SEXUAL PHASES IN WOOD-BORING MOLLUSKS

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It has been demonstrated previously that the well-known shipworm *Teredo navalis* is typically protandric, nearly all individuals functioning as males when young and later changing to the female phase (Coe, 1936; Grave and Smith, 1936). Under favorable conditions the female phase may be followed by an additional sequence of male and female phases.

In no other species of the wood-boring mollusks (Teredinidae) is the sexual sequence fully known, although Yonge (1926) recognized protandry in *Teredo norvegica* and Siegerfoos (1908) concluded that it was present in "*Xylotrya gouldi*" = *Bankia fimbriata* (Jeffries).

During the past few years the writer has had the opportunity of investigating the biology of three species, *Teredo navalis, T. diegensis* and *Bankia setacea,* with particular reference to the development of the gonads and the sequence of the sexual phases. The results of this study may be briefly summarized and compared with previous reports on the sexuality of the shipworms.

Sexual Phases of Teredo navalis

This widely distributed species occurs on both the Atlantic and Pacific coasts of the United States and has been particularly destructive in past years in San Francisco Bay. Individuals in the female phase are larviparous, the fertilized eggs developing through about half the larval period in the maternal gill chambers. A free-swimming period follows the discharge of the larvae into the water. After settling upon a piece of wood, transformation to the adult condition takes place and boring into the wood begins (Kofoid and Miller, 1927; Grave, 1928).

The primary male phase becomes functional within four to six weeks after the completion of the free-swimming larval condition in the warmer season of the year or in warm localities, but may be delayed for six months or more under colder conditions. The body is then only 20 to 30 mm. in length and about 2 mm. in diameter. The female phase may begin at the age of eight to ten weeks.

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Growth is rapid under favorable conditions. At the end of one year the body may have attained a length of 10 to 40 cm. and a diameter of 4 to 9 mm. In the meantime the individual has normally transformed to the female phase and has produced perhaps 1,000,000 young. A second sequence of male and female phases may have occurred.

Because of the long breeding season and the sequence of sexual phases, the proportion of the two sexes in each piece of wood will obviously depend upon the ages represented in the colony. In a recently attacked timber nearly every individual will be in the male phase. A few weeks later, after the sexual transformation has occurred, 60 to 90 per cent of the original colony will be functioning as females.

But in the meantime there may have been daily additions of recently arrived young from other pieces of wood, resulting in a continuing supply of male-phase individuals. These, together with the few so-called true males, and a small proportion of second male-phase individuals, are then available for the fertilization of the eggs produced by such individuals as are at that time functioning as females. Because of this overlapping of sexual phases all the older colonies are at all times represented by both sexual phases in varying proportions. Most of the smaller and consequently younger individuals will be functioning as males, while most of the larger, older individuals are in the female phase.

A rhythmical sequence of four sexual phases may be considered to represent the normal life cycle but this is seldom realized because of an earlier death due to parasites or to the exhaustion of the wood supply or to other unfavorable environmental conditions. Most individuals die after only two of these phases have been completed and many others survive only the primary male phase.

There are some variations in this sequence, however, because a second female phase may sometimes follow the first without an intervening male phase. Other individuals, known as true males, retain the male phase long after their contemporaries have changed to the female condition, and this may sometimes mean throughout their entire lifetimes.

Sexual Phases in Teredo diegensis

This species, like *T. navalis,* is protandric and larviparous, but the two species differ considerably both in the conditions of sexuality and in larval development.

T. diegensis Bartsch occurs abundantly and causes considerable damage along the coast of Southern California, and has been reported as far north as San Francisco (Kofoid and Miller, 1927). It is also found at the Hawaiian Islands. On the coast of Southern California this species breeds through all except the two or three cooler months of the year and through the entire year when the winter is warmer than usual. At the lower temperatures the larvae may remain within the maternal gill chambers for several months before they are discharged.

Ovulation occurs at intervals of a few weeks, the later broods of larvae often becoming established in the gills before an earlier brood has left. This condition occurs throughout the year. With the exception of young individuals and a few " true males " a sexually mature individual without a brood of larvae is seldom found.

Large individuals, 120 mm. or more in length, may have more than 1000 larvae in the gill chambers, while dwarfs may have less than 100. The bivalve larvae reach a shell length of 0.35 to 0.38 mm. before leaving the gills. In this species, as in *T. pedicellata* (Roch, 1940), the larvae remain within the gill chambers until nearly ready for metamorphosis. The free-swimming stage consequently lasts but a few hours if wood is available for attachment. The total period of larval development is about four weeks and is therefore of about the same length as in *T. navalis* (Coe, 1933*a*). In this latter species, however, only about two weeks of this time are spent in the maternal gill chambers, followed by a free-swimming period of about the same duration.

