Pacific Science (1985), vol. 39, no. 3

Development of the Seastar, *Astropecten gisselbrechti* Döderlein[1]

MIÉKO KOMATSU[2] and SATOSHI NOJIMA[3]

ABSTRACT: The entire process of development from eggs to juveniles in the seastar *Astropecten gisselbrechti* was observed, with special attention to the external morphology and formation of the skeletal system. The breeding season of this seastar along the coast of Tsuyazaki (33°47′ N, 130°28′ E), Fukuoka Prefecture, Japan, is in June. The eggs are 353 μm average diameter, semitranslucent, and pale brown in color. Development proceeded as follows at 25°C: Embryos develop through a wrinkled blastula stage that lasts about 5 hr (from 5 hr after insemination) by total and equal cleavage. Gastrulae bearing an expanded distal portion of the archenteron hatch from the fertilization membrane 15 hr after insemination. Gastrulae develop into barrel-shaped larvae $1\frac{1}{2}$ days after insemination. The larva is free-swimming, and is neither bipinnaria nor brachiolaria because it lacks an open larval mouth, arms, and ciliary bands. Rudiments of the adult skeletal plates appear at this time. Metamorphosis is completed 4 days after insemination, mostly by absorption of the stalk, a larval organ, or rarely by rupture of the stalk. The newly metamorphosed juvenile is 650 μm in diameter and bears two pairs of tube-feet on each arm. This is the third reported observation of a barrel-shaped larva in asteroids.

DEVELOPMENT OF SEASTARS belonging to the genus *Astropecten* has so far been described in six species. Among these, the entire process of development from eggs to juveniles has been observed in only three species: *A. aranciacus* (Hörstadius 1939), *A. latespinosus* (Komatsu 1975*a*), and *A. scoparius* (Oguro, Komatsu, and Kano 1976). Although larvae of the remaining species, *A. irregularis*, *A. polyacanthus*, and *A. velitaris*, have been reported, descriptions of their development are fragmentary (Mortensen 1921, 1937; Newth 1925; Oguro, Komatsu, and Kano 1975). The larvae of all these *Astropecten* species, except *A. latespinosus*, are bipinnariae. Since their bipinnariae begin to metamorphose without passing through a brachiolaria stage, the development of *Astropecten* is fundamentally nonbrachiolarian. On the other hand, the larvae of *A. latespinosus* are barrel-shaped. *Ctenopleura fisheri*, which also belongs to Astropectinidae, is the only other species reported to have a barrel-shaped larva (Komatsu 1982). Eggs of *A. latespinosus* and *C. fisheri* are 300 and 460 μm in diameter, respectively. The largest egg among the other five *Astropecten* species, whose larvae are bipinnariae, is observed in *A. scoparius* and measures 230 μm. The authors are of the opinion that the occurrence of the barrel-shaped larvae is intimately associated with the size of the ova in the Astropectinidae, whose development is generally of the nonbrachiolarian type. The mature ova of *A. gisselbrechti* are larger than those of the other members of *Astropecten* whose development has been reported. It is therefore of interest to observe the development of this species.

The present paper describes the development of *Astropecten gisselbrechti* through metamorphosis, with special attention to the

[1] This study was supported in part by grant no. 574290 to M. Komatsu from the Ministry of Education, Science and Culture of Japan. Manuscript accepted 20 February 1985.

[2] Toyama University, Department of Biology, Faculty of Science, Toyama 930, Japan.

[3] Kyushu University, Amakusa Marine Biological Laboratory, Amakusa, Kumamoto 863–25, Japan.

external morphology and formation of the skeletal system. One notable finding of the present study is that, as predicted because of the fairly large egg size, this seastar is the third species among the Astropectinidae found to have a barrel-shaped larva, as in *A. latespinosus* and *C. fisheri*.

MATERIALS AND METHODS

Adults of *Astropecten gisselbrechti* Döderlein were collected along the coast of Tsuyazaki (33°47′ N, 130°28′ E), Fukuoka Prefecture, Japan, on 18–19 June 1981. A number of fertilized eggs were obtained as a result of natural spawning that occurred while adult specimens were being transported in an ice chest with seawater.

