THE SPAWNING CYCLE OF SOFT-SHELL CLAM, *MYA ARENARIA*, IN SAN FRANCISCO BAY

SHELLY E. ROSENBLUM AND THOMAS M. NIESEN[1]

ABSTRACT

Four populations *Mya arenaria* in San Francisco Bay were studied for 1 year to determine the spawning cycle. The spawning cycle was well synchronized among the four populations. Gametogenesis had commenced by late February and spawning occurred uninterrupted from April through summer. Cessation of spawning occurred from September to October. The protracted spawning period of *M. arenaria* populations in San Francisco Bay is probably related to the long period of moderate water temperatures (March-October) which occur there. Size at first reproduction was placed at a shell length of 25 mm. Sex ratios of *M. arenaria* > 25 mm in shell length did not differ significantly from 1:1. No evidence of hermaphroditism was observed.

The soft-shell clam, *Mya arenaria*, was once popular with clam diggers in San Francisco Bay. During the early 20th century, owners of bay front property fenced off portions of the mud flats in order to exclude clam predators, thus insuring bountiful harvests of *M. arenaria* (Bonnot 1932). Today as the "trend toward the improvement of San Francisco Bay water continues,"[2] the potential for a recreational shellfishery exists again. Agencies for communities on the bay have begun to look at this potential. Recently (1982), the digging of clams in San Francisco Bay received official clearance for the first time in 30 yr.[3]

The spawning cycle of the soft-shell clam has been studied extensively on the east coast. Ropes and Stickney (1965) examined populations from the Cape Cod-New England region. They did not encounter clams in the ripe stage of gametogenesis until May, and by September spawning was over. Brousseau (1978) reported a biannual cycle of spawning for *M. arenaria* from Cape Ann, MA. The first spawning occurred between March and April and was of short duration. A separate, second spawning took place from June through July. Porter (1974) studied *M. arenaria* from populations at Skagit Bay, WA. He noted a single yearly spawning from late May to early September.

The climate of the San Francisco Bay area, and hence the seasonal water temperature fluctuations of San Francisco Bay, are much less extreme than that of the New England or Washington areas and most of the other locations from which *M. arenaria* has been examined. The question investigated in this study is whether the spawning cycle of *M. arenaria* from San Francisco Bay would differ from that of other areas reported in the literature.

MATERIALS AND METHODS

Description of Study Sites

Specimens of *M. arenaria* were collected from September 1979 through December 1980 from four sites around central San Francisco Bay (Fig. 1): 1) Candlestick Point–adjacent to the causeway leading to the Candlestick Park Stadium (lat. 37°42′32″N, long. 122°23′28″W); 2) Burlingame Lagoon–just south of San Francisco International Airport (lat. 37°35′12″N, long. 122°20′10″W); 3) Foster City–immediately north of the San Mateo Bridge, off Third Street (lat. 37°34′20″N, long. 122°23′28″W); 4) Point Isabel–north of the Golden Gate Fields race track on the eastern shore of San Francisco Bay (lat. 37°53′59″N, long. 122°23′28″W). These areas were selected because they experience annual variations in temperature and salinity (Conomos 1979), factors which are known to affect bivalve spawning cycles (Loosanoff and Davis 1951; Swan 1952; Matthiessen 1960, Pfitzenmeyer 1962; Stickney 1964). Substratum conditions were classified according to field observations; no particle size analyses were conducted.

[1]Department of Biological Sciences, San Francisco State University, 1600 Holloway Ave., San Francisco, CA 94132.

[2]Jones and Stokes Associates, Inc. 1977. San Francisco Bay shellfish: an assessment of the potential for commercial and recreational harvesting. Prepared for the Association of Bay Area Governments, 171 p.

[3]Champion, D. 1982. Clam digging OK'd on part of San Francisco Bay. San Francisco, Chronicle, 27 August 1982, p. 1.

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The Candlestick Point site has a sandy substratum and is adjacent to a broad expanse of mud flat. Temperatures and salinities at this site reflect those of the central San Francisco Bay (Conomos 1979). Clams were collected high on the sandy beach front 0.6 m above Mean Lower Low Water (MLLW) in the areas exposed as the tide begins to recede.

Burlingame Lagoon is separated from San Francisco Bay by a levee with a narrow channel connecting to the open body of the Bay (Fig. 1). Salinity and temperature can vary dramatically with heavy rains (8 to 12 ppt) (pers. obs.). The area has a heavy clay-mud substratum. The collecting site was 0.6 m above MLLW.

