LIFE HISTORY STUDIES OF THE SANDWORM, *NEREIS VIRENS* SARS, IN THE SHEEPSCOT ESTUARY, MAINE

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ABSTRACT

Little information is available on the life history of the sandworm, *Nereis virens*, in Maine despite their commercial importance over more than 40 years. Life history studies were performed in a flat along the Sheepscot River at Wiscasset, Maine, which was closed to commercial digging. Salinity varied between 17 and 29‰ at the surface and between 24 and 29‰ on the bottom, and temperature varied between −1° and 15°C at the surface and −1° and 14°C on the bottom. The proportions of potential male and female spawners changed with size; for worms <30 cm, the proportions were equal whereas a preponderance of females existed for worms >30 cm. Thirty percent of the largest worms displayed no sign of sexual development. Single eggs of 50 μ diameter were first observed in the coelom from October to November. These eggs entered a rapid growth phase between August and December and attained a maximum diameter of from 183 μ (1967) to 194 μ (1968) at time of spawning during April and May. Maturation could take as long as 18-20 months or as little as 12 months. The numbers of eggs laid by sandworms were found to vary between 0.05 (16 cm worm) and 1.3 million eggs (54 cm worm). The onset of spawning occurred when the surface water temperature was between 7.0°C (1968) and 8.1°C (1967) and when the bottom water temperature was between 6.7°C (1968) and 7.6°C (1967). During both years, spawning occurred 4 days after full moon during the period of spring tides. Scuba observations revealed that male spawners emerged from the mud about 3 hours after high water. At the peak of spawning, densities of epitokes may reach 1 worm/m^2. Male spawners are readily consumed by herring gulls, *Larus argentatus*.

The sandworm, *Nereis virens* Sars, commonly occurs on the Atlantic coast from Virginia northward to the Arctic region. It is also found in Iceland, Norway, Ireland, and the North Sea to France (Pettibone 1963).

Nereis virens is known to inhabit coarse and fine muddy sand, mussel beds, and the roots of decaying marsh and eelgrass (Pettibone 1963). The sandworm population in the Sheepscot River study area at Wiscasset, Maine (lat. 44°N, long. 70°40′W), inhabits a gray, silty clay which is moderately burrowed and contains shell fragments, mica flakes, and 2% organic carbon (Reynolds et al. 1975[2]). The mean tidal amplitude in this region is 2.9 m.

Ecologically, sandworms occupy an important position in the food web of other invertebrates, fish, and shorebirds. They have been harvested commercially for bait along the Maine coast for more than 40 years, with landings of 26.9-38.1 million worms/yr and a landed value of $0.5-1.1 million reported between 1966 and 1980 (NMFS 1966-80).

Previous research on Maine sandworms included studies on digging (Ganaros 1951[3]) and dispersion (Gustafson 1953; Dean 1978). Although intensive harvesting qualifies the sandworm for management considerations, only reports by Glidden (1951)[4] and Dow and Creaser (1970) contain life history information pertinent to management of sandworm populations in Maine. The present study was undertaken to provide life history information for a sandworm population in the Sheepscot Estuary at Wiscasset, Maine. It also includes some information on subjects not previously investigated or which differ from findings reported from other geographical locations.

Other studies on the life history and reproduction of *Nereis virens* include Brafield and Chapman (1967) and Bass and Brafield (1972) in the Thames Estuary at Southend, England; Sveshnikov (1955) in Rugozerski Bay near the White Sea,

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[2]Reynolds, L., J. Bowman, and E. Kelly. 1975. Unpublished summary of sediment size, x-radiography, chemistry, and mass physical properties of six cores and two grabs from Maine. U.S. Naval Oceanographic Office, Washington, D.C.

[3]Ganaros, A. 1951. Commercial worm digging. Bull. Dep. Sea Shore Fish., Augusta, Maine, 6 p.

[4]Glidden, P. E. 1951. Three commercially important polychaete marine worms from Maine. Rep. Dep. Sea Shore Fish., Augusta, Maine, 25 p.

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Russia; and Snow and Marsden (1974) at Brandy Cove, St. Andrews, New Brunswick, Canada.

