Temperature and pressure tolerance of embryos and larvae of the Atlantic seastars *Asterias rubens* and *Marthasterias glacialis* (Echinodermata: Asteroidea): potential for deep-sea invasion

Francisco Benitez Villalobos[1], Paul A. Tyler[1],*, **Craig M. Young[2]**

[1]School of Ocean and Earth Science, University of Southampton, National Oceanography Centre, Southampton SO14 3ZH, UK
[2]Oregon Institute of Marine Biology, PO Box 5389, Charleston, Oregon 97420, USA

ABSTRACT: Eggs of the shallow-water asteroids *Asterias rubens* and *Marthasterias glacialis* were fertilized *in vitro* and incubated through the early embryonic cleavages until the larval stage. Early embryos, blastulae, gastrulae, and swimming bipinnaria were subjected to a temperature/pressure matrix of 5, 10, 15 and 20°C and 1, 50, 100, 150 and 200 atm. Early embryos of both species were able to tolerate pressures up to 150 atm at 15°C and 100 atm at 10°C. Survivorship of *A. rubens* swimming bipinnaria remained high (>70%) after incubation at all the temperature/pressure combinations. Swimming larvae ranged from 100% survival at 10°C/50 atm to 72% at 15°C/200 atm. For *M. glacialis* the highest survival of swimming larvae was 100% at 5, 15 and 20°C/1 atm and 15 and 20°C/50 atm, but decreased to 56.85% at 5°C/200 atm. In general, survivorship decreased as pressure increased; nevertheless larvae generally tolerated pressures of 200 atm. Data for the temperature and pressure effects on the later stages of development suggest that all the larval stages are more temperature/pressure tolerant than the early embryos and survivorship increases with larval age. All the developmental stages of both species have a potentially wider depth distribution than their respective adults. Therefore, the larvae of shallow-water species *A. rubens* and *M. glacialis* could survive transport to deeper waters and may be capable of acting as colonists in the deep sea.

KEY WORDS: *Asterias rubens* · *Marthasterias glacialis* · Embryos · Larvae · Deep-sea invasion · Temperature · Pressure

INTRODUCTION

Deep-water formation in the ocean occurs at 3 main sites: the great embayments around Antarctica, the Norwegian Sea in the North Atlantic, and the northern Mediterranean (Gage & Tyler 1991). The deepest water in the ocean originates from shallow water around the Antarctic continent where very dense cold, high-saline water (Antarctic Bottom Water: AABW) is formed by intense cooling of surface waters (Mantyla & Reid 1983, Gage & Tyler 1991). In the Norwegian Sea, North Atlantic Deep Water (NADW) is formed during winter when high-salinity surface water from the North Atlantic cools and sinks to form a deep homo-genous water column. This water flows south over the Scotland-Faroes-Iceland-Greenland Ridge and sinks and spreads throughout the ocean as a deep, cold water mass (Gage & Tyler, 1991). In the Mediter-ranean, deep water is formed in winter in the Gulf of Lions by the cooling of surface water by the Mistral (Tyler 2003). The sill of Gibraltar prevents the incur-sion of the dense, cold water from the North Atlantic; this results in the bottom water temperature in the Mediterranean being ca. 13°C whilst elsewhere in most of the ocean, the abyssal temperature is below 4°C. (Sverdrup et al. 1942, Tyler 1995, 2003). In addi-tion to these sites of deep-water formation, there are a number of sites where water cascades down the conti-nental slope to depths in excess of 500 m (Ivanov et al. 2004).

The sites of deep- and bottom-water formation have been invoked as potential sites of invasion of the deep sea by larvae of shallow-water invertebrates. To test this hypothesis, the pressure and temperature tolerances of echinoid embryos from the shallow waters of the North Atlantic, the Antarctic Peninsula and the northern Mediterranean have been determined *in vitro* (Young et al. 1996a,b, 1997, Tyler & Young, 1998, Tyler et al. 2000). The data from these experiments suggest that larvae of shallow-water echinoids are sufficiently tolerant of high pressures to follow an isothermal layer into, at least, bathyal depths and could, subsequently, colonise the deep sea within a single generation (Tyler et al. 2000). Concomitant experiments on bathyal and upper abyssal echinoids suggest that the embryos of bathyal species have the widest tolerance (Tyler & Young 1998), whilst those of the upper abyssal *Echinus affinis* are truly barophilic (Young & Tyler, 1993, Tyler & Young 1998)

Young et al. (1996a) provide data on the temperature/pressure tolerance of developing embryos of the lower bathyal seastar *Plutonaster bifrons*. They found that the highest percentage of normal development occurred at 200 atm ($\equiv$2000 m depth), which is the peak of the species' distribution (Howell et al. 2002). Virtually no normal development occurred at a pressure corresponding to 3000m depth. These results indicate that embryonic tolerances could determine the bathymetric limits of distribution for this species.

In this paper we present temperature/pressure tolerance data for the embryos and larvae of the shallow-water Atlantic seastars *Asterias rubens* and *Martasterias glacilais*. We test the hypothesis that the early embryos and bipinnaria of both species have a similar temperature/pressure tolerance to those of shallow-water echinoids and could use the same pathway for invasion of the deep sea.

