Marine Biology 104, 41–46 (1990)

Marine Biology
International Journal on Life in Oceans and Coastal Waters

Developmental types of shallow-water asteroids of McMurdo Sound, Antarctica

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Abstract

The mode of development was ascertained for 14 of the 16 species of sea stars known to occur in shallow waters of McMurdo Sound, Antarctica (77°51′S; 166°40′E). The species were collected between September 1984 and December 1985. Females of three species, *Odontaster validus, O. meridionalis* and *Porania antarctica,* spawn small to moderate eggs (0.17 to 0.55 mm), have a high fecundity, and produce feeding larvae. Females of an undescribed *Porania* species spawn a few eggs (150 to 310) that are 0.55 mm in diameter and develop into demersal non-feeding larvae. Females of *Diplasterias brucei* and *Notasterias armata* produce a few (<300) large eggs (2.8 to 3.5 mm) and brood their young. Females of the remaining eight species have moderate fecundity and produce pelagic non-feeding larvae, as determined from egg type (buoyant, 0.54 to 1.28 mm diam) and direct observations of spawning and development. The high incidence (11 out of 14 species; 79%) of non-feeding development is consistent with predictions that environmental conditions in high-latitude regions are unfavorable for planktotrophic development. Nonetheless, most of the species surveyed (11 out of 14) had pelagic larvae, which contradicts inferences of unusual selection for benthic development in the Antarctic.

Introduction

Marine benthic invertebrates exhibit a spectrum of developmental types which includes pelagic or non-pelagic embryos and larvae and planktotrophic (particulate feeding) or lecithotrophic (non-feeding) modes of nutrition (Mileikovsky 1971, Chia 1974). Large-scale latitudinal shifts in the relative proportion of these developmental types were first detailed by Thorson (1936, 1950), who reported a trend toward brooded or protected lecithotrophic development with increasing latitude. Thorson's conclusions were based primarily on studies of prosobranch gastropods in the eastern North Atlantic. His observations have been substantiated by studies of reproductive patterns in bivalves from the northern hemisphere (Ocklemann 1965) and are consistent with predictions of theoretical models of life-history evolution in the seas (Vance 1973, Christiansen and Fenchel 1979, Roughgarden 1989). In addition, available information suggests that the majority of benthic invertebrates from Antarctic regions also develop non-pelagically. For example, more than 80% of sponge species whose development is known exhibit brood protection (Arnaud 1974). The incidence of protected development is high in antarctic bivalves (Dell 1972, Richardson 1977), gastropods (Simpson 1977, 1982), some marine parasites (Rohde 1985), and other taxa (Arnaud 1974, Picken 1980). The notion that pelagic and planktotrophic types of larval development are suppressed with increasing latitude is firmly established and is referred to as "Thorson's rule" (Mileikovsky 1971).

The Asteroidea of the Southern Ocean is another group presumed to have an unusually high proportion of species that brood their young (Arnaud 1974, White 1984). This notion is based primarily on the finding of a few brooders in general faunal collections (Fisher 1940, Clark 1962, Clark 1963, Arnaud 1974). Long-term observations and sampling in the Antarctic are lacking, particularly along the more southern regions of the continental shore. Because individuals carrying young are easily recognized, these records overestimate the incidence of brooding. The reproduction of only 35 of 132 species of sea stars in the Antarctic has been reported (MacBride and Simpson 1908, Simpson 1982, Emlet et al. 1987), and it remains to be shown that brooding is the predominant mode of reproduction in this fauna.

The present paper describes the mode of reproduction of 14 of the 16 species of sea stars known from shallow waters in McMurdo Sound, Antarctica (77°51′S; 166°40′E).

