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DEVELOPMENT, SUBSTRATUM SELECTION, DELAY OF META-MORPHOSIS AND GROWTH IN THE SEASTAR, *MEDIASTER AEQUALIS* STIMPSON

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To understand the functional organization of benthic marine communities, it will be necessary to know more about the nature of recruitment(Thorson, 1957, 1966; Loosanoff, 1964). In general, larvae of benthic animals are selective as to the nature of substratum or micro-habitat in which they set (for examples see Wilson, 1960 and Thorson, 1966), though the degee of specificity may vary with the adult food requirements (Scheltema, 1961). Larvae of certain predators with specific food requirements are known to undergo metamorphosis selectively on the epidermis or other surfaces of the adult's prey (Thompson, 1964). In this report we examine the larval biology of an asteroid which is capable of exploiting a wide range of both foods and habitats, and we examine one habitat which appears favorable for a variety of juvenile asteroids.

Mediaster aequalis Stimpson has the most catholic diet recorded for a seastar (Mauzey, Birkeland and Dayton, 1968). It feeds on plants of at least four phyla, sessile and motile animals of at least nine phyla, detritus and apparently suspended material. *M. aequalis* is found commonly on mud, sand, cobble and rock substrata and is recorded from the low intertidal (unpublished observations) to depths of at least 274 m (Fisher, 1911, page 200). The adults are thus quite broad in their survival requirements and it might be predicted that *M. aequalis* would settle and undergo metamorphosis under a wide variety of conditions. As the larvae are lecithotrophic, possessing no functional mouth nor gut, it might also be predicted that their ability to prolong their larval life when failing to encounter environments suitable for metamorphosis might be severely limited. Neither prediction appears to be true for *M. aequalis.*

Observations and Results

Spawning

The breeding season of *Mediaster aequalis* in Puget Sound and near the San Juan Islands is probably late March through May. Specimens of *M. aequalis* were seen spawning in the field in late April of 1967 and those kept in running sea water at Friday Harbor Laboratories spawned in late March of 1969. Larvae

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which appeared to be *M. aequalis* were found in the plankton near Friday Harbor on 30 May 1970. Animals collected in late July 1970 had spent gonads. However, animals held for long periods in aquaria at Friday Harbor spawned as late as July in 1967 and 1968.

An upper estimate of egg number was calculated for a ripe *M. aequalis* 13 cm in diameter, about the median size of the *M. aequalis* at the field site. The egg volume is about 0.7 mm^3; the gonad volume before spawning about 1.25 ml. If spawning occurs once a year, such an individual contributes less than 1800 eggs annually.

Development

The oocytes are opaque and bright orange and are about 1.0 to 1.2 mm in diameter (Fig. 1). The color persists throughout development and metamorphosis

TABLE I

Chronology of normal development of M. aequalis *at 9 to 11° C and with tubes of* Phyllochaetopterus *as a substratum for settling*

Time	Stage
0 hr	Eggs fertilized
4 hr	1st cleavage
2 days	Morula; early blastula with numerous surface furrows
3 days	Late blastula with few surface furrows
4 days	Gastrula with large blastopore
5 days	Hatched gastrula with small blastopore, surface furrows disappear, elongating along A-V axis
9–10 days	Developing brachiolar arms visible
16 days	Adhesive disk developed
30 days	Larvae fully developed with adult spines visible; larvae have sunk to the bottom and temporarily attached by the brachiolar arms
38 days	Attachment by adhesive disk and completion of metamorphosis by some larvae
14 months	Larvae still capable of metamorphosis

and is similar to that of the adult. The slightly pear-shaped oocytes are buoyant and float at the surface of the water with the large end up. They are surrounded by a layer of striated jelly and the polar bodies appear after shedding.

The fertilization membrane is low. Cleavage appears to be holoblastic and seems to follow the typical pattern of radial cleavage in echinoderms. The chronology of development is given in Table I.

The surface of the blastula is furrowed and is probably infolded like that of *Leptasterias hexactis* (Chia, 1968). The number of surface furrows decreases so that eventually the bastula resembles an embryo at the earlier cleavage stages. One of the surface furrows of the blastula becomes recognizable as the blastopore, which is at first large and irregular. The embryos hatch as ciliated, swimming gastrulae which are still buoyant. As the larva elongates to about 1.9 mm, the blastopore becomes small and round, moving to the ventral side about 0.5 mm from the posterior end. The other furrows disappear.

