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Metabolism and development of pelagic larvae of Antarctic gastropods with mixed reproductive strategies

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ABSTRACT: The Antarctic gastropods *Marseniopsis mollis* (Smith, 1902) and *Torellia mirabilis* (Smith, 1907) lay eggs in the late austral summer and autumn; these hatch the following late winter and early summer. Field observations indicate that *M. mollis* lays eggs in the tests of ascidians in January to March. Ascidians with *M. mollis* broods were collected in April and held in culture. Larvae hatched between mid-October and mid-December, a brooding period of 8 to 11 mo. *T. mirabilis* egg masses laid in aquaria in April took 6 to 7 mo to hatch. Both species released large veliger larvae (presumably planktotrophic). Natural phytoplankton were provided, but feeding was not confirmed. These larvae were maintained in culture for 25 to 50 d, during which period they were regularly offered a range of substrata, but no settlement behaviour was observed. Metabolism was estimated in individual larvae using microrespirometers of 30 to 45 µl volume, and a couloximeter system to measure water oxygen-content. Average *M. mollis* veligers contained 14.1 µg ash-free dry mass (AFDM) and consumed 310 pmol O_2 h^{-1}. Corresponding values for *T. mirabilis* veligers were 17.6 µg AFDM and 221 pmol O_2 h^{-1}. The periods of protected development here were shorter than those previously reported for Antarctic gastropods, including *T. mirabilis*, by a factor of ×4, although previous reports were for species hatching as juveniles. The protected periods here were, however, around 5 time longer than for temperate gastropods. The oxygen-consumption rates for *M. mollis* and *T. mirabilis* veligers were around ×10 less than those for comparable temperate gastropod and bivalve veligers.

KEY WORDS: Gastropod · Larva · Veliger · Brooding · Oxygen consumption · Antarctic

INTRODUCTION

The larval phase is the critical life-history stage for many marine invertebrate species. Mortality is often orders of magnitude higher for larvae than for any other stage (Pechenik 1999). For species with adults of low mobility the larva represents the predominant dispersal mechanism, and the only such mechanism for sessile species. Many species, however, exhibit protected development, whereby embryonic development takes place in well-protected egg masses. There are both advantages and disadvantages to protected compared with pelagic development (Pechenik 1979, 1986, 1999). Mortality is reduced in protected strategies, and the likelihood of any individual embryo reaching juvenile stages is thereby enhanced. However, protected development generally involves the production of larger, but fewer embryos, and requires more investment per embryo from the parents (Strathmann 1985). Some species exhibit a mixed reproductive strategy in which a long period of protected development is followed by an extended pelagic larval phase, but few of these have been studied to date (Peck & Robinson 1994, Meidlinger et al. 1998).

In the middle of the last century, work carried out in Europe and the Arctic, mainly by Thorson (1936, 1946,

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1950), and based predominantly on molluscs, suggested a decline in the incidence of pelagic development with a concomitant increase in protected development towards the poles. This trend was named 'Thorson's rule' by Mileikovsky (1971). A decrease in the proportion of taxa reproducing via pelagic larva with latitude has been confirmed in the southern hemisphere for gastropod molluscs (Clarke 1992), but patterns are very different for other taxa. Thus, the proportion of echinoderm taxa with protected development is similar in California and Antarctica (Bosch & Pearse 1990, Pearse 1994). Furthermore, a detailed year-round survey of pelagic, marine-invertebrate larvae in waters around Signy Island, South Orkney Islands, found numbers of larval taxa similar to those in Denmark in Thorson's (1936, 1946, 1950) studies, and over 10 times as many as found in the Arctic (Stanwell-Smith et al. 1999). This suggests that, although there is a strong latitudinal cline in the proportion of taxa with pelagic planktotrophic larvae in gastropods, Thorson's rule is not a general ecological feature (Pearse 1994, Pearse & Lockhart 2004)

All studies of development rates and larval lifetimes in polar marine invertebrates undertaken to date have found markedly slow development and dramatically extended larval periods (Bosch et al. 1987, Peck 1993, Peck & Robinson 1994, Powell 2001). In some cases larvae may be able to spend more than 6 mo in the water column, facilitating very long dispersal distances. This is thought to be a consequence of direct temperature effects slowing the development rate of polar taxa rather than an adaptive feature per se (Hoegh-Guldberg & Pearse 1995). Metabolic assessments of polar larvae have, so far, been restricted to echinoderms (Marsh et al. 1999, Peck & Prothero-Thomas 2002), and these have revealed very low metabolic rates compared with temperate larvae.

Herein we report a mixed development strategy with long brooding periods followed by an extended pelagic phase in 2 Antarctic gastropods, *Marseniopsis mollis* (Smith, 1902) and *Torellia mirabilis* (Smith, 1907). The aim of the investigation was to identify the length of the brooding periods in these species, and to measure the metabolic rates of newly released individuals. A secondary aim was to compare these rates with those previously measured for other Antarctic taxa.

MATERIALS AND METHODS

Specimen collection and maintenance. Velutinid (previously lamellariid) gastropods are typically predators of ascidians (Fretter & Graham 1962, Young 1986) and in Antarctica the common shallow-water velutinid *Marseniopsis mollis* (Smith, 1902) lays broods of eggs in the test of the abundant ascidian *Cnemidocarpa verrucosa* (see Fig. 1). At sites near Rothera research station on Adelaide Island, Antarctica (67° 34′ S, 68° 08′ W) SCUBA divers have observed broods being laid between the months of January and March, although the frequency of such observations varies between years, suggesting strong interannual variability in reproductive activity (British Antarctic Survey [BAS] unpubl. data). In April, ascidians previously observed being utilised by *M. mollis* for laying broods were collected and maintained in a flow-through aquarium system. They were held in 25 cm deep, flowing-water tables and observed at approximately twice-weekly intervals, until hatching, to evaluate any visible development stages. Aquarium temperatures over this period were monitored continuously and ranged between –1.5 and –0.5°C; at all times they were within ±0.5°C of ambient seawater temperatures. When larvae began to hatch, ascidians with broods were transferred to beakers containing 4 l of clean seawater to prevent loss of larvae. Newly hatched larvae were removed to separate 1 l beakers of clean seawater using wide-bore pipettes, until used in experiments. The seawater was taken directly from the sea and contained natural levels of phytoplankton that were, therefore, available for larvae to consume. Natural phytoplankton levels varied markedly during the larval period, but total chlorophyll typically reaches a maximum value of 20 to 25 mg m^{-3} in January, with nanophytoplankton levels peaking in the 0.5 to 1.5 mg m^{-3} range (data for 1997 to 2005: BAS unpubl. obs.). However, no checks were made to confirm whether larvae were feeding or not. During the whole process, beakers were held in flowing-water tables to maintain temperatures as close as possible to the long-term maintenance temperatures.

Specimens of *Torellia mirabilis* (Smith, 1907) were collected by divers, introduced into the station aquarium system in February and March, and held in large (0.75 m^3) flow-through holding tanks. They were observed to begin laying broods on the sides of the tanks in April. Throughout April, 2 females were observed in detail; one laid 23 egg masses attached to the side of a tank, while the other laid 30 broods. Culture conditions were the same as for *M. mollis*, with egg masses being held until hatching in water tables, and larvae held in beakers until used in experiments.

Oxygen consumption measurements. Oxygen consumption was measured on individual larvae following the protocols of Peck & Prothero-Thomas (2002). Respirometers of 35 to 45 µl volume were made from 2.35 mm internal diameter (ID), glass capillary tubing. This was cut into 12 mm lengths and heat-sealed at one end to form small chambers. Individual larvae were introduced into each microrespirometer, which

were then 'capped' by inserting a 20 mm length of narrow-bore peristaltic pump tubing (black, ID = 0.76 mm, outer diameter [OD] = 2.35 mm) into the top. At the end of the experiment, samples of 25 µl were taken using gas-tight syringes for analysis of oxygen content. They were obtained by passing the syringe needle through the narrow-bore tubing, taking great care to avoid incorporating air bubbles or the larva with the sample. For the duration of the experiment the chambers were held in a small metal rack suspended in a shallow flow-through aquarium, in which the general larval culture was also held. This allowed the experimental temperatures to be maintained at the set temperature ±0.2°C. The oxygen content of the chamber water was determined using couloximetric methods (Peck & Uglow 1990, Peck & Whitehouse 1992), which allowed oxygen content in the 25 µl sample to be measured to a routine accuracy of ±1%. The oxygen consumed by larvae was obtained from comparison of experimental respirometers with controls (identical respirometers submitted to the whole procedure but containing no larva). Controls all decreased in oxygen content by less than 1% of the start value, compared to depletions of 5 to 30% for respirometers with larvae.

In each experimental trial, 20 respirometer chambers were set up: 5 of these were used as controls and were filled with seawater (using a Pasteur pipette) before being capped with the narrow-bore tubing; the remaining 15 were half-filled with seawater; an individual larva (already held in filtered water) was then placed in each chamber with great care. The respirometers were then topped-up and sealed, ensuring there were no air bubbles present. All chambers were placed in the rack for the duration of the experiments, which ran for up to between 15 and 25 h. During trials, maximum oxygen depletions of 30% were allowed. Maintaining oxygen levels above 70% of saturation minimised stress effects during the experiments, and avoided problems associated with oxygen diffusing into chambers (Peck & Prothero-Thomas 2002).

At the end of each experiment, larvae in the respirometers were checked using a field microscope to ensure they were still alive. The couloximeter was regularly calibrated with injections of fully saturated seawater at known temperature whose actual oxygen content was obtained from previously published sources (Benson & Krause 1984). Calibrations were always in the range 97 ± 2%.

Larval mass measures. Concurrently with respiration trials, samples of larvae of each species were transferred from culture vessels in as little seawater as possible to pre-ashed 5 mm, tin, elemental-analysis vials. When 25 larvae had been added to a vial, any excess seawater was carefully removed using a Pasteur pipette. Because of the disturbance of transfer, at this stage larvae were tightly closed. Samples were then rinsed quickly in freshwater to remove excess salt before drying for 24 h at 60°C; 1 control sample was immediately returned to seawater after the freshwater rinse, and 24 of the 25 larvae opened and were swimming normally within 1 h. After drying, samples were cooled in a desiccator and weighed on a microbalance. Samples were then transferred to a muffle furnace and ignited at 450°C for 12 h, cooled in a desiccator and reweighed on a microbalance. Ash-free dry mass (AFDM) was obtained as the difference between dry mass and remaining mass post-ignition; 5 groups of 25 larvae were evaluated for each species. Mass measures were made on *Marsenioposis mollis* larvae approximately 45 d post-release and on *Torellia mirabilis* larvae approximately 40 d post-release.

RESULTS

Brooding and larval observations

At Rothera, female *Marseniopsis mollis* laid eggs in batches in the cuticle of the common ascidian *Cnemidocarpa verrucosa* (Fig. 1). It is not known for certain whether a given female utilised more than 1 ascidian for her eggs, or whether any ascidian was utilised by more than 1 gastropod.

In *Marseniopsis mollis* egg masses, veliger stage embryos were first noted in early August, and hatching took place between early October and mid-December. By the end of August embryos were noted as being motile within the egg capsule. Larvae hatched as mature veligers (Fig. 2a). Since this species was observed laying

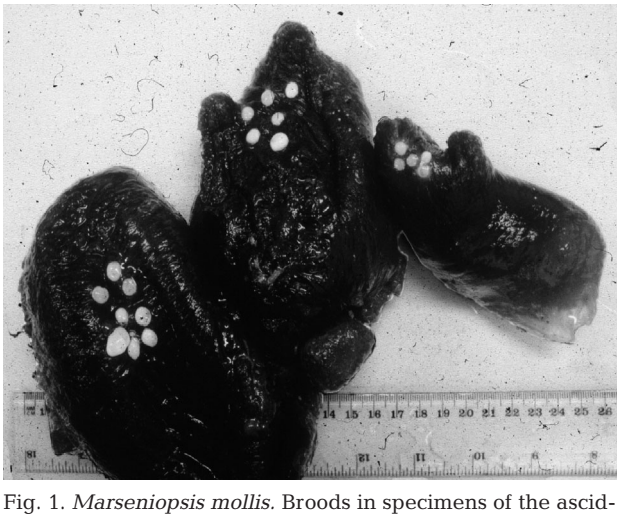

Fig. 1. *Marseniopsis mollis.* Broods in specimens of the ascidian *Cnemidocarpa verrucosa*. Sample was collected near Rothera station, Antarctica. Each pale spot on the photograph is a separate 'batch' of eggs, and broods are made up of several 'batches'

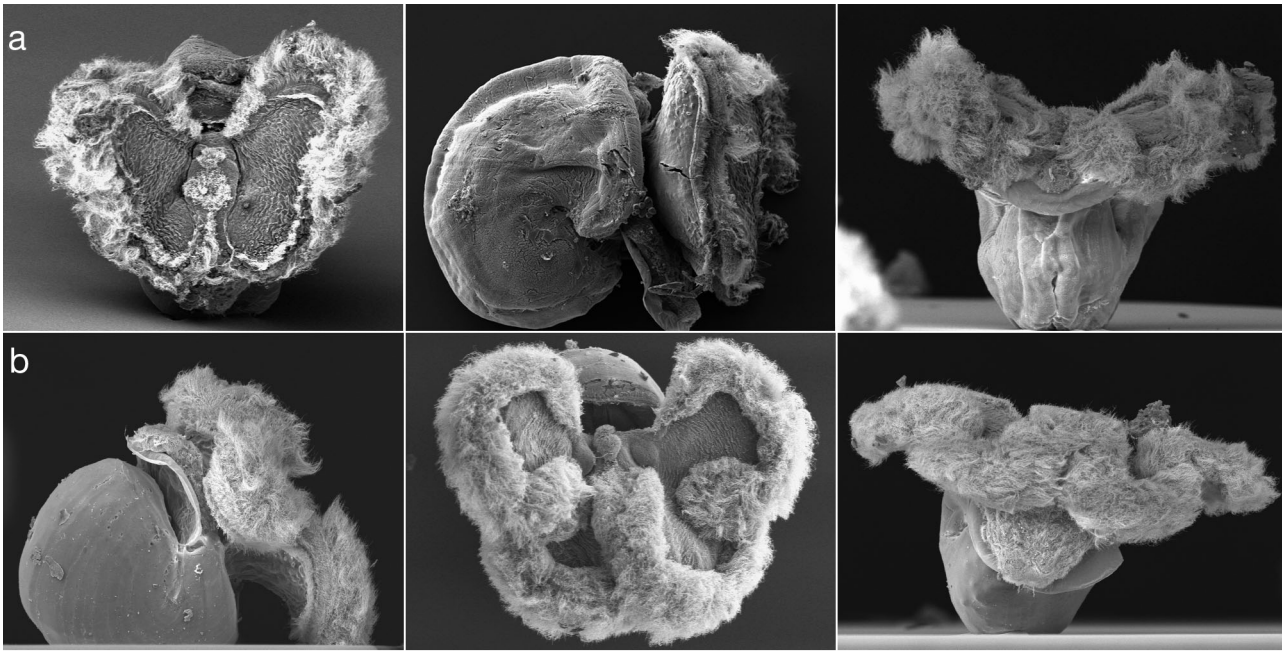

Fig. 2. (a) *Marseniopsis mollis*; (b) *Torellia mirabilis*. SEM images of hatched veliger larvae, note 4-lobed velum, closing operculum and ciliated foot. In life, larval length was 678 µm (SE = 11, n = 10) for *M. mollis*, and 729 µm (SE = 5, n = 10) for *T. mirabilis*

egg masses between January and March, the brooding period is 9 to 10 mo, and the time needed to reach the veliger stage is 5 to 6 mo. This development takes place over the austral winter. After release in the laboratory, larvae were held in culture for up to 55 d before experiments were ended because of logistic constraints. At the end of this culture period, the larvae had not changed visibly and no settlement behaviour was exhibited, even in the presence of a range of potential substrata including natural rock (with and without encrusting red algae), adults of the same species, and specimens of the host ascidian *Cnemidocarpa verrucosa*.

Torellia mirabilis egg masses were first noted to contain fully formed, veliger-stage embryo larvae in mid-August, and hatching took place in mid-October to mid-November. Embryos were noted as being motile in mid-September. As in *Marseniopsis mollis*, larvae hatched as well-developed veligers (Fig. 2b). Egg masses were laid in the aquarium in April, and the brooding period was therefore 6 to 7 mo, again over winter, and the veliger stage was reached after around 4 mo. After hatching, larvae were maintained in culture for 25 to 45 d until experiments ceased. As for *M. mollis*, no settlement behaviour was observed, even in the presence of local rock, encrusting red algae, or shells of adult *T. mirabilis*. The complete length of the larval period in both species is not known, but is extensive, and clearly well in excess of the 45 to 55 d culture periods completed here.

Oxygen consumption measurements

In *Marseniopsis mollis*, larval oxygen consumption was assessed approximately 35 to 40 d post-release, and in *Torellia mirabilis*, 25 to 30 d post-release. For *M. mollis* oxygen consumption of individual larvae ranged from 165 to 442 pmol h^{-1}, mean = 317 pmol h^{-1} (SE = 14; n = 17). Mean, larval, ash-free dry mass was 14.1 µg (SE = 0.07, on mean of 5 pooled samples each of 25 individuals). For *T. mirabilis* these figures were range = 122 to 298 pmol O_2 h^{-1}; mean = 208 pmol O_2 h^{-1} (SE = 11, n = 15); mean larval mass = 17.6 µg AFDM (SE = 0.11, on mean of 5 samples each of 25 individuals) (Fig. 3).

DISCUSSION

Reproductive strategies of marine invertebrates are generally classified into those with protected development and those (predominantly broadcast fertilizers) with pelagic development (Strathmann 1985). The reproductive strategy exhibited here by both *Marseniopsis mollis* and *Torellia mirabilis*, of a long period of brooding followed by an extensive period of planktonic larval development, is relatively unusual in marine invertebrates in general, but has been seen previously in gastropods (Pechenik 1979, 1999). It has also been reported previously in Antarctica for the

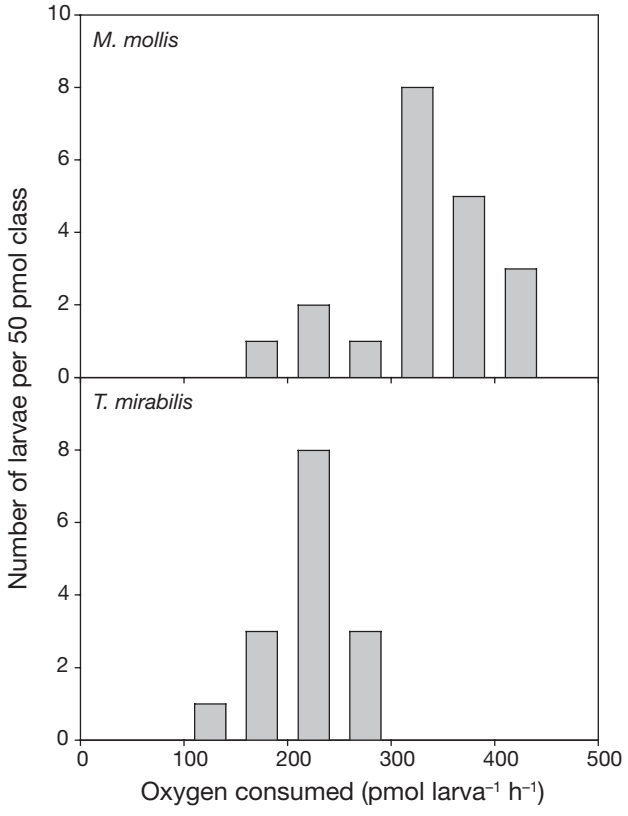

Fig. 3. *Marseniopsis mollis* and *Torellia mirabilis*. Frequency distribution of oxygen consumption for veligers. Each determination represents respiration rate of a single larva

brachiopod *Liothyrella uva* (Meidlinger et al. 1998). For species that have very long development times, conducting the early part of their development phase in an egg mass provides protection from predators and other mortality factors. Release at a late stage, but combined with a lengthy pelagic period, allows protected development to a size that may provide a refuge from predation, combined with the potential for colonisation at distance, and areas made newly available by ice-scour. The protected period here also covers the Antarctic winter for both species. Producing broods that develop over winter would provide some protection from ice-scour, because scouring intensity is considerably reduced in winter when the sea surface is frozen. It is also possible that this allows release to be keyed with the timing of enhanced water-column productivity, or the provision of suitable food supplies for newly settled juveniles. It should be noted here that no larvae similar to those described here were collected in a 3 yr larvae-sampling programme at Signy Island (Stanwell-Smith et al. 1999), or in a similar study at Rothera station between 2001 and 2004 (D. Bowden pers. comm.), suggesting that *M. mollis* and *T. mirabilis* larvae may be demersal.

The periods of protected development measured here for *Marseniopsis mollis* and *Torellia mirabilis* of 9 to 10 mo and 5 to 6 mo, respectively, are much longer than those typical of temperate and tropical brooding gastropods (Fig. 4). The few previous studies of fully protected development in Antarctic gastropods found even longer development times than those recorded here for *M. mollis* and *T. mirabilis*. Hain (1991) and Hain & Arnaud (1992) maintained egg masses of *Trophon scotianus*, *Neobuccinum eatoni* and *Austrodoris kerguelensis* in aquaria at 0 ± 0.5°C and found juveniles emerged between 19 and 26 mo after egg-

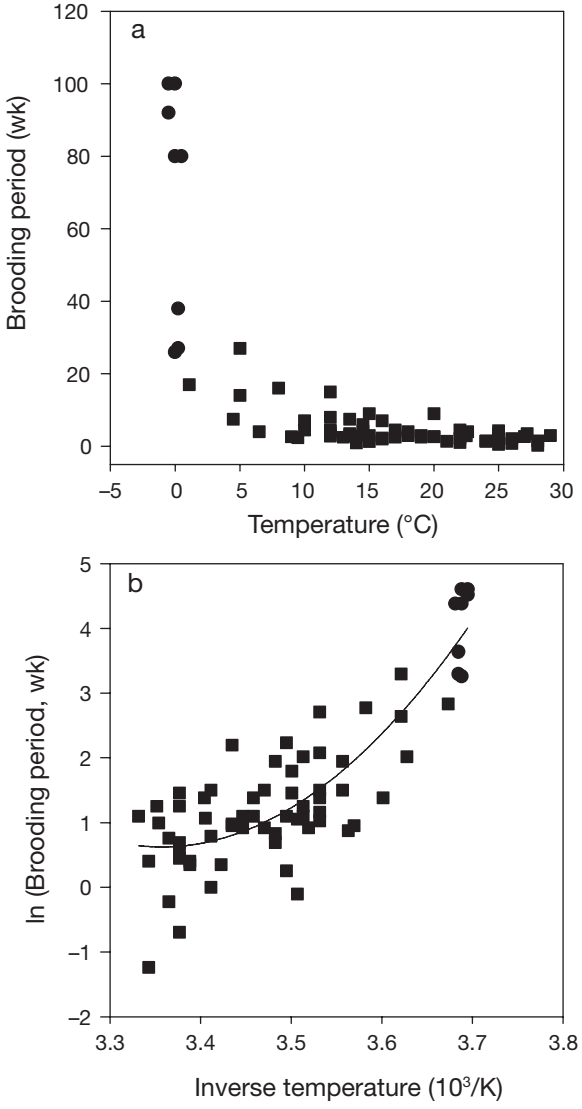

Fig. 4. (a) Brooding periods for Antarctic (●) and for temperate and tropical (■) molluscs (data are primarily for gastropods, but also include aplacophoran and polyplacophoran species) plotted against habitat temperature (data from Fretter & Graham 1962, Hadfield 1979, Pearse 1979, Fretter 1984, Hadfield & Switzer-Dunlap 1984, Hughes 1986, Hain 1991, Gonzales & Gallardo 1999); (b) Arrhenius plot of data in (a)

laying. This compares with a range of between <1 and 26 wk (90% = ≤5 wk, Fig. 4) for temperate and tropical gastropods. They also cultured broods of *Torellia mirabilis* that hatched after 24 mo, 4 times as long as the brooding period recorded here. Their cultures hatched at the crawling juvenile stage rather than the veliger stage in the present study. This suggests that either the brooding period in some of these species is highly variable, or that small changes in environmental conditions (e.g. temperature, light regime, etc.) can markedly affect development rate.

With pelagic trawls Hain & Arnaud (1992) also collected limacospaeran larvae that they assumed came from *Marseniopsis conica* and *M. mollis*. These larvae were over 10 mm in length and clearly different from the larvae produced in the present study. Either the Limacosphaeran larvae collected by Hain & Arnaud (1992) were not *M. mollis* larvae, or our specimens still had a long developmental period to complete that would include this stage. Velutinid gastropods have a characteristic echinospiran larva that has a double shell. The SEM images of the present study suggest that the *M. mollis* veligers in this study could be of the echinospiran type, but no effort was made to establish this.

The dramatic slowing in development rate at temperatures around 0°C, as shown by the markedly increased brooding periods matches the pattern previously reported for Antarctic echinoderms (Fig. 4a, Table 1) (Bosch et al. 1987, Hoegh-Guldberg & Pearse 1995, Stanwell-Smith & Peck 1998) and bivalve mollusks (Powell 2001). Hoegh-Guldberg & Pearse (1995) showed that temperature is the most important determinant for development rates in marine invertebrates. Both Stanwell-Smith & Peck (1998) and Powell (2001) showed that Q_{10} values calculated for development rates above polar temperatures produce values between 1 and 4, the normally accepted range for non-pathological thermodynamic effects on physiological processes (Clarke 1983). Below 1°C, development rates slowed dramatically and produced high Q_{10} values, above 10. The data presented herein show a similar marked slowing of development around 0°C. Average brooding period ranges from about 2 to 5 wk in species living at temperatures between 10 and 30°C. At 5 to 10°C, this rises to over 10 wk, but at temperatures below 5°C the period rises to over 60 wk (Table 1). The Q_{10} values for these temperature effects are between 2.0 and 4.5 for temperatures between 5 and 30°C, but rise to over 35 when temperatures lower than 5°C are compared to those in the 5 to 10°C range (Table 1). Such high Q_{10} values are so far outside those expected for biological systems as to indicate that some factor other than direct thermodynamic control becomes important. Thus, either the rate of development of marine invertebrates is constrained by different factors or processes at polar temperatures than at higher temperatures, or neither the van t'Hoff relationship (Table 1) nor the Arrhenius relationship (which is non-linear for brooding periods in gastropod molluscs, Fig. 4b) are meaningful descriptions of the effect of temperature on development in marine invertebrates (Clarke 1992).

Table 1. Q_{10} values for brooding period of gastropods, apalacophoran and polylacophoran molluscs for 5°C temperature blocks across whole temperature range (data from Fig. 4), showing means calculated for brooding period for each 5°C block between 0 and 30°C and Q_{10} values calculated for adjacent temperature blocks (i.e. for comparison with next temperature step)

Temp. step (°C)	Brooding period (wk)	Q_{10}
<5	62.20	35.10
5–10	10.50	4.46
10–15	4.97	2.43
15–20	3.19	1.12
20–25	3.02	2.03
25–30	2.12	