In addition to the natural fertilization, successful artificial fertilization was realized as follows: Fertilizable ova were obtained by treating excised ovaries with 1-methyladenine according to Kanatani (1969). A dilute sperm suspension was added to the vessels containing mature ova to effect insemination. Embryos and juveniles were reared in glass vessels at about 25°C. Observations were made with a dissecting microscope and a light microscope. Measurements of living embryos were performed with an ocular micrometer. For microscopic examination of the skeletal system, larvae and juveniles were fixed in 70% alcohol, then macerated in a 10% aqueous solution of potassium hydroxide.

RESULTS

Astropecten gisselbrechti is dioecious. The gonads of both sexes are composed of tufted tubules and are restricted to the base of each arm. Each gonad is furnished with a gonoduct that opens on the aboral side of the arm base. Ovaries are pale brown and testes are milky white. The breeding season of *A. gisselbrechti* along the coast of Fukuoka Prefecture was estimated to be June because of the occurrence of spawning and the success of artificial fertilization.

Mature ova were spherical, pale brown in color, and semitranslucent; the mean diameter was $353 \pm 4.6\,\mu m$ (mean $\pm$ SE, $n = 17$). Ova were enclosed in a jelly layer about 15 μm thick and were heavier than seawater, so they settled to the bottom of the culture vessel. The fertilization membrane was apparent about 5 min after insemination. The height of the perivitelline space was about 50 μm 30 min later (Figure 1*A*). The first and second polar bodies were visible in the perivitelline space. First cleavage occurred on a plane through the animal and vegetal poles 60 min after insemination, and subsequent cleavages took place at intervals of about 20 min. Cleavage was total and equal (Figure 1*B*). The embryos were in the 4-cell stage 1.5 hr after insemination and in the 32-cell stage 1.0 hr later. They developed into coeloblastulae 4.0 hr after insemination. The wrinkled blastula stage began with the appearance of egression tracts on the surface 5.0 hr after insemination (Figure 1*C*). Subsequently, the egression tracts gradually increased in number and size. Wrinkling of the blastula reached its most prominent stage 7.0 hr after insemination (Figure 1*D*). Thereafter, the egression tracts decreased in number and complexity. The wrinkled stage lasted about 5 hr. Gastrulation took place at the vegetal pole 9.5 hr after insemination, before the complete disappearance of the egression tracts. Twelve hours after insemination, early gastrulae were nearly spherical and were 450 μm in diameter (Figure 1*E*). A conspicuous rounded blastopore about 150 μm in diameter was noticed in the vegetal polar area. At this time, the gastrulae were slowly rotating within the fertilization membrane.

Hatching took place and the gastrulae became free-swimming larvae 15 hr after insemination. They were oval in shape, 525 μm in length, and 500 μm in width. The blastopore, now about 100 μm in diameter, was noticed at the center of the broadened posterior portion of each larva. The archenteron, extending half the length of the larva, consisted of two distinguishable parts, an expanded distal portion and a basal portion, the stem. At this stage mesenchyme cells were released from the tip of the expanded portion of the archenteron. Twenty hours after insemination, coelomic pouches appeared as lateral bulges on

