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Slow developing demersal embryos and larvae of the antarctic sea star *Odontaster validus*

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Abstract

The early development of *Odontaster validus* at McMurdo Sound, Antarctica, is indirect and includes equal cleavage, a convoluted blastula, a free-swimming coeloblastula, a gastrula, and a feeding bipinnaria larva. Development differs from that of other asteroids in two respects: (1) The developmental rate is extremely slow; blastulae form nearly 2 days after fertilization, gastrulation begins after 7 days, and the bipinnaria develops in about 40 to 55 days. The slow developmental rate appears to be only partly related to the low environmental temperature (−1.5 °C). (2) The embryos and larvae are largely demersal. Such behavior may be an adaptation to keep the larvae out of antarctic surface waters, as does brooding in many other polar echinoderms.

Introduction

The early development of asteroids has been described for many temperate and tropical species (e.g. MORTENSEN, 1921, 1931, 1937, 1938). However, in polar regions where harsh conditions have made long-term laboratory observations difficult, little comparable information is available. The recent establishment of permanent biological laboratories in the antarctic, particularly in McMurdo Sound (WOHLSCHLAG, 1963), provides new opportunities to make such observations.

The asteroid *Odontaster validus* KOEHLER is one of the most abundant animals around the antarctic coast. Embryos and larvae of this species were maintained during 1961 at McMurdo Station (PEARSE, 1962). The present paper provides more details on these embryos and larvae and draws special attention to their unusually slow rates of development and their demersal habit.

Materials and methods

Specimens of *Odontaster validus* were collected in McMurdo Sound with meat-baited traps set at about 20 m, as described previously (PEARSE, 1965).

Odontaster validus spawns during the austral winter from May through mid-September (PEARSE, 1965, 1966). Spawning occurred in the laboratory on only one occasion; 10 of 35 exceptionally ripe animals collected on September 4, 1961, from Cape Evans, McMurdo Sound, spawned within 5 to 105 min after being left out of water at room temperature. A similar spawning response to being left out of water was reported by NEWMANN (1925) for *Patiria miniata*. Oocytes spawned from 1 female were mixed with sperm spawned from 1 male of the September Cape Evans sample. Ninety-six percent of the spawned oocytes underwent fertilization, indicating that only ripe oocytes were spawned. These fertilized oocytes were maintained and their development followed.

Gametes for other cultures of embryos were obtained from excised gonads. Ovaries were dissected from females and placed in finger bowls containing filtered seawater kept at −1.5 ± 1 °C. After the oocytes were shed from the excised ovaries for 5 min, the ovaries were removed and a few drops of sperm collected from a freshly dissected male were added. Cultures were started from excised gonads on the following dates in 1961: June 25 (3 cultures), July 15 (7 cultures), August 6 (5 cultures), and September 4 (6 cultures). Attempts were also made to establish cultures from gametes collected from excised gonads in January, February, April, late September, October, November and December, 1961; these attempts were unsuccessful because all the oocytes were immature (PEARSE, 1965).

The percentage of oocytes shed from excised ovaries that underwent fertilization varied from less than 1 to 36%. These variations reflected the ripeness of the ovaries; large ripe ovaries from females with high gonadal indices generally yielded the highest percent of fertilizable oocytes. Procedures for handling ovaries and oocytes that might affect the percent fertilized were also tested in July. Single ovaries were dissected from each of 4 animals and treated together for each of 5 treatments. Twelve to 14 h after the shed oocytes were mixed with sperm, 50 to 100 cells were collected and the number of zygotes counted. The treatments and percent fertilized were: (1) ovaries placed directly in seawater at −1.5 °C for shedding, 32% fertilized; (2) ovaries rinsed in seawater at −1.5 °C, and then placed in shedding dishes at −1.5 °C, 2 cultures, 21 and 20% fertilized; (3) ovaries rinsed and placed in seawater with 2% coelomic fluid at −1.5 °C, 17% fertilized; (4) ovaries exposed in the dissected animals at room temperature (c. 20 °C) for 5 and 10 min, rinsed and placed in seawater at −1.5 °C, 13 and 14% fertilized, respectively; (5) ovaries rinsed and placed in seawater at +5° ± 2 °C, 18% fertilized. The highest percent fertilized was obtained with the unrinsed ovaries; rinsing probably washed away many ripe oocytes. Although JUST (1939) found that coelomic fluid tended to be toxic to asteroid oocytes, addition of 2% coelomic fluid to the filtered seawater had little effect. There was little difference in percent fertilized between rinsed oocytes at −1.5 °C and +5.0 °C. Moreover, many of the oocytes appeared to tolerate 5 and 10 min exposures to room temperatures.