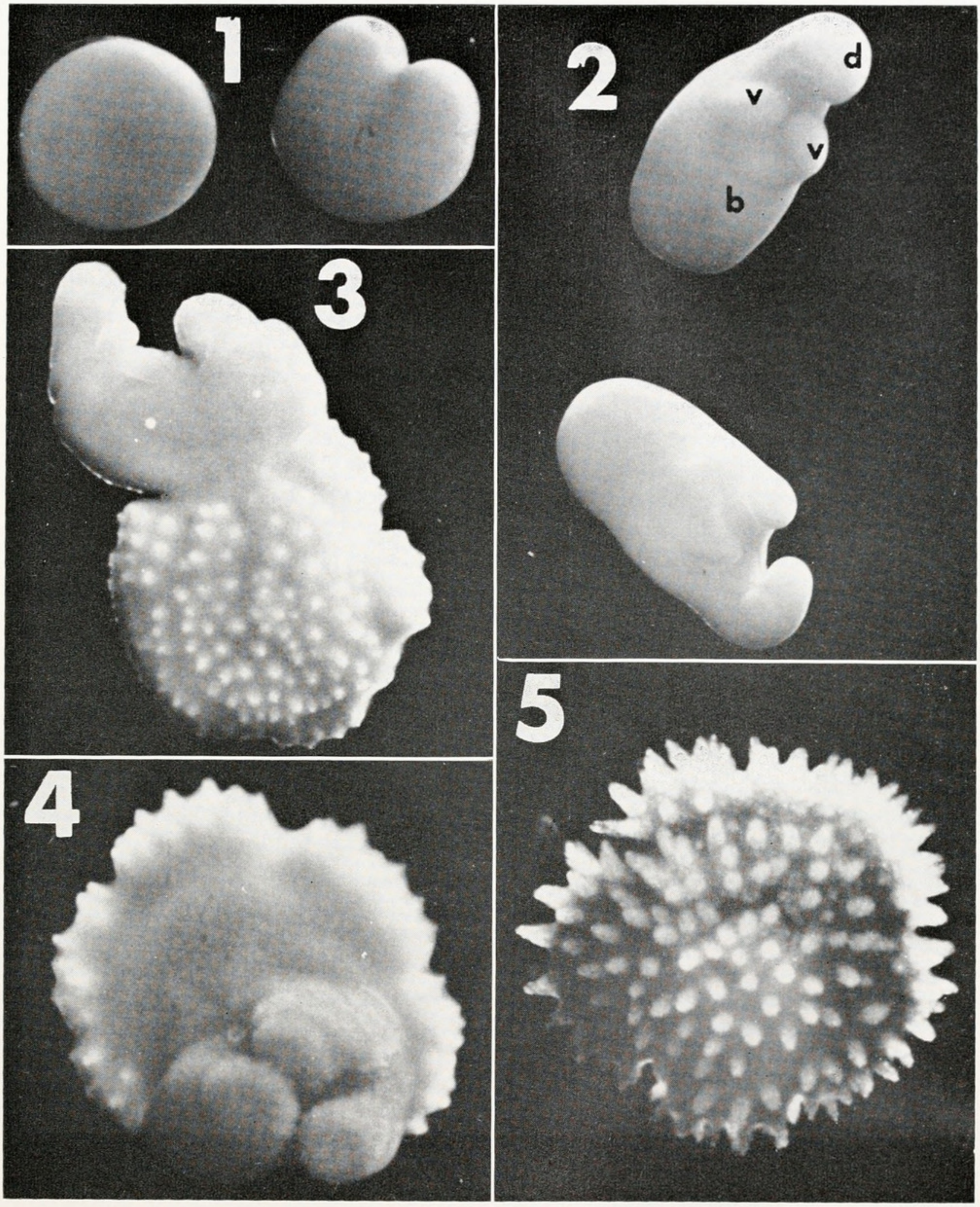

FIGURE 1. Zygote (left); first cleavage beginning (right).

FIGURE 2. Young brachiolaria larvae showing the preoral lobe with three brachiolar arms, one median antero-dorsal (d) and two ventro-lateral (v), and the larval body (b).

FIGURE 3. Advanced brachiolaria larva. Adult spines and rudiments of rays are seen on the larval body.

