

Reproduction of Antarctic Benthic Marine Invertebrates: Tempos, Modes, and Timing¹

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SYNOPSIS. Work on the life histories of common antarctic benthic marine invertebrates over the past several decades demands a revision of several widely held paradigms. First, contrary to expectations derived from work on temperate species, there is little or no evidence for temperature adaptation with respect to reproduction (gametogenesis), development, and growth. It remains to be determined whether the slow rates of these processes reflect some inherent inability to adapt to low temperatures, or are a response to features of the antarctic marine environment not directly related to low temperature, such as low food resources. Secondly, contrary to the widely accepted opinion designated as "Thorson's rule," pelagic development is common in many groups of shallow-water marine invertebrates. In fact in some groups, such as asteroidea, pelagic development is as prevalent in McMurdo Sound, the southern-most open-water marine environment in the world, as in central California. In other taxonomic groups, especially gastropods, there does seem to be a genuine trend toward non-pelagic development from tropical to antarctic latitudes. Although this trend has been predicted by theoretical models, its underlying causes appear to be group specific rather than general. Thirdly, pelagic lecithotrophic development, often considered to be of negligible importance, occurs in many shallow-water antarctic marine macroinvertebrates. Pelagic lecithotrophy may be an adaptation to a combination of poor food conditions in antarctic waters most of the year and slow rates of development. Nevertheless, some of the most abundant and widespread antarctic marine invertebrates have pelagic planktotrophic larvae that take very long times to complete development to metamorphosis. These species are particularly prevalent in productive regions of shallow water (<30 m), which are frequently disturbed by anchor ice formation, and the production of numerous pelagic planktotrophic larvae may represent a strategy for colonization. Although planktotrophic larvae tend to be seasonal in occurrence, their production is not linked particularly closely to the mid-summer pulse of phytoplankton production. These larvae show no evidence of starvation, even during times when phytoplankton abundance is very low, and they may depend on unusual sources of food, such as bacteria. How they escape the selective conditions that apparently led to a predominance of non-feeding modes of development in antarctic marine invertebrates remains as a major challenge for antarctic marine biology.

INTRODUCTION

Waters around Antarctica are often viewed as being extremely hostile to marine life. They are perpetually near freezing, variable in salinity as ice forms and melts, often stormy with generally offshore currents, usually poor in food, and continually

dark or continually light for many months of the year. Nevertheless, since the expeditions of the late 19th and early 20th century, these waters have been known to be home to a rich and diverse fauna with representatives of most major groups of marine plants and animals (Hedgpeth, 1969a, b; Dell, 1972; Arnaud, 1974; White, 1984). Living in such apparently hostile conditions, the organisms of this biota might be expected to possess unusual adaptations. Indeed, Thomson (1878) noted some "peculiar" modes of reproduction by spec-

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imens collected during the Challenger Expedition, and Giard (1905) proposed that there was an overall tendency for antarctic animals to brood their offspring and bypass pelagic larval stages. Moreover, Orton (1920) predicted that the timing of reproduction by polar marine invertebrates in general would tend to be aseasonal and more or less continuous.

During the past 30 years, since the establishment and maintenance of permanent shore-based research facilities in Antarctica, a variety of benthic marine animals have been studied and their life histories characterized. Their tempo of metabolism, development, and growth seemed unaccountably slow, especially as knowledge about temperature adaptation developed (Clarke, 1982, 1983, 1987, 1989, 1990). Moreover, while some species fit previously predicted non-pelagic modes of reproduction, more and more "exceptions" have been noted among others (Pearse *et al.*, 1986). Reproduction was found to be strongly seasonal for some species, despite Orton's (1920) prediction, and new paradigms linking reproduction to the summer period of high phytoplankton production have developed (Thorson, 1950; White, 1977, 1984; Clarke, 1988). In the present paper we review current knowledge about reproduction of antarctic marine invertebrates in light of theoretical predictions, and reveal that some of our most established theories about life history patterns need to be abandoned or greatly modified, while others continue to be inadequate.

THE ENVIRONMENT AND PREDICTED RESPONSES

There are a number of characteristic features of the antarctic nearshore marine environment which are strikingly unlike those in most other parts of the world ocean, and which would be expected to have a major influence in shaping physiological and ecological functioning of antarctic fauna, including reproduction. In some cases, available information from other parts of the world has led to reasonable predictions about how the fauna would be expected to have responded. In this sec-

tion, we briefly examine this information and the predictions it has generated.

Temperature

Sea temperatures, even near the surface, are the most stable in the world, hovering around the freezing point of sea water between -2.0 to -1.5°C along the continental shores (Littlepage, 1965; Hicks, 1974) and ranging from about -2.0 to $+2.0^{\circ}\text{C}$ in northern portions of the Antarctic Peninsula and the subantarctic islands (Foster, 1984). Although the range is small, these temperatures can fluctuate with a clear seasonal pattern; Littlepage (1965) found that even in McMurdo Sound, the southern-most open-water region in the world, sea temperatures ranged from brief periods of -2.1°C in midwinter to -1.7°C in midsummer. On the basis of this evidence Pearse (1965) argued that seasonal activities such as reproduction might be cued by seasonally changing sea temperatures, as, in fact, appears to be the case for spawning activity in several populations of the antarctic limpet *Nacella concinna* (Shabica, 1976; Picken, 1980).