The developing embryos and larvae were maintained in filtered seawater in finger bowls placed in polyethylene pans filled with seawater. The pans, with the finger bowls, were placed in ethylene glycol coolant in a Labline Tempmobile. The temperature was kept at -1.5 ± 0.5 °C. One culture maintained at $+5 \pm 2$ °C was kept in a refrigerator. The cultures were kept in complete darkness except for brief periods of observation. Water changes were made every 4 days by decanting off $^1/_2$ to $^3/_4$ of the culture water and replacing it with freshly filtered seawater. In the few cases when the animals were swimming off the bottom, the upper half of the cultures, with the healthy specimens, were decanted into bowls with fresh filtered seawater.

Observations of the embryos and larvae were made by sucking 25 to 100 individuals into a small pipette and spreading them on a glass slide. The various stages were quickly counted and the specimens replaced in the culture dishes. When extended observations and photographs were made (taking more than a few minutes) the specimens were discarded.

Results

Fertilization

Changes after fertilization proceeded in close synchrony in the one culture established from spawned

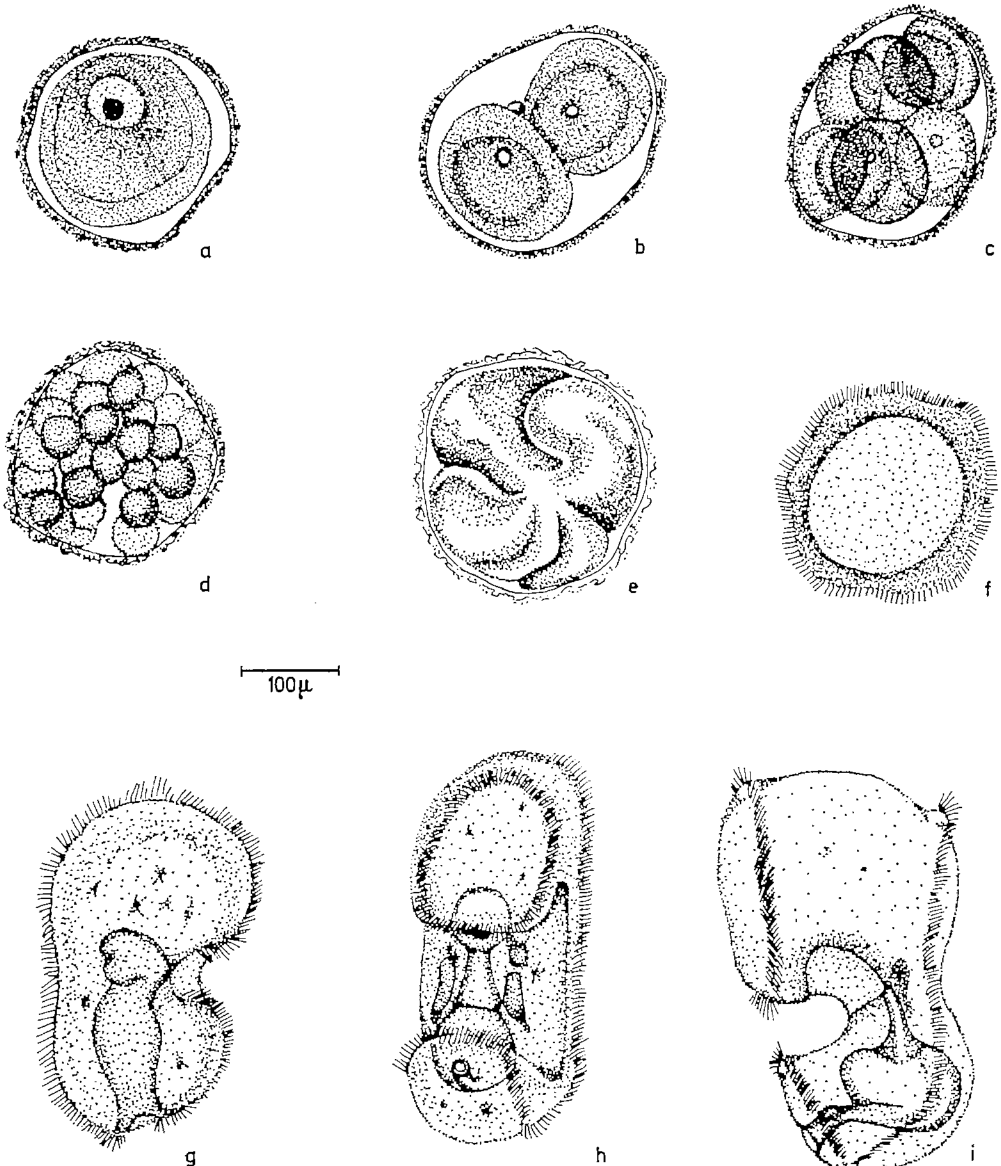

Fig. 1. Developmental stages of *Odontaster validus*. (a) Zygote before female maturation divisions showing prominent germinal vesicle, 30 min; (b) two-celled stage showing polar body within fertilization membrane, 13 h; (c) eight-celled stage, 32 h; (d) morula, 68 h; (e) convoluted blastula, 5 days; (f) free-swimming coeloblastula shortly after release from fertilization membrane, 8 days; (g) late gastrula with mesenchyme cells and the formation of enterocoels and the stomodaeum, 44 days; (h) early bipinnaria larva with complete gut, enterocoels, and 2 ciliary bands, 62 days; (i) bipinnaria larva with resorbed enterocoels, 80 days. All were drawn from photographs and adjusted to the same magnifications and actual times after fertilization given

gametes. Only primary oocytes with intact germinal vesicles were spawned, and no germinal vesicle breakdown occurred for at least 35 min after the oocytes were spawned. Ten min after the sperm were introduced, fertilization membranes appeared (Fig. 1a), but the germinal vesicles remained intact at least 1 h after fertilization. All the zygotes had undergone maturation division after 7 h, and the polar bodies were present under the fertilization membranes (Fig. 1b).

Similar changes occurred in oocytes shed from excised ovaries. Germinal vesicle breakdown did not occur in artificially shed oocytes for up to 3.5 h before sperm introduction. Maturation divisions usually occurred several hours after fertilization. However, maturation divisions did not occur in up to 35% of the oocytes that formed fertilization membranes. Apparently many immature oocytes shed from the excised ovaries were capable of raising a fertilization membrane, but incapable of undergoing maturation divisions.

