The effects of temperature on the behaviour of the Antarctic sea star *Odontaster validus*

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Abstract: Many Antarctic marine benthic invertebrates are adapted to specific environmental conditions (*e.g.* low stable temperatures, high salinity and oxygen content). Changes caused by global climatic shifts can be expected to have significant impact on their physiology and distribution. *Odontaster validus*, an ubiquitous, omnivorous sea star is one of the "keystone species" in the Antarctic benthic communities. Laboratory experiments were carried out to study the effect of temperature rise (from 0 to 5°C) on some vital biological functions that sea stars must perform in order to survive in their environment. Parameters such as behavioural reaction of sea stars to food and food odour, locomotory performance and ability to right were measured. Temperature increase significantly impaired the ability of *O. validus* to perform these functions (*e.g.* lowering the number of sea stars able to right, increasing time-to-right, reducing locomotory activity, weakening chemosensory reaction to food and food odour). At temperatures of 4 and 5°C a loss of motor coordination was observed, although at all tested temperatures up to 5°C there were single individuals performing successfully.

Key words: Antarctica, asteroid, temperature, stress, behaviour.

Introduction

Antarctic marine benthic invertebrates outside the intertidal zone live at permanently low and stable temperatures, with the total annual variation rarely exceeding 3°C in the region of Antarctic Peninsula, and 1.5°C at high Antarctic (Peck 2005). Such stenothermal environmental conditions prevailed in this part of the world for at least 10 million years (Peck 2005; Pörtner *et al.* 2007). Adaptation to such conditions has resulted in physiological rates (*e.g.* metabolic, growth, development or activity rates) being considerable lower than in temperate species (*e.g.* Pearse *et al.* 1991; Brey and Clarke 1993; Arntz *et al.* 1994; Peck and Robinson 1994; Chapelle and Peck 1995; Peck *et al.* 2000, 2004a; Peck 2002; McClintock *et al.* 2008a).

In the last 50 years a significant climatic shift has been observed along the Antarctic Peninsula, with air temperatures having risen by *ca*. 3°C at some localities (King *et al.* 2003). Antarctic seawater temperatures are also on the rise, both in sub-surface water masses (Gille 2002; Robertson *et al.* 2002), and in shallow waters along the Western Antarctic Peninsula (Meredith and King 2005). Such changes, if continuing, may have significant impact on species survival and distribution.

Previous investigations showed that some Antarctic benthic invertebrates are strictly stenothermal (Peck *et al.* 2004b; Peck 2005). Many of them die in temperatures below 10°C or lose the ability to perform vital biological functions (Peck *et al.* 2004b; Young *et al.* 2006). Nevertheless, studies concerning this problem are scarce, and there is no information on the temperature impact on the behavioural reactions of the Antarctic marine invertebrates to food signals.

The aim of this study was to evaluate the effects of temperature on the behaviour of the Antarctic sea star *Odontaster validus* Koehler, 1906, and its ability to perform vital biological functions, such as righting when turned over, locomotion, behavioural reactions to food and food odour. We hypothesize that at increased water temperature sea stars will fail to perform these functions successfully. If sea stars are incapable of righting after disturbance or unable to find food, their survival is seriously compromised. Therefore, future climatic changes can result in the reduction of their numbers or even disapearence from benthic communities.

Odontaster validus is a circumpolar, long-lived, moderately sized Antarctic sea star occurring in benthic environments from shallow subtidal to 940 m (Dearborn 1977; McClintock 1994). It is an omnivorous species, which may act as active predator, a scavenger, a herbivore and a suspension feeder (Pearse 1965; 1969; Dayton *et al.* 1974; McClintock 1994). Complex intra- and interspecific behaviour in *O. validus* was observed (McClintock *et al.* 2008a, b). It is also regarded as one of the "keystone species" regulating the distribution and abundance of other Antarctic benthic invertebrates (Dayton *et al.* 1974; McClintock *et al.* 1988). *O. validus* was previously shown to use chemical information to locate food items (Kidawa 2005) and to respond to chemical signals produced by its conspecifics, distinguishing between fed and starved ones (Kidawa 2001).