The seastar *Asterias rubens* L. is one of the most abundant and widespread echinoderms of the Northern Hemisphere. It is distributed from Labrador southwards to the Carolinas (infrequently to Florida) in the western North Atlantic and from the Arctic to southern Portugal in the east. It is found from the intertidal to depths of 900 m (Vevers 1949, Clark & Downey 1992), and though normally completely marine, may be found in waters with a salinity close to 10. This species is synonymous with *Asterias vulgaris* (Clark & Downey 1992), which is widely distributed on the eastern coast of the USA (Franz et al. 1981). The reproductive periodicity and larva of *A. rubens* are well known (Gemmill 1914, Jangoux & Vloeberg 1973, Barker & Nichols 1983). Nichols & Barker (1984) suggested a planktotrophic pelagic life of ca. 90 d, and settlement of larvae on a wide range of substrata. Bipinnaria of *A. rubens* are present in the plankton mainly between

March and April. Late bipinnaria and brachiolaria appear from the end of April until early July, and late brachiolaria reach a peak in mid-late June, being found occasionally in plankton samples until mid- to late July. Delage (1904) and Barker & Nichols (1983) suggested that larvae of *A. rubens* undergo very prolonged development to allow for wide dispersal under appropriate hydrological conditions.

Marthasterias glacialis is distributed from Finmark, south to the west coast of the UK, the North Sea and as far south on the east side of the Atlantic as the Cape Verde Islands (Penney & Griffiths 1984). It is also found in the Mediterranean, the Canaries and the Azores (Mortensen 1927). It is not commonly found intertidally, but it has a depth distribution from sub-littoral down to ca. 180 m (Mortensen 1927, Madsen 1950). Little is known of the reproduction of *M. glacialis*. Delage (1904) reared the larvae to brachiolaria stage and described 'parthenogenetic' development. Subsequently, Mortensen (1913) reared larvae to the brachiolaria stage. Mortensen noted that spawning takes place in summer and this was refined to June to late September (Boolootian 1966) and May to June in UK waters (Barker & Nichols 1983). Barker (1977) determined the length of larval life to be ca. 127 d. Thus both species fall into the category of marine invertebrates with teleplanic larvae (Scheltema 1971, 1989) with a long larval life and potentially wide dispersal.

MATERIALS AND METHODS

Field sampling and spawning. The experimental work was carried out in the aquarium of the National Oceanography Centre, Southampton (NOC), during April and May 2002 and 2003. Individuals of *Asterias rubens* were collected from Southampton Water by divers. Individuals *of Marthasterias glacialis* were collected from Plymouth Sound by divers of the Plymouth Diving Centre. All individuals were maintained in running seawater at 15ºC until used. To obtain gametes the individuals were placed in separate, small plastic aquaria with seawater. In order to induce spawning, each animal was injected with 5 ml of a solution of 1×10^{-4} M 1-methyladenine into the coelomic cavity. The males started to spawn 15 to 20 min after injection. The females started to spawn 15 to 20 min after the males. Eggs were pipetted into a shallow crystallizing dish with seawater and examined under a compound microscope to determine if they had undergone germinal vesicle breakdown.

Temperature/pressure effects on fertilized eggs. 1 ml of concentrated sperm was added to a 2 l beaker containing a suspension of eggs in seawater. Successful fertilization was recognized by the appearance of a

fertilization membrane. Excess sperm was removed by allowing the fertilized eggs to settle, decanting off the excess sperm in seawater and replacing it with fresh seawater. Zygotes in suspension were placed into 8 ml plastic vials that were filled to overflowing with seawater at 15°C and carefully capped to avoid trapping any air. Three replicate vials were assigned to each temperature/pressure combination in a modified pressure chamber (see Young et al. 1996b). Pressure was applied using an Enerpac Model 11100 hand pump with the pressure vessel under water at 15°C. The cultures were incubated at 5, 10, 15 and 20°C and at 1, 50, 100, 150 and 200 atm. Individual treatments were maintained at temperature, either in a constant temperature room or in a temperature-controlled water bath. Cultures were examined at 6, 12, 24 and 48 h. Pressure vessels were depressurised, and the contents of incubations vials were emptied into a counting chamber. Full-sized eggs in each culture were examined under a compound microscope at 10× magnification. The cleavage stage of each normal embryo was noted, and all embryos that had undergone irregular cleavage were counted. Cultures were depressurised, examined and repressurised within 15 min. At least 50 embryos from each replicate were staged according to

Fig. 1. *Asterias rubens*. Embryonic development (mean ± 1 SD) after 6 h under different temperature/pressure regimes, U: uncleaved; 2: 2 cell stage; 4: 4 cell stage; 8: 8 cell stage; 32: 32 cell stage; B: blastula; A: abnormal

embryonic development, and the data for each stage were presented as histograms with mean and SD. Zygotes that appeared normal with fertilization membranes but no cleavage were classified as uncleaved. Embryos with irregular cleavage or with distortion of the cytoplasm were classified as abnormal.

Temperature/pressure effects on larvae. Embryos were cultured to swimming bipinnaria at 15°C and 1 atm. The cultures did not develop to the brachiolaria stage. Three replicate cultures of larvae were then subjected to each of 16 temperature/pressure combinations, which included temperatures of 5, 10, 15 and 20°C and 1, 50, 100, 150 and 200 atm. At least 50 developing larvae from each culture were examined by dissecting microscope after 24 h and the stage attained noted.