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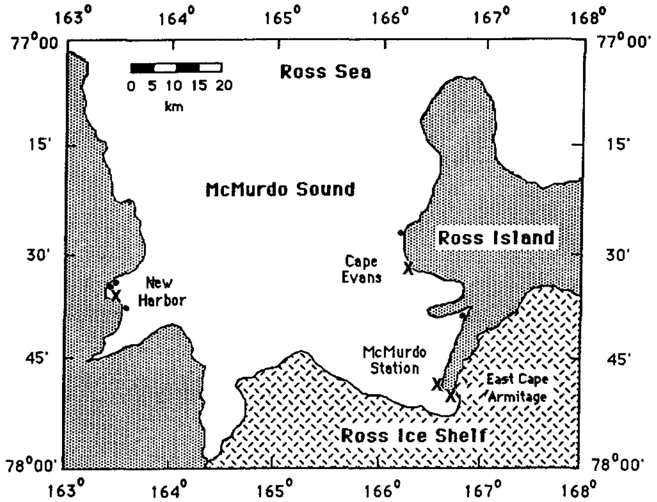

Fig. 1. McMurdo Sound, Antarctica, showing location of our four primary study sites (×) and of five additional sites (●) where survey dives were made. Benthic environment at each of our primary sites (East Cape Armitage, McMurdo Station, Cape Evans and New Harbor) has been described by McClintock et al. (1988), Dayton et al. (1974), Pearse (1965) and Dayton and Oliver (1977), respectively

Table 1. Systemic account of sea stars (*sensu* Blake 1987) collected from shallow waters (<33 m) of McMurdo Sound during this study, their bathymetric range, and list of stations where collections were made. All species except *Porania* sp. have a circumantarctic distribution, with some extending into the sub-Antarctic. Distributional data compiled from Fisher (1940), Clark (1962), Clark (1963), Fell and Dawsey (1969) and this study. ECA: East Cape Armitage; McM: McMurdo Station; CE: Cape Evans; NH: New Harbor

Species	Depth (m)	Station
Valvatida		
Odontasteridae		
Odontaster validus	0– 914	ECA, McM, CE, NH
Odontaster meridionalis	0– 519	ECA, McM, CE, NH
Acodontaster capitatus	15– 647	McM, NH
Acodontaster conspicuus	25– 274	McM, CE, NH
Acodontaster elongatus	15– 600	McM
Acodontaster hodgsoni	15– 549	ECA, McM, CE, NH
Poraniidae		
Porania antarctica	4–3 200	McM, CE, NH
Porania sp.	15–?	ECA, McM, CE, NH
Paxillosida		
Astropectinidae		
Bathybiaster loripes	78–1 266	NH
Psilaster charcoti	15–3 900	NH
Macroptychaster accrescens	15– 640[a]	ECA, McM, NH
Velatida		
Solasteridae		
Lophaster gaini	15– 578[a]	NH
Cuenotaster involutus	15– 578	NH
Spinulosiuda		
Echinasteridae		
Perknaster fuscus	3– 362[a]	ECA, McM, CE, NH
Forcipulatida		
Asteriidae		
Diplasterias brucei	0– 752	ECA, McM, CE, NH
Coscinasteriniae		
Notasterias armata	15– 752	NH

[a] New shallow-depth record

Materials and methods

Sea stars were collected over a 15 mo period (September 1984 to December 1985) from four sites in shallow waters of McMurdo Sound: East Cape Armitage, McMurdo Station and Cape Evans on the eastern shore of McMurdo Sound, and Explorers Cove, New Harbor, on the western shore of McMurdo Sound (Fig. 1). In addition, survey dives were made during the austral summers of 1984 and 1985 at five other sites within McMurdo Sound.

Collections and observations were made using SCUBA diving to a maximum depth of approximately 33 m. Sea stars were transported to McMurdo Station and kept for extended periods of time in aquaria with running seawater (−1.5 °C). Attempts to induce spawning were initiated within 48 h of collection by injecting 1-methyladenine (1-MA) at 10^{-3}–10^{-6} *M* in seawater into the coelom. In some cases, excised ovaries were placed in seawater with 1-MA. Ova obtained by these methods were immediately washed in 5 μm-filtered seawater and inseminated with sperm collected from spawning or dissected males. In cases where spawning was not induced by 1-MA, unspawned individuals (1 to 10) were dissected and the excised gonads were examined. The diameters of 20 to 25 spawned ova or 10 to 20 of the largest oocytes from dissected females were measured using a compound microscope with an ocular micrometer. Qualitative observations of buoyancy were made by placing ova or oocytes in ambient seawater.