FIGURE 4. Oral view of metamorphosing juvenile. The preoral lobe is being absorbed (bottom). The mouth has not yet opened.

FIGURE 5. Aboral view of a post-metamorphosis juvenile with extended tube foot visible at upper left.

The larva is lecithotrophic and entirely lacking in feeding structure or mouth, but can be considered a modified brachiolaria. Ten days after fertilization three brachiolar arms, one median anterodorsal and two ventrolateral, begin to form. After 16 days the brachiolar arms are able to adhere to glass needles and pipets and the adhesive disk is visible (Fig. 2). As the brachiolar arms and adult structures develop, the larvae become less buoyant and spend more time at the bottom of the culture dish. Eventually swimming becomes greatly reduced or stops altogether. The fully developed brachiolaria (Fig. 3) is about 2.2 mm long. The form of the brachiolar arms is quite variable. Most individuals have three distinct arms, but some appear to have four, apparently from a division of the antero-dorsal arm. The disk of the starfish at the posterior end of the larva is about 1.2 to 1.3 mm across. The adult mouth and tube feet do not form until after the larva has permanently attached to the bottom. We could see no further development prior to settling.

Fully developed larvae temporarily attach themselves to the glass dish by their brachiolar arms, but in settling, the final attachment is with the adhesive disk. The preoral lobe, which includes the brachiolar arms and adhesive disk, is absorbed (Fig. 4). Metamorphosis is then considered to be complete. The juvenile, about 1.3 mm in diameter, begins its benthic life with two pairs of tube feet per arm. The five arms are of uneven size and difficult to distinguish in aboral view (Fig. 5).

Choice of substratum and delay of metamorphosis

At 25 to 30 days after fertilization the larvae from the 28 March 1969 spawning were temporarily attaching to the glass by their brachiolar arms and appeared ready to settle. At 29 days after fertilization, four substrata which seemed favorable for settling were provided in separate culture dishes. These were (1) two juvenile *Mediaster aequalis* (2.5 cm diameter); (2) sand from an area where adult *M. aequalis* are found; (3) same as (2) but with two small sea pens *Ptilosarcus gurneyi* Gray (1.0 to 1.5 cm tall); and (4) same as (2) but with tubes of the polychaete *Phyllochaetopterus prolifica* Potts (hereafter referred to as *Phyllochaetopterus*). *Ptilosarcus gurneyi* was chosen because it makes up a major portion of the diet of adult *M. aequalis* in the field. *Phyllochaetopterus* tubes were chosen because juvenile specimens of *M. aequalis* are regularly found on them in the field. We set up 3 separate bowls for each kind of substratum, and 3 clean bowls as controls, for a total of 15 cultures. We then placed 15 brachiolaria larvae into each bowl and maintained them at a temperature of 10–14° C on a water table. The results of this test are given in Table II.

The small specimens of *M. aequalis* ate the larvae. We do not know the cause of mortality in the other bowls. Larvae did not settle in plain glass bowls or in the presence of *Ptilosarcus gurneyi*. Larvae first began to settle in the bowls with tubes of *Phyllochaetopterus*, and at 56 days after fertilization, the specimens of *Phyllochaetopterus* appeared to be about 4 times as effective as the sand in inducing settling. Although the larval development in *M. aequalis* had appeared quite synchronous, the fully developed larvae are quite variable in their readiness to settle. At 56 days only half the larvae had settled on the tubes of *Phyllochaetopterus*.

TABLE II

Metamorphosis and mortality of Mediaster aequalis *with different substrata or species present. Test begun 29 days after fertilization*

Substratum or species tested	Dish number	38 days after fertilization			56 days after fertilization		
		# larvae	# died	# metamorphosed	# larvae	# died	# metamorphosed
	1	15	0	0	15	0	0
glass only	2	12	3	0	12	3	0
	3	15	0	0	14	1	0
	1	0	15	0	0	15	0
juvenile *Mediaster*	2	1	14	0	0	15	
	3	2	13	0	1	14	0
	1	15	0	0	10	3	2
sand	2	15	0	0	14	0	1
	3	14	1	0	9	4	2
	1	13	2	0	11	4	0
Ptilosarcus and sand	2	15	0	0	9	6	0
	3	15	0	0	13	2	0
	1	12	1	2	8	3	4
Phyllochaetopterus and sand	2	12	1	2	6	1	8
	3	12	0	3	6	2	7

Tubes of *Phyllochaetopterus* were more effective in inducing settling and metamorphosis in older larvae. When the larvae were 128 days old, 32 of the 33 larvae that were offered *Phyllochaetopterus* tubes settled and metamorphosed within 9 days. None of the 33 control larvae in a plain glass bowl had metamorphosed. By this age a few larvae had settled and metamorphosed in those culture dishes in which algae had been allowed to grow on the glass. Most larvae did not metamorphose until a more favorable substratum (*Phyllochaetopterus*) was available.

