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Temperature and pressure tolerances of embryos and larvae of the Antarctic sea urchin *Sterechinus neumayeri* (Echinodermata: Echinoidea): potential for deep-sea invasion from high latitudes

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ABSTRACT: Early embryos, blastulae, prisms and 4-arm plutei of the Antarctic shallow-water echinoid *Sterechinus neumayeri* were subjected to a temperature/pressure regime from −1.2 to +2.5°C and from 1 to 250 atm. Early embryos were able to tolerate pressures up to 150 atm at +2.5 to +0.9°C and 100 atm at −1.2°C. Blastulae and prisms showed an increasing sensitivity to pressure with decreasing temperature. Four-arm plutei were more sensitive than early larval stages to pressure and were also more sensitive to pressure at lower temperatures. These data suggest that the embryonic and larval stages of *S. neumayeri* are capable of surviving low temperatures in surface waters, but only tolerate higher pressures when water column temperatures are >0°C. Such a pattern of temperature increase is seen in the formation of Antarctic Bottom Water in the Weddell Sea and we infer that the larvae of *S. neumayeri* are capable of penetrating the deep sea through the agency of this deep water formation.

KEY WORDS: *Sterechinus* · Antarctica · Deep sea · Larvae · Pressure · Temperature

INTRODUCTION

The origin of the modern deep-sea fauna remains controversial, in part because the various hypotheses advanced over the past century do not lend themselves to rigorous experimental testing. Definitive answers cannot be obtained, as the presumed invasion, extinction and vicariance events that resulted in the modern deep-sea fauna took place in the past and cannot be directly observed. Evidence, mostly correlative in nature, is of necessity based on the biogeographic and bathymetric distributions, and phylogenetic relationships, of extant species. A fundamental premise of virtually every hypothesis is that thermal tolerances of organisms invading the deep sea were, and remain, narrow and conservative. If this assumption is true, then, recent invasions of the deep sea from shallow water should have occurred only through cold, near-isothermal water columns at high latitudes (Kussakin 1973, Menzies et al. 1973). From a physiological standpoint, this explanation is the most parsimonious, since animals in polar seas are preadapted to the thermal conditions of the present deep sea. Alternatively, however, animals could have invaded the deep sea even at low latitudes during the late Mesozoic or early Cenozoic when the ocean was vertically homogenous and warm (Menzies et al. 1973, Hessler & Wilson 1983, Young et al. 1997). The vertical pressure gradient in the sea is the longest continuous environmental gradient on earth. Pressure increases by 10^5 Pa (1 atm or bar) with every 10 m increase in depth. By contrast, vertical thermal gradients are variable, and may be short and abrupt, especially near discontinuity layers. Pressure affects the growth and survival of a number of deep-sea organisms from bacteria to metazoans (see Gage & Tyler 1991) in all life-history stages.

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Early studies of the effect of pressure on embryonic development were driven by an interest in the properties of the mitotic spindle and cell membranes (Marsland 1970). A pressure of 275×10^5 Pa (~275 atm) was found to inhibit division of zygotes of shallow-water sea urchins (Marsland 1938, 1950, 1970, Zimmermann & Marsland 1964, Swezwy et al. 1987). More recently, the physiological effects of pressure have been studied extensively (reviewed by Somero 1992) and pressure has been implicated as an important ecological factor that limits vertical distributions of animals in the sea (Kinne 1972, Carney et al. 1983).