Embryos and larvae were reared in stirred or unstirred 4-liter culture vessels at −1.8° to −1.0 °C, generally following the methods of Strathmann (1971) as modified by Pearse and Bosch (1986). Non-feeding larvae were reared in 5 μm-filtered seawater that was changed every 4 d. Development to hatching was monitored every 8 h, and subsequent development was monitored every other day. Competent larvae were induced to settle and metamorphose with substrates (e.g. sediment, shell debris) collected from adult habitats or by placing glass slides covered with bacterial-algal films in the culture vessels (Hinegardner and Tuzzi 1981). The diameter of newly metamorphosed juveniles was measured with a dissecting microscope using an ocular micrometer.

Results

Individuals of 7 families and 16 species of sea stars were collected from shallow waters of McMurdo Sound (Table 1). An unreported species was placed in the genus *Porania* (H. E. S. Clark personal communication); it is referred to as *Porania* sp. Reproductive mode was determined for 14 of the 16 species directly by observing spawning and development, or indirectly by regularly monitoring ovarian characteristics (Table 2).

Table 2. Developmental characteristics and occurrence of ripe females of sea stars collected between September 1984 and December 1985 in shallow waters of McMurdo Sound. Unless otherwise stated, data are based on observations of females induced to spawn in the laboratory with 1-methyladenine. Mean diameter of brooded early-stage embryos, spawned ova, and maximum oocyte diameter are provided for brooders, broadcasters, and probable broadcasters, respectively. Sample size ranged from 10 to 30. –: no ripe females collected

Species	Egg diam (mm)	Ripe females
Broadcasters with feeding larvae		
Odontaster validus	0.17	July to mid October
Odontaster meridionalis	0.19	July to late October
Porania antarctica	0.55	September to November
Broadcasters with non-feeding larvae		
Bathybiaster loripes	0.93	November to January
Psilaster charcoti	0.95	Late October
Acodontaster conspicuus[a]	0.70	Early December
Acodontaster elongatus[a]	0.54	Mid September
Acodontaster hodgsoni	0.55	Late September
Porania sp.	0.55	Year-round
Lophaster gaini[a]	1.28	Early February
Probable broadcasters with non-feeding larvae[b]		
Macroptychaster accrescens	1.28	–
Perknaster fuscus *	1.20	–
Brooders[c]		
Diplasterias brucei	2.80	Year-round
Notasterias armata	3.50	August to February

[a] Spawned spontaneously in the laboratory
[b] Determined from observations of dissected ovaries
[c] Determined from field observations of females carrying broods
* Added at proof: 1 female *P. fuscus* collected from McMurdo Sound broadcast spawned eggs when injected with 1-MA on 27 September 1989

Broadcasters with feeding larvae

Female *Odontaster validus* and *O. meridionalis* broadcast-spawn large numbers of small oocytes (0.17 to 0.19 mm) that undergo germinal vesicle breakdown at the time of fertilization and develop into feeding bipinnaria and brachiolaria larvae. The development to metamorphosis of *O. validus* was described by Pearse and Bosch (1986). The rate of embryonic and larval development of *O. validus* and *O. meridionalis* was extremely slow: at −1.5 °C, the shortest time from fertilization to an early and late bipinnaria stage was approximately 38 and 93 d, respectively. Time of development to metamorphosis was 165 d for *O. validus* (Table 3).

The reproduction of *Porania antarctica* is intermediate between planktotrophic and lecithotrophic types (Bosch 1989). The eggs produced were large (0.55 mm diam), opaque and of yellowish color. Development proceeded through bipinnaria and brachiolaria larval stages that were yolky and ingested small suspended particles, such as bacteria (Rivkin et al. 1986). Metamorphosis first occurred 65 d after fertilization. This is the shortest period of development to a juvenile stage recorded for the species surveyed (Table 3).

Table 3. Egg size, development mode, minimal days to juvenile stage and juvenile size of five species of sea stars from shallow waters of McMurdo Sound. P: planktotroph; PL: pelagic lecithotroph; DL: demersal lecithotroph; BL: brooded lecithotroph

Species	Egg size (mm)	Devel. mode	Days to juvenile stage	Juvenile size (mm)
Odontaster validus	0.17	P	167	0.6
Porania antarctica	0.55	P	65	0.8
Porania sp.	0.55	DL	78	0.6
Acodontaster hodgsoni	0.55	PL	106	0.6
Diplasterias brucei	2.80	BL	165[a]	3.0

[a] Determined from field observations; the length of the brooding period may be underestimated

Table 4. *Acodontaster hodgsoni.* Chronology of lecithotrophic development at −1.5° to −1.0 °C. Sizes represent diameter of eggs and blastulae and total length of larvae. Times are based on observations of four cultures initiated from three females and a single male

Developmental stage	Days to first appearance	Size (mm)
Eggs fertilized	0	0.55
Second cleavage	3	0.55
64-cell embryo	5	0.58
Ciliated blastula	13	0.60
Hatched blastula	15	0.60
Bilobed larva	33	1.30
Modified brachiolaria	80	1.85
Well developed rudiment	98	1.85
Metamorphosis	106	0.59

Broadcasters with non-feeding larvae

Large (0.54 to 1.28 mm diam) yolky eggs were free-spawned by females from 7 of the 11 remaining species.

Embryos of *Acodontaster hodgsoni* obtained from induced spawnings of individuals held in laboratory sea-tables were reared through metamorphosis (Table 4). The larvae of *A. hodgsoni* are large and buoyant; they have well-developed anterior and posterior lobes, but lack feeding structures and distinct ciliated bands. Competent larvae attached to the substrate by a modified brachiolarian complex 106 d after fertilization and metamorphosed.

Bathybiaster loripes and *Psilaster charcoti* were induced to spawn in the laboratory. Embryos of both species hatched as large (0.9 to 1.0 mm diam), buoyant, ciliated blastulae, passed through a modified gastrula stage and developed into non-feeding larvae. *B. loripes* were reared to an advanced larval stage. After 52 d in culture, the fully grown larva (2.5 mm length) had well-developed anterior and posterior lobes, the latter containing a prominent rudiment. They lacked distinct ciliated bands and a brachiolarian complex.

Eggs (0.55 mm diam) obtained from induced spawnings of *Porania* sp. were inseminated with sperm obtained from dissected males. The resulting embryos were negatively buoyant and immediately settled on the bottom of culture vessels. Embryogenesis was followed by the formation of a pear-shaped demersal larva that had no feeding structures or distinct ciliated bands. Development proceeded through a modified, non-feeding brachiolaria which attained a maximum length of 1.1 mm near the time of settlement, 78 d after fertilization (Bosch 1989).

Acodontaster conspicuus, A. elongatus and *Lophaster gaini* did not respond to treatment with 1-MA. At least one female of each species spawned spontaneously in the laboratory. The eggs released (ca. 3 to 5×10^3 per female) were positively buoyant and measured 0.70, 0.54, and 1.28 mm in diameter for *A. conspicuus, A. elongatus,* and *L. gaini,* respectively.

Probable broadcasters with non-feeding larvae

Individuals of *Macroptychaster accrescens* and *Perknaster fuscus* were collected from populations at East Cape Armitage and McMurdo Station every two to three months throughout our 15 mo study period. Neither species responded to 1-MA. Two or three size-classes of oocytes were always present in the ovaries of dissected females. Vitellogenic oocytes were buoyant and had a maximum diameter of 1.28 mm in *M. accrescens* and 1.2 mm in *P. fuscus.*

Brooders

The development of *Diplasterias brucei* to an advanced juvenile stage takes place within a suboral maternal brood chamber. Only a few offspring are produced (<300), judging from brood size in six females carrying early stage embryos. The period of incubation was estimated by following brood development of two females during subsequent sampling dives. Large (long radius, $R = 3.0 \pm 0.6$ mm, $n = 105$ for 1 female) juveniles were released after brooding periods of 5.5 and 6.2 mo. Because the actual spawning dates of the two females were unknown, these times represent a minimum brooding period. Brooding activity showed no marked seasonality at East Cape Armitage over a 12 mo study period, with ca. 10% of all adults ($n = 199$) carrying broods on each of five sampling dates.

Individuals of *Notasterias armata* occurred in low numbers at New Harbor and only five brooding females were examined. Fecundity is low (ca. 50 eggs), as indicated by brood size in two females. The eggs are large (up to 3.5 mm diam) and develop to a juvenile stage within a suboral brood chamber.

Discussion

Thirty seven species of sea stars have been reported from the Ross Sea region of the Antarctic, with 11 ranging into shallow-water areas (<100 m) of McMurdo Sound (Clark 1963, Dearborn 1965). Five species (*Acodontaster capitatus, A. elongatus, Bathybiaster loripes, Lophaster gaini,* and the undescribed poraniid *Porania* sp.) are added here. Of the 14 species studied, two brood their embryos and have no larvae, one has demersal non-feeding larvae, three have planktonic feeding larvae (including one with a previously undescribed yolk-rich feeding larva) and eight have pelagic non-feeding larvae. The mode of spawning and development was not observed directly for *Macroptychaster accrescens* and *Perknaster fuscus.* However, the maximum egg sizes of these two species are well within the range reported by Emlet et al. (1987) for sea stars with non-feeding pelagic larvae. Moreover, their individual female fecundity and reproductive effort (see McClintock and Pearse 1986, 1987) are intermediate between planktotrophic and brooding sea stars. This evidence supports the conclusion that *M. accressens* and *P. fuscus* are broadcasters with non-feeding larvae.

Fisher (1940) and Clark (1962) listed 132 species of sea stars from Antarctic and sub-Antarctic biogeographical provinces. The mode of reproduction is known for 48 of these. Most (33 out of 48; 69%) brood their young to a juvenile stage (Fisher 1940, Clarke 1962, Clarke 1963, Arnaud 1974, Simpson 1982, this study). This apparent widespread curtailment of a pelagic larval phase may be a result of sampling biases, or it may be a consequence of the fauna studied. For example, among the known brooders, most species (20 out of 33; 61%) are of three forcipulate genera (*Anasterias, Diplasterias* and *Lysasterias*) that have no known non-brooding representatives. Moreover, their distribution is limited predominately to shallow waters of isolated Antarctic and sub-Antarctic islands. The preponderance of brooding among these genera may be a consequence of phylogenetic history, or it may be an adaptation that avoids the loss of larvae from favorable shallow-water island habitats (Jablonski and Lutz 1980) rather than a response to ongoing selection in the Antarctic environment *per se.*

The shallow-water sea star fauna of McMurdo Sound has no apparent phylogenetic or distributional biases that might influence patterns of development (Fisher 1940, Hyman 1955, Clark 1963; see present Table 1). The high incidence of lecithotrophic development among these species lends credence to Thorson's (1950) hypothesis that environmental conditions in high latitudes are unfavorable for planktotrophic larvae. Thorson (1950), Vance (1973), and others (e.g. Christiansen and Fenchel 1979, Roughgarden 1989) further predicted that polar species would tend to develop non-pelagically, avoiding the high risk of predation associated with a slow-growing pelagic larval stage. Our finding that non-pelagic development is not prevalent among shallow-water sea stars in McMurdo Sound is therefore unexpected on the basis of both predicted and observed patterns of development in Antarctic and sub-Antarctic regions (Picken 1980, White 1984). There does appear to be a genuine predominance of non-pelagic development in some Antarctic benthic invertebrates. In particular, the data for Antarctic prosobranch gastropods, which are both empirical and comprehensive, indicate that most species produce embryos that develop to a juvenile stage within benthic egg masses or capsules (Dell 1972, Simpson 1977, Picken 1979, 1980). This is to be anticipated on the basis of developmental trends in Arctic prosobranchs (Thorson 1936, 1965). Such a marked disparity in patterns of development between representative sea star and gastropod faunas subject to comparable physical and biotic conditions suggests that phylogenetic history may have a considerable influence on the evolution of reproductive mode (Radwin and Chamberlin 1973, Strathmann 1978). Although generalities can be made (e.g., planktotrophy *tends* to be suppressed in high-latitude benthic marine invertebrate faunas), the underlying adaptive significance of a particular reproductive trait must be understood within the context of each taxon.

