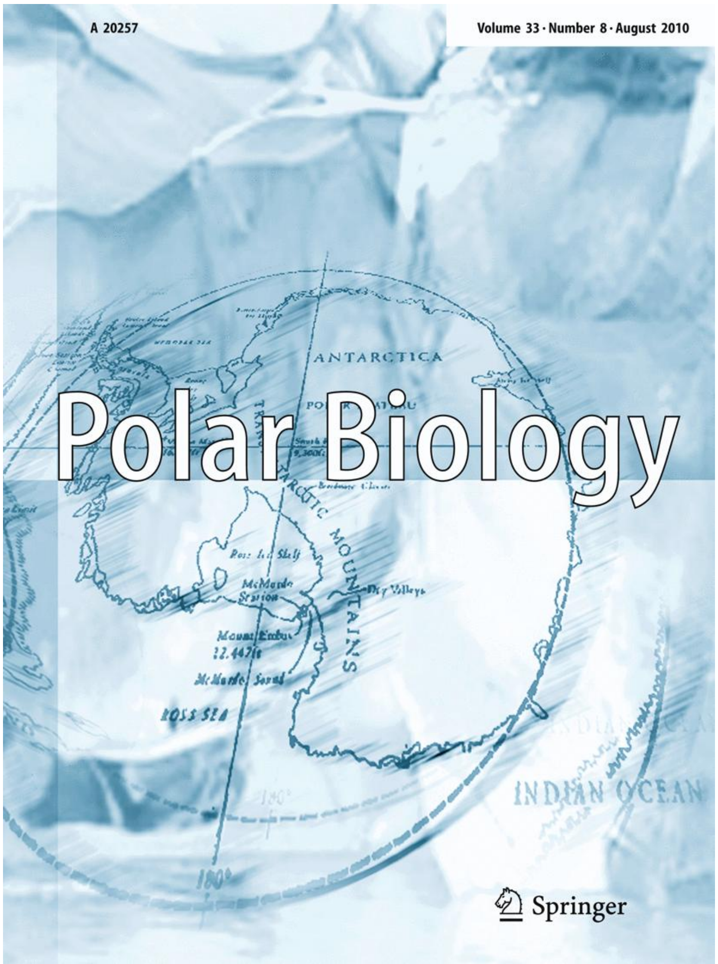
ISSN 0722-4060, Volume 33, Number 8



Polar Biol (2010) 33:1013–1020
DOI 10.1007/s00300-010-0779-y

ORIGINAL PAPER

The effects of temperature and salinity on vital biological functions of the Antarctic crustacean *Serolis polita*

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Received: 20 October 2009 / Revised: 20 January 2010 / Accepted: 4 February 2010 / Published online: 7 March 2010

Abstract Effects of temperature rise (from 0 to +5°C) and salinity decline (from 34 to 30 psu) on vital biological functions of the Antarctic isopod *Serolis polita* were studied in laboratory experiments. Behavioural reactions to food odour, as well as righting responses and reburying in the sediments, were measured. Both temperature increase and salinity decline impaired the ability of *S. polita* to perform these biological functions critical for their long-term survival, by lowering the number of isopods able to right and rebury in the sediment, increasing time-to-right, reducing locomotory activity and weakening isopod reaction to food odour. Significant interactive effects between temperature and salinity on time-to-right and time spent swimming were observed, with isopods being more vulnerable to lower salinities when exposed to higher temperatures. Some biological functions (righting, reburying) were more sensitive to temperature and salinity changes than others (swimming). In conclusion, our findings strongly suggest that Antarctic isopods are vulnerable to environmental changes, and their ability to cope with them is limited.

