

# Ion regulatory capacity and the biogeography of Crustacea at high southern latitudes

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**Abstract** Brachyuran and anomuran decapod crabs do not occur in the extremely cold waters of the Antarctic continental shelf whereas caridean and other shrimp-like decapods, amphipods and isopods are highly abundant. Differing capacities for extracellular ion regulation, especially concerning magnesium, have been hypothesised to determine cold tolerance and by that the biogeography of Antarctic crustaceans. Magnesium is known to have a paralysing effect, which is even more distinct in the cold. As only few or no data exist on haemolymph ionic composition of Sub-Antarctic and Antarctic crustaceans, haemolymph samples of 12 species from these regions were analysed for the concentrations of major inorganic ions ( $\text{Na}^+$ ,  $\text{K}^+$ ,  $\text{Ca}^{2+}$ ,  $\text{Mg}^{2+}$ ,  $\text{Cl}^-$ ,  $\text{SO}_4^{2-}$ ) by ion chromatography. Cation relationships guaranteed neuromuscular excitability in all species. Sulphate and potassium correlated positively with magnesium concentration. The Antarctic caridean decapod as well as the amphipods maintained low (6–20% of ambient sea water magnesium concentration), Sub-Antarctic brachyuran and anomuran crabs as well as the Antarctic isopods high (54–96% of ambient sea water magnesium concentration) haemolymph magnesium levels. In conclusion, magnesium regulation may explain the biogeography of decapods, but not that of the peracarids.

**Keywords** Antarctic · Haemolymph ion composition · Decapoda · Isopoda · Amphipoda · Magnesium

## Introduction

Decapod crustacean diversity is low in Antarctic compared to Sub-Antarctic regions (Gorny 1999). Over 130 benthic and pelagic decapod species occur in the Southern Ocean, but only 27 species are present south of the Polar Frontal Zone (PFZ). Brachyuran crabs are completely absent, whereas at least nine species of the anomuran family Lithodidae have been found south of the PFZ (Gorny 1999; García Raso et al. 2005; Thatje et al. 2005). Anomuran and brachyuran crabs still inhabited nearshore habitats of Antarctica in the late Eocene (Feldmann and Zinsmeister 1984a, b). The extinction or migration of brachyuran crabs, which today are restricted to warmer shallow waters of the Sub-Antarctic (Gorny 1999), likely happened during cooling trends in the Miocene, when isopods radiated in the Antarctic and occupied ecological niches vacated by the decapods (Aronson et al. 2007 and references therein; Brandt 1999; Held 2000). Accordingly, amongst the Crustacea the taxon Peracarida is the most abundant and speciose in the Antarctic today, with over 400 isopod and over 500 amphipod species (Brandt 1999; Gutt et al. 2004).

Antarctica is encircled by a strong water current (Antarctic Circumpolar Current or ACC), which developed during the Oligocene and led to climatic cooling of the Southern Ocean (Lawver and Gahagan 2003). At about 50°S cold water masses coming from the South (surface temperature ca. 2°C) meet warmer waters from the North (surface temperature ca. 8°C; Orsi et al. 1995). The sharp change in water temperature is detectable to significant depth and may pose an oceanographic barrier, called the Polar Front. However, near the bottom this difference will be less distinct, depending on the depth of the seabed (Orsi et al. 1995). Potential seabed temperatures at 50°S are ca. 2°C on continental shelf (0–1,000 m), 0–2°C on continental slope

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(1,000–3,000 m) and  $-1-0^{\circ}\text{C}$  in deep-sea areas ( $>3,000$  m; Clarke et al. 2009). At high southern latitudes, seabed potential temperature is highest on the shelf of the western Antarctic Peninsula (ca.  $1^{\circ}\text{C}$ ), whereas it is lowest on the shelves of the Weddell and Ross Seas (ca.  $-1.5^{\circ}\text{C}$ ; Clarke et al. 2009).

The repeated extension and retreat of the Antarctic shelf ice and formation and melting of a multiyear sea-ice layer during earth history might have contributed to the current distribution pattern of Antarctic crustaceans. Expansion periodically reduced the space of the shelf habitat and due to a decline of light penetration decreased primary productivity. This may have selected for species, which were able to adapt to or were already adapted to continental slope or deep-sea environments. This may explain why the recent invertebrate shelf fauna is characterised by a large number of eurybathic species (Brey et al. 1996) and of groups, which are important components of the deep-sea fauna, like echinoderms and isopods (Aronson et al. 2007). Furthermore, skeleton-crushing predators amongst crabs and fish are missing. These predators disappeared at about the same time when climatic cooling occurred. Declining predation pressure caused a fundamental shift in the structure of the Antarctic benthic community and a reestablishment of its archaic character that we observe today (Aronson et al. 2007).

South of the PFZ, species-level endemism is high in the ocean (Arntz et al. 1997). However, endemism may have been overestimated and there are species, which occur both north and south of the PFZ (Barnes and Peck 2008; Thatje et al. 2005). Furthermore, larvae of South American decapod species have been found in Antarctic water masses (Thatje and Fuentes 2003). This indicates that isolation of the Antarctic continent may not be as pronounced as formerly thought and that reinvasion is possible (Clarke et al. 2005). However, the establishment of a species on the Antarctic shelf requires adaptations to constantly low temperature, high pressure and pronounced seasonality of available resources (Aronson et al. 2007; Clarke 1988; Clarke et al. 2009).