Our observation that pelagic non-feeding larval development is common among sea stars in McMurdo Sound is paralleled by observations of developmental types in deep-sea sea stars. Females of most (9 out of 11; 82%) species collected from the Rockall Trough (2 200 m) in the northeast Atlantic produce relatively small numbers of moderately sized (0.85 to 1.10 mm) yolky eggs that probably develop into dispersive non-feeding larvae (Pain et al. 1982, Tyler et al. 1982). Studies by Einarsson (1948) on Icelandic echinoderms suggest that a similar developmental tendency may exist in asteroids of Arctic regions. Of the 21 species surveyed, 47% had non-feeding, dispersive larvae and 14% had planktotrophic larvae. These observations stand in sharp contrast to the predominance of planktotrophic development in temperate and tropical shallow-water asteroid faunas (Emlet et al. 1987).

Deep-sea and shallow-water polar environments have many important physical and biotic similarities (Lipps and Hickman 1982). It is not surprising to find similar reproductive adaptations in comparable deep-sea and polar sea stars. The trend toward non-feeding development in these faunas is probably related to low food levels for larvae, although larval growth in at least one Antarctic species, the sea star *Odontaster validus*, is not limited by food supply (Olson et al. 1987). The adaptive causes and consequences of pelagic and non-pelagic lecithotrophic development are not understood. Deep-sea and polar benthos are physically stable and the turnover of populations in these communities are extremely slow (Grassle and Sanders 1973, Dayton et al. 1974, White 1984). Under such conditions, the advantages of a dispersive larval stage may be minimized relative to reproductive adaptations that enhance competitive capabilities, as might be expected of the more robust, early-stage juveniles typically produced by species with protected development. On the other hand, adaptations that enhance the dispersal of offspring can be advantageous in stable habitats (Hamilton and May 1977). The relative costs and advantages of pelagic and non-pelagic development need further consideration, particularly in the context of polar and deep-sea environments where planktotrophic types of development tend to be suppressed and a diversity of lecithotrophic developmental types co-exist.

Acknowledgements. We thank K. Miller, S. Alexander and especially R. Britton and B. Marinovic for diving assistance; the Antarctic Services Inc. of ITT and the U.S. Navy Antarctic Support Force for logistic support; and M. F. Barker, J. B. McClintock, and A. T. Newberry for valuable comments on earlier versions of this manuscript. We are indebted to H. E. S. Clark for identifying several of the species surveyed. This study was supported in part by National Science Foundation Grant No. DPP-8317082 and a Harbor Branch Institution Postdoctoral Fellowship. Contribution No. 727 to the Harbor Branch Oceanographic Institution.