Introduction

Throughout the twentieth century, global air temperatures increased by 0.3–0.6°C (Hughes 2000), and current climatic models predict further warming (IPCC 2001, 2007). Global seawater temperatures have risen by 0.06°C during the last half century (Levitus et al. 2000) with a predicted increase of 2°C over the next 100 years (IPCC 2001, 2007). Rapid changes especially were observed along the Antarctic Peninsula, with air temperatures having risen by ca 3°C in the last 50 years at some localities, and winter minimums by over 5°C (King et al. 2003). Antarctic seawater temperatures are also rising, 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) and around South Georgia (Whithehouse et al. 2008). These changes are accompanied by dramatic melt increase along the Antarctic Peninsula, with 87% of glacier termini retreating (Cook et al. 2005) and some indication of significant reductions in sea ice extent (Curran et al. 2003). Localized instances of lowered shallow waters salinities resulting from melted freshwater discharge were also observed (Nihashi et al. 2005; Kidawa and Janecki, personal observations).

Climate change is already having significant impact on some components of the Antarctic food web. Changes in phytoplankton concentration and composition along the western shelf of the Antarctic Peninsula associated with long-term climate modification were noted (Montes-Hugo et al. 2009) as well as significant shifts in bird and seal populations sizes in the Southern Ocean (Barbraud and Weimerskirch 2001; Croxall et al. 2002; Weimerskirch et al. 2003). There are also indications that populations of *Pleuragramma antarcticum*, a key fish species of the trophic web, whose reproduction is closely associated with sea ice, declined locally, to be replaced by myctophids, a new food item for predators (after SCAR Report 2009).

Many unique Antarctic marine invertebrate species living on the sea bed are adapted to a very precise set of environmental conditions, such as low stable temperatures, stable salinities, high oxygen content and strong seasonality of primary production which have existed in this region for the last 10 million years (Peck 2005). In consequence,

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Antarctic marine invertebrates are temperature limited, they have slow growth, development, metabolic and activity rates and may be energy limited (Pearse et al. 1991; Arntz et al. 1994; Peck and Robinson 1994; Peck 1996; Peck et al. 2000, 2004; Peck 2002). Therefore, it can be assumed that they are characterized by a poor ability to cope with environmental changes predicted by prevailing global warming models.

Temperature and salinity are two of major environmental factors influencing growth, development and survival of marine invertebrates (Kinne 1964; Pörtner 2001; Somero 2005). Although there is a considerable number of publications on the effects of temperature on Antarctic benthic invertebrates (e.g. Peck et al. 2004, 2009a, b; Peck 2005; Young et al. 2006; Clark et al. 2008), there are only scant data on the salinity impact on Antarctic (Cowart et al. 2009) and sub-Antarctic invertebrates (Simpson 1976; Davenport and Macalister 1996). No information is available on the combined effects of temperature and salinity on the ability to perform vital biological function by Antarctic marine crustaceans.

The isopod crustacean *Serolis polita* is a significant component of Antarctic benthos living in soft bottom areas composed of sand at depths of up to 900 m. It spends most of the time buried under the surface of the sediment, although it was also observed swimming in short bursts of activity (Luxmoore 1982, 1985). Its geographical distribution is restricted to the region of Antarctic Peninsula and the Scotia Arc (Kusakin 1967). It attains body lengths of about 30 mm and has a life span exceeding 6 years (Luxmoore 1985). It breeds at a mean age of 28 months, and the eggs are incubated in a ventral marsupium for a period of 20 months before the release of juveniles in spring. (Luxmoore 1982). *S. polita* is an unspecialized predator eating mostly amphipods and polychaetes (Luxmoore 1985), although some instances of cannibalistic behaviour were also observed (Janecki personal observations). It uses chemical information to locate food items, responding to chemical cues such as glutamic acid, serine, leucine and arginine (Janecki in prep.). In Admiralty Bay, *S. polita* is common on sandy bottom (Arnaud et al. 1986), with maximum concentrations of 274 individuals m^{-2} (Nonato et al. 2000). Mean annual temperature in Admiralty Bay at 10 m is −0.11°C (Szafrański and Lipski 1982; Zwolska and Janecki 1999), and mean salinity at 30 m is 34.1 psu (Rakusa-Suszczewski 1996).

The aim of this study was to analyse the effects of temperature and salinity on the ability of *S. polita* to perform vital biological functions such as righting after being overturned, reburying in the sediment and responding to food odour. We hypothetize that at lowered salinities and raised water temperatures, isopods will have reduced capabilities to perform these essential functions.