The Foster City site was selected because it reflects conditions more closely associated with the south bay (Conomos 1979). The substratum is sandy-mud with rocks and cobble intermixed. The area juts into the bay and is exposed to wave action and temperatures and salinities characteristic of the bay waters (Conomos 1979). It is adjacent to outflow from the tidal channel that winds through Foster City. The collecting site was 0.24 m above MLLW.

The Point Isabel site is on the mud banks of a narrow (4 m wide) tidal channel that bisects the Point Isabel promontory. The substratum is clay-mud with rock and debris intermixed. Clams were collected from 0.15 to 0.46 m above MLLW.

The depths of the collection sites (relative to MLLW) at the four locations were dictated by the presence of *M. arenaria* at each site. *Mya arenaria* signals its presence by distinct siphon holes at the surface of the substratum. After an initial excavation of each collection site to a depth of 10 cm, it became obvious that clams were present only in the specific areas clearly marked by their siphon holes. Thereafter only these areas were sampled.

Temperature and salinity were recorded with a field hydrometer (marked at ppt) and thermometer at each site each month, beginning in October 1979 and continuing through November 1980.

Collecting Methods

A gardener's hand rake and careful hand digging was used for excavating the deep-dwelling *M. arenaria*. At least 25 clams were collected from each of the four sites each month for 1 yr (with the following exceptions: 4 October–Foster City, 12 collected; 3 November–Foster City, 20 collected; 25 December–Foster City, 24 collected; 2 November–Candlestick Point, 20 collected; 24 September–Point Isabel, 20 collected; 3 November–Burlingame, 7 collected). A total of 1,625 clams were examined in this study. Clams were collected, placed in a Thermos[4] jug of cool bay water, and returned to the laboratory.

Processing Methods

Analysis of gonadal stage was made by microscopical examination of histological preparations (Ropes and Stickney 1965). The presence and development of gametes was used to infer the spawning stage or readiness of the clam. Specimens were measured for shell length to the nearest 0.1 mm. The anterior one-third of the visceral mass (Ropes and Stickney 1965) was removed, labeled, and placed in Bouin's seawater fixative. During dissection, tissues were submerged in cool seawater to prevent drying or osmotic changes. The time between collection and preservation was under 3 h to prevent any gonadal changes.

The tissues were subjected to standard histological procedures (dehydrated in alcohol and embedded in paraffin). Embedded tissues were thin sectioned (5 μ) on a rotary microtome. Sections were mounted on glass slides, stained with Harris' hematoxylin and eosin, and examined using standard light microscopy.

Each slide of gonadal tissue was studied to determine the presence of male or female gametes and the condition of the gonadal tissues. This allowed clams to be placed into one of the five classes of spawning readiness (inactive, active, ripe, partially spawned, spent) employed and described by Ropes and Stickney (1965) for *M. arenaria*.

Categories of Spawning Readiness (adapted from Ropes and Stickney 1965)

Female Gonads

INACTIVE PHASE.–Ropes and Stickney (1965) used the term "inactive" to describe this phase. Brousseau (1978) preferred the term "indifferent" because cellular activity is continuing although no gametogenic activity is obvious. The term "inactive" is employed here and refers to individuals which are not seen to be producing gametes whether due to seasonal quiescence or immaturity. Thus in this research which presents pooled male and female data, the "inactive phase" may contain sexually undifferentiated individuals along with inactive animals clearly recognizable as male and female.