Methods

Odontaster validus individuals with a radius (measured from the centre of the disc to the tip of the longest arm) of 3.5–4.5 cm were collected by SCUBA divers in January–February 2008 in Admiralty Bay (King George Island, South Shetlands, Antarctica). Animals were maintained in well-aerated tanks (*ca.* 30 l each) at a temperature of 0°C and water salinity of 34.0–34.2 psu. For 10 days animals were fed *ad libitum* with *Notothenia* sp. muscle meat to minimize differences in

their feeding status and then starved for 30 days. Non-feeding sea stars were excluded from the experiments. During the whole experimental period no instances of natural death or cannibalism were observed and no animal was used for the same type of test more than once. No individual was tested more than once in three days.

Laboratory experiments were conducted in temperatures of 0, 1, 2, 3, 4 and 5°C and salinity of 34 psu. Tests done in temperature 0°C were treated as a control. Sea stars were taken from the holding tanks and placed individually in 5-liter aquariums in a room with temperature control (0°C). Afterwards, temperature in the room was set to the planned value (0, 1, 2, 3, 4 or 5°C). Experiments were conducted 24 hrs later, during which the temperature of seawater in the aquaria matched the desired value. Two such rooms were used – one for housing sea stars at 0°C, and the other for the experiments. All experiments were conducted in 5-liter aquaria with static water. Water in the aquaria was changed after each trial. All tests were filmed with a digital video camera. Timed recordings were then analyzed to determine time each sea star took to right itself, way of righting, locomotory activity, behavioural reaction to food odour and numbers of sea stars feeding on bait.

Righting tests were conducted by turning sea stars upside-down and placing them individually on the bottom of the aquarium; one seastar per tank. Numbers of sea stars capable of righting, time-to-right, the way of righting and walking speed were noted in 5 successive righting attempts. The time to right was measured as the time between the initiation of the righting behaviour and the moment when the sea star righted completely, returning to the initial posture.

Each variant of the experiment was replicated 15 times with a different sea star used in each trial.

Food stimuli tests were conducted by placing sea stars individually on the bottom of the aquarium. After 60 minutes 5 ml of meat extract (consisting of 100 ml seawater and 50 g of *Notothenia* sp. muscle meat left for 24 hrs) was slowly released from a syringe kept above 3 cm from the tip of the sea star arm. Animals were than observed for 20 minutes. Number of reacting sea stars and types of reaction were noted. Each variant of the experiment was replicated 15 times with a different sea star used in each trial. Additional experiments with pure sea water instead of meat extract were also conducted.

Food finding tests were conducted by placing food bait (50 g of *Notothenia* sp. muscle meat) on the bottom of the aquarium where 5 sea stars were put 60 minutes earlier. The distance between each sea star and meat bait was *ca*. 20 cm. Numbers of sea stars feeding on bait after 60 minutes of experiment were noted. Each variant of the experiment was replicated 5 times with a different set of sea stars used in each trial.

After the experiments, all sea stars were returned to their natural environment.

Data analysis were performed using the statistical package Statistica 5.5. (StatSoft). To establish the statistical significance of differences between data

from subsequent variants of the experiments χ² test, ANOVA and Tukey HSD test were used. Test values at p-value of 0.05 were considered significant. When necessary logarithmic transformation of data was performed.

Results

Three ways of righting in sea stars *O. validus* were observed. In the first (called "typical") *O. validus*, after being placed upside-down, flexed its arms outside and attached tube foot at the arms' ends to the bottom. Two arms were anchoring the sea star, three were pushing up, arching the sea star's body above the sediment. Then two arms were withdrawn from the sediment, pulling upwards and towards the anchoring arms, and rolling the sea star over. In the second way (called "untypical I") *O. validus* raised all five arms upwards, with their tips almost touching. Then it rolled to one side, attached two arms's ends to the bottom, strightened the body and proceeded as in the "typical" way. This way of righting was often observed in fed *O. validus*, which were pumped up with dissolved food particles and could not flex its arms outside (Kidawa, personal observations). The third way (called "untypical II") is a lump category, enclosing all instances during which sea stars changed (one or two times) the way of righting during its execution. This phenomenon was previously not observed by the authors.

Two types of motor activity were observed in sea stars after a successful righting: locomotion and turning around while staying in the place of righting.

