

Temperature limits to activity, feeding and metabolism in the Antarctic starfish *Odontaster validus*

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ABSTRACT: Cold-blooded Antarctic marine species are highly stenothermal and possibly the most temperature-sensitive group on Earth. Studies to date have produced upper lethal temperatures in the range of 4 to 10°C. Although invertebrates have not been acclimated to temperatures above 3°C, some Antarctic fish have been acclimated to 4°C. Activity competence has been evaluated in several Antarctic marine invertebrates and shown to be very sensitive to temperature, with 50% failures in the range of 1 to 3°C for clams, limpets and scallops. The starfish *Odontaster validus* is much more capable of coping with elevated temperatures than any of these species. Turning speed increased with temperature, reaching a maximum at 7.5°C. Temperature increase led to a clear hierarchy of response loss in the starfish, with lethal limits occurring at a higher temperature (15°C) than loss of activity (9°C) and loss of feeding competence (Specific Dynamic Action, or SDA) and coelomic oxygen level collapse both occurring at 6°C. The higher temperature limit for activity than coelomic oxygen level could be explained by body design or taxonomic factors, which may also explain the markedly enhanced ability to cope with elevated temperature over other Antarctic marine species. Long-term acclimation and survival up to 6°C should be possible for this species, which is important for species living on the west coast of the Antarctic Peninsula, possibly the fastest warming marine environment on Earth. The markedly higher resistance to elevated temperature and maintenance of function in a common Antarctic predator compared to the abilities of several of its prey species suggests that a warming environment could have dramatic consequences on the community-level ecological balance for large areas of the Antarctic benthos.

KEY WORDS: Aerobic scope · Climate change · Specific Dynamic Action · SDA · Critical temperature · Temperature change · Competition

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INTRODUCTION

Antarctic marine species are highly stenothermal, with the vast majority having experimental upper lethal temperatures between 5 and 10°C (Somero & DeVries 1967, Peck & Conway 2000). The most stenothermal species can only survive in a temperature window between –2 and 4°C (Peck 1989, Pörtner et al. 1999a). The physiological processes setting the temperature tolerance limits, at least in marine ectotherms, are associated with reductions in whole animal aerobic scope (Pörtner et al. 1998, 1999b, Peck et al. 2002). Recently, Pörtner (2002) elucidated the physiological

basis of temperature limits at different levels and showed a hierarchy of tolerance from the molecular level to the whole animal. This showed that the tightest limits were set at the whole animal level. There is then wider tolerance at each step down the physiological hierarchy to tissues, cells and molecules, and he argued that, in general, adding organismal complexity reduces thermal tolerance. Thus, the physiological processes evident in response to varying temperature, at least in acute to medium-term experiments, are a progressive reduction in aerobic scope to a point where it is lost completely and tissues transfer to anaerobic metabolism. This is the critical physiological

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limit of Pörtner et al. (1998), and this may have a basis in mitochondrial function (Pörtner et al. 2007). Beyond this point survival is dictated by organismal tolerance to anaerobiosis.

In longer-term studies, several Antarctic fish species have been shown to be able to acclimate to 4°C but not above this temperature (Gonzalez-Cabrera et al. 1995, Lowe & Davison 2005, Seebacher et al. 2005, Jin & DeVries 2006, Podrabsky & Somero 2006). Invertebrates, however, appear less able to acclimate to elevated temperatures; attempts to acclimate the scallop *Adamussium colbecki* to temperatures above 2°C failed (Bailey et al. 2005). In long-term temperature elevation trials the brachiopod *Liothyrella uva* survived at 3.0°C but failed at 4.5°C (Peck 1989) and the bivalve *Limopsis marionensis* failed at 4°C (Pörtner et al. 1999a). Attempts to acclimate the clam *Laternula elliptica* (S. Morley pers. comm.) and the brittle star *Ophionotus victoriae* (M. Clark pers. obs.) to 3°C have also failed.

The important criteria for population or species survival in a given area is not, however, dictated directly by its physiological tolerance limits, but by the eco-physiological constraints on its ability to perform critical biological functions such as feeding, locomotion and reproduction, and how changes in these characteristics, affect ecological balances. Recently, investigations of activity in a range of Antarctic marine herbivores indicated a surprising sensitivity to temperature and a progressive decline in capability consistent with declining aerobic scope (Peck et al. 2004). The large infaunal bivalve mollusc *Laternula elliptica* has an experimental upper lethal temperature of 9°C and transfers to anaerobic metabolism at ca. 6°C (Peck et al. 2002). However, it ceases to rebury after removal from sediment at 5°C, and 50% of the population loses this ability when temperatures reach 2.5°C (Peck et al. 2007). Likewise, the limpet *Nacella concinna* has an upper lethal temperature of 9.5°C (Peck 1989), but 50% of the population loses the ability to right themselves when turned over at ca. 2°C, and the scallop *Adamussium colbecki* dies at 5 to 6°C, but loses the ability to swim between 1 and 2°C. These are all major activities that involve extensive muscular activity.