The pressure and temperature tolerances of echinoderm (mainly echinoid) embryos, from both deep- and shallow-water adults, have been determined for species living in Hawaii, the Bahamas, the northern Mediterranean and the deep and shallow North Atlantic (Young & Tyler 1993, Young et al. 1996a,b, 1997, Tyler & Young 1998). The species from the North Atlantic and the northern Mediterranean were chosen because deep-water formation (North Atlantic Deep Water and Western Mediterranean Deep Water, respectively) is known to occur in these areas (Gage & Tyler 1991). The data suggest that the larvae of shallow-water echinoids are sufficiently tolerant of high pressures to follow an isothermal layer into, at least, bathyal depths and could, therefore, send colonists to the deep sea within a single generation. We have also shown (Tyler & Young 1998) that embryonic pressure tolerances of bathyal *Echinus acutus* var *norvegicus* are broader than those of shallow-water conspecifics, suggesting that this species may presently be invading the deep sea by slowly adapting to increased pressure. In the North Atlantic the vertically overlapping species of *Echinus* have retained both planktotrophy and seasonal reproduction at all depths from the intertidal zone to the abyssal plain (Tyler et al. 1996). This evidence supports the hypothesis that at least 1 genus of echinoid radiated into the deep sea from an origin in shallow water.

Although the deepest waters in the world's ocean (Antarctic Bottom Water) originate from shallow water around the Antarctic continent (Mantyla & Reid 1983, Gage & Tyler 1991), no data on embryonic pressure tolerances are available for any shallow-water Antarctic invertebrate. It is known, however, that many species of Antarctic benthos are eurybathic in their vertical distribution (Brey et al. 1996), a feature that may be related to the unusually deep continental shelves around Antarctica and Cenozoic glacial history (Clarke & Crame 1992). The aim of the present study was to determine the effects of temperature and pressure combinations on the early embryogenesis and later larval stages of the common Antarctic echinoid *Sterechinus neumayeri*. Specifically, we wished to determine if pressure would limit the ability of larvae of *Sterechinus* to disperse to bathyal depths through a cold isothermal water column.

The genus *Sterechinus* is comprised of 5 species, all found primarily in Antarctic waters (Hedgepeth 1969). *S. agassizii* is confined to the maritime Antarctic and *S. diadema* exclusively to the Kerguelen Islands. Of the continental Antarctic species, *S. neumayeri* is most common in shallow water down to ~450 m depth, but may be found as deep as 850 m, whereas *S. antarcticus* occurs at all depths from 100 to 1200 m (Brey & Gutt 1991). These are remarkably broad distributions for essentially shallow-water sea urchins and may be permitted by the isothermal water column. *S. dentifer* is known only from 2 deep localities in the Indian Ocean sector of Antarctica (Hedgepeth 1969).

In shallow water, *Sterechinus neumayeri* can be the most abundant macrobenthic organism (Bosch et al. 1987, Brey & Gutt 1991). In this species, the larvae are planktotrophic and the rate of development is very sensitive to temperature (Bosch et al. 1987, Stanwell-Smith & Peck 1998). Moreover, larvae and embryos are extraordinarily stenothermal. Development occurs down to −1.9°C, whilst above +1.7°C the number of non-viable eggs increases dramatically (Stanwell-Smith & Peck 1998). Larvae of *S. neumayeri* are found in the plankton between November and February (Stanwell-Smith et al. 1998) and, although once believed to be demersal (Pearse & Giese 1966), are now known to occur throughout the water column (Bosch et al. 1987). At the British Antarctic Base at Rothera Point, Adelaide Island, *S. neumayeri* is abundant in both the South and North Cove. The South Cove population spawns in November whereas the North Cove population will have spawning individuals to late January (S. Brockington pers. obs.).

Within the deep sea, juvenile echinoids and ophiuroids are often found outside the adult vertical range (Gage & Tyler 1981, Sumida 1998) where they grow, and may even start gametogenesis, but die shortly afterwards (P.A. Tyler pers obs.). The very existence of such pseudopopulations shows that larvae of some echinoderms are capable of dispersing to and settling at depths greater than where the adults can survive. Permanent colonization therefore depends not only on the dispersal phase, but also on the abilities of benthic stages to survive and reproduce under physical and dietary conditions that prevail in the deep sea.

