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Extreme sensitivity of biological function to temperature in Antarctic marine species

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Abstract

Biological capacities to respond to changing environments dictate success or failure of populations and species over time. The major environmental character in this context is often temperature, and organisms across the planet vary widely in their capacity to cope with temperature variation. With very few exceptions Antarctic marine species are more sensitive to temperature variation than marine groups elsewhere, having survivable temperature envelopes between 5°C and 12°C above the minimum sea temperature of -2°C. Here we show, that in biological functions important to long-term survival, these animals are even more tightly constrained. The Antarctic bivalve mollusc *Laternula elliptica* and limpet *Nacella concinna* both survive a few days in experiments at 9-10°C, but suffer 50% failure in essential biological activities at 2-3°C and complete loss at 5°C. The Antarctic scallop *Adamussium colbecki* is even more sensitive, and loses the ability to swim as temperature approaches 2°C. This failure of activity is caused by a loss of aerobic capacity. A 2°C rise in sea temperature could remove these animals from the Southern Ocean.

INTRODUCTION

Organism responses to changing environments are complex, and species survival usually determined by changes in the balance of ecological factors, rather than direct effects of alterations to the physical environment (Davis *et al.* 1998; Convey *et al.* 2002). Recent models mainly focus on higher scale metrics, such as habitat loss, that encompass multiple environmental characters (Travis 2003). The relative importance of balance of ecological factors vs direct effect of changed physical factors differs from site to site, and with evolutionary history.

Most species on earth probably live either in the deep-sea (Grassle & Maciolek 1992; Snelgrove & Smith 2002), mid to deep ocean depths, or in the polar oceans (Clarke & Johnston 2003), where temperatures are below 5°C, are very stable,

and have been so for long evolutionary periods. Adaptation to these conditions has resulted in reduced rates of growth, development, and metabolism (Peck 2002). In these environments changes in physical environmental characters may be more important than elsewhere.

Antarctic marine species are stenothermal, being much less able to survive elevated temperatures than species from elsewhere (Peck & Conway 2000). Thus polar fish generally die at temperatures around, or slightly above 5°C (Somero & De Vries 1967), and most cold-water marine invertebrates die in experiments at temperatures of 5-10°C. These temperature envelopes are 2-4 times smaller than those for lower latitude species (Peck & Conway 2000). Metabolic rates in ectotherms vary with ambient temperature. Recent studies in Antarctic marine invertebrates have shown that as temperature rises oxygen consumption and heartbeat rate increase while blood oxygen content declines (Peck 1989; Pörtner *et al.* 1999; Peck *et al.* 2002; Pörtner 2002). As demand increases a point is reached where oxygen supply cannot meet the total requirements of the animal, anaerobic pathways are entered and anaerobic metabolic end products accumulate (Peck *et al.* 2002; Pörtner *et al.* 1998). This point is termed the critical temperature, and indicates the long-term physiological limit, as anaerobiosis cannot be sustained indefinitely. Above the critical temperature a point is eventually reached where the short-term oxygen debt is beyond the capacity of the animal, and death occurs at the experimental upper lethal temperature. The temperature where this is reached depends on time of exposure to elevated temperature and species tolerance of hypoxia. A faster increase in resting, compared with maximum aerobic metabolic costs, at elevated temperature has also recently been shown in the Antarctic stenothermal fish *Pagothenia borchgrevinki* (Wilson *et al.* 2003).

Frederich & Pörtner (2000) set the physiological responses of temperate species into a wider framework, identifying optimum, sub-optimum (pejus) and non-survivable (pessimum) temperatures, while explaining physiological responses of the spider crab *Maja squinado*. They related these changes to Shelford's law of tolerance (Shelford 1931), which states "the survival of an organism depends on the completeness of a complex of conditions", here termed the survival envelope. This law was important in the development of the niche and ecological hypervolume concept. Pörtner *et al.*

(1998) suggested that translocating the survival curves to lower temperatures truncated them, and the decline in survival and aerobic capacity at the lower end of survivable temperatures was lost in polar species, because it fell below the freezing point of seawater.

Recently the data showing Antarctic ectotherms to have very low temperature limits, and for this to be associated with transfer of tissues to anaerobic metabolism has been postulated to be a function of declining aerobic scope with elevated temperature (Mark *et al* 2002, Peck *et al* 2002, Pörtner 2002). Thus, as temperature rises the difference between maintenance metabolism and maximum aerobic metabolic rate decreases because maintenance costs outstrip the ability to raise oxygen supply.

In any changing environment, the important criteria for survival are not the conditions that can be endured, but the conditions where essential biological functions cannot be maintained, and the balance of these conditions over time. Thus, the temperature where tissues turn to anaerobic pathways is not important in this context, but the temperatures where functions such as feeding, locomotion or reproduction are compromised are critical. These functional upper limits will set the survival envelope for species, either by setting immediate limits, or altering the balance of ecological interactions. Where the physical environment dominates survival factors, or organisms have insufficient physiological flexibility (as for polar benthos), physical limits may dominate over biological interactions.

We tested the hypothesis that the stenothermal nature of Antarctic marine species is caused by limited aerobic scopes. To do this we measured the animal's abilities to perform activity, and predicted that the loss of essential biological functions would occur progressively with very small temperature elevations. In our experiments we investigated critical activity functions in the Antarctic limpet *Nacella concinna*, the infaunal bivalve *Laternula elliptica* and the scallop *Adamussium colbecki*. In the limpet we evaluated the ability to right itself when turned over. If limpets are incapable of righting after disturbance their survival is compromised. In *L. elliptica* we measured its ability to rebury in sediment. *L. elliptica* is a large infaunal bivalve, living deeply buried in sediments. Specimens move vertically in the

sediment during normal activity cycles, and also need to rebury when ploughed from the sediment by ice disturbance. In *A. colbecki* we assessed the proportion of animals that swam in response to stimuli.

MATERIALS AND METHODS

Experimental animals were collected by scuba divers from 8-15 m depth in Hangar Cove, Rothera Point, Adelaide Island (67°34'20"S, 68°07'50"W). Specimens of *L. elliptica* and *N. concinna* were held for 24 h in aquaria at ambient temperature before being used in experiments. Constant low-light levels were maintained, to mimic Antarctic summer conditions. In studies at ambient temperature animals were used immediately after the 24 h acclimation period. For elevated temperatures animals were held in jacketed water baths and temperatures raised at 0.1°C h⁻¹, until the required temperature was reached. Video recordings were made to determine burrowing or turning rate and times to completion. Data were collected using a Panasonic AG6124HB 24h time-lapse video recorder, and subsequently analysed using a JVCBR-S610E video analysis machine. At each temperature for each species between 18 and 26 animals were evaluated. A total of 145 *L. elliptica* were used, and measurements were only made in 2002. For *N. concinna*, measurements were made in both 2001 and 2002 and a total of 190 specimens were used from the same population in South Cove, Rothera Point.

Specimens used to evaluate swimming in *A. colbecki* were collected from Hangar Cove, Rothera Point, from 5-25m depth. Animals were stimulated initially at the ambient water temperature. Tank temperatures were then varied over a -1.9°C to +1.9°C range to compare acute responses. Temperature changes were made in 0.5°C increments at a maximum rate of change of 1°C · day⁻¹ (Bailey 2001). Light conditions were the same as previous. Prior to experiments animals were moved into a swim tank and allowed to rest for a minimum of 6 h before the first escape response was stimulated (6 h was the maximum time to 90% recovery recorded in this species for exhaustive exercise by Bailey *et al.* (2003)) 6 h was the maximum time to 90% recovery recorded in this species for exhaustive exercise by Bailey *et al.* (2003).. Handling was minimised and animals transported between tanks in water. The water

in the original tank was slowly mixed with the water in the new tank to minimise any differences in temperature or salinity. Escape responses were then stimulated using freshwater within 1°C of tank temperature. Water was introduced to the rear of the animal, directly beneath the hinge, using a tube attached to a 20 cm³ syringe. Typically 10 cm³ was injected at approximately 2 cm³ · s⁻¹. Freshwater is known to stimulate swimming in wild *A. colbecki* (Berkman 1988). There was minimal disturbance of the water around the animal and no force was exerted on the body of the scallop itself. The area of reduced salinity visible around the animal typically dispersed before adduction.

RESULTS

For *N. concinna* between 95 and 100% of individuals are capable of righting themselves within 24 h at 0°C (Fig. 1a). Righting ability falls progressively with temperature, until no limpets can perform this activity at 5°C. 50% of individuals are incapable of righting between 2°C and 2.5°C. For *L. elliptica* at 0°C, around 90% reburying in 24 h, whereas none rebury at 5°C, and 50% of the population lose the ability at 2°C (Fig 1b). In both species half the population have lost the ability to perform critical biological functions at, or very slightly above, 2°C.

Swimming in the scallop *A. colbecki* also declined with rising temperature, but the rate of decline was more rapid (Fig 2). Below 0°C the proportion of scallops swimming when stimulated varied between 28% and 50%. Above 0°C the proportion swimming declined monotonically. Above 2°C no scallops could be induced to swim.

Times required for limpets to right themselves are difficult to evaluate accurately, as the process involves a period of probing the substratum, followed by attachment and then turning. The turning element takes a short time, of the order of 5-20 seconds. Burrowing in *L. elliptica* varied with size, and was completed at 0°C in around 1 h in small individuals and up to 16 h in large specimens.

Between 1997 and 2000, sea temperatures at 15m depth at Rothera point ranged between -1.9°C and $+1.4^{\circ}\text{C}$ (Fig 3). The stability of winter temperatures varies with sea ice extent and duration, and the 1997 and 1998 winters had more sea-ice than the 1999 winter. In each year temperatures rose above 0°C for periods between 2 weeks and around 3 months (1999). Temperatures only rose above 1.0°C in the 1997/98 and 1998/99 summers, and then only for periods of around 1-2 weeks.

