The excretion of nitrogen and phosphorus and changes in nitrogen content in the Antarctic amphipod *Waldeckia obesa* and isopod *Glyptonotus antarcticus* during long-term starvation

A. NĘDZAREK & K. STEPanowska

Department of Aquatic Bioengineering and Aquaculture, Faculty of Food Sciences and Fisheries, West Pomeranian University of Technology Szczecin, Poland

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Abstract

Seasonal food availability for benthic feeders in Antarctica can influence the level of excreted metabolites, which may then be a source of N and P for autotrophs. In this study, we examined the effects of starvation of *Waldeckia obesa* and *Glyptonotus antarcticus* on the excretion of both N and P, and the chemical composition of their bodies. N-NH$_4^+$ dominated in the pool of excreted nitrogen (93% and 77% of inorganic nitrogen, and 76% and 67% of total nitrogen, for *W. obesa* and *G. antarcticus*, respectively). Reactive phosphorus dominated in the pool of excreted phosphorus (72% and 65% of total phosphorus for *G. antarcticus* and *W. obesa*, respectively). The excretion of N-NH$_4^+$ (in μmol N h$^{-1}$ 100 g$^{-1}$) dropped from 3,687 (W. obesa) and 1,336 (G. antarcticus) in the first day to about 0.6 after 10 days of starvation (for both species). Phosphorus excretion was generally lower than that of nitrogen (on average 0.046 and 0.017 μmol P h$^{-1}$ 100 g$^{-1}$ for *G. antarcticus* and *W. obesa*, respectively), but no clear trend appeared with N as a result of starvation. The greatest decrease in nitrogen and protein content in *W. obesa* was recorded on the 3rd day of starvation (nitrogen: from 1.30% to 0.93%; protein: 8.15% to 5.80%) and in *G. antarcticus* on the 5th day of starvation (nitrogen: from 2.22% to 1.43%; protein: from 13.86% to 8.94%). Conclusions: (i) nitrogen and phosphorus compounds released by crustaceans may be a supplementary source of biogenic salts for autotrophs, (ii) nitrates constituting approx. 20% nitrogen may be used by phytoplankton in the period of new production, (iii) starvation reduces the excretion of N and P and the content of nitrogen and protein in crustaceans.

Keywords: Southern Ocean, invertebrates, protein, primary production, nutrient regeneration

1. Introduction

Global climate change is affecting the Antarctic Peninsula ecosystem, where warming in the second half of the twentieth century was greater than in other regions of Antarctica. Clear consequences of this have been observed in the terrestrial ecosystem, such as a growth in ice-free areas, expansion of native plants and invasions of alien species (Znój et al. 2017; Galera et al. 2018; Convey & Peck 2019; Chwedorzewska et al. 2020). Changes are occurring in the marine ecosystem: e.g. increases in temperature and acidification of the waters, changes in ice conditions, increases in the flow of meltwater, forced animal migrations in search of safe suitable habitats and food, and colonization of new areas (Henley et al. 2019; Potocka et al. 2019). Forced migrations can extend regular periods of restricted access to food, especially for benthic organisms, with food from the Australian pelagic zone reaching them mainly in the short summer (Clarke 1983; Obermüller et al. 2010). Of great significance are changes in the food web, where the key species of Antarctic krill (*Euphausia* sp.) depends to a great degree on the phytoplankton biomass (Atkinson et al. 2019) that relies directly on the stability of the water and light column and on the availability of
biogenic elements. These inter-relationships are still poorly understood (Saba et al. 2014). In addition, the environmental and oceanographic changes taking place also generate further changes in primary production patterns (Pinkerton et al. 2021).

Despite the fact that the waters of the Southern Ocean are considered rich in biogenic salts (e.g. Nędzarek 2008; Polukhin et al. 2021), it should be borne in mind that changes in environmental conditions may in the future also result in a change of factors limiting primary production (Pinkerton et al. 2021). For example, Elser et al. (2007) indicate that reduced nitrogen availability may limit the photosynthesis of algae in many aquatic ecosystems.

