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The giant Antarctic amphipod *Paraceradocus miersi* will not fare well if freshening continues in the Southern Ocean

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ABSTRACT

Sea water provides a stable environment for marine animals. Most oceanic invertebrates have body fluids similar in ionic composition to sea water. However, Antarctic coastal ecosystems are increasingly exposed to *freshening*—a reduction in salinity driven by glacial melt, increased precipitation, and extreme weather events. Such changes can cause mortality in Antarctic invertebrates, which generally are intolerant to reduced salinity. This study investigated osmotic and ionic regulation of the Antarctic amphipod *Paraceradocus miersi* exposed to simulated freshening. When salinity was reduced (from S = 34.6 to 28.0) for 12–48 h, haemolymph osmolality and sodium concentration declined, while calcium remained stable; magnesium increased markedly, suggesting poor regulation. At S = 22.1, irreversible, catastrophic gill damage was clearly visible. We conclude that *P. miersi* is an osmoconformer capable of limited osmo- and variable iono-regulation, at least on the timescale investigated, and so is vulnerable to hyposaline damage, *via* compromised gill integrity Compared with Arctic amphipods, which possess stronger osmoregulatory capacity, *P. miersi* reflects adaptation to the historically stable Antarctic salinity regime. Haemolymph ion composition was broadly similar to sea water for Na^{+} but differed markedly for K^{+} and Mg^{2+}, with values more closely-aligned with Antarctic isopods. Freshening events in Ryder Bay have been rare but not absent; a 2017 event (S = 28.4) may have impaired osmotic and ion balance or even caused mortality in shallow-dwelling individuals. Continued 'summer' coastal freshening may therefore pose a significant physiological threat to this Antarctic amphipod and other marine invertebrates.

1. Introduction

It has long been regarded that sea water provides the most constant environment for marine invertebrates, while coastal environments, even in polar waters, may often exhibit substantial variation in salinity (Dittmar, 1884; Potts and Parry, 1964). Many oceanic invertebrates have extracellular fluids that, with some notable exceptions, differ little from sea water in terms of their osmotic and ionic content (Robertson, 1949; Mantel and Farmer, 1983). Osmotic and ionic regulation by marine animals has been studied for over a century mainly in connection with the invasion of land, optimisation of conditions for aquaculture or aquatic animal shipping, and predominantly the challenge posed by invasion and colonisation of brackish or estuarine waterbodies, and the brackishwater/estuarine species that become invasive, *via* anthropogenic dispersal (Potts and Parry, 1964; Little, 1990; Willmer et al., 2005; Charmantier et al., 2008, Bradley, 2009). Originally of heuristic interest, understanding these physiological regulations has recently grown in importance as we seek to understand the biological implications of biological invasions and a changing climate.

While increasing temperatures, altered sea ice and ocean acidification are considered the major threats to Antarctic biodiversity, a fourth, changing salinity and in particular coastal freshening, has been increasing since the early 1980s (Haumann et al., 2016). Generally the Southern Ocean has a higher and less variable mean surface salinity (33.5-34.5) than the Arctic (30-33 and sometimes even lower) (Timmermans and Marshall, 2020; Yu, 2026). This is because while the Southern Ocean surrounds a continent with almost no river input, the Arctic is a largely enclosed ocean with massive river, and precipitation input. Coastal freshening is driven largely by temperature-related increases in terrestrial ice loss, releasing fresh water into the marine environment, which is common in both regions (Röthig et al., 2023). Coastal and shelf waters are subject to greater freshening than the

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Antarctic Bottom water, but even in deep water there is evidence of freshening (Rintoul et al., 2026). A recent study by Silvano et al. (2025) suggested that while there is a long-term freshening trend in the Southern Ocean, surface salinity may actually be increasing due to limited freshwater input and warming. Much still depends on future changes in precipitation in the region. The IPCC AR6 forecast suggests it 'very likely' that precipitation will increase as air temperatures rise (IPCC et al., 2021). They also add there is increased likelihood of extreme precipitation events ('atmospheric rivers') (Maclennan et al., 2025), which will further increase freshening. What is clear is that shallow water Antarctic species are likely to be exposed to increased freshening or freshening events, even if those events are complicated by other factors. In the intertidal zone glacial run-off has been seen to dramatically reduce the salinity of intertidal pools to <12 (Waller et al., 2006). Large acute freshwater inputs have been correlated with mass mortalities in Antarctic waters even of motile invertebrates such as krill (Fuentes et al., 2016) and an inability to survive sudden large salinity changes has been recorded for many Antarctic invertebrates (Peck, 2018; González-Aravena et al., 2018; Navarro et al., 2020; Röthig et al., 2023; Barrett et al., 2024, 2025). At a depth of 10 m in Cierva Cove, Western Antarctic Peninsula water salinity fell to 33.0 as a result of glacial meltwater as opposed to direct sea-ice melt, a reduction not uncommon in the region (Micallef et al., 2026).