Methods

Serolis polita specimens with lengths measuring from 1.8 to 2.3 cm were collected by SCUBA divers equipped with hand-drag net during January–February 2008. Collections were made at Arctowski Cove (Admiralty Bay, King George Island, South Shetlands, Antarctica) from a population living at depth of ca 6 m on bottom covered with fine sand. Animals were maintained in well-aerated tanks (ca 30 L each) at a temperature of 0.0°C and water salinity of 34.0–34.3. For 3 days isopods were fed *Notothenia* sp. muscle meat to minimize differences in their feeding status and then starved for 14 days. Damaged or non-feeding isopods were excluded from the experiments.

All experiments were conducted at temperatures of 0, +1, +2, +3, +4 and +5°C, and salinities 34, 33, 32, 31 and 30. Tests done in salinity 34 and temperature 0°C were treated as control. Isopods were taken from the holding tanks and placed in aquariums in a temperature-controlled room. Afterwards, temperature in the room was set to the planned value (0, +1, +2, +3, +4 and +5°C). Experiments were conducted 24 h later, allowing the temperature of seawater in the aquaria to match the desired value. Two temperature-controlled rooms were used—one for housing the isopods at 0°C, and the other for the experiments. The temperature in the second room was set to a higher temperature after the completion of previous tests. Isopods were collected several times to ensure that all were starved for 30 days. Each group of isopod was warmed independently from 0°C to the planned experimental temperature.

Seawater was combined with distilled water to attain the appropriate salinity level, which was measured with conductometer LF 197 (WTW GmbH). Two hours before the experiment, isopods were placed in seawater of desired salinity.

All experiments were conducted in 2-l aquaria with static water of desired temperature and salinity. Each aquarium contained 2-cm layer of fine sand similar to the substratum from the location where the isopods were living. All tests were recorded with a digital video camera. Timed recordings were then analysed to determine time each isopod took to right itself and time spent swimming by each animal in response to food stimuli.

All righting tests were conducted by turning isopods upside-down and placing them individually on the bottom of the aquarium. Time-to-right was measured as the time between the initiation of the righting behaviour and its completion. Afterwards, the behaviour of isopods was observed, and the number of animals reburying themselves immediately in sand after successful righting attempt was noted. Each variant of the experiment was replicated 15 times. No individual was tested more than once in any of the combined righting/reburying tests. The total number of 450 isopods was used in the experiment.

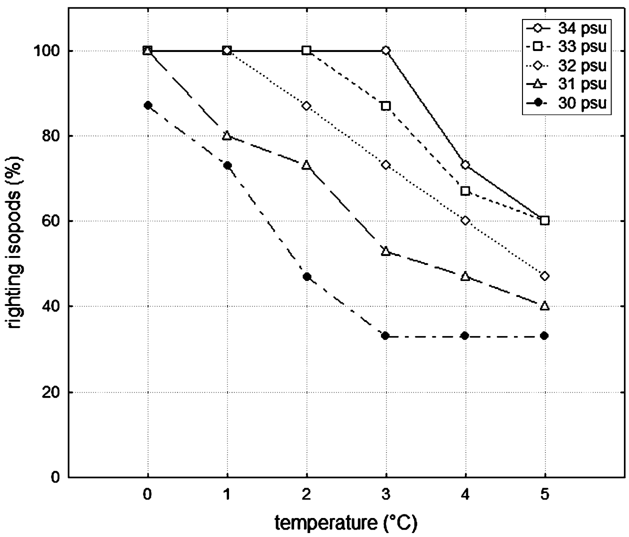

Fig. 1 The effect of temperature and salinity on the righting behaviour of isopods *S. polita*. Righting isopods—percentage of isopods righting after being overturned