DISCUSSION

Populations of both *L. elliptica* and *N. concinna* at Rothera exhibit high levels of ability to perform critical biological functions at 0°C , with nearly 100% of individuals reburying (*L. elliptica*) or righting (*N. concinna*). These abilities are rapidly lost with rising temperature, such that half the population have lost these abilities at $+2.0$ to $+2.5^{\circ}\text{C}$, and all individuals lost the ability to bury or right at $+5.0^{\circ}\text{C}$. For the scallops it was not possible to elicit swimming responses from more than 50% of the animals studied at any temperature. This may have been because swimming is a more energetically costly activity than righting in limpets or burrowing in *Laternula*, and other factors such as feeding or reproductive condition interfered with swimming ability. Brokordt *et al* (2000) showed that swimming was markedly reduced in animals near to or post spawning in *Chlamys islandica*. These experiments were conducted during the Antarctic summer, when animals would be feeding on the intense phytoplankton bloom, and also in the post-spawning period (Tyler *et al* 2003). The variability in swimming at temperatures below 0°C may therefore reflect natural variation at this time of the year. It is also possible that stronger stimuli may have elicited more swimming and Bailey *et al.* (2003) obtained higher swimming responses from *A. colbecki* that had been returned to the UK and Germany prior to experimentation and were not recently collected. However, their experiments were conducted in June, when *A. colbecki* is building gonad.

The scallops in this study rapidly lost the ability to swim, and none swam at 2°C and above. *A. colbecki* has a lower upper lethal temperature than the other two species. Bailey (2001) was unable to acclimate specimens to temperatures above $+3^{\circ}\text{C}$ because at 4°C animals rapidly lost condition and 50% mortality occurred in 19 days.

L. elliptica and *N. concinna* both have experimental upper temperatures below 10°C (Peck 1989, Peck et al 2002).

The ability to perform work in animals is part of the aerobic scope of individuals in that population. Aerobic scope is used for many functions, including growth, and processes associated with feeding, as well as activity. Each individual at any time will have a range of factors reducing or enhancing aerobic scope, and individuals will vary in this respect. Thus evaluations of population capacities are a measure of average capacity in those conditions.

Previous studies showing that upper experimental temperatures and transfers to anaerobic metabolism set the various short, medium and long-term temperature limits for marine species living in polar conditions, fit a model where the underlying control is aerobic scope (Fig 4), as suggested by Pörtner (2002). As temperature increases for ectotherms, underlying metabolic costs rise. Usually maximum aerobic rate either rises slightly, or stays the same. Thus with rising temperature aerobic scope, the difference between maintenance cost and maximum rate, decreases. At some point costs equal the maximum sustainable rate, tissues begin to turn to anaerobic metabolism, and the critical long-term physiological limit is reached (Pörtner *et al.* 1998; Peck *et al.* 2002; Pörtner 2002). With even higher temperatures the anaerobic deficit (magnitude of excess of metabolic costs over oxygen supply) increases until the short-term anaerobic limit is reached and the animals die. The final limits are dictated by anaerobic tolerances, and death occurs by processes similar to asphyxiation. Prior to the critical physiological temperature being reached functional limits dictate that progressively more biological functions are not possible, as indicated by the hatched zone in Fig. 4. Our experiments are a test of this hypothesis. If rising temperature progressively reduces aerobic scope, then the ability to perform work should decline progressively as upper limits are approached. These limits to work should also be at lower temperatures than the experimental or physiological upper limits. The monotonic decreases in the capacity to perform various behaviours requiring work in limpets, scallops and burrowing bivalve molluscs, combined with cessation of these activities at significantly lower temperatures than previously identified upper temperatures for survival all support the aerobic scope model. It should be noted here that swimming in scallops is an anaerobic activity. However,

recovery from exercise is aerobic, and the ability of an individual to swim will depend on its aerobic condition when acclimated to any given temperature. It should also be noted that isolated muscle fibres from *A. colbecki* adductor muscle continue to contract normally at least to temperatures above 4°C (Bailey 2001), and possibly much higher.

Sea temperatures at Rothera point, where this study was conducted are typical of the maritime Antarctic, ranging from -1.8°C in winter to maxima around 1°C in summer. Our data would indicate that cold-blooded species inhabiting the maritime Antarctic are close to their upper temperatures for the initiation of significant loss of biological function in summer. A 1°C rise in summer sea temperatures would take most of them to 50% loss of biological functions, and this during the short summer bloom period, that only last for 2-3 months (Clarke *et al.* 1988), when most herbivores need to be active to exploit their major food supply. The most sensitive species, like *A. colbecki*, would lose completely their ability to swim in summer with a 1°C temperature rise. Predictions of future sea temperatures around Antarctica are difficult, because of the complexity added by sea-ice interactions, but most models predict global sea temperature to rise by 2°C or more in the next 100 years (Mitchell *et al.* 1998). Clearly sea temperatures of 2-3°C would pose extreme, and possibly insurmountable problems for many species.

Times to complete burial at 0°C in *L. elliptica* were very similar to those reported by Peck *et al.* (in press) at the same temperature, and were around x10 slower than rates for temperate burrowing bivalve molluscs (Peck *et al.* in press). When Antarctic and temperate marine species were compared at their normal habitat temperatures, activity rates were between x3 and x10 slower for 8 comparisons of activity (Peck *et al.*, in press). The only exception was sustained swimming in fish, which is compensated because of markedly increased mitochondrial densities in red pectoral muscles of cold-water fish (Johnston *et al.* 1998). The lack of compensation of activity elsewhere suggests the increase of mitochondrial density seen in fish red muscle might not be widespread, leading to poor abilities to compensate work rate for temperature.