One source of biogenic elements is the excretion of nitrogen and phosphorus compounds by aquatic organisms (Elser et al. 2007; Nędzarek 2008; Vanni et al. 2017; Stepanowska & Nędzarek 2020). Various studies have shown that aquatic invertebrates can significantly affect the abundance of N and P in the ecosystem through such excretion. Some researchers postulate that closely related species or species fulfilling similar functional roles in the ecosystem show similarities in their contribution to the process of supplying the environment with nitrogen and phosphorus, with others suggesting significant differences in this contribution (Alves et al. 2010; Vanni et al. 2017; Balik et al. 2018).

In the Antarctic ecosystem, high variability in trophic conditions is an important factor shaping the metabolism of organisms (Obermüller et al. 2010). The seasonality of food access means that many organisms (including benthic necrophages), especially during winter, must endure long periods of starvation (Clarke 1983, 1988). They are adapted to food deprivation and their tolerance increases with age – for example, krill larvae can survive from a few days to a few weeks without food while adults for more than 200 days (Siegel 2016). Starvation is associated with changes in body chemistry, such as a reduction in lipid or protein content (Chapelle et al. 1994; Comoglio et al. 2005; Watts et al. 2014; Stepanowska & Nędzarek 2020). To our knowledge, the effect of starvation of Antarctic benthic crustaceans on the magnitude of excreted metabolites which may provide a source of N and P for autotrophs has not been well described.

Researchers usually examine the excretion of ammonium nitrogen and phosphates, as these are forms easily assimilated by first-order producers (e.g. Alcaraz et al. 2010; Comoglio et al. 2005; Ikeda 2013; Balik et al. 2018). The possibility of enriching the ecosystem with oxidized forms of inorganic nitrogen (nitrates and nitrites) is often neglected. Although the uptake of nitrates, rather than the reduced form, by autotrophs is less energy efficient, the oxidized form may constitute an important part of the nitrogen nutrition of microplankton in the case of ammonium deficiency/utilization (Priddle et al. 1995; Whitehouse et al. 1999). Therefore, when the concentration of ammoniacal nitrogen is reduced to a lower effective level, the availability of nitrates may positively affect primary production, a growing trend in many areas of the Southern Ocean (Pinkerton et al. 2021).

The aim of this research (simulating environmental conditions with low levels of trophic resources) was (i) to assess the capabilities of two scavenger species of benthic invertebrates: amphipod Waldeckia obesa and isopod Glyptonotus antarcticus to supply the Antarctic ecosystem with excretions of nitrogen (including oxidized forms of inorganic nitrogen) and phosphorus, (ii) evaluation of the impact of long-term starvation on this process, (ii) assessing the change in body chemical composition of these crustaceans.

2. Material and methods

2.1. Study area

The research was carried out at the H. Arctowski Polish Antarctic Station (Figure 1), located on the west coast of Admiralty Bay, the largest bay of King George Island (West Antarctica). The shoreline of the bay is about 83.4 km, the area is about 122.08 km², and the water volume is estimated at 24.24 km³. The water depth varies from shallow water to 530 m deep, with an average depth of ca. 200 m (Rakusa-Suszczewski 1995). The drainage basin of Admiralty Bay covers an area of ca. 361 km². To the south, the bay is open to the influence of sea currents from the Bransfield Strait (Sailing directions for Antarctica 1985; Battke 1990).

2.2. Crustacea

The Southern Ocean has a high abundance of benthic species. The shallow sublittoral zone is particularly densely inhabited by macrozoobenthos (Jazdewska & Siciński 2017). Researchers such as De Broyer et al. (2004) also confirm a great number and diversity, and hence their importance, in the Antarctic bathyal and abyssal zones.

Two species of invertebrates were tested in this experiment: the amphipod Waldeckia obesa and isopod Glyptonotus antarcticus, both common in the marine benthic environment of Antarctica from the
littