

REPRODUCTIVE CYCLE OF THE SOFT-SHELL CLAM, *MYA ARENARIA*, AT SKAGIT BAY, WASHINGTON

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ABSTRACT

The annual reproductive cycle of the soft-shell clam, *Mya arenaria* L., was studied at Skagit Bay in northern Puget Sound, Wash. Spawning occurred from late May to early September in both 1971 and 1972 with peak spawning in July and June respectively. Small clams (less than 60 mm in length) had a spawning peak that coincided with other size classes although the spawning period was shorter in duration. The single yearly spawning period at Skagit Bay corresponds with east coast populations in Canada and Maine.

The soft-shell clam, *Mya arenaria* L., is found on virtually all coastlines in the northern hemisphere (Hanks, 1963) and is still extending its range as evidenced by its recent movement into the Black Sea (Zambriborshch, Marchenko, and Telegin, 1968; Ivanov, 1969). On the North American continent, it is native to the east coast from which it reportedly was accidentally introduced into San Francisco Bay, Calif., about 1874 (Fitch, 1953). However, there is some evidence from Indian middens that the soft-shell clam is also native to the west coast (Craig, 1927). Its range on the west coast presently extends from California to Alaska (Morris, 1966).

The reproductive cycle of the soft-shell clam has been described from a variety of locations on the east coast, but no data have been presented for west coast populations except for one brief note from Oregon (Edmondson, 1920). The first detailed study on the histology of the gonad of *Mya arenaria* was conducted by Coe and Turner (1938) in New England. They found that spawning occurred in the summer. At Martha's Vineyard in Massachusetts spawning was found to occur over a 6-mo period from spring through early fall (Deevey, 1948). In northern Massachusetts, spawning occurs in late summer and early fall (Ropes and Stickney, 1965), while in New Jersey, spawning takes place in the spring (Belding, 1930; Nelson and Perkins, 1931). Two spawnings per year (spring and fall) have been reported for the Chesapeake Bay in Maryland (Pfitzenmeyer, 1962, 1965) and for Narragansett Bay, R.I. (Landers, 1954). Ropes and Stickney

(1965) have tabulated the results of most east coast studies for easy comparison.

This paper describes the annual reproductive cycle for a soft-shell clam population from Puget Sound, Wash. Skagit Bay was selected as the study area since it has a potential for commercial operations, a commercial soft-shell clam fishery is in the beginning stages, and it appears to be the area with the greatest abundance of soft-shell clams in Puget Sound.

DESCRIPTION OF AREA

Skagit Bay, Wash., is located in northern Puget Sound 60 miles north of Seattle. The Skagit River, which has an average discharge of 16,560 ft³/s (U.S. Department of Interior, 1971:190),² empties into the end of the bay via the South Fork and at the northern entrance of the bay via the North Fork. The northern side of the bay is made up of a large broad mud flat approximately 13 square miles in area. The study area was located on the mud flat off Fir Island between Hall Slough and Browns Slough.

The mean tide range at Skagit Bay is 6.5 feet, and the diurnal range 10 feet. The soft-shell clam beds are located at a tidal level of approximately +3.5 feet.

Water temperatures and salinities in the vicinity of Skagit Bay may vary widely on both an annual and a diurnal basis due to river discharge and tidal effects. During 1971, surface temperatures at Strawberry Point varied from 4.79° to 15.68°C, while salinities ranged from 2.54 to 24.53‰. The maximum recorded daily variation

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²Thirty-year period—maximum recorded flow: 144,000 ft³/s, minimum recorded flow: 2,740 ft³/s.

in surface water temperature at Strawberry Point was 4°C.

METHODS AND MATERIALS

The study began in November 1970 and was completed in November 1972. Samples were collected once a month from November thru February and twice a month from April thru October in 1971 and March thru October in 1972. The bimonthly samples were taken at 2-wk intervals: generally during the first and third weeks of the month. No sample was collected in January 1971 because river flooding prevented access to the study area. Each sample consisted of 50 clams which was separated from a larger random sample to represent five size classes: clams less than 60 mm in length, those in the 60-, 70-, and 80-mm length ranges, and those larger than 90 mm. As far as possible the 50 clams selected for each sample were equally distributed between the five size classes. The samples taken during the first 3 mo of the study consisted of only 10, 10, and 15 clams respectively. A total of 1,785 clams were collected which ranged from 22 to 105.5 mm in length. Of this total 2.6% were immature, leaving a total of 1,739 mature clams that were utilized in the analysis of the reproductive cycle.

The samples were returned to the laboratory where they were measured and weighed and the gonadal mass removed and preserved in Davidson's acetic acid fixative (Shaw and Battle, 1957). In smaller clams the entire visceral mass was preserved and sectioned; for larger clams a cube of gonadal tissue was removed from the mid-lateral portion of the visceral mass. Usually dissection and preservation were accomplished the day of collection. Clams not dissected until the following day were held in a refrigerated saltwater system overnight.

Slides were prepared by standard histological techniques: tissues were dehydrated in alcohol, cleared in xylene, embedded in paraffin, sectioned at 5-8 microns, and stained with Mayer's hematoxylin and alcoholic eosin (Galigher and Kozloff, 1971).

The number of gonadal stages used to describe bivalve reproductive cycles varies widely. Lamens (1967) distinguished 11 stages and measured the nuclear-cytoplasmic ratio. Previous investigations on *Mya* reproductive biology generally have recognized five phases of development (Shaw, 1962, 1965; Ropes and Stickney, 1965); therefore the following five phases were used: in-

active, active, ripe, spawning, and spent. These five phases were distinguished by the following characteristics.

Males

Inactive (Figure 1a)

During this phase the alveoli are filled with follicle cells which contain the typical male type inclusions as described by Coe and Turner (1938). Primary spermatocytes may be visible along the alveolar wall, but are not abundant.

Active (Figure 1b-d)

This phase is typified by the proliferation and maturing of the spermatocytes. In staging the slides, an early active, middle active, and late active stage were identified. The early active stage (Figure 1b) is characterized by the proliferation of primary spermatocytes at the basal membrane of the alveoli and the appearance of some spermatids. The middle active stage (Figure 1c) is characterized by the disappearance of the follicle cells and the migration of spermatids toward the center of the alveoli where they begin aligning in radial columns. The late active stage (Figure 1d) is characterized by the greatly increased number of radially aligned spermatids and the formation of a central lumen in the alveoli.

Ripe (Figure 1e)

In the ripe male clam, the sperm are distinctly bunched in radial columns around the alveoli with their tails, which stain pink with eosin, projecting into the central lumen.

Spawning (Figures 1f and 2a)

When spawning commences a single row of follicle cells form at the alveolar membrane (Figure 1f). These follicle cells contain the typical inclusions of the male, and the number of rows increases as spawning proceeds (Figure 2a).

Spent (Figure 2b)

In the spent clam most all sperm have been discharged, but a few may remain. The alveoli are almost completely filled with follicle cells.

Females

Inactive (Figure 2c)

In the inactive phase the alveoli are filled with follicle cells which contain the distinctive female

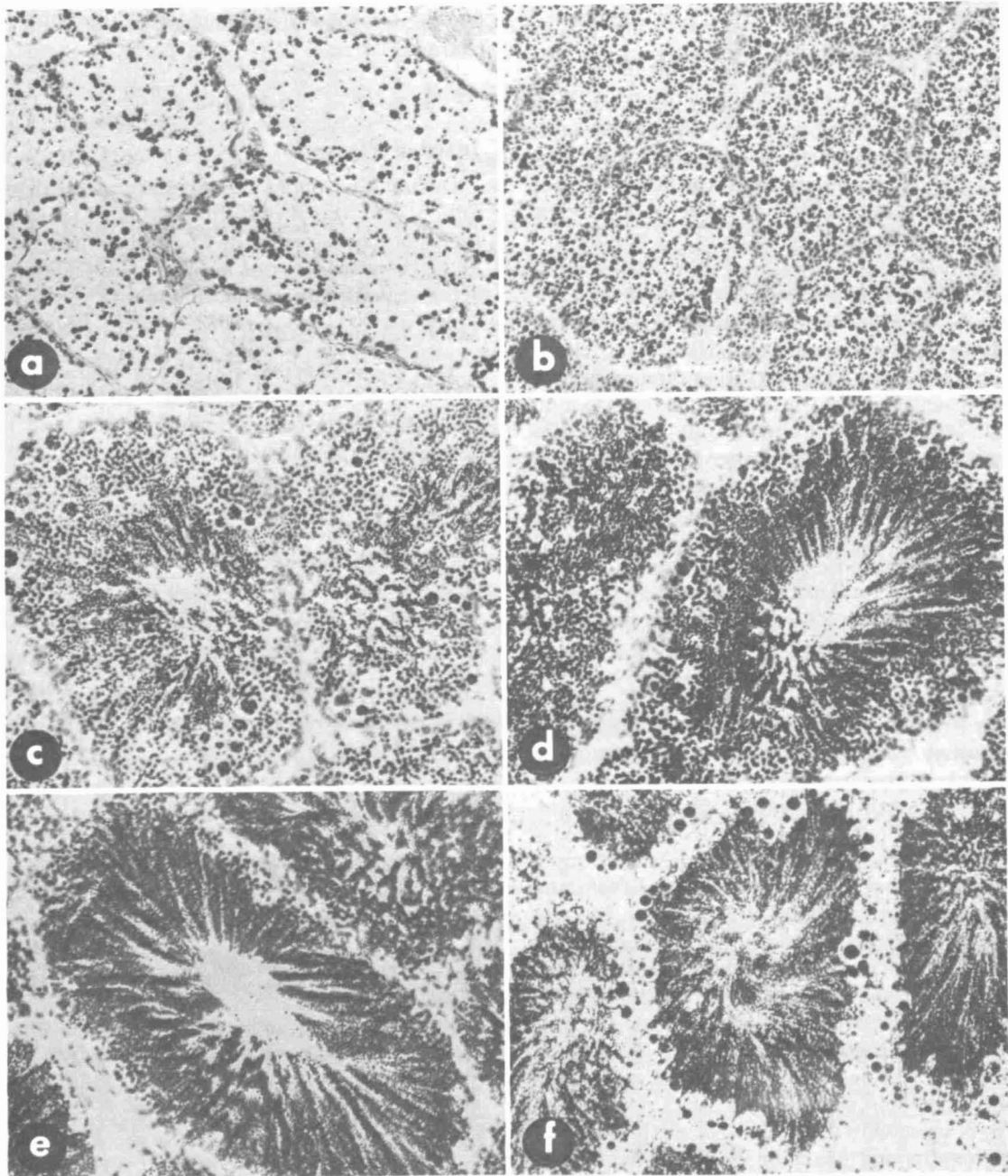


FIGURE 1.—Gonadal stages of the soft-shell clam, *Mya arenaria*, at Skagit Bay, Wash. a) Inactive male (160 \times), 22 Sept. 1972. Follicle cells with inclusions fill the alveoli. b) Early active male (160 \times), 17 Feb. 1972. Proliferation of the primary spermatocytes is visible along the basal membrane of the alveoli. c) Active male (250 \times), 30 Apr. 1971. Spermatids begin aligning in radial columns toward the central lumen of the alveoli. A few sperm balls are visible near the periphery of the alveolus. d) Late active male (250 \times), 14 May 1971. e) Ripe male (250 \times), 11 June 1971. The sperm are aligned in radial columns, their tails projecting into the central lumen. f) Early spawning male (250 \times), 1 June 1972. A single row of follicle cells containing inclusions forms at the basal membrane of the alveoli.

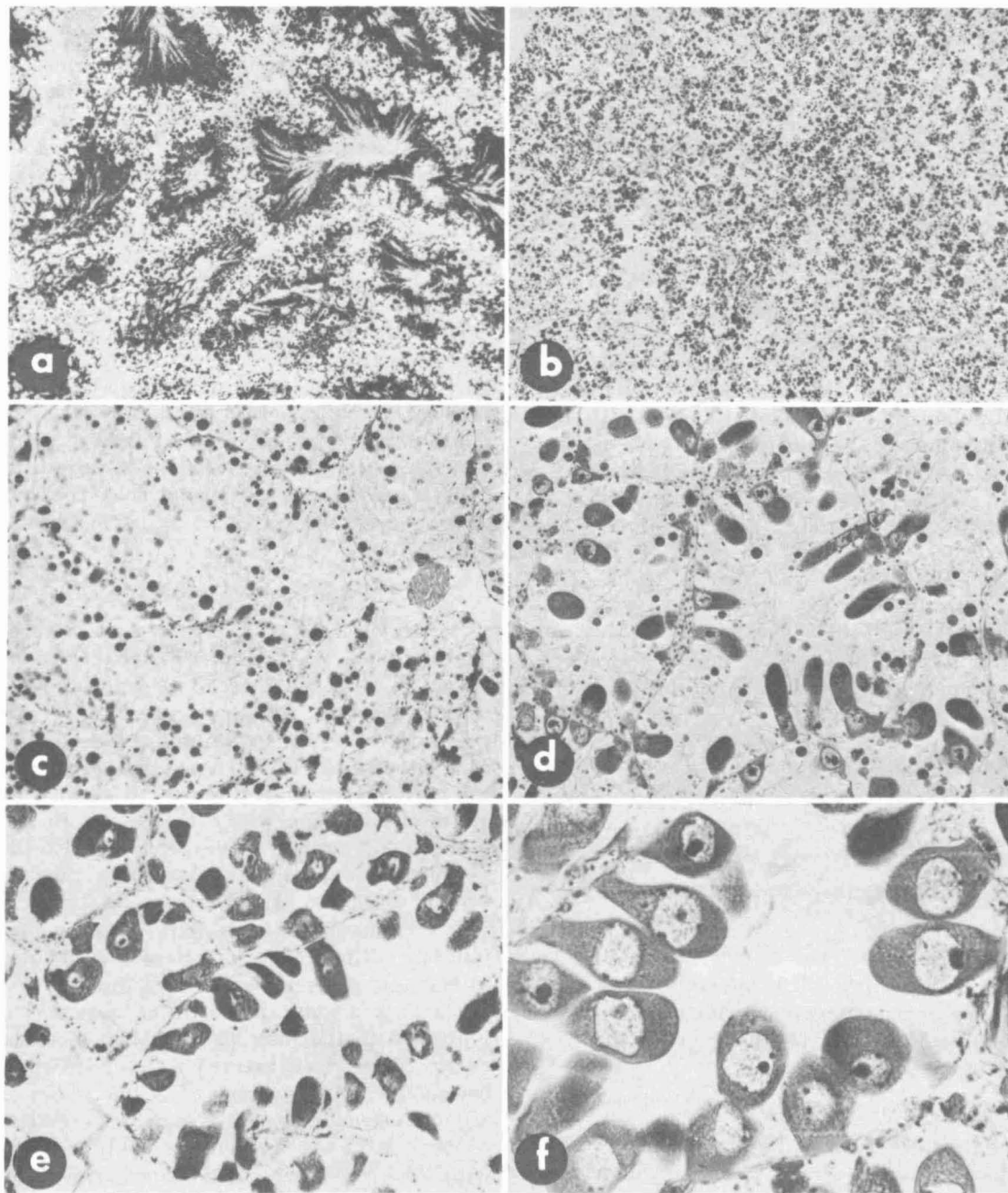


FIGURE 2.—Gonadal stages of the soft-shell clam, *Mya arenaria*, at Skagit Bay, Wash. a) Spawning male (100 \times), 6 Aug. 1971. The follicle cells reappear as spawning progresses. b) Spent male (100 \times), 8 Sept. 1972. c) Inactive female (100 \times), 12 Oct. 1971. Follicle cells containing the typical female inclusions fill the alveoli. d) Early active female (145 \times), 3 Mar. 1972. The primary oocytes begin enlarging forming stalked oocytes. e) Active female (136 \times), 8 May 1972. The follicle cells and their inclusions have disappeared. f) Late active female (240 \times), 14 June 1972. The nucleolus and amphinucleolus of the ova have appeared, but most ova are still attached to the basal membrane of the alveoli.

type inclusions (Coe and Turner, 1938). A few primary ovocytes are visible along the alveolar membrane.

Active (Figure 2d-f)

As in the male, three stages were identified for this phase: early, middle, and late active. The early active stage (Figure 2d) is characterized by the proliferation of primary ovocytes and their elongation producing stalks which protrude toward the center of the alveolus between the follicle cells. In the middle active stage (Figure 2e) the follicle cells and their inclusions have disappeared leaving a central lumen in each alveolus. An increasing number of stalked ovocytes attached to the alveolar wall protrude into this lumen. In the late active stage (Figure 2f) the ovocytes are beginning to become spherical with slender stalks, and in many the nucleolus and amphinucleolus are readily visible.

Ripe (Figure 3a, b)

In the ripe phase a majority of the ova are free of the alveolar wall and have taken on spherical shape (Figure 3a). In some individuals the ova are quite abundant, and almost all will be free of the alveolar wall (Figure 3b).

Spawning (Figure 3c)

The spawning phase is characterized by the emptying of the alveoli of ripe ova, leaving behind a few ovocytes that are still attached to the alveolar wall.

Spent (Figure 3d)

In the spent clam the alveoli are empty, and follicle cells begin to fill in the alveoli from the basal membrane inward. Inclusions reappear with the follicle cells, and some of the primary ovocytes are visible.

Immature

The immature gonad (Figure 3e) has a much smaller number of alveoli which are filled with follicle cells devoid of any inclusions.

Each clam was identified as to sex and staged in accordance with the above phases. The percentage of clams in each phase was then calculated. For the purposes of analyzing the reproductive cycle (Figure 4), the three stages of the active phase: early, middle, and late were combined under the single term active phase. In addition, mean monthly percentages were utilized in analyzing

the reproductive cycle (Figure 4) for those months during which two samples were collected.

In the presentation of results, the terms 1971 and 1972 reproductive cycle refer to the cycle whose spawning phase occurred during that respective calendar year. However, the reproductive cycle as a whole does not necessarily coincide with, nor is it restricted to, a particular calendar year. The reproductive cycle was assumed to begin with the active phase and end with the inactive phase.

RESULTS

The histological examinations revealed a single yearly spawning period which occurred from late May to early September. This was true for both sexes and for both the 1971 and the 1972 reproductive cycles although the period of peak spawning varied slightly (Figure 4). The sex ratio of the 1,739 clams utilized in the analysis of the reproductive cycle was 48% males (837) and 52% females (902).

1971 Reproductive Cycle

During the 1971 reproductive cycle (Figure 4) clams in the active phase were encountered from February through July for males and February through June for females. Active clams were undoubtedly first present in January although no samples were collected that month. Individuals in the early active stage (Figures 1b and 2d) first appeared in February for both sexes, while those in the middle active stage (Figures 1c and 2e) first appeared in March and the late active stage (Figures 1d and 2f) in early April.

Ripe clams of both sexes were first observed in late April. Ripe males (35%) were most abundant in May and ripe females (47%) in June.

Clams in a spawning condition were first encountered in the later part of May, peaked in July, and were last observed in the early September sample. During July 75% of the males and 55% of the females were in a spawning condition.

Spent clams were present from July to October with the highest percentage occurring in August when 38% of the males and 65% of the females were in this phase.

There was no observed difference in reproductive cycle with size class, except for clams under 60 mm in length. In general the period of peak spawning for those clams was the same as other size classes, but the duration of the spawning period was shorter. It began about 1 mo later than other size classes and ended a month earlier.

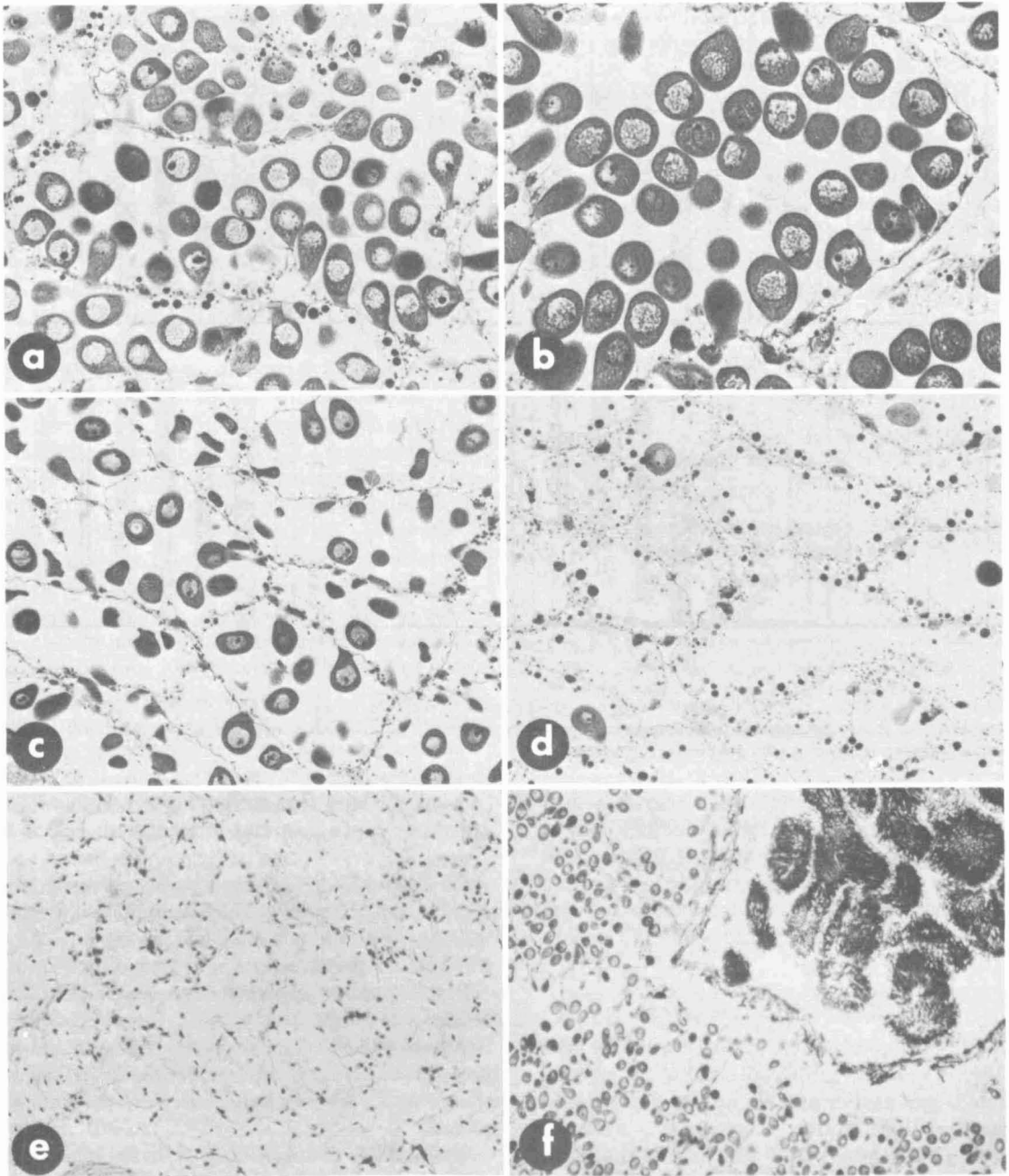


FIGURE 3.—Gonadal stages of the soft-shell clam, *Mya arenaria*, at Skagit Bay, Wash. a) Ripe female (180 \times), 14 June 1972. The ova are now free of the alveolar wall and have taken on a spherical shape. b) Ripe female (145 \times), 14 June 1972. c) Spawning female (180 \times), 1 June 1972. d) Spent female (100 \times), 24 Aug. 1972. The ova have been discharged, and follicle cells with inclusions are forming along the basal membrane of the alveoli. e) Immature clam (160 \times), 24 Aug. 1972. Follicle cells devoid of inclusions, but containing the small black follicular nuclei, fill the alveoli. From an individual 38.4 mm in length. f) Hermaphrodite (40 \times) in a spawning condition (14 June 1972).

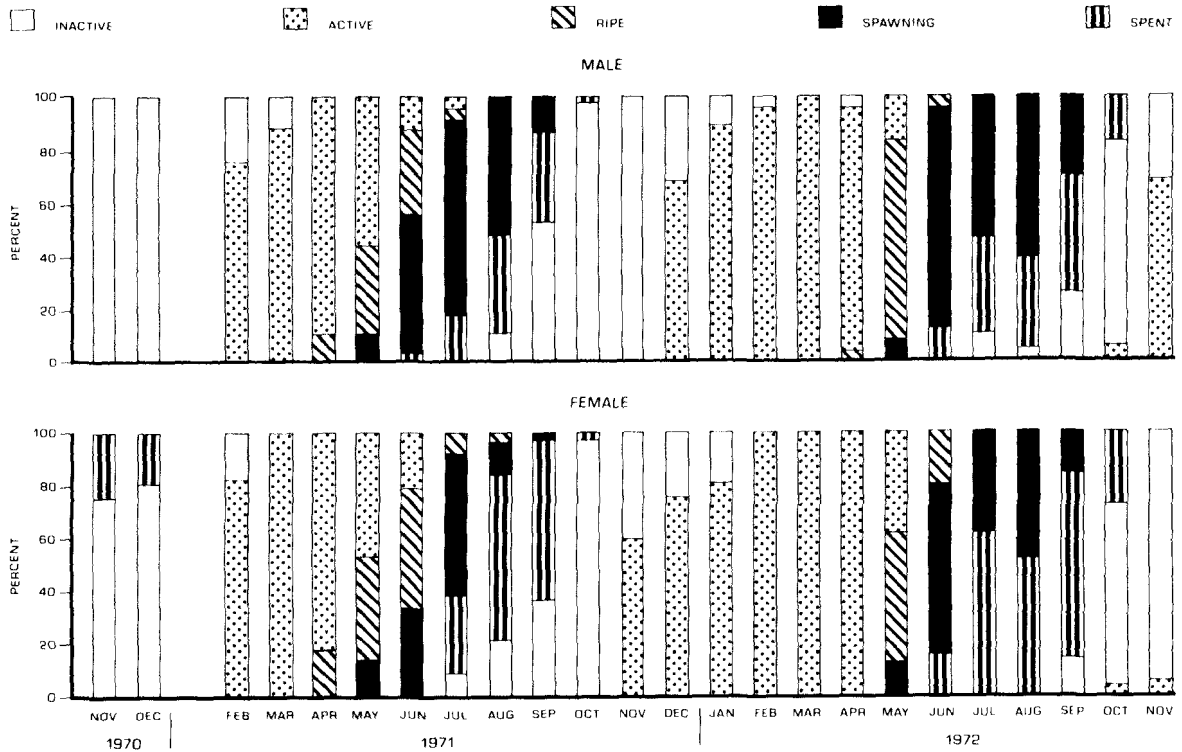


FIGURE 4.—Male and female reproductive cycles of the soft-shell clam, *Mya arenaria*, during 1971 and 1972 from Skagit Bay, Wash. The length of each shaded area represents the percentage frequency of clams in each reproductive phase. A total of 1,739 clams (48% males and 52% females) were examined during the 2-yr study.