In control experiments (T = 0°C) all sea stars were capable of righting for 5 successive attempts (Tables 1, 2). Almost all of them (97%) did it in the "typical" way (Table 2). After righting, all of them moved with the mean speed of 0.85±0.045 cm/min (Table 3). *O. validus* showed no behavioural response to pure sea water, but all of them reacted to the food odour (Table 4). Their reaction consisted of tube foot waving, arm(s) movement and locomotion. About 80% of animals displayed all three types of reactions simultaneously. Mean number of reaction types displayed simultaneously by *O. validus* was 2.8±0.11 (Table 4). All tested sea stars found bait and began to feed within 60 minutes of experiment (Table 5).

Temperature increase caused significant changes in the ability of *O. validus* to perform all tested biological functions. Numbers of sea stars capable of righting declined, and at 5°C only one individual was capable of righting 5 times in succession (Tables 1, 2). The differences between observed and theoretical (control variant – T = 0°C) numbers of *O. validus* able and unable to right were statistically significant for the sea stars at 5°C (1 attempt), and at 4 and 5°C (all other righting attempts) (test χ², p < 0.05). Statistically significant differences were found among the impacts of various temperatures on number of successful righting attempts per sea star (ANOVA $F_{84,5} = 37.25$, p < 0.001), with *O. validus* at temperature 0, 1, 2

Table 1

The effect of temperature on the proportion of *Odontaster validus* capable of successive righting attempts. Statistically significant differences between observed and theoretical (control variant – T = 0°C) numbers of sea stars able and unable to right when turned over were marked with an (*). Test χ^2, p < 0.05 was considered significant. n – number of sea stars tested. Each variant of the experiment was replicated 15 times with a different sea star used in each trial.

Temperature	n	Sea stars capable of righting (%)				
		1 attempt	2 attempt	3 attempt	4 attempt	5 attempt
0°C	15	100	100	100	100	100
1°C	15	100	100	100	100	100
2°C	15	100	100	100	100	100
3°C	15	100	100	100	93	87
4°C	15	93	80*	67*	53*	40*
5°C	15	73*	40*	20*	7*	7*

Table 2

The effect of temperature on the mean number of successful righting attempts, time-to-right and proportion of *Odontaster validus* righting in different ways. Time-to-right – time between the initiation of the righting behaviour and its completion. n – number of sea stars tested. Each variant of the experiment was replicated 15 times with a different sea star used in each trial. As there were no statistically significant differences between time-to-right for succesive attempts, data for each temperature were pooled together. Means sharing the same letter (a, b *etc.*) are not significantly different (Tukey HSD test, p < 0.05).

Temperature	n	Number of successful righting attempts		Time-to-right		Proportion of sea stars righting in different ways (%)		
		mean	SE	mean	SE	typical	untypical I	untypical II
0°C	75	5.0[a]	0.0	4.91[a]	0.25	97	3	0
1°C	75	5.0[a]	0.0	4.88[a]	0.34	97	3	0
2°C	75	5.0[a]	0.0	4.78[a]	0.24	83	17	0
3°C	72	4.93[a]	0.07	6.29[a,b]	0.56	57	43	0
4°C	50	3.33	0.45	6.68[b,c]	0.41	30	36	34
5°C	22	1.47	0.36	9.28[b,c]	1.40	23	45	32

and 3°C capable of more successful righting attempts than sea stars at 4 and 5°C (Tukey HSD test, p < 0.05).

As there were no statistically significant differences among times-to-right for succesive attempts, data for each temperature were pooled together. Time-to-right rose from 4.91±0.25 min at 0°C to 9.28±1.40 min at 5°C (Table 2). Statistically significant differences were found among the impact of temperature on time-to-right (ANOVA $F_{360,5} = 9.96$, p < 0.001), with time-to-right at 5°C significantly longer than at any other temperature except 4°C (Tukey HSD test, p < 0.05). The proportion of sea stars righting in "typical" way declined with the rise of temperature

The effect of temperature on the proportion of *Odontaster validus* capable of locomotion and their speed of movement. Each variant of the experiment was replicated 15 times with a different sea star used in each trial. As there were no statistically significant differences between movement speed for succesive trials, data for each temperature were pooled together. Statistically significant differences between observed and theoretical (control variant – T = 0°C) numbers of sea stars able and unable of locomotion were marked with an (*). Test χ^2, p < 0.05 was considered significant. Means sharing the same letter (a, b *etc.*) are not significantly different (Tukey HSD test, p < 0.05). n1 – number of sea stars capable of righting, n2 – number of sea stars capable of locomotion.