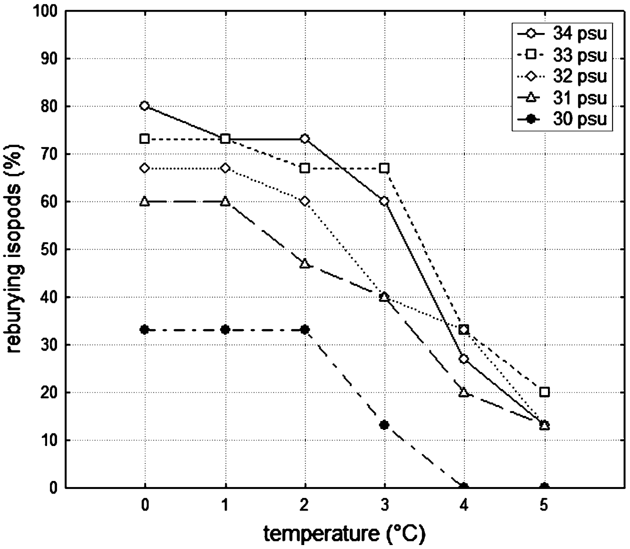

Fig. 2 The effect of temperature and salinity on the reburying behaviour of isopods *S. polita*. Reburying isopods—percentage of isopods able to rebury in the sediment

Food stimuli tests were conducted by placing isopods individually on the bottom of the aquarium. After 15 min, 1 ml of meat extract (consisting of a leachate of 100-ml seawater and 50 g of *Notothenia* sp. muscle meat left for 24 h) was slowly released from a syringe kept at 3 cm above the animal. Isopod activity level was measured as time spent swimming. Each variant of the experiment was replicated 15 times. No individual was tested more than once, and none of them was used previously in the righting/reburying experiments. The total number of 450 isopods was used in the experiment.

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

Data analysis was performed using the statistical package Statistica 5.5. (StatSoft). To establish the statistical significance of differences between data from subsequent variants of the experiments, χ^2 test, two-way ANOVA and Tukey HSD test were used. A P value of 0.05 was considered significant. When necessary, logarithmic transformation of data was performed.

Results

In control experiments, all *S. polita* were capable of righting and 80% reburied in the sediments (Figs. 1, 2). Time-to-right was less than 3 s (Fig. 3). All isopods reacted to the food odour with swimming for 1.4 min (Figs. 4, 5).

The percentage of isopods able to right after being placed upside-down on the bottom of the aquarium was significantly affected by both temperature (two-way ANOVA, $F_{5,20} = 33.06$, $P < 0.001$) and salinity (two-way ANOVA, $F_{4,20} = 17.07$, $P < 0.001$), decreasing with the rise of temperature and decline of salinity from 100 to 33% (Fig. 1).

The differences between observed and theoretical (control variant—salinity 34, temperature 0°C) numbers of isopods able and unable to right were statistically significant for the isopods at $T = 1$ and 2°C (31 and 30 psu), $T = 3$°C (32, 31 and 30 psu) and $T = 4$ and 5°C (all salinities) (test χ^2, $P < 0.05$).

Mean time-to-right ranged from 2.4 s ($T = 1$°C, salinity 34 and $T = 0$°C, salinity 33) to 30.4 s ($T = 4$°C, salinity 31). It was significantly affected by both temperature (two-way ANOVA, $F_{5,313} = 57.14$, $P < 0.001$) and salinity (two-way ANOVA, $F_{4,313} = 13.20$, $P < 0.001$). Significant interactive effects between temperature and salinity on time-to-right were also found (two-way ANOVA, $F_{20,313} = 3.35$, $P < 0.001$). At temperatures of 0 and 1°C combined with salinities of 34, 33 and 32, low variability of time-to-right was noted. In other variants of the experiment, variability was much higher, especially at a temperature of 4°C (all salinities). Two groups of isopods with short (<10 s) and long (50–69 s) time-to-right were observed.

Time-to-right lengthened with rising temperature and declining salinity (Fig. 3). No statistically significant differences were noted between time-to-right of isopods exposed to $T = 0$ and 1°C in salinities of 34, 33 and 32 (Tukey HSD test, $P < 0.05$). Similarly, no differences were observed between time-to-right of isopods exposed to $T = 2$, 3 and 4°C in all tested salinities, and $T = 0$ and 1°C in salinities of 31 and 30 (Tukey HSD test, $P < 0.05$).