Metabolic-rate measurements of larvae of Antarctic marine invertebrates have, in the past, been carried out predominantly on echinoderm larvae (Olson et al. 1987, Hoegh-Guldberg et al. 1991, Shilling & Manahan 1994, Marsh & Manahan 1999, Peck & Prothero-Thomas 2002). Thus, values for oxygen consumption in the range 2 to 107 pmol O_2 $larva^{-1}$ h^{-1} have been reported for larvae of the starfish *Odontaster validus* (Peck & Prothero-Thomas 2002). Factors such as temperature, the method of measuring water oxygen-content and numbers of larvae per respirometer appear to have significant effects on the results obtained. The few studies comparing the metabolism of Antarctic larvae with that of larvae elsewhere have shown markedly lower respiration rates of Antarctic compared to temperate species, but have generally only been able to include a few species in their comparisons (e.g. Hoegh-Guldberg et al. 1991 for asteroid larvae). The relative paucity of data on metabolic rates of larvae from temperate and tropical latitudes also makes large-scale comparisons difficult.

Expressed on an AFDM basis, the oxygen consumption of *Marseniopsis mollis* and *Torellia mirabilis* larvae is near the middle of the range reported for Antarctic echinoderm larvae, suggesting that the cost of development and maintaining organic tissue in larvae of polar echinoderms and molluscs is similar. The values for Antarctic larvae overall are significantly lower than data for larvae of gastropod and bivalve molluscs from temperate and subtropical latitudes (Fig. 5). The mean oxygen consumption of gastropod and bivalve larvae at 20°C (from Fig. 5) is 265 pmol

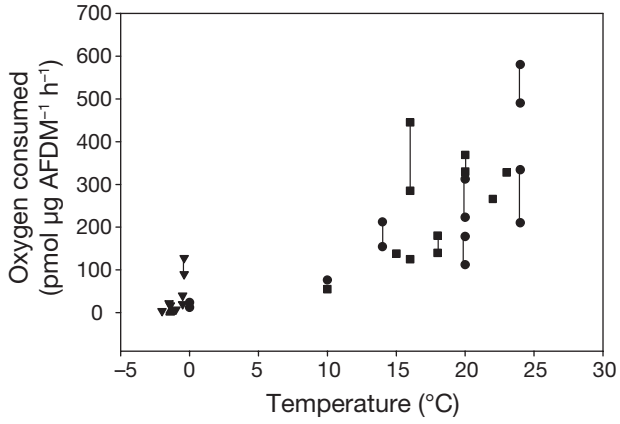

Fig. 5. *Marseniopsis mollis* and *Torellia mirabilis*. Oxygen-consumption rates of veliger larvae at 0°C compared with rates of Antarctic echinoderm larvae (▲ = asteroid larvae, ▼ = echinoid larvae) (data from Olson et al. 1987, Hoegh-Guldberg et al. 1991, Shilling & Manahan 1994, Hoegh-Guldberg & Manahan 1995, Marsh et al. 1999, Marsh & Manahan 1999, Peck & Prothero-Thomas 2002), and temperate gastropod mollusc larvae (■) (data from Pechenik 1980, Doberteen & Pechenik 1987 and bivalve mollusc larvae (●) (data from Holland 1978, Bayne 1983, Laing & Utting 1994, Hoegh-Guldberg & Manahan 1995)

µg AFDM^{-1} h^{-1}, compared with 22.6 and 11.8 pmol µg AFDM^{-1} h^{-1} for *M. mollis* and *T. mirabilis* veligers, respectively. These values equate to a Q_{10} for larval metabolic rate of 3.5 to 4.8; these values are high, but not unusual for biological systems. The form of the relationship in Fig. 5 is similar to data for adult perciform-fish species across latitudes (Clarke & Johnston, 1999), and also for adult bivalve molluscs (Peck & Conway 2000).

In ecological terms, low energy-use may underpin the developmental and larval strategy exhibited by *Marseniopsis mollis* and *Torellia mirabilis* of slow development and combined protected development with an extended pelagic period. The low polar temperatures allow metabolic costs to be markedly reduced. They may also result in species having long development periods that allow protected development through phases where mortality losses in the water column would be high, combined with a long dispersal phase that optimises colonisation of new sites. This could be more advantageous at polar than at other latitudes, because of the regular physical disturbance from ice experienced in the former.

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