The Antarctic has an abundant and rich benthos with high levels of endemism (Arntz et al. 1994, Clarke & Johnston 2003). Current data for invertebrates suggest that they are highly sensitive to rising temperatures, but analyses to date are limited to herbivores or scavengers. To move analyses to other trophic levels and identify ecologically important relations, we evaluated the ability to perform work, metabolism, aerobic status and feeding, including Specific Dynamic Action (SDA) of feeding, with rising temperature in a common predatory species, the starfish *Odontaster*

validus. *O. validus* is common in Antarctica, circumpolar and a major element of the predator/scavenging organism complex of the benthic food web. A better ability to cope with rising temperature than species it preys upon, including scallops, limpets and burrowing bivalves, may significantly alter the ecological balance during any future environmental warming event. This is the first step towards making ecologically relevant predictions of climate change effects based on temperature tolerance capacities of different ecological guilds for a region where significant change has already been documented and the fauna appear sensitive to change.

MATERIALS AND METHODS

Odontaster validus were collected by SCUBA from sites at 10 to 20 m depth near the British Antarctic Survey's Rothera research station, Adelaide Island, Antarctica (67° 34' 07" S, 68° 07' 30" W). For experiments on whole animal oxygen consumption, coelomic oxygen content and activity in relation to temperature, specimens were held in a flow-through aquarium at conditions close to ambient for 2 to 3 wk before being transported to the UK. In transit and in the UK, starfish were held in recirculating seawater systems at $0 \pm 1.5^\circ\text{C}$, in a 12:12 h light:dark regime, and fed either frozen krill or fish. Measurements of the effect of temperature on the post-prandial rise in metabolic rate were made in Antarctica in the station flow-through aquarium, where temperatures were within 0.5°C of ambient.

Turning activity in relation to temperature. Prior to initiating investigations of ability of species to right themselves (turn the right way up) in relation to temperature, specimens were starved for a minimum of 3 wk to ensure individuals had low resting metabolic rates. Groups of between 5 and 10 starfish were then transferred to jacketed tanks connected to thermocirculator units, and the whole system was held in a controlled-temperature room. In this fashion, temperatures were held at the set temperature $\pm 0.1^\circ\text{C}$. Initially, temperatures were held at 0.3°C. Temperatures were then changed at a rate of 0.1 to 0.2°C h⁻¹ until the required experimental temperature was reached. Specimens were allowed 24 h to acclimate at each temperature before experiments began. In each experiment, starfish were turned upside down, and the time taken for them to right themselves was recorded. Starfish were well spread in the tanks to avoid the possibility of interference or interactions affecting results. Each starfish was inverted up to 26 times at 0.3 and 9.5°C to evaluate any effect of fatigue. At other temperatures, 5 starfish were inverted between 7 and 12 times. Turning rate was calculated as the reciprocal of

the number of minutes needed for an individual to right itself.

Metabolism and temperature. For all oxygen consumption experiments in the UK, specimens were starved for 4 wk prior to measurements being made to ensure that metabolic rates were close to standard. The specimens were then transferred to temperature control systems similar to those described above. Whole animal oxygen consumption measures were made using closed bottle respirometry methods similar to those of Chapelle & Peck (1995). Preliminary trials were run to assess suitable times to run experiments, and oxygen concentrations were not allowed to fall below 70% saturation. Experiments were run using 1 μm filtered, aerated seawater. Animal volumes were measured by displacement after trials and respirometer volume adjusted accordingly in the calculation of oxygen consumption rate. Oxygen concentrations in chambers were obtained from 25 μl samples taken with a gas tight syringe through a rubber septum seal. These samples were injected into a fuel cell-based coulometer, which measured oxygen content of the sample to $\pm 1\%$ (Peck & Uglow 1990, Peck & Whitehouse 1992). Replicate samples were taken to ensure accuracy. Five starfish of similar size were selected for this experiment and their rates of oxygen consumption measured at $-1.5, 0, 3, 6, 9$ and 12°C . After each temperature rise oxygen consumption was measured daily, and the move to the next temperature step was made when respiration rates appeared to have stabilised. The experiment was terminated at 15°C when $>50\%$ of the starfish had died.

Oxygen content of coelomic fluid was obtained from replicate 25 μl samples taken from the coelomic cavity through the epidermis using a gas tight syringe. These samples were also analysed using a coulometer. For measures of coelomic fluid oxygen content, separate individuals were used from those in the respirometry trials. These individuals were, however, held in the same temperature control system and therefore under identical conditions.

Feeding and SDA. These trials were conducted in Antarctica on 75 freshly collected specimens held in flow-through aquaria at temperatures between 0.5 and 0.9°C , which were close to but slightly above ambient (0.3 to 0.6°C). Initially, specimens were starved for 4 wk to exclude any effects of prior feeding. The first experiment evaluated the temperature at which feeding ceased. Experiments started by transferring 48 starfish to the temperature control system and initially, at 0°C , they were individually fed blocks of fish muscle (*Notothenia coriiceps*), ca. 10% of their own wet body weight to ensure that all individuals would take food. After 48 h all uneaten food was taken from each starfish and weighed. Specimens were then held for

10 d without food to ensure the initial feeding at 0°C would not affect readiness to feed. In subsequent trials 8 specimens were placed in the temperature control system and temperatures raised at 0.5°C h^{-1} until the required temperature was reached. They were then allowed to acclimate to the new temperature for 24 h before being offered food (ca. 10% body weight). At all temperatures, food remaining after 48 h was removed and weighed, allowing the amount of food eaten by each individual to be obtained by subtraction. Different groups of 8 were used at each temperature step, to avoid any pretreatment effects. At temperatures where some or all individuals did not take the offered food, a different group of 8 individuals was tested for ability to feed 3 d after reaching the set temperature.

In the second experiment the increase in metabolism following SDA of feeding was assessed using a protocol similar to Peck (1996). Initially, 5 specimens were transferred to the temperature control system and held at 0°C . Individuals were allowed 2 d to acclimate to the experimental conditions and then standard metabolism was measured as oxygen consumption over the next 3 d using the methods described above. They were then allowed to feed on meals of ca. 10% body weight for 48 h, after which remaining food was removed and weighed. Oxygen consumption was then measured daily over the subsequent period of elevated metabolism. This whole process was then repeated on a new group of 5 starfish at 6°C , the highest temperature at which all *Odontaster validus* fed in the feeding trials.

After trials were complete, starfish volumes were measured as before. Specimen live weight was obtained by weighing after surface drying, dry weight after drying for 24 h at 60°C , and ash weight following ignition at 475°C for 24 h. After drying and ashing, samples were allowed to cool in a desiccator prior to weighing.

Data were tested for normality prior to parametric analysis using the Anderson-Darling test, where appropriate. Statistical treatments were made using the MINITAB 14 package.

RESULTS

Turning activity

At 0°C the starfish took on average 4.7 min (SE = 0.24) to right themselves after being turned over. There was a significant effect of size, with smaller starfish turning more rapidly than larger specimens (ANOVA, $F = 3.95$, $p < 0.01$, $df = 111$). There was no discernible fatigue exhibited by the starfish being forced to right themselves repeatedly by turning them

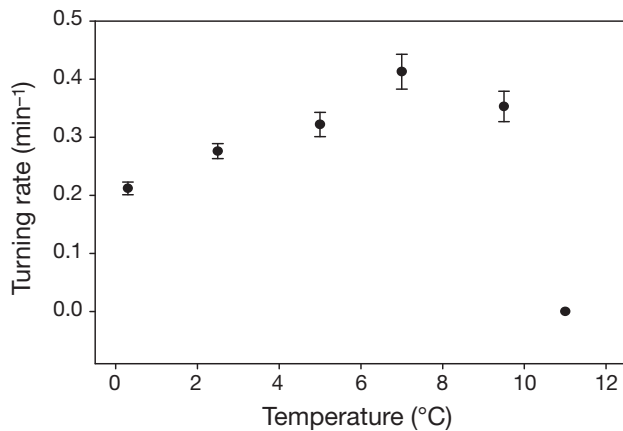


Fig. 1. *Odontaster validus*. Rate of turning from upside down versus temperature. Data shown are mean (\pm SE). At each temperature 5 starfish were assessed, and 12 assessments were made on each starfish

back over immediately following righting at 0.3 or 9.5°C; there was no change in the speed of turning (ANOVA, $F = 0.74$, $p = 0.81$, $df = 362$).

