shaded area represents the percentage frequency of clams in each gonad condition.

five other areas. More than half of the Lubec and Pembroke clams were in the active phase in January and February. After February, clams in this condition were almost equally as numerous from all seven eastern Maine areas. An earlier spawning in Lubec and Pembroke was not definitely indicated by the data.

Boothbay Harbor

Gametogenesis had commenced in about 75% of Boothbay Harbor clams during February and March (Fig. 13). More ripe clams occurred during May in the Boothbay Harbor than eastern Maine samples. Some partially spawned clams were observed as early as June in Boothbay Harbor, but both areas yielded numerous partially spawned clams during July. Completely spawned clams did not appear until July in Boothbay Harbor, or nearly one month later than in eastern Maine. More Boothbay Harbor than eastern Maine clams were in the ripe, partially spawned or spent condition in late August. The three-month spawning period of Boothbay Harbor clams, extending from late June to August, was not only later, but longer by a half a month than that of eastern Maine clams.

Plum Island Sound

The spawning season was still later in clams from Plum Island Sound than in clams from all Maine study areas (Fig. 13). Relatively few clams began gametogenesis during February and March. Ripe clams appeared first in June, a month later than clams from Maine. Correspondingly, the earliest occurrence of spawned clams was later. Spawning, indicated by the appearance of partially spawned clams from July through September, lasted for three months in Plum Island Sound. Many spent clams were seen as late as October.

Discussion

The results of gonad examinations suggested several generalizations about the reproductive cycle of *Mya arenaria*. Gametogenesis began during the late winter or early spring in all areas sampled. Thereafter a progressive development of the gametes was seen until ripe cells filled the tissues and spawning began in late spring and early summer. A spawning peak occurred during the middle and late summer, after which gametogenesis ceased. The inactive condition prevailed during the fall and most of the winter. No more than a single reproductive cycle occurred in the clams from nine sample areas north of Cape Cod. No failure to spawn was indicated in clams from any of the sample areas.

Despite the more southern latitude, the reproductive period in Plum Island Sound was characterized by a later rather than an earlier spawning season than that in Maine (Fig. 13). Furthermore, a still later spawning season than that of 1952 was indicated by the occasional gonad samples taken in Plum Island Sound during the preceding year. A few ripe clams first appeared during July, 1951. Both ripe and partially spawned clams were most numerous during late July and early August. All were spent by late October, 1951.

Most reports of larval occurrence and sex cell development indicated that *Mya* begins spawning at an earlier date in areas north of Plum Island Sound (Fig. 14). At Malpeque Bay, Canada, the earliest soft-shell clam larvae were found during early June by Stafford (1912) and during late May by Sullivan (1948). Stafford (1912) found an abundance of *Mya* larvae during July and August at St. Andrews, Canada. Most of the clams in Battle's (1932) samples from St. Andrews, Canada, contained ripe gonads during early June. She found some spent gonads by late June, indicating the beginning of the spawning season.

After finding an early abundance of larvae, Welch (1953, unpublished report) [2] deduced that some were probably in the plankton of Robinhood Cove, Maine, during early May, 1951. He also caught a few larvae during June of 1952 (oral communication), even though maximum numbers occurred during the middle of August to the middle of October that year.

A late spawning season was reported for *Mya* in northern Massachusetts areas. Belding (1907) observed that *Mya* spawns from the middle of August until early October (Fig. 14). Stevenson (1907) caught no larvae at Ipswich, Massachusetts, before late August, and reported the last half of September as the period of peak spawning. He also caught large numbers of larvae at Plymouth, Massachusetts, during late July and early August. Later Belding (1930) reported July and August as the spawning season for soft-shell clams north of Boston. These reports agreed with our observations of a late active phase and spawning period of *Mya* in Plum Island Sound.