Description of development

Development to an armless bipinnaria larva was similar to that in other asteroids with indirect development. Holoblastic, equal cleavage (Fig. 1b, c) led to a morula composed of relatively large blastomeres (Fig. 1d). The morula stage was followed by a much convoluted, generally 4-lobed, blastula stage (Fig. 1e) typical of other phanerozonid asteroids with indirect development (Mortensen, 1913a; Hörstadius, 1939; Newth, 1925). A ciliated coeloblastula (Fig. 1f) developed from the convoluted blastula, and escaped from the fertilization membrane. Gastrulation occurred by invagination, mesenchyme became scattered in the blastocoel, and eventually paired enterocoelic pouches appeared (Fig. 1g). Following stomodaeal breakthrough, the early bipinnaria larva developed with pre- and postoral ciliary bands[1] (Fig. 1h). No auricularian stage with a single ciliary band was seen.

The early bipinnaria larvae showed little further change even though some were maintained for up to 60 days. Failure of continued development was probably due to lack of suitable food; the enterocoels began to be resorbed about 80 days after fertilization (Fig. 1i). These larvae all reached the bipinnaria stage during the late austral winter before the beginning of the summer phytoplankton bloom (Littlepage, 1965). Because there was little phytoplankton present, and because these larvae were demersal (see below), their normal food might have consisted of bottom material. Fine suspensions of bottom material obtained from a grab, and consisting mainly of detritus, ciliates and flagellates, were offered periodically to the larvae. Material was often present in the larval stomachs after such feedings, yet the larvae still resorbed their enterocoels and eventually died.

Rate of development

The rates of development of these cultures were extremely slow. As shown in Fig. 2, however, the developmental rates were similar in the cultures begun on different dates. The chronology of the first observed appearances of well defined developmental stages was: cleavage, 0.67 day; convoluted blastula, 1.67 days; coeloblastula, 5 days; gastrula, 7 days; mesenchyme appearance, 20 days; enterocoel appearance,

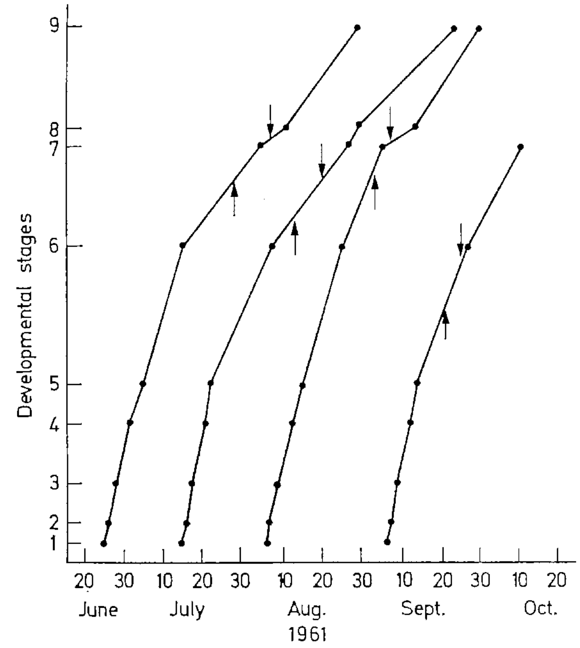

Fig. 2. Chronology within the 4 sets of cultures of *Odontaster validus* embryos. The earliest appearance of each developmental stage is followed. The developmental stages are: *1* zygote; *2* cleavage; *3* convoluted blastula; *4* coeloblastula; *5* gastrula; *6* mesenchyme appearance; *7* enterocoel appearance; *8* stomodaeal breakthrough; *9* bipinnaria. The arrows indicate when the embryos began to swim on the surface (↑) and when they settled again on the bottom (↓)

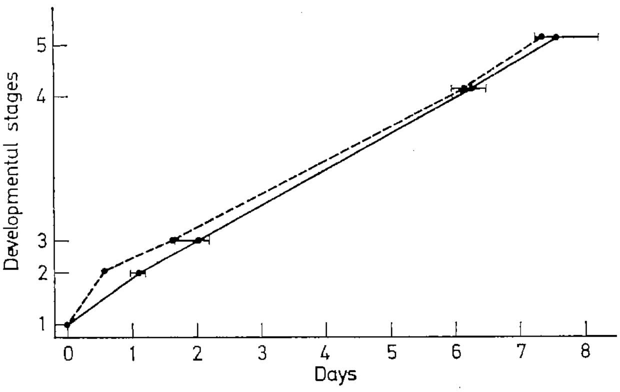

Fig. 3. *Odontaster validus*. Developmental rates to gastrulation in 1 culture of embryos maintained at +5° ± 2 °C (- - - -) and 6 cultures of embryos maintained at −1.5° ± 0.5 °C (mean and range). Developmental stages as given in Fig. 2

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[1] Usage of the term bipinnaria for this stage follows Mortensen (1931, 1937, 1938) and Hörstadius (1939). Costello et al. (1957) refer to this stage as the dipleurula.

30 days; stomodaeal breakthrough, 38 days; completed early bipinnaria, 55 days. Because these larvae fed little or not at all, the time taken to reach the bipinnaria may have been abnormally long; with food, perhaps the early bipinnaria stage could be reached shortly after stomodaeal breakthrough in as little as 40 days.

One culture was begun on July 15, 1961 and maintained to gastrulation in a refrigerator at +5° ± 2 °C. Fig. 3 compares the rate of development in this culture with the rates of development of 6 other cultures begun with gametes from the same animals and maintained at −1.5° ± 0.5 °C. (These were the cultures resulting from the fertilization tests given in the Materials and methods section.) Time to cleavage after fertilization in the +5 °C culture was about half that in the cultures at −1.5 °C. However, no difference could be detected in the times to reach later stages of development.

Behavior of the embryos and larvae

The embryos and larvae of *Odontaster validus* almost always stayed close to the bottom of the culture dishes. After release from the fertilization membranes, they seemed to actively seek the lowest portions of the dishes (the outer ring of the finger bowls), and large numbers of healthy embryos concentrated in these depressions. Each culture, however, went through a brief period (3 to 6 days) when the late gastrula embryos swam off the bottom and near the surface; this period is indicated in Fig. 2. Embryos in all the cultures begun on the same day went through the surface-swimming behavior at the same time. After the brief surface-swimming period, the embryos again concentrated in the lowest portions of the dishes and were rarely found off the bottom.

Discussion

Development rate

A comparison among different asteroids shows a generally direct relationship between latitude and developmental rate (Table 1); most tropical forms develop faster than most temperate forms. This relationship between developmental rate and latitude almost certainly reflects a temperature relationship. Development of *Luidia savignyi* in the Red Sea (about 30 °C), for example, is close to 3 times as rapid as that of *Porania pulvillus* off Scotland (about 15 °C). With such a comparison, the Q_{10} for asteroid developmental rate appears to be approximately 2. The developmental rate to gastrulation of *Odontaster validus* at −1.5 °C is in fair accordance with such a Q_{10}; it is about half that of *P. pulvillus*. Early development of *O. validus*, therefore, shows no evidence of temperature adaptation. Moreover, as diagrammed in Fig. 4, post-gastrula development in *O. validus* is much slower than would be predicted by comparisons with other asteroids; development to the bipinnaria in *P. pulvillus* is about 6 to 8 times faster than in *O. validus*.

As also indicated in Table 1, developmental rates in asteroids are undoubtedly influenced by factors other than temperature. Some tropical asteroids have relatively slow developmental rates (e.g. *Linckia multifora*), some temperate forms have relatively rapid developmental rates (e.g. *Patiria miniata*), and 3 species of *Astropecten* from different latitudes are reported to have the same developmental rates. It is probable that the slow rate of development in *Odontaster validus*, particularly after gastrulation, results from factors other than low temperature.

There is some evidence that other indirectly developing echinoderms in cold waters have extremely

Table. 1. *Comparison of asteroid developmental rates. (Approximate times in days)*

Species	Locality	Beginning of gastrulation	Early bipinnaria	Investigator
Luidia savignyi	Red Sea	1	2	Mortensen (1938)
Pentaceraster mammillatus	Red Sea	1	2	Mortensen (1938)
Patiria pectinifera	Japan	1	2	Mortensen (1921)
Patiria miniata	California	1	3	Newmann (1925)
Linckia laevigata	Java Sea	?	3	Mortensen (1931)
Astropecten polyacanthus	Red Sea	1	3	Mortensen (1937)
Astropecten aranciacus	Italy	1	3	Hörstadius (1939)
Astropecten irregularis	England	1	3	Newth (1925)
Asterias forbesi	Connecticut	1	3—4	Larsen (1937)
Ophidiaster guildingii	Tobago	?	4	Mortensen (1921)
Asterope carinifera	Red Sea	1	6	Mortensen (1937)
Acanthaster planci	Java Sea	1	6	Mortensen (1931)
Asterias vulgaris	Massachusetts	1	6	Field (1892)
Pisaster ochraceus	British Columbia	2	4—5	Mortensen (1921)
Gymnasteria carinifera	Hawaii	2	5	Mortensen (1921)
Linckia multifora	Red Sea	2	5	Mortensen (1938)
Asterias rubens	Scotland	2	6	Gemmill (1914)
Evasterias troscheli	British Columbia	2—3	4—5	Mortensen (1921)
Pycnopodia helianthoides	Washington State	2—3	5	Greer (1962)
Luidia ciliaris	England	3	6	Mortensen (1913a)
Porania pulvillus	Scotland	3—4	7	Gemmill (1915)
Odontaster validus	Antarctica	7	40—55	this paper

slow developmental rates. Development of the arctic ophiuroid *Ophiocten sericeum* is extremely slow and metamorphosis occurs about 6 months after spawning (Pearse, 1965). Perhaps development to metamorphosis of the abyssal ophiuroid *Ophiura ljungmani* is as slow (Schoener, 1968). If metamorphosis in *Odontaster validus* occurs 6 months after spawning, it would take place sometime during the latter half of the austral summer.

The unmodified rate of development after cleavage at +5 °C contrasts sharply with similar experiments done with echinoids. Only a three-degree rise in temperature (from 20° to 23 °C) decreases the time to gastrulation by more than 25% in *Arbacia punctulata* (Costello et al., 1957). With only one experiment at only one higher temperature, however, it is by no means conclusive that the developmental rate of *Odontaster validus* is insensitive to temperature. In several antarctic fish, respiration increases markedly with temperature rises from – 1.5° to about 5 °C, but decreases above 5 °C (Wohlschlag, 1964). Respiration in the antarctic euphausid *Euphausia superba* increases from 0° to 5 °C, but no further increase occurs at higher temperatures; indeed, temperatures above 4 °C are lethal within 24 h (McWhinnie, 1964). The developmental rate of *O. validus* embryos may also increase with temperature, up to about 4° to 5 °C, but deleterious effects of higher temperatures may well counter any further stimulatory effects. It is also of interest that the time to cleavage was halved at 5 °C; perhaps the disruptive effects of 5 °C are less pronounced on the relatively few enzyme systems involved in very early development, than later when more enzyme coordination probably comes into play.

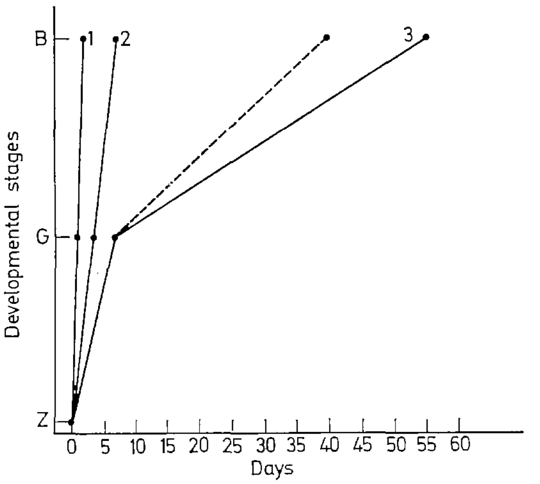

Fig. 4. Comparison of developmental rates of (1) fast developing asteroid *Luidia savignyi* in the Red Sea at about 30 °C (Mortensen, 1938); (2) slow developing asteroid *Porania pulvillus* off Scotland at about 15 °C (Gemmill, 1915); (3) *Odontaster validus* at –1.5 °C. Dotted line indicates possible post-gastrula developmental rate in *Odontaster validus* with suitable food present. Development stages: Z zygote, G gastrula, B bipinnaria

Demersal behavior

The maintained *Odontaster validus* embryos and larvae spent the great majority of the time as bottom swimmers. This behavior suggests that they are demersal rather than pelagic. Such a suggestion is supported by consideration of the antarctic plankton. Only a few pelagic echinoderm larvae (including a bipinnaria) are known from the antarctic (e.g. Mortensen, 1913b), and echinoderm larvae (as well as trochophores, veligers, and similar larvae) have long been notable by their scarcity in the antarctic plankton (Hardy, 1960). Bunt (1960) made at least monthly plankton collections at Mawson, Antarctica, from 1 May 1956 to 10 February 1957, and failed to find a single echinoderm larva, yet *O. validus* is common at Mawson (J. S. Bunt, personal communication). Extensive plankton collections taken from McMurdo Sound between December, 1960 and December, 1961, also contained no echinoderm larvae (J. L. Littlepage, personal communication). *O. validus* is very abundant in the relatively shallow water of McMurdo Sound (Dearborn, 1967) and, except for a possible brief early pelagic period, the embryos and larvae must be demersal in habit.

Other echinoderms with indirect development also have demersal embryos and larvae. Newth (1925) found that blastulae and early gastrulae of *Astropecten irregularis* swam near the bottom of his culture dishes (he did not mention the behavior of later stages), and Mortensen (1921) reported the same behavior for bipinnaria of *Patiria pectinifera* and *Evasterias troscheli*. Mortensen (1921) also noted that the embryos and plutei of the echinoid *Laganum diplopora* swam near the bottom of the culture dishes. Moreover, the antarctic echinoid *Sterechinus neumayeri* probably develops through pluteus stages, yet these are rare in the plankton and probably demersal in habit (Pearse and Giese, 1966).

Demersal larvae that are morphologically similar to comparable pelagic larvae have been reported for other phyla. Sanders (1963) found that the demersal cephalocarid, mystacocarid, and harpacticoid copepod nauplii are very similar to pelagic calanoid copepod nauplii. This similarity "...is due to the fact that they move and feed in the same manner, one swimming through the water and feeding on fine suspended matter, the other moving on the bottom and feeding on a detrital material suspended by a sweeping action of the (appendages)" (Sanders, 1963, p. 24). Young larvae of the polychaete *Nereis diversicolor* off Finland also are demersal in habit, in this case staying out of the low surface salinities, but later stages with wider tolerances become planktonic (Smith, 1964).

With the establishment of a demersal habit for *Odontaster validus* embryos and larvae, indirect development in echinoderms can no longer be viewed as leading only to pelagic larvae (e.g. Hörstadius, 1939; Thorson, 1950; Feder and Christensen, 1966).

In deep seas as well as polar seas, indirectly developing embryos and feeding larvae of echinoderms that are demersal may be of more importance than previously thought. MORTENSEN (1921) noted that deep-sea echinoderms with pelagic larvae had never been definitely found and, from this and other observations, it has been generalized that all deep-sea animals have non-pelagic, non-feeding larvae (e.g. THORSON, 1950; MADSEN, 1961). *O. validus* occurs to depths of at least 914 m (CLARK, 1963) and can be considered as a species occurring in moderately deep water (bathyal zone) with non-pelagic, yet feeding, larvae. Similarly, the echinoid *Laganum diplopora* from 800 m has pluteus larvae that are probably demersal (MORTENSEN, 1921). More recently, SCHOENER (1968) has given evidence that an abyssal (1 to 4000 m) ophiuroid has indirectly developing larvae that are likely to be bottom feeders.

As has long been known, an unusually high proportion of antarctic echinoderms brood their embryos and larvae (THOMSON, 1876; THORSON, 1950). Several reasons have been proposed for this high incidence of brooding, including: (1) low surface salinities due to ice melt (ÖSTERGREN, 1912; HARDY, 1960), and (2) poor planktonic food conditions, with a short summer productive period, which might favor yolky rather than feeding larvae (THORSON, 1950). HARDY (1960) pointed out that crustacean larvae are especially abundant in the antarctic plankton and, because of their thick cuticle, these may be less vulnerable to osmotic stresses than more delicate larvae such as those of echinoderms. Consideration of the plankton of McMurdo Sound (J. L. LITTLEPAGE, personal communication), Mawson (BUNT, 1960), and Heard Island (EALEY and CHITTLEBOROUGH, 1956) supports this hypothesis. The most abundant meroplankters in these areas are young polychaetes which are all well segmented and may have a wide salinity tolerance as is found in comparable stages of *Nereis diversicolor* (SMITH, 1964). Also indicative of the importance of occasional low surface salinities, adult specimens of *Odontaster validus* have some coelomic water volume control that may be an adaption to freshwater runoff (PEARSE, 1967).