Reproductive and developmental adaptations have been discussed to determine decapod distribution patterns (Thatje et al. 2003). Many subpolar and polar marine invertebrate groups have evolved a high degree of endotrophy and an abbreviation of larval development to compensate for scarcity and pronounced seasonality of food supply (Thorson's rule, Mileikovsky 1971; Clarke 1988). Whereas lithodid crab species as well as caridean shrimp species have adopted these characteristics to various degrees, there are only few subpolar brachyuran species, which have developed these traits (Thatje et al. 2003). By contrast, peracarids keep their young in a brood pouch until they have completed direct development to juveniles (Luxmoore 1982; Ruppert and Barnes 1994). The female will protect

their young from predators and might even provide nutrition to the more advanced offspring (Heilmayer et al. 2008; Janssen and Hoese 1993). It is interesting to note in this context, that similar to the echinoderms of the Antarctic shelf (Poulin et al. 2002), the number of crustacean species with planktonic larvae (decapods) has declined during earth history, whereas brooding crustaceans (peracarids) have radiated.

The biogeography of lithodid crabs is probably constrained by temperature, as this group has only been found in waters warmer than  $0^{\circ}\text{C}$  (Hall and Thatje 2009) with their southernmost habitat being the continental slope of the western Antarctic Peninsula in the Bellingshausen Sea (García Raso et al. 2005; Thatje et al. 2008). In contrast, caridean decapods as well as amphipods and isopods tolerate temperatures as low as  $-1.8^{\circ}\text{C}$ , and are frequently observed in shallower waters of the continental shelf of Antarctica (Brandt 1999; Gutt et al. 1991). Most rates of locomotory activity as well as metabolic and developmental rates are slower in polar than in temperate species with similar ecological function. This indicates that these processes are not or only poorly temperature-compensated (Barnes and Peck 2008; Young et al. 2006).

Furthermore, the activity level (quantified as righting or walking speed, relative heart rate and oxygen consumption) is negatively correlated with haemolymph magnesium concentration in decapods (Sartoris et al. 1997; Walters and Uglow 1981; Watt et al. 1999) and amphipods (Spicer et al. 1994), as reviewed by Morritt and Spicer (1993). This might be based on the fact that magnesium slows down neuromuscular transmission by blocking calcium channels, which makes it useful as anaesthetic (Iseri and French 1984; Katz 1936; Lee et al. 1996; Pantin 1948; Waterman 1941). Quantal content of crayfish axons, a direct measure of transmitter release, is reduced at high extracellular magnesium concentration (Parnas et al. 1994). Magnesium inhibits the secretion of neurohormones from the X-organ sinus gland of the land crab *Cardisoma carnifex* at physiological extracellular levels of  $10-15\text{ mmol L}^{-1}$  by blocking calcium currents (Richmond et al. 1995). Similarly, low temperature reduces the amount of transmitter release in crayfish axons, which is thought to be the result of reduced calcium influx through calcium channels (Dunn and Mercier 2003). High haemolymph magnesium concentration and low temperature may therefore work in concert to decline neuromuscular transmission and rates of activity. For example Frederich et al. (2000b) observed that the spider crab *Hyas araneus* was threefold slower at righting itself at  $-2^{\circ}\text{C}$  (18.5 s) than at temperatures above  $0^{\circ}\text{C}$  (6.5 s). When magnesium concentration was experimentally reduced from the natural level of  $50$  to  $6\text{ mmol L}^{-1}$ , the mean time-to-right remained at 6.5 s over the entire investigated thermal range ( $-2-6.5^{\circ}\text{C}$ ).

Moreover, all muscular systems, including those of ventilation and circulation may be affected (Frederich 1999; Frederich et al. 2000a, b). Low temperature may constrain physiological functions and this may influence the distribution pattern of crustaceans, following the rationale of the concept of oxygen limited thermal tolerance (Pörtner 2002). In the temperate spider crab *Maja squinado*, tolerance to cold was constrained by inefficient ventilation of the gills and reduced circulation of the haemolymph, which led to a decline of haemolymph oxygenation and finally to the onset of anaerobic metabolism during progressive cooling (Bock et al. 2001; Frederich and Pörtner 2000). Judged from a threefold increase in mean cardiac output, the low threshold for optimal performance (pejus temperature) of *Maja squinado* was shifted from 8 to 6°C in an incubation of low magnesium concentration (6 mmol L<sup>-1</sup>) compared to natural conditions (50 mmol L<sup>-1</sup>, Frederich et al. 2000a). Based on these and further results, the hypothesis was brought forward that crustaceans which are thought to have a high capacity for haemolymph magnesium extrusion (caridean shrimps, amphipods and isopods) would be more cold tolerant than those crustaceans which are thought to be poor magnesium regulators (brachyuran and anomuran crabs, Sartoris et al. 1997; Frederich et al. 2000b). Today, this seems to be accepted as the primary explanation for the biogeography of crustaceans in Antarctica (Aronson et al. 2007; Thatje et al. 2005). Whereas there is experimental evidence for the relationships between temperature, magnesium and physiological functions in temperate and subpolar brachyuran crabs (Frederich et al. 2000a, b), temperate and polar caridean shrimps (Sartoris and Pörtner 1997a, b) and temperate amphipods (Spicer et al. 1994), we do not know whether there is a relation between temperature, the capacity for magnesium extrusion and other physiological functions in anomuran crabs, amphipods, isopods and other crustacean groups from the Southern Ocean.