Females in the inactive phase exhibit small oocytes

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

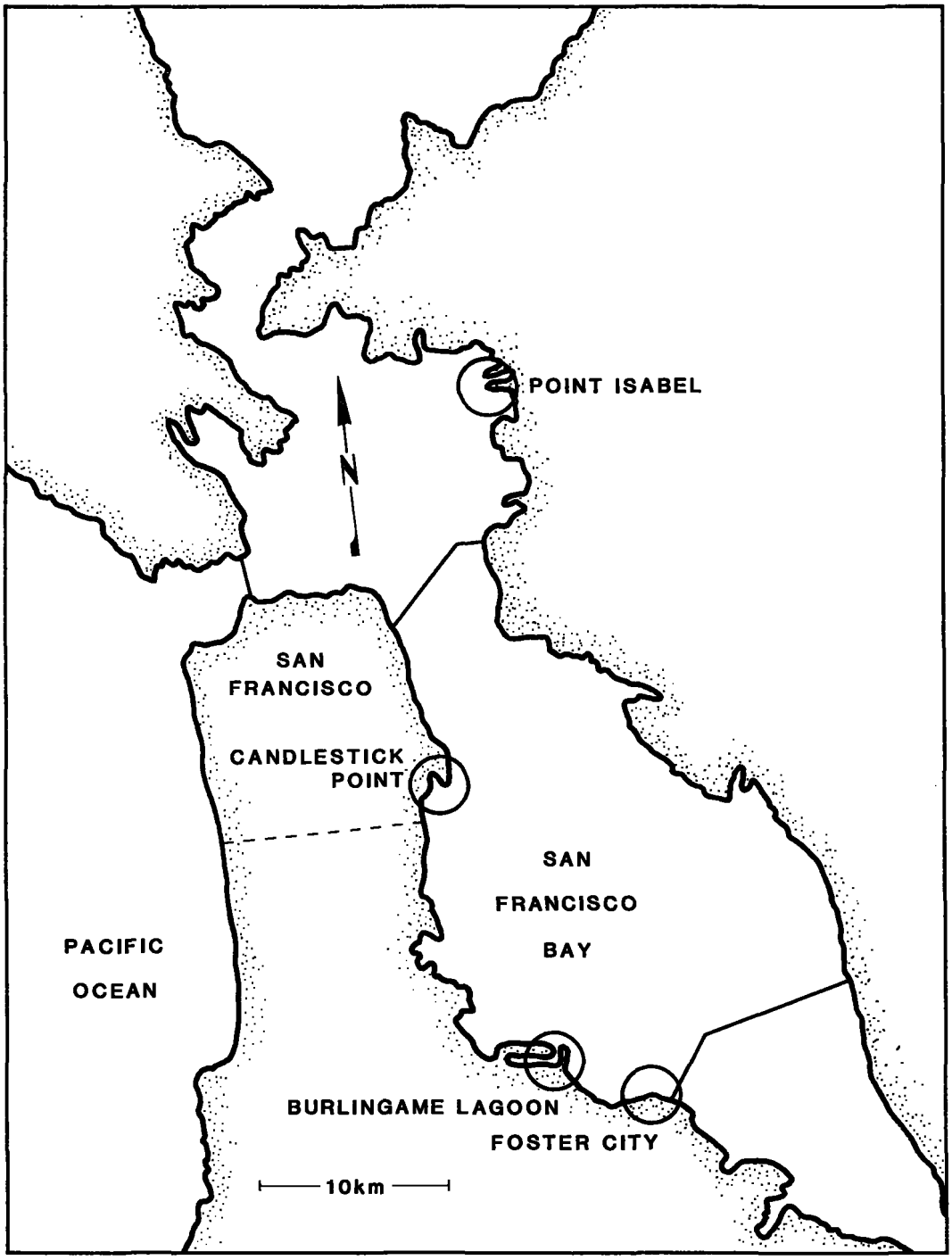

FIGURE 1.–Study sites on San Francisco Bay indicated by circles.

at the periphery of alveoli. Follicle cells completely imbed the oocytes and may fill the lumina of alveoli.

ACTIVE PHASE.–Enlarging oocytes grow between follicle cells towards the center of alveoli. Oocytes are irregular in shape but are attached to the wall of the alveolus by broad cytoplasmic bases.

RIPE PHASE.–In the ripe phase, oocytes appear as round cells in the lumina of the alveoli as if free of attachment to the basal membrane, yet they may be attached by a very slender stalk. The large oocytes fill the lumina of the alveoli and are usually more numerous than less developed oocytes.

PARTIALLY SPAWNED PHASE.–Gonadal tissues contain a few ripe oocytes. Small oocytes are imbedded in follicle cells at the periphery of an empty alveolus. Many alveoli are devoid of ripe oocytes.

SPENT PHASE.–Very few ripe oocytes are present, usually darkly staining with obscure nuclei. Numerous spherical droplets of lipoids and other products of cytolysis are characteristic. The spent phase progresses into the inactive phase.

Male Gonads

INACTIVE PHASE.–During the inactive phase, male tissues contain products of atypical spermatogenesis (Coe and Turner 1938). Tissues appear quite active, yet this activity will not result in viable male gametes. Pycnotic cells and multinucleated cells appear in the follicles. A few spermatogonia and primary spermatocytes may be seen at the periphery of alveoli while aberrant cells can be seen throughout the alveoli. As indicated in the description of the inactive phase for female gonads, this phase category is expanded to include sexually undifferentiated individuals along with pooled male and female inactive phase animals.

ACTIVE PHASE.–Proliferating primary spermatocytes exist at the basal membrane of the alveoli. These are small and uniformly sized cells which are similar to the earliest oocytes. They can be seen growing between follicle cells, extending toward the centers of the alveoli. Early stages of meiosis occur at the periphery of the alveoli, while later spermatids occur at the alveolar centers where they later form a distinct mass. Follicle cells eventually disappear.