Small plants and animals grow on the tubes of *Phyllochaetopterus* and we made no attempt to determine whether the attraction lay in the tubes themselves or the associated organisms.

Six larvae from the 28 March 1969 spawning were still alive after 14 months. They lay on the bottom of the glass bowl, no longer swimming. Deep divisions of the brachiolar arms gave the appearance of a preoral lobe with 6 to 8 brachiolar arms. The spines on the larval body were well developed. The bright orange larvae now appeared translucent. On 23 May 1970 all six were placed in a bowl with *Phyllochaetopterus*. None had undergone metamorphosis 18 days later, but all had undergone metamorphosis after 51 days.

Growth

Juvenile *Mediaster* were collected from beds of *Phyllochaetopterus prolifica* (at a depth of 20 m MLLW) during four dives in fall and winter, 1968–1969.

The mean and range of size of the smallest 10% of those measured are given in Table III. Changes in mean size at the lower end of the size range could result from settling of larvae during this period, differential mortality, or growth. It seems unlikely that many larvae would be settling more than 5 months after spawning. If we attribute increased size to growth alone, then we find growth rates up to 2 mm/month between November and January or 0.5 mm/month over the whole period from September to March. The increases between November and January and between September and March are significant, but so is the unexplained decrease between January and March ($P < 0.01$, 1-way ANOVA). Juveniles reared at 10–14° C in the laboratory with running sea water, sand, and either small *Ptilosarcus gurneyi* or *Phyllochaetopterus* tubes grew only about 0.3 to 0.4 mm/month, attaining diameters of only 2.7 to 3.7 mm at 6 months after metamorphosis (May to November).

One hundred specimens of *Mediaster aequalis* were tagged by hypodermic insertion of individually numbered FD-67 Floy Tags. These are numbered plastic tubes with an internal cross-bar anchor. Only 3 were recovered after periods of greater than 6 months (Table IV). The absolute rate of increase in mean diameter

TABLE III

Size of the smallest 10% of the Mediaster aequalis *found on* Phyllochaetopterus prolifica *in the field*

Date	Size range (dia. in mm)	Mean size (dia. in mm)	No. in 10% of the sample
13 Sept. 1968	2 to 7	4.2	22
24 Nov. 1968	4 to 7	5.8	9
20 Jan. 1969	7 to 12	9.6	11
25 March 1969	4 to 10	7.4	13

of adults (0.7 to 1.1 mm per month) does not appear to be much greater than that of the juveniles. These estimates of juvenile and adult growth rates are similar to the lower estimates reported for other species of asteroids (Kenny, 1969; Swan, 1966). Some observations (Feder and Christensen, 1966) indicate slower growth in the colder part of the year, when our field estimates of juvenile growth were made.

Field observations on juvenile asteroids

The tubes of the polychaete *Phyllochaetopterus* may play a significant role as an "asteroid nursery" in Puget Sound. Recently metamorphosed asteroids (less than 10 mm in diameter) can be found regularly in *Phyllochaetopterus* beds where small *Mediaster aequalis*, *Crossaster papposus* (Linnaeus), *Luidia foliolata* Grube, *Pteraster tesselatus* Fisher, *Henricia leviuscula* Stimpson, *Solaster stimpsoni* Verrill, *S. dawsoni* Verrill and unidentified forcipulates are all common. Small asteroids of all species are often found crawling along the worm tubes with their stomachs everted. They are rarely found on the sand beneath the worm tubes. *Crossaster* (3 and 4 mm in diameter) and *Mediaster* (2 to 4 mm in diameter) have been found on ectoprocts, *Bugula* sp., their stomachs inserted into individual zooecia. Small *Mediaster* and *Pteraster* have been found with their stomachs everted onto the surface of sponges which were growing attached to the *Phyllochaetopterus* tubes. Thus *Phyllochaetopterus* seems to harbor food for very small asteroids of generalized diet. In sand-bottom habitats, tubes of these worms are the only abundant attachment sites for ectoprocts, sponges, colonial and solitary ascidians, brachiopods, hydroids and so on; these animals do not grow to large size on the tubes. Asteroids less than 10 mm in diameter must have a difficult time capturing food; sponges and ectoproct zooids would seem to be suitable prey. Most of the asteroids, however, seem to be feeding generally on microscopic growth of detritus coating the surfaces of the worm tubes. Fifty-one of sixty-four specimens of *M. aequalis* were found with their stomachs everted on the *Phyllochaetopterus* tubes.