All of the 12 polar marine species so far evaluated have upper experimental temperatures below, or around 10°C (Peck & Conway 2000; Peck *et al.* 2002), and the most stenothermal species, the bivalve mollusc *Limopsis marionensis*, the brachiopod *Liothyrella uva* and the scallop *Adamussium colbecki* all die in experiments at temperatures around 4°C (Peck 1989; Pörtner *et al.* 1999; Bailey 2001). The species studied here, therefore represent the broad range of responses to elevated temperature identified in polar marine ectotherms. All species so far studied transfer to anaerobic metabolism 2-4°C below their upper experimental temperatures, and here we show functions are lost 2-8°C below upper experimental temperature limits. On this basis the majority of Antarctica's in excess of 4000 marine benthic species so far described (Clarke & Johnston 2003) would be at risk of at least population level losses from only a very minor increase in summer sea temperatures.

Individual to population level responses to environmental change that enhance survival fall into 3 main categories, (1) using inherent physiological capacities or scopes, (2) adapting to new conditions, or (3) migrating to areas consistent with survival. We have shown that the Antarctic marine fauna has a very poor ability to cope physiologically, possibly the poorest so far described. The Antarctic marine fauna is characterised by slow growth, increased longevity and deferred maturity (Peck 2002). Of the species studied, several live in excess of 40 to 50 years (Peck & Bullough 1993; Arntz *et al.* 1994; Brey *et al.* 1995; Peck & Brey 1996; Peck *et al.* 1997; Peck 2002). Generation times are typically 10-20 years. Abilities to adapt to changing conditions are, therefore, poor. Finally, most continents have long coastlines covering large latitudinal ranges that, at least theoretically, allow migration to more hospitable conditions in a warming scenario. The outline of Antarctica covers less degrees of latitude than any other. The animals on the Southern Ocean seabed have less scope to migrate away from poor conditions than faunas elsewhere, irrespective of dispersal capabilities. The combination of very poor functional scopes, with slow rates of adaptation and restricted available dispersal ranges make Antarctic marine species amongst the most fragile to environmental change on earth.

REFERENCES

- Arntz, W.E., Brey, T. & Gallardo, V.A. 1994 Antarctic zoobenthos. *Oceanogr. Mar. Biol. Annu. Rev.* 32, 241-304.
- Bailey D.M. (2001) The thermal dependence of swimming and muscle physiology in temperate and Antarctic scallops. PhD Thesis, p. 138. University of St. Andrews, St. Andrews
- Bailey D.M., Peck L.S., Bock C. & Pörtner H.O. (2003) High-energy phosphate metabolism during exercise and recovery in temperate and Antarctic scallops - an in vivo ³¹P-NMR study. *Physiological and Biochemical Zoology*, 76, 622-633.
- Berkman P.A. 1988 Ecology of the circumpolar Antarctic Scallop, *Adamussium colbecki* (Smith, 1902). PhD Thesis. 215pp. University of Rhode Island
- Brey, T., Peck, L.S., Gutt, J., Hain, S. and Arntz, W. 1995 Population dynamics of *Magellania fragilis*, a brachiopod dominating a mixed-bottom macrobenthic assemblage on the Antarctic shelf. *J. Mar. Biol. Assoc. UK.*, 75, 857-870.
- Brokordt K.B., Himmelman J.H. & Guderley HE 2000 Effect of reproduction on escape responses and muscle metabolic capacities in the scallop *Chlamys islandica* Muller 1776. *J. Exp. Mar. Biol. Ecol.* 251 (2), 205-225
- Clarke, A. & Johnston, N. 2003 Antarctic marine benthic diversity. *Oceanogr. Mar. Biol. Annu. Rev.* 41, 47-114.
- Clarke, A., Holmes, L.J. & White, M.G. 1988 The annual cycle of temperature, chlorophyll and major nutrients at Signy Island, South Orkney Islands, 1969-82. *British Antarctic Survey Bulletin* 80, 65-86.
- Convey, P., Pugh, P.J.A., Jackson, C., Murray, A.W., Ruhland, C.T., Xiong, F.S. & Day, T.A. 2002 Response of Antarctic terrestrial arthropods to long-term climate manipulations. *Ecology* 83, 3130-3140.
- Davis, A.J., Jenkinson, L.S., Lawton, J.H., Shorrocks, B., & Wood, S. 1998 Making mistakes when predicting shifts in species range in response to global warming. *Nature* **391**, 783-786.
- Frederich, M. & Pörtner H.O. 2000 Oxygen limitation of thermal tolerance defined by cardiac and ventilatory performance in spider crab, *Maja squinado*. *Am. J. Physiol. Integr. Comp. Physiol.* 279, R1531-R1538.
- Grassle, J.F & Maciolek, N.J. 1992 Deep sea species richness: regional and local diversity estimates from quantitative bottom samples. *Am. Nat.* 139, 313-341.