RIPE PHASE.–Masses of spermatozoa arranged in more or less radial columns exist in rounded alveoli with tails oriented toward the center.

PARTIALLY SPAWNED PHASE.–Relatively few spermatozoa can be seen. Follicle cells start to refill the alveoli. Some pycnotic cells occur.

SPENT PHASE.–Spent male tissues contain no or very few spermatozoa in the central alveolar area. Numerous follicle cells with multinucleated cells and pycnotic cells from atypical spermatogenic activities surround small groups of spermatozoa. Tissues lack cells in the active phase of spermatogenesis. The spent phase progresses into the inactive phase.

RESULTS

Of the 1,674 clams examined in this study, 1,361 were distinguishable as male or female; the remaining 313 were indistinguishable as to sex. The male: female ratio (670:691) did not vary significantly from a 1:1 sex ratio ($P = 0.25$; $\chi^2 = 0.294$). No hermaphrodites were found. The possibility of asynchrony between males and females was considered. Separate histograms were prepared for the male and female data. Upon visual inspection the histograms showed no clear pattern of asynchrony between the sexes. As no discernable asynchrony was apparent, further analysis was considered unnecessary. The data for both sexes were pooled and are reported here.

The clams sampled in this study ranged from 15 to 88 mm in shell length. Of the 28 clams < 25 mm sampled, only a single 15 mm female in the active stage could be distinguished, the remainder showing no gonadal activity of any kind, sex being indistinguishable.

No consistent relationship between spawning condition and size could be discerned for clams over 25 mm in length. Correlation coefficients between size and spawning condition were calculated and subjected to a *t*-test, but the results were inconclusive. Clams of all sizes occurred in the various spawning categories throughout the spawning season. Mean shell lengths varied from 44.9 to 61.6 mm among the four populations studied (Fig. 2).

Candlestick Point

Sampling began in September 1979 and it was apparent that spawning was ending at that time. While 15% of *M. arenaria* were still ripe, 65% were inactive and the remaining 20% partially spawned or spent (Fig. 3). By late November, 95% of the clams