Primary sites for extracellular ion regulation are the gills and the antennal (decapods, amphipods) or maxillary (isopods) glands (Ruppert and Barnes 1994). These tissues possess high concentrations of the enzyme Na<sup>+</sup>/K<sup>+</sup>-ATPase, which provides at least part of the driving force for trans-epithelial ion transport (Khodabandeh et al. 2005; Lucu and Towle 2003). Sodium, chloride and calcium ion uptake and secretion may take place across the gill epithelium. In osmoregulating brachyuran crabs, ionocytes are especially abundant in the posterior gills. These exhibit a higher Na<sup>+</sup>/K<sup>+</sup>-ATPase activity than the anterior portion of the gills, which are characterised by a thin epithelium facilitating gas exchange (Copeland and Fitzjarrell 1968; Neufeld et al. 1980). Urine formation together with magnesium and sulphate excretion occurs in the antennal glands. Furthermore, calcium and potassium ions may be reabsorbed in exchange for sodium at this site (reviewed by Freire et al. 2008).

In those crustaceans, which have been investigated so far, haemolymph sodium, chloride and potassium concentrations are usually kept at levels similar to those in sea water (Mantel and Farmer 1983). Extracellular calcium concentration varies during the molt cycle (Robertson 1960). Magnesium concentration is strongly hyporegulated in caridean shrimp, amphipod and most isopod species ( $[Mg^{2+}]_{HL} < 20 \text{ mmol L}^{-1}$ ) and to a much lesser extent in anomuran and brachyuran crab species ( $[Mg^{2+}]_{HL} = 20\text{--}50 \text{ mmol L}^{-1}$ , Burton 1995 and references therein; Frederich 1999; Robertson 1953). Sulphate seems to show the same pattern, but only few measurements have been undertaken, particularly few in amphipods and isopods (Mantel and Farmer 1983).

In this study, we present the first analyses of ionic composition of the haemolymph of Antarctic amphipods and isopods and of lithodid crab species occurring near Sub-Antarctic islands. Altogether, we provide information on 12 species of decapods, isopods and amphipods and discuss the results with a focus on the hypothesis that extracellular magnesium regulation shapes the biogeography of crustaceans in the Southern Ocean.

## Materials and methods

### Sample collection

Haemolymph samples of *Lithodes confundens*, *Paralomis formosa*, *Paralomis spinosissima* and *Peltarion spinosulum* were collected during the ICEFISH Cruise in June 2004 (<http://www.icefish.neu.edu/>). Specimens of *Notocrangon antarcticus*, *Eurythenes gryllus*, *Abyssoorchomene plebs*, *Eusirus propeperdentatus*, *Glyptonotus antarcticus*, *Natatolana* sp. and *Ceratoserolis trilobitoides* were obtained during Polarstern expedition ANT XXIII/8 in the Antarctic summer 2007. Haemolymph samples were collected either on board directly (RV Nathaniel B. Palmer or RV Polarstern) or from live animals transported back to the Alfred Wegener Institute for Polar and Marine Research in Bremerhaven, Germany (AWI) after an acclimation period of 1 week at 0°C and 32.5 ppt. Male specimens of *Paralomis granulosa* were obtained from local fishermen in Punta Arenas, Chile in April 2008, the collection site is therefore not known precisely (Table 1). These animals were transported to the AWI on board RV Polarstern and kept in a recirculating aquarium system at 4°C and 32.5 ppt for 1 year until haemolymph samples were taken. Laboratory-kept animals were fed ad libitum with pieces of *Mytilus edulis*, *Cerastoderma edule* or *Crangon crangon*.

Animals were blotted dry before haemolymph was withdrawn either with a syringe and hypodermic needle, which was inserted through an arthrodistal membrane at the coxa of

**Table 1** Collection sites, mean fishing depth (m) of the sampled crustaceans and approximate ambient water temperature (°C) at the time of collection (Locarnini et al. 2006)

Taxon	Species	Collection sites	Depth (m)	Temperature (°C)
Decapoda, Brachyura	<i>Peltarion spinosulum</i>	51°41' S, 57°27' W	130	6.0
Decapoda, Anomura	<i>Lithodes confundens</i>	53°39' S, 40°44' W	410	2.0
	<i>Paralomis formosa</i>	56°19' S, 27°27' W	340	1.0
	<i>Paralomis granulosa</i>	Magellan region	Unknown	5.0–8.0?
	<i>Paralomis spinosissima</i>	53°39' S, 40°44' W	410	2.0
Decapoda, Caridea	<i>Notocrangon antarcticus</i>	65° 32' S, 61° 30' W	490	–1.0 to –0.5
Peracarida, Amphipoda	<i>Abyssorhomene plebs</i>	60° 57' S, 55° 55' W	231	0.0
	<i>Eurythenes gryllus</i>	62° 58' S, 57° 58' W	839	1.5
	<i>Eusirus propeperdentatus</i>	62° 58' S, 57° 58' W	839	1.5
Peracarida, Isopoda	<i>Glyptonotus antarcticus</i>	61° 20' S, 55° 32' W	137	–1.0
		62° 19' S, 60° 27' W	109	–1.0
	<i>Natanolana</i> sp.	60° 57' S, 55° 55' W	231	0.0
	<i>Ceratoserolis trilobitoides</i>	70° 31' S, 8° 48' W	297	0.0
		61° 22' S, 56° 1' W	353	–0.5