Temperature	n1	Sea stars capable of locomotion (%)	n2	Locomotion speed (cm/min)	
				mean	SE
0°C	75	100.0	75	0.85[b,c,d]	0.045
1°C	75	100.0	75	1.21[a,c]	0.051
2°C	75	100.0	75	0.99[a,b,c]	0.045
3°C	72	87.5*	63	0.89[b,c,d]	0.061
4°C	50	70.0*	35	0.78[b,c,d]	0.051
5°C	22	40.9*	9	0.55[b,d]	0.037

from 97 to 23% (Table 2). At temperatures 4 and 5°C as much as one third of sea stars righted in an "untypical II" way. At temperatures 2 and 3°C time-to-right done in "typical" way was significantly lower (4.21 ± 0.201 and 4.71 ± 0.387 min) than in "untypical I" way (7.41 ± 0.629 and 8.38 ± 1.090 min) (Student's t test, p < 0.001). No statistically significant differences were observed at 4 and 5°C due to high data variability.

Percentage of sea stars capable of motion declined from 100% at 0, 1 and 2°C to 40.9% at 5°C (Table 3). The differences between observed and theoretical (control variant – T = 0°C) numbers of *O. validus* able and unable to move were statistically significant for the sea stars at 3, 4 and 5°C (test χ^2, p < 0.05).

As there were no statistically significant differences between motion speed for succesive trials, data for each temperature were pooled together. The highest motion speed – 1.21±0.051 cm/min – was observed in sea stars at 1°C (Table 3). At temperatures between 2 and 5°C motion speed decreased from 0.990.045± to 0.55±0.037 cm/min. Statistically significant differences were found among the impact of temperature on motion speed (ANOVA $F_{326,5}$ = 8.42, p < 0.001), with motion speed at 1°C significantly higher than at any other temperature except 2°C (Tukey HSD test, p < 0.05).

All individuals, irrespective of temperature, reacted to food odour (Table 4). Their reaction consisted of tube foot waving, arm(s) movement and motion. Temperature increase reduced number of sea stars reacting with arm(s) movement and motion (to 53 and 33% respectively). At 4 and 5°C, only one sea star displaying all three types of reactions simultaneously was observed. At temperatures between 0 and 5°C mean number of behavioural reaction types displayed by sea stars fell

Table 4

The effect of temperature on the behavioural responses of *Odontaster validus* to food odour. Positive responses are divided into types: I – tube foot waving, II – arm(s) movement, III – locomotion. n – number of sea stars tested. Each variant of the experiment was replicated 15 times with a different sea star used in each trial. Means sharing the same letter (a, b *etc*.) are not significantly different (Tukey HSD test, p < 0.05).

Temperature	n	Positive responses (%)			Number of reaction types/sea star	
		I	II	III	mean	SE
0°C	15	100	87	87	2.8[a,b]	0.11
1°C	15	100	80	73	2.5[a,b,c]	0.13
2°C	15	100	87	80	2.6[a,b,c]	0.13
3°C	15	100	67	47	2.1[b,c,d]	0.13
4°C	15	100	67	33	2.0[c,d]	0.10
5°C	15	100	53	33	1.8[c,d]	0.17

Table 5

The effect of temperature on the number of *Odontaster validus* feeding on fish meat bait after 60 minutes from experiment. n – number of sea stars tested. Each variant of the experiment was replicated 5 times with a different set of sea stars used in each trial. Means sharing the same letter (a, b *etc*.) are not significantly different (Tukey HSD test, p < 0.05).

Temperature	n	Number of sea stars feeding on bait	
		mean	SE
0°C	5	5.0[a]	0.0
1°C	5	4.8[a]	0.20
2°C	5	4.8[a]	0.20
3°C	5	3.6	0.24
4°C	5	2.4[b]	0.24
5°C	5	1.6[b]	0.40

from 2.8±0.11 to 1.8±0.17 (Table 4). Statistically significant differences were found among the impact of temperature on mean number of behavioural reaction types (ANOVA $F_{84,5} = 7.91$, p < 0.001), with number of reaction types at 5°C significantly lower than at any other temperature except 3 and 4°C (Tukey HSD test, p < 0.05).