Our knowledge of the effects of low salinity on the physiology, and in particular the capacity to regulate the osmotic and ionic content of extracellular fluids of Antarctic invertebrates is limited. Exposure to low salinities affects the righting rate, response to food odour, swimming and reburying behaviours of the Antarctic isopod *Paraserlis* (=*Serolis*) *polita* (Janecki et al., 2010), the activity, feeding and metabolism of urchins (Barrett et al., 2024, 2025), and energy (re)allocation (towards survival and somatic maintenance) and upregulation of genes associated with cellular stress response in the limpet *Nacella concinna* (Navarro et al., 2020). While Arctic benthic amphipods tend to display well developed powers of osmoregulation (e.g. Aarset and Aunaas, 1987a, b; Aarset and Zachariassen, 1988; Kiko et al., 2009); to our knowledge there is no information on benthic Antarctic amphipods. Currently we have very little information on whether Antarctic invertebrates are able to osmo- and iono-regulate or not. One might predict that because of the relatively stable salinities that characterise the Antarctic compared with the Arctic (see above) that there is little requirement for active (expensive) osmoregulation in Antarctic invertebrates. While regulation of particular ions may still be necessary, osmoconforming is a 'good' fit, for an animal that is iso-osmotic with full strength sea water and historically has inhabited a very stable environment. Recent work by Barrett et al. (2024, 2025) which showed that though the starfish *Odontaster validus* and the sea urchin *Sterechinus neumayeri* were osmoconformers, they survived low salinity exposure (12 weeks at S = 24 and 29) by using amino acids in cell volume regulation in a way not recorded for temperate echinoderms.

Therefore, the aim of our study was to test the hypothesis that the 'giant' (max length 5 cm) Antarctic amphipod *Paraceradocus* (*Megamoera*) *miersi* (Pfeffer, 1888) will be isosmotic with the sea water it inhabits, sea water which has been relatively constant in temperature and salinity for millions of years. We predict *P. miersi* will bean osmoconformer, so that when it is challenged with hyposaline stress its haemolymph will shift to be iso-osmotic with the new dilute media, with a concomitant change in haemolymph ions. To this end we investigated osmotic and ionic regulation of amphipods exposed to a simulated freshening event. To do this we examined the number and intensity of freshening events that have occurred where the amphipods were collected (1999 - 2018) to inform our choice of test salinities, and provide context for interpretation of physiological findings. We then exposed individuals acutely to reduced salinities and measured the osmolality and cation content (namely Na^+, K^+, Ca^{2+} and Mg^{2+}) of the haemolymph. The opportunity was also taken to briefly compare the ionic content of haemolymph of *P. miersi* with the small number of Antarctic amphipod and isopod species for which there are comparable data.

Paraceradocus miersi is a benthic detritivore/scavenger which lives under stones in burrows in sediment which they excavate (Coleman, 1989). The salinity and oxygen content of the burrow water (burrows at 6 m water depth) was tested in February 2017 and was not significantly different from surface waters (Spicer and Morley, Unpubl.Obs.). It occurs at depths 0 - 344 m in east and west Antarctic Provinces and South Georgia district (de Broyer et al., 2007). Little is known of the physiology of most Antarctic invertebrates but *P. miersi* is an exception perhaps because of its large size. It exhibits intermediate thermal tolerance (Clark et al., 2017; Peck et al., 2009; Varas et al., 2024), a relatively low and temperature/season insensitive metabolism (Q_{10} = 1.45), (Obermüller et al., 2010; Varas et al., 2024), low temperature sensitivity of neuronal conduction (Young et al., 2006), has no ability to acclimate to different temperatures (Peck et al., 2010), and does not always exhibit an HSP70 heat shock response when challenged with a thermal shock (Clark et al., 2008, 2017). It is unable to regulate rates of oxygen uptake when exposed to acutely declining oxygen tensions, and its crawling speed is not significantly altered by temperature increase (Spicer and Morley, 2019). There is no published information on osmotic or ionic regulation by this species.

2. Materials & methods

2.1. Collection and maintenance of amphipods

Amphipods (wet mass = 1.229 – 2.778 g, N = 25) were collected by divers beneath cobbles/boulders at a depth of 6 - 8 m from South Cove, Ryder Bay, Adelaide Island, Graham Land, Western Antarctic Peninsula (lat. 67°34′11′′S, long. 68°08′89″ W, Fig. 1) during Jan/Feb 2017. Individuals were transferred to the laboratory within 60 min of capture. They were maintained in a number of Aquarium Tank Fish Hatchery and Fry Breeder Units (All Pond Solutions, Uxbridge, UK) that floated, partially submerged, in large aquaria supplied with sand filtered running sea water (T = 0°C, DO = 100–106 % air saturation, S = 34.6 with measured ions (Na^+ = 464, K^+ = 10.4, Ca^{2+} = 10.3, Mg^{2+} = 53.4; expressed as mmol.L^{-1}) pumped directly from South Cove, Rothera Point, adjacent to the laboratory. Temperature and DO was measured using a hand-held probe (YSI ProODO), DO using a Presens system and salinity using a salinometer (Guildline Autosal 8400 B) calibrated using IAPSO standard sea water (S = ±0.002). Ion concentrations were measured using the ICP-OES used for haemolymph analysis (see below). Amphipods were kept for 48 h before use in the experiment described below and were not fed during this time. All individuals were in Drach's molt Stage C (intermolt), determined by inspecting setal development through the cuticle (Graf, 1986). All experiments were carried out at the beginning of Feb 2017.