RESULTS

Temperature/pressure effects on fertilized eggs

Asterias rubens

At 6 h. At 5°C there was almost no evidence of cleavage at any pressure (Fig. 1). At 10°C/1 atm, a high percentage of embryos reached the 8 and 16 cell stage, at 50 and 100 atm there were a few at 4, 8, and 16 cell, but most remained uncleaved. At 150 and 200 atm most zygotes were uncleaved. At 15°C/1 atm, a high percentage of embryos reached the 32 cell stage; at 50 atm most of them were at the 16 cell stage, whilst at 100 and 150 atm there were many zygotes uncleaved and the number of abnormal embryos started to increase. At 200 atm most of the embryos were abnormal. At 20°C/1 and 50 atm, a number of embryos reached the 32 cell stage but between 100 and 200 atm almost all embryos were abnormal (Fig. 1).

At 12 h. At 5°C/1 atm most embryos reached the 32 cell stage (Fig. 2). At 50 atm, the number of abnormal embryos increased, whilst at 100 atm almost 50% were uncleaved with the remainder abnormal. At 150 and 200 atm, the majority of embryos were uncleaved. At 10°C/1 and 50 atm, most of the embryos reached the 32 cell, 64 cell or blastula stage. At 100 atm, some embryos reached the 32 cell stage. At 150 and 200 atm, all embryos were abnormal. At 15°C/1 to 150 atm, most of the embryos were blastulae, although the number of abnormal embryos increased with pressure. At 200 atm, all embryos, with very few exceptions, were abnormal (Fig. 2).

At 24 h. At 5°C/1 atm most of the embryos were at the 64 cell stage whilst at 50 and 100 atm most were abnormal (Fig. 3) At 150 atm, most of the zygotes remained uncleaved, and at 200 atm all embryos were abnormal. At 10°C/1 and 50 atm, most of the embryos were blastu-
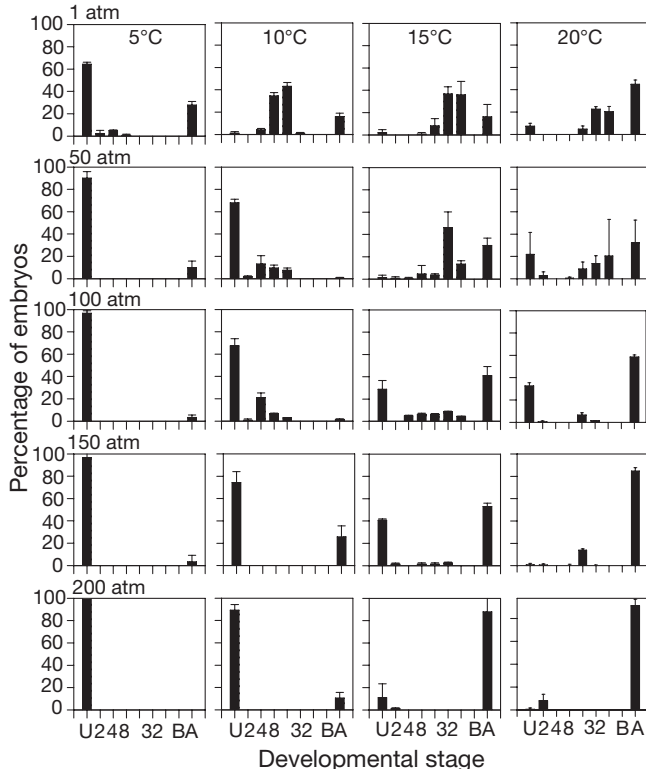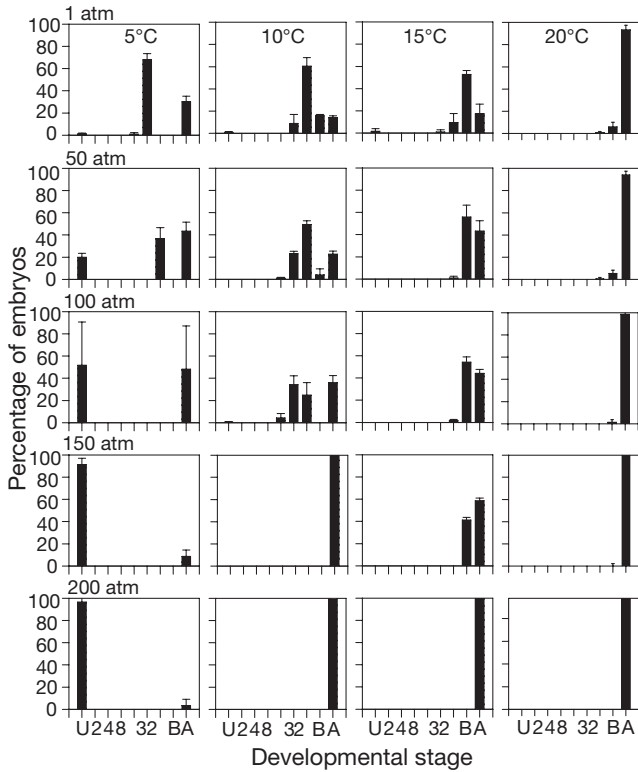
Fig. 2. *Asterias rubens*. Embryonic development (mean ± 1 SD) after 12 h under different temperature/pressure regimes. For abbreviations see Fig. 1
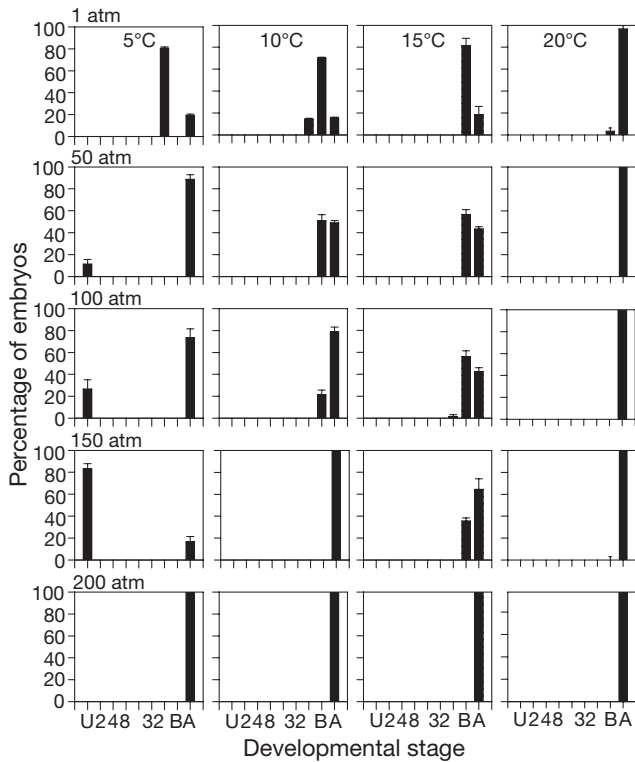
lae; at 100 atm, most were abnormal, and at 150 and 200 atm all the embryos were abnormal. At 15°C/1 to 100 atm, most of the embryos had reached the blastula stage; at 150 atm most were abnormal, and at 200 atm all the embryos were abnormal. At 20°C/1 atm, >95% of embryos were abnormal with the occasional blastula. From 50 to 200 atm, all embryos were abnormal (Fig. 3).

