Our experience in growing larvae of *M. solidissima* was confined to the period from the middle of January to the end of June. During that time morphologically-ripe eggs and spermatozoa were always present in the gonadal follicles. Possibly, equally well-developed sex cells could have been found in the gonads several weeks earlier than January because, apparently, the most important period of gametogenesis in *M. solidissima* begins immediately after the end of spawning, as in *M. mercenaria*, in which gonads of both sexes present a ripe appearance in December (Loosanoff, 1937b). Allen (1953) obtained ripe eggs of *M. solidissima* from early spring until late autumn.

Spermatozoa, taken from clams brought from their natural beds early in January, when placed in a drop of water at room temperature quickly began to move. However, eggs taken from clams of the same groups usually could not be fertilized, probably because they were not physiologically ripe. Nevertheless, placing female clams in water of about 15°C for only a few days was sufficient to ripen them. Later in the season, when the temperature of the water in Milford Harbor increased to 12°C, no conditioning was needed.

Fertilizable eggs could be obtained either by stripping or by inducing spawning. Sometimes, stripped eggs obtained from a ripe female were as viable as those discharged during a normal spawning. More often, however, a culture started with stripped eggs contained many abnormal individuals. Costello *et al.* (1957) suggested a different method of obtaining gametes, which consisted of straining the eggs through a cheesecloth.

Spawning was induced by the usual method of thermal and chemical stimulation. On several occasions thermal stimulation alone was sufficient. Normally, addition of a suspension of sex cells was required and, even then, many conditioned clams did not spawn.

Spawning was induced at temperatures ranging from 18° to 25°C. Temperatures of 30°C and over unfavorably affected the clams. They gaped and abnormally extended their feet which, like the rest of their bodies, became limp and soft. If, after exposure to such high temperatures the clams were quickly returned to cooler water of about 25°C, they often began to spawn, but the eggs obtained in such a manner did not develop past the formation of polar bodies. Apparently, exposure of clams to temperatures over 30°C caused serious injuries to their eggs. Our observations in this respect agree with those of Imai *et al.* (1953) who, while working on a closely-related species, *Mactra sachalinensis*, found that at a temperature of about 32°C none of the eggs underwent normal cleavage.

Observations were made on the growth of larvae of *M. solidissima*

at two different temperatures. Eggs obtained from several females and fertilized with spermatozoa of three ripe males were mixed together and then divided into two groups, one to be grown at a temperature of about 22°C and the other at 14°C. The concentration of eggs per ml of water was the same in both cultures. During the experiment the larvae were fed equal quantities of phytoplankton composed largely of *Chlorella* sp.

Eggs placed in water at 14°C were in the trochophore stage at the end of 40 hr. After 72 hr the culture contained normal and active straight-hinge larvae averaging 85 μ in length, which were quite uniform in size and appearance. At 22°C this stage was reached after only 28 hr. Young straight-hinge larvae of *M. solidissima* were usually

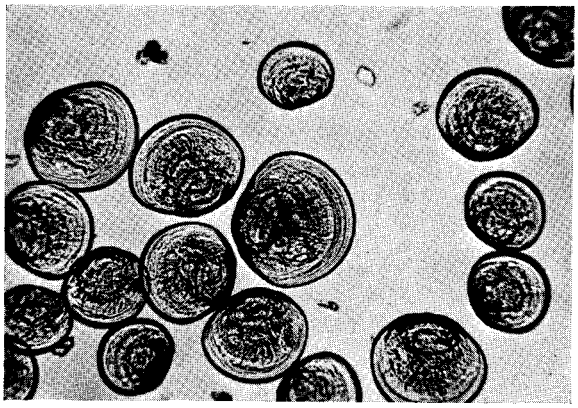

FIG. 41. Larvae of *Mactra solidissima*. Largest larva, 219 μ long and 193 μ wide, is approaching metamorphosis. Note differences in sizes of larvae that originated from the same group of eggs and were reared under identical conditions.

almost transparent and had a granular appearance with the internal organs at this time not too well defined. Later, as in the case of most larvae, the color began to deepen.