- Johnston, I.A., Calvo, J., Guderley, H. Fernandez, D. & Palmer, L. 1998 Latitudinal variation in the abundance and oxidative capacities of muscle mitochondria in perciform fishes. *J. Exp. Biol.* 201, 1-12.
- Mark F.C., Bock C. & Pörtner H.O. 2002 Oxygen-limited thermal tolerance in Antarctic fish investigated by MRI and P-31-MRS. *Am. J. Physiol.- Reg. Int. & Comp Physiol.* 283 (5), r1254-r1262.
- Mitchell, J.F.B., Johns, T.C. & Senior, C.A. 1998. Transient response to increasing greenhouse gases using models with and without flux adjustment. *Hadley Centre Technical Note No 2*, 26pp.
- Peck, L.S. 1989 Temperature and basal metabolism in two Antarctic marine herbivores. *J. Exp. Mar. Biol. Ecol.* 127, 1-12.
- Peck, L.S. 2002. Ecophysiology of Antarctic marine ectotherms: limits to life. *Pol. Biol.* 25, 31-40.
- Peck, L.S. & Bullough, L.W. 1993 Growth and population structure in the infaunal bivalve *Yoldia eightsi* in relation to iceberg activity at Signy Island, Antarctica. *Mar. Biol.* 117, 235-241.
- Peck, L.S. & Brey, T. 1996 Bomb signals in old Antarctic brachiopods. *Nature* 380, 207-208.
- Peck L.S. & Conway L.Z. 2000 The myth of metabolic cold adaptation: oxygen consumption in stenothermal Antarctic bivalves. In: *The Evolutionary Biology of the Bivalvia* (eds Harper E.M., Taylor J.D. & Crame J.A.). *Geological Society, London, Special Publications* 177, 441-45.
- Peck, L.S. Ansell, A.D., Webb, K., Hepburn, L. & Burrows, M. in press. Movements and burrowing activity in the Antarctic bivalve molluscs *Laternula elliptica* and *Yoldia eightsi*. *Pol. Biol.*
- Peck, L.S., Brockington, S & Brey, T. 1997 Growth and metabolism in the Antarctic brachiopod *Liothyrella uva*. *Phil. Trans. R. Soc. Lond. B.* 352, 851-858.
- Peck, L.S., Portner, H.O. & Hardewig, I. 2002 Metabolic demand, oxygen supply, and critical temperatures in the Antarctic bivalve *Laternula elliptica*. *Physiol & Biochem. Zool.* 75, 123-133.
- Pörtner, H.O. 2002 Physiological basis of temperature-dependent biogeography: trade-offs in muscle design and performance in polar ectotherms. *J. Exp. Biol.* 205, 2217-2230.
- Pörtner, H.O., Hardewig, I., Sartorius, F.J. & van Dijk P. 1998 Energetic aspects of

- cold adaptation: critical temperatures in metabolic, ionic and acid base regulation?
In: *Cold Ocean Physiology* (eds, Pörtner, H.O. & Playle, R.), *Society for Experimental Biology Seminar Series* 66, 88-120, Cambridge University Press, Cambridge.
- Pörtner, H.O., Peck, L.S., Zielinski, S. & Conway, L.Z. 1999 Intracellular pH and energy metabolism in the highly stenothermal Antarctic bivalve *Limopsis marionensis* as a function of ambient temperature. *Pol. Biol.* 22,17-30.
- Shelford, V.E. 1931 Some concepts of bioecology. *Ecology* 123, 455-467.
- Snelgrove, P.V.R. & Smith, C.R. 2002 A riot of species in an environmental calm: the paradox of the species-rich deep-sea floor. *Oceanogr. Mar. Biol. Annu. Rev.* 40, 311-342.
- Somero, G. N. & DeVries, A.L. 1967 Temperature tolerance of some Antarctic fishes. *Science* 156, 257-258.
- Travis, J.M.J. 2003 Climate change and habitat destruction: a deadly anthropogenic cocktail. *Proc. R. Soc. Lond.* 270B, 467-473.
- Tyler, P.A., Reeves, S., Peck, L.S., Clarke, A. & Powell, D. 2003 Seasonal variation in the gametogenic ecology of the Antarctic scallop *Adamussium colbecki*. *Pol. Biol.* 26, 727-733.
- Wilson, R.S., Kuchel, L.J., Franklin, C.E. & Davison, W. 2003 Turning up the heat on subzero fish: thermal dependence of sustained swimming in an Antarctic notothenioid. *J. Therm. Biol.* 27, 381-386.