At temperatures between 0 and 5°C mean number of *O. validus* feeding together on bait fell from 5.0±0.0 (100%) to 1.6±0.40 (32%) (Table 5). Statistically significant differences were found among the impact of temperature on mean number of sea stars feeding (ANOVA $F_{24,5} = 34.07$, p < 0.001), with number of *O. validus* at 0°C significantly higher than at any other temperature except 1 and 2°C (Tukey HSD test, p < 0.05). Number of *O. validus* feeding at 5°C was significantly lower than at any other temperature except 4°C (Tukey HSD test, p < 0.05).

Discussion

Our experiments showed that acute temperature increase had a significant effect on all tested biological functions of the Antarctic sea star *Odontaster validus*. Time-to-right rose from 4.91 min to 9.28 min, and at 5°C only one individual was capable of righting 5 times successively. The proportion of sea stars righting in a "typical" way declined to 23%. The mean number of behavioural reaction types displayed by sea stars in response to food odour fell from 2.8 to 1.8, the speed of motion decreased significantly and the proportion of sea stars losing the ability of motion rose to 59.1%. In the result the proportion of *Odontaster validus* capable of finding food bait at 5°C fell to 32%. At temperatures above 3°C a loss of motor coordination was observed.

Most previously tested Antarctic marine invertebrates were found to be temperature limited. Species such as the bivalve *Limopsis marionensis* (Pörtner *et al.* 1999) and the brachiopod *Liothyrella uva* (Peck 1989) died at temperature of 4°C. Other, such as the bivalve *Laternula elliptica* (Peck *et al.* 2002) and the limpet *Nacella concinna* (Peck 1989) survived in experiments with temperatures of about 10°C. Common Antarctic echinoderm, the brittle star *Ophionotus victoriae*, was shown to be unable to acclimate at 3°C (Peck *et al.* 2009a).

In contrast, recent study on the sea star *O. validus* showed that it can maintain activity at higher temperatures than in our experiments, righting itself when turned over at temperatures up to 8°C and feeding up to 7°C (Peck *et al.* 2008). In these experiments temperatures were changed at a rate of 0.1–0.2°C per hour with 24 hours acclimation period, whereas in our experiments an acute rate of warming was applied, with temperature being raised by 5°C per day maximum and no acclimation period. The mean time-to-right at 0°C was similar in both studies (4.7 min – Peck *et al.* 2008, 4.9 min – our data). The rate of warming is one of the factors that can have a significant impact on the species' thermotolerance (Peck *et al.* 2009b). When temperatures were raised by 1°C per day invertebrates belonging to several taxa (among them *O. validus*) survived in much higher temperatures (8.3–17.6°C) than when the warming process was prolonged (survival in 4.0–12.3°C for weekly temperature elevations, and only in 1–6°C for long-term acclimation) (Peck et al. 2009b). Animal reaction to temperature increase can also be influenced by the length of acclimation period. After 24 hrs of acclimation at 8°C all sea stars *O. validus* fed on proffered food, whereas sea stars acclimated for 3 days ignored food (Peck *et al.* 2008). All these differences suggest that further experiments with strict and comparable protocols are needed to solve this problem completely. The potential success (or its lack) of one of the benthic predator species can have a significant impact at community and ecosystem levels (Peck *et al.* 2008).

Other factors that can influence thermotolerance of Antarctic benthic invertebrates are: individual size (Peck *et al.* 2009b) and geographical location (Morley *et al.* 2009). When temperatures were raised acutely smaller individuals

belonging to several taxa survived to higher temperatures than large animals, which can strongly affect the species' reproductive potential (Peck *et al.* 2009b). It was also established that limpets *N. concinna* from South Georgia have a lower critical limit (5.1–10.0°C) than *N. concinna* from the colder environments of Signy Island and Adelaide Island (10.0–12.5°C) (Morley *et al.* 2009).