Materials and Methods

All sandworms were collected in the vicinity of a small intertidal mud flat at Wiscasset, Maine, closed to commercial digging. Within this area, a section running parallel to the low-water mark and measuring 91 m × 24 m was used for experimental purposes. Differences in tidal height between the upper and lower extremities of this experimental area were about 22 cm. Monthly, three 1 m^2 sample plots were randomly chosen and dug within the experimental site. The sampling device consisted of a 1 m^2 frame with deep walls (45 cm) that could be pushed into the mud to prevent escape. Within each plot, the surface ooze was removed with a dustpan to a depth of 2-3 cm and deposited within a square framed receptacle constructed of 1 mm mesh fiberglass screen. The receptacle was then partially immersed in the river and carefully agitated to remove sediment. The remaining debris and worms were poured into a plastic container and transported to the laboratory. Small portions of debris, together with seawater, were deposited in dissecting trays and dispersed with a needle probe. The contents were thoroughly searched and all small sandworms, swimming or hiding among the debris, were removed with forceps. Clumps of deeper and firmer mud were removed from the sampling device in the field to the maximum depth of burrowing activity (about 30 cm) and carefully broken by hand to remove the larger worms intact. These worms were also transported to the laboratory in plastic buckets.

All sandworms were acclimated to high salinity water (about 32‰) at the laboratory prior to immersion in anesthetic (7.5% $MgCl_2$). Lengths were obtained using a V-shaped measuring trough containing ample anesthetic to cover the worms. Coelomic fluid was withdrawn with the aid of capillary pipettes, and sex was determined by microscopic examination of the contents. Egg diameters were measured with an ocular micrometer and without a cover slip. Usually 10 eggs were measured from each worm. The relationship of sandworm length to numbers of eggs laid was corrected for transformation bias following the methodology of Bradu and Mundlak (1970).

Worms used in the study to determine the percent of mature males and females and immature females in each length increment were obtained during February (prior to spawning) from pooled samples dug independently of the regular monthly sample. The distinction between mature and immature females was made after examining eggs in the coelomic fluid; large eggs from mature worms would be spawned in April or May, and small eggs would be spawned approximately 1 yr later. We were unable to make a distinction between mature and immature males.

Sandworms designated "nonspawners" include worms of all sizes that have not spawned and whose coelomic contents present no clue about sexuality. "Spent" worms include both males and females that have spawned and are deteriorating and approaching death.

Female sandworms used for egg counts were anesthetized, measured, and preserved. The worms were then split lengthwise and washed thoroughly to remove as many eggs as possible. Next, the body was chopped into 1 cm pieces, immersed in seawater, and stirred magnetically. After three or four changes of water, most eggs were dislodged. Egg samples were diluted in 0.1-2.7 l seawater, depending upon size of the worm and numbers of eggs present. Two 1 ml aliquots were withdrawn from this mixture during agitation, placed on Sedgwick-Rafter[5] counting cells, and the number of eggs counted under the 10× objective. The mean value was then multi-

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

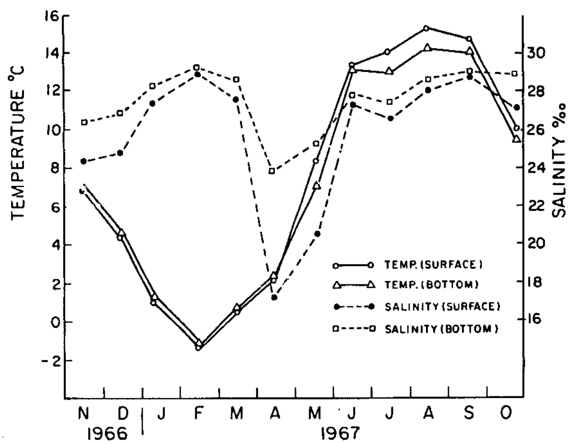

FIGURE 1.—Summary of temperature and salinity data collected from the Sheepscot River near the Wiscasset closed area between November 1966 and October 1967.

plied by the dilution factor to obtain the final egg count.