A study of Figure 14, summarizing available information on the reproductive cycle of *Mya*, shows clearly two important phenomena: (1) the tendency for clams to develop gametes and spawn progressively earlier in the season northward and southward from northern Massachusetts, and (2) the bimodal nature of spawning activity south of Cape Cod. It is not entirely certain from this information that the bimodality results from two distinct reproductive cycles. It may result merely from an interruption in the spawning activity during a single reproductive cycle. Lacking observations on gametogenesis in the clams from their study areas, Bumpus (1898), Mead and Barnes (1904), Belding (1907; 1930), Stevenson (1907), Nelson and Perkins (1931), Deevey (1948), and Landers (1954) neither described nor implied more than a single annual reproductive cycle to *Mya*, even though Mead and Barnes (1904), Belding (1907; 1930), and Stevenson (1907) found two distinct groups of newly settled juveniles, and Landers (1954) observed two distinct swarms of larvae. In addition, Coe and Turner (1938) and Rogers (1959) believed that *Mya* probably spawned more than once each year, but did not mention the possibility of more than a single annual reproductive cycle.

Nevertheless, some evidence is available from several studies which suggests two separate reproductive cycles per year in southern latitudes. The clams from southern areas were reported to begin spawning earlier in the year than those from northern Massachusetts areas (Fig. 14). Deevey (1948) found that *Mya* larvae were dominant in Tisbury Great Pond on Martha's Vineyard, Massachusetts, from late April to June. Landers (1954) obtained larvae as early as the middle of April in samples from Wickford Harbor, Rhode Island, whereas Pfitzenmeyer (1962) captured larvae in the plankton of Chesapeake Bay, Maryland, throughout May. More important, however, both Landers (1954) and Pfitzenmeyer (1962) caught no larvae during the middle of the summer, after a late spring to early summer larval swarm. This period of larval absence in the plankton corresponded to observations of gonads by Rogers (1959) and Pfitzenmeyer (1962) which were apparently in the inactive phase during the middle of

[2] Welch, W. R., 1953. Seasonal abundance of bivalve larvae in Robinhood Cove, Maine. Fourth Annual Conference on Clam Research, U. S. Fish and Wildlife Service, Clam Investigations, Boothbay Harbor, Maine. (Mimeographed report).

the summer. Hence, the clams were unable to spawn because ripe sex cells were not present in the gonads.

Further evidence of biannual spawning can be drawn from our own histological examinations of clams collected in the Woods Hole, Massachusetts, area.

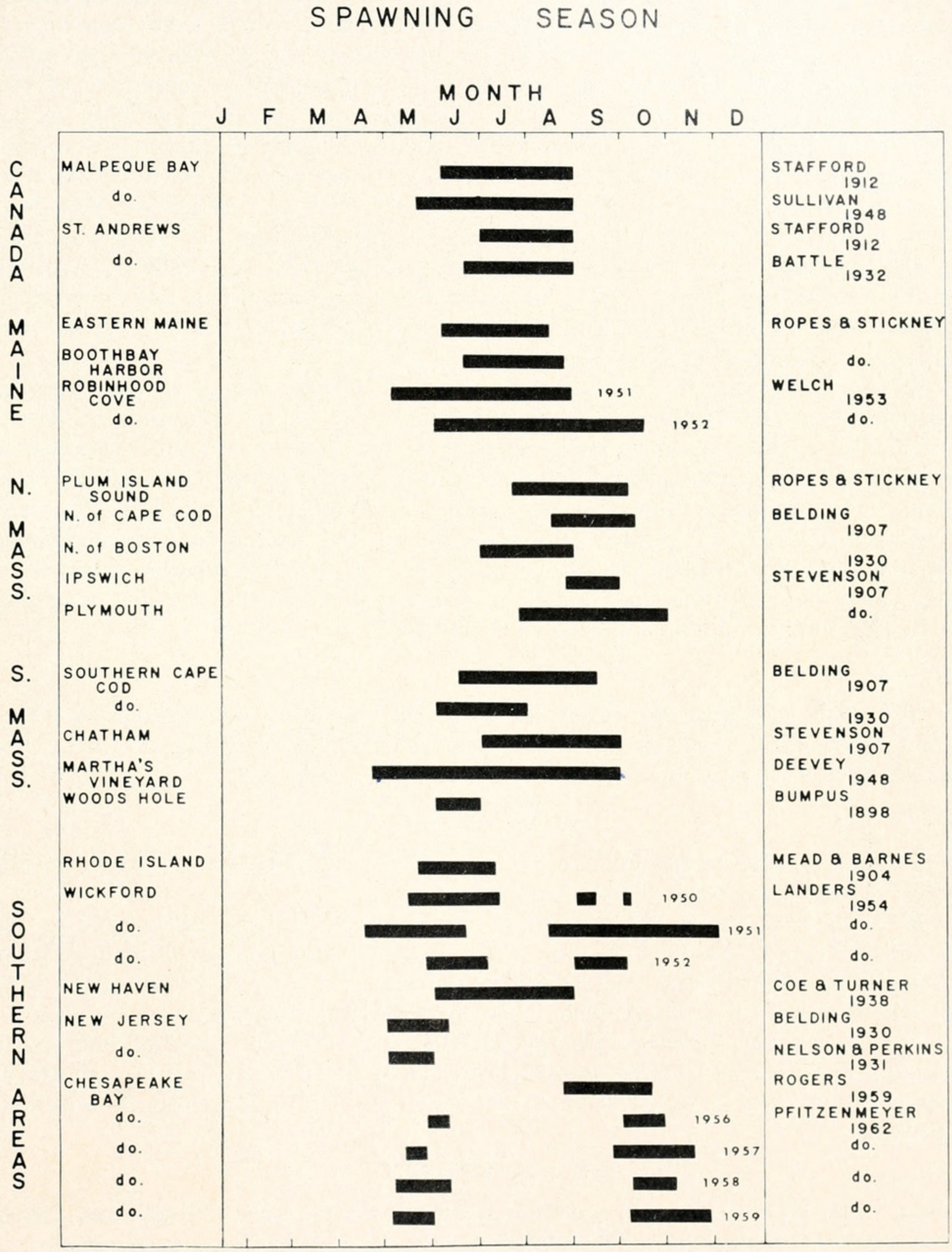


FIGURE 14. The duration of the spawning season of *Mya arenaria* reported in the literature for areas along the Northwestern Atlantic coast.

Samples of clams collected July 19 and 31, 1950, from Falmouth Inner Harbor contained none with ripe or developing gametes. Some live clams from these samples were held in outdoor tanks of sea water at seasonal temperatures until September 1, 1950, at which time most of them were fully ripe. The numerous nutritive granules, typically products of cytolyzed, unspawned gametes in females and the products of aberrant spermatogenesis in males, which were seen in July samples suggest that the clams from this population had also been ripe earlier in the year. This inference was supported by subsequent observations of ripe clams which were common in samples collected from Woods Hole both in late September, 1961, and in late May, 1962. The occurrence of ripe gonads during the early spring and fall corresponded to the times when larval swarms were found by both Landers (1954) and Pfitzenmeyer (1962). When the gonads of clams in the southern latitudes were in the inactive condition the gonads of clams in the northern latitudes were either ripe or partially spawned. Therefore, the two periods of gametogenesis in clams from southern areas were completely out of phase with the single annual reproductive period of northern clams, and indicated a biannual reproductive cycle.

We used clams with an apparent biannual reproductive cycle in spawning experiments at the Boothbay Harbor laboratory. Spawnings were induced during a period of a month or more after collecting clams from Woods Hole, Massachusetts, in late September, 1961, and also in late May, 1962, as well as from Chesapeake Bay, Maryland, in the middle of October, 1961. The Maryland clams remained in the inactive condition during the winter, and ripened again the following April in the laboratory tanks. These clams produced larvae when local clams were neither ripe enough to spawn, nor were the gametes developed to the ripe condition by the methods we tried.

We wish to thank Mr. Malcolm E. Richards, Marine Resources Scientist of the Maine Department of Sea and Shore Fisheries, for providing us with gonad samples from eastern Maine.

Summary

1. Only a single reproductive cycle was observed in *Mya arenaria* gonads collected from areas north of Cape Cod.

2. In eastern Maine, the spawning season extended from early June to the middle of August. Boothbay Harbor clams spawned from late June to late August. Clams from Plum Island Sound began spawning in July, a month later than eastern Maine clams, and completed spawning by late September.

3. Observations of gonadal changes in *Mya* from southern Cape Cod indicated a biannual cycle occurs. These observations are supported by previous reports of spawning activities, larval occurrence, and gametogenesis in *Mya* from the southern latitudes.

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