a walking leg (crabs), in the heart region (*N. antarcticus*, *E. gryllus*, *E. propeperdentatus*) or by inserting a pointed glass capillary dorsally into the heart region of the animals (remaining species). Samples were stored at –20°C or –80°C until being analysed.

Sea water ion composition at 35 ppt salinity was taken from Atkinson and Bingman (1997) for comparison with field-sampled individuals and calculated for 32.5 ppt for comparison with laboratory-kept animals (Table 2).

#### Ion chromatography

Ion composition of haemolymph was determined by ion chromatography (ICS-2000, Dionex®, Idstein, Germany) after dilution of the samples with deionised water. A conductivity cell and a self-regenerating suppressor were used to reduce background conductivity. Cations ( $\text{Na}^+$ ,  $\text{K}^+$ ,  $\text{Mg}^{2+}$ ,  $\text{Ca}^{2+}$ ) were separated on an IonPac® CS16 column with methane sulfonic acid ( $30 \text{ mmol L}^{-1}$ ) as eluent at a flow rate of  $0.36 \text{ mL min}^{-1}$  at 40°C. Anions ( $\text{Cl}^-$ ,  $\text{SO}_4^{2-}$ ) were separated on an IonPac® AS11-HC column with potassium hydroxide ( $30 \text{ mmol L}^{-1}$ ) as eluent at a flow rate of  $0.30 \text{ mL min}^{-1}$  at 30°C. Ion concentrations were calculated in  $\text{mmol L}^{-1}$  relative to the Dionex® Six Cation-II or Five Anion Standards and are also given in percent of the ambient sea water ion concentrations to make data of field-sampled and laboratory-kept animals comparable.

#### Statistical analyses

Before calculating means  $\pm$  standard deviation (SD), outliers were identified by use of the Nalimov test on the sum of

all ions of each individual. One-way ANOVA and post hoc Dunnett's multiple comparison tests were run to compare means of percentages of ions in haemolymph with those of sea water (always 100%). Differences were termed "significant" if *p* values were below 0.05. ANOVA as well as linear regression and Pearson correlation analyses were performed by use of Prism 4.0a.

#### Results

For each collection site monthly means of water temperatures at the respective depth were taken from Locarnini et al. (2006, Table 1). Anomuran and brachyuran decapods were found in waters with temperatures above 0°C while the caridean decapod *Notocrangon antarcticus* as well as most of the peracarids were collected in waters of or below 0°C.

All species except *Peltarion spinosulum* displayed significantly lower haemolymph magnesium levels compared to sea water (Fig. 1, Table 2). Despite of this, there are differences in the extent of downregulation of magnesium between groups. Whereas brachyuran and anomuran decapods as well as isopods maintained rather high haemolymph magnesium levels between  $54 \pm 2\%$  and  $82 \pm 6\%$  of sea water, those of the caridean decapod *Notocrangon antarcticus* and the amphipods were well below half of the value of sea water, between 6% (*E. propeperdentatus*) and  $20 \pm 2\%$  (*E. gryllus*).

Likewise, the haemolymph sulphate content of all species except that of *Peltarion spinosulum* was significantly lower than that in sea water (Table 2). The amphipod *E. gryllus* exhibited the lowest value of  $7 \pm 2\%$ .

**Table 2** Haemolymph inorganic ion composition of Sub-Antarctic and Antarctic crustaceans determined by ion chromatography (mmol L<sup>-1</sup>) and expressed as percent of ambient sea water ion concentrations given as means  $\pm$  SD, *n* number of individuals sampled