The thermal range within which normal physiological functioning can occur is usually narrower than the tolerance limits of any species (Newell and Branch 1980; Peck *et al.* 2004b; Rupp and Parsons 2004). Antarctic marine invertebrates, such as the limpet *N. concinna* and the large bivalve *L. elliptica*, suffered 50% failure in vital biological functions (righting and reburying) at 2–3°C and complete loss at 5°C (Peck *et al.* 2004b). The Antarctic scallop *Adamussium colbecki* was even more temperature limited, and lost the ability to swim at 2°C (Peck *et al.* 2004b). In our experiments on *O. validus* 50% loss in motion and bait finding was noted at the temperatures between 4 and 5°C, but even at 5°C more than 70% of sea stars were capable of one successful righting attempt. Complete loss of any tested biological functions was not observed, and even at 5°C there was a small proportion of sea stars able to perform successfully. Similar observations were done by Cowart *et al.* (2009) during the experiments on the sensitivity to changing salinity in early embryos of the Antarctic sea urchin *Sterechinus neumayeri*, and by Janecki (unpublished data) on the effect of temperature and salinity on the behaviour of the Antarctic isopod *Serolis polita*. Further experiments are needed to validate this observation and ascertain its possible significance for benthic populations.

Motion speed of sea stars *O. validus* in our experiments were similar to those previously reported (Kidawa 2005; McClintock *et al.* 2008b). Temperature rise caused at first (at 1°C) an increase in locomotion speed, and then its reduction. Time-to-rise increased at temperatures above 3°C. There are only scant data on this subject, but Young *et al.* (2006) showed that motion speed of the Antarctic amphipod *Paraceradocus gibber* increased between test temperatures ranging from -2.5 to 4.5°C. Similar, but statistically insignificant trend was observed for the Antarctic isopod *Glyptonotus antarcticus* (Young *et al.* 2006). These authors also noted that at temperatures below 1.5°C the time-to-right of *G. antarcticus* decreased with successive attempts. Large variation in the mean time-to-right of *G. antarcticus* in higher temperatures was caused by long times and repeated attempts to right observed in some individuals (Young *et al.* 2006). The authors ascertain that elevating temperatures up to 4.5°C did not led to acute breakdown of movement coordination in both tested species. They also propose that the ability of *G. antarcticus* and *P. gibber* to perform righting and walking must fall rapidly between 5 and 11°C, which is the upper temperature at which *G. antarcticus* showed 33% mortality after 5 h exposure (Wells 1979 after Young *et al.* 2006). In our experiments a loss of movement coordination was observed at temperatures of 4 and 5°C ("untypical" way of righting, lack of motion). The time-to-right increase ob-

served in these conditions was mainly caused by sea stars switching from "typical" to "untypical" ways of righting. It suggests that at higher temperatures sea stars were unable to generate sufficient force to successfully complete the behaviour in their "typical" way. Although the two-fold increase in the time-to-right will not probably impair the sea star survival, it is a significant indicator of the change in the physiological capacity of an animal. Temperature sensitivity of Antarctic benthic invertebrates can be explained by the oxygen limitation hypothesis (Pörtner 2002; Pörtner *et al.* 2007). Oxygen limitation results in a temperature range where all functions of an organism can be completed using solely aerobic metabolism. Outside this range organism progressively loses aerobic scope and needs to use anaerobic pathways to provide the required energy (Pörtner 2002). Data collected for some Antarctic benthic invertebrates (bivalve *L. elliptica*, isopod *G. antarcticus*, limpet *N. concinna*, brachiopod *L. uva*) suggest that at higher temperatures oxygen demands can rapidly outstrip oxygen supply mechanism (Robertson *et al.* 2001; Peck 2002, 2005; Peck *et al.* 2002).

In conclusion, our data suggest that temperature increase impaired the ability of *O. validus* to perform vital biological function critical for their long term survival. Therefore, it can be assumed that barring acclimation or a sufficient period of time for adaptation, the ability of sea stars to cope with future environmental change is limited, and this species can successfully perform only in a narrow range of temperatures. *O. validus* is an important component of the Southern Ocean benthic ecosystem, and one of the "keystone species" regulating the distribution and abundance of other Antarctic benthic invertebrates (Dayton *et al.* 1974; McClintock *et al.* 1988). Future regional climate change in the area of the Antarctic Peninsula can result in the reduction of its numbers, with sublethal effects influencing ecological interactions and food-web operation, especially if different species or different functional groups (*e.g.* prey *versus* predator) will be affected to a different degree (Clarke *et al.* 2007). However, the phenomenon of single sea stars performing successfully even at 5°C implies the existence of considerable physiological variability within this species, which can make it less vulnerable to future warming trends.