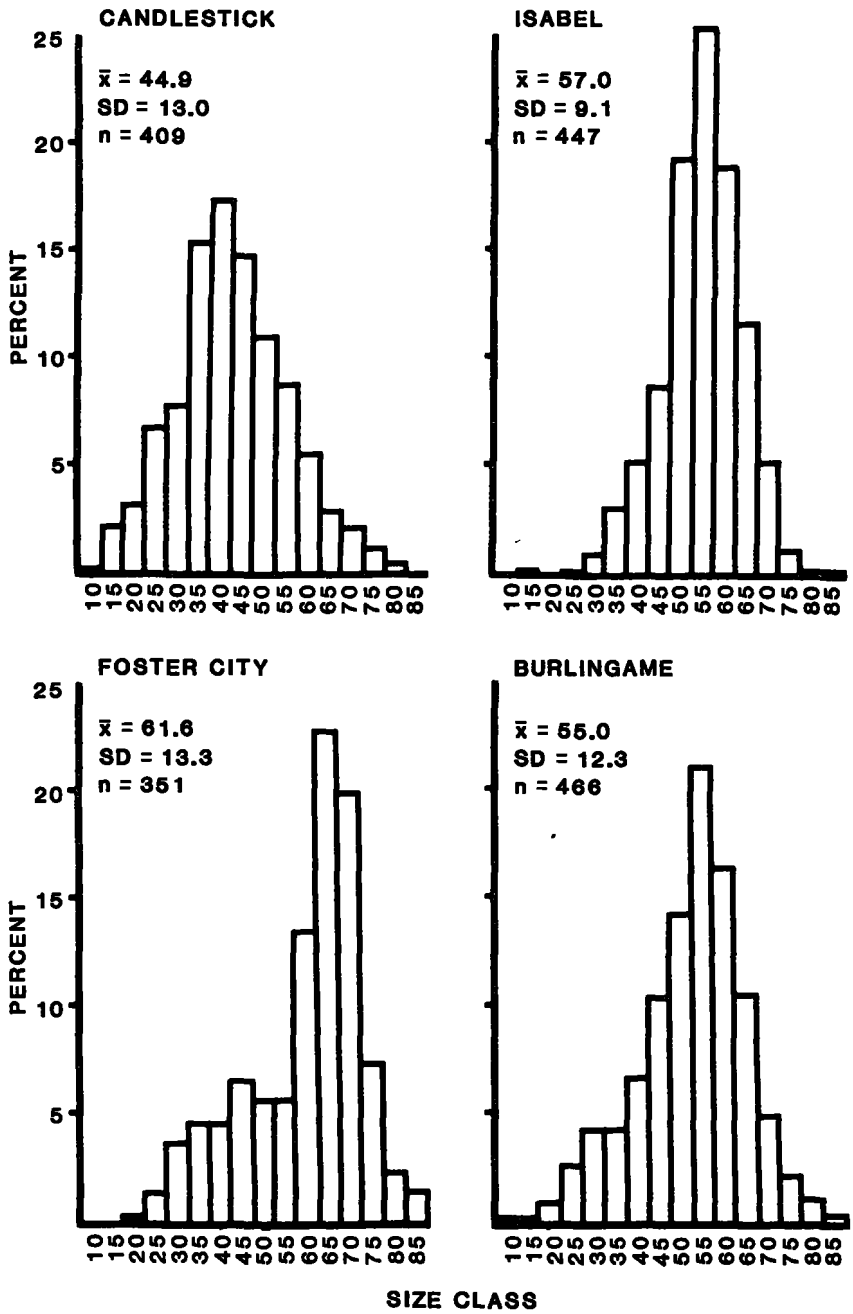

FIGURE 2. – Size-frequency histograms for the four populations studied. Size classes are (in mm) 10.0-14.9, 15.0-19.9, etc.

sampled were inactive and 5% still showed a few mature gametes which would probably have been resorbed. All individuals were inactive by the end of December 1979.

The first sign of gonadal activity appeared at the end of January 1980; by March, 82.1% of the clams sampled were active. In April, all individuals were either ripe or spawning. Peak spawning occurred