On the 19th day, when larvae in the warmer culture began to metamorphose, the length of the modal class of larvae grown at 14°C was only 117 μ, and the larger individuals in the cultures were only 153 μ long. The first metamorphosing clams were observed in this culture after 35 days. When the experiment was discontinued on the 50th day the remaining larvae showed a wide range in size, the smallest being only 109 μ long (Fig. 41).

A partial description of development and dimensions of larvae of *M. solidissima* was given earlier in this article. Here we may add

that the most recent description of what were assumed to be larvae of *Mactra* (= *Spisula*) *solidissima* was reported by Sullivan (1948). She gave the minimum size of straight-hinge larvae as about 95 × 80 μ, which is approximately 15 μ longer than usually found in our cultures, while the maximum size of 270 × 245 μ closely agreed with our measurements. In both instances the length–width relationship given by Sullivan falls near the median line of length–width relationships which we found for larvae of *M. solidissima.*

In describing larvae of a related form, *Spisula subtruncata*, Jørgensen (1946) reported that veligers are about 400 μ at the time of metamorphosis. Kändler (1926) stated, however, that the length of this species at metamorphosis is only 310 μ. Considering that Imai *et al.* (1953) found the maximum size of larvae of *Mactra* (= *Spisula*) *sachalinensis* to be about 270 μ, virtually the same as we found for *M. solidissima*, and because Imai's conclusions and ours are based on measurements of larvae of a known origin, we think that Kändler's measurements are more realistic than Jørgensen's and that the latter was probably describing larvae other than those belonging to the genus *Mactra* (= *Spisula*). The same consideration leads us to believe that the descriptions and measurements offered by Rees (1950) of advanced stages of larvae presumably of the superfamily Mactracea, including *Spisula solida* (360 μ) and *Spisula elliptica* (355 μ), are really those of some other species.

R. *Mya arenaria* Linné

Our efforts to induce spawning of *M. arenaria* were confined largely to the period extending from March until the middle of July. Several groups of these clams were also conditioned and spawned in winter. Moreover, to induce spawning of even well-conditioned and apparently ripe *M. arenaria* is difficult, nevertheless.

In developing a method to induce spawning of these clams we tried many approaches, including sudden and gradual changes in water temperature, changes in pH, salinity, hydrostatic pressure, light intensities and the addition of sex products. Usually, none of these worked. The only method that proved to be successful with some regularity consisted of subjecting ripe clams to water of relatively high temperature, of about 26° to 28°C, for long periods often extending from 6 to 8 hr and adding, during this time, a suspension of sex products. Many clams spawned profusely when this method was employed and discharged a large number of eggs, but a high percentage of these eggs usually developed into abnormal larvae.

Belding (1931) reported the diameter of the average egg of the

soft shell clam as 62·5 μ, while Battle (1932) gave the egg size as varying from 70 to 80 μ. Our measurements of hundreds of eggs discharged by different females and on different occasions showed that the majority were between 68 and 73 μ in diameter, with a modal size of 70·5 μ.

Belding (1931) expressed the opinion that artificial cultivation of *M. arenaria* is virtually impossible because the eggs either fail to develop normally or else never pass the young veliger stage. Nevertheless, Belding was able to show that, unlike other pelecypods, eggs stripped from *M. arenaria* can be artificially fertilized.

The smallest normal straight-hinge larvae recorded in our cultures measured only about 86 $\times$ 71 μ. These were, however, extremely uncommon and normal, fully-formed straight-hinge larvae were usually about 93 $\times$ 77 μ. As in most pelecypod larvae, they were light in color at this stage and their internal organs were not well defined. They remained quite light, almost transparent, until a length of about 110 μ was reached. As the larvae grew, they became darker. Nevertheless, as mentioned on several occasions, these larvae do not possess characteristic colors that would help to distinguish them from members of other genera or species of bivalves. In our experiments, where larvae of this species were fed different foods, their color ranged from a dark reddish-brown to dark green. We cannot, therefore, agree with Sullivan (1948) that brown pigmentation in large larvae of *M. arenaria* is diagnostic of that species.