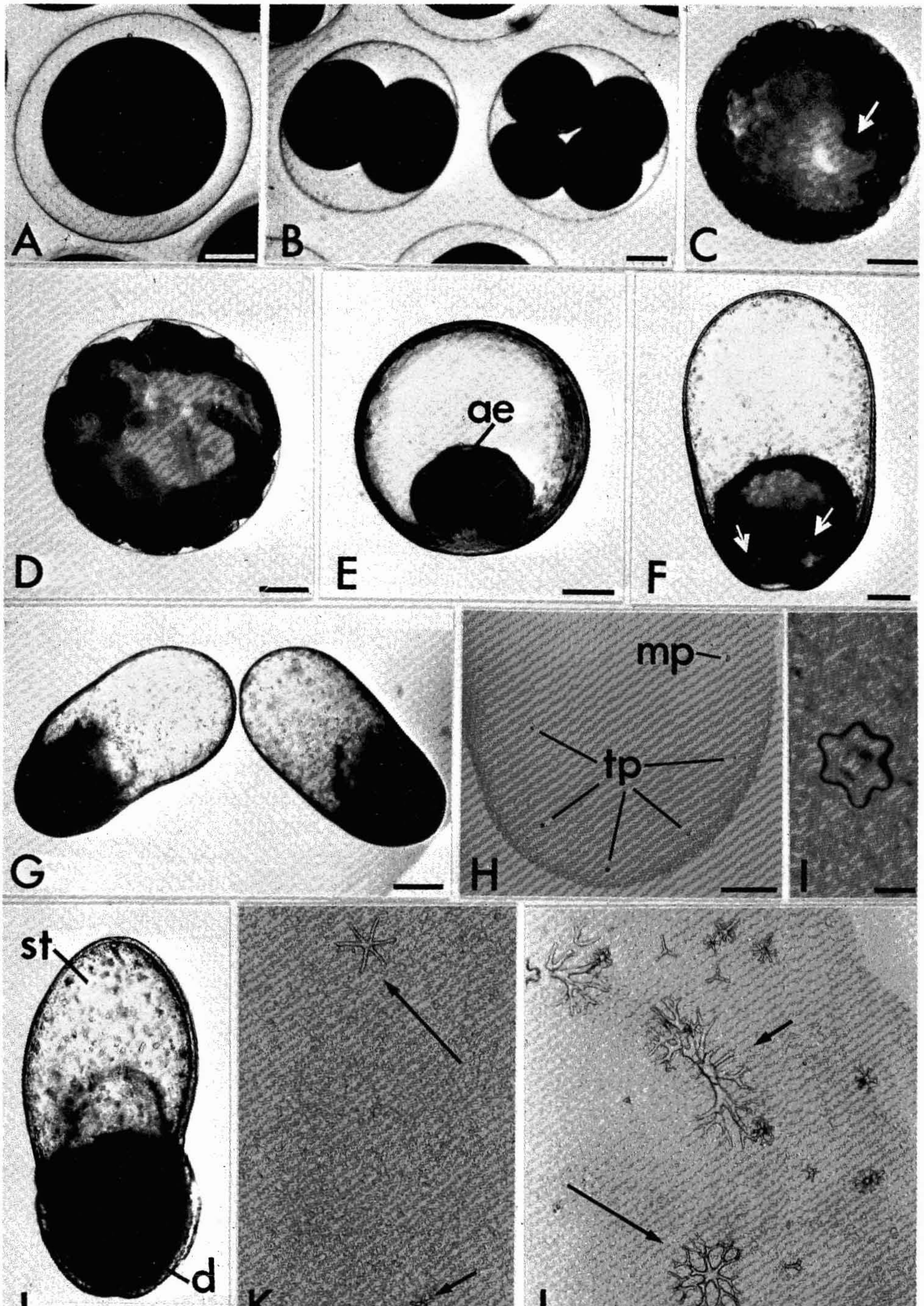

FIGURE 1. Development of *Astropecten gisselbrechti*: *A*, fertilized egg; *B*, two-cell and four-cell stages; *C*, early wrinkled blastula, arrow points to egression tract; *D*, blastula in its most wrinkled stage; *E*, early gastrula, 12 hr after insemination; *F*, gastrula with coelomic pouches (arrows) in the archenteron, 24 hr after insemination; *G*, two barrel-shaped larvae oriented opposite to each other, one (right) shows the future aboral side of the larval disk and the other the future aboral side, 1.5 days after insemination; *H*, larval disk showing rudimentary skeletal plates, same stage as shown in Figure 1*G*; *I*, magnified view of one terminal plate of the specimen shown in Figure 1*H*; *J*, larva, 2 days after insemination; *K*, central plate (short arrow) and madreporic plate (long arrow), same stage as shown in Figure 1*J*; *L*, part of the skeletal plates of a larva, 2.5 days after insemination, view of future aboral side of the disk (short and long arrows indicate terminal plate and madreporic plate, respectively). ae, archenteron; d, disk; mp, madreporic plate; st, stalk; tp, terminal plate. Scale = 100 μm in *A–F*, *H*, *J*; scale = 200 μm in *G*; scale = 5 μm in *I*; scale = 50 μm in *K*, *L*.

either side of the expanded distal portion of the archenteron. Four hours later, the posterior end of each coelomic pouch had almost reached the inner part of the posterior body wall of the larva (Figure 1*F*). By this stage, the larvae had grown to 800 μm in length and most of them swam near the bottom of the culture vessels. Subsequently, organogenesis commenced in the posterior portion of the larvae, but this could not be observed in detail because of the opacity of this portion.