2.2. Experimental design

To investigate the effect of exposure to reduced salinities on the osmotic and ionic regulation of *P. miersi*, the following experiment was carried out. Individuals were removed from their holding conditions and carefully placed in aquaria (vol. = 10 L, n = 1 - 2 indiv. per aquarium to avoid crowding) filled either with the water they had been held in (S = 34.6) or the same water diluted with distilled water (S = 28.0 and 22.1). All aquaria and their contents were held at T = 0 ^{0}C in a controlled temperature facility. Individuals were removed 12 and 48 h after transfer and the haemolymph of survivors sampled as follows. Control individuals were not sampled at 12 h, but only at the start and end of the experiment in order to reduce the number of these large amphipods required to achieve our aim. The whole experimental design was constructed to minimise the number of these large and presumably extremely old animals used in the experiment. Test conditions were informed by the lowest salinity shown to occur in surface waters over the

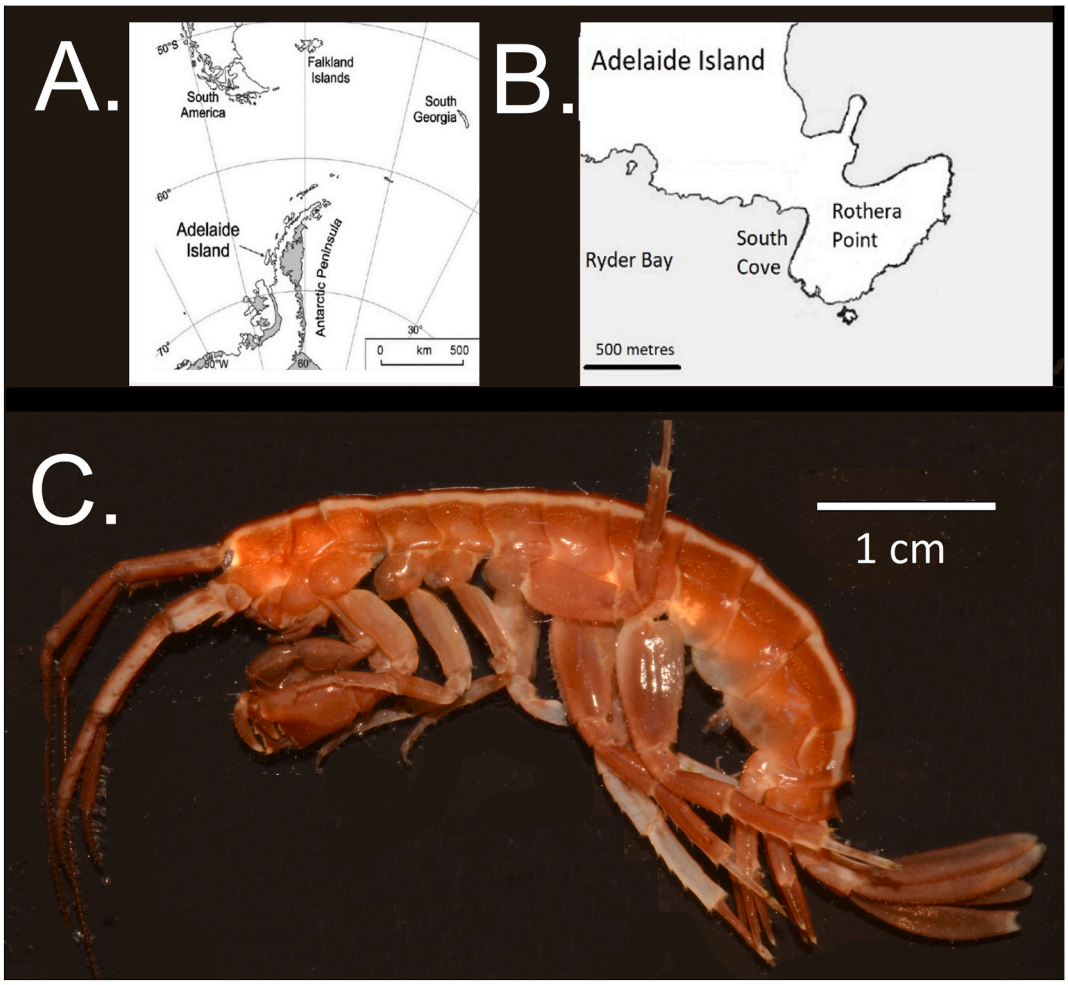

Fig. 1. (A) Adelaide Island relative to the Western Antarctic Peninsula, (B) location of the collection site (South Cove) and Rothera point on Adelaide Island and (C) the giant Antarctic amphipod *Paraceradocus miersi*.