Regardless of which factors are important in restricting echinoderm and similar larvae from polar pelagic waters, *Odontaster validus* is very probably responsive to these factors. The response, though, is not by the development of direct development and brooding, but by the demersal behavior of feeding larvae. This behavioral response weakens THORSON'S (1950) proposal that poor food conditions are involved in limiting the occurrence of pelagic polar larvae. *O. validus* larvae indeed must feed, but this should be no more of a problem than it is for other small animals inhabiting the bottom.

Odontaster validus is a widespread antarctic asteroid, being circumcontinental and occurring near islands as far north as South Georgia and the Bouvet islands (CLARK, 1963). The development of a predominately demersal larva with brief pelagic phases, may be considered an adaptive "compromise," serving for effective dispersion, yet preventing excessive larval wastage in the apparently hazardous antarctic surface waters. The common arctic ophiuroid, *Ophiocten sericeum*, also has partly demersal, partly pelagic, embryos and larvae (PEARSE, 1965), and this behavior may account for its wide distribution. Although many polar echinoderms have direct development [according to THORSON (1950) perhaps 95% of the polar species have direct development], there is still a paucity of known pelagic larvae to account for the remaining species. This paucity is especially evident when it is considered that common, widespread polar species (such as *Odontaster validus* and *Sterechinus neumayeri* of the Antarctic and *Ophiocten sericeum* and *Strongylocentrotus dröbachiensis* of the Arctic) have indirect development, with feeding larvae (THORSON, 1950). It is likely that other common polar echinoderms have undergone larval adaptations leading to demersal behavior. Future investigators should be especially cognizant of possible differences in distributional ranges between brooding species and species which may have predominately demersal, feeding larvae such as *O. validus*.

Summary

1. The development of the antarctic asteroid *Odontaster validus* is indirect, and includes a feeding bipinnaria stage.

2. The rate of development of *O. validus* at ambient sea temperatures (−1.5 °C) is extremely slow; blastulae form nearly 2 days after fertilization, gastrulation begins after 7 days and the bipinnaria develops in about 40 to 55 days. The rate of development after cleavage is not increased at +5 °C. The rate of development to gastrulation is similar to that of most tropical and temperate asteroids if compensation is made for temperature differences, and there is no evidence of temperature adaptation. Post-gastrula developmental rate is even much slower than would be expected from studies on asteroids of other areas.

3. The embryos and larvae are largely demersal in habit. They spend most of the time on the bottom of culture dishes and are absent in plankton. This behavior protects the larvae from exposure to apparent harsh conditions of the antarctic surface water, and is analogous in effect to brooding in many other antarctic forms. It is suggested that demersal feeding larvae may be important for the dispersal of both polar and deep-sea echinoderms.

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Literature cited

Bunt, J. S.: Introductory studies: hydrology and plankton, June, 1956 — February, 1957. A. N. A. R. E. Rep. (Ser. B) **3**, 1—135 (1960).

Clark, H. E. S.: The fauna of the Ross Sea. Pt 3. Asteroidea. Bull. N. Z. Dep. scient. ind. Res. **151**, 1—84 (1963).

Costello, D. P., M. E. Davidson, A. Eggers, M. H. Fox and C. Henley: Methods for obtaining and handling marine eggs and embryos, 247 pp. Woods Hole, Mass.: Marine Biological Lab. 1957.

Dearborn, J. H.: The fauna of the Ross Sea. Pt 5. Stanford University invertebrate studies in the Ross Sea 1958—61: general account and station list. Bull. N. Z. Dep. scient. ind. Res. **176**, 31—47 (1967).

Ealey, E. H. M. and R. G. Chittleborough: Plankton, hydrology and marine fouling at Heard Island. Interim Rep. Aust. natn. Antarct. Res. Exped. **15**, 1—81 (1956).

Feder, H. and A. M. Christensen: Aspects of asteroid biology. *In:* Physiology of Echinodermata, pp 87—127. Ed. by R. A. Boolootian. New York: Interscience Publ. 1966.

Field, G. W.: The larvae of *Asterias vulgaris*. Q. Jl microsc. Sci. **34**, 105—128 (1892).

Gemmill, J. F.: The development and certain points in the adult structure of the starfish *Asterias rubens* L. Phil. Trans. R. Soc. (B) **205**, 213—294 (1914).

— The larva of the starfish *Porania pulvillus* (O. F. M.), Q. Jl microsc. Sci. **61**, 27—50 (1915).

Greer, D. L.: Studies on the embryology of *Pycnopodia helianthoides* (Brandt) Stimpson. Pacif. Sci. **14**, 280—285 (1962).

Hardy, A.: Remarks. *In:* A discussion on the biology of the southern cold temperate zone. Proc. R. Soc. (Ser. B) **152**, 641—642 (1960).