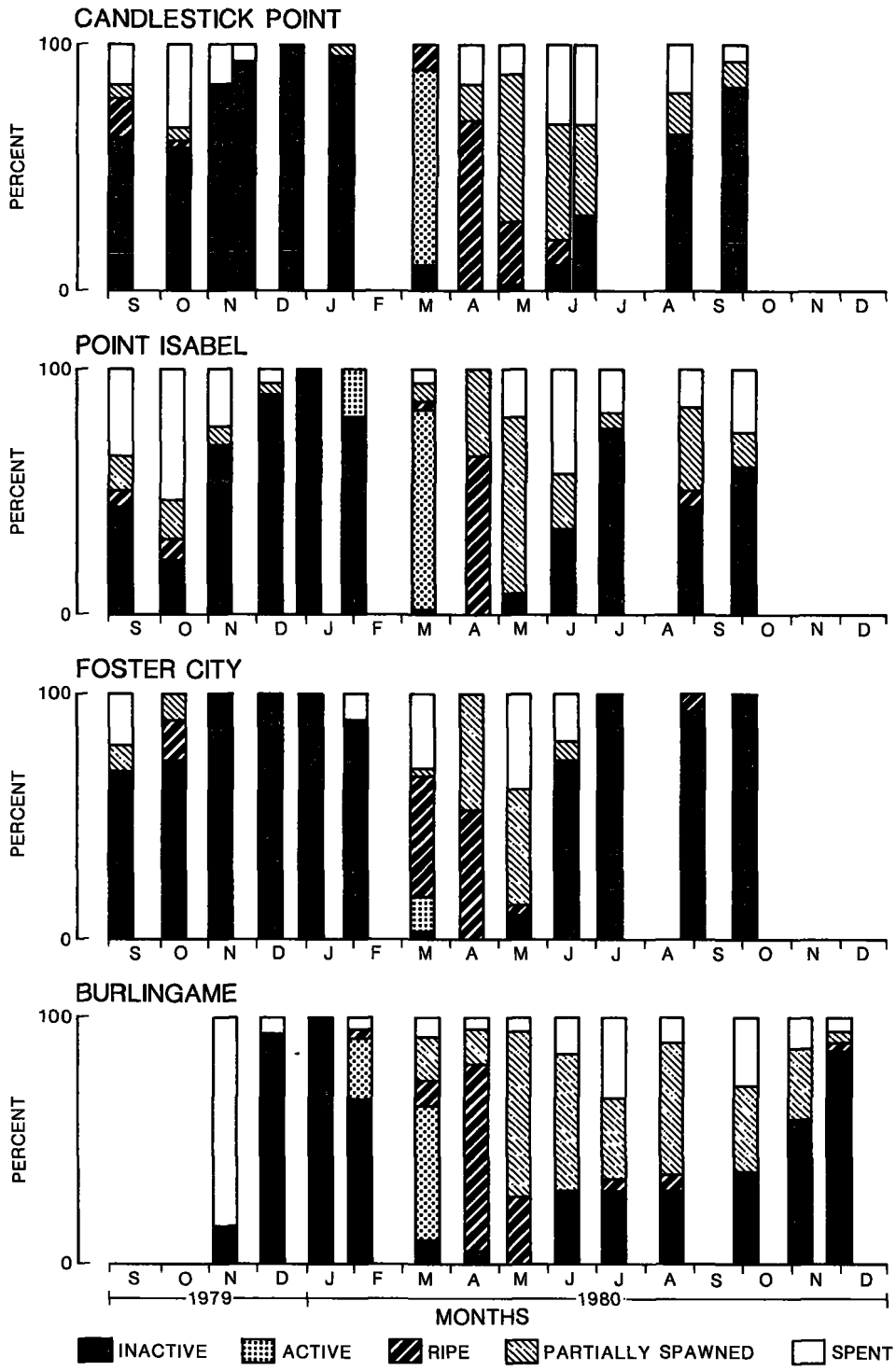

FIGURE 3.—Percentage of the clams sampled that were in each of the five categories of spawning readiness. Male and female data are pooled.

during May and June. By the end of June, the sample was roughly divided into thirds among the partially spawned, spent, and inactive stages. Some spawning could still be seen through the end of August, but by late September 85% were inactive, 10% partially spawned, and 5% spent.

Foster City

September-October 1979 marked the end of the Foster City population spawning, with most clams (70%) being inactive during this period (Fig. 3). From early November through the end of December 1979, no activity could be found. The late January 1980 sample showed a 90% active:10% spent ratio with no intermediate stages represented. It is unclear whether this indicated a rapid maturing and spawning of a few precocious individuals or an overwintering of residual gametes. By mid-March, every stage was represented, most (50%) being in the ripe stage. Peak spawning extended from the beginning of April through May, with a complete maturation-spawning season extending from late February through May. From July to late September no appreciable gonadal activity could be discerned. This lack of activity from mid- to late summer distinguished the Foster City population by its short spawning season relative to other populations (Fig. 3).

Burlingame Lagoon

Sampling of the Burlingame Lagoon population did not begin until November 1979. At the time 85% of the clams sampled were spent and only 15% were inactive (Fig. 3). This suggests a protracted spawning in 1979, similar to that which was seen in 1980. By December all but 5% were inactive and by 1 January 1980 all were inactive. Gonadal activity appeared again by the end of January 1980. Peak spawning occurred during May and June; however, spawning continued well into September and October with a full 30% of the clams of each sample being in the partially spawned stage. The Burlingame Lagoon population had the longest spawning season of the populations examined.

Point Isabel

Sampling of the Point Isabel population began in September 1979. The September and October samples still contained ripe individuals (< 10%), but most of the clams sampled were spent or inactive. By November, 70% of the clams sampled were inactive and by the end of December all were inactive (Fig. 3). The 1979 spawning season had ended for the Point Isabel population by early November.

Gonadal activity had resumed by late January. By March, 80% of the clams sampled were active. Only ripe and partially spawned individuals could be found in mid-April, and by May inactive individuals were being found (10%). Peak spawning occurred during May. Spawning continued through June and by July almost 80% were inactive and 20% partially spawned or spent. Spawning appeared to be over; however, the August sample contained almost 35% partially spawned and 5% ripe individuals. It is tempting to suggest a possible second spawning in August, but the May and June samples lacked active or ripe individuals, which suggest the August observation be attributed to sampling error. Spawning was still occurring in late September, as 15% were still in the partially spawned stage. At this time, however, 60% were inactive and 25% spent.

The four study sites showed similar trends (Fig. 4) in temperature and salinity. Temperatures fell from November through mid-January and rose from mid-January through the beginning of April and then stabilized. Temperature then climbed again from mid-May through July. The July-September temperatures were steadier at the Foster City and Burlingame sites than at Point Isabel or Candlestick Point, where they dropped markedly during this period. Salinity followed a similar trend, falling during the late winter months, and rising during spring and summer (Fig. 4). Salinity ranged from 8 to 33 ppt and temperature from 12° to 23°C.

DISCUSSION

The spawning cycle of *M. arenaria* in San Francisco Bay in 1980 was an extended one. Gametogenesis had begun by late January for three of the four populations sampled (Candlestick Point, Burlingame Lagoon, and Point Isabel), and by mid-March all five stages of gonadal development were represented in the Burlingame Lagoon, Point Isabel, and Foster City populations. Spawning had begun at all four sites by April; over 20% of the individuals from each sample were in the partially spawned or spent stages. The number of clams in these spawning stages reached a maximum during May and June 1980. Spawning continued through September and October and then ceased.

