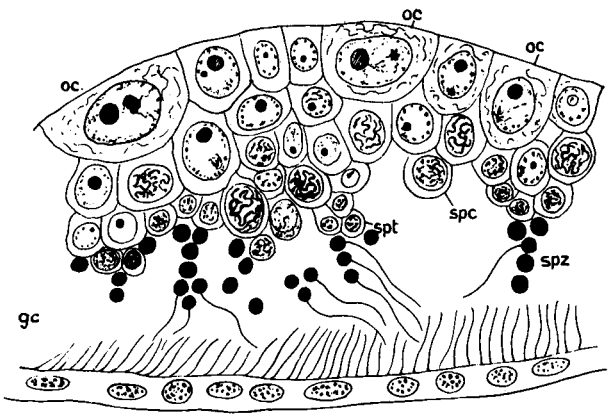

FIGURE 284.—Portion of bisexual gonad in young male *C. virginica*. gc—genital canal; oc—ovocytes; spt—spermatid; spc—primary spermatocyte; spz—spermatozoa. Photographically reproduced from Coe, 1934, fig. 5.

(fig. 284). At this stage the *C. virginica* gonad resembles that of *O. lurida* at the completion of the male phase and transition to female (fig. 285). In *C. virginica* the spermatogonia proliferate more rapidly than do the ovogonia and soon the young gonad attains a predominantly male appearance. Variation in the rhythm of gonad development in the oysters from different localities and even among those occupying the same bed results in different "categories" or "phases" of maleness or femaleness.

Development of the primary bisexual gonad in young *C. virginica* in New England waters is checked by the approach of winter when the growth of ovocytes is inhibited while the number of spermatogenic cells increases. A small number of spermatids may be formed early in November when the oysters are about 4 months old. The spermary of these secondary males contain scattered ovocytes, many of which degenerate, but some of them continue to develop into ova capable of fertilization. Even at the stage designated by Coe (1934) as "true male" the spermary at sexual maturity still retains a small number of ovocytes on the walls of the follicles.

At the close of the first breeding season many undifferentiated cells remain in the gonad to form the germinal cells of the following year.

Transformation of a bisexual gonad of *C. virginica* into an ovary begins before the formation of spermatozoa. At this stage the spermatogenesis is inhibited by the growth of ovocytes and the female phase is attained in a certain percentage of young oysters. The protandry, i.e., the development of maleness before the female phase, is well pronounced in *C. virginica*.

At their first breeding season young oysters form several sex classes: immature individuals in which the sex cells have not differentiated; males; hermaphrodites in which functional spermatozoa and ova are found in the gonad; and females. Hermaphroditic oysters are capable of self-fertilization and produce apparently normal larvae. The relative abundance of different sex phases of young oysters varies greatly, as can be seen from table 34,

TABLE 34.—*Frequency of different sex phases among* C. virginica *at first breeding season*

[According to Coe, 1934]

Locality	Immature	Hermaphrodite	Males	Females	Total examined
W. Sayville, N.Y.	77	4	154	48	283
Great South Bay, N.Y.	21	0	197	7	225
New Haven, Conn. (1932)	17	4	389	13	423
New Haven, Conn. (1933)	3	0	129	7	139
Woods Hole, Mass.	373	3	9	4	389