Hörstadius, S.: Über die Entwicklung von *Astropecten aranciacus* L. Pubbl. Staz. zool. Napoli **17**, 222—312 (1939).

Just, E. E.: Basic methods for experiments on eggs of marine animals, 89 pp. Philadelphia: P. Blakiston's Son & Co. 1939.

Larsen, E. J.: The laboratory culture of the larvae of *Asterias forbesi*. *In:* Culture methods for invertebrate animals, pp 550—553, Ed. by P. S. Galtsoff, F. E. Lutz, P. S. Welch and J. G. Needham. Ithaca, New York: Comstock Publ. Co., Inc. 1937.

Littlepage, J. L.: Oceanographic investigations in McMurdo Sound, Antarctica. *In:* Biology of the Antarctic Seas. 2. Antarctic Res. Ser. **5**, 1—38 (1965).

McWhinnie, M. A.: Temperature responses and tissue respiration in antarctic Crustacea with particular reference to the krill *Euphausia superba*. *In:* Biology of the Antarctic Seas. 1. Antarctic Res. Ser. **1**, 63—72 (1964).

Madsen, F. J.: On the zoogeography and origin of the abyssal fauna in view of the knowledge of the Porcellanasteridae. Galathea Rep. **4**, 177—218 (1961).

Mortensen, T.: On the development of some British echinoderms. J. mar. biol. Ass. U. K. **10**, 1—18 (1913a).

— Die Echinodermenlarven der Deutschen Sud-polar Expedition 1901—1903. Dt. Südpol.-Exped. **14** (Zool. 6), 69—111 (1913b).

— Studies of the development and larval forms of echinoderms, 261 pp. Copenhagen: G. E. D. Gad 1921.

— Contributions to the study of the development and larval forms of echinoderms I and II. K. danske Vidensk. Selsk. Skr. (Naturv. — math. Afd.) Raekke 9. **4** (1), 1—39 (1931).

— Contributions to the study of the development and larval forms of echinoderms III. K. danske Vidensk. Selsk. Skr. (Naturv. — math. Afd.) Raekke 9. **7** (1), 1—65 (1937).

— Contributions to the study of the development and larval forms of echinoderms IV. K. danske Vidensk. Selsk. Skr. (Naturv. — math. Afd.) Raekke 9. **7** (3), 1—59 (1938).

Newman, H. H.: An experimental analysis of asymmetry in the starfish *Patiria miniata*. Biol. Bull. mar. biol. Lab., Woods Hole **49**, 111—138 (1925).

Newth, H. G.: The early development of *Astropecten irregularis* with remarks on duplicity in echinoderm larvae. Q. Jl microsc. Sci. **69**, 520—554 (1925).

Östergren, H.: Über die Brutpflege der Echinodermen in den südpolaren Küstengebieten. Z. wiss. Zool. 101, 325—341 (1912).

Pearse, J. S.: Early development of the antarctic asteroid *Odontaster validus* Koehler. Am. Zool. **2**, 436 (1962).

— Reproductive periodicities in several contrasting populations of *Odontaster validus* Koehler, a common antarctic asteroid. Biology of the Antarctic Seas. 2. Antarctic Res. Ser. **5**, 39—85 (1965).

— Antarctic asteroid *Odontaster validus*: constancy of reproductive periodicities. Science, N. Y. **152**, 1763—1764 (1966).

— Coelomic water volume control in the antarctic sea-star *Odontaster validus*. Nature, Lond. **216**, 1118—1119 (1967).

— and A. C. Giese: Food, reproduction and organic constitution of the common antarctic echinoid *Sterechinus neumayeri* (Meissner). Biol. Bull. mar. biol. Lab., Woods Hole **130**, 387—401 (1966).

Sanders, H. L.: The Cephalocarida. Functional morphology, larval development, comparative external anatomy. Mem. Conn. Acad. Arts Sci. **15**, 1—80 (1963).

Schoener, A.: Evidence for reproductive periodicity in the deep sea. Ecology **49**, 81—87 (1968).

Smith, R. I.: On the early development of *Nereis diversicolor* in different salinities. J. Morph. **114**, 437—463 (1964).

Thomson, C. W.: Notice of some peculiarities in the mode of propagation of certain echinoderms of the Southern Sea. J. Linn. Soc. (Zool.) **13**, 55—79 (1876).

Thorson, G.: Reproductive and larval ecology of marine bottom invertebrates. Biol. Rev. **25**, 1—45 (1950).

Wohlschlag, D. E.: The biological laboratory and field research facilities at the United States "McMurdo" Station, Antarctica. Polar Rec. 11, 713—718 (1963).

— Respiratory metabolism and ecological characteristics of some fishes in McMurdo Sound, Antarctica. Biology of the Antarctic Seas. 1. Antarctic Res. Ser. **1**, 33—62 (1964).

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