Raising the temperature (T) increased the turning rate (TR) of the *Odontaster validus* linearly from 0.21 min^{-1} at 0.3°C to 0.41 min^{-1} at 7.0°C ($\text{TR} = 0.20 + 0.029T$, $r^2 = 0.20$, $F = 63.43$, $p < 0.001$, $df = 256$, Fig. 1). When temperatures were raised to 9.5°C , the turning rate declined to 0.35 min^{-1} . At all temperatures up to 7°C , all starfish were capable of turning; at 9.5°C , 1 specimen failed, and at 11.0°C no starfish were capable of righting themselves. At this temperature all starfish adopted a position where the arms were held raised above the body.

Whole animal oxygen consumption, coelomic oxygen content and temperature

The starfish used in this experiment were selected to be of similar size. They had a mean volume of 7.87 cm^3 ($\text{SE} = 2.11$, $n = 5$), a dry weight of 1.21 g ($\text{SE} = 0.099$) and an ash-free dry mass (AFDM) of 0.61 g ($\text{SE} = 0.064$). At -1.5°C mean oxygen consumption was $107.5 \mu\text{g g}^{-1} \text{ AFDM h}^{-1}$, and this rose with temperature to a maximum of $300.1 \mu\text{g g}^{-1} \text{ AFDM h}^{-1}$ at 12°C before declining rapidly at 15°C (Fig. 2). At this point specimens began to die and the experiment was terminated. In a Generalised Linear Model (GLM) analysis temperature had a significant effect on oxygen consumption ($F_{1,196} = 37$, $p < 0.001$), as did individual ($F_{1,196} = 22.4$, $p < 0.001$), but the interaction term was not significant ($F_{1,196} = 0.01$, $p = 0.91$). A Tukey comparison of means showed that rates of oxygen consumption at different temperatures were significantly different ($p = 0.05$) for all pairwise comparisons with the exception of -1.5°C

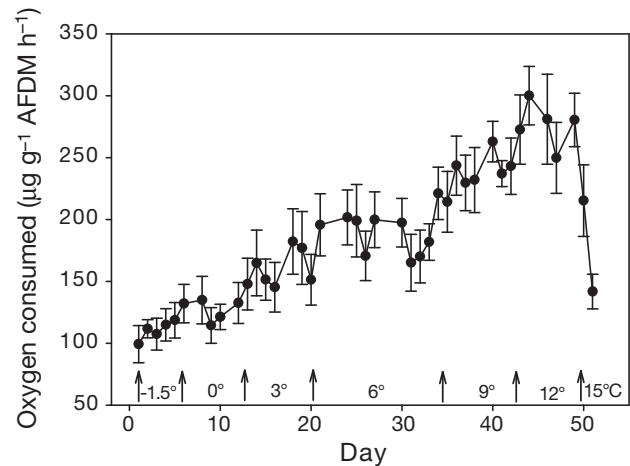


Fig. 2. *Odontaster validus*. Oxygen consumption in relation to temperature. Five specimens were held initially at -1.5°C , and then temperatures were raised incrementally to 0 , 3 , 6 , 9 , 12 and 15°C . Temperatures were raised after oxygen consumption values had appeared to stabilise. Arrows indicate days when temperatures were changed. Data shown are mean values for the group \pm SE. Experiments were terminated when more than 50% of the starfish died. AFDM: ash-free dry mass

vs. 0°C and 9°C vs. 12°C . The oxygen consumption rate at 15°C was significantly lower than the value at 12°C . Q_{10} values for each temperature step between -1.5 and 12.0°C were 3.1 (-1.5 to 0°C), 2.3 (0 to 3°C), 1.7 (3 to 6°C), 2.3 (6 to 9°C), and 1.29 (9 to 12°C). The overall Q_{10} for the change in metabolic rate between -1.5 and 12°C was 1.95 . Control starfish held at 0°C without food for the whole experimental period survived for more than 1 mo after experimental trials ceased with no mortality, showing that the effects of starvation in these trials were small.

The oxygen concentration of coelomic fluid declined markedly from 6.9 to $4.1 \text{ mg O}_2 \text{ l}^{-1}$ at 1.5 and 0°C , respectively (Fig. 3). When temperatures were raised initial measurements were made within 24 h of the temperature change to measure acute responses, and further measures were made 4 to 8 d after the temperature rise to assess acclimated responses. Acute coelomic oxygen concentrations leveled off at values of 2 to $3 \text{ mg O}_2 \text{ l}^{-1}$ between 3 and 12°C . Acclimated values, on the other hand, increased significantly from these low values to 4.8 and $4.2 \text{ mg O}_2 \text{ l}^{-1}$ at 0 and 3°C ($t = 3.2$, $p < 0.05$; $t = 4.8$, $p < 0.01$), respectively. Recovery was poorer at 6°C , with only a value just below $3 \text{ mg O}_2 \text{ l}^{-1}$ being achieved (only ca. $0.5 \text{ mg O}_2 \text{ l}^{-1}$ higher than acute values). At 9 and 12°C the acclimated coelomic oxygen concentrations were lower than the acute measures, but values overlapped. At 15°C coelomic oxygen concentration collapsed to close to 0 , indicating an inability to maintain oxygen supply to the tissues.

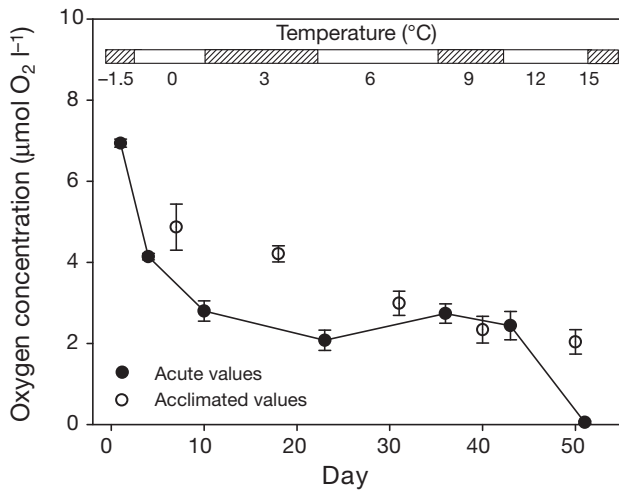


Fig. 3. *Odontaster validus*. Oxygen content of coelomic fluid with temperature. Each data point represents the mean for the 3 specimens measured at each temperature (each value was the mean of triplicate measures per individual). ●: acute values taken within 24 h of the temperature being raised; ○: acclimated values taken between 4 and 7 d after the temperature was raised. Note that there was no compensation (sensu Precht et al. 1955) of acclimated values from acute levels at temperatures of 6°C and above

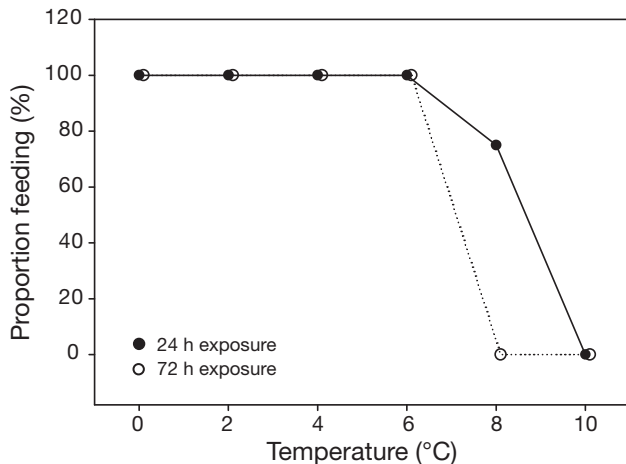


Fig. 4. *Odontaster validus*. Proportion of starfish (n = 8) feeding 24 and 48 h after being offered food in relation to temperature. ●: offered food after 24 h exposure to the experimental temperature; ○: counts for separate starfish offered food after 72 h at the set temperature

Feeding, SDA and temperature

All starfish acclimated for 24 h at the set temperatures, fed immediately when offered food, and were still feeding 24 h later at 0, 2, 4 and 6°C (Fig. 4). At 8°C all starfish accepted food when offered, but 24 h later only 6 of the 8 were still feeding. When starfish acclimated for 3 d at 8°C were tested, none fed. At 10°C no starfish fed after 24 h or 3 d exposure.

Table 1. *Odontaster validus*. Size data (volume, wet weight, dry weight, and ash-free dry mass [AFDM]) for starfish held at 0 and 6°C in the Specific Dynamic Action (SDA) experiment. All values are mean ± SEM. Starfish held at 6°C were significantly larger than those at 0°C (*t*-test on volume: *t* = 6.03, *df* = 9, *p* < 0.001)

Temp. (°C)	Volume (cm ³)	Wet weight (g)	Dry weight (g)	AFDM (g)
0	5.46 ± 0.38	5.30 ± 0.33	1.19 ± 0.07	0.64 ± 0.04
6	11.28 ± 0.89	11.76 ± 0.94	2.23 ± 0.18	1.34 ± 0.12

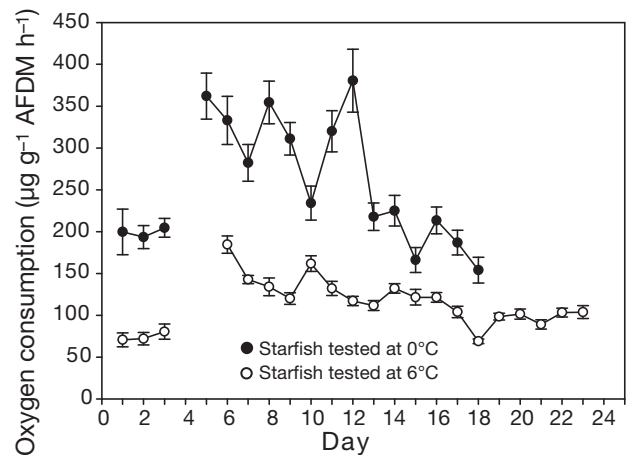


Fig. 5. *Odontaster validus*. Oxygen consumption in relation to feeding for starfish held at 0 and 6°C. At both temperatures starfish were fed on Day 3 after oxygen consumption measures had started. ○: starfish tested at 0°C; ●: starfish tested at 6°C. AFDM: ash-free dry mass

SDA trials were run at 0 and 6°C, the latter because this was the highest temperature in feeding trials where all starfish fed. Starfish were chosen at random from the holding stock, but specimens used were larger in the 6°C trials than in the 0°C ones (Table 1). Because the sizes of the starfish were different, but not markedly so, pre- and post-prandial metabolic rates were expressed on a mass-specific basis.

At 0°C standard metabolic rate was 78.5 µg O₂ g⁻¹ AFDM h⁻¹. After feeding, oxygen consumption rose to a peak 181 µg g⁻¹ AFDM h⁻¹, a factorial rise of ×2.30 (Fig. 5). Oxygen consumption remained elevated above pre-feeding for 15 d. At 6°C pre-prandial standard metabolic rate was 194.2 µg O₂ g⁻¹ AFDM h⁻¹ and the post-prandial peak was 372.0 µg O₂ g⁻¹ AFDM h⁻¹, a rise of ×1.92. The post-prandial rise in metabolism remained elevated above pre-feeding levels for 10 d.

DISCUSSION

Activity and temperature

Recent studies by Gonzalez-Cabrera et al. (1995), Lowe & Davison (2005), Jin & DeVries (2006) and Podrabsky & Somero (2006) have shown that a range of Antarctic fish species are capable of acclimating and functioning long-term to a temperature of 4°C, with enhanced thermal tolerance when temperatures are subsequently raised acutely to values in excess of 10°C. In contrast, Peck et al. (2004) showed that Antarctic limpets, clams and scallops rapidly lose the ability to perform work in the face of increasing temperatures. At temperatures of 5°C the limpet and clam were incapable of righting and burying, respectively, and at 2 to 3°C 50% of the individuals studied failed to right or bury. The scallop was even more tightly constrained with no specimens capable of swimming at 2°C. Recently this limitation to activity has been shown to be an oxygen supply dependency, because lowering or raising ambient oxygen levels lowered and raised, respectively, the successful performance of burying activity in the clam *Laternula elliptica* (Peck et al. 2007). Furthermore attempts to acclimate various Antarctic invertebrate species to 3°C have failed for the scallop *Adamussium colbecki* (Bailey et al. 2005). Upper temperature limits for brachiopods have been shown to be between 3.0 and 4.5°C (Peck 1989) and for the bivalve *Limopsis marionensis* to be below 4°C (Pörtner et al. 1999a). The clam *L. elliptica* (S. Morley pers. comm.) and the brittle star *Ophionotus victoriae* (M. Clark pers. obs.) cannot acclimate to 3.0°C. These measures of ability to perform activity and capacity to acclimate to elevated temperatures are better predictors of the ability of a species to cope in a changing environment than earlier studies of purely upper lethal limits, which in themselves showed Antarctic marine species to be highly stenothermal (Somero & DeVries 1967, Peck & Conway 2000).

Data here showing that all *Odontaster validus* studied were capable of performing activity up to 7°C, and the vast majority up to 9.5°C, are markedly different from data for other Antarctic marine invertebrates (Peck et al. 2004). This indicates that this species is significantly more eurythermal than previous invertebrate species studied. This is the first echinoderm to be evaluated in this way, and it is possible that there is a taxonomic effect here, especially as Antarctic fish appear more capable of acclimation than the invertebrates investigated, or there may be a bauplan effect.