Hydrographic data were usually obtained shortly after the collection of worm samples. Mean monthly water temperature was calculated from 25 thermister recordings collected in situ at 30-min intervals at hydrographic stations occupied for 12 h. Mud temperature records were collected in situ by digging a shallow hole in the mud flat and inserting a thermometer horizontally at a depth of about 10 cm. Water samples used in salinity analysis were obtained using a 1 l water sampler. Water samples of 5 ml were analyzed for salinity by the Knudsen method.

Sandworms were captured during spawning using scuba techniques or dip nets.

RESULTS

Salinity and Temperature of the Study Area

The salinity and temperature regime of the river water at the study area during the period November 1966-October 1967 is summarized in Figure 1. During these studies, surface salinity varied between 17 and 29‰, surface temperature between −1° and 15°C, bottom salinity between 24 and 29‰, and bottom temperature between −1° and 14°C.

Length Frequency

Preliminary digging in the Wiscasset closed area indicated that sandworms were most abundant in the region of the low-water mark. Within this region, significant variations in both abundance and size were recorded for three randomly selected 1 m^2 plots dug from one tidal height during one time period. Because of this variation, digging more than 1 sample plot/mo was desirable. We elected to dig and combine the results of 3 randomly selected plots/mo because the combined results produced fairly consistent length-frequency trends between months. Considerable breakage of all sizes of sandworms was encountered during handling and processing. During agitation, the presence of sharp shells and debris in the upper layer of organic ooze resulted in additional breakage of juvenile sandworms prevalent there. Some unavoidable bias has therefore resulted in the numbers of juvenile worms reported. Length-frequency results for all whole worms collected during August, September, and October are shown in Figure 2. Sandworms captured varied in length between <1 and 31 cm. Numbers of whole individuals captured during these months varied between 546 and 701. Figure 2 indicates some recruitment of small individuals into the sampled population during the summer. Additional length-frequency information collected during this study is presented in Creaser and Clifford (1981)[6].

The August-October 1967 length-frequency data, when combined to produce sufficient number, was analyzed by the method of Harding (1949), as explained by Cassie (1950), to determine the number of assumed age modes. Although five assumed modes and linear growth were detected by this analysis, there is considerable overlap in length at age; the results are therefore questionable until they can be verified against other aging techniques.

[6]Creaser, E. P., and D. A. Clifford. 1981. Life history studies of the sandworm *Nereis virens* Sars, in the Sheepscot Estuary, Maine. Maine Department Marine Resources Research Laboratory, Res. Ref. Doc. 81/16, 37 p.

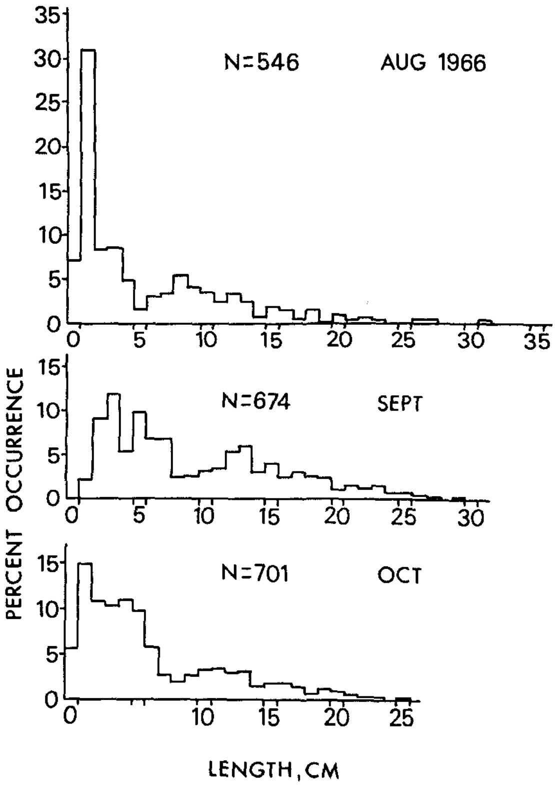

FIGURE 2.—Monthly length frequency distributions for three combined plots dug from the Wiscasset closed area.

Proportions of male, female, and nonspawning sandworms of various lengths are shown in Figure 3. There is an increase in numbers of mature males and females with increasing size. Worms >30 cm show a preponderance of mature females over mature males. More than 30% of the largest worms showed no sign of sexual development.

Oocyte Development

The results of oocyte growth studies are presented in Figure 4A, and water temperatures associated with these data are shown in Figure 4B. Eggs of about 50 μ were first observed in the coelom in October-November. Diameter increased from 80 to 160 μ during the rapid-growth phase which occurred between August and December. Prior to spawning, the rate of egg growth decreased. Maximum mean egg diameters obtained were 183 μ (1967) and 194 μ (1968). A Student's t-test revealed a significant difference between these mean diameters ($t = 4.65910$; $P<0.05$; 14 df). Spawning occurred in April and May during a 4-5 wk period, and few egg-bearing worms were found after the beginning of June. The maturation of gametes required 18-20 mo, or as little as 12 mo, depending upon when the eggs were ovulated into the coelom. Annual spawning, together with a maximum development period of 18-20 mo, accounted for the presence of two general egg sizes in sandworms inspected between October-November and April-May. Eggs approaching spawning size varied the least in diameter (the smallest standard deviation) (see Figure 4A). During the period of rapid egg growth, both mud and bottom river temperatures were decreasing (see Figure 4B).

Numbers of Eggs Laid

The numbers of eggs laid by sandworms of various lengths are recorded in Figure 5. The range varies between about 0.05 and 1.3 million eggs for worm lengths of 16 and 54 cm, respectively.

Environmental Conditions During Spawning

Spawning first occurred in the Wiscasset region on 28 April 1967 and 17 April 1968. A summary of hydrographic conditions associated with spawning on 2 May 1967 and 19 April 1968 is presented in Table 1. Table 1 shows that mean surface-water temperatures of 7.0°C (1968) and 8.1°C (1967) and bottom water temperatures of 6.7°C (1968) and 7.6°C (1967) were associated with the onset of spawning. During both years, initial activity in the Wiscasset area occurred 4 d after full moon during the period of spring tides. The stage of the tide during which spawning activity occurs was investigated on 23 April 1968, using scuba techniques. During a series of six dives beginning just after high water (08:28

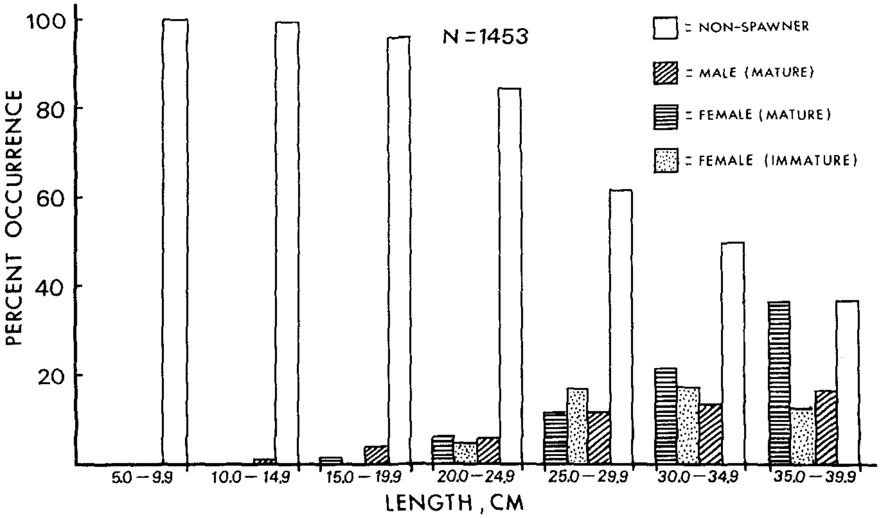

FIGURE 3.—Proportions of male, female, and nonspawning sandworms of various lengths collected prior to spawning during February 1967.

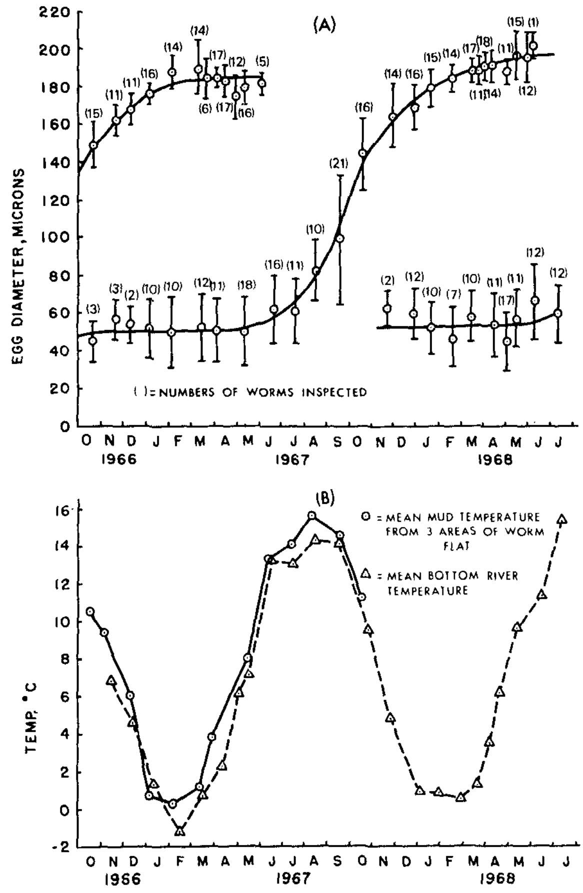

FIGURE 4.—(A) Oocyte growth occurring simultaneously in two groups of Wiscasset sandworms at different stages of maturation (lines fitted by eye). (B) Monthly mean mud and bottom water temperature from the Sheepscot River at Wiscasset.

TABLE 1.—Summary of temperature and salinity associated with sandworms spawning at Wiscasset, Maine, on 2 May 1967 and 19 April 1968.

	2 May 1967 1030-1430 h			19 April 1968 0730-1200 h		
	Temp. (°C)	Salinity (‰)	*N*	Temp. (°C)	Salinity (‰)	*N*
Surface						
$\bar{x} \pm 1$ SE	8.1±0.3	19.98± 0.38	9	7.0±0.2	23.55± 0.25	10
Range	6.8–9.1	18.51–21.58	9	5.8–7.8	22.75–25.08	10
Bottom						
$\bar{x} \pm 1$ SE	7.6±0.2	23.18± 0.43	9	6.7±0.2	25.34± 0.26	10
Range	6.6–8.4	21.24–25.32	9	5.3–8.0	23.80–26.09	10

EST) and ending just before low water (14:34 EST), no spawning worms were observed until about 3 h after high water (Table 2). Although the possible role of water temperature in initiating spawning cannot be completely eliminated, the tidal-condition results in Table 2 are consistent with numerous visual observations on spawning activity in the Wiscasset area over many years.

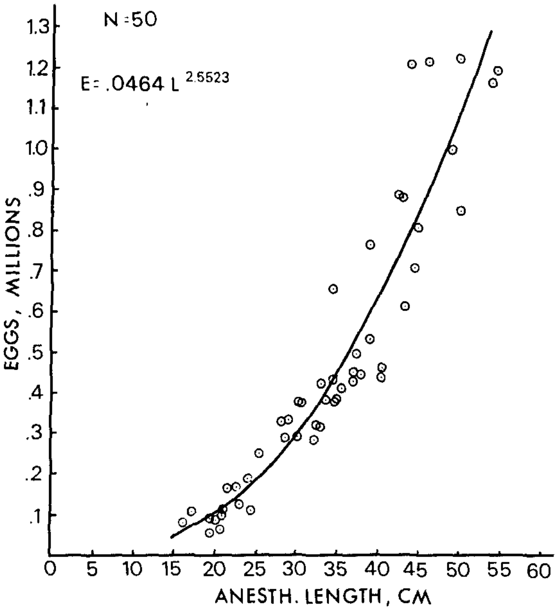

FIGURE 5.—Number of eggs produced as a function of sandworm length.

Spawning Characteristics

Nearly all sandworms captured during spawning were males. Females were only rarely encountered in the latter part of the spawning season. Scuba observations revealed that male sandworms emerge from the mud anterior-end

TABLE 2.—Data collected during scuba investigation of tidal conditions between high water and low water at onset of spawning activity on 23 April 1968.

Time of dive	Tide height (m)	Temperature (°C) Surface	Temperature (°C) Bottom	Salinity (‰) Surface	Salinity (‰) Bottom	No. worms collected ♂	No. worms collected ♀
(High water 0828 h EST)							
0910-0930	3.4	7.3	6.1	24.24	26.64	0	0
1010-1028	2.9	7.6	6.5	25.12	26.24	0	0
1103-1123	2.1	8.1	7.7	24.87	24.74	0	0
1200-1222	1.2	8.8	8.2	24.61	24.69	127	0
1305-1335	0.6	9.4	9.1	25.16	25.26	118	0
1400-1410	0.5	11.2	10.4	24.72	24.98	96	0
(Low water 1434 h EST)							

first. These free-swimming spawners displayed two characteristic types of swimming behavior: 1) Swimming more or less in a straight path (with occasional tumbling and back swimming) with typical lateral undulations of the body, and 2) swimming in circles typically 10-15 cm in diameter. Spawning worms appeared to be distributed randomly over the flats. During peak spawning, the density of worms observed swimming near the surface of the mud was about 1 worm/m^2. All male spawners collected in the Wiscasset area were definitely epitokous individuals, having undergone morphological changes. Mature female sandworms dug from the flats were typically dark green, males that had just emerged to spawn were lighter green, and males that were "spawned out" but still swimming were a dark, bluish green. Some male sandworms may spawn during more than one tide. Numerous male sandworms were observed burrowing back into the flats during scuba dives. None, however, burrowed deeply into the mud. The reproductive strategy of the sandworm qualifies it as a "monotelic" species, i.e., it breeds once in its lifetime, all gametes are released in one or two large batches, and the spent animals die immediately or shortly afterwards without developing more gametes (Clark cited in Stancyk 1979). Some nearly "spent" individuals were observed to contain large numbers of a parameciumlike ciliate.

Predation

During receding tides in the Wiscasset vicinity during April, an increasing number of herring gulls, *Larus argentatus* Pontoppidan, circling the flats, anticipated the ensuing spawning activity of *Nereis virens*. At the height of spawning, thousands of gulls could be observed feeding on male spawners.

DISCUSSION AND CONCLUSIONS

Salinity and Temperature of the Sandworm Habitat

The salinity and temperature regime encountered by *Nereis virens* in other geographical areas is incomplete. Brafield (1968)[7] indicated that water and interstitial salinity encountered by the Southend, England, sandworm population varied between 28-32‰ and 27.5-31.5‰, and water temperature varied between 3.2°C (January) and 22.5°C (August). The Wiscasset population is subjected to more estuarine salinity conditions and cooler water temperatures than in England. The temperatures recorded for Brandy Cove, New Brunswick, by Snow (1972) are very similar to the temperatures recorded in Figures 1 and 4B.

Length-Related Observations

The concave nature of the length-frequency data presented in Figure 2 is consistent with a highly variable recruitment pattern resulting from larval mortality and intense predation soon after settlement (Warwick cited in Coull 1979).

The absence of sexual products in the coelom of a proportion of the largest sandworms (see Fig. 3) appears to be characteristic of the species. Both Snow and Marsden (1974) and Brafield and Chapman (1967) have made similar observations. The fate of these large nonspawners is not known. They possibly emigrate to subtidal or downriver habitats or succumb to natural or digging mortality without spawning.