	<i>n</i>	Unit	Na <sup>+</sup>	Cl <sup>-</sup>	K <sup>+</sup>	Ca <sup>2+</sup>	Mg <sup>2+</sup>	SO <sub>4</sub> <sup>2-</sup>
Sea water		%	100	100	100	100	100	100
32.5 ppt		mmol L <sup>-1</sup>	446	522	9.7	9.8	50.3	26.6
35 ppt		mmol L <sup>-1</sup>	481	563	10.4	10.5	54.2	28.6
<i>Peltarion spinosulum</i> <sup>a</sup>	4	%	99 $\pm$ 4	85 $\pm$ 7	112 $\pm$ 12	51 $\pm$ 34*	96 $\pm$ 4	104 $\pm$ 12
		mmol L <sup>-1</sup>	477 $\pm$ 19	479 $\pm$ 39	11.6 $\pm$ 1.2	5.4 $\pm$ 3.5	51.7 $\pm$ 1.9	30.3 $\pm$ 3.4
<i>Lithodes confundens</i> <sup>a</sup>	9	%	100 $\pm$ 6	88 $\pm$ 7	133 $\pm$ 20*	119 $\pm$ 14	68 $\pm$ 15*	77 $\pm$ 12*
		mmol L <sup>-1</sup>	478 $\pm$ 28	505 $\pm$ 43	13.9 $\pm$ 2.0	12.5 $\pm$ 1.4	37.0 $\pm$ 7.6	22.4 $\pm$ 3.4
<i>Paralomis formosa</i> <sup>a</sup>	7	%	106 $\pm$ 5	100 $\pm$ 3	101 $\pm$ 10	104 $\pm$ 17	73 $\pm$ 7*	79 $\pm$ 14*
		mmol L <sup>-1</sup>	508 $\pm$ 24	563 $\pm$ 17	10.6 $\pm$ 1.0	10.9 $\pm$ 1.8	39.5 $\pm$ 3.8	22.8 $\pm$ 4.1
<i>Paralomis granulosa</i> <sup>b</sup>	8	%	97 $\pm$ 2	94 $\pm$ 3	118 $\pm$ 13	110 $\pm$ 5	80 $\pm$ 4*	63 $\pm$ 8*
		mmol L <sup>-1</sup>	431 $\pm$ 11	491 $\pm$ 15	11.4 $\pm$ 1.3	10.8 $\pm$ 0.5	40.0 $\pm$ 1.9	16.9 $\pm$ 2.2
<i>Paralomis spinosissima</i> <sup>a</sup>	10	%	99 $\pm$ 3	95 $\pm$ 5	105 $\pm$ 10	106 $\pm$ 16	75 $\pm$ 5*	71 $\pm$ 8*
		mmol L <sup>-1</sup>	475 $\pm$ 15	533 $\pm$ 29	10.9 $\pm$ 1.0	11.2 $\pm$ 1.7	40.7 $\pm$ 2.6	20.5 $\pm$ 2.4
<i>Notocrangon antarcticus</i> <sup>a</sup>	6	%	98 $\pm$ 7	82 $\pm$ 9*	72 $\pm$ 16*	140 $\pm$ 20	16 $\pm$ 11*	33 $\pm$ 10*
		mmol L <sup>-1</sup>	476 $\pm$ 34	477 $\pm$ 60	7.7 $\pm$ 1.7	14.5 $\pm$ 2.0	11.0 $\pm$ 8.5	10.6 $\pm$ 4.0
<i>Abyssorhomene plebs</i> <sup>b</sup>	5	%	89 $\pm$ 5	77 $\pm$ 4*	60 $\pm$ 6*	112 $\pm$ 16	20 $\pm$ 2*	33 $\pm$ 9*
		mmol L <sup>-1</sup>	397 $\pm$ 22	404 $\pm$ 21	5.9 $\pm$ 0.6	11.0 $\pm$ 1.6	10.0 $\pm$ 0.8	8.9 $\pm$ 2.3
<i>Eurythenes gryllus</i> <sup>a</sup>	10	%	101 $\pm$ 5	95 $\pm$ 5	68 $\pm$ 4*	95 $\pm$ 40	20 $\pm$ 2*	7 $\pm$ 2*
		mmol L <sup>-1</sup>	479 $\pm$ 29	530 $\pm$ 36	7.1 $\pm$ 0.4	9.9 $\pm$ 4.0	11.1 $\pm$ 0.9	2.0 $\pm$ 0.6
<i>Eusirus propeperdentatus</i> <sup>a</sup>	2	%	119	112	59	99	6	33
		mmol L <sup>-1</sup>	574	629	6.2	10.4	3.5	9.7
<i>Glyptonotus antarcticus</i> <sup>b</sup>	5	%	93 $\pm$ 4	93 $\pm$ 4	126 $\pm$ 12	101 $\pm$ 6	54 $\pm$ 2*	31 $\pm$ 2*
		mmol L <sup>-1</sup>	415 $\pm$ 15	509 $\pm$ 53	12.2 $\pm$ 1.2	9.8 $\pm$ 0.6	30.4 $\pm$ 8.5	12.4 $\pm$ 9.6
<i>Natanolana</i> sp. <sup>b</sup>	6	%	87 $\pm$ 10*	83 $\pm$ 10*	106 $\pm$ 19	111 $\pm$ 7	82 $\pm$ 6*	46 $\pm$ 10*
		mmol L <sup>-1</sup>	390 $\pm$ 47	437 $\pm$ 52	10.3 $\pm$ 1.8	10.9 $\pm$ 0.7	41.0 $\pm$ 3.0	12.5 $\pm$ 2.6
<i>Ceratoserolis trilobitoides</i> <sup>b</sup>	6	%	87 $\pm$ 6*	83 $\pm$ 8*	99 $\pm$ 10	97 $\pm$ 11	60 $\pm$ 12*	69 $\pm$ 10*
		mmol L <sup>-1</sup>	388 $\pm$ 25	435 $\pm$ 41	9.6 $\pm$ 0.92	9.5 $\pm$ 1.0	29.8 $\pm$ 5.8	18.7 $\pm$ 2.7