MATERIALS AND METHODS

This study was carried out in the Bonner Laboratory of the British Antarctic Survey Base at Rothera

on Adelaide Island to the west of the Antarctic Peninsula during January 1999. Samples of *Sterechinus neumayeri* were collected by divers in the North Cove of Rothera (67° 34' S, 68° 07' W). Individuals were transported to the Bonner Laboratory in 25 l plastic buckets and were placed in aquaria within 10 min of collection. Urchins were maintained in running seawater at +0.9°C until used; this is the typical summer temperature for shallow-water habitats locally. To obtain gametes, urchins were inverted over finger bowls and injected with 1 ml of 0.55 M KCl. Urchins were left for 30 min, as spawning was slow. Eggs were pipetted into fresh seawater and sperm were diluted with seawater at +0.9°C. Viability of eggs and sperm was checked before use. Eggs were fertilized with dilute sperm, left for 15 min, then checked for fertilization envelopes.

Temperature/pressure effects on fertilized eggs. Fertilized eggs were used in a temperature/pressure matrix. Zygotes were pipetted into 8 ml plastic scintillation vials filled to overflowing with seawater. Three replicate vials were assigned randomly to each pressure/temperature combination. Embryos were incubated at −1.2 (±0.1), +0.9 (±0.1) and +2.5°C (±0.2°C) and, within each temperature, at 1, 50, 100, 150 and 200 atm. The SI unit for pressure is the pascal (1 atm = 10^5 Pa) but we have retained the use of atmospheres for clarity of presentation and recognition of the depths they represent (50 atm ~500 m). Because development rate in *Sterechinus neumayeri* is known to be slow (Bosch et al. 1987) cultures were examined only at 24 and 48 h. At 24 h, each culture was depressurized, examined and repressurized within 20 min. Wherever possible, at least 50 embryos from each replicate were examined. The percentage of embryos at each cleavage stage was determined for each replicate.

Temperature/pressure effects on embryos and larvae. Cultures of embryos were maintained in 1 l beakers partially submerged in flowing seawater at +0.9°C. Mesenchyme, prism and 4-arm plutei (as defined by Young et al. 1997) were incubated at −1.2, +0.9 and +2.5°C and at 1, 50, 100, 150, 200 and 250 atm. Three replicates of each temperature/pressure combination were incubated for 24 h, then examined. The number of dead and swimming larvae was recorded for each replicate.

RESULTS

Temperature/pressure effects on zygotes and early embryos at 24 h

One-atmosphere controls developed normally at all 3 temperatures, attaining the 16- and 32-cell stages at −1.2°C (Fig. 1) and the 32-cell stage at +2.5 and +0.9°C. At 50 atm, embryos at −1.2°C attained no more than the 4-cell stage, while embryos incubated at +2.5 and +0.9°C reached the 32-cell stage. At 100 atm, no cleavage occurred at −1.2°C, but embryos were at the 4-cell stage at +0.9°C and at the 16 and 32-cell stages at +2.5°C. At 150 atm and +2.5°C, embryonic development was slightly slower than at lower pressures, with embryos attaining only the 16-cell stage. This effect was even more dramatic at +0.9 and −1.2°C, where a few zygotes initiated first cleavage, but most remained as uncleaved zygotes. At 200 atm, there was no normal cleavage at any temperature. Uncleaved zygotes at the