References

ARNTZ W.E., BREY T. and GALLARDO V.A. 1994. Antarctic zoobenthos. *Oceanography and Marine Biology, an Annual Review* 32: 241–304.

BREY T. and CLARKE A. 1993. Population dynamics of marine benthic invertebrates in antarctic and subantarctic environments. *Antarctic Science* 5: 253–266.

CHAPELLE G. and PECK L.S. 1995. The influence of acclimation and substratum on the metabolism of the Antarctic amphipods *Waldeckia obesa* (Chevreux, 1905) and *Bovallia gigantea* (Pfeffer, 1888). *Polar Biology* 15: 225–232.

CLARKE A., MURPHY E.J., MEREDITH M.P., KING J.C., PECK L.S., BARNES D.K. and SMITH R.C. 2007. Climate change and the marine ecosystem of the western Antarctic Peninsula. *Philosophical Transactions of the Royal Society B* 362: 149–166.

COWART D.A., ULRICH P.N., MILLER D.C. and MARSH A.G. 2009. Salinity sensitivity of early embryos of the Antarctic sea urchin, *Sterechinus neumayeri*. *Polar Biology* 32: 435–441.

DAYTON P.K., ROBILLIARD G.A., PAINE R.T. and DAYTON L.B. 1974. Biological accomodation in the benthic community at McMurdo Sound, Antarctica. *Ecological Monographs* 44: 105–128.

DEARBORN J.H. 1977. Foods and feeding characteristics of Antarctic asteroids and ophiuroids. *In*: G.A. Llano (ed.) *Adaptations within Antarctic Ecosystems*. Gulf Publishing, Houston: 293–326.

GILLE S.T. 2002. Warming of the Southern Ocean since the 1950s. *Science* 295: 1275–1277.

KIDAWA A. 2001. Antarctic starfish *Odontaster validus*, distinguish between fed and starved conspecifics. *Polar Biology* 24: 408–410.

KIDAWA A. 2005. The role of amino acids in phagostimulation in the shallow-water omnivorous Antarctic sea star *Odontaster validus*. *Polar Biology* 28: 147–155.

KING J.C., TURNER J., MARSHALL G.J., CONNOLLEY W.M. and LACHLAN-COPE T.A. 2003. Antarctic Peninsula climate variability and its causes as revealed by instrumental records. *Antarctic Research Series* 79: 17–30.

MCCLINTOCK J.B. 1994. The trophic biology of Antarctic echinoderms. *Marine Ecology Progress Series* 111: 191–202.

MCCLINTOCK J.B., DUCKLOW H. and FRASER B. 2008a. Ecological impacts of climate change on the Antarctic Peninsula. *American Scientist* 96: 302–310.

MCCLINTOCK J.B., ANGUS R.A., HO C., AMSLER C.D. and BAKER B.J. 2008b. A laboratory study of behavioural interactions of the Antarctic keystone sea star *Odontaster validus* with three sympatric predatory sea stars. *Marine Biology* 154: 1077–1084.

MCCLINTOCK J.B., PEARSE J.S. and BOSCH I. 1988. Population structure and energetics of the shallow-water Antarctic sea star *Odontaster validus* in contrasting habitats. *Marine Biology* 99: 235–246.

MEREDITH M.P. and KING J.C. 2005. Rapid climate change in the ocean west of the Antarctic Peninsula during the second half of the 20th century. *Geophysical Research Letters* 32: L19604–L19609.

MORLEY S.A, HIRSE T., PÖRTNER H.O. and PECK L.S. 2009. Geographical variation in thermal tolerance within Southern Ocean marine ectotherms. *Comparative Biochemistry and Physiology, Part A* 153: 154–161.

NEWELL R.C. and BRANCH G.M. 1980. The effects of temperature on the maintenance of metabolic energy balance in marine invertebrates. *Advances in Marine Biology* 17: 329–396.

PEARSE J.S. 1965. Reproductive periodicities in several contrasting populations of *Odontaster validus* Koehler, a common Antarctic asteroid. *Antarctic Research Series* 5: 39–85.