Sea temperatures have been low, and probably very stable, since the late Miocene cooling about 14 million years ago (Shackleton and Kennet, 1975; Lipps and Hickman, 1982). With such a long period of continually low temperatures, well-adapted temperature compensation for all life processes might be expected. After all, many temperate species acclimatize metabolic responses, including growth and development, to seasonal temperature fluctuations (Kinne, 1970; Horstadius, 1975). Metabolic, physiological, and reproductive processes "should" all be temperature adapted in antarctic marine invertebrates, and proceed at rates comparable to those in temperate, or even tropical, waters.

Physical hazards in shallow pelagic areas

Being always close to freezing, and being overlain with air that is either above or below (sometimes far below) freezing, antarctic surface waters continually are either freezing or melting. During freezing, fresh water is extracted as ice, leaving

a hyperosmotic solution behind. Alternatively, as the sea ice melts, fresh water is released, diluting the salt content of surface waters. In addition, as ice and snow on land melt during the summer, fresh water pours out over nearshore surface waters. In the Arctic, seasonal freshwater dilution can be very marked as melting occurs on the surrounding lands (Graininger, 1959), but nearshore antarctic waters can be subject to substantial seasonal salinity fluctuations as well (Bunt, 1960). Such salinity fluctuations might be expected to be particularly hazardous to larval stages with little osmoregulatory capability, and Hardy (1960) suggested that they would select against pelagic larvae of benthic animals.

Other factors also might be hazardous to pelagic animals, including larvae, that are near the surface. Storms are notorious in the Southern Ocean, and when the sea is not covered with solid ice, waves will throw water over the shore and floating ice, stranding organisms which then freeze. Moreover, winds almost always blow off the antarctic continent and out to sea, carrying surface waters offshore, and presumably away from areas suitable for settlement of the larvae of benthic animals. Ostregren (1912) proposed that such offshore currents would select against pelagic larvae in antarctic waters, although Mortensen (1913) argued against that proposal.

Seasonal production and oligotrophy

Antarctic seas are among the most seasonal habitats in the world (Clarke, 1988), with high primary production in mid-summer, and little or no primary production from late fall to early spring (Holm-Hansen, 1985; Perrin *et al.*, 1987; Rivkin, 1990). Three alternative reproductive "strategies" by benthic marine invertebrates may be predicted to occur as a response to such extreme seasonality. First, planktotrophic pelagic larvae might be produced in spring and summer when food for the larvae is plentiful. Second, lecithotrophic larvae that are independent of larval food, and therefore of the seasonal production of phytoplankton, might be produced. Third,

embryos may be retained by the parent or in benthic egg cases that hatch out as benthic juveniles, thereby avoiding the plankton altogether.

After reviewing the information available to him, Thorson (1950) concluded that most polar marine invertebrates have taken the third option and have benthic embryonic development without any pelagic larval stages. He attributed this pattern to the restricted summer food conditions for pelagic larvae, and argued that the trend toward benthic brood protection and viviparity is particularly pronounced in the Antarctic. Additional information reviewed by Mileikovsky (1971) appeared to add support to this trend, which Mileikovsky termed "Thorson's rule." Other more recent workers largely agree that there is a trend toward non-pelagic development by benthic antarctic invertebrates (Dell, 1972; Arnaud, 1974; White, 1977, 1984; Simpson, 1977; Picken, 1980). And Crisp (1986, p. 70) believed that the "one valid generalization" concerning the question of whether a species produces pelagic larvae is "that pelagic larvae are found in the majority of tropical invertebrates . . . but in few high latitude species of invertebrates."

Comparing the various types of larvae of benthic marine invertebrates, Thorson (1950) concluded, mainly from his experience with molluscs, that non-feeding pelagic lecithotrophic larvae were of minor importance in general and were restricted to temperate and tropical areas. Thus, non-feeding lecithotrophic development by polar species was always considered by Thorson to be non-pelagic as well. Other workers have focused on the contrast between feeding and non-feeding modes of development, also usually assuming that the non-feeding modes are non-pelagic. In particular, nutritional mode of development in gastropods and bivalves can be inferred by the size and shape of the larval shell, and comparative studies suggest that non-feeding modes of development predominate in polar forms (reviewed by Jablonski and Lutz, 1983). In addition, theoretical modelers have considered trade-offs between producing (1) many small eggs

that develop into feeding larvae and (2) relatively few large eggs that develop without a feeding larval stage, and concluded that when food supplies are low, and developmental rates slow, as in polar seas, non-feeding modes of development should predominate (Vance, 1973; Grant, 1983; Strathmann, 1985). Roughgarden (1989) reached a similar conclusion with his models, and equated non-feeding modes with non-pelagic modes of development; thus theory predicts non-pelagic (=non-feeding) development in polar seas, as the empirical data had suggested.