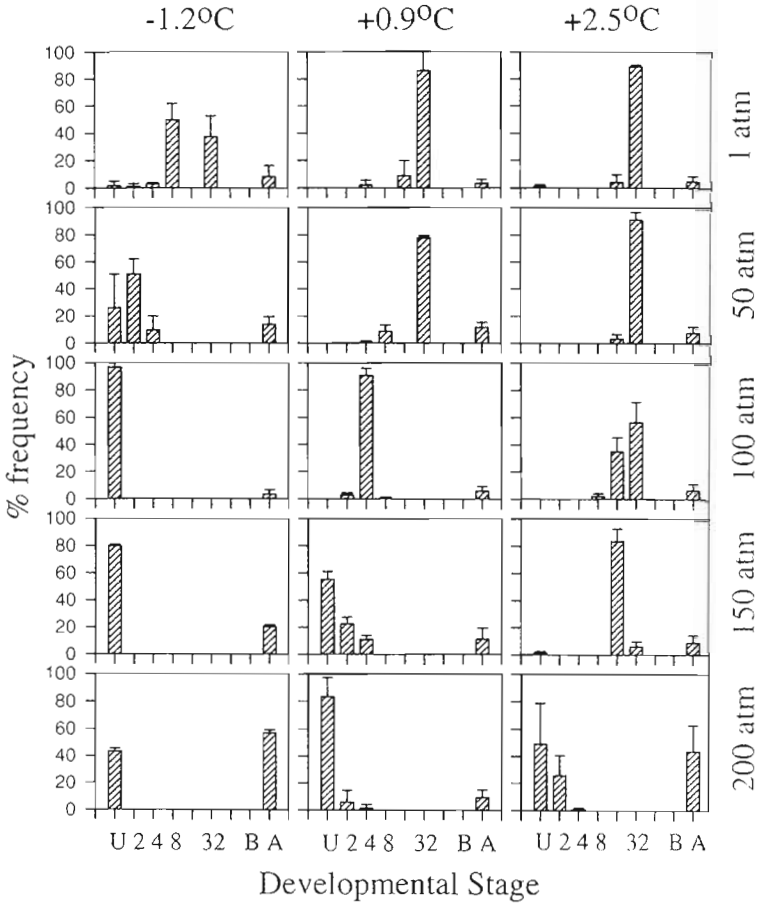

Fig. 1. *Sterechinus neumayeri* embryos incubated at +2.5, +0.9 and −1.2°C at 1 to 200 atm for 24 h. Histograms represent % mean and SD. Development stages are (U) Uncleaved, 2 to 64 cell, (B) Blastula and (A) Abnormal

2 higher temperatures looked normal after 24 h, but at −1.2°C and 200 atm, we observed a number of zygotes with unusually rough surfaces. Abnormal embryos at lower pressures generally cleaved, but the blastomeres were in abnormal spatial configurations.

Temperature/pressure effects on zygotes and early embryos at 48 h

At −1.2°C, the control cultures at 1 atm yielded blastulae, the 50 atm culture had a mixture of 64-cell stages and blastulae, and the 100 atm cultures contained a few 2- and 4-cell embryos. Most zygotes or embryos at 100 atm were uncleaved or abnormally cleaved (partially cleaved, or irregularly cleaved) (Fig 2). At 150 and 200 atm, no zygotes had cleaved, and some had a rough surface. At +0.9°C, embryos had reached the blastula stage from 1 to 100 atm, but had become abnormal at higher pressures. These abnormalities included a mixture of disaggregated blastomeres in embryos that had cleaved abnormally, and uncleaved zygotes with rough surfaces. At +2.5°C, embryos attained the blastula stage at all pressures from 1 to 150 atm. The zygotes incubated at 200 atm remained mostly uncleaved and showed an irregular surface. Those few embryos at 200 atm that had undergone first cleavage after 24 h were showing irregular cleavages after 48 h.

Temperature/pressure effects on blastulae at 24 h

At +2.5°C more than 90% of all embryos were swimming after 24 h incubation at pressures up to and including 250 atm (Fig. 3). Mortality at +0.9°C was only slightly higher (most cultures with more than 70% swimming) except at 200 atm, where an average of 24% of embryos was still swimming after incubation. At −1.2°C the number of swimming embryos remained high from 1 to 150 atm but declined to 46% at 200 atm. Only a single swimming blastula survived at 250 atm.

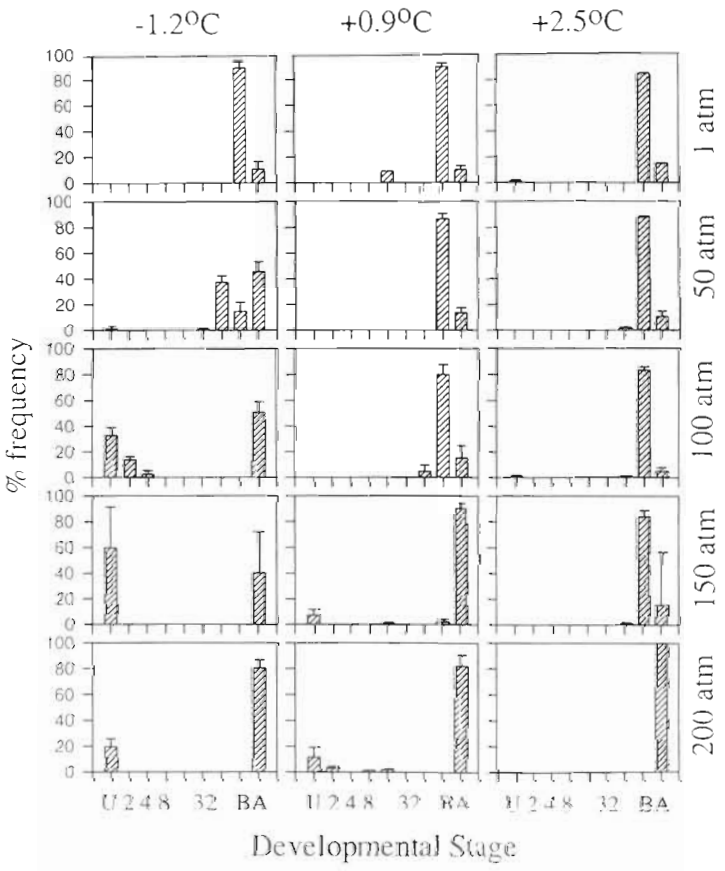

Fig. 2. *Sterechinus neumayeri* embryos incubated at +2.5, +0.9 and −1.2°C at 1 to 200 atm for 48 h. Histograms represent % mean and SD. Development stages are (U) Uncleaved, 2 to 64 cell, (B) Blastula and (A) Abnormal

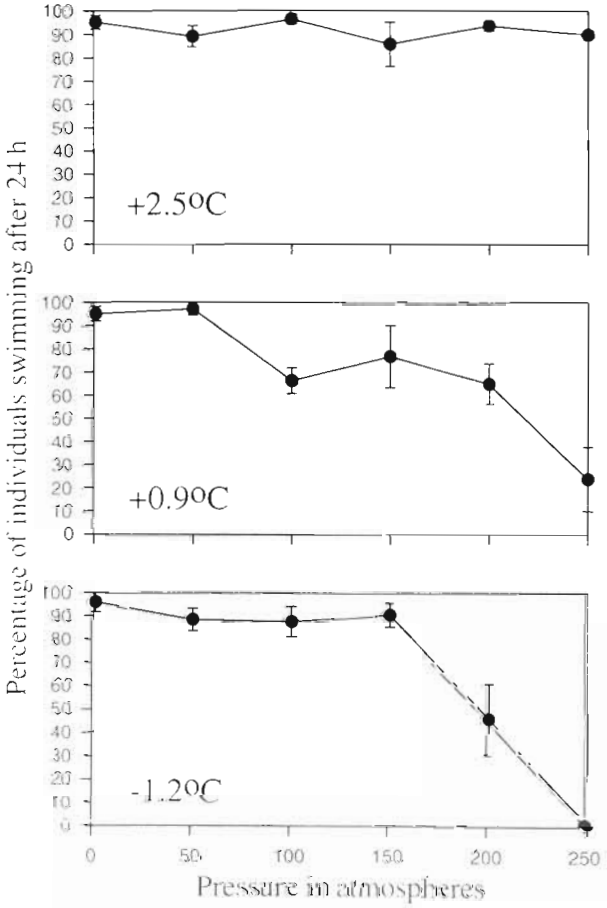

Fig. 3. *Sterechinus neumayeri*. Survival of blastulae (mesenchyme stage) at +2.5, +0.9 and −1.2°C at 1 to 250 atm for 24 h. Data are mean and SD of 3 replicates