Considerable variation exists in the maximum size of *Nereis virens* reported from different geographical locations. The largest individual reported in Figure 2 was 31 cm. Sandworms of 70-75 cm (anesthetized length) have been dug from the Back River in Boothbay, Maine (lat. 43°54′15″ N, long. 69°40′ W). Sveshnikov (1965) reported catching epitokous individuals 45 cm in length and also reported that the heteronereid form of *N. virens* reached a length of 90 cm along the coast of England and 1 m in Japan. Khlebovich (1963) reported mature individuals reaching 38.5 cm in the White Sea.

The sex ratio of *Nereis virens* collected prior to spawning varies with geographical location. In our studies, the sex ratio of small potential spawners was approximately 1 female:1 male, whereas the sex ratio of individuals ≥30 cm was approximately 2 females:1 male. There is no reason to believe that these changes in sex ratios with size result from nonspawners (in February) becoming sexually mature by spawning onset in April. Our observations reveal that the maturation rate of both eggs (see Figure 4A) and sperm requires considerably more than 2 mo. The change in sex ratio may indicate that larger potential males are more disposed to either free-swimming in the

[7]A. E. Brafield, Department of Biology, Queen Elizabeth College (University of London), Campden Hill Road, London, England, pers. commun. 1968.

water or exposing themselves on the surface of the mud, and are therefore subject to greater natural mortality through predation. The free-swimming habits of *Nereis virens* (especially at night) have been well documented (Crowder 1923; Gustafson 1953; Dean 1978). Brafield and Chapman (1967) reported that by the onset of spawning, males and females occurred in about equal numbers. Snow (1972), on the other hand, reports a 3:1 ratio of males to females prior to spawning.

Oocyte Development

Some similarities exist between our studies of oocyte development (see Figure 4A) and those of Brafield and Chapman (1967) and Snow and Marsden (1974). Brafield and Chapman (1967) reported that ovulation occurred in February or March at 50 μ and the oocyte diameters increased from 80 μ to 160 μ during the period of rapid growth between September and December. The increase in oocyte diameters to 170-180 μ prior to spawning required about 14 mo. Snow (1972) reported that the smallest eggs found free in the coelom of *Nereis virens* measured 10 μ in diameter. The eggs usually remained in clumps until they measured 25 μ and appeared singly above 50 μ. Snow and Marsden (1974) stated that the rapid-growth phase began in September, and their egg growth figure showed that this extended at least until December. They stated that maturation required 1-2 yr, depending upon the time of year when the eggs were produced. Ova measured 210-240 μ when spawned in May.

The standard deviation for oocyte diameters recorded in both the present study and that of Brafield and Chapman (1967) reveals that small oocytes are more variable in size than large oocytes. The large standard deviation for small oocytes results from ovulation occurring over a long period. Eventually, the maturation rate of oocytes produced late in this period accelerates so that all oocytes mature at a certain size at the same time (Clark cited in Stancyk 1979). Similar observations have been recorded for *Nereis diversicolor* Müller (Clark and Ruston 1963).

Oocyte development in *Nereis virens* follows the typical sigmoid growth curve. Similar observations have been recorded for all or part of the oocyte maturation processes in *Arenicola marina* Linnaeus (Howie 1964 pers. commun. cited in Clark 1965), *Nereis diversicolor* (Clark and Ruston 1963), and *Glycera dibranchiata* Ehlers (Creaser 1973).

Although no length measurements were obtained for the sandworms used in Figure 4A, it was generally evident to us that no relationship existed between size of the adult and size of the eggs; potential spawners of all sizes at one time possessed eggs of similar size.

Numbers of Eggs Laid

Sandworms >37 cm long were not found in the Wiscasset closed area (Creaser and Clifford footnote 6). However, a few larger worms, up to 54 cm long, were captured adjacent to the closed area after extensive digging, and egg counts from these as well as the more typical sizes were included in this study. Sandworms contained considerably fewer eggs than were found in similar-sized bloodworms, *Glycera dibranchiata*, collected from the same closed area but higher on the flat (Creaser 1973). The relatively large numbers of eggs produced (0.05-1.3 million), however, are consistent with the observation that macrofauna species generally produce large numbers of gametes (Thorson 1950 cited in Coull 1979).