At 48 h. At 5°C/1 atm, most of the embryos were blastulae. From 50 to 150 atm, most embryos underwent abnormal cleavage, and at 200 atm all embryos were abnormal (Fig. 4). At 10°C/1 atm most embryos reached the late gastrula stage, whereas at 50 and 100 atm only a few were gastrulae. At 150 and 200 atm, all embryos were abnormal. At 15°C/1 atm, most of the embryos were late gastrulae, whilst from 50 to 150 atm the number of abnormal embryos increased. At 200 atm, all the zygotes underwent abnormal cleavage. At 20°C, all embryos were abnormal although a few had reached the early gastrula stage at 1 atm (Fig. 4).

Marthasterias glacialis

At 6 h. At 5°C there was no evidence of cleavage at any pressure (Fig. 5). At 10°C/1 atm, the majority of embryos remained uncleaved. At 50 atm, a high percentage of embryos were at the 4 cell stage, and
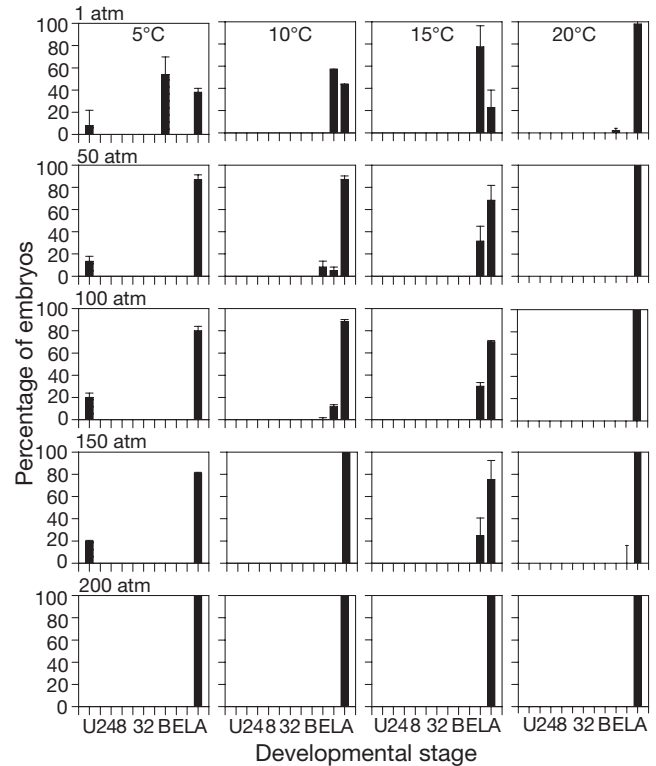

Fig. 3. *Asterias rubens*. Embryonic development (mean ± 1 SD) after 24 h under different temperature/pressure regimes. For abbreviations see Fig. 1

Fig. 4. *Asterias rubens*. Embryonic development (mean ± 1 SD) after 48 h under different temperature/pressure regimes, E: early gastrula; L: late gastrula. For other abbreviations see Fig. 1