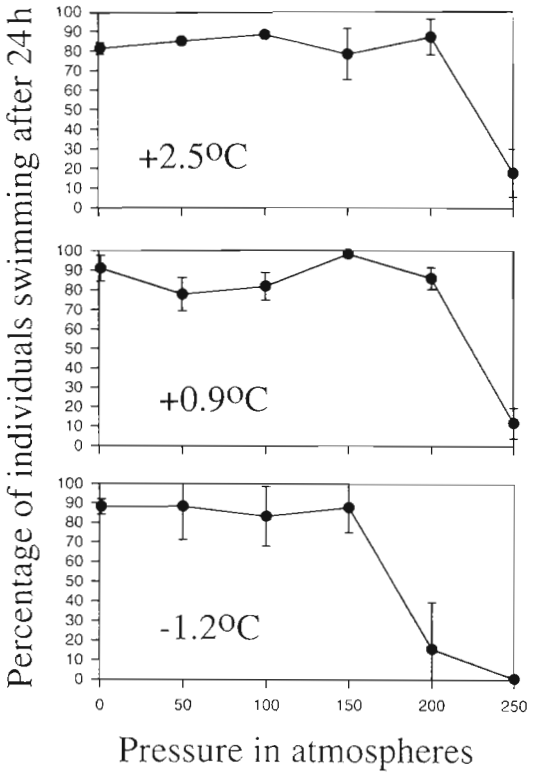

Fig. 4. *Sterechinus neumayeri*. Survival of prisms at +2.5, +0.9 and -1.2°C at 1 to 250 atm for 24 h. Data are mean and SD of 3 replicates

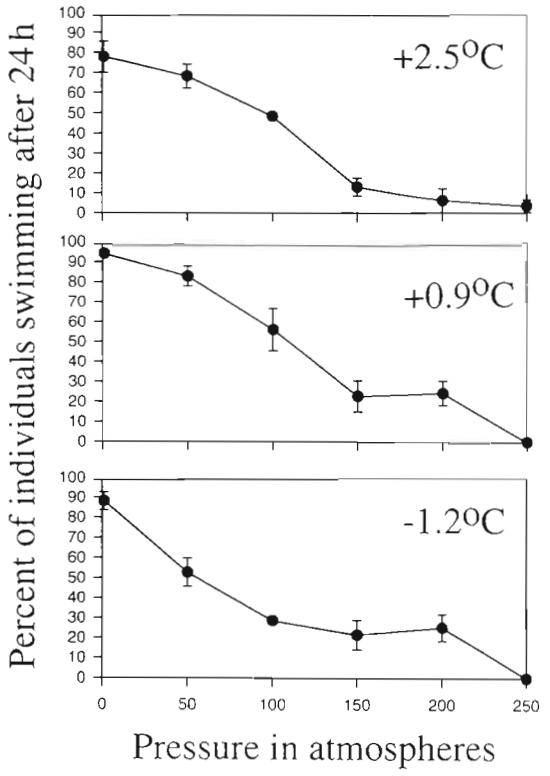

Fig. 5. *Sterechinus neumayeri*. Survival of 4-arm plutei at +2.5, +0.9 and -1.2°C at 1 to 250 atm for 24 h. Data are mean and SD of 3 replicates

Temperature/pressure effects on prisms at 24 h

At +2.5°C and +0.9°C, the number of swimming prisms remained high (>75%) after incubation at 1 to 200 atm, but at 250 atm, the number of surviving prisms was reduced to <20% (Fig. 4). At -1.2°C, the percentage of survivors remained high between 1 and 150 atm but was reduced substantially to <16% at 200 atm and <1% (2 prisms total in all 3 replicates) at 250 atm

Temperature/pressure effects on 4-arm plutei at 24 h

Survivorship of 4-arm plutei was variable among treatments (Fig. 5). At +2.5 and +0.9°C, survival was >70% at 1 and 50 atm but substantially lower at pressures above 100 atm. At -1.2°C, survival had decreased to 58% at 50 atm, remained low between 100 and 200 atm, and declined to zero at 250 atm.