The percentage of isopods *S. polita* able to rebury in sand was significantly affected by both temperature (two-

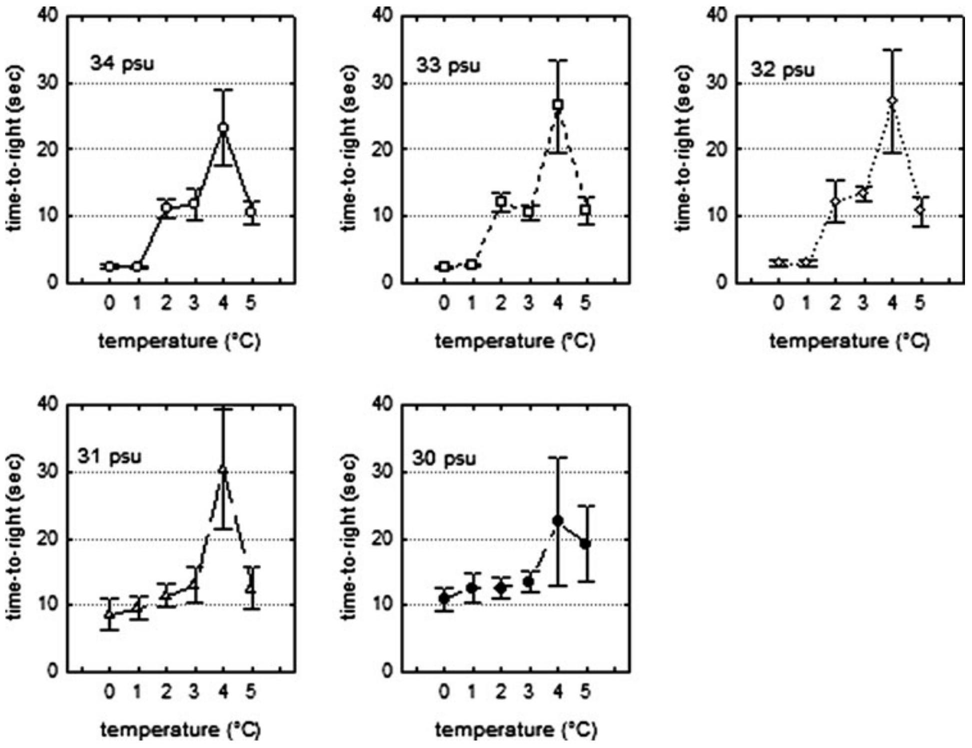

Fig. 3 The effect of temperature and salinity on the time-to-right of isopods *S. polita*. Time-to-right—time between the initiation of the righting behaviour and its completion. Data shown as mean ± SE

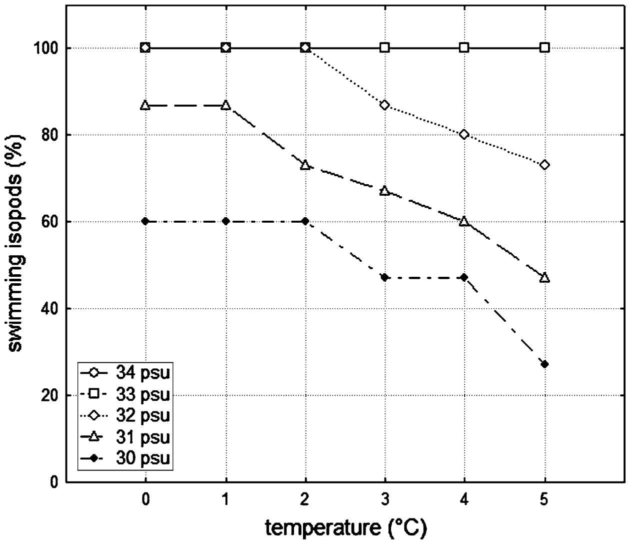

Fig. 4 The effect of temperature and salinity on the behavioural reaction (swimming) of isopods *S. polita*. Swimming isopods—percentage of isopods swimming in response to food odour. Values for 34 and 33 psu were the same for all tested temperatures

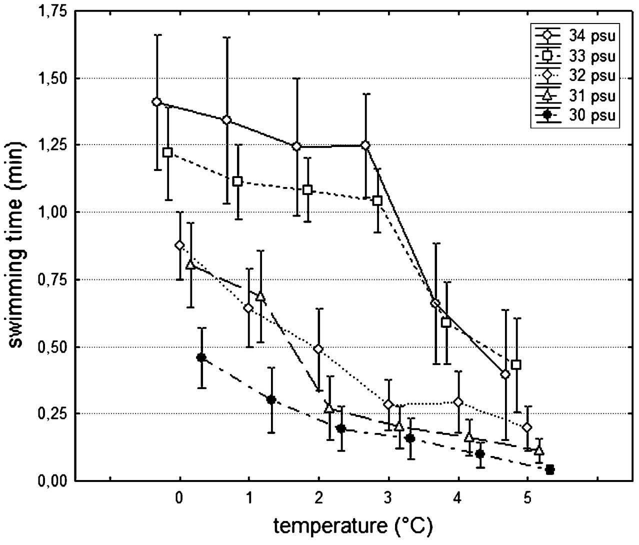

Fig. 5 The effect of temperature and salinity on the behavioural reaction (swimming) of isopods *S. polita* in response to food stimuli. Data shown as mean ± SE

way ANOVA, $F_{5,20} = 49.18$, $P < 0.001$) and salinity (two-way ANOVA, $F_{4,20} = 39.74$, $P < 0.001$), decreasing from 80 to 0% with the rise of temperature and decline of salinity (Fig. 2).

The differences between observed and theoretical (control variant—salinity 34, temperature 0°C) numbers of isopods able and unable to rebury were statistically significant for isopods at temperatures 0, 1 and 2°C (salinity 32, 31 and 30), 3, 4 and 5°C (all salinities) (test χ^2, $P < 0.05$).

The percentage of isopods *S. polita* reacting to food odour was significantly affected by both temperature (two-way ANOVA, $F_{5,20} = 5.26$, $P < 0.01$) and salinity (two-way ANOVA, $F_{5,20} = 47.00$, $P < 0.001$), decreasing with the rise of temperature and decline of salinity from 100 to 26.7% (Fig. 4).

The differences between observed and theoretical (control variant—salinity 34, temperature 0°C) numbers of isopods reacting and not reacting to food odour were statistically significant for isopods at temperatures of 0 and 1°C (salinity 30), 2 and 3°C (salinity 31 and 30), and 4 and 5°C (salinity 32, 31 and 30) (test χ^2, $P < 0.05$).

Mean time spent swimming by isopods exposed to food odour ranged from 1.41 min ($T = 0$°C, salinity 34) to 0.04 min ($T = 5$°C, salinity 30). Activity was significantly affected by both temperature (two-way ANOVA, $F_{5,339} = 71.15$, $P < 0.001$) and salinity (two-way ANOVA, $F_{4,339} = 100.37$, $P < 0.001$), and significant interactive effects (two-way ANOVA, $F_{20,339} = 3.39$, $P < 0.001$).

Time spent swimming decreased gradually with rising temperature and declining salinity (Fig. 5). In statistical analysis (Tukey HSD test), 17 groups with no statistical difference within them were distinguished. No significant differences were noted between time spent swimming of isopods exposed to temperatures of 0, 1, 2 and 3°C (salinities of 34 and 34), temperatures of 0 and 1°C (salinities of 32 and 31) and temperature of 1°C (salinity of 31) (Tukey HSD test, $P < 0.05$). Time spent swimming of isopods exposed to the highest experimental temperature (5°C) and the lowest experimental salinity (30 psu) was significantly lower than in all other conditions except in temperatures of 3 and 4°C (salinity 30) and temperature of 5°C (salinity 31) (Tukey HSD test, $P < 0.05$).