In older larvae measuring about 175 μ and longer we noticed the presence, in the margins of the mantle, of irregular opaque spots varying in size from 5 to 15 μ. These granules occurred with such regularity that we are inclined to consider them as characteristic of the species, at least during late larval stages. Jørgensen (1946) noticed a somewhat different pigmentation of the soft parts of larvae of *M. arenaria* measuring about 200 μ and larger. He also suggested that this may be a reliable specific character.

The size of larvae of *M. arenaria* at setting is extremely varied. Metamorphosis may occur at any length from 170 to 228 μ. The latter is the size of the largest free-swimming larva ever recorded in our cultures. The majority metamorphosed at a length between 200 and 210 μ.

The smallest larva in which the foot was present was about 165 μ long but many of the larvae had a well-developed foot by the time they reached 175 μ in length. The presence of a large foot does not necessarily indicate that the velum has already become non-functional. Larvae as long as 210 μ have been seen at times swimming about using both the velum, which still appeared to be of normal size, and also

the large foot. However, the velum normally begins to disappear soon after a length of 172 to 175 μ is reached and sometimes even earlier. In most individuals 200 μ in length the velum is already resorbed. Some larvae measuring only 175 μ in length, and having no velum, were seen actually crawling, using their feet.

The balancing organ, the otocyst, can be clearly seen at the base of the foot of larvae measuring about 175 μ in length. The byssus gland also can be seen in larvae less than 200 μ in length, and the gills may be clearly discerned in some individuals of about the same size. The byssus thread is strong, and our attempts to break it by directing a strong jet of water from a pipette caused the larvae to sway from side to side, but did not break the thread.

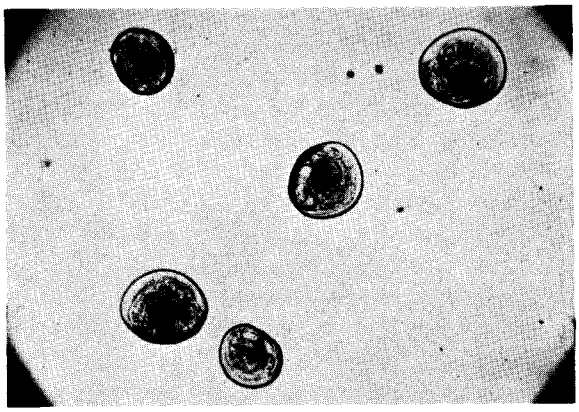

FIG. 42. Young larvae of *Mya arenaria*. Largest larva shown is about 140 μ long.

No systematic studies on the rate of growth of larvae of *M. arenaria* at different temperatures, such as those conducted with larvae of *M. mercenaria*, were made. Our attempts to grow larvae at low temperatures ranging from 12° to 15°C were usually unsuccessful because of slow growth. For example, at a temperature of about 14°C larvae, even after 15 days, were only about 110 to 115 μ long. Larvae grown at low temperatures, probably because of the slow rate of growth, were usually of extremely uniform size.

Most of our cultures were grown at room temperatures which ranged from about 19° to 24°C. Under those conditions the rate of growth was quite rapid, although it varied, of course, from culture to culture, depending upon the temperature, concentration of larvae, and quality and quantity of food given. At about 23°C the average length of larvae 2 days after fertilization was approximately 109·5 μ

and the maximum 117 μ. After 5 days larvae averaged 120 μ in length and the largest individuals were 140 μ long (Fig. 42). After 10 days some of the largest larvae approached a length of 180 μ at which setting is possible. By the 15th day many individuals had already set, and the average size of the larvae in the cultures had increased to about 175 μ. A few large larvae, measuring about 225 μ in length but still free swimming, were also found in our samples. In some cultures setting began when the larvae were about 10 days old and continued until the end of the 35th day.

As has already been mentioned, the smallest straight-hinge larvae of *M. arenaria* in our cultures measured about 86 $\times$ 71 μ. The largest free-swimming individuals were 228 $\times$ 207 μ, although most of them metamorphosed before that size was reached. Our measurements, therefore, differ from those given by Stafford (1912), who stated that the smallest straight-hinge larva of *M. arenaria* that he found was only 75·9 $\times$ 62 μ, while the largest measured 414 $\times$ 345 μ. Of the latter he said, "The largest measurement I have is 64 $\times$ 53, and I have seen them attached by a byssus-thread, their siphons protruded, and the big hinge-tooth on the left valve." Since, according to Stafford, each unit of his measurements was equal to 6·9 μ, the dimensions of his larvae were as given above. It is quite possible, if his measurements were correct, that Stafford was working with larvae of a species other than *M. arenaria* and, possibly, his large individuals were already juvenile mollusks and not free-swimming larvae. Another possibility is that Stafford's microscope was not correctly calibrated.