DISCUSSION

The origin of the deep-sea fauna has been a point of discussion for decades. One view maintains that many of the major deep-sea taxa originated within and radiated from the deep sea (Hessler & Thistle 1975). Proponents of the alternative view, that animals invaded the deep sea from shallow water, have suggested that invasions could have occurred either during the Mesozoic or early Cenozoic. During these eras the water column was vertically homogenous and warm (Menzies et al. 1973, Hessler & Wilson 1983). More recently invasion of the deep-sea could have taken place through near-isothermal cold water at high latitudes (Kussakin 1973, Menzies et al. 1973). Both possibilities require adaptation to high pressure, and the former additionally requires that animals slowly adapt to cold temperatures (Clarke 1983).

Experimental work on the pressure and temperature tolerances of embryos and larvae of shallow-water echinoids from the northern Mediterranean (Young et al. 1997) indicates that larvae should be able to enter the deep sea through a warm water column. In this region, Western Mediterranean Deep Water is formed during the winter when mistral winds from the Maritime Alps cool the sea surface and convection overturns the water column to form a nearly homogenous water column to 2500 m depth. Embryos and larvae of the shallow-water echinoids *Paracentrotus lividus*,

Arbacia lixula, and *Sphaerechinus granularis* were able to tolerate pressures as high as 150 atm at 15°C. Lower temperatures (<11°C) exacerbated the effects of pressure. Thus, invasion of the deep sea by these species would require relatively high temperatures initially, followed by slow adaptation to the more normal cold temperatures that prevail there. Although *P. lividus* and *A. lixula* have very shallow distributions, living larvae have been collected from depths as great as 400 m (Pedrotti 1990), indicating that invasion of deep waters could actually occur within a single generation (Young et al. 1997).

In the Norwegian Sea, North Atlantic Deep Water is formed during winter when high salinity surface water from the North Atlantic cools and sinks to form a deep homogenous water column. This water flows south over the Scotland-Faroes-Iceland-Greenland Ridge, sinks and spreads throughout the world's ocean as a deep, cold water mass (Gage & Tyler 1991). Tyler & Young (1998) have examined the temperature/pressure tolerance of embryos and larvae of the shallow-living *Echinus esculentus*, shallow and bathyal (~900 m depth) population of *E. acutus* and lower bathyal (~2000 m) populations of *E. affinis*. Embryos and larvae of both *E. esculentus* and *E. acutus* tolerated pressures up to more than 250 atm, which is far beyond those encountered in the adult range. Unlike the Mediterranean urchins, developmental arrests and abnormalities decreased with lower temperatures, suggesting that single-generation invasion of the deep sea could be difficult for temperate species that normally reproduce between 5 and 15°C. Evidence that slower invasion may take place at these latitudes comes from embryos of the bathyal population of *E. acutus*. These embryos developed more rapidly at cold temperatures and high pressures than did embryos of shallow conspecifics, suggesting an adaptation to depth. Truly barophilic embryos were observed in *E. affinis*, which failed to cleave at low pressure and showed maximal development above 100 atm (Young & Tyler 1993, Tyler & Young 1998).