The environmental envelope (range of suitable environmental conditions) in which there were no statistically significant differences between control and experimental values was much wider in the case of time spent swimming by isopods exposed to food odour than time-to-right of isopods placed upside-down on the bottom of the aquarium. Similar phenomenon was observed in the case of numbers of isopods able to right after being overturned, rebury in the sediments and react to food odour.

Discussion

In our experiments, simultaneous temperature increase and salinity decline caused significant changes in the ability of *S. polita* to perform all tested biological functions. Time-to-right rose from 2.4 s to half a minute. In salinity of 30 and at temperatures 4 and 5°C, no isopod was capable of reburying in the sediments. The proportion of isopods swimming when exposed to food odour fell to 27%, and time spent swimming dropped from 1.41 min to only a few seconds, impairing the ability of isopods to find food.

Temperature and salinity are main abiotic environmental factors affecting survival and distribution of marine organisms (Kinne 1964). The environmental range in which growth and normal physiological functioning can occur is usually narrower than the tolerance limits of any species (Newell and Branch 1980; Peck et al. 2004; Rupp and Parsons 2004).

All previously tested Antarctic benthic invertebrates are also strongly stenothermal (Peck et al. 2004; Peck 2005; Young et al. 2006). Many of them die at temperatures between 5 and 10°C (Peck 1989; Peck et al. 2002, 2004). Species such as limpet *Nacella concinna*, bivalves *Laternula elliptica* and *Adamussium colbecki* lost the ability to perform vital biological functions (righting, reburying, swimming) at elevated temperatures (50% failure at 2–3°C, complete loss at 5°C) (Peck et al. 2004), although elevating temperatures up to 4.5°C did not led to acute breakdown of motor coordination in two Antarctic crustaceans, isopod *Glyptonotus antarcticus* and amphipod *Paraceradocus gibber* (Young et al. 2006). Authors propose that the ability of *G. antarcticus* and *P. gibber* to perform righting and walking must therefore 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). A recent study on the sea star *Odontaster validus* showed that it can maintain activity at higher temperatures than other studied Antarctic benthic invertebrates, righting itself when turned over at temperatures up to 8°C and feeding up to 7°C (Peck et al. 2008).

The rate of warming can have a significant impact on the species' thermotolerance (Peck et al. 2009a, b). When temperatures were raised by 1°C per day, invertebrates survived to much higher temperatures (8.3–17.6°C) than when the warming process was prolonged (survival to 4.0–12.3°C for weekly temperature elevations and only to 1–6°C for long-term acclimation) (after Peck et al. 2009a, b). In our experiments, a more acute rate of warming was applied, with temperature being raised by 5°C per day maximum. In spite of it, the temperature at which the loss of ability to perform vital biological functions by *S. polita* was observed was similar to previously tested Antarctic benthic invertebrates subjected to short-time warming (Peck et al. 2004, 2008; Young et al. 2006).

There are only scant data on the effect of salinity decline on Antarctic marine invertebrates. Measuring the impact of decrease in salinity from 34 to 30 psu on sea urchin *Sterechinus neumayeri* embryo development, Cowart et al. (2009) noticed that small salinity changes (2–4 psu) not only slowed development rate and decreased the percentage of embryos reaching morula stage but also reduced viability of embryos. Comparison with tropical and temperate species of sea urchins suggested a greater stenohaline limitation in *S. neumayeri* (Cowart et al. 2009). Davenport (2001) observed significant behavioural responses in limpets exposed to meltwater, including rapid detachment in limpets on vertical surfaces, short-term clamp down of the shell and retraction of the head and tentacles in other individuals. It was also established that sub-Antarctic limpets *Nacella concinna* from South Georgia were stenohaline, showing 100% mortality in water of 20.5 psu within 96 h (Davenport and Macalister 1996). During the research on sub-Antarctic molluscs in the rocky littoral zone of Macquarie Island, Simpson (1976) noticed that environmental temperatures and salinities there did not reach lethal levels, but the debilitating effects of unfavourable conditions in combination with other adverse factors (e.g. combination of high temperature and predation) can be lethal.