Only a single clam < 25 mm in length was found to have active gonads. This suggests that 25 mm might be generally recognized as the size at first reproduction for San Francisco Bay *M. arenaria.*

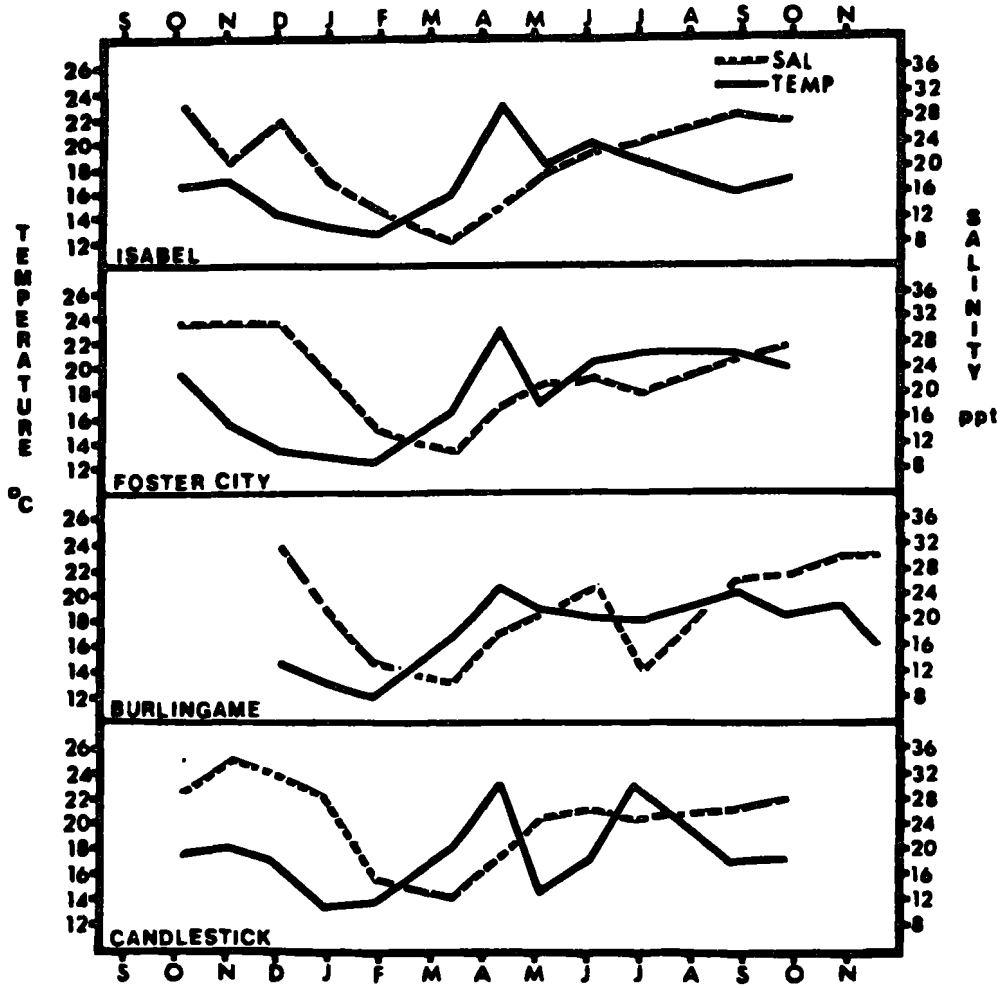

FIGURE 4.—Temperature and salinity variations during the collection period for the four collection sites, 1979 and 1980.

Although no growth or age measurements were performed in this study, the 25 mm shell length indicating a lower limit to sexual maturity corresponds to the east coast *M. arenaria* found to be late in their first year (Brousseau 1979).

Of the 313 clams that were indistinguishable as to sex, only 28 were < 25 mm in length, therefore we cannot attribute this lack of discernable sex to immaturity. Furthermore, clams of indeterminate sex were seen only during the fall and winter months (September-March) when most clams were found to be in the inactive stage. During the period of March-September or spring-fall when the active, ripe, partially spawned, and spent stages were well represented, all clams could easily be determined to be male or female. The difference between inactive male and female gonads is obvious and was seen in many clams, yet many clams which were larger than 25 mm in length and should have been sexually mature showed no signs of sexually distinguishable tissue at all. No evidence of even small oocytes or atypical spermatogenesis was seen in these clams. For the sake of simplicity, these clams were placed in the inactive stage. Perhaps this condition was a kind of "gonadal exhaustion" due to the prolonged spawning period.