Literature cited

Arnaud, P. M. (1974). Contribution à la bionomie marine benthique des regions antarctiques et subantarctiques. Téthys 6: 465–556

Blake, D. B. (1987). A classification and phylogeny of post Paleozoic sea stars (Asteroidea: Echinodermata). J. nat. Hist. 21: 481–528

Bosch, I. (1989). Contrasting modes of reproduction in two antarctic asteroids the genus *Porania*, with a description of unusual feeding and nonfeeding larval types. Biol. Bull. mar. biol. Lab., Woods Hole 177: 77–82

Chia, F. S. (1974). Classification and adaptive significance of developmental patterns in marine invertebrates. Thalassia jugosl. 10: 121–130

Christiansen, F. B., Fenchel, T. M. (1979). Evolution of marine invertebrate reproductive strategies. Theor. Popul. Biol. 16: 267–282

Clark, A. M. (1962). Asteroidea. Rep. B.A.N.Z. antarct. Res. Exped. 9: 1–104

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

Dayton, P. K., Oliver J. S. (1977). Antarctic soft bottom benthos in oligotrophic and eutrophic environments. Science, N.Y. 97: 55–58

Dayton, P. K., Robilliard, G. A., Paine, R. T., Dayton, L. B. (1974). Biological accommodation in the benthic community at McMurdo Sound, Antarctica. Ecol. Monogr. 44: 105–128

Dearborn, J. H. (1965). Ecological and faunistic investigation of the marine benthos at McMurdo Sound Antarctica. Ph. D. thesis, Stanford University, California, USA

Dell, R. K. (1972). Antarctic benthos. Adv. mar. Biol. 10: 1–216

Einarsson, H. (1948). Echinodermata. Zool. Iceland 4: 1–67

Emlet, R. B., McEdward, L. R., Strathman, R. R. (1987). Echinoderm larval ecology viewed from the egg. In: Jangoux, M., Lawrence, J. M. (eds.) Echinoderm studies. Vol. 2. Balkema Press, Rotterdam, p. 55–136

Fell, H. B., Dawsey, S. (1969). Asteroidea. Antarctic Map Folio Ser. 11: 42–43

Fisher, W. K. (1940). Asteroidea. 'Discovery' Rep. 20: 69–306

Grassle, J. F., Sanders, H. L. (1973). Life histories and the role of disturbance. Deep-Sea Res. 20: 643–649

Hamilton, W. D., May, R. M. (1977). Dispersal in stable habitats. Nature, Lond. 269: 578–581

Hinegardner, R. T., Tuzzi, M. M. R. (1981). Laboratory culture of the sea urchin *Lytechinus pictus*. In: Hinegardner, R. T. (ed.) Laboratory animal management of marine invertebrates. National Academic Press, Washington D.C., p. 291–302

Hyman, L. H. (1955). The invertebrates: Echinodermata. Vol IV. McGraw Hill Book Co., Inc. New York

Jablonski, D., Lutz R. A. (1980). Molluscan larval shell morphology, ecological and paleontological applications. In: Rhoads, D. C., Lutz, R. A. (eds.) Skeletal growth of aquatic organisms. Plenum Publishing Co., London, p. 323–377

Lipps, J. H., Hickman, C. S. (1982). Origin, age, and evolution of antarctic and deep-sea faunas. In: Ernst, W. G., Morin, J. G. (eds.) The environment of the deep sea. Prentice-Hall Inc., Englewood Cliffs, N.J., p. 324–356

MacBride, E. W., Simpson, J. C. (1908). Echinodermata II. Echinoderm larvae. Natn. Antarct. Exped. 1901–1904 (Nat. Hist.) 4: 1–9

McClintock, J. B., Pearse, J. S. (1986). Organic and energetic content of eggs and juveniles of antarctic echinoids and asteroids with lecithotrophic development. Comp. Biochem. Physiol. 85A: 341–345

McClintock, J. B., Pearse, J. S. (1987). Biochemical composition of antarctic echinoderms. Comp. Biochem. Physiol. 86B: 683–687

McClintock, J. B., Pearse, J. S., Bosch, I. (1988). Population structure and energetics of the shallow-water antarctic sea star *Odontaster validus* in contrasting habitats. Mar. Biol. 99: 235–246

Mileikovsky, S. A. (1971). Types of larval development in marine bottom invertebrates, their distribution and ecological significance: a re-evaluation. Mar. Biol. 10: 193–213