Small specimens of *Solaster dawsoni* are found in *Phyllochaetopterus* where they prey upon small asteroids and holothrurians. A 4.8 cm *S. dawsoni,* for example, was seen successfully capturing a 4.9 cm *S. stimpsoni.*

TABLE IV

Growth of adult Mediaster aequalis *in the field*

Total diameter in mm		Time interval in months	Growth (mm diameter)/ month
Beginning	End		
112	123	11.7	0.9
132	138	9.0	0.7
134	141	6.5	1.1

Small (9 and 11 mm) specimens of *Mediaster* on the sand below the worm tubes were, on two occasions, eating ostracods, their stomachs inserted between the valves. Very small bivalves regularly fall prey to slightly larger *Mediaster* and *Crossaster* (10 to 20 mm).

DISCUSSION

Although adult *Mediaster aequalis* occur in many habitats and eat a variety of foods, their larvae are quite selective as to sites for metamorphosis. *M. aequalis* will not settle on clean glass and can postpone metamorphosis for over a year, if suitable substrata are not available. The pelagic larvae of many benthic marine invertebrates delay settling and metamorphosis in the absence of a suitable substratum, becoming less specific in their requirements as time progresses (Thorson, 1966). *Mediaster aequalis* demonstrates the extraordinary length to which such delay of metamorphosis can be carried. Other lecithotrophic, pelagic asteroid larvae have not delayed so long in the laboratory (see, for example, Chia, 1966; Gemmill, 1912, 1920; Kempf, 1966; Mortensen, 1938).

We were surprised that the larvae could survive 14 months and still complete metamorphosis. The larvae cannot feed during this time. If the larva subsists entirely on energy reserves from the egg, the metabolic rate must be quite low.

The larvae might take up dissolved organic matter, as has been reported for adult starfish (Ferguson, 1967), polychaete larvae (Bass, Chapman and Chapman, 1969), and brooded ophiuroid larvae (Fontaine and Chia, 1968), but at least some small organisms excrete more organic matter than they take up (Johannes, Coward and Webb, 1969), so there may be no net gain.

Since the larvae of *M. aequalis* can survive 14 months, they might be termed "long-distance larvae" in the sense of Thorson (1961). However, these larvae probably could not remain pelagic for this long under natural conditions. During the period of delay they tend to sink. Once near the bottom they would probably come in contact with a favorable substratum or be eaten within a fairly short time.

At the location of this study, juvenile *Mediaster aequalis*, and also juvenile *Luidia foliolata*, *Crossaster papposus*, *Henricia leviuscula*, *Solaster stimpsoni*, *S. dawsoni* and *Pteraster tesselatus* were commonly found on tubes of the polychaete *Phyllochaetopterus prolifica* and were rarely found elsewhere. *Phyllochaetopterus* tubes were more effective in inducing settling by *Mediaster* than the other substrata tested. It is therefore tempting to speculate that the beds of *Phyllochaetopterus* tubes, with the associated small organisms, are a favorable "nursery ground" for juvenile starfish, providing an attractive site for settling and an abundance of food in the form of epizoites. After a few years the starfish presumably would move out to the sandy areas and eat larger prey. Our data are consistent with this view but do not prove it correct. Other substrata in nature may be more attractive, or just as attractive, as the tubes of *Phyllochaetopterus prolifica*.