Environmental Conditions During Spawning

Clark and Olive (1973) reported that "In the family Nereidae, sexual maturation and epitoky are caused by a decline in the rate of production of a cerebral hormone." Clark (1965) suggested that changes in the secretion rate of cerebral hormone might be controlled by environmental conditions or by some feedback mechanism. A distinction is made between (a) necessary environmental conditions and (b) specific environmental signals (Clark cited in Stancyk 1979).

Results of the present study suggest that a water temperature of about 7°-8°C might be one of the necessary environmental conditions required to initiate spawning. This hypothesis is strengthened by the fact that Snow and Marsden (1974) successfully fertilized *Nereis virens* ova and reared the young in the laboratory at 7°C. Sveshnikov (1955) recorded that surface temperature varied between 8.9° and 9.5°C at time of spawning in the White Sea. Some investigators (Thorson 1946; Korringa 1957) have reported that a rise in seawater temperature triggers spawning in a number of marine organisms. Bass and Brafield (1972) induced premature spawning in *Nereis virens* with an artificial rise in temperature from ambient (5°C) to 22°C over a 10-h period.

The specific environmental signals required to initiate spawning may be associated with the phase of the moon and the stage of tide. Our observations of initial spawning activity shortly after full moon are in partial agreement with Pettibone (1963) who reported that the spawning activity of *Nereis virens* on the New England coast centered around both full and new moon. Brafield and Chapman (1967), Bass and Brafield (1972), and Snow and Marsden (1974) have reported that swarming coincided with the time of new moon. The sandworms at Wiscasset spawn during the second half of the outgoing tide through the first part of the incoming tide. Pettibone (1963) reported similar observations from Barnstable, Mass. Bass and Brafield (1972) reported swarming in the Thames population only during periods of day and night high tides. Our only observation of some exceptionally large *Nereis virens* swarming at high water occurred in the Damariscotta River, Maine, in the vicinity of Fort Island (lat. 43°53′30″ N, long. 69°31′30″ W).

Spawning Characteristics

Some of the characteristics of spawning *Nereis virens* recorded by different investigators are summarized in Table 3.

Nereis virens has been described as atokous (Brafield and Chapman 1967; Snow and Marsden 1974) and epitokous (Gustafson 1953; Sveshnikov 1955; Khlebovich 1963). Clark (1961) reported that the structural modification associated with epitoky may be subtle and consist only of an elongation of the setae, modification of the sense organs, and reconstruction of the musculature. According to this description, spawning individuals captured in the vicinity of Wiscasset were obviously epitokes; the same morphological changes recorded in England by Bass and Brafield (1972) for adult males were observed in the Wiscasset population. There is no reason to doubt that *Nereis virens* display different reproductive characteristics in different geographical locations. Dales (1950) reported that nereids are well known for displaying variable reproductive habits within a given species.

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TABLE 3.—Some characteristics of spawning *Nereis virens* recorded by different investigators.

Investigators	Location of spawning males	Location of spawning females	Male swimming behavior during spawning	Color of spawners	Fate after spawning
Bass and Brafield (1972)	males in free-swimming swarms	believed females spawned in burrows	observed circular swimming in both vertical and horizontal plane; anterior portion of gravid worm becomes rigid.	4% of males deep red with white lines marking margin of anterior segments; a few were creamy white	worms swarmed several times before becoming spent but die after spawning
Brafield and Chapman (1967)	males in free-swimming swarms	believed females spawned in burrows or possibly spent short period swarming at surface		females lime green males milky green	worms die after spawning
Clark (1961)	males often dominate breeding swarms of nereids		swimming in tight circles is common to all swarming nereids		
Snow and Marsden (1974)	males in free-swimming swarms	believed females spawned in burrows			survival after spawning is highly unlikely
Our observations	males in free-swimming swarms	believed females spawned in burrows; some evidence that they emerge from mud to die after spawning	2 types: 1) swimming in straight lines is characteristic of new spawners that have just emerged from the mud; 2) circular swimming of spent or nearly spent individuals caused by anterior portion curved downward and worm tipped on side when swimming	females dark green males pale green becoming darker as worms become spawned out	individual worms sometimes spawn on more than one tide but die after spawning

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