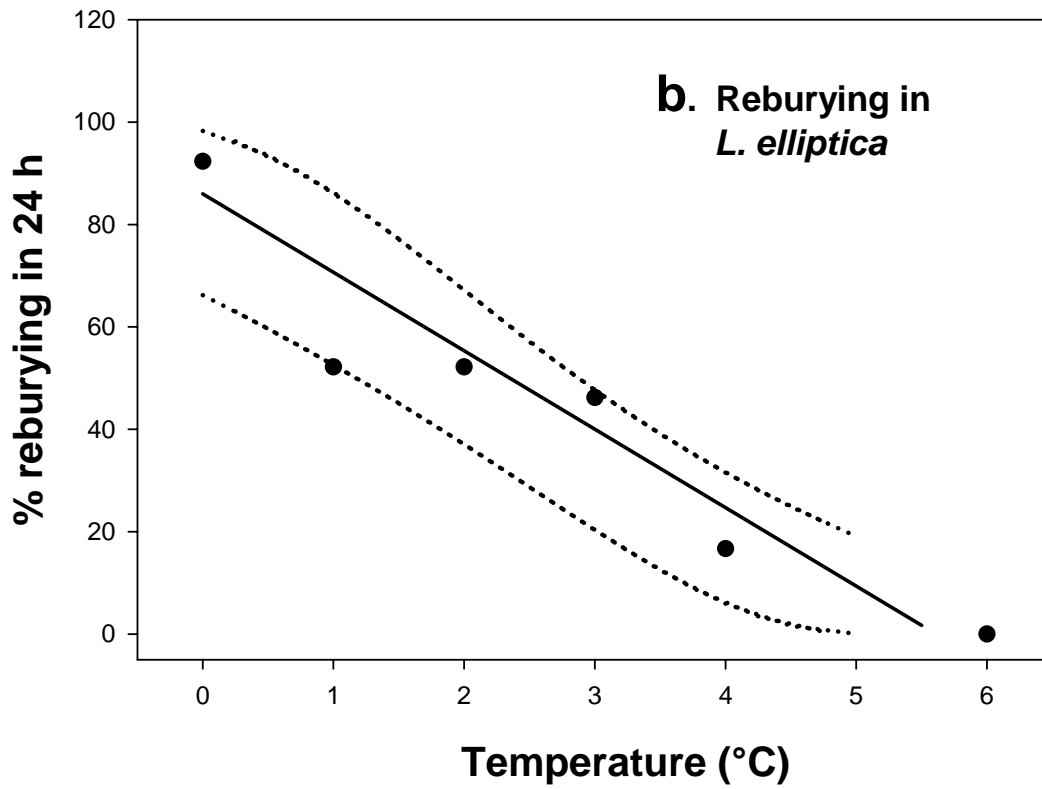
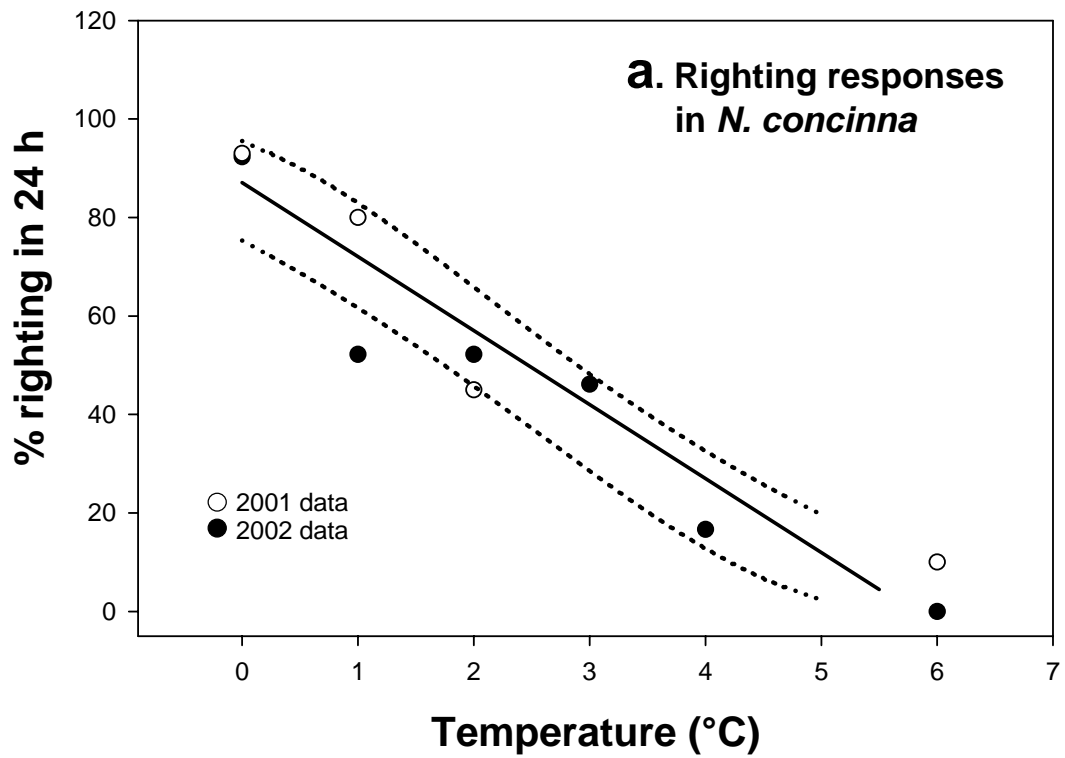
Figure legends.

Figure 1. **a.** righting responses in the Antarctic limpet *N. concinna* with temperature. Data shown are the proportion of limpets righting in 24 h. Data are from experiments in 2001 and 2002. For each point n= 20-31. All regressions were made following square root and arcsin transforms of % data ($\arcsin(\sqrt{\% \text{righting}}) = 1.20 - 0.180T^{\circ}\text{C}$; $r^2 = 0.90$, $F = 77.9$, $P < 0.001$, 9 df). **b.** reburying in the bivalve mollusc *L. elliptica* with temperature. Data show the proportion of animals reburying in 24 h (n = 18-26). Regression line: $\arcsin(\sqrt{\% \text{burying}}) = 0.95 - 0.173T^{\circ}\text{C}$ ($r^2 = 0.85$, $F = 22.4$, $P=0.009$, 5df). A total of 190 limpets and 145 *L. elliptica* were used. In both figures dotted lines indicate 95% confidence intervals for regressions. For both plots lines and confidence intervals shown were plotted following sine back transforms.

Figure 2. The proportion of Antarctic scallops, *A. colbecki*, swimming in response to freshwater stimulation. Each point is the proportion swimming at that temperature. The number tested is given above each point and varied between 57 and 175. The total number of animals used in the experiments was 858. A regression was fitted to data for temperatures above -0.3°C , where a clear temperature effect was apparent. This regression was fitted to square root and arcsin transformed percentage values. Regression Line: $\arcsin(\sqrt{\% \text{swimming}}) = 0.682 - 0.230T^{\circ}\text{C}$ ($r^2 = 0.93$, $F = 51.5$, $P=0.006$, 4df).