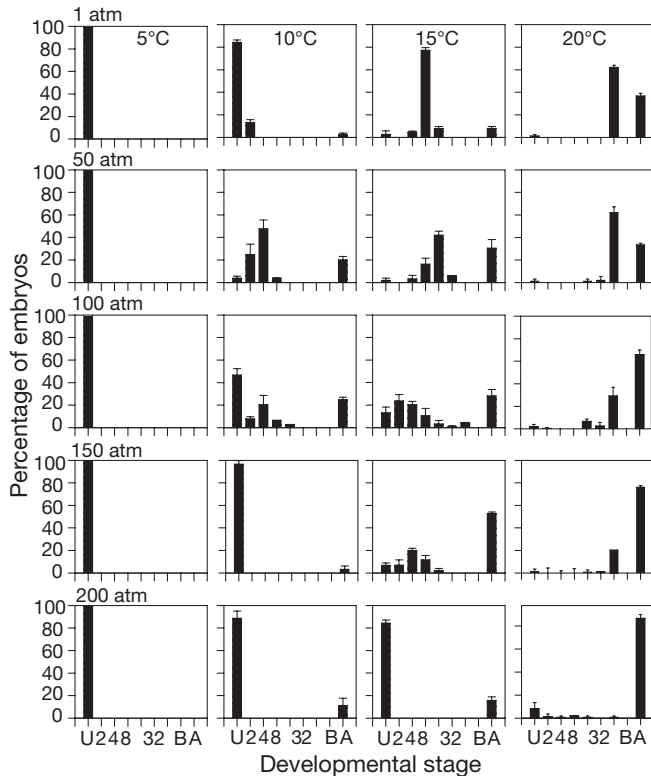Fig. 5. *Marthasterias glacialis*. Embryonic development (mean ± 1 SD) after 6 h under different temperature/pressure regimes. For abbreviations see Fig. 1

were some at the 2 cell stage, and the number of abnormal ones increased. At 150 and 200 atm, all the zygotes were uncleaved. At 15°C/1 atm, most embryos were at the 32 cell stage; at 50 atm, 53.8% were 32 cell embryos, whilst the rest were 16 cell stage or abnormal. At 100 and 150 atm, almost 60% of embryos were abnormal, the remainder being uncleaved or 8 and 16 cell entities. At 200 atm, almost all embryos remained uncleaved. At 20°C/1 to 100 atm, a high percentage of embryos reached the blastula stage, but the number of abnormalities was high also. At 50 atm, virtually all embryos underwent an abnormal cleavage with just a few developing to 64 cell stage and blastulae. At 200 atm, 90% of embryos were abnormal, the remainder remaining uncleaved (Fig. 6).

At 24 h. At 5°C/1 atm, most embryos were abnormal with just a few remaining uncleaved (Fig. 7). At 50 and 100 atm, most embryos were uncleaved, but the number of abnormal ones increased with pressure. At 150 atm, 93% of the embryos underwent abnormal cleavage, whilst at 200 atm all of the them were abnormal. At 10°C/1 atm, 37% of the embryos became blastulae, the remainder reaching the 16, 32 cell stage with

the remainder were 2 cell embryos or abnormal; at 100 atm there were a few at 2, 4, 8, and 16 cell stages, but most remained uncleaved and a small number were abnormal. At 150 and 200 atm, most embryos were uncleaved. At 15°C/1 atm, there was a high percentage of embryos at the 8 cell stage: However, at 50 atm most of them were 16 cell embryos and the number of abnormal ones increased. At 100 and 150 atm, zygotes were distributed among 2, 4, 8, and 16 cell stages, whilst the number of abnormal embryos increased with the pressure. At 200 atm, most zygotes remained uncleaved. At 20°C/1 to 150 atm, a number of embryos reached the 32 cell stage, although there were many abnormal ones. At 200 atm, all embryos were abnormal except for a small number of apparently normal uncleaved zygotes (Fig. 5).

At 12 h. At 5°C almost all zygotes remained uncleaved and showed no irregularities, with just a few abnormalities appearing at 1 and 50 atm (Fig. 6). At 10°C/1 atm the majority of embryos remained uncleaved; at 50 atm, the embryos started to cleave and were at early 2 cell stage, but almost 50% remained uncleaved and some were abnormal. At 100 atm, most of the embryos were uncleaved; there