Shortly after being set free in the water the larvae of *T. diegensis* attach themselves to any available piece of wood but do not immediately penetrate the surface. Some of them may remain two weeks or more on the surface of the wood before beginning to bore. Their stomach contents show that minute particles of organic food materials are ingested in the meantime. Because there is no necessity for feeding during the brief free-swimming stage, this species may be reared from generation to generation in the aquarium. By supplying a fresh piece of wood occasionally the stock may be continued for at least several years. The aquarium water evidently contains sufficient materials to supplement the wood as sources of nourishment. After penetrating the wood the young teredos grow rapidly and reach the primary male phase within four to five weeks. The body is then about 8 to 12 mm. in length.

The primary gonad is composed of branching follicles filled with large, vacuolated cells and having a few proliferating germinal cells scattered along the walls of the follicles as shown for *Bankia setacea* (Fig. 1, *A*). This condition is closely similar to that described by Coe and Turner (1938) for the developing gonads of *Mya*. As the germinal cells increase in number they become differentiated into the two sexual types of gonia and then further differentiated into ovocytes and spermatocytes.

By their rapid proliferation and differentiation the spermatogenic cells encroach upon the spaces occupied by the vacuolated follicle cells and eventually fill the entire lumen of the follicle (Fig. 1, *B*). In some individuals the follicle cells contain numerous fragmenting and degenerating nuclei, representing a kind of atypical spermatogenesis, as described by Coe and Turner (1938) for *Mya*.

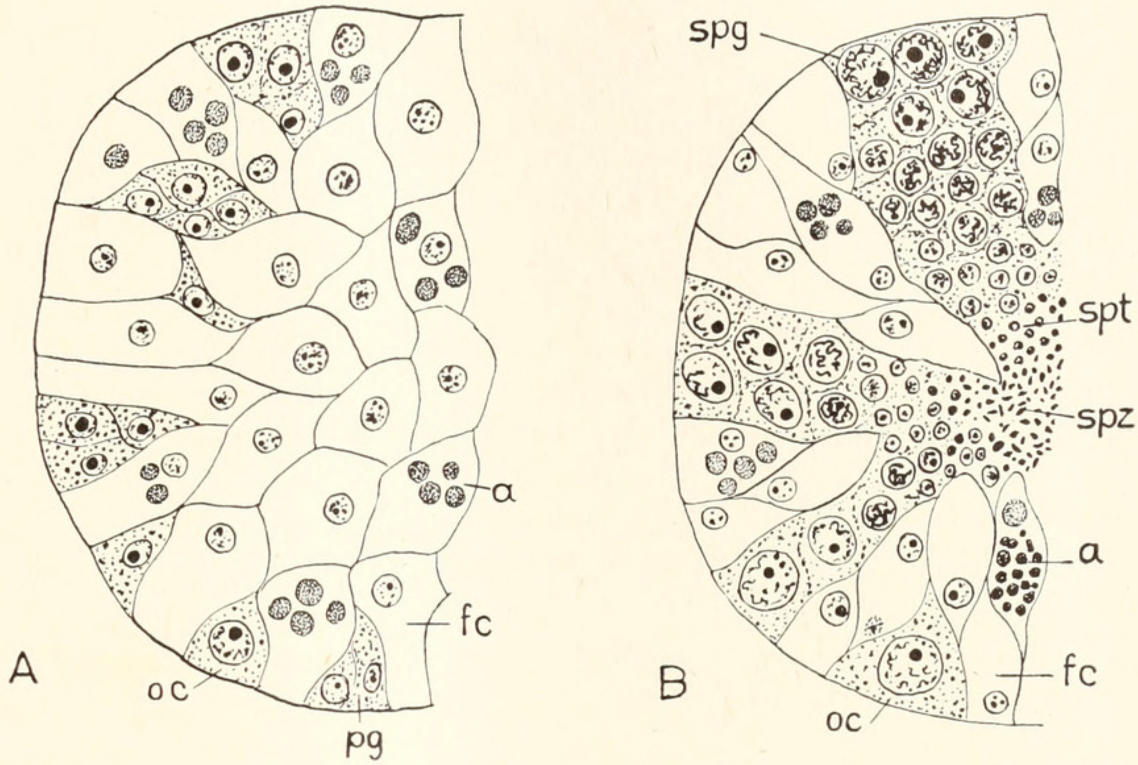

FIG. 1. *Bankia setacea.* Development of the primary ambisexual gonad. *A*, portion of section of young follicle, showing large vacuolated follicle cells (*fc*), with a few primary gonia (*pg*) and a single young ovocyte (*oc*) peripherally; several follicle cells contain atypical, degenerate nuclei (*a*), derived from original primary gonia. *B*, portion of follicle in early male phase, with a few remaining vacuolated follicle cells (*fc*) and various stages of spermatogenesis; *a*, atypical degenerate nuclei; *oc*, ovocyte; *spg*, spermatogonia; *spt*, spermatids; *spz*, spermatozoa.

There is considerable variation in the number and size of the ovocytes which are always present on the walls of the follicles during spermatogenesis. Some individuals, corresponding with the so-called true males of *T. navalis,* have only a few small ovocytes in each of the follicles (Fig. 3, *A*), while others show a preponderance of ovocytes in some or all of the follicles before the spermatozoa are fully ripe (Fig. 2).

Occasionally all the spermatozoa are discharged before ovulation occurs, resulting in a distinctly female phase (Fig. 3, *B*), but more frequently a functionally hermaphroditic condition is found. Both spermatozoa and ova may ripen at the same time and evidently both may be discharged simultaneously. Under experimental conditions self-fertilization occurs readily; this is followed by the formation of the polar bodies and cleavage, but only as far as the blastula and gastrula stages. For the normal processes of larval development the environmental conditions peculiar to the maternal gill chambers appear to be necessary.

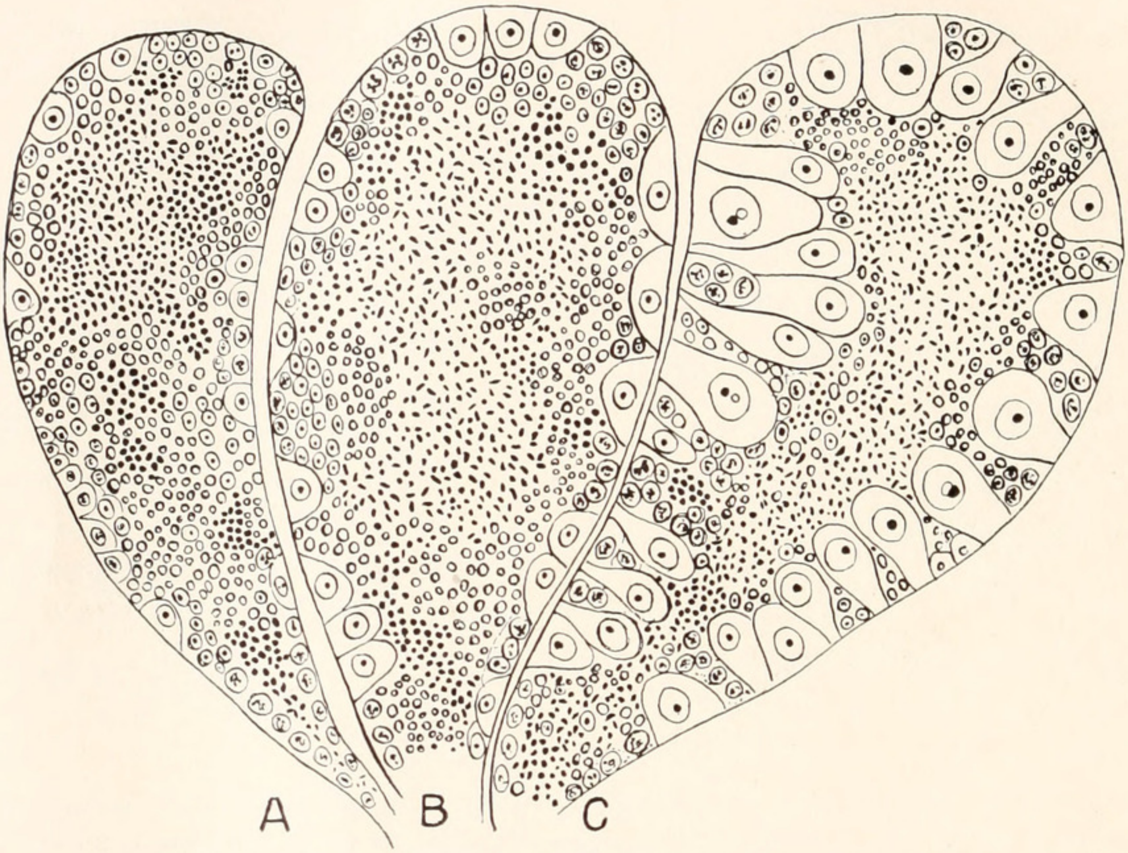

FIG. 2. *Teredo diegensis.* Sections of three follicles from gonad of second male-phase individual which had branchial brood pouches distended with larvae. *A*, immature follicle, principally in male phase, with relatively few ripe spermatozoa and with only small ovocytes in basal layer of germinal cells. *B*, more nearly mature follicle in male phase, distended with spermatogenic cells and many ripe spermatozoa; numerous half-grown ovocytes in basal layer of germinal cells. *C*, ripe follicle in hermaphroditic male phase; lumen filled with ripe spermatozoa and with nearly mature ovocytes densely crowded on periphery.

During some seasons this species becomes particularly injurious by boring in mooring ropes. A similar habit has been reported for *T. navalis* (Coe, 1933). Under such conditions only dwarf individuals are produced but many of these are nevertheless capable of forming a small number of ripe gametes. A single change of sexual phase, from male to female, may occur, although many individuals are killed by the disintegration of the rope before even the primary male phase is completed.

Sexual Phases of Bankia setacea

This species differs from *Teredo diegensis*, with which it is often associated in the cooler waters on the coast of southern California, in being oviparous rather than larviparous. On reaching the female phase vast numbers of minute ova are produced and these are discharged directly into the water. Fertilization of these ova by sperm of other individuals takes place in the water. Then follows a free-swimming larval period of perhaps four weeks before the larva is ready to settle on a piece of wood and transform to the adult condition.

It is evident that all individuals pass through a functional male phase a few weeks after entering the wood. The two types of males are more

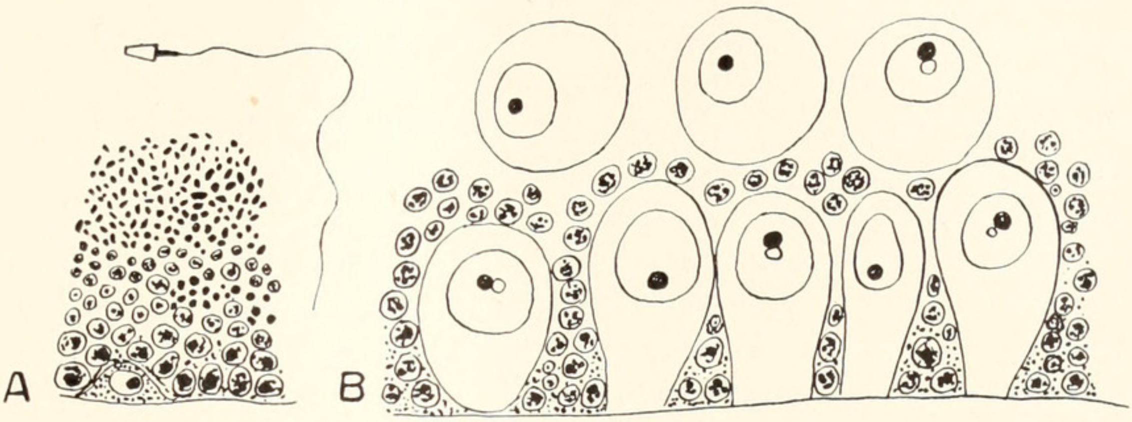

FIG. 3. *Teredo diegensis*. *A*, portion of gonad of young individual in "true male" phase, showing spermatogenesis and a single, more highly enlarged spermatozoön; a single ovocyte is shown at the base of the spermatogenic cells. *B*, portion of gonad in female phase, with ripe ova; those ova still attached to wall of follicle are surrounded by follicle cells with undifferentiated gonia basally.

easily distinguished than in either *Teredo navalis* or *T. diegensis*. About half of the young, male-phase individuals are apparently hermaphroditic; these complete spermatogenesis early and then change to the female phase. These are evidently genetically protandric females, while an approximately equal number retain the primary male phase much longer. The latter presumably represent the "true males" of other species (Coe, 1933*a*, 1936). Fully adult individuals, measuring 20 to 50 cm. in length, usually have the appearance of being either males or females, with little indication of ambisexuality. Only occasionally do their gonads reveal distinctly their essentially hermaphroditic nature. Careful examination of the gonad in full spermatogenesis, however, usually reveals a few ovocytes on the walls of the follicles and these may be considered as an indication that a change of sexuality may later occur. In the female phase likewise indifferent gonia show the potentiality of a sex change.

The sexual conditions in this species are therefore similar to those of the oyster *Ostrea virginica* (Coe, 1938), which is seasonally of separate sexes but in which the sexual phase of any season cannot be predicted from the sexual condition of the preceding season. In *Bankia*, however, many of the females experience but a single change of sex, from male to female, while the true males may retain the male phase throughout life.

On the coast of southern California some individuals of *B. setacea* are found in spawning condition throughout the year. The majority of individuals, however, spawn only during the autumn and spring months, with resting periods in the winter and summer. Consequently wooden blocks and timbers become much more quickly and more heavily infested in the spring and autumn than at other times of the year.

Johnson and Miller (1935) found that settlement of this species in Puget Sound occurred principally from October to December and less abundantly from March to September. Kofoid and Miller (1927) also observed that in San Francisco Bay settlement of this species was confined to the cooler months of the year.

When removed from the body the eggs of *Bankia* develop rapidly to the free-swimming larval condition after artificial fertilization by sperm from another individual. The eggs of juvenile protandric females are sometimes capable of self-fertilization.

Conclusions

It is evident that the sexuality of these three species of pelecypods represents a graded series of ambisexual or hermaphroditic conditions intermediate between such dioecious forms as *Mya* or *Mytilus*, which are almost strictly of separate sexes, and those that are uniformly monoecious, as the larviparous oysters, *Ostrea edulis* or *O. lurida*. In all the dioecious pelecypods of which the sexuality has been extensively investigated hermaphroditism is found occasionally and this may include a large or only a small portion of the gonad.

Even the monoecious species usually have some dioecious tendencies, with some individuals ("true males") showing a preponderance of masculine characteristics, while others are more nearly feminine. A sequence of functional male and female phases is of common occurrence and in the case of long-lived species this may constitute an alternating rhythm. The wood-boring mollusks are of this type.

Protandry is characteristic of many species. This represents a juvenile type of sexuality and often occurs when the individual is very young and when the body has reached but a small fraction of its definitive size.

As mentioned above for *Bankia* and as Loosanoff (1937) found in *Venus,* the genetic females pass through a juvenile male phase before adult sexuality is realized. This has been reported for other species. In the oviparous oyster *Ostrea virginica* the proportion of the genetic females which pass through a functional male phase during their first breeding season depends both upon the particular local race concerned and upon the environmental conditions. This juvenile male phase is more frequently aborted or omitted under conditions favorable to rapid growth, thereby increasing the proportion of juvenile females. This species also shows a rhythmical tendency toward seasonal change of sex in later life (Coe, 1938).

In all the examples mentioned and in many others belonging to the various classes of mollusks, the sex-differentiating mechanism is so delicately balanced between the two sexual tendencies that relatively slight differences in environmental conditions may be potent in determining which of the two contrasted aspects of sexuality shall be realized. In some the entire population functions as male when young and as female when fully adult. An intervening functionally hermaphroditic phase may occur.

Summary

1. The three species of wood-boring mollusks *Teredo navalis, T. diegensis* and *Bankia setacea,* are all protandric, with a strong tendency toward rhythmical changes of functional male and female phases.

2. Each species differs as to the degree of ambisexuality characteristic of the primary male phase and of the subsequent sexual phases.

3. The primary gonad in all three species develops from branching follicles filled with large vacuolated follicle cells and having the primary gonia scattered along walls of the follicles.

4. In each of these species the gonads of young animals indicate that there are two types of primary male-phase individuals: (1) ambisexual males or protandric females, characterized by many ovocytes on the walls of the spermatic follicles, and (2) true males with few ovocytes. In those of the former type the male phase is of short duration, while true males retain the male phase longer or in some cases indefinitely.

5. In *T. navalis* the first female phase does not usually become functional until nearly all the sperm of the primary male phase have been discharged. Functional hermaphroditism is not usual, although the gonad is histologically ambisexual during the change of sexual phase in both directions.

6. In *T. diegensis,* on the other hand, functional hermaphroditism is of usual occurrence and the sexual phases are not sharply demarcated.

7. In *B. setacea* functional hermaphroditism occurs only occasionally in the primary male phase; the subsequent sexual phases are clearly differentiated, often with a resting stage intervening between two sexual phases. The sexual phases are of the alternative type in that any sexual phase, after the first, may be followed by either a male or female phase if the length of life suffices. The relatively short life of many individuals, however, allows but a single change of sex, from male to female, in the genetic females, and none at all in true males.

8. In all of the three species the eggs begin development after artificial fertilization. In *Bankia* the larvae may be reared to the free-swimming veliger stage, but in the other two species the larval stages require the peculiar environmental conditions of the maternal gill chambers. Under experimental conditions self-fertilization and apparently normal cleavage occurs readily in the two species of *Teredo* and occasionally in *Bankia*.

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