We do not know the extent to which juvenile *M. aequalis* are preyed upon in the beds of *Phyllochaetopterus*. Small *Solaster dawsoni*, a major predator of asteroids, are particularly abundant on *Phyllochaetopterus* tubes, so safety from predation may not be a feature of this habitat. Laboratory observations of the cannibalism by the juveniles on settling larvae suggests a mechanism by which further recruitment might be limited after a heavy set. The observation of *M. aequalis* up to 35 mm in diameter, on *Phyllochaetopterus* suggests that *M. aequalis* may remain on *Phyllochaetopterus* for 2 or 3 years, patrolling the tubes on which the branchiolariae of their species set. A particularly abundant recruitment of *Mediaster* in one year could impose higher mortality on the next two year classes.

The evidence available suggests a very slow growth rate for *M. aequalis*. If *M. aequalis* increases in diameter at a rate no greater than 2 mm per month, then at least 4 years would be required to reach sexual maturity. A median-size adult produces less than 1800 eggs in a single spawning and probably spawns only once a year. The larvae spend at least 4 weeks exposed to the dangers of a planktonic existence. Settling in a favorable habitat and the characteristic of the juvenile formed at metamorphosis are obviously of critical importance to the perpetuation of this abundant species.

Hyman (1955, page 305) remarks that "The baby stars are of microscopic dimensions, less than 1 mm across when developing from small nonyolky types of eggs, 1 to 2 mm across when coming from large yolky eggs." A review of the literature indicates that this remark also applies to planktotrophic development as compared to lecithotrophic development in asteroids. This is confirmed by our experience in regions near Puget Sound where *Pteraster tesselatus, Mediaster aequalis, Solaster stimpsoni* and *Hippasteria spinosa* Verrill with pelagic lecithotrophic larvae form juveniles greater than 1 mm, and *Pisaster ochraceus* (Brandt), *Pycnopodia helianthoides* (Brandt), *Luidia foliolata* and *Patiria miniata* Brandt with pelagic planktotrophic development form juveniles closer to 0.5 or 0.6 mm diameter (Chia, 1966; Greer, 1962; and unpublished observations). A notable exception to this trend in asteroids are the planktotrophic larvae of some species of *Luidia* which produce very large juveniles (Tattersall and Sheppard, 1934). The production of large juveniles by lecithotrophic larvae must necessitate more organic material per egg and therefore fewer eggs than would otherwise be possible. The production of larger juveniles by planktotrophic development probably would require a longer period in the plankton. Presumably larger juveniles have an advantage in obtaining food or avoiding predation. If these assumptions are correct, then the advantage gained by producing a larger juvenile generally exceeds the cost of fewer eggs in asteroids with lecithotrophic development, but is generally less than the cost of a longer period in the plankton in asteroids with planktotrophic development.

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Summary

1. The eggs of *Mediaster aequalis* (Asteroidea, family Goniasteridae) are 1.0 to 1.2 mm in diameter. Development is lecithotrophic with a wrinkled blastula and modified brachiolaria larva. The metamorphosed juveniles are about 1.3 mm diameter. Estimated growth rates are less than 2 mm per month.

2. In the laboratory, *M. aequalis* larvae settled on tubes of the polychaete *Phyllochaetopterus prolifica,* but not on other substrata tested, 38 days after fertilization.

3. If *Phyllochaetopterus* tubes were not present, metamorphosis was postponed. Some larvae survived 14 months and still completed metamorphosis when offered tubes of *Phyllochaetopterus.*

4. In the laboratory, juvenile *M. aequalis* ate settling *M. aequalis* brachiolaria larvae.

5. Juvenile *M. aequalis* and juveniles of several other asteroid species were found commonly on tubes of *Phyllochaetopterus.* Their feeding was observed in the field. Tubes of *Phyllochaetopterus* may play a significant role in the life of asteroids in Puget Sound.

6. In asteroids, lecithotrophic development is generally associated with formation of larger juveniles at metamorphosis (Hyman, 1955). Possible implications of this phenomenon are discussed.

LITERATURE CITED

BASS, N., G. CHAPMAN AND J. M. CHAPMAN, 1969. Uptake of leucine by larvae and adults of *Nereis*. *Nature*, **221**: 476–477.

CHIA, F-S., 1966. Development of a deep-sea cushion star, *Pteraster tesselatus*. *Proc. Calif. Acad. Sci., Series 4*, **34**: 505–510.