period 1999 - end of 2017 (Venables et al., 2023). The lowest salinity (S = 28.4) was then taken as one of the reduced salinities the amphipods from Ryder Bay would be exposed to (Fig. 2) In the Spring of 2017 when the investigation presented here was carried out the extreme surface layer was almost S = 0 for a time and a number of amphipod carcasses were seen in the water (S. Morley, unpubl. Obs.). The second test salinity was an extreme value (S = 22.1) representing lower values than S = 28 experienced at other locations in Antarctic Peninsula bays during pulsed meltwater events (Meredith et al., 2018).

Haemolymph samples (vol. = 20 – 30 μL) were obtained, *via* direct

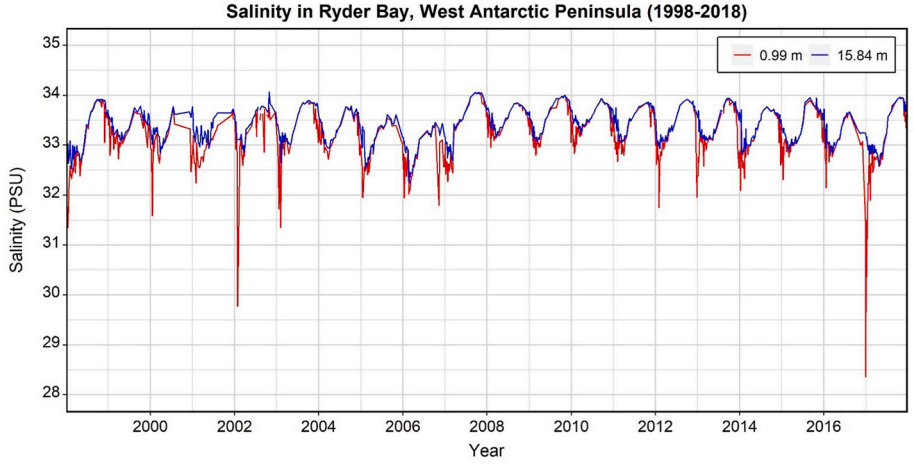

Fig. 2. Salinity data from CTD profile, at 0.99 m (red) and 15.85 m (blue) depth (1998 - 2018), Ryder Bay, Western Antarctic Peninsula (UK Polar Data Centre, 2025), Data downloaded from British Antarctic Survey (BAS) Rothera Time Series Dataset (RaTS). (For interpretation of the references to colour in this figure legend, the reader is referred to the Web version of this article.)

cardiac puncture, using a microsyringe (Hamilton, 50 μL), the needle of which was inserted dorsally through the arthrodial membrane between pereon segments 2 and 3. The haemolymph sample was gently aspirated into a microcentrifuge tube (Eppendorf, vol. = 1.6 mL) which was then frozen at T = −20^{0}C until required for analysis.

2.3. Measurement of osmolality and ions

The osmotic pressure (mOsm.kg^{-1}) of each haemolymph and water sample was determined on duplicate samples (vol. = 8 μL) using a vapour pressure osmometer (Wescor 5520, USA), calibrated using standards (Optimol® Osmolality standards 1000 and 290 mOsm.kg^{-1}). The concentration of selected ions (Na^+, K^+, Ca^{2+} and Mg^{2+}; expressed as mmol.L^{-1}) in haemolymph samples was determined after appropriate dilution with double distilled water, using Inductively Coupled Plasma Optical Emission Spectrophotometry (ICP-OES Agilent (Varians) 725, Agilent Technologies, USA).

There was no significant effect of time on any of the parameters measured in control conditions (0 and 48 h, (Students 't' test $t \leq 0.52$, $df = 7$, $P \geq 0.618$). Therefore, the effect of reduced salinity exposure on all measured parameters was tested using a one-way ANOVA having tested for normality (Anderson Darling ≤ 0.501, $P \geq 0.106$) and variance (Bartlett's test ≤ 3.68, $P \geq 0.159$). All values are expressed as means ± 1 S.D. Data analytics were carried out using Minitab© 18.

2.4. Long term record of seawater salinity

Salinity data for the sea water in Ryder Bay where the amphipods were collected, was obtained from the Rothera Oceanographic and Biological Time Series (RaTS) programme (1999 - 2017) (Venables et al., 2023). Salinity measurements from depths of 0.99 m and 15.84 m were retrieved. This information was used to inform the experimental design.