<sup>a</sup> Field sampling, % values calculated in relation to ambient sea water with salinity 35 ppt

<sup>b</sup> Animals kept in the laboratory prior to sampling, fed ad libitum, % values calculated in relation to ambient sea water with salinity 32.5 ppt

\* Significantly different from ambient sea water (100%)

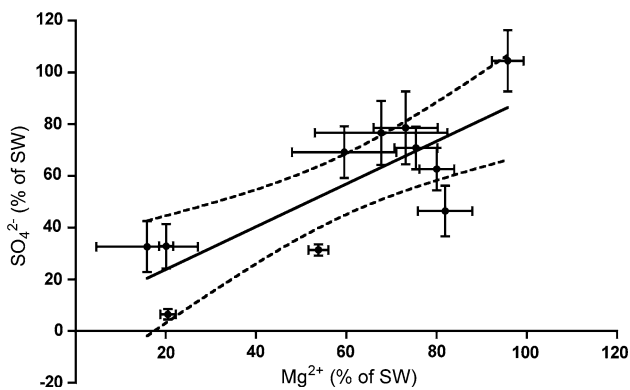
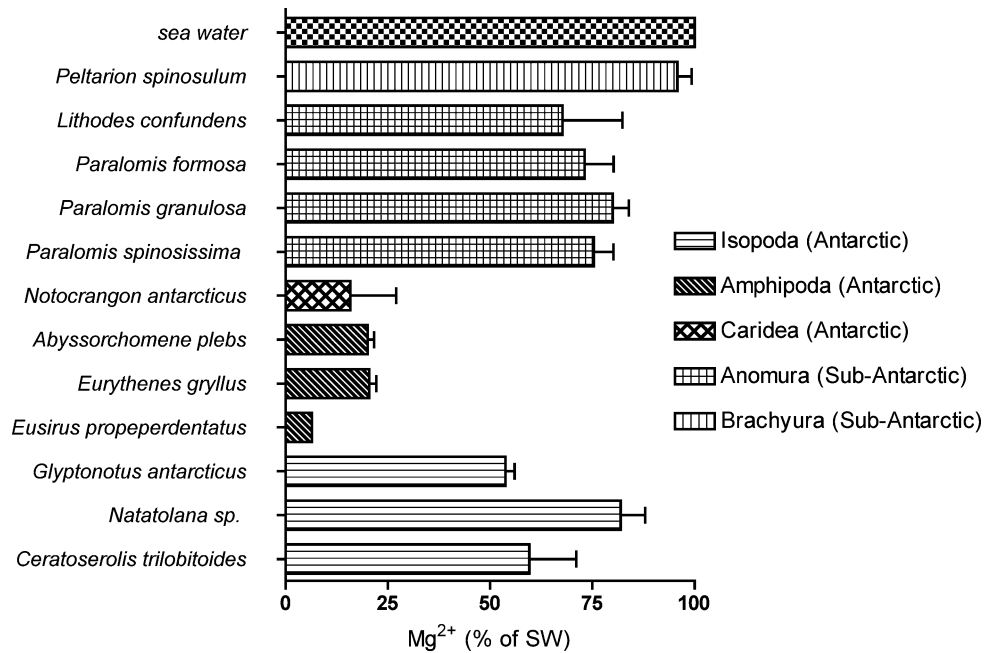
Species which maintained low haemolymph magnesium concentrations usually maintained low sulphate levels as well (Fig. 2). This resulted in a significantly ( $p = 0.0023$ ) positive, linear correlation between magnesium and sulphate percentages with Pearson  $r = 0.8147$  and  $r^2 = 0.6638$  where all investigated species were considered, except *E. propeperdentatus*, which was excluded because of the small sample size. Only the isopod *Natanolana* sp., which showed a significantly reduced sulphate percentage in spite of a high magnesium percentage deviated from this relationship.

Haemolymph sodium content was equal to or slightly lower than in sea water in most species and only significantly reduced in *Natanolana* sp. and *C. trilobitoides* with values of  $87 \pm 10\%$  and  $87 \pm 6\%$  (Table 2).

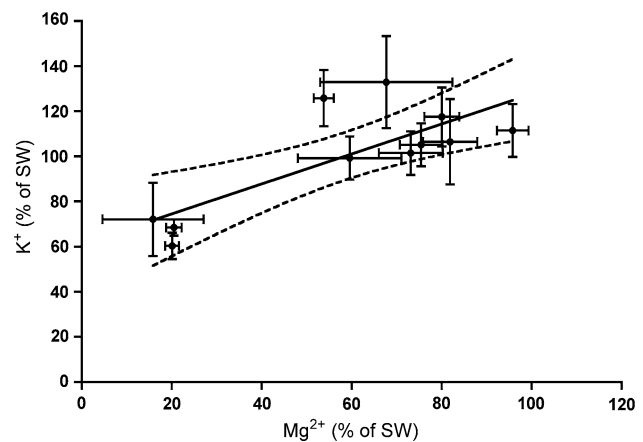
In most investigated species haemolymph calcium was not significantly different from the sea water level. Only *Peltarion spinosulum* exhibited a remarkably low value of  $54 \pm 34\%$  of sea water calcium concentration (Table 2).