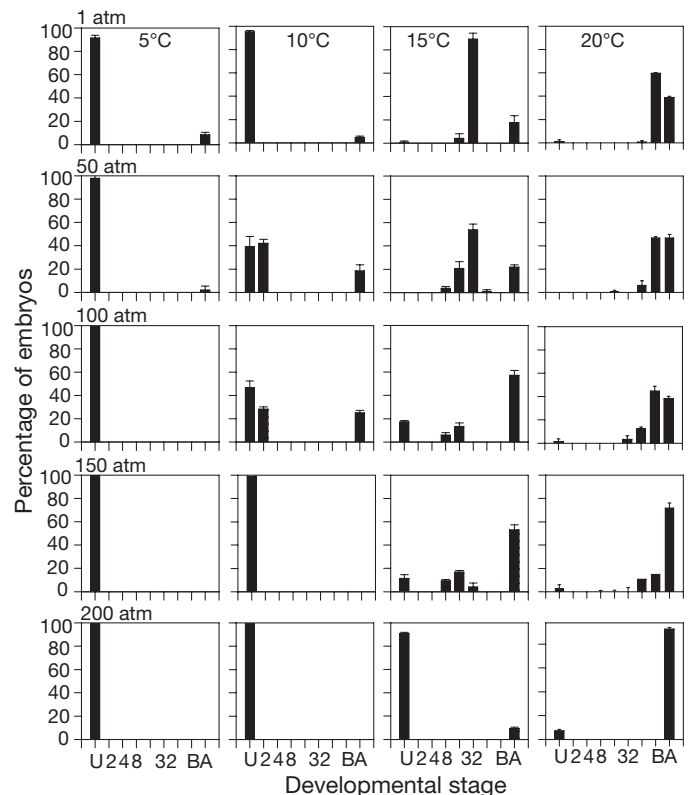

Fig. 6. *Marthasterias glacialis*. Embryonic development (mean ± 1 SD) after 12 h under different temperature/pressure regimes. For abbreviations see Fig. 1
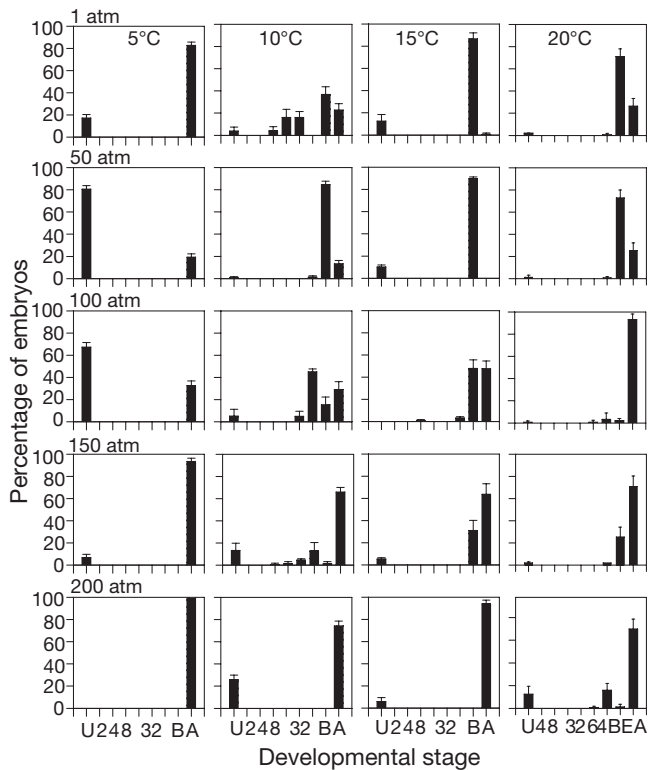
Fig. 7. *Marthasterias glacialis*. Embryonic development (mean ± 1 SD) after 24 h under different temperature/pressure regimes, 64: 64 cell stage. For abbreviations see Figs. 1 & 4

150 atm, almost all embryos remained uncleaved, whilst at 200 atm most embryos underwent abnormal cleavage and the rest remained uncleaved. At 10°C/1 atm, 87% of embryos reached the blastula stage, whilst at 50 atm 92% of embryos reached the same stage. At 100 atm, more than a half of the embryos were abnormal, the rest being blastulae and uncleaved. At 150 atm, all embryos underwent an abnormal cleavage, whilst at 200 atm 60% showed abnormal cleavage and 40% were uncleaved. At 15°C/1 and 50 atm, almost all embryos were late gastrulae; at 100 atm, half of the embryos were abnormal and the remainder were blastulae or gastrulae. At 150 atm, 68% of the embryos were abnormal and the rest were gastrula. At 200 atm, almost all zygotes underwent abnormal cleavage, with a very small proportion developing to early gastrulae. At 20°C/1 atm, most of the embryos were abnormal and 8% were early gastrulae. At 50 and 100 atm, the number of gastrulae decreased, and the number of abnormalities increased with increasing pressure. At 200 atm, all embryos underwent abnormal cleavage (Fig. 8).
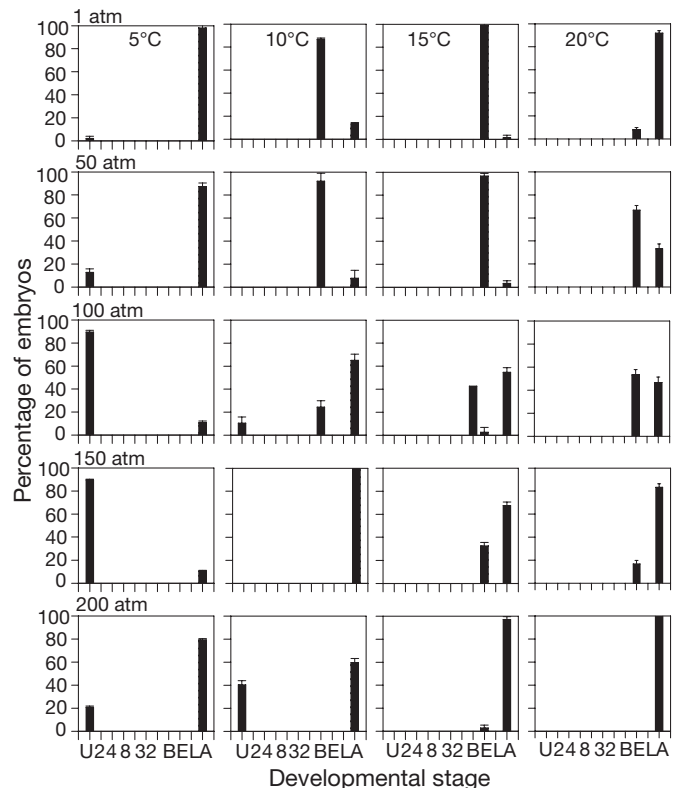
ca. 20% abnormal. At 50 atm, almost all the embryos were blastulae, with the occasional abnormal cleavage. At 100 atm, development had reached the 32, 64 cell stage or blastulae with about 25% abnormalities. At 150 atm, 66% of the embryos were abnormal; the remainder were a mixture of 8, 16, 32 and 64 cell stages, with the percentage of uncleaved embryos being higher than at 100 atm. At 200 atm, 74% of the embryos were abnormal, the remainder being uncleaved. At 15°C/1 and 50 atm, most of the embryos were blastulae. At 100 atm, the proportion of blastulae and abnormal embryos was equal, whilst at 150 atm 63% were abnormal, 31% were blastulae and just very few were uncleaved. At 200 atm, 94% of the embryos were abnormal, the remainder were uncleaved. At 20°C/1 atm, 71% of the embryos were at the early gastrula stage and the rest were abnormal. At 50 atm, 73% of embryos were early gastrulae and the rest were abnormal. At 100 atm, almost all embryos were abnormal and there were very few blastulae. At 150 atm, 71% of the embryos were abnormal, whilst 25% were early gastrulae. At 200 atm, 70% of the embryos were abnormal, 16% were blastula and 13.5% remained uncleaved (Fig. 7).