3. Results

3.1. Long term record of seawater salinity

Presented in Fig. 2 is the salinity profile (1999 - 2018) for the body of sea water where the amphipods were collected. There was no difference in the mean salinity (S ~ 33) of the water bodies at depths of 0.99 and 15.84 m. At 15.84 m the mean maximum salinity was S ~34 reducing slightly to a minimum of S ~32 during the austral summers. In the top 0.99 m of the water column the variation between summer and winter was greater than recorded in the deeper water. What is most noticeable are the large spikes particularly in 2002 and 2017 where the salinity of the water fell to below S = 30 and ~28.4 respectively. Therefore S = 28.0 was chosen as one of our test salinities.

3.2. Haemolymph osmolality and ion concentrations

Amphipod extracellular fluids were close to isosmotic in sea water (S = 34.6) but fell rapidly within 12 h upon exposure to reduced salinity (S = 28.0) ($F_{2,14} = 47.32$, $P < 0.001$); extracellular fluids were isosmotic within 48 h (Fig. 3). There are no equivalent osmolality (or ion concentration) data for the exposure to S = 22.1 as it seemed clear after short time periods that the individuals were unlikely to survive even a few hours exposure. After minutes they became moribund, were unable to right themselves, and showed swelling, within the ventral surface of the ventral groove, and of the gills (see below); and were consequently moved back to full strength sea water (S = 34.6).

Fig. 4 depicts the concentrations of the four cations in the amphipod haemolymph collected after exposure to S = 28.0 for 12 and 48 h. There was a significant ($F_{2,14} = 28.9$, $P < 0.001$) reduction in the Na^+ concentration of the haemolymph over the 48 h period in reduced salinity water (Fig. 4A). Over the same period there were no significant differences in the K^+ (Fig. 4B) or Ca^{2+} (Fig. 4C) concentrations of the haemolymph ($F_{2,14} \leq 1.85$, $P \geq 0.199$).

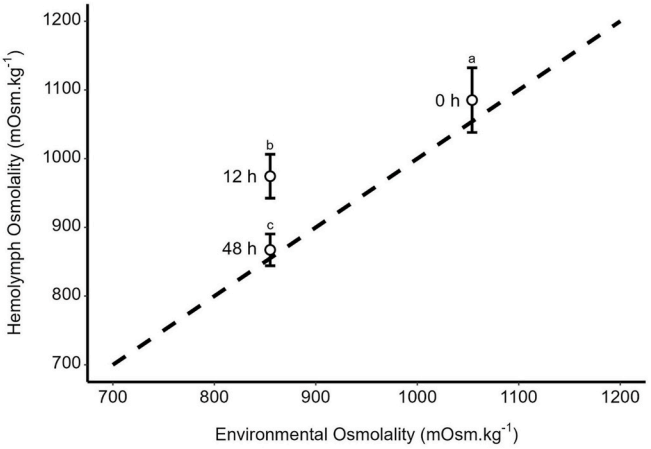

Fig. 3. Changes in haemolymph osmotic pressure over time of *Paraceradocus miersi* exposed to reduced salinity (S = 28.0). Values are means ± 1 S.D. Dashed line is the isosmotic line.

The greatest proportional change in haemolymph ion concentration was Mg^{2+} which increased significantly ($F_{2,14} = 18.87$, $P < 0.001$) by almost 55 % after 48 h in the reduced salinity treatment (Fig. 4C).

3.3. Gill damage

There was no mortality amongst the 10 individuals exposed to S = 22.1 and returned after a few minutes to S = 34.6 (without haemolymph being removed) in an effort to preserve the lives of these individuals. Within the experimental treatment (S = 22.1) these amphipods initially moved around, exploring their environment, but within 60 min had become quiescent, haemolymph was no longer passing through the gill, and they were only exhibiting slow sporadic beating of the pleopods (<40 beats.min^{-1} compared with 60 - 70 beats.min^{-1} under control conditions. However, 5 individuals when investigated closely and compared with control individuals (Fig. 5A) had clearly visible signs of catastrophic gill damage (Fig. 5B). This took the form of rupture and loss of integrity of the haemolymph sinuses and lacunae within the gills caused by disruption of connective damage clearly visible in the enlarged cuticle areas pictured (Fig. 5, right hand pane). The gills were swollen and clearly filled with large amounts of haemolymph (Fig. 5B). The flattened lamellae (Fig. 5A) were transformed into pockets of static haemolymph (Fig. 5B). Interestingly within 24 h of return to full strength sea water those individuals were indistinguishable from the others in terms of their behaviour, despite still having visibly damaged gills.