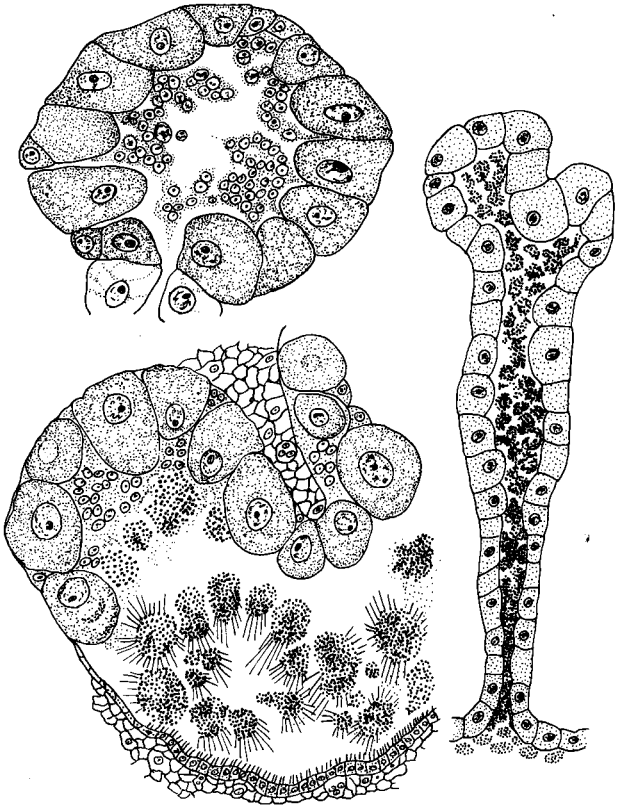

FIGURE 285.—Transition from male to female phase in *O. lurida*. Lower left—genital canal filled with sperm balls ready to be discharged; spermatogonia on the surface of large ovocytes. Right—advanced male phase in an older oyster; ovarian follicle is packed with cells in the later stages of spermatogenesis. Upper left—female phase preceding ovulation; many spermatogonia in the lumen of the follicle. Redrawn from Coe, 1932c.

which summarizes Coe's observations (1934) made on oysters from four different places along the coast of Massachusetts, Connecticut, and New York.

During the second breeding season the number of males may still exceed that of the females, but generally the sex ratio approaches equality. Great differences in the degree of protandry among the 1-year-old oysters is associated with the differences in the growth rate. Coe's observations suggest that there is a correlation between the development of ovocytes in the bisexual gonad and the rate of body growth. At the first breeding season the average size of the females is much larger than that of males (Needler, 1932a, 1932b). Coe (1934) found that the mean height of 389 yearling males from the New Haven area was 31.28 mm. (Std. dev. ±6.33) and that of the 13 females of the same age 38.54 mm. (Std. dev. ±8.12). The difference does not seem to be statistically significant, and several interpretations were advanced by Coe. He suggested that the females require more favorable conditions in order to mature, that they are metabolically more active, and that at the critical period of sex differentiation the metabolic factor determines the predominance of the male or female cells in the primary bisexual gonad. These proposals require corroboration. Since it is known that the growth rate of young oysters is accelerated by keeping them suspended above the bottom, there apparently would be no difficulties in conducting a comparative test using slow and fast growing oysters selected from a single population.

After spawning the gonad of *C. virginica* retains its bisexual potencies and its sex may alternate in either direction. Needler (1932a, 1932b) was the first to demonstrate that such a change actually occurs among adult *C. virginica*. She found that out of 24 surviving oysters which were known to be males during one summer, 5 became functional females the following year, and out of 12 females 5 changed to males. Among the 57 *C. virginica* studied by Needler (1942) for a period of 4 years there was a high proportion of males which remained unchanged while other oysters changed sex at least once. Some of the individuals changed sex every year. Needler suggested, without providing corroborative evidence, that the sex of the males which remained unchanged was genetically determined and that the other oysters in which sex alternation occurred at random were hermaphrodites.

Adult Japanese oysters, *C. gigas*, may change their sex during the interval between the two breeding seasons. Amemiya (1929), who established this fact, found that the rate of change was higher in the males (60 percent) than in the females (25 percent). Sex change occurs also in *C. commercialis;* 95 percent of the very young oysters of this species were found by Roughley (1933) to be males, but among the adult specimens of large size the females predominated at the rate of 270 to 100 males.

The sex of the oysters used in the investigations by Needler and Amemiya was determined by drilling a hole in the shell and pinching off a piece of gonad for microscopy. The injury caused by the operation constitutes a factor which may affect the unstable gonad and influence its sex change. By removing about one-third of all gill lamellae in adult *C. gigas* at the time when the gonad was at the indifferent phase after spawning, Amemiya (1936) demonstrated that the percentage of males in the mutilated group in all cases was larger than those in the control. Removal of the gill tissue may have indirectly influenced the development of male sex by reducing the rate of feeding and growth. This assumption also needs further corroboration.

Injury to the oyster used for observation on sex change can be avoided by inducing spawning in each individual oyster, obtaining kymograph tracings of muscular contractions, and examining the discharged sex cells. This technique was employed in the Woods Hole laboratory. In a test which continued for 5 consecutive years, 4-year-old oysters were obtained from one of the private oyster beds near Onset, Mass. During the first summer 202 oysters were induced to spawn, their sex was recorded, and an identifying number was engraved on the right (upper) valve. Upon completion of the tests the oysters were returned to outdoor tanks or were placed in the harbor and remained there until the next reproductive season. The testing was repeated every summer (Galtsoff, 1961).

Because the males respond to spawning stimuli more readily than the females, their number at the beginning of the experiment was greater than that of the females. The disparity does not represent an actual sex ratio of the population of 4-year-old oysters which was found to be about 1 to 1. The mortality, especially among the 7-year-old oysters

used in the test, was high, and the number of nonspawning oysters gradually increased toward the end of the experiment (table 35).

When oysters failed to respond to spawning stimulation, the testing was repeated at 4- to 5-day intervals for 5 consecutive weeks. Negative results were assumed to indicate the oysters were nonfunctional sexually, and they were returned to the holding tanks for another year. In several instances the oysters that failed to spawn became sexually active the following breeding season. It is not known at present whether the increased number of failures to spawn and increased mortality (table 35) should be attributed to aging or to unfavorable conditions in the winters. On several occasions the holding tanks and live cars in which the oysters were kept were swept by stormy waters and everything inside was covered with a deposit of mud.

TABLE 35.—*Changes in the percentage of sexes in a selected group of* C. virginica *tested consecutively for 4 years*

[Initial number of males and females 4 years old does not represent the normal sex ratio which was about 1 to 1]

Age in years	Males	Females	Non-spawning	Total survivors
Number	*Percent*	*Percent*	*Percent*	*Number*
4	64.4	35.6	0	202
5	65.2	32.6	2.2	181
6	61.2	31.6	7.2	139
7	50.1	40.3	9.6	104
8	44.1	41.2	14.7	68

During the 5-year period of observations the number of spawning males decreased from 119 to 15 in 9-year-old mollusks. The number of females decreased from 63 to 18. Consequently the sex ratios of males to females of the experimental oysters changed from 1.9:1 at the beginning to 0.8:1 at the end of the observations. The predominance of oysters of female sex in the surviving oysters can not be attributed to more frequent sex changes from male to female. In table 36 no significant differences were recorded in the rates of sex alternation in the two groups. The predominance of females at the end of the test could be explained, therefore, by greater survival rate of oysters at the female phase. This interesting point requires further corroboration.

Out of the 68 survivors at the end of the breeding season of the fourth year, 31 had alternated their sex at least once during the period of testing (Galtsoff, 1961). The frequency of changes were as follows:

One change	18 instances.
Two changes	10 instances.
Three changes	2 instances.
Four changes	1 instance.

The oyster which changed sex every year was a male at the beginning and returned to the male phase at the last test. No distinct pattern is apparent in the rhythm of changes except the greater persistence of the female phase. The sex ratio within the sex-reversed oysters changed from 23 males and 8 females at the beginning to 11 males and 20 females at the end of the observations.

TABLE 36.—*Frequency of sex alternation in adult* C. virginica *from 5 to 9 years old*

[The figures in the table indicate the number of males (column 2) and females (column 5) of each age and the number and percentage of changes to females (columns 3 and 4) and to males (columns 6 and 7) that occurred during each year]

Age in years	Males	Changes to females		Females	Changes to males	
Number	*Number*	*Number*	*Percent*	*Number*	*Number*	*Percent*
5	119	10	9.2	63	11	17.4
6	88	10	11.3	38	9	23.7
7	65	15	23.1	33	3	9.1
8	25	3	12.0	24	6	25.0
9	15	1	6.7	18	1	5.6

The cause of sex instability and the factors which may influence the shift of a gonad from one sex to another are not known. Coe believed that the physiological state of the organism in each breeding season is the key to the determination of the sexual phase of the oyster. No concrete proof to substantiate this idea can be found in his experiments. Egami (1952) attempted to transplant pieces of gonad of *C. gigas* to another oyster of the same or of the opposite sex. He found no evidence that the sex of the host affected the sex differentiation of the graft and concluded that the sex of the grafted pieces has been determined at the operating season (December) at their morphologically undifferentiated state. In another work (Egami, 1953), he corroborated the results of Amemiya's observation on the decrease of growth rate of *C. gigas* by the removal of gill tissue and the increase in the percentage of males among the mutilated oysters. He concluded that maleness could not be attributed directly to mutilation but was associated with the decreased growth rate of oysters without gills. Egami found that among normal individuals of *C. gigas* those growing more rapidly during the autumn tended

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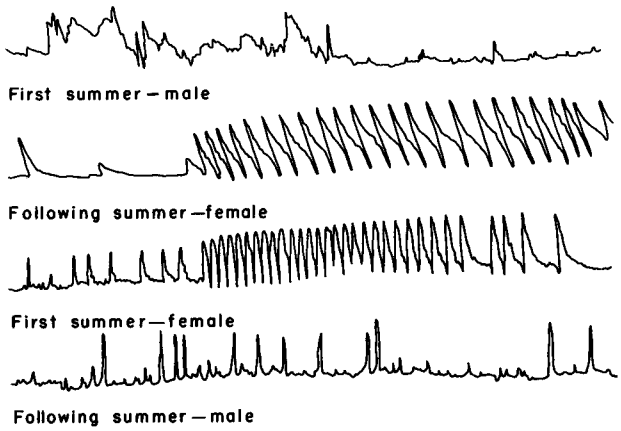
to develop into females the following reproductive season.

The conclusions may be considered only tentative since they are based on a small number of experiments which need to be repeated on a larger and more comprehensive scale. Sex alternation in oysters offers fascinating possibilities for further research on this fundamental biological problem.

The spawning reactions of sex-reversed oysters, as reflected in the type of shell movements and in the manner of dispersal of sex cells, are in every respect identical to those of the reactions of true males and females (fig. 286). In some sex-reversed oysters the change from male to female behavior is however delayed. Examination of records shows that in several instances females which were males during the preceding year spawned at the beginning of the reproductive season in a male fashion, discharging the eggs through the cloaca. Full female reaction involving rhythmical contractions of the adductor muscle was fully developed toward the end of the spawning season (fig. 287). It can be inferred from these observations that the mechanism of female sexual behavior develops at a slower rate than the morphological changes in the gonads. There was no retention of female behavior in oysters which returned to the male phase. The male reaction was apparent in them at the beginning of the season.



FIGURES 286.—Kymograph records of sex-reversed male (two upper lines) and sex-reversed female (two lower lines) *C. virginica* recorded at two consecutive breeding seasons. Both oysters were 5 years old at the "first" summer. In both instances eggs were dispersed through the gills, the sperm through the cloaca. Time interval, 1 minute.

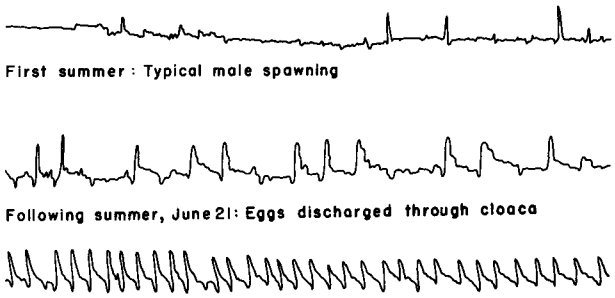


FIGURE 287.—Spawning of the sex-reversed male *C. virginica*. First line—spawning at the male phase. Second line—sex of the gonad changed to female; spawning proceeds in the male fashion. Third line—typical female spawning. Oyster was 5 years old during the "first" summer. Time interval, 1 minute.

In one instance the spawning of an hermaphroditic oyster was recorded (Galtsoff, 1961). Both eggs and sperm were discharged simultaneously through the cloaca, and the rhythmical contractions of the adductor muscle were not fully developed (fig. 288). A small portion of the gonad of this oyster is shown in fig. 289. Microscopic examination of the tissue revealed the presence of relatively few mature eggs in the follicles occupied by spermatozoa. Spawning of this oyster was induced by raising the water temperature. Eggs removed from the spawning tank were found to be fertilized and their development traced to trochophore stage was normal.

LUNAR PERIODICITY

The modern zoologist may disregard the early popular beliefs and superstitions which endowed the moon with mysterious effects on human affairs, on animals, and plants; nevertheless, he is confronted with several undeniable instances of lunar periodicity in the reproduction of marine invertebrates. Probably the most famous and generally known examples are the swarming and breeding of the Palolo worm (*Eunice viridis* Gray) of the South Pacific at the moon's last quarter of

FIGURE 288.—Shell movements of a spawning hermaphroditic *C. virginica*. Temperature 24.5° C. Time interval, 1 minute.

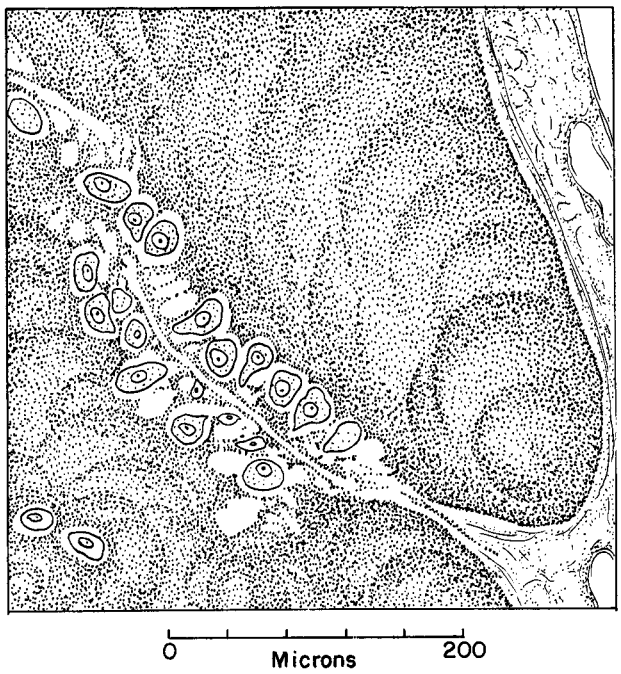


FIGURE 289.—Section of a small portion of an hermaphroditic gonad of *C. virginica*. Bouin, hematoxylin-eosin.

October and November; the swarming of the Atlantic Palolo (*Odontosyllis enopla* Verrill) at Bermuda and *Eunice fucata* Ehlers, at Tortugas, Florida (Mayer, 1908); and the breeding habits of *Heteronereis* form of *Nereis limbata* at Woods Hole (Lillie and Just, 1913). Legendre (1925) gives an interesting historical account of the effect of the moon on marine organisms. A comprehensive review of the instances of lunar periodicity of breeding among many marine invertebrates, including several species of pelecypods, is given by Korringa (1947).

Evidence of a relationship of breeding of *O. edulis* to moon phases was first presented by Orton (1926), who examined weekly samples of adult oysters from Fal estuary and found two important maximums in spawning at the full moon spring tides in the year 1925. He further concluded that the population as a whole gave maximal percentage of spawn (based on presence of embryos in the oysters) in the weeks after the July and September full moons. Later observations by Korringa (1941, 1947) in the commercial oyster district of Oosterschelde, Holland, confirmed the existence of a relationship between breeding of *O. edulis* and moon phases. He found that the full moon exercises the same influence on the breeding of oysters as does the new moon. Korringa based his studies on determinations of the time and abundance of oyster larvae in plankton and found a marked periodicity in the maximums of oyster larvae occurring about 10 days after full and new moon. Fluctuations in water temperatures, according to Korringa's view, are apparently of little or no importance in causing the periodicity in swarming which appears to be correlated with the spring tides. Unfortunately no experimental evidence is available to substantiate this inference which is based entirely on the concurrence of the two phenomena.

Spawning of *C. virginica* has no relationship to lunar phases. The existence of such a relationship was postulated by Prytherch (1929), who stated that Long Island Sound oysters spawn "at the end of full moon tidal period, or eight days after the time of full moon," but the correlation could not be corroborated by careful studies of Loosanoff and Nomejko (1951a), who continued the observations in Long Island Sound over a period of 13 years after the termination of Prytherch's work. Negative results were also reported by Hopkins (1931) in Galveston Bay, Tex., and by R. O. Smith in South Carolina waters (unpublished reports on file in the Bureau of Commercial Fisheries).

BIOLOGICAL SIGNIFICANCE OF SPAWNING REACTION

The most outstanding single factor in oyster reproduction is the difference in spawning behavior of the two sexes. The males are more responsive to sexual stimulation than the females and are easily stimulated to spawn by rising temperatures and by a great variety of organic substances, some of them not found in natural sea water. The spawning response of the male is nonspecific.

The less responsive, sexually mature females require stronger stimuli and are highly specific to chemical stimulation; they respond only to suspensions of sperm of the same or related species and are indifferent to the sperm of other bivalves and various chemical substances tested. The specificity of females is an insurance that eggs cannot be discharged when there is no sperm in the water.

Males are usually the first to initiate spawning; the discharge of sperm by even one individual induces spawning by those next to it, and the process spreads over the entire oyster community. This sequence has been observed among oysters

FIGURE 290.—Spawn of *C. gigas* carried down by the tidal river near Vancouver, British Columbia. Courtesy of D. Quayle. Black and white enlargement of Kodachrome slide.

kept on floats and among specimens living under natural conditions on oysters beds near low tide level. The spawning of an entire oyster population can be artificially initiated by mincing the meats of several sexually mature oysters and spreading them into the waters of the oyster bed. This method, based on my laboratory experiments, has been applied on a commercial scale by oyster growers in British Columbia (Elsey, 1936).

Simultaneous spawning of oyster populations is essential for the production of a large brood of oyster larvae and for obtaining setting of commercial value. In the estuaries where the majority of oyster beds are located, the tides carry the released spawn for some distance before the eggs sink to the bottom. A transport of oyster spawn by a strong current can be seen in the photograph (fig. 290) taken by Quayle near Vancouver, British Columbia, and kindly given to me for reproduction. The white streak in the foreground of the clear river water was formed by billions of eggs and sperm discharged by a population of *C. gigas* several miles up river.

The method of discharging sperm and eggs is also of considerable significance. Spermatozoa carried away by the respiratory current remain in suspension for several hours. When eggs are discharged in the same manner by some sex-reversed oysters, they rapidly sink to the bottom only a few inches away from the female. Laboratory observations indicate that under such conditions only a very small percent of them are fertilized or have even a slim chance of developing. On the other hand, eggs discharged in the usual manner through the gills and forcibly ejected from the mantle cavity, have a much better chance to be fertilized and survive. Furthermore, because of the specificity of female response to sperm, eggs are ejected only when the water contains free spermatozoa of the same species. The female spawning reaction is an adaptation of an oviparous organism to the conditions of its existence and assures the survival of the species.

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