Figure 1*G* shows two larvae 1.5 days after insemination. As is obvious from the figure, each larva is ellipsoid and is furnished with neither arms nor suckers; they were 875 μm in length and 370 μm in width. No definite ciliary bands were observed nor was there an opening of the larval mouth. The blastopore was no longer visible at this stage. The larva of this species is thus very similar in appearance to the barrel-shaped larvae of *Astropecten latespinosus* and *Ctenopleura fisheri*. At this stage, formation of the adult skeletal plates began as fine spicules in the embryo's posterior portion, which forms the main part of the adult disk after metamorphosis (Figure 1*H*). These spicules correspond to the rudiments of the madreporic plate and the terminal plate. They were hexagonal with a knob in their center and were approximately 10 μm in diameter (Figure 1*I*). Two days after insemination, the posterior portion of the larva was thicker than the anterior portion and it was distinct from the anterior portion (Figure 1*J*). The former may be called a larval disk since it forms a main part of the adult disk after metamorphosis as mentioned above. The anterior portion of the larva corresponds to the stalk, a larval organ. At this time, five hydrolobes were recognized within the future oral side of the larval disk. Near the center of the future aboral side of the larval disk, a pentaradiate primary central plate about 20 μm in diameter was noticed (Figure 1*K*). The rudimentary madreporic plate, which was hexaradiate and about 50 μm in diameter, was situated between a pair of the terminal plates in an interradius. Thereafter, development of the skeletal system further proceeded in the larval disk. Two and a half days after insemination, the madreporic plate and the terminal plates became larger and more branched (Figure 1*L*). The terminal plate was furnished with several spines, the longest of which was 35 μm in length.

Metamorphosis climaxed about 2.5 days after insemination. It was interesting that the stalk of the larva disappeared in two different ways. In most larvae, the stalk began to grow smaller while the larvae were swimming near the bottom of the culture vessels (Figure 2*A*), and soon thereafter, the regressing stalk shrank rapidly (Figure 2*B*). It was finally absorbed into the larval disk within half a day after the beginning of its reduction. In a few larvae,the stalk began to rupture (Figure 2*K*, *L*). When the stalk partly ruptured in its anterior portion, the remainder was completely absorbed into the larval disk. On the other hand, when almost all the stalk ruptured, the remainder proceeded to collapse entirely while the larvae were floating near the surface of the water (Figure 2*M*). Regardless of whether the stalk disappeared by absorption or rupture, the larvae were 500 μm in diameter 3 days after insemination (Figure 2*C*). They sank to the bottom and produced one pair of tube-foot buds on the future oral side of each arm. The skeletal system was well formed at this stage (Figure 2*D*). Each of the terminal plates bore more than 12 spines, of which the longest was 100 μm in length. On the future oral side, five pairs of oral plates were recognized. Several dorsal plates, which could not be identified as radial plates or interradial plates, were formed around the central plate.

Four days after insemination, the mouth opened, signaling the completion of metamorphosis (Figure 2*E*). Juveniles were about 650 μm in diameter just after the completion of metamorphosis. They were white except for the disk, in which the digestive organ was visible as a yellowish structure. Two pairs of tube-feet and one terminal tentacle were present on each arm. Figures 2*F* and 2*G* show the skeletal system of the juvenile in this stage. The madreporic plate, measuring about 70 μm in diameter, was situated in an interradius of the aboral side of the disk. Dorsal plates, including the central plate, had a spine in the center. On the oral side, five pairs of ambulacral plates, in addition to the oral plates,

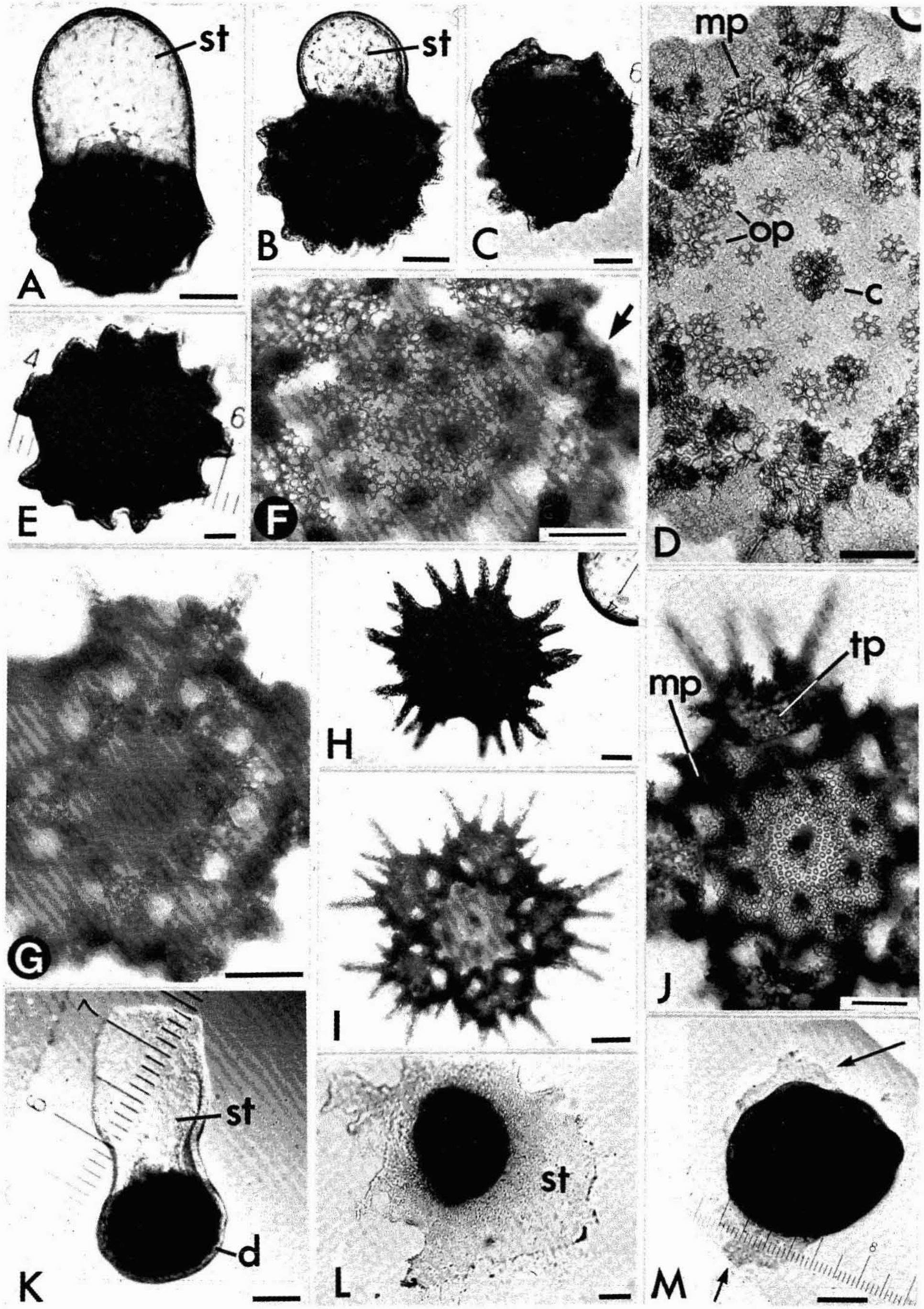

FIGURE 2. Development of *Astropecten gisselbrechti*: *A*, larva with shrunken stalk, 2.5 days after insemination; *B*, larva with a more reduced stalk; *C*, larva without the stalk, 3 days after insemination; *D*, skeletal plates, same stage as shown in Figure 2*C*, future aboral view; *E*, juvenile just after the completion of metamorphosis, aboral view; *F*, aboral skeletal plates of a juvenile, same stage as shown in Figure 2*E* (arrow indicates madreporic plate); *G*, opposite side of the specimen shown in Figure 2*F*; *H*, juvenile, 5 days after insemination, aboral view; *I*, skeletal system of a juvenile, 10 days after insemination, oral view; *J*, part of the aboral skeletal system of the speciman shown in Figure 2*I*; *K*, larva that has lost the anterior portion of its stalk by rupture; *L*, larva with ruptured stalk; *M*, larva with remainder of its collapsed stalk (arrows). c, central plate; d, disk; mp, madreporic plate; op, oral plate; st, stalk; tp, terminal plate. Scale = 100 μm in *A–E*, *G–M*; scale = 10 μm in *F*.

were clearly recognized. Five days after insemination, juveniles, which had four long spines about 100 μm in length at the top of each of five arms, moved around on the bottom using tube-feet (Figure 2*H*). At this stage, an eyespot of brilliant red appeared on the base of the oral side of each terminal tentacle. Five days later, the juveniles grew to about 800 μm in diameter. Each arm bore one pair of adambulacral plates, each of which was furnished with one spine on the oral side (Figure 2*I*). The aboral side was covered with many porous dorsal plates (Figure 2*J*).

DISCUSSION

Although the larval forms of the asteroids have been established as bipinnaria and brachiolaria, a barrel-shaped larva was reported in *Astropecten latespinosus* (Komatsu 1975*a*). This peculiar type of larva has since been reported only in *Ctenopleura fisheri*, which also belongs to the family Astropectinidae (Komatsu 1982). In the present study, it was found that *A. gisselbrechti* develops through a barrel-shaped larva similar to that reported in *A. latespinosus* and *C. fisheri*. This is thus the third reported observation of this type of larvae.

It is of interest that all the barrel-shaped larvae so far described occur in species belonging to the family Astropectinidae. All *Astropecten* species whose development has been described so far, except for *A. latespinosus* and the present species *A. gisselbrechti*, develop through only bipinnaria; therefore, their development is of the nonbrachiolarian type (Oguro, Komatsu, and Kano 1976). The bipinnaria of the nonbrachiolarian type differs from that in the indirect type of development which passes through both the bipinnaria and the most advanced larval stage, a brachiolaria, since it undergoes metamorphosis without passing through the brachiolaria. During metamorphosis, the brachiolariae in either direct or indirect type of development generally attach to the substratum by their arms and fixing disk (Barker 1977, Gemmill 1914, Greer 1962, Yamaguchi 1973). On the other hand, the bipinnariae of the *Astropecten* species initiate metamorphosis while they are pelagic. Initiation of metamorphosis in the pelagic state was also observed in the barrel-shaped larvae at metamorphosis. In fact, the barrel-shaped larva lacks both arms and fixing disk.

It has been pointed out that early formation of the madreporic plate is associated with the nonbrachiolarian type of development (Oguro, Komatsu, and Kano 1976), which is so far limited to the species of only two genera, *Astropecten* and *Luidia* (Komatsu, Oguro, and Kano 1982, Oguro, Komatsu, and Kano 1976). In the seastars belonging to these two genera, the madreporic plate appears at the same time that rudimentary adult skeletal plates form during metamorphosis and is distinguishable from the other dorsal plates (Hörstadius 1939; Komatsu, Oguro, and Kano 1982; Mortensen 1938; Oguro, Komatsu, and Kano 1976). On the other hand, newly metamorphosed juveniles belonging to genera other than *Astropecten* and *Luidia* bear no madreporic plate, and the rudiment of the madreporic plate appears long after the completion of metamorphosis (Fewkes 1888, Komatsu 1975*b*, Komatsu et al. 1979, MacBride 1896). In *Leptasterias ochotensis similispinis*, for instance, the madreporite becomes recognizable in specimens with 20 pairs of tube-feet in each arm (Kano, Komatsu, and Oguro 1974). In *A. gisselbrechti*, the madreporic plate, as well as the rudiments of some other dorsal plates, was formed during metamorphosis. Likewise, early formation of the madreporic plate was observed in *A. latespinosus* and *Ctenopleura fisheri*. This is a characteristic of the nonbrachiolarian type of development also observed in the species having a barrel-shaped larva. These facts all suggest that development with a barrel-shaped larva is a modification of the nonbrachiolarian type of development.

Among asteroids of different species, the size of the eggs ranges from 100 μm diameter in *Acanthaster planci* (Henderson 1969) to 1.0–1.2 mm diameter in *Mediaster aequalis* (Birkeland, Chia, and Strathmann 1971), although exceptionally large eggs (more than 2.5 mm diameter) were reported in some species (Hayashi 1972). The egg diameters in

Astropecten latespinosus, *A. gisselbrechti*, and *Ctenopleura fisheri*, whose larvae are barrel-shaped, are 300, 353, and 465 μm, respectively. Thus, the eggs that develop into barrel-shaped larvae seem to be of medium size among those of asteroids. Small seastar eggs that develop into brachiolariae through bipinnariae (indirect development) are generally translucent, while large ones that develop directly into brachiolariae (direct development) are opaque and colored. Eggs of *A. latespinosus*, *C. fisheri*, and *A. gisselbrechti* that develop into barrel-shaped larvae are all semitranslucent. The largest egg among the *Astropecten* species passing through a bipinnaria stage (nonbrachiolarian type of development) is that of *A. scoparius*; it measures 230 μm in diameter and is translucent (Oguro, Komatsu, and Kano 1976). Eggs forming barrel-shaped larvae are thus larger than those forming bipinnaria.