4. Discussion

Exposure of the Antarctic amphipod *Paraceradocus miersi* to a reduction in salinity from S = 34.6 to S = 28.0 for 12 - 48 h resulted in concomitant reductions in haemolymph osmolality and Na^+ concentration, but not K^+ or Ca^{2+} concentrations. Haemolymph Mg^{2+} concentration increased over the same time period, the greatest proportional change of any of the ions investigated. Exposure to a slightly greater salinity reduction (S = 22.0) resulted in substantial, visible (to the unaided eye), gill damage and a loss of coordinated movement and would most likely have resulted in death had the experiment not been terminated early. Amphipod coxal gills, are flattened oval plates which, in most crustaceans, are lined by a single layer of epithelial cells, where both respiratory gas exchange and ion transport takes place (Sutcliffe, 1984). Even a cursory visual inspection revealed that the structural integrity of the gill was compromised by hyposaline exposure, as was haemolymph supply to those gills. This will

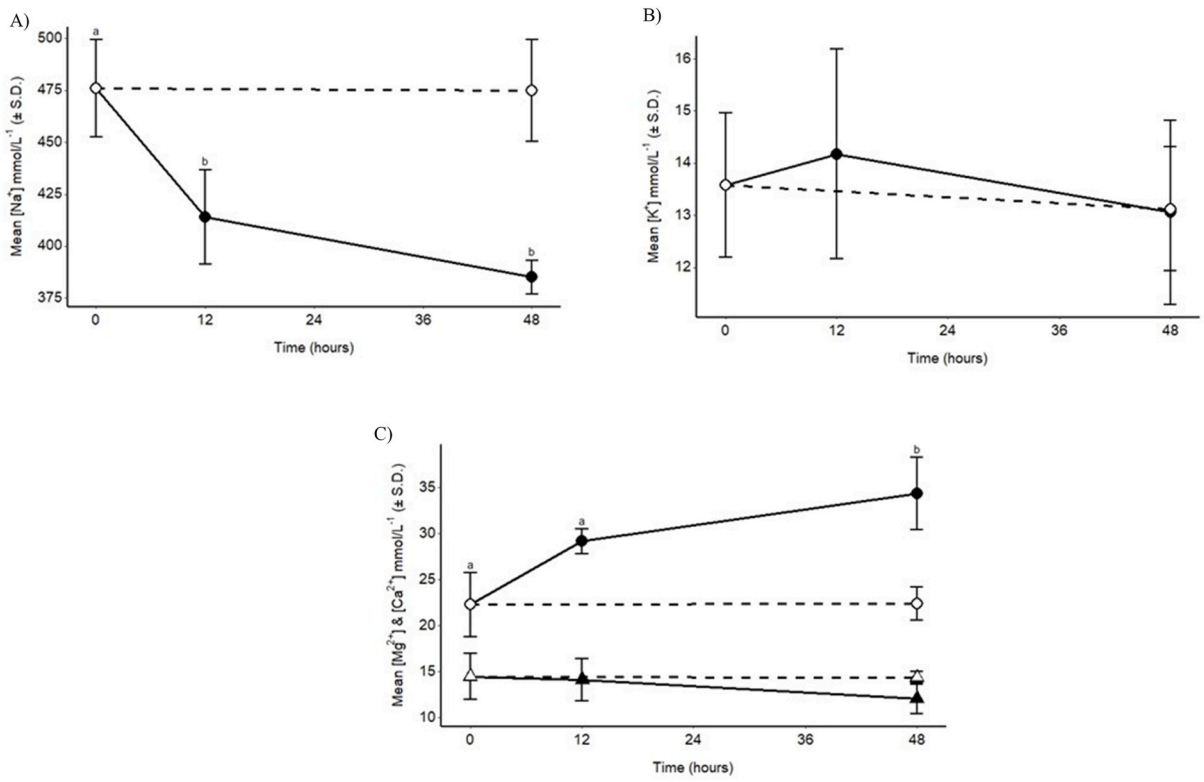

Fig. 4. Changes in haemolymph cations (A) Na^+ (B) K^+ and (C) Ca^{2+} (=triangles) and Mg^{2+} (=circles) over time for *Paraceradocus miersi* exposed to reduced salinity (S = 28.0). Open symbols = controls, Closed symbols = experimental. Different letters represent significant differences, no letters, or the same letter, signify no significant differences. Values are expressed as means ± 1. S.D.