The dimensions of larvae in our cultures were not too different from Sullivan's (1948). Nevertheless, her smallest size of 105 $\times$ 90 μ is considerably larger than we found and her largest, 250 $\times$ 230 μ, also somewhat exceeds ours. Yoshida's (1938) observation that larvae of *M. arenaria* in Japanese waters metamorphose upon reaching a size ranging from 240 to 300 μ also disagrees with ours because, while the length of 240 μ does not differ radically from the measurements of our largest larvae, the maximum size of 300 μ given by Yoshida exceeds ours by about 70 μ.

The length of early straight-hinge larvae of *M. arenaria* given by Jørgensen (1946) is similar to ours. This is to be expected because his early larvae were laboratory-reared, as were ours, and, therefore, there is no doubt that we and Jørgensen were working with the same species. However, we disagree with Jørgensen that larvae of *M. arenaria* may reach 300 μ in length before metamorphosis. His conclusion regarding the setting size is based not on laboratory-reared *M. arenaria*, but on specimens collected in the field and only assumed to be this

species. The fact that Jørgensen stated on several occasions that metamorphosis of *M. arenaria* may occur upon attainment of a much smaller size than 300 μ strongly supports our opinion. For example, Jørgensen mentioned that in Ringkbing Fjord the size of larvae at metamorphosis in shallow water varies between 200 and 225 μ, thus being within the size range observed in our cultures.

S. *Teredo navalis* Linné

Larvae of *T. navalis* have been described by many authors, including Jørgensen (1946), Sullivan (1948) and, also, Imai, Hatanaka and Sato (1950), who gave a good description of the method of rearing them.

In our laboratory adult *T. navalis* were conditioned to spawn as early as the first part of December. This was done by placing pieces of wood, containing wood-borers, in sea water maintained at a temperature between 15° and 20°C. Spawning occurred at temperatures of 14°C and higher, and larvae were released at temperatures ranging from about 16° to 20°C. Grave (1928) reported that spawning of *T. navalis* began when the water temperature reached 11° to 12°C. Imai *et al.* (1950b), however, found that spawning begins when the water temperature reaches 18°C. Sullivan's (1948) data closely agree with ours, that spawning and swarming may occur at approximately 15°C.

Although *T. navalis* is naturally larviparous, both recently-fertilized eggs and immature larvae removed from the gill chambers of the parents developed normally past metamorphosis. The diameter of unfertilized eggs varied between 50 and 60 μ, agreeing with measurements given by Jørgensen (1946) and Costello *et al.* (1957). In the dissected adults, however, most of the eggs found were either already fertilized or immature, thus presenting difficulty in obtaining reliable egg measurements.

The smallest larvae released in natural swarmings at our laboratory measured only 80 $\times$ 70 μ, while the largest larvae found in the gill chamber of the mother were 90 μ long, or approximately 10 μ longer than reported by Jørgensen (1946). Evidently, the length of larvae at the time of release may vary by at least 20 μ. Imai *et al.* (1950b) indicated that the mean size at the time of release is 85 $\times$ 72 μ. Our observations that the average size of just-released *Teredo* larvae is between 85 and 95 μ are in agreement with those of Sullivan (1948), Jørgensen (1946) and Imai *et al.* (1950a). We cannot, however, accept the conclusion of Lane *et al.* (1954) who maintained that larvae are about 250 μ in size when released from the gill chamber.

Eggs, in early stages of development, taken from the gill chamber

of a female *Teredo* were cultured to metamorphosis in 28 days at a temperature of about 20°C. Grave (1928) thought that the entire period of development of *Teredo* from the moment of fertilization to metamorphosis takes about 5 weeks. Judging by data offered by Imai *et al.* (1950a), setting in their cultures occurred between the 24th and 34th days.