Haemolymph potassium concentrations were close to sea water level in the majority of species. However, *E. propeperdentatus* displayed an extremely low value of 59%, *N. antarcticus*, *A. plebs* and *E. gryllus* had significantly decreased potassium values and *L. confundens* had a significantly increased level compared to sea water (Table 2). Furthermore, there was a significantly ( $p = 0.0044$ ) positive correlation between magnesium and potassium percentages amongst all species in this study (*E. propeperdentatus* was excluded) with Pearson  $r = 0.7824$  (Fig. 3).

**Fig. 1** Magnesium concentration in the haemolymph of Sub-Antarctic and Antarctic crustaceans (% of ambient sea water magnesium concentration). Values are means  $\pm$  SD. All values except that of *Peltarion spinosulum* are significantly different from ambient sea water (100%)



**Fig. 2** Relationship between magnesium and sulphate in the haemolymph (% of ambient sea water ion concentrations) of all species investigated except *Eusirus propeperdentatus*, which was excluded because of the low sample size. Significant positive correlation with Pearson  $r = 0.8147$ ,  $p = 0.0023$ , and linear regression of  $r^2 = 0.6638$  with 95% confidence bands. Values are means  $\pm$  SD



**Fig. 3** Relationship between magnesium and potassium in the haemolymph (% of ambient sea water ion concentrations) of all species investigated except *Eusirus propeperdentatus*, which was excluded because of the low sample size. Significant positive correlation (Pearson  $r = 0.7824$ ,  $p = 0.0044$ ) and linear regression of  $r^2 = 0.6122$  with 95% confidence bands. Values are means  $\pm$  SD

Haemolymph chloride levels of most investigated animals were equal to or lower than that in sea water. In *N. antarcticus*, *A. plebs*, *Natatolana sp.* and *C. trilobitoides* haemolymph chloride content even was significantly below that of sea water and comprised only  $82 \pm 9\%$  of the sea water concentration in *N. antarcticus* (Table 2).

## Discussion

Sub-Antarctic lithodid crab species exhibited a relatively low but significant capability for magnesium extrusion from the haemolymph. Our data compare well to those

obtained in previous studies on the northern species *Lithodes maja* (where  $[Mg^{2+}]_{HL} = 50 \text{ mmol L}^{-1}$ , which corresponds to about 92% of sea water concentration, Robertson 1953), *Paralithodes camtschatica* ( $[Mg^{2+}]_{HL} = 37 \text{ mmol L}^{-1}$ ,  $\approx 69\%$ , Mackay and Prosser 1970) and *Neolithodes grimaldii* collected during summer ( $[Mg^{2+}]_{HL} = 33 \text{ mmol L}^{-1}$ ,  $\approx 61\%$ , McAllen et al. 2005). However, our value for *P. granulosa* is twice as high as that recorded by Frederich (1999) for this species ( $17\text{--}24 \text{ mmol L}^{-1}$ ,  $\approx 31\text{--}44\%$ ). This difference might be attributable to a different nutritional state of the animals because McAllen et al. (2005) found significantly lower haemolymph magnesium levels

( $[Mg^{2+}]_{HL} = 20 \text{ mmol L}^{-1}$ ,  $\approx 37\%$ ) in *N. grimaldii* along with significantly lower haemolymph protein levels during spring when food was presumably scarce. Extracellular protein concentration decreases during starvation (Dall 1974). Whereas the activation of energy demanding magnesium excretion appears paradoxical during food deprivation, its physiological role could be an activation of the organism to trigger foraging activity (McAllen et al. 2005). An increase in walking activity was observed when brachyuran crabs were experimentally exposed to artificial sea water with reduced magnesium concentration (Frederich et al. 2000b).

The haemolymph magnesium concentration of the brachyuran *Peltarion spinosulum* from the Falkland Islands did not differ significantly from that of sea water. Our data were similar to those previously recorded for *P. spinosulum* and for other subtidal brachyuran species from the Sub-Antarctic (e.g. *Eurypodius latreillei*; Frederich 1999) and from temperate northern latitudes (e.g. *Dromia vulgaris*, *Hyas araneus*; Robertson 1953; Frederich 1999).

Previous analyses of haemolymph ion composition in isopods were focused on species from intertidal, estuarine or semiterrestrial habitats. These species regulate magnesium down to below  $20 \text{ mmol L}^{-1}$  (Burton 1995 and references therein; Parry 1953; Ziegler et al. 2000). In contrast, the extracellular magnesium concentration of the deep-sea isopod *Bathynomus doderleini* does not differ from that of sea water (F.-Tsukamoto et al. 2000). Despite this, the relatively well-developed ability to downregulate magnesium in temperate intertidal isopods has been extrapolated to be valid for polar species and has served as a possible explanation for their advantage over decapod crabs to colonise high Antarctic waters (Frederich et al. 2000b; Thatje et al. 2005). Here, we showed that the capacity for magnesium regulation of the polar isopods was in the same range as that of the lithodid crabs. A high level of magnesium in the haemolymph therefore does not constrain the isopods to warmer waters. However, a correlation between the general life style/activity and haemolymph magnesium concentration may be postulated. *Glyptonotus antarcticus* exhibited a relatively low magnesium fraction and is described as a “rude carnivorous benthic scavenger and predator” (Janssen and Hoese 1993) and actively forages for food (C. Held, personal observation). *Natatolana* sp. possessed a high haemolymph magnesium fraction and are burrow dwellers similar to *Natatolana borealis* from Scottish waters (Taylor and Moore 1995). These animals adopt a sit-and-wait strategy (C. Held, personal observation): when dwelling in the burrow, the animals remain inactive except for ventilatory burrow irrigation. However, they exhibit excellent swimming behaviour once carrion or prey is detected by them. After feeding, they return to an inactive mode and digest while staying in their burrows. High extra-

cellular magnesium concentration and reduced activity levels may increase tolerance to hypoxia (Sartoris and Pörtner 1997a), which is frequently encountered by infaunal species. Whereas investigations on the relationships between nutritional state, activity, cold tolerance and haemolymph magnesium levels in isopods are still missing, we may hypothesise that neuromuscular transmission of isopods is less sensitive to magnesium than that of decapods. Furthermore, it is possible that haemolymph magnesium concentration varies according to the nutritional condition of the animals and that this influences their activity level. These adaptations may allow them to thrive in the extremely cold waters of the Antarctic shelf despite relatively high haemolymph magnesium concentration as observed in our well-fed laboratory animals.

The Antarctic amphipods as well as the caridean shrimp were found to be excellent magnesium regulators similar to their temperate counterparts (Mantel and Farmer 1983; Normant et al. 2005) or tropical oceanic relatives (Tentori and Lockwood 1990). Therefore, ion regulation is not constrained by low temperature but is compensated by these cold adapted species. This was also found in the Arctic amphipod *Apherusa glacialis* (Kiko et al. 2009), the northern caridean prawn *Pandalus borealis* (Sartoris and Pörtner 1997b) and the Antarctic caridean shrimp *Chorismus antarcticus* (Frederich 1999). In contrast, when the temperate amphipod sandhopper *Talitrus saltator* was exposed to winter cold, it ceased to extrude magnesium from the haemolymph and fell into a torpor state (Spicer et al. 1994). Similarly, the capacity for magnesium regulation was hampered in tropical pelagic amphipods, when experimentally exposed to temperatures far below their natural temperature range (Tentori and Lockwood 1990). Amongst the caridean shrimps, the temperate *Crangon crangon* exhibited increased haemolymph magnesium concentrations during short-term exposure to cold (Sartoris and Pörtner 1997a).

The strong positive correlation between haemolymph magnesium and sulphate levels indicates that sulphate is regulated in parallel to magnesium for compensation of osmotic equilibrium (Robertson 1953). The mechanisms for magnesium and sulphate excretion in the antennal gland are not known in detail, but there is evidence that they function independently of each other. When exposed to salinity variations, sulphate extrusion ceased earlier than magnesium extrusion in e.g., an amphipod (Kiko et al. 2009) and a brachyuran decapod (Zanders 1980). Furthermore, it is known from both lobster hepatopancreas and flounder kidney, that sulphate is exported by use of sulphate-anion exchangers (Gerencser et al. 2001). Sulphate excretion in the antennal gland may be based on a similar mechanism and therefore may work independently of magnesium transport.

Extracellular sodium, chloride and potassium were kept close to equilibrium with sea water in most species. This is a general pattern found in marine crustaceans (Mantel and Farmer 1983). Calcium is the major component of the carapace, therefore extracellular concentrations vary during the molt cycle (Mantel and Farmer 1983; Robertson 1960). Cation relationships were similar to those collected by Burton (1995) in over 70 sea water and freshwater crustacean species. He concluded that “haemolymph composition has evolved in such a way as to preserve the transmembrane potential” across the cell membrane. Maintenance of the transmembrane potential is crucial for animals, because it guarantees the excitability of nerve and muscle and drives ion transport processes (Eckert et al. 2000). If so, we can conclude from this, that our sampled individuals were in good health.

In summary, our results comply with previous assumptions and findings (Frederich et al. 2000b; Thatje et al. 2005), that lithodid crabs from the Southern Ocean are rather poor haemolymph magnesium regulators and do not thrive in waters colder than 0°C and that caridean shrimps which exhibit a high capacity for magnesium regulation can be found in high Antarctic waters of temperatures below 0°C. Amongst the peracarids, the Antarctic amphipod species displayed a magnesium regulatory capacity similar to species examined in previous studies from tropic, temperate and polar latitudes (Kiko et al. 2009; Mantel and Farmer 1983; Spicer et al. 1994; Tentori and Lockwood 1990). In contrast, the Antarctic isopods only regulated extracellular magnesium to the same extent as the lithodids. The isopods must therefore possess different physiological and ecological adaptations, which give them an advantage over the decapod crabs and which enable them to thrive in high Antarctic waters. Concerning the physiology, this could be a reduced sensitivity of neuromuscular systems to magnesium compared to the lithodid crabs. Apart from this, different reproductive traits, like a direct development of the young, which may remain rather inactive as they are carried in a brood pouch or different food preferences could have contributed to the success of the peracarids in the Antarctic (Janssen and Hoese 1993; Brandt 1999).

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**Conflict of interest statement** The authors declare that they have no conflict of interest

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