PEARSE J.S. 1969. Antarctic sea star. *Australian Natural History* 16: 234–238.

PEARSE J.S., MCCLINTOCK J.B. and BOSCH I. 1991. Reproduction of Antarctic benthic marine invertebrates – tempos, modes, and timing. *American Zoologist* 31: 65–80.

PECK L.S. 1989. Temperature and basal metabolism in two Antarctic marine herbivores. *Journal of Experimental Marine Biology and Ecology* 127: 1–12.

PECK L.S. 2002. Ecophysiology of Antarctic marine ectotherms: limits to life. *Polar Biology* 25: 31–40.

PECK L.S. 2005. Prospects for survival in the Southern Ocean: vulnerability of benthic species to temperature change. *Antarctic Science* 17: 497–507.

PECK L.S. and ROBINSON K. 1994. Pelagic larval development in the brooding Antarctic brachiopod *Liothyrella uva*. *Marine Biology* 120: 279–286.

PECK L.S., ANSELL A.D., WEBB K.E., HEPBURN L. and BURROWS M. 2004a. Movements and burrowing activity in the Antarctic bivalve molluscs *Laternula elliptica* and *Yoldia eightsi*. *Polar Biology* 27: 357–367.

PECK L.S., CLARK M.S., MORLEY S.A., MASSEY A. and ROSSETTI H. 2009b. Animal temperature limits and ecological relevance: effects of size, activity and rates of change. *Functional Ecology* 23: 248–256.

PECK L.S., COLMAN J.G. and MURRAY A.W.A. 2000. Growth and tissue mass cycles in the infaunal bivalve *Yoldia eightsi* at Signy Island, Antarctica. *Polar Biology* 23: 420–429.

PECK L.S., MASSEY A., THORNE M.A.S and CLARK M.S. 2009a. Lack of acclimation in *Ophionotus victoriae*: brittle stars are not fish. *Polar Biology* 32: 399–402.

PECK L.S., PÖRTNER H.O. and HARDEWIG I. 2002. Metabolic demand, oxygen supply and critical temperatures in the Antarctic bivalve *Laternula elliptica*. *Physiological and Biochemical Zoology* 75: 123–133.

PECK L.S., WEBB K.E. and BAILEY D.M. 2004b. Extreme sensitivity of biological function to temperature in Antarctic marine species. *Functional Ecology* 18: 625–630.

PECK L.S., WEBB K.E., MILLER A., CLARK M.S. and HILL T. 2008. Temperature limits to activity, feeding and metabolism in the Antarctic starfish *Odontaster validus*. *Marine Ecology Progress Series* 358: 181–189.

PÖRTNER H.O. 2002. Climate variations and the physiological basis of temperature dependent biogeography: systemic to molecular hierarchy of thermal tolerance in animals. *Comparative Biochemistry and Physiology, Part A* 132: 739–761.

PÖRTNER H.O., PECK L.S. and SOMERO G. 2007. Thermal limits and adaptation in marine Antarctic ectotherms: and integrative view. *Philosophical Transactions of the Royal Society B* 362: 2233–2258.

PÖRTNER H.O., PECK L.S., ZIELINSKI S and CONWAY L. 1999. Temperature and metabolism in the highly stenothermal bivalve mollusc *Limopsis marionensis* from the Weddell Sea, Antarctica. *Polar Biology* 22: 17–30.

ROBERTSON R., EL-HAJ A.J., CLARKE A., PECK L.S. and TAYLOR E.W. 2001. The effects of temperature on metabolic rate and protein synthesis following a meal in the isopod *Glyptonotus antarcticus* Eights (1852). *Polar Biology* 24: 677–686.

ROBERTSON R., VISBECK M., GORDON A.L. and FAHRBACH E. 2002. Long-term temperature trends in the deep waters of the Weddell Sea. *Deep Sea Research II* 49: 4791–4806.

RUPP G.S. and PARSONS G.J. 2004. Effects of salinity and temperature on the survival and byssal attachment of the lion's paw scallop *Nodipecten nodosus* at its southern distribution limit. *Journal of Experimental Marine Biology and Ecology* 309: 173–198.

YOUNG J.S., PECK L.S. and MATHESON T. 2006. The effects of temperature on walking and righting in temperate and Antarctic crustaceans. *Polar Biology* 29: 978–987.