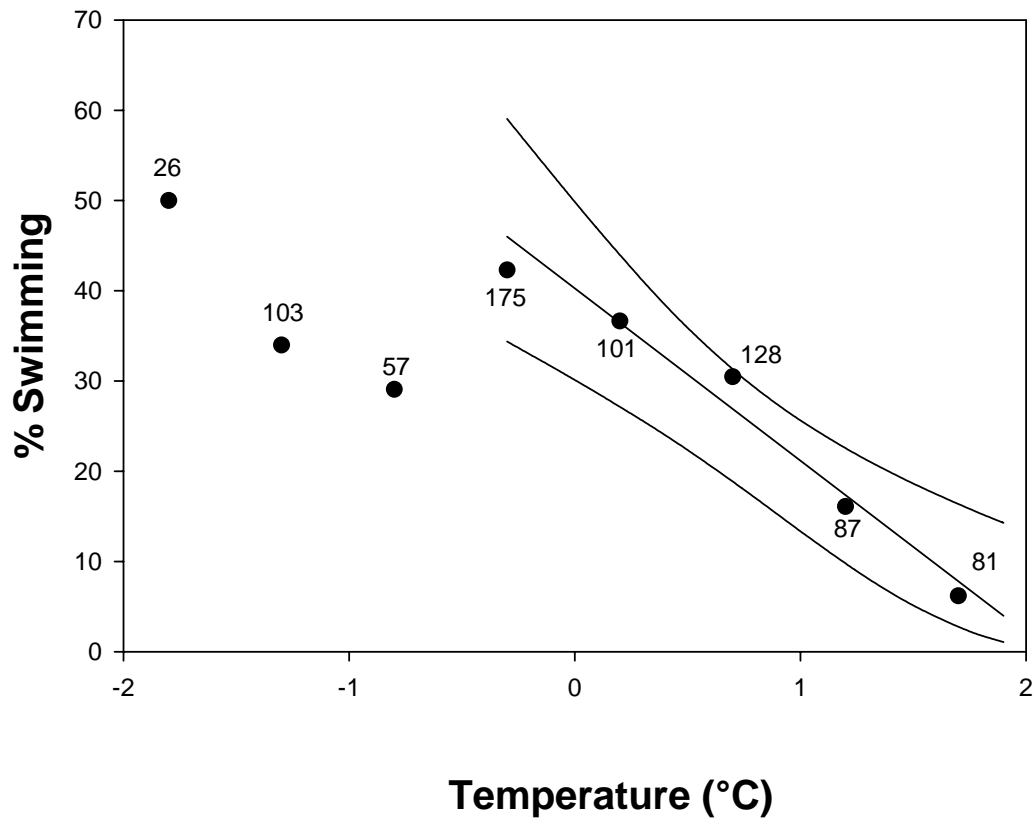
Figure 3. Temperature recordings from 15 m depth in Ryder Bay, Adelaide Island. Recordings were made 800 m from the site of collection of the experimental animals used, and were continuously logged throughout. Minimum temperatures in winter were around -1.8°C , but in summer rose to values between 0.2°C and 1.4°C .

Figure 4. Schematic of the effects of rising temperature on aerobic capacity in Antarctic marine stenotherms. Aerobic scope declines with temperature and biological functions lost up to a point where aerobic balance becomes negative and tissues enter an anaerobic state (the critical temperature). Eventually hypoxic levels become too great and the short-term temperature limit is reached.