In seastars belonging to the genus *Astropecten*, species with a barrel-shaped larva complete metamorphosis in a shorter time than those passing through a bipinnaria. For example, *A. gisselbrechti* and *A. latespinosus*, whose larvae are barrel-shaped, complete metamorphosis within 4 and 5 days after insemination at 25°C, respectively. It takes 15 days to complete metamorphosis in *Ctenopleura fisheri* (at 17°C). On the other hand, it takes about 80 days to complete metamorphosis in *A. aranciacus* at 15°C (Hörstadius 1939) and 18 days in *A. scoparius* at 25°C (Oguro, Komatsu, and Kano 1976). Larvae of these latter two species are bipinnariae. The barrel-shaped larvae depend totally on stored yolk for their nutrition because the mouth is not open. It is known that the majority of species undergoing direct development, whose larvae are brachiolariae also without a larval mouth, have an extremely long larval life before the completion of metamorphosis. It takes 36, 38, 38–42, and 49 days to complete metamorphosis in *Certonardoa semiregularis* (Hayashi and Komatsu 1971), *Mediaster aequalis* (Birkeland, Chia, and Strathmann 1971), *Crossaster papposus* (Gemmill 1920), and *Leptasterias hexactis* (Chia 1968), respectively. Eggs of these species are large, approx. 1.0 mm in diameter, and opaque. Although the composition of the material stored in their eggs has not been determined, it seems likely that relatively large and opaque eggs contain more yolk than the smaller and translucent eggs that give rise to feeding bipinnaria larvae.

As mentioned above, the eggs that develop into barrel-shaped larvae are medium-sized and semitranslucent. Therefore, it is very probable that the storage content of the eggs is less than that of large and opaque eggs. Thus, the barrel-shaped larva is nonfeeding but does not have enough yolk to complete metamorphosis after passing through a long larval life. If this is the case, then it is quite predictable that the barrel-shaped larvae complete metamorphosis within a short term.

Mortensen (1972) noted that in *Luidia*, the stalk, a larval organ, is thrown off during metamorphosis. However, the larval organ of the bipinnaria of *L. quinaria* is not thrown off, but is absorbed into the future body of the juvenile through metamorphosis (Komatsu, Oguro, and Kano 1982). It has been suggested that the separation of the larval organ is one of the characters of the large-size larvae of asteroids. This idea is also realized in the barrel-shaped larvae of *Astropecten latespinosus* and *Ctenopleura fisheri* (Komatsu 1982). The larva of *C. fisheri* is 1500 μm in length, and this is about twice the length of the *A. latespinosus* larva (700 μm). The larval organ of *C. fisheri* disappears by one of two different processes: absorption into the future body of the juvenile or rupture and collapse (Komatsu 1982). On the other hand, in *A. latespinosus*, the only way the larval organ disappears is by absorption (Komatsu 1975*a*). It was observed that in the majority of the barrel-shaped larvae of *A. gisselbrechti* the stalk disappeared through absorption into the future bodies of the juveniles during the metamorphic climax. In a few larvae, however, the stalk ruptured. It is probable that the larvae of *A. gisselbrechti*, which are 900 μm in length and larger than in *A. latespinosus*, exhibit not only absorption but rupture of the stalk in some cases as a normal process.

ACKNOWLEDGMENTS

The authors are indebted to Yasuo Yone, Akinobu Nakazono, and members of the Fishery Research Laboratory, Kyushu University, for their kind cooperation in providing facilities. They wish to express their cordial thanks to Chitaru Oguro, Toyama University, for his critical reading of the manuscript.

LITERATURE CITED

BARKER, M. F. 1977. Observations on the settlement of the brachiolaria larvae of *Stichaster australis* (Verrill) and *Coscinasterias calamaria* (Gray) (Echinodermata: Asteroidea) in the laboratory and on the shore. J. Exp. Mar. Biol. Ecol. 30:95–108.

BIRKELAND, C., F.-S. CHIA, and R. R. STRATHMANN. 1971. Development, substratum selection, delay of metamorphosis and growth in the seastar, *Mediaster aequalis* Stimpson. Biol. Bull. 141:99–108.

CHIA, F.-S. 1968. The embryology of a brooding starfish, *Leptasterias hexactis* (Stimpson). Acta Zool. 49:321–364.