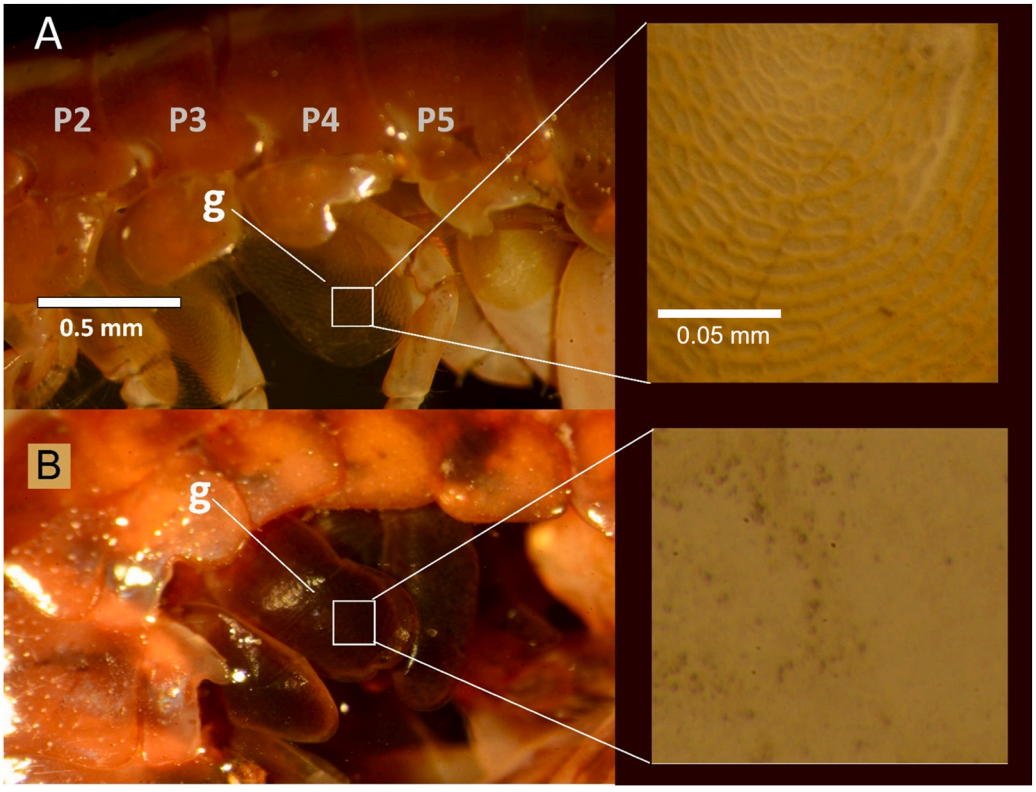

Fig. 5. Coxal gills of *P. miersi* kept in control (A, S = 34.6) and experimental (B, S = 22.1) conditions for 48 h. The limbs have been removed to make the gills visible. g = gill. P = pereon segment. On the right hand side are close up views of the same gills excised after having been washed out with isosmotic saline.

undoubtedly result in disruption of ion transport across these surfaces (Spicer, 2013; Kiko et al., 2009). Therefore, we suggest that although *P. miersi* is capable of regulating extracellular K^+ and Ca^{2+} concentrations when exposed to reduced salinities over the range investigated here, it is an osmoconformer that can sustain structural damage to the gills, consistent with osmotic swelling, even with only a modest reduction in salinity. Furthermore, reductions in salinity will likely compromise any regulatory ability that is present and that involves those gills. This stands in stark contrast to the benthic Arctic amphipods investigated to date, many of which show reasonably well developed hyper-iso-osmotic regulation. That said it is consistent with the inability of many other Antarctic invertebrate species to osmoregulate and (apart from the two echinoderm species investigated by Barrett et al., 2024, 2025) cope with reduced salinity (see Introduction for references). This is perhaps unsurprising given that Arctic waters experience much greater and more frequent salinity changes particularly in nearshore and estuarine environments (where many amphipod species are found), compared with the Antarctic (Silvano et al., 2025). Thus, there is likely to be stronger ecological pressure to evolve (or retain) a strong osmoregulatory capacity in the Arctic than in the relatively stable Antarctic environments.

The increase in haemolymph Mg^{2+} in hyposaline conditions was striking. Wittmann et al. (2010) interpreted the high values of Mg^{2+} that we see in isopod haemolymph as evidence that this ion is poorly regulated. If correct we may hypothesise that haemolymph Mg^{2+} in *P. miersi* is also poorly regulated. This hypothesis is lent support from the fact that when *P. miersi* was exposed to low salinity conditions haemolymph Mg^{2+} showed the most pronounced rise in concentration (from 25.32 to 39.04 mmol.L^{-1}, but did not become iso-ionic (46.2 mmol.L^{-1}) with the dilute sea water (S = 28.0). So the difference between seawater and haemolymph Mg^{2+} (indicative of regulatory ability) was 17.08 mmol.L^{-1} under control conditions compared to 7.16 mmol.L^{-1} at S = 28.0, a 62 % reduction. Therefore, we might infer that this reduction points to impaired, but not no, Mg^{2+} regulation as there is still a difference between sea water and haemolymph Mg^{2+} concentrations.

In many crustaceans including amphipods the antennal gland, and not just the gills, is involved in regulating Mg^{2+} a known narcotising agent – in the haemolymph. This suggests that the antennal gland may also be affected by hyposaline exposure and not just the gills. In the freshwater amphipod *Gammarus pulex,* and other (but by no means all) crustaceans, an increase in Mg^{2+} concentration resulted in a reduction (by substrate inhibition) in the activity of the gill Na^+/K^+ ATPase and other enzyme activity (Holliday, 1985; Brooks and Mills, 2006) which presumably affect physiological functions even in an osmoconformer, The proportions of the four cations (as a proportion of ion concentrations in sea water, S = 34.6) in the haemolymph of *P. miersi* are presented in Fig. 6 together with other Antarctic amphipod and isopod species for which we have information (Wittmann et al., 2010). In all cases extracellular Na^+ is very similar to the concentration of this ion in sea water.