At 48 h. At 5°C/1 and 50 atm, most of the embryos underwent abnormal cleavage (Fig. 8). At 100 and

Fig. 8. *Marthasterias glacialis*. Embryonic development (mean ± 1 SD) after 48 h under different temperature/pressure regimes. For abbreviations see Figs. 1 & 4
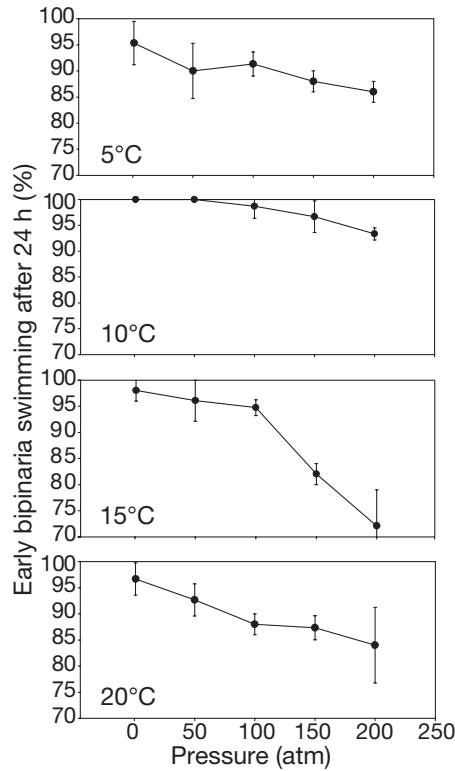
Fig. 9. *Asterias rubens.* Survival of early bipinnaria (mean ± 1 SD) after 24 h at different temperatures and pressures
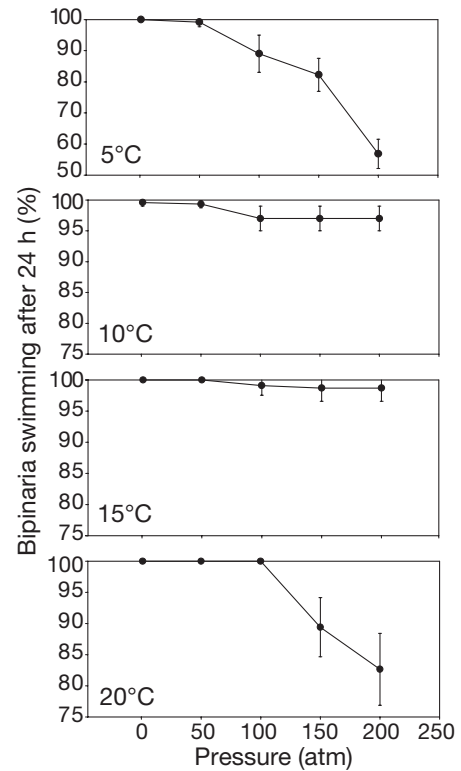

Fig. 11. *Marthasterias glacialis.* Survival of bipinnaria (mean ± 1 SD) after 24 h at different temperatures and pressures. Note scale change at 5°C
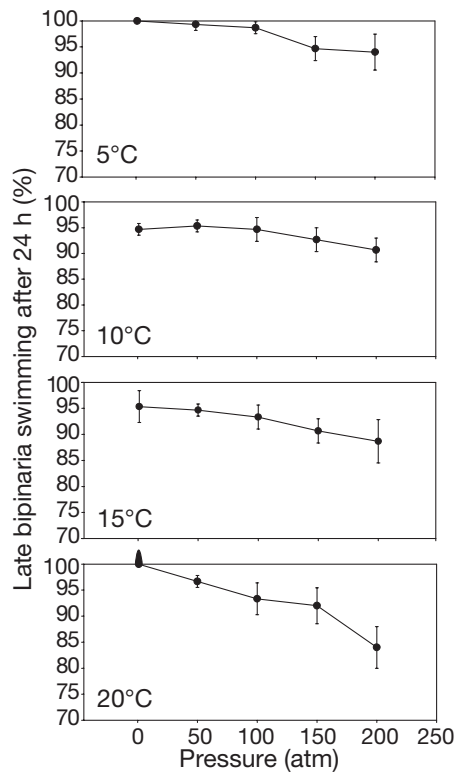
Temperature/pressure effects on swimming bipinnaria at 24 h

Asterias rubens

Survivorship of swimming (15 to 20 d) early and late bipinnaria remained high (>70%) after incubation at all the temperature/pressure combinations (Figs. 9 & 10). Surviving swimming bipinnaria ranged from 100% at 10°C/50 atm to 72% at 15°C/200 atm (Fig. 9). Survivorship decreased as pressure increased; nevertheless, most early bipinnaria tolerated a pressure of 200 atm for 24h. Survivorship remained high for late bipinnaria (Fig. 10).