Rates of activity in *Odontaster validus* increased with temperature monotonically from 0.21 min⁻¹ at 0°C to 0.41 min⁻¹ at 7°C, where they peaked before complete failure at 11°C. The increase produces a Q_{10} of 2.71 for

the temperature effect on activity, which is well within the expected range for biological functions. This type of relationship, increasing activity up to a maximum followed by a decline, is widespread in marine ectotherms and may be a characteristic of animals in general. In polar species this has been shown for the infanual clam *Laternula elliptica* (Morley et al. 2007), where a maximum rate that was closer to upper critical temperature limits, and is also above the normally experienced range of temperatures, was also found. However, maximum activity rates occurred at 2 to 3°C in *L. elliptica*, a much lower temperature than that for *O. validus*. Lower temperatures for maximum activity rates would also be expected in the scallop *Adamussium colbecki*, the brittle star *Ophionotus victoriae* and the limpet *Nacella concinna*, as their upper limits for activity are 5°C or lower. *O. validus* activity is also markedly different from the changes demonstrated by the Antarctic fish *Pagothenia borchgrevincki*. Although the latter can survive up to 10°C, has its maximum thermal scope measured at 3°C, and swimming performance follows a similar pattern (Wilson et al. 2002, Lowe & Davison 2005).

Oxygen consumption and temperature

Oxygen consumption in *Odontaster validus* rose consistently with temperature (Fig. 2) in a similar fashion to the pattern seen for *Laternula elliptica* (Peck et al. 2002), the limpet *Nacella concinna*, and the brachiopod *Liothyrella uva* (Peck 1989). The rise from a mean oxygen consumption of 106 µg O₂ g⁻¹ AFDM h⁻¹ at -1.5°C to 281 µg O₂ g⁻¹ AFDM h⁻¹ at 12°C produces a Q_{10} of 2.06 and is in the range of typical effects of temperatures on biological systems. As with previous investigations a rise to a peak is followed by a rapid fall in oxygen consumption and death of the specimens under study. This matches the predictions of the oxygen limitation of thermal tolerance (Pörtner 2002), where a failure in oxygen supply mechanisms is the proximate mechanism causing death. The difference in these data from previous studies on Antarctic ectotherms is that the *O. validus* survived up to 12°C, whereas the limpet *N. concinna* and the bivalve mollusc *L. elliptica* failed at ca. 9°C, and the brachiopod *L. uva* and the bivalve *Limopsis marionensis* did not survive above 4.5°C (Peck 1989, Pörtner et al. 1999a, Peck et al. 2002).

It is interesting that coelomic oxygen content increased in short-term acclimated specimens over acute values at 0, 3 and 6°C, but not at 9°C (Fig. 3). Combined with the results showing that activity was maintained up to 9°C, this suggests that the upper pejus temperature (sensu Pörtner 2002) is around this temperature. This also matches previous studies that have

found the pejus temperature to be a few degrees below the upper thermal limit in Antarctic marine species (Pörtner et al. 2007). These data would also suggest that *Odontaster validus* should be able to acclimate to temperatures possibly as high as 6°C, and that this is one of the most, if not the most, eurythermal Antarctic marine species investigated to date.

Feeding, metabolism and temperature

In line with the above data showing that *Odontaster validus* can perform physical activity up to 9°C in medium-term temperature elevation experiments and can survive temperatures up to 12°C with similar rates of rising temperature, it would be expected that it would maintain its ability to feed at temperatures well above those experienced in its natural environment (−1.8 to 1.8°C at Rothera station). All specimens in trials up to 6°C fed immediately on food made available and continued to feed 3 d later (Fig. 4). At 8°C nearly 80% of individuals fed over the first 24 h of reaching the set temperature, but none were feeding after 3 d. No specimens fed at 10°C at any time interval. These data again reinforce the implication that the upper pejus temperature for this species is between 8 and 10°C, because this is the temperature range where the capacity to perform metabolic work (aerobic capacity) is lost. Again it should be noted that this upper limit for activity is above the upper survival limit for all Antarctic marine invertebrates so far reported.

The rise in metabolism following feeding is a ubiquitous response in animals, and it is termed the SDA or Heat Increment (HIF) of feeding. Two main measures are made of the SDA: the factorial rise from pre-feeding to peak levels of oxygen consumption and the duration of the effect. In coldwater species the duration of the SDA is longer than for species at warmer temperatures, but the factorial rise is similar (Peck 1998). The overall energetic cost involved as a proportion of the energy content of the meal, the SDA coefficient, stays the same across temperatures.