FEWKES, J. W. 1888. On the development of the calcareous plates of *Asterias*. Bull. Mus. Comp. Zool., Harvard 17:1–56.

GEMMILL, J. F. 1914. The development and certain points in the adult structure of the starfish *Asterias rubens* L. Phil. Trans. R. Soc. London, Ser. B 205:213–294.

———. 1920. The development of the starfish *Crossaster papposus*, Müller and Troschel. Quart. J. Micr. Sci. 64:155–189.

GREER, D. 1962. Studies on embryology of *Pycnopodia helianthoides* (Brandt) Stimpson. Pac. Sci. 16:280–285.

HAYASHI, R. 1972. On the relations between the breeding habits and larval forms in asteroids, with remarks on the wrinkled blastula. Proc. Jap. Soc. Syst. Zool. 8:42–48.

HAYASHI, R., and M. KOMATSU. 1971. On the development of the sea-star, *Certonardoa semiregularis* (Müller et Troschel) I. Proc. Jap. Soc. Syst. Zool. 7:74–80.

HENDERSON, J. A. 1969. Preliminary observations on the rearing and development of *Acanthaster planci* (L.) (Asteroidea) larvae. Fish. Notes 3:69–75.

HÖRSTADIUS, S. 1939. Über die Entwicklung von *Astropecten aranciacus* L. Pubbl. Staz. Zool. Napoli 17:221–312.

KANATANI, H. 1969. Induction of spawning and oocyte maturation by 1-methyladenine in starfishes. Exp. Cell Res. 57:333–337.

KANO, Y. T., M. KOMATSU, and C. OGURO. 1974. Notes on the development of the sea-star, *Leptasterias ochotensis similispinis*, with special reference to skeletal system. Proc. Jap. Soc. Syst. Zool. 10:45–53.

KOMATSU, M. 1975*a*. On the development of the sea-star, *Astropecten latespinosus* Meissner. Biol. Bull. 148:49–59.

———. 1975*b*. Development of the sea-star, *Asterina coronata japonica* Hayashi. Proc. Jap. Soc. Syst. Zool. 11:42–48.

———. 1982. Development of the sea-star *Ctenopleura fisheri*. Mar. Biol. 66:199–205.

KOMATSU, M., C. OGURO, and Y. T. KANO. 1982. Development of the sea-star, *Luidia quinaria* von Martens. Pages 497–530 *in* J.M. Lawrence, ed. Echinoderms: Proceedings of the International Conference, Tampa Bay. A. A. Balkema, Rotterdam.

KOMATSU, M., Y. T. KANO, H. YOSHIZAWA, S. AKABANE, and C. OGURO. 1979. Reproduction and development of the hermaphroditic sea-star, *Asterina minor* Hayashi. Biol. Bull. 157:258–274.

MACBRIDE, E.W. 1896. The development of *Asterina gibbosa*. Quart. J. Micr. Sci. 38: 339–411.

MORTENSEN, T. 1921 Studies of the development and larval forms of echinoderms. G. E. C. Gad, Copenhagen.

———. 1927. Handbook of the echinoderms of British Isles. Oxford University Press, Oxford.

———. 1937. Contributions to the study of the development and larval forms of echinoderms III. K. Dansk. Vidensk. Selsk. Skr., Naturvid. Math. Afd. 9, 7(1):1–65.

———. 1938. Contributions to the study of the development and larval forms of echinoderms IV. K. Dansk. Vidensk. Selsk. Skr., Naturvid. Math. Afd. 9, 7(3):1–59.

NEWTH, H. G. 1925. The early development of *Astropecten irregularis*, with remarks on duplicity in echinoderm larvae. Quart. J. Micr. Sci. 69:519–554.

OGURO, C., M. KOMATSU, and Y. T. KANO. 1975. A note on the early development of *Astropecten polyacanthus* Müller et Troschel. Proc. Jap. Soc. Syst. Zool. 11:49–52.

———. 1976. Development and metamorphosis of the sea-star, *Astropecten scoparius* Valenciennes. Biol. Bull. 151:560–573.

YAMAGUCHI, M. 1973. Early life histories of coral reef asteroids, with special reference to *Acanthaster planci* (L.). Pages 369–387 *in* O. A. Jones and R. Endean, eds. Biology and geology of coral reefs. Vol. 2, Biol. 1. Academic Press, New York.