Physically unstable shallow benthos

The shallow benthos around the antarctic continent is in one of the most unstable and physically disrupted marine habitats known. Ice forms along the shore down to about 10 m, effectively eliminating the intertidal and shallow subtidal along most of the coast. Where there is bare rock, the community is relatively simple and largely ephemeral (Hedgpeth, 1969b; Dayton *et al.*, 1974; DeLaca and Lipps, 1976). In addition to the shore-bound ice, ice-bergs are often grounded in shallow water of some areas, ploughing up the bottom and disrupting the benthos (Kauffman, 1974). Moreover, anchor ice forms during the winter on rocks and organisms down to depths of about 20–30 m. When enough forms, it can break free of the bottom, lifting rocks and organisms to the surface where they freeze into the undersurface of floating sea ice (Pearse, 1962; Dayton *et al.*, 1969). Dayton *et al.* (1970) suggest that anchor ice formation causes a faunal zonation in shallow water, with motile species that can escape entrapment or ephemeral species that can colonize open space predominating at depths less than about 30 m. Nevertheless, such shallow depths may be among the most productive of the antarctic benthos as indicated by standing stocks and activities of microbes and algae (White *et al.*, 1985; Dayton *et al.*, 1986; Miller and Pearse, 1990), by the rich infaunal assemblage of small polychetes and arthropods (Oliver, 1979), and by the abundance and size of omnivores such as the asteroid *Odonaster validus* (McClintock *et al.*, 1988). Ben-

thic invertebrates in such an environment would be expected to have life-history characteristics that provide for rapid colonization, and include possession of dispersive larvae. Non-pelagic development that would localize populations should not be favored.

Physically stable deeper benthos

In contrast to the shallow benthos, which is impacted by ice scour and anchor ice disruption, deeper portions of the antarctic benthos are physically very stable, as are other deeper water marine habitats. Moreover, rays and other fishes that cause bioturbation are virtually absent, as are bottom-feeding cetaceans, in contrast to arctic seas (Oliver and Slattery, 1985). In some areas, such as the southeast corner of McMurdo Sound, sponges form thick mats at depths greater than 20–30 m, down to 50 m or more, and some of the larger sponges appear to attain great ages (Dayton *et al.*, 1974; Dayton, 1979). In other, more oligotrophic areas under thick layers of sea ice, such as on the west side of McMurdo Sound (Dayton and Oliver, 1977), or under ice shelves (Littlepage and Pearse, 1962) the benthos resembles that of the deep sea and is dominated by scavengers and predators. In both types of areas, physical stability appears to be very high, and turnover of populations quite slow, suggesting a K-selected environment (White, 1984). In such an environment, biological interactions may determine community organization more strongly than physical disturbance, and component species would be selected for strengths in competitive interactions as well as in predator-prey relationships. Animals may be expected to invest relatively large amounts of resources into individual offspring so that the juveniles would be large and well established early on, enhancing their competitive capabilities. High investment in individual offspring would result in lower fecundity (Strathmann, 1977; Emlet *et al.*, 1987), decreasing the potential for pelagic larvae. In such an environment, one might expect lecithotrophic development resulting in large juveniles, with embryonic and larval stages that spend a relatively short

time in the plankton, or undergo completely non-pelagic development.

EMPIRICAL STUDIES

Tempo of reproduction, development, and growth

Although studies in temperate latitudes have suggested that organisms would be expected to show temperature compensation at polar latitudes, such as in the Antarctic, and rates of activities associated with reproduction, development, and growth would be comparable to those in warmer environments, no marked compensation has been seen in most of the animals investigated to date. Indeed, in nearly all cases, these processes are very slow, and they show little or no evidence of temperature adaptation. Oogenesis in echinoderms (Pearse, 1965; Pearse and Giese, 1966; McClintock and Pearse, 1987; but see Yakovlev, 1984), molluscs (Picken, 1979, 1980; Richardson, 1979; Seager, 1979), and crustaceans (Pearse, 1963; Marinovic, 1987) takes more than a year to complete, so that two or even three annual cohorts of growing oocytes can be found in the same animal at one time. The same slow rate of oogenesis is found in antarctic fishes (Hourigan and Radtke, 1989). Developmental rates are also very slow; pelagic lecithotrophic asteroid larvae take 2 to 3 months before settling and metamorphosing (Bosch and Pearse, 1990) compared to less than 1 month for most temperate and tropical pelagic lecithotrophs; pelagic planktotrophic asteroid and echinoid larvae take 5 to 6 months (Pearse and Bosch, 1986; Bosch *et al.*, 1987); and brooding echinoderms release their embryos only after more than 6 months (Morrison, 1979; Simpson, 1982; Blankley and Branch, 1984; Schatt, 1984; Bosch, 1989). Incubation periods determined for several crustaceans (Pearse, 1963; White, 1970; Bregazzi, 1972; Clarke, 1983; Marinovic, 1987) and molluscs (Simpson, 1977; Richardson, 1979; Seager, 1979; Picken, 1979, 1980) are also lengthy, extending beyond 18 months in some cases. Similarly, nearly all growth rates that have been determined for marine invertebrates are surprisingly

slow (reviewed by Clarke, 1983, 1987), as are those for fishes (Hourigan and Radtke, 1989).

The reasons that rates of reproduction, development, and growth in antarctic marine invertebrates are so slow compared to those of temperate species are unknown. Clarke (1990) argues that the comparatively slow rates cannot even be taken as evidence of lack of temperature compensation, but rather they may be adaptations to low food supplies during most of the year. Nevertheless, it is difficult to see how development of lecithotrophic embryos and larvae, which are provisioned with nutrients by the parent, could be nutrient limited. Moreover, selection for rapid development through these precarious stages might be expected to be as severe in polar marine environments as elsewhere, so that slow developmental rates should not persist if change is possible. Developmental rates of antarctic invertebrates can be extraordinarily sensitive to temperature changes; an increase of only a few degrees nearly doubles the rate of development, from about -1.8°C to 0.0°C for sea urchin embryos (Bosch *et al.*, 1987) or 0.0°C to 2.0°C for krill embryos (Ross and Quetin, 1986). Consequently, temperature itself appears to be closely involved with the slow developmental rates observed in antarctic (polar) marine invertebrates.

Regardless of the causes, it is now firmly established that the tempo of reproduction and growth of antarctic marine invertebrates is generally very slow. Gametogenesis typically takes a year or more for completion, embryonic and larval development several months to half a year or more, and growth to adulthood many years. Such a slow tempo would be expected to have a profound effect on all aspects of the life history of a species, and on how rapidly (or slowly) a species or community can respond to perturbation and change.

Mode of development: pelagic versus non-pelagic

As already discussed, the early evidence of Thomson (1878), Giard (1905), Ostregren (1912), and others led Thorson (1950, p. 37) to conclude that in the antarctic shore

TABLE 1. Developmental modes of shallow-water asteroids in McMurdo Sound, Antarctica and Monterey Bay, California.*

| McMurdo Sound | Monterey Bay |
|---|--|
| Brooders: <i>Diplasterias brucei</i> <i>Notasterias armata</i> | <i>Leptasterias hexactis</i> <i>Leptasterias pusilla</i> <i>Henricia leviuscula</i> (small form) |
| Benthic nonfeeding larva: <i>Porania</i> species | |
| Pelagic nonfeeding larva: <i>Macroptychaster accressens</i> <i>Psilaster charcoti</i> <i>Bathybiaster loripes</i> <i>Lophaster gaini</i> <i>Acodontaster hodgsoni</i> <i>Acodontaster conspicuus</i> <i>Acodontaster capitatus</i> <i>Perknaster fuscus</i> | <i>Mediaster aequalis</i> <i>Pteraster tessellatus</i> <i>Solaster dawsoni</i> <i>Henricia leviuscula</i> (large form) |
| Pelagic feeding larva: <i>Odontaster meridionalis</i> <i>Odontaster validus</i> <i>Porania antarctica</i> | <i>Luidia foliata</i> <i>Astropecten californicus</i> <i>Dermasterias imbricata</i> <i>Poraniopsis inflata</i> <i>Asterina miniata</i> <i>Orthasterias koehleri</i> <i>Pisaster brevispinus</i> <i>Pisaster giganteus</i> <i>Pisaster ochraceus</i> <i>Pycnopodia helianthoides</i> |

* Data from Pearse *et al.* (1985), Bosch (1989) and Emlet *et al.* (1987).

fauna "... non-pelagic development is the rule, ... where brood protection and viviparity is dominant." More recent evidence reveals that for many groups the proportion of shallow-water species with pelagic development in the antarctic is similar to that found elsewhere. For example, among the 14 species of shallow-water asteroids known from McMurdo Sound, Antarctica, only 3 have non-pelagic development (2 are brooders); in comparison, of the 17 species of shallow-water asteroids known from Monterey Bay, California, 3 have non-pelagic development (Table 1). Pelagic development is also known or suspected for some of the other more abundant larger shallow-water invertebrates in McMurdo Sound (Table 2), including species of nemertean, polychetes, bivalves, and echinoids, as well as the crinoid *Promachocrinus kerguelensis* (McClintock and Pearse, 1987).

There are several reasons why development of antarctic species has been con-

sidered to be mainly non-pelagic for the past century. First, examples of brooding by antarctic species are unusual and noteworthy, as shown by Thomson (1878) with the deeply sunken marsupiums in antarctic spatangoid echinoids, all of which brood. Thus, these examples became well known early on. Subsequent workers were particularly alert to other examples and even attributed brooding to species that do not brood, using flimsy evidence. For example, Burne (1920) concluded that the large antarctic bivalve *Laternula elliptica* brooded its young because he found eggs in the mantle cavity of a crushed specimen; this bivalve is a broadcast spawner and develops pelagically within a protective egg capsule (Bosch and Pearse, 1988). Similarly, Gravier (1911) concluded that the large antarctic polychete *Flabelligera munda* brooded its young because he found eggs entangled in the anterior setae. No individuals of *F. munda* collected regularly

over a 15 month period in McMurdo Sound were observed brooding (Pearse *et al.*, 1985); the eggs noted by Gravier were most likely discharged at death after collection rather than through natural spawning.

More important, brooding animals are usually relatively easy to recognize in collections of preserved animals, and by selectively noting only those species that brood, information can be severely biased. Arnaud (1974), for example, lists known (or suspected) examples of brooders on the Adélie Coast and concludes that they are unusually abundant in accordance with "Thorson's rule," but he presents little comparable information on non-brooders. Fisher (1940) compiled a similar list from his systematic account of known species of antarctic asteroids and found an unusual proportion of brooding species. However, the mode of reproduction was known only for a small percentage (25%) of the total fauna. When the reproductive modes of all the asteroids in a given area were compared, as was done for the shallow waters of McMurdo Sound, no such high proportion of brooders was found (Bosch, 1989; Table 1). Indeed, the majority of species (12/14) free spawn their gametes and produce dispersive larvae.

Despite the fact that non-pelagic development may not be all that prevalent among large shallow-water antarctic invertebrates, as previously believed, there are some groups that do appear to display high incidences of brooding. Nearly all 43 known species of antarctic echinoids are members of the orders Cidaroida and Spatangoida, and all antarctic cidaroids and spatangoids brood their embryos, bypassing pelagic larval stages (Fell, 1976). The remaining echinoids are 3 species of the echinoidan genus *Sterechinus*, one of which (*S. neumayeri*) is widespread in shallow waters around the antarctic continent and has typical echinoid planktotrophic development (Bosch *et al.*, 1987). The antarctic cidaroids and particularly spatangoids appear to represent speciose taxons with relatively restricted and isolated populations, as might be expected of species with limited dispersal abilities (Jablonski and Lutz, 1983). Species within such taxons are

not independent examples of brooding, but belong to lineages of brooding taxons, and it is misleading to tabulate them separately as is often done.

Bivalves and gastropods are also well documented to have an unusually high number of species with non-pelagic development (Simpson, 1977; Richardson, 1979; Picken, 1980; Simpson and Harrington, 1985), and indeed, Thorson (1950) based his conclusions on patterns of developmental modes mainly on data from gastropods. In both groups, there is a high proportion of species with very small adult sizes, and it has been well established that brooding is associated with small size (Strathmann and Strathmann, 1982). Pelagic development is found among the common larger bivalves in McMurdo Sound (*Adamussium colbecki*, *Laternula elliptica*, *Limatula hodgsoni*; Pearse *et al.*, 1985). On the other hand, non-pelagic development appears to be the rule among gastropods, even the larger neogastropods (*Amauropsis grisea*, *Neobuccinum eatoni*, *Trophon longstaffi*) and opisthobranchs (*Austro-doris mcmurdensis*, *Philine antarctica*; Pearse *et al.*, 1985). Pelagic lecithotrophic development in the limpet *Nacella concinna* is exceptional (Picken, 1980). "Thorson's rule" does appear to hold with gastropods, the group Thorson (1950) used for his major supporting data, and the group referred to mainly by most other workers (Mileikovsky, 1971; Dell, 1972; Arnaud, 1974; Picken, 1980).

Mode of development: planktotrophic versus lecithotrophic

Although non-pelagic development is not particularly prevalent among antarctic shallow-water invertebrates as previously supposed, lecithotrophic development is unusually common. For example, most shallow-water asteroids in McMurdo Sound have pelagic lecithotrophic larvae, while most asteroids in shallow tropical and temperate regions such as Monterey Bay, California produce pelagic planktotrophic larvae (Emlet *et al.*, 1987; Table 1). These data are surprising in view of Thorson's (1950) conclusion that pelagic lecithotrophic development is rare in general and

TABLE 2. Mode of development and months during the year when shallow-water marine invertebrates spawn in McMurdo Sound, Antarctica.*

| | Months | | | | | | | | | | | | Evidence ^a |
|--|--------|---|---|---|---|---|---|---|---|---|---|---|-----------------------|
| | J | F | M | A | M | J | J | A | S | O | N | D | |
| Pelagic embryos, planktotrophic larvae | | | | | | | | | | | | | |
| Polychete | | | | | | | | | | | | | |
| <i>Flabelligera munda</i> ^c | | | | | | | S | S | | | | | 1a, 2, 3 |
| Bivalve | | | | | | | | | | | | | |
| <i>Limatula hodgsoni</i> ^c | | | | | X | X | X | X | S | S | | | 1a, 2, 4 |
| Asteroids | | | | | | | | | | | | | |
| <i>Odontaster validus</i> | | | | | | S | S | S | S | | | | 1b, 2, 3, 4, 5, 7 |
| <i>Odontaster meridionalis</i> | | | | | | S | S | S | S | | | | 1c, 2, 3, 4, 5, 7 |
| <i>Porania antarctica</i> | | | | | | | | S | S | S | | | 1c, 2, 5 |
| Echinoid | | | | | | | | | | | | | |
| <i>Sterechnus neumayeri</i> | | | | | | | | | | X | S | X | 1d, 2, 3, 4, 5, 6, 7 |
| Euphausiid | | | | | | | | | | | | | |
| <i>Euphausia crystallorophias</i> | S | X | | | | | | | | X | S | S | 1e, 2 |
| Nemertean | | | | | | | | | | | | | |
| <i>Parborlasia corrugatus</i> ^c | X | X | X | X | X | X | X | X | X | X | S | S | 1f, 2, 6, 7 |
| Pelagic embryos, pelagic lecithotrophic larvae | | | | | | | | | | | | | |
| Copepod | | | | | | | | | | | | | |
| <i>Euchaeta antarctica</i> | | | | | | X | S | S | X | | | | 1e, 7 |
| Cnidarian | | | | | | | | | | | | | |
| <i>Edwardsia meridionalis</i> ^c | X | X | X | X | X | X | X | X | X | X | X | X | 1g, 2 |
| Asteroids | | | | | | | | | | | | | |
| <i>Acodontaster hodgsoni</i> | X | X | X | X | X | X | X | X | X | X | X | X | 1h, 2, 3, 4, 5 |
| <i>Perknaster fuscus</i> ^c | X | X | X | X | X | X | X | X | X | X | X | X | 1h, 2, 3 |
| Pelagic embryos, no larvae | | | | | | | | | | | | | |
| Bivalve | | | | | | | | | | | | | |
| <i>Laternula elliptica</i> | | X | S | X | | | | | | | | | 1i, 2, 4, 5, 6, 7 |
| Benthic embryos, benthic lecithotrophic larvae | | | | | | | | | | | | | |
| Asteroid | | | | | | | | | | | | | |
| <i>Porania</i> sp. | X | X | X | X | X | X | X | X | X | X | X | X | 1c, 2, 5 |

TABLE 2. Continued.

| | Months | | | | | | | | | | | | Evidence ^a |
|----------------------------------|--------|---|---|---|---|---|---|---|---|---|---|---|-----------------------|
| | J | F | M | A | M | J | J | A | S | O | N | D | |
| Brooded embryos (no larvae) | | | | | | | | | | | | | |
| Peracaridians | | | | | | | | | | | | | |
| <i>Monoculodes scabriculosus</i> | S | S | S | S | X | X | X | X | | | | S | lg, 7 |
| <i>Eudorella splendida</i> | S | S | S | S | X | X | X | X | | | X | S | lg, 7 |
| <i>Heterophoxus videns</i> | | | | | | | | | X | X | X | X | lg, 7 |
| <i>Austrosignum grande</i> | S | X | X | X | X | S | S | S | X | S | S | S | lg, 7 |
| <i>Nototanaid dimorphus</i> | | X | X | X | X | S | S | S | S | X | | | lj, 7 |
| <i>Orchomene plebs</i> | | X | X | X | X | S | S | S | S | | | | lk, 7 |
| <i>Glyptonotus antarcticus</i> | X | X | X | X | X | X | X | X | X | X | X | X | ll, 7 |
| Asteroid | | | | | | | | | | | | | |
| <i>Diplasterias brucei</i> | X | X | X | X | X | X | X | X | X | X | X | X | lf, lh, 2, 7 |
| Echinoids | | | | | | | | | | | | | |
| <i>Abatus nimrodi</i> | X | X | X | X | X | X | X | X | X | X | X | X | la, m, 2, 7 |
| <i>Abatus shackletoni</i> | X | X | X | X | X | X | X | X | X | X | X | X | la, m, 2, 7 |

^a Symbols: S, main spawning period; X, some spawning probable because mature gametes present, or in the case of suspected continuous breeders, brooding animals and/or larvae found irregularly throughout the year.
^b 1. Literature: a. Pearse *et al.*, 1986; b. Pearse, 1965, Pearse and Bosch, 1990; i. Bosch and Pearse, 1988; j. Marinovic, 1987; k. Pearse, 1963, Rakusa-Suszczewski, 1964; f. Dearborn, 1965; g. Oliver, 1979; h. Bosch and Pearse, 1988; j. Marinovic, 1987; k. Pearse, 1963, Rakusa-Suszczewski, 1964; l. Dearborn, 1967; m. McClintock and Pearse, 1988. 2. Fresh gonadal smears. 3. Gonadal size analyses. 4. Histological analyses of the gonads. 5. Spawning in the laboratory. 6. Spawning observed in the field. 7. Embryos or larvae collected in the field.
, Developmental mode based on size and buoyancy of eggs and lack of observation of brooding; small eggs less than 200 micrometers, planktotrophic; large eggs more than 500 micrometers, lecithotrophic.

virtually absent in polar environments. On the other hand, several workers (*e.g.*, Vance, 1973; Grant, 1983; Strathmann, 1985; Roughgarden, 1989) have used mathematical models to contrast conditions that would lead to planktotrophic or lecithotrophic development; they conclude that in areas where food resources are poor and where developmental rates are slow ("because" of low temperatures), lecithotrophic development would be favored. These conditions are those of polar regions and the deep seas, and Thorson (1950) evoked them to explain the rarity of species with pelagic planktotrophic larvae in these regions. Indeed, he appears to have proposed the right reasons but only for part of the phenomenon that needed explanation, that is, for non-pelagic development rather than for non-feeding development. Vance (1973) further argued that where development is very slow and mortality is much greater for pelagic larvae than for brooded embryos, as might be envisioned in polar seas, there would be a shift toward non-pelagic development. However, as we have shown (Tables 1 and 2) such restrictive conditions apparently do not occur even in the highest latitudes of the antarctic marine environment.

Lecithotrophic development has several consequences besides freeing the embryo or larva from dependence on particulate food. The eggs are typically much larger than those that develop into planktotrophic larvae, and the juveniles produced from lecithotrophic development are generally much larger than those that result from planktotrophic development (Ockelmann, 1965; Jablonski and Lutz, 1983; Strathmann, 1977; Emler *et al.*, 1987). Moreover, because relatively small amounts of the organic material in the large lecithotrophic eggs of brooding antarctic spatangoids are consumed during development, Lawrence *et al.* (1984) and McClintock and Pearse (1986) suggested that the material in the eggs served primarily to form large juveniles and not as a source of nourishment for the embryos. Consequently, under conditions where juvenile mortality is high and restrictive, and is size dependent, lecithotrophy (whether with non-pelagic or

pelagic development) might be favored. If such mortality is the primary selective agent leading to lecithotrophy in antarctic environments, low nutrient levels in pelagic waters may not be of such importance as supposed by Thorson (1950) and theoretical modelers (Vance, 1973; Roughgarden, 1989).

Another major consequence of lecithotrophy is that developmental time in the plankton is generally shortened (Emler *et al.*, 1987). This effect may be particularly important in polar environments where development rates are very slow. Thus, pelagic lecithotrophic development could be interpreted as an adaptation that lowers larval mortality by decreasing the time larvae spend among the hazardous plankton. Nevertheless, producing relatively large eggs invariably lowers the potential fecundity of an animal, and when development is pelagic at all, there is still the problem of how, as stated by Grant (1983), "species with long-lived lecithotrophic larvae overcome the combined effects of lowered fecundity and high mortality during the larval period." The adaptive attributes of pelagic lecithotrophic development by antarctic marine invertebrates beg for further explanation.

Despite the prevalence of lecithotrophic development, some of the most common and widespread shallow-water antarctic marine invertebrates have pelagic planktotrophic larvae. These include the asteroid *Odontaster validus* (Pearse, 1969; Pearse and Bosch, 1986), the echinoid *Sterechinus neumayeri* (Bosch *et al.*, 1987), the bivalve *Adamussium colbecki* and the nemertean *Parborlasia corrugatus* (Pearse *et al.*, 1985). Larvae of *O. validus* are abundant and can be collected in early spring when little phytoplankton food is available (Pearse and Bosch, 1986; Bosch, 1988); they appear healthy and adequately nourished, and they survive and continue to develop when held within chambers in the field for over a month (Olson *et al.*, 1987). Experiments using radio-labeled tracers suggest that all these larvae feed on bacteria (Rivkin *et al.*, 1986). It is not yet known, however, whether bacterivory is a key adaptation allowing species with feeding larvae to

thrive in an environment that appears to select for non-feeding modes of development.

Timing of reproduction

As might be expected, shallow-water antarctic species with planktotrophic larvae tend to have more restricted and seasonal spawning times than those with non-feeding modes of development (Table 2). However, the correspondence between spawning times and period of mid-summer phytoplankton production is not particularly close. In the asteroids *Odontaster validus*, *O. meridionalis*, and *Porania antarctica*, all with planktotrophic larvae, spawning occurs in late winter (mid-June) to early spring in McMurdo Sound, 3 to 4 months before the mid-summer pulse of phytoplankton enters the area. Larvae of these species begin to feed when they are 1 to 2 months old (Bosch, 1988), well before the phytoplankton bloom. Moreover, planktotrophic pilidium larvae are present in the plankton throughout the year, presumably reflecting spawning by the common large nemertean *Parborlasia corrugatus* throughout the year (Pearse and Bosch, unpublished). Larvae of all of these species are known to feed on bacterioplankton that are relatively abundant all year (Rivkin *et al.*, 1986); they may not be as dependent on the mid-summer phytoplankton bloom as has been suspected (White, 1977; Picken, 1980).

Pelagic lecithotrophic larvae would be expected to be independent of the plankton for food, and data collected throughout the year for three benthic species in McMurdo Sound that produce pelagic lecithotrophic larvae show them to reproduce throughout the year (Table 2). The contrast between the three asteroid species known to have pelagic lecithotrophic larvae versus two other asteroid species with pelagic planktotrophic larvae is particularly notable. Nevertheless, our data are presently quite limited, and as more are gathered, we can expect more examples of seasonal reproduction by species with pelagic lecithotrophic larvae. One such species is the crinoid *Promachocrinus kerguelensis*, which McClintock and Pearse

(1987) suggested spawned in early summer, based on gonad condition and egg sizes of summer-collected samples. Moreover, there are other species with non-feeding pelagic developmental modes that have seasonal reproduction. For example, the carnivorous pelagic copepod *Euchaeta antarctica* produces pelagic lecithotrophic larvae in late winter and early fall. Littlepage (1964) suggested that the early production of these larvae allowed them to develop into carnivorous juveniles in early summer, when nauplii of the euphausiid *Euphausia crystalloporhys* and other crustaceans are produced and can be preyed upon. Conversely, Daniels (1978) suggested that reproduction is timed in the antarctic plunder fish, *Harpagifer bispinis*, so that hatchlings are released before predatory zooplankters build up in association with the summer plankton bloom. In another interesting example, the bivalve *Laternula elliptica* produces pelagic embryos during a restricted period in the fall that develop without feeding (or even hatching from the egg membranes) into tiny juveniles, which then settle in large numbers (Bosch and Pearse, 1988). These embryos are in the plankton after the mid-summer plankton bloom, and the timing of their hatching follows settlement of the phytoplankton onto the sea floor, which could provide juveniles with an early nutrient source. These examples indicate the abundance of larval food is not the only factor that could select for restricted timing of reproduction.

Species with non-pelagic lecithotrophic development also tend to spawn throughout the year in McMurdo Sound, but there are exceptions (Table 2). In particular, different species of peracaridian crustaceans have restricted breeding seasons at different times of the year. The highly motile amphipod *Orchomene plebs* and the tubiculous tanaid *Nototanais dimorphus* both begin brooding embryos in late summer, fall, and winter, and the juveniles are released after 5–6 months, in spring and summer, in phase with benthic diatom production upon which they feed (Pearse, 1963, unpublished observation; Marinovic, 1987). Subantarctic species that brood embryos and

have no larvae also are known to have restricted spawning times, for example, the echinoid *Abatus cordatus* on Kerguelen Island (Magniez, 1983) and the asteroid *Anasterias perrieri* on Marion Island (Blankley and Branch, 1984). These examples of seasonal spawning by species without larvae further reinforce the conclusion that spawning times can be selected by factors other than the seasonal presence of suitable food for planktotrophic larvae.

Animals in physically unstable shallow environments

Dayton *et al.* (1970) provided a clear description of a shallow-water antarctic habitat strongly influenced by seasonal formation of anchor ice. This area, in the southeast corner of McMurdo Sound, is disrupted in the winter as anchor ice forms on surfaces on the bottom, picking up small and loose particles, living and dead, and carrying them to the undersurface of the overlying sea ice, where they are frozen into place. Such disruption apparently prevents the development of a rich community of sponges and other sessile organisms that occur at greater depths (>10–20 m).

Despite the frequent disruption in this shallow-water area, productivity is high as determined by standing stock estimates (Dayton *et al.*, 1986), the diverse and abundant infauna (Oliver, 1979; Marinovic, 1987), and the abundance and size of the generalist omnivorous asteroid *Odontaster validus* (McClintock *et al.*, 1988). Productivity appears to be light limited, and at sites where more light is available because of less cover of sea ice and snow, such as Cape Evans, a rich cover of red algae flourishes (Miller and Pearse, 1990). Prominent mobile macroinvertebrates in these areas include the nemertean *Parborlasia corrugatus* and the echinoid *Sterechinus neumayeri*, as well as *O. validus* (Dayton *et al.*, 1970). These abundant and widespread antarctic animals all produce pelagic, planktotrophic larvae (Table 2). Most of the infauna are very small peracaridean crustaceans and polychetes; at least some of the species of polychetes also produce pelagic larvae (Oliver, 1979).

Animals in deeper, more stable and biotically complex environments

At depths greater than about 20–30 m in the southeast corner of McMurdo Sound, the habitat appears to be much more stable, and a rich and diverse fauna of sponges and other sessile organisms develop into what Dayton *et al.* (1974) term a “biologically accommodated community.” More oligotrophic areas on the western side of McMurdo Sound also appear to be stable and biologically accommodated, but are dominated by predators and scavengers (Dayton and Oliver, 1977). Although we know less about the reproduction of the major macroinvertebrates in these areas, many produce pelagic lecithotrophic larvae. This mode of reproduction would produce relatively large juveniles that may be more capable of resisting predation than the smaller juveniles that develop from planktotrophic larvae.

NEW PERSPECTIVES AND FUTURE RESEARCH

The key environmental characteristics of the antarctic shallow-water marine environment, and their predicted influence on the reproductive biology of benthic marine invertebrates, are summarized in Table 3. It is evident that recent empirical studies do not agree with our previous theoretical predictions. Although seen in many cold water biological systems, temperature compensation may not occur in such characters as gametogenesis, embryonic and larval development, and juvenile and adult growth of antarctic benthic invertebrates. Studies are needed to determine whether this is in fact the case and to evaluate possible causes of such slow rates including nutrient limitation.

The prediction that embryos and larvae of antarctic benthic invertebrates avoid hazardous pelagic conditions does not apply to many groups, as evidenced by the large numbers of species with pelagic development. Although most of these species produce non-feeding larvae, some of the most numerically abundant species produce larvae that must feed in the plankton for long

TABLE 3. Features of the Antarctic shallow-water environment, how they have been predicted to influence the reproductive biology of benthic marine invertebrates, and current status of our knowledge.

| Environmental feature | Predicted influence | Observed characters |
|---|--|---|
| Constant low temperature | Marked temperature compensation | Slow rates of gametogenesis, development and growth |
| Physically "hazardous" near surface | Larvae avoid surface; non-pelagic development | Many species with pelagic larvae |
| Extreme oligotrophy most of year | Select against feeding larvae, favor lecithotrophy | Many species with lecithotrophic larvae, but common species with planktotrophic larvae |
| Extreme seasonality of primary production | Feeding larvae produced in phase with primary production, non-feeding larvae or brooding without synchrony | Feeding larvae do not seem closely linked to primary production, some brooders well phased |
| Shallow benthos (<30 m) very productive but very unstable | Populated with motile colonizing species with dispersive larvae | Major species motile with dispersive larvae or juveniles |
| Deeper benthos (>30 m) very stable | Populated with sessile species, "biologically accommodated," high juvenile mortality | Populated by sessile species when food supplies high. Tendency for lecithotrophic development producing large juveniles |

periods of time. Additional work is needed to further understand how feeding larvae survive in phytoplankton-depauperate antarctic waters, apparently decoupled from primary production. Moreover, the potential advantages and disadvantages of producing a relatively small number of pelagic offspring need to be explored, including possible trade-offs of increased dispersal, decreased length of embryonic development, decoupling from planktonic nutritional resources and production of large-sized juveniles at metamorphosis.

The prediction that shallow, productive, but unstable antarctic benthos are colonized by motile opportunistic species seems to fit quite well. However, there are some interesting exceptions to this rule, such as the common irregular spatangoid sea urchins, all of which brood. It would be of interest to further study such expectations to learn how species with low motility and non-dispersive larvae can survive in shallow-water ephemeral habitats. Finally, the prediction that deeper more stable benthic environments are "biologically accommodated" and colonized by more sessile species which suffer high juvenile mortality is supported in part by empirical work. There is a preponderance of sessile species, many of which produce lecithotrophic larvae that metamorphose into large juve-

niles, as do most of the motile asteroids, presumably attaining some refuge in size in a community where predation is high.

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