The data in the present study for *Odontaster validus* match this pattern (Fig. 5). At 0°C the factorial rise to peak from pre-feeding levels was $\times 2.3$, and metabolism was raised for 15 d. At 6°C the rise to peak was $\times 1.9$, and the SDA lasted 10 d. However, it should be noted that specimens were only offered meals of 10% body mass, and both variation in rise to peak and larger peaks might have been obtained with larger meals. Despite the factorial SDA rise to peak being slightly larger at 0°C, because the pre-feeding standard metabolic rate was higher at 6°C ($194 \mu\text{g O}_2 \text{g}^{-1} \text{AFDM h}^{-1}$ compared to $78.5 \mu\text{g O}_2 \text{g}^{-1} \text{AFDM h}^{-1}$ at 0°C), the actual rise in metabolism was greater at the

higher temperature ($178 \mu\text{g O}_2 \text{g}^{-1} \text{AFDM h}^{-1}$ at 6°C compared to $102.5 \mu\text{g O}_2 \text{g}^{-1} \text{AFDM h}^{-1}$ at 0°C). This explains the reduction in duration of the SDA at 6°C, as similar amounts of total energy were used in the overall SDA (area under the curve in Fig. 5). Interestingly, the SDA at both 0 and 6°C appeared to be composed of 3 phases. At 0°C the peaks on each phase declined in size, but each phase was progressively longer, whereas at 6°C peaks were the same height and durations were also similar. Multiple peaks in an SDA have been reported previously for the limpet *Nacella concinna* (Peck & Veal 2001) and the nemertean *Parborlasia corrugatus* (Clarke & Prothero-Thomas 1997). The latter authors also noted that different metabolic processes occurred at different times during the SDA cycle. Thus, urea excretion was predominantly associated with the last phase.

Physiological and ecological implications

The fact that *Odontaster validus* survives in medium-term warming trials to at least 12°C, continues to perform activity up to 9°C, can complete a full feeding cycle and appears able to recover its coelomic fluid oxygen content with acclimation at 6°C indicates that this is easily the most eurythermal Antarctic marine invertebrate so far studied, and it may be the most eurythermal of all Antarctic marine ectotherms to date, including fish. The possible reasons for this include taxonomic effects or physiological constraints, although taxonomic constraints seem unlikely as clams, scallops, limpets and brittle stars are highly temperature sensitive. It may, however, be possible to explain these data via the oxygen limitation hypothesis (Pörtner 2002, Pörtner et al. 2007). Under this hypothesis, oxygen use, availability and delivery dictate rate of loss of aerobic scope with rising temperature. Fish have much higher levels of oxygen carrying blood pigments than either molluscs or fish, and their delivery system (the circulatory system) is more efficient. Thus, aerobic scope loss may be less in fish because of an enhanced delivery system. The major tissue in animals in terms of oxygen demand is muscle because of its mitochondrial content and the activity functions it performs. Muscle mass relative to whole animal mass is much lower in *O. validus* than in either molluscs or fish. Thus the loss of aerobic scope in the starfish with warming may be less than in other groups because its main locomotory mechanism is not muscle-based. Animals with poor circulatory capacities and larger muscle masses, such as scallops, would therefore be more vulnerable to environmental warming than those with better oxygen delivery systems or those with lower relative muscle mass.

The success of *Odontaster validus* in surviving elevated temperatures is clearly important given the 1°C rise in sea temperatures observed in the Bellingshausen Sea off the Antarctic peninsula over the last 50 yr (Meredith & King 2005). However, other considerations than the direct survival of this species may be of more interest. In ecological terms the success of a starfish predator at temperatures well above those where some of its known prey fail has a significant potential impact at community and ecosystem levels. All 3 mollusc species studied by Peck et al. (2004) lost significant capacity to perform activity at 2 to 3°C. The clam *Laternula elliptica* avoids predators such as *O. validus* by burying in sediment, while swimming is the scallop's main mechanism of predator avoidance. Rates of activity and processing meals increase in *O. validus*, at least to 6°C. Thus the ability of the prey species to avoid *O. validus* will decrease with every rise in temperature above the current position, because their ability to perform activity declines more rapidly with rising temperature than does that of the starfish. It is these types of change in ecological balance that are the most likely mechanisms for extinction of species at the population level (Peck 2005). This is the first evaluation of the capacity of a predatory benthic Antarctic invertebrate to continue to perform biological functions in elevated temperatures. The fact that it is far more capable than previously studied suspension-feeders or grazers raises important questions that need urgent attention. Are Antarctic marine benthic predators in general better at coping with rising temperatures, and thus could ecological imbalance be caused by relatively minor temperature changes? Or are the data here phenomena that are peculiar to starfish predators or even to *O. validus* itself, and if so why? Clearly such questions of differing capacities to cope among different feeding guilds are of wide significance in all major marine ecosystems and not just Antarctica.

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