The four study populations were dominated by clams ranging from 40 to 75 mm in length (Fig. 2). This size range corresponds to the 1.5 to 4.0 year classes determined by Brousseau (1979) for *M. arenaria* from Gloucester, MA. While total correspondence in growth rates between Massachusetts

and San Francisco Bay populations cannot be assumed, the age classes can be used as a first estimate of approximate age with size.

Studies of the spawning cycle of soft-shell clams from the east and west coasts of the United States reveal both similarities and differences in spawning pattern. Spawning on both coasts begins in early spring as the water warms from the lower winter temperatures. The majority of east coast populations studied show two separate spawnings each year, while populations studied on the west coast show a single more protracted spawning. Differences in the length of spawning and the number of separate spawning episodes are probably partially related to the phenology of water temperature change and the difference in the range of water temperatures that occur on either coast.

Mya arenaria in San Francisco Bay, studied during the 1979-80 season, began ripening earlier than *M. arenaria* of the New England region studied previously. Ropes and Stickney (1965) encountered active clams in eastern Maine by late January; however, ripe clams were not discovered until mid-May, and at that time none appeared to have spawned. Clams from their Booth Bay Harbor samples showed the earliest ripening, which was in April and May; by September spawning was over.

Brousseau (1978) reported a biannual cycle of spawning for *M. arenaria* from Cape Ann, MA. The first spawning at Cape Ann occurred as early as that in San Francisco Bay (March); however, it was of short duration, being over by April. A separate second spawning took place during June through July. Brousseau's figures indicate water temperatures began to rise from a low of 1°C around Cape Ann as early as mid-February, but did not rise above 10°C before May. It is possible that the increase in temperature triggered an early spawning, but the continuing, relatively cold temperature prevented an adequate build-up of mature gametes to sustain a prolonged spawning. Once spawning had taken place, the clams may have had to undergo another period of gametogenesis prior to a second spawning. Brousseau (1978, page 159) stated, "The presence of cytolyzed unspawned gametes in the summer samples suggested that the same individuals had also been ripe earlier in the year. Thus the observed spawning pattern was due to repeated spawning by the same individuals rather than asynchronous spawning of individuals within the population."

Pfitzenmeyer (1962) also reported two annual periods of spawning in *M. arenaria* at Solomons, MD. He noted that "The first umbone larvae of the year usually were found in May after the surface waters rise above 15°C or a mean temperature of 16.7°C." Salinities which remained constant throughout the spring remained near 10 ppt. This corresponds to the March temperature-salinity patterns in San Francisco Bay. During March, San Francisco clams were just beginning to spawn. Pfitzenmeyer also noted the disappearance of larvae from the Maryland waters as the temperature rose above a mean of 21.4°C. The larvae did not reappear until temperatures had fallen below this point. He concluded an optimal temperature range exists during which spawning may occur. In San Francisco Bay, temperatures rose to or above 21°C only in the following instances: Foster City–11 April - 23°C, 2 July - 21°C, 25 August - 21°C; Candlestick Point–9 April - 23°C, 30 June - 23°C; Point Isabel–10 April - 23°C (Fig. 4).

Porter (1974) noted a single yearly spawning from late May to early September among *M. arenaria* from Skagit Bay, WA. This is a shorter spawning season than seen among San Francisco Bay *M. arenaria* and may be a result of lower temperatures (4.8°-15.7°C) encountered in Washington.

Simel[5] reported a single spawning from late March through April for soft-shell clams from Humboldt Bay, CA. Generally, this more northerly part of California has a cooler climate than the San Francisco Bay area. Simel indicated that the later stages of gametogenesis corresponded with a peak in the phytoplankton abundance.

Studies of the spawning cycles of *M. arenaria* from the east and west coasts of the United States suggests a pattern of spawning behavior. Spawning begins as the water temperature rises in the spring. Pfitzenmeyer's (1962) work suggests *M. arenaria*'s optimal spawning range falls between 15° and 21°C. Differences between the spawning cycle of *M. arenaria* from San Francisco Bay and that of *M. arenaria* from New England, Canada, Washington, and northern California may be explained as the logical result of the different seasonal warming patterns and extremes encountered in the different areas. San Francisco Bay does not cool to the same temperatures as the other areas and has a much longer period of moderate water temperatures, extending from late March through summer and into September and October. Consequently, *M. arenaria*'s spawning season is equally protracted in San Francisco Bay.

[5]N. Simel, Humboldt State University, Arcata, CA 94542, pers. commun. 1982.

ACKNOWLEDGMENTS

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