Marthasterias glacialis

Survivorship of swimming bipinnaria (30 d) of *Marthasterias glacialis* also remained high after incubation at 1 atm at all temperatures (Fig. 11). At 5°C and 20°C survivorship decreased with pressure increase but remained above 50% and 80% survival respectively. Survival remained high at all pressures at 10 and 15°C (Fig. 11).

Fig. 10. *Asterias rubens.* Survival of late bipinnaria (mean ± 1 SD) after 24 h at different temperatures and pressures

DISCUSSION

Experimental work on the temperature and pressure tolerances of embryos and larvae of shallow water echinoids suggests that they are capable of entering the deep sea along isotherms, but across isobars. In the northern Mediterranean embryos and larvae of the shallow-water echinoids *Paracentrotus lividus*, *Arbacia lixula*, and *Sphaerechinus granularis* tolerated pressures as high as 150 atm at 15°C (Young et al. 1997). Lower temperatures (<11°C) exacerbated the effects of pressure. Living larvae of shallow-water Mediterranean echinoids have been collected from depths as great as 400 m (Pedrotti 1990), indicating that invasion of deeper waters could take place in a single generation. These data suggest that such embryos and larvae could have colonised the deep-sea under the warm deep-sea conditions that prevailed in the late Mesozoic or early Cenozoic (Menzies et al. 1973).

In the North Atlantic, Tyler & Young (1998) examined the temperature and pressure tolerances of embryos and larvae of the shallow-water species *Echinus esculentus*, shallow (10 m) and bathyal (ca. 900 m) populations of *E. acutus* and lower bathyal populations of *E. affinis*. Embryos and larvae of both *E. esculentus* and *E. acutus* were able to tolerate pressures of more than 250 atm, far greater than the adult range, although unlike the Mediterranean species developmental arrests and abnormalities did not increase with lower temperatures. Embryos of *E. acutus* var. *norvegicus* from the bathyal zone tolerated a significantly broader range of temperature and pressure than did embryos of *E. acutus* from shallow subtidal habitats and also developed more rapidly at lower temperatures. These observations suggested that *E. acutus* is a very plastic species and may be currently in the process of invading the deep sea by slowly adapting to increased pressure. Embryos of the lower bathyal species *E. affinis* were truly barophilic (Young et al. 1993). These data support the hypothesis that the deep sea could have been invaded during or since the last ice age by larvae capable of tolerating lower temperatures and greater pressures (Kussakin 1973, Menzies et al. 1973).

In the present study, early embryos of *Asterias rubens* were able to tolerate pressures up to 150 atm at 15°C and 100 atm at 10°C, whilst embryos of *Marthasterias glacialis* were able to tolerate pressures up to 150 atm at 15 and 20°C and up to 100 atm at 10°C. At the lowest temperatures (5°C), there was abnormal embryonic development at 1 and 50 atm, whilst at 100 and 150 atm the zygotes remained uncleaved. Although survivorship of early embryos was variable with temperature and pressure, the survivorship of swimming bipinnaria at all temperature and pressures remained effectively high (>70%). Comparison of these data with those of shallow-water and deep-sea Atlantic echinoids suggests that the early embryos of echinoids are more tolerant of temperature/pressure changes but that the later larval stages of asteroids tolerate change more readily than the larval stages of echinoids.

There is increasing evidence for accelerated deep-water formation at the end of glacial periods (Knorr & Lohmann 2003). During deglaciation, the Atlantic thermohaline circulation became more vigorous changing from a weak glacial mode into a strong interglacial mode. There is also recent evidence that there may be a variety of sites of deep-water formation in the North Atlantic (Pickart et al. 2003). Cascading may also be an important mechanism by which cold surface water enters the deep sea (Ivanov et al. 2004). If more vigorous formation of deep water occurs at the end of a glacial period, it may be that the warming of surface waters stimulates (1) accelerated reproduction, both through temperature and primary production, and (2) that the resultant larvae using the thermohaline 'conveyer belt' to penetrate the deep sea.

If larvae can tolerate pressures significantly higher than those where adults normally live, then why are the adults of these species not found in deeper waters? It is possible that the temperature/pressure tolerance of different shallow, bathyal and abyssal species may determine their zonation. Howell et al. (2002) have shown that the zonation of asteroids varies with depth, with individual species having relatively narrow bands where they are common, but a few individuals within a species having a wide zonation. In a number of species, the apparent zonation is wide because juveniles especially are found outside the adult zone (Howell et al. 2002). This pattern has been observed in the bathyal ophiuroid *Ophiocten gracilis* and the upper abyssal ophiuroid *Ophiura ljungmani* (Gage & Tyler 1981a,b). Juveniles of both species settle well outside the adult zone. The juveniles grow and initiate gametogenesis, but only those individuals settling in the normal adult depth region survive to complete reproduction. These data suggest that in some deep-sea species, the post-larvae and juveniles have a wider pressure tolerance than the adults, although survival of juveniles outside the adult zonation is very poor. It is probable that post-selective forces other than pressure tolerance may exist, such as suitability of habitat or food availability, which eliminates juveniles outside the adult range.

We propose that the ability to tolerate increasing pressure may be cumulative over many generations until an individual species has adapted to the deep-sea environment. It is possible that this adaptation may have been rapid as a number of deep-sea invertebrate species retain the seasonal growth and reproductive patterns seen in shallow water congeners (Young 2003).

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