A brief description of early stages of development of eggs and larvae of *T. navalis* are given by Costello *et al.* (1957) and of later stages, by Sigerfoos (1908). Imai *et al.* (1950b) gave a good account for all stages. In our cultures the shells of straight-hinge larvae appeared heavy and thick. The larvae were also characterized by a dark band

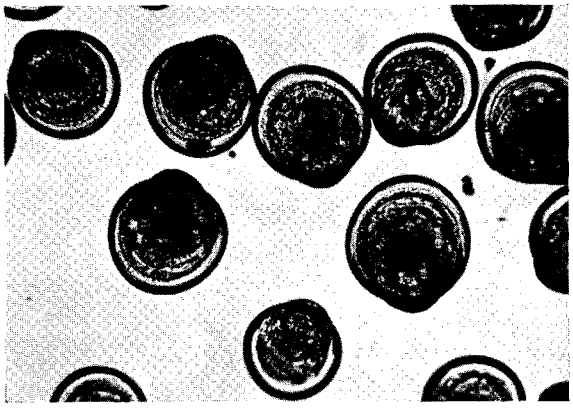

FIG. 43. Late larval stages of *Teredo navalis*. Largest larva in the group is about 185 μ long and 200 μ wide. Note dark band around edge of shell characteristic of larvae of this species.

around the edge of the shell from one end of the hinge to the other (Fig. 43). A light band was quite conspicuous inside of this dark band. Although these bands are probably optical illusions resulting from curvature of the shell seen under the microscope, they are well pronounced. The bands are quite narrow and less conspicuous in larvae smaller than 90 μ in length but, nevertheless, they are present even in these small individuals. As larvae approach setting size, the bands become less sharply delineated, although they remain quite prominent.

The color of larvae begins to darken soon after they reach 100 μ in length. Imai *et al.* (1950a) also came to the same conclusion. However, while Imai reported that neither the foot, otocyst or gill filament appears before larvae reach the size of 200 $\times$ 215 μ, we observed their appearance in larvae at least 15 μ smaller.

Imai *et al.* (1950b) gave a table showing growth of *T. navalis* larvae from day to day, indicating length–width relationships during different stages of growth. These data closely resemble ours. Other observations of these authors on appearance and behavior of larvae are also in close agreement with ours.

Larvae of *T. navalis* are extremely active and usually swim vigorously and virtually continuously. This is particularly true of younger stages. We noticed that the larvae have some substance on the outside of their shells by means of which they adhere readily to glassware and, as a result, it is extremely difficult to rinse them from beakers, pipettes, slides, etc.

Larvae began to metamorphose soon after a length of 200 μ was reached. However, several fully-metamorphosed individuals measuring only 190 μ in length and 206 μ in width were seen. The largest swimming larvae were approximately 200 $\times$ 231 μ. Our maximum size of free-swimming larvae of the wood-borer is, therefore, somewhat smaller than the 220 $\times$ 250 μ reported by Sullivan (1948), but closely approaches that given by Imai *et al.* (1950).

Larvae of advanced stages do not develop an " eye " that is characteristic of larvae of corresponding stages of other species, such as *C. virginica*. The foot of recently set borers is extremely slender and worm-like. The set attach themselves to the substratum by means of a byssus.

The time required for larvae in our cultures to reach metamorphosis varied. Early in our work, before good food organisms became available, the first metamorphosing larvae were observed 20 days after swarming, when grown at room temperature. If better growing conditions were provided, the free-swimming period could undoubtedly be shortened. Nevertheless, we strongly disagree with the conclusions of Lane *et al.* (1954) that the normal free-swimming period of *Teredo* larvae does not exceed 4 days.

Teredo larvae are quite susceptible to fungus diseases. Such infections were observed on numerous occasions and were probably responsible for the complete mortalities of *Teredo* larvae in some of our cultures.

VI. Acknowledgments

Our studies, which provided most of the material for this article, have been continuous since 1944 and, naturally, during this time many people have participated either directly or indirectly. We want to express our appreciation to all biologists of our laboratory, especially to Mr. Paul E. Chanley, who grew larvae of the several species of

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