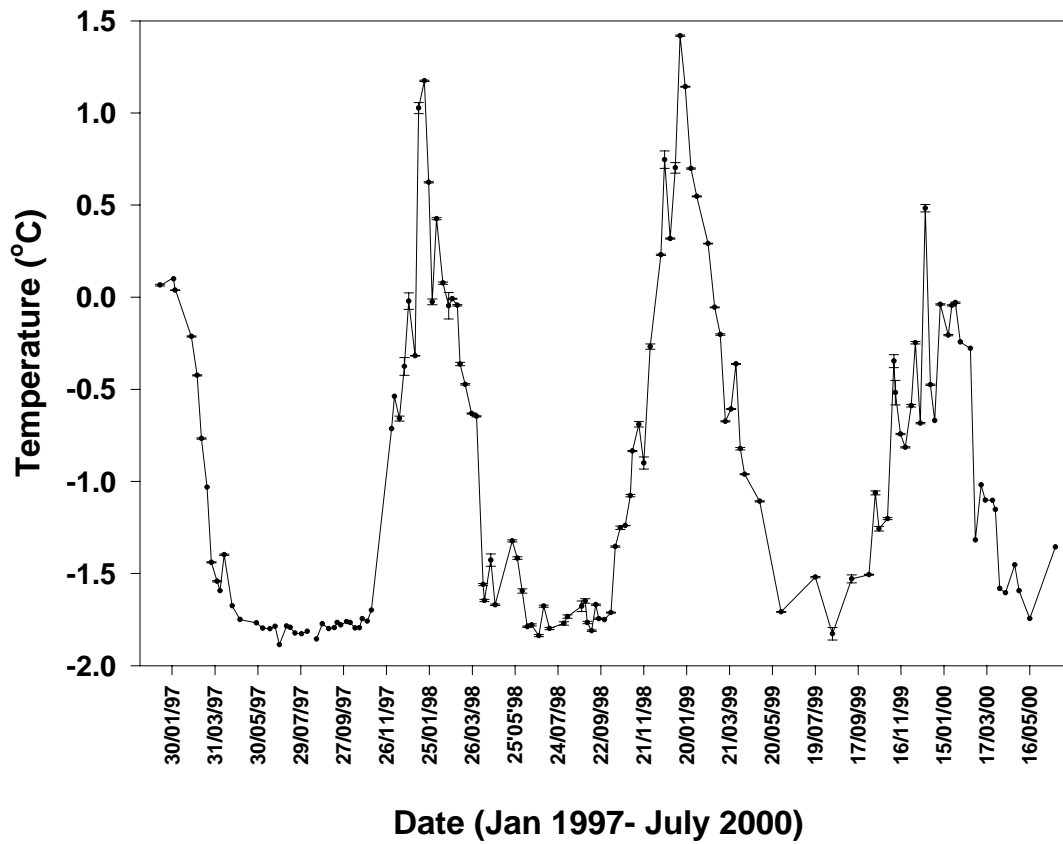
Peck et al. Fig 1

Proportion of *Adamussium colbecki* swimming with temperature

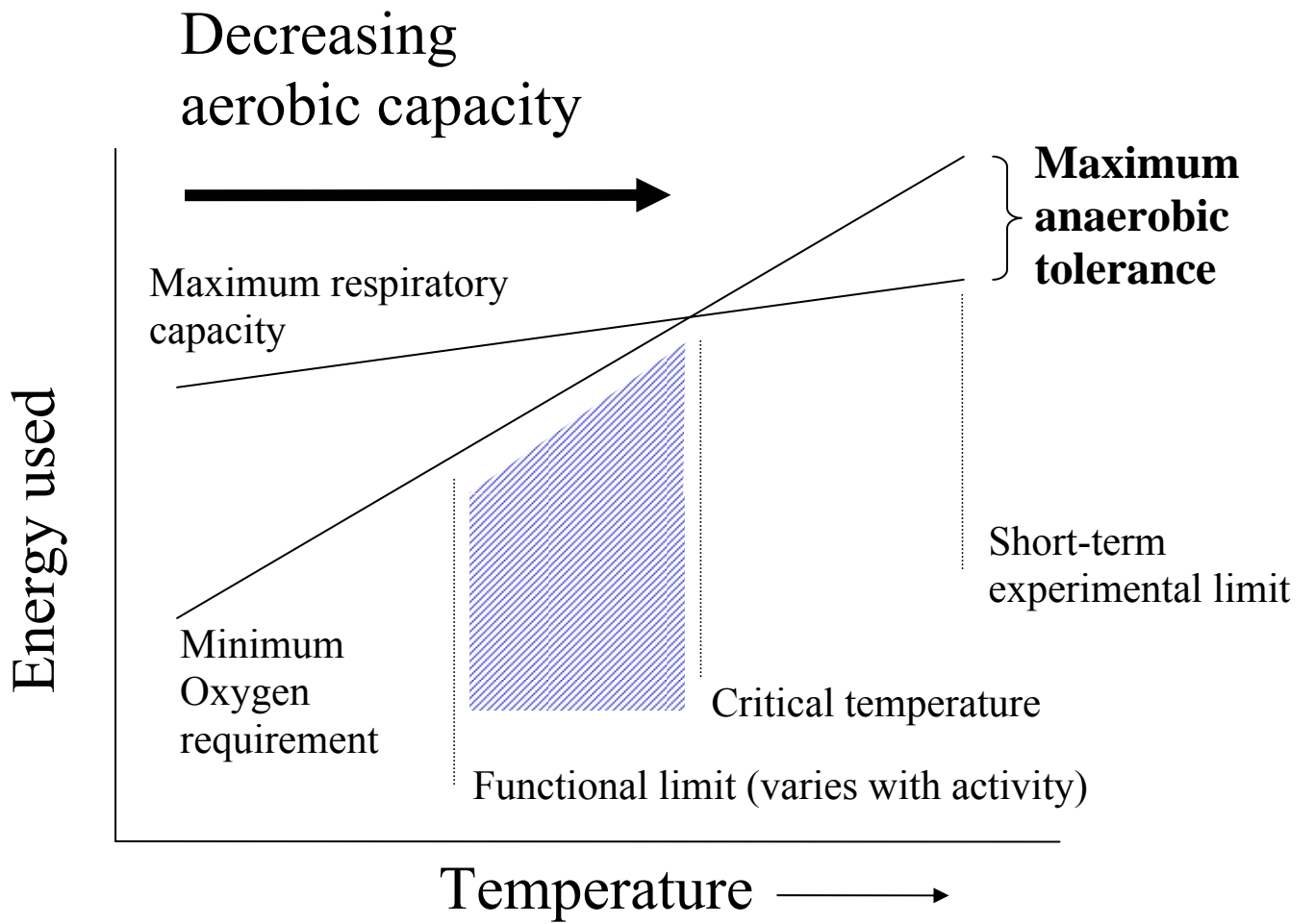


Peck et al Fig 2

seasonal temperature variation at 15m in Ryder Bay.



Peck et al Fig 3



Peck et al Fig 4