The deepest (and most dense) water mass in the world's oceans is formed around Antarctica where the very dense, cold, high-saline water is formed by freezing of the surface waters. Antarctic Bottom Water (a generic term for cold water formed in the Weddell Sea, the Ross Sea and off Terre Adelie coast; Gage & Tyler 1991) has a temperature of −0.4°C and a salinity of 34.66. Analysis of the temperature/pressure tolerance of *Sterechinus neumayeri* embryos shows that decreasing temperature and increasing pressure, even over the very stenothermal range of the adult, have variable effects. As previously observed (Bosch et al. 1987, Stanwell-Smith & Peck 1998), 1 atm controls showed a decrease in the rate of development with decreasing temperature. In contrast to Stanwell-Smith & Peck (1998), we observed normal development at +2.5°C, almost 1°C above the temperature at which they obtained normal development. At 50 atm embryonic development was slowed at −1.2°C, and at >100 atm zygotes remained uncleaved. After 24 h at +0.9 and +2.5°C development was normal, although retarded, to 150 atm. At 48 h development was only normal up to pressures of 150 atm at +2.5°C. At 48 h embryos were abnormal from 100 atm at +0.9°C to 200 atm at +2.5°C. Interestingly, the potential effect of this pattern on deep-sea invasion potential varies between north and south polar species because of the thermal structure of the water column. In the North Atlantic, water becomes colder with depth, increasing the pressures that the embryos can tolerate. By contrast, the temperature in Antarctic seas may *increase* with depth (depending on season), the coldest water being near the surface where ice melts, and the water warming at greater depths as various water masses mix.

The response of later stages of embryonic development in *Sterechinus neumayeri* are in contrast to the effects seen in the Mediterranean and North Atlantic. Of the 3 stages tested, the mesenchyme blastulae were the most tolerant of pressure particularly at +2.5°C but were able to tolerate 150 atm at −1.2°C. Prisms were tolerant of pressure to 200 atm at +0.9 and +2.5°C, but only to 100 atm at −1.2°C. The reason for this non-linear response is not known. The 4-arm plutei showed the least tolerance to pressure increase, with a steady decline in survival with increased pressures, resulting in <20% survival at pressures greater than 150 atm. The reduced survival at 1 atm at +2.5°C may be a result of exceeding the upper temperature tolerance levels of larvae of *S. neumayeri*.

These data imply that embryonic stages of *Sterechinus neumayeri* have the ability to invade deep water at temperatures within their normal development range. The extreme cold water of the Antarctic (−1.9°C in Western Shelf Water of the Weddell Sea) may retard the ability of larvae to tolerate pressure, although development will occur at that temperature (Bosch et al. 1987, Stanwell-Smith & Peck 1998). However, in deeper water, typical Antarctic water temperatures are on the order of ~0°C and we believe this temperature would not inhibit larval invasion of deep water. Because of the increase in water temperature with depth, we conclude that echinoid larvae are more likely to invade the deep sea during a single generation in Antarctic waters than in either the Norwegian or Mediterranean Seas.

As observed in the genus *Echinus* in the North Atlantic (Tyler et al. 1996, Tyler & Young 1998) congeneric species with overlapping vertical ranges can

be found for the genus *Sterechinus* in the Antarctic. Two deep water forms are known: *S. antarcticus* overlaps the lower depth distribution of *S. neumayeri* in the Weddell Sea (Brey & Gutt 1991) and *S. dentifer* is found in the, as yet, poorly sampled Indian Ocean sector of Antarctica. The reason an analagous situation is not found in the Mediterranean, the echinoids being confined to shallow water, is perhaps the young age of the Mediterranean Sea (~5 million yr). Most of the deep-water fauna is believed to have invaded from the Atlantic through the Straits of Gibraltar rather than being formed in the Mediterranean and there has been insufficient time for the evolution of an endemic deep-water fauna (Pérès 1985). In contrast, the circum-Antarctic benthic fauna is very old (Lipps & Hickman 1982, Clarke & Crame 1989).

We believe these empirical data suggest that the embryos and larvae from at least 1 taxonomic group are capable of invading deep water along either a warm- or cold-water isotherms. It is significant that the formation of a deep-water mass coincides temporally with spawning and larval development in these Antarctic species.

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