The three Amphilochidon amphipods for which we have data have approximately the same proportions of ions in the haemolymph as are found in sea water, and according to Wittmann et al. (2010) are very similar to what we see in temperate amphipods. The main difference is that *Eusirus propeperdentatus* has a much lower haemolymph Mg^{2+} concentration than the other two species. *Paraceradocus miersi* belongs to a completely different suborder from these three species and while it has a similar haemolymph Na^+ concentration, differs dramatically in the remaining three ions, particularly Mg^{2+} which is X 2.5 greater than the Amphilochidon species. Apart from haemolymph Na^+, the ionic content of *P. miersi* is more similar to the Antarctic isopods (high K^+ and Mg^{2+} ions) for which we have data, despite the phylogenetic distance between them (see Fig. 5). This raises the possibility of convergent evolution although it is difficult to envisage what the advantage of high Mg^{2+} (which acts as a relaxant) is in the two largest species within the Antarctic amphipods and isopods. Furthermore, it is interesting that our data fit the relationship found by Burton (1995) who demonstrated a significant positive relationship between haemolymph K^+ and both Mg^{2+} (and Na^+) concentrations across 77 crustacean species. He concluded that haemolymph composition has evolved in such a way as to preserve the transmembrane potential across the cell membrane.

In conclusion, significant 'summer' freshening events have been rare in Ryder Bay where *Paraceradocus miersi* were collected but not absent. The most severe event on record (minimum S ~ 28) occurred in 2017 immediately before the experiments reported here were carried out. It would have been sufficient to, at best, result in impaired extracellular ion balance, and at worst result in the death of this osmoconforming species. Giant marine invertebrates are already at risk from a warming ocean primarily because of a temperature related reduction in dissolved oxygen (Spicer and Morley, 2019). We suggest that the Antarctic amphipod *Paraceradocus miersi* will not fare well if freshening continues in a warming world. They are osmoconformers and internal ion balance (particularly Mg^{2+}) is impaired or even breaks down even under moderate freshening conditions.

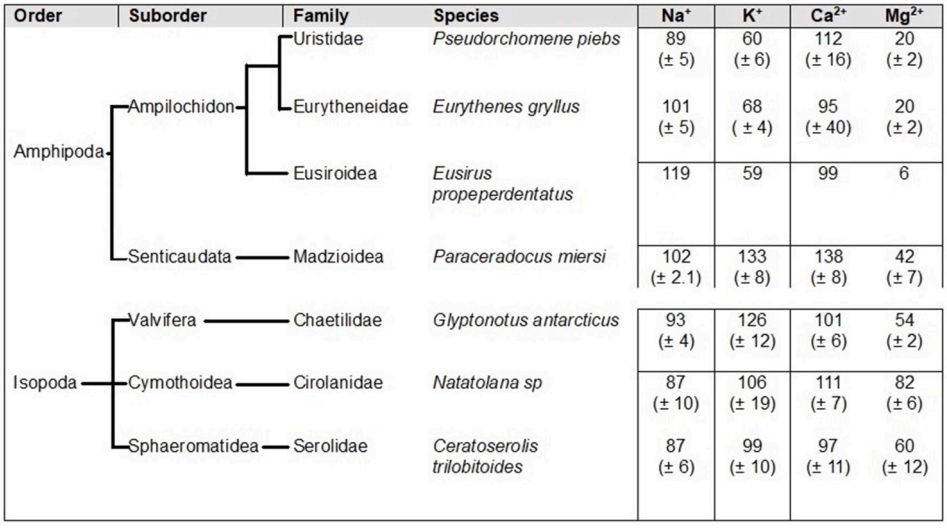

Fig. 6. Cation concentrations for the Antarctic amphipod and isopod species for which information is available (from Wittmann et al., 2010 except *Paraceradocus miersi*, which is this study) presented within a phylogenetic framework. Ions are expressed as percentages of the ions concentration in the sea water they were kept in.

CRediT authorship contribution statement

John I. Spicer: Conceptualization, Formal analysis, Funding acquisition, Investigation, Methodology, Writing – original draft. **Simon A. Morley:** Conceptualization, Funding acquisition, Methodology, Writing – review & editing. **Katie N.G. Thiessen:** Investigation, Methodology, Writing – review & editing. **Lloyd S. Peck:** Conceptualization, Funding acquisition, Writing – review & editing.

Data accessibility

The datasets supporting this article will be uploaded as part of the Supplementary Material.

Ethics statement

All research was conducted under Antarctic Treaty permits (28/2016) issued by the UK Foreign, Commonwealth and Development Office to British Antarctic Survey. Experiments were conducted on marine invertebrate species not protected under the UK Animals (Scientific Procedures) Act 1986 and although ethical approval was not required the highest possible standards of animal welfare were applied.

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Declaration of competing interests

The authors declare that they have no known competing financial interests or personal relationships that could have appeared to influence the work reported in this paper.

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Data availability

Data will be made available on request.

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