Ocklemann, K. W. (1965). Developmental types in marine bivalves and their distribution along the Atlantic coast of Europe. Proc. 1st Eur. malac. Congr. 1962: 25–35. [Cox, L. R., Peake, J. F. (eds.) Conchological Society of Great Britain and Malacological Society of London]

Olson, R. R., Bosch, I., Pearse, J. S. (1987). The antarctic larval food limitation hypothesis examined for the asteroid *Odontaster validus*. Limnol. Oceanogr. 32: 686–690

Pain, S. L., Tyler, P. A., Gage, J. D. (1982). The reproductive biology of the deep-sea asteroids *Benthopecten simples, Pectinaster filholi,* and *Pontaster tenuispinus* (Phanerozonia: Benthopectinidae) from the Rockall Trough. J. exp. mar. Biol. Ecol. 65: 195–211

Pearse, J. S. (1965). Reproductive periodicities in several contrasting populations of *Odontaster validus* Koehler, a common antarctic asteroid. Biology of the antarctic seas. II. Antarctic Res. Ser. 5: 39–85

Pearse, J. S., Bosch, I. (1986). Are the feeding larvae of the most common antarctic asteroid really demersal? Bull. mar. Sci. 39: 477–484

Picken, G. B. (1979). Non-pelagic reproduction of some antarctic gastropods from Singy Island, South Orkney Islands. Malacologia 19: 109–128

Picken, G. B. (1980). Reproductive adaptations of antarctic benthic invertebrates. Biol. J. Linn. Soc. 14: 67–75

Radwin, G. E., Chamberlin, J. L. (1973). Patterns of larval development in stenoglossan gastropods. Trans. S Diego Soc. nat. Hist. 17: 107–117

Richardson, M. G. (1977). The ecology and reproduction of the brooding antarctic bivalve, *Lissarca miliaris*. Br. Antarct. Surv. Bull. 49: 91–155

Rivkin, R. B., Bosch, I., Pearse, J. S., Lessard, E. J. (1986). Bacterivory: a novel feeding mode for asteroid larvae. Science, N.Y. 223: 1311–1314

Rohde, K. (1985). Increased viviparity of marine parasites at latitudes. Hydrobiologia 127: 197–201

Roughgarden, J. (1989). The evolution of marine life cycles. In: Feldman, M. W. (ed.) Mathematical evolutionary theory. Princeton University Press, Princeton, New Jersey, p. 270–300

Simpson, R. D. (1977). The reproduction of some littoral molluscs from Macquarie Island (Sub-Antarctic). Mar. Biol. 44: 125–142

Simpson, R. D. (1982). The reproduction of some echinoderms from Macquarie Island. Mem. Aust. Mus. 16: 39–52

Strathmann, R. R. (1971). The feeding behavior of planktotrophic echinoderm larvae: mechanisms, regulation, and rates of suspension feeding. J. exp. mar. Biol. Ecol. 6: 109–160

Strathmann, R. R. (1978). The evolution and loss of feeding larval stages of marine invertebrates. Evolution, Lawrence, Kansas 32: 894–906

Thorson, G. (1936). The larval development, growth and metabolism of Arctic marine bottom invertebrates. Meddr Grønland 100: 1–155

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

Thorson, G. (1965). The distribution of benthic marine mollusca along the N.E. Atlantic shelf from Gibraltar to Murmansk. Proc. 1st Eur. malac. Congr. 1962: 5–25. [Cox, L. R., Peake, J. F. (eds.) Conchological Society of Great Britain and Malacological Society of London]

Tyler, P. A., Grant, A., Pain, S. L., Gage, J. D. (1983). Is annual reproduction in deep-sea echinoderms a response to variability in their environment? Nature, Lond 300: 747–750

Vance, R. R. (1973). On reproductive strategies of marine benthic invertebrates. Am. Nat. 107: 353–361

White, M. G. (1984). Marine benthos. In: Laws, R. M. (ed.) Antarctic ecology. Vol. 2. Academic Press, London, p. 421–461

Date of final manuscript acceptance: August 18, 1989.
Communicated by J. M. Lawrence, Tampa