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

FEDER, H. M., AND A. M. CHRISTENSEN, 1966. Aspects of asteroid biology. Pages 87–127 in R. A. Boolootian, Ed., *Physiology of Echinodermata*. Interscience, New York.

FERGUSON, J. C., 1967. An autoradiographic study of the utilization of free exogenous amino acids by starfishes. *Biol. Bull.*, **133**: 317–329.

FISHER, W. K., 1911. Asteroidea of the North Pacific and adjacent waters. Part 1. *Phanerozonia* and *Spinulosa*. *Bull. U. S. Nat. Mus., No.* **76**: 1–255.

FONTAINE, A. R., AND F-S. CHIA, 1968. Echinoderms: an autoradiographic study of assimilation of dissolved organic molecules. *Science*, **161**: 1153–1155.

GEMMILL, J. F., 1912. The development of the starfish, *Solaster endeca* (Forbes). *Trans. Zool. Soc. London*, **20**: 1–58.

GEMMILL, J. F., 1920. The development of the starfish, *Crossaster papposus* (Müller and Troschel). *Quart. J. Microscop. Sci.*, **64**: 156–184.

GREER, D. L., 1962. Studies on the embryology of *Pycnopodia helianthoides* (Brandt) Stimpson. *Pacific Science*, **16**: 280–285.

HYMAN, L. H., 1955. *The Invertebrates: Echinodermata*. McGraw-Hill, New York, 763 pp.

JOHANNES, R. E., S. J. COWARD AND K. L. WEBB, 1969. Are dissolved amino acids an energy source for marine invertebrates? *Comp. Biochem. Physiol.*, **29**: 283–288.

KEMPF, M., 1966. On the development of *Echinaster echinophorus*. *Ann. Acad. Brasileira Ciencias*, **38**: 505–507.

KENNY, R., 1969. Growth and asexual reproduction of the starfish *Nepanthia belcheri* (Perrier). *Pacific Science*, **23**: 51–55.

LOOSANOFF, V. I., 1964. Variations in time and intensity of settling of the starfish, *Asterias forbesi*, in Long Island Sound during a twenty-five year period. *Biol. Bull.*, **126**: 423–439.

MAUZEY, K. P., C. BIRKELAND AND P. K. DAYTON, 1968. Feeding behavior of asteroids and escape responses of their prey in the Puget Sound area. *Ecology*, **49**: 603–619.

MORTENSEN, T., 1938. Contributions to the study of the development and larval forms of echinoderms. IV. *Kgl. Dan. Vidensk. Selsk. Skr. Natuurvid. Math. Afd., Series 9*, **7**(3): 1–59.

SCHELTEMA, R. S., 1961. Metamorphosis of the veliger larvae of *Nassarius obsoletus* (gastropoda) in response to bottom sediment. *Biol. Bull.*, **120**: 92–109.

SWAN, E. F., 1966. Growth, autotomy, and regeneration. Pages 397–434 in R. A. Boolootian, Ed., *Physiology of Echinodermata*. Interscience, New York.

TATTERSALL, W. M., AND E. M. SHEPPARD, 1934. Observations on the bipinnaria of the asteroid genus *Luidia*. Pages 35–61 in *James Johnstone Memorial Volume*. University of Liverpool Press, Liverpool, England.

THOMPSON, T. E., 1964. Grazing and the life cycles of British nudibranchs. Pages 275–297 in D. J. Crisp, Ed., *Grazing in Terrestrial and Marine Environments*. [*British Ecol. Soc. Symp. No. 4*.] Blackwell, Oxford.

THORSON, G., 1957. Bottom communities. Pages 461–534 in J. W. Hedgpeth, Ed., *Treatise on Marine Ecology and Paleoecology, I, Ecology*. Geological Society of America, New York.

THORSON, G., 1961. Length of pelagic larval life in marine bottom invertebrates as related to larval transport by ocean currents. Pages 455–474 in M. Sears, Ed., *Oceanography*. American Association Advancement of Science Publication 67, Washington, D. C.

THORSON, G., 1966. Some factors influencing the recruitment and establishment of marine benthic communities. *Netherlands J. Sea Res.*, **3**: 267–293.

WILSON, D. P., 1960. Some problems in larval ecology related to the localized distribution of bottom animals. Pages 87–104 in A. A. Buzzatti-Traverso, Ed., *Perspectives in Marine Biology*. University of California Press, Berkeley.