The effect of salinity decline was also observed in some marine invertebrates living outside the Southern Ocean. Salinity decrease caused the significant reduction in larval oxygen consumption and growth in marine polychaete *Arenicola cristata* (Richmond and Woodin 1999), reduced survival rate in giant clams *Tridacna gigas* larvae (Blidberg 2004), lowered synthesis of byssal threads by *Nodipecten nodosus* spat (Rupp and Parsons 2004), or decreased growth rates of scallop *Pecten maximus* (Laing 2002). However, there are also species which exhibit no reaction to salinity changes. Marshall et al. (2003) noticed that oxygen consumption rate of crustacean *Gastrosaccus brevifissura* from the South African estuaries, where salinity usually varies between 20 and 30 psu and temperatures range from 17 to 25°C, was largely independent of salinity changes between 20 and 35 psu. Authors hypothetized that such independence of physiological rate from abiotic factors may be observed in euryhaline species experiencing highly variable environmental conditions.

In our experiments, significant interactive effects between temperature and salinity on time-to-right and time spent swimming were observed, so that isopods were more vulnerable to lower salinities when exposed to higher temperatures. Similar interactions were noted in some other species. Tolerance of scallop *Nodipecten nodosus* to low salinity decreased as temperature increased (Rupp and Parsons 2004). The mortality and egg production of adult copepod *Gladioferens pectinatus* were influenced by temperature and salinity with salinity tolerance decreasing at elevated temperatures (Hall and Burns 2002). Similarly, supercooling abilities of copepods *Tigriopus brevicornis* were affected by salinity changes (McAllen and Block 1997).

Our data on isopods *S. polita* showed large variation in time-to-right at higher temperatures, with two groups of isopods distinguished. The number of isopods used in our experiments was too low to allow for more detailed analysis. Similarly, Young et al. (2006) also observed large variation in the mean time-to-right of *G. antarcticus* at higher temperatures, which was caused by the long times taken to right by some individual animals.

Although most of *S. polita* exposed to high temperature (5°C) and low salinity (30 psu) were unable to right when turned over or swim in reaction to food odour, there was small percentage of animals able to perform these functions. Further experiments are needed to validate this observation, ascertain size of this group and its possible significance for isopod populations. Same phenomenon was also noted by Cowart et al. (2009), showing that a small number of Antarctic sea urchins *S. neumayeri* embryos was able to survive despite the lowered salinity. High biological diversity was also observed in the Antarctic sea stars *Odontaster validus* exposed to amino acids such as arginine, asparagine, lysine and leucine, where two groups of animals differing in mobility level were observed (Kidawa 2005).

From our experiments, it can be ascertained that some biological functions (righting, reburying) seem more sensitive to temperature rise and salinity decline than others (swimming). Further experiments are needed to validate this observation, but it seems to underscore necessity of the careful choice of studied physiological parameters.

In conclusion, isopods *S. polita*, like other organisms living in a narrow range of environmental factors such as temperature and salinity, are vulnerable to potential climatic changes and have only limited ability to cope with them.

Isopods represent an important component of the Southern Ocean benthic ecosystem, contributing to a high degree to the overall Antarctic biodiversity (Brandt 1999; Clarke and Johnston 2003; De Broyer et al. 2003; Choudhury and Brandt 2009). Recent studies increased the number of isopod species in the Southern Ocean to nearly 1,000 species (after Choudhury and Brandt 2009). Our data showed that even small temperature rise and salinity decline have significant effect on *S. polita* physiological performance (e.g. shortening time spent swimming in response to food odour which reduce their chances to find food). Future regional climate change in the area of the Antarctic Peninsula can result in the reduction of their numbers or even their removal from the benthic ecosystem, disrupting ecological interactions which stabilize benthic communities and reducing functional diversity in the Antarctic food-web (Clarke et al. 2007).

Acknowledgments Data presented in this paper were collected during the 32. Polish Antarctic Expedition at "Arctowski" Station (King George Island, South Shetlands, Antarctica). The work was financed by the Ministry of Scientific Research and Higher Education, Grant No. IPY/268/2006 (years 2007–2010). Particular thanks are addressed to two referees for their most helpful comments, which greatly improved the paper.

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