The smallest mature male clam examined during the 1971 reproductive cycle was 22.9 mm in length, and the smallest female 31.0 mm. Both were taken in the September sample and were in the inactive phase. The largest immature clam was collected in late May and was 45.2 mm in length.

1972 Reproductive Cycle

The 1972 reproductive cycle (Figure 4) was similar to 1971 with the exception that the cycle as a whole began earlier and the active phase was of longer duration. Active female clams first appeared in November 1971 and active males in December 1971. The active phase lasted until May 1972. During the period from February until April the majority of all clams sampled of both sexes were in the active phase.

Ripe male clams first appeared in April and ripe females in May. Ripe clams of both sexes, 78% of the males and 49% of the females, were most abundant in May.

Spawning commenced in late May and peaked

in June for both males (86%) and females (65%) and then continued at a diminished rate until September.

Spent clams of both sexes were present from June through October. They were most abundant in September when 45% of the males and 72% of the females were in the spent phase.

Inactive male clams first appeared in July (10%), while inactive females first appeared in September (13%). The highest percentage of inactive clams occurred in October with 79% of the males and 70% of the females in the inactive phase.

As in 1971, the spawning cycle for most of the clams under 60 mm in length commenced about 1 mo later than the normal cycle and ended 1 mo earlier. The smallest mature clam collected was a 36.3-mm spawning male obtained in July. The smallest mature female was 38.9 mm in length and was in the active phase in March. The largest immature clam was 51.5 mm in length and was collected in March.

In 1971 spawning was quite complete in both

sexes, while in 1972 many of the females failed to spawn completely although the discharge of male sex products seemed complete.

DISCUSSION

The gonadal inclusions of male and female soft-shell clams are distinctive. Coe and Turner (1938) state that the origin of these inclusions is partly from cytoplasmic activity of follicle cells and partly from cytolysis of gametes. The fact that all immature clams in the process of sexual differentiation were found to be developing inclusions characteristic of their sex seems to verify cytoplasmic activity of the follicle cells as one origin of these inclusions. In older male clams, the method of formation of the multinucleated cells first described by Coe and Turner (1938) as pycnotic nuclei and later by Shaw (1965) as sperm balls, needs further study. If the unspawned sperm are retained by the male clam as sperm balls as reported by Shaw (1965) and as my observations indicate (Figure 1c), then perhaps cytoplasmic activity of the follicle cells is the major method by which the inclusions are formed. In female clams the exact relationship between cytolysis of unspawned ova and the formation of inclusions is not known. The single row of follicle cells which form almost immediately at the basal membrane of the alveoli in spent female clams already contain a number of inclusions (Figure 3d) before any of the unspent ova have undergone cytolysis. The origin and function of gonadal inclusions in both sexes requires further investigation.

The gametogenic cycle of the soft-shell clam at Skagit Bay is identical to that reported for clams from the east coast (Coe and Turner, 1938; Shaw, 1962, 1965; Pfitzenmeyer, 1965; Ropes and Stickney, 1965). The single spawning cycle per year, from late May to early September, is similar to that described for studies in eastern Canada (Stafford, 1912; Battle, 1932; Sullivan, 1948) and the New England area (Welch, 1953³; Ropes and Stickney, 1965).

The slight variations noted between the spawning cycles of 1971 and 1972 and the incomplete spawning of females in 1972 cannot be explained at present.

Few hermaphroditic *Mya* are reported from

other areas (Coe and Turner, 1938; Shaw, 1965). A single hermaphroditic specimen was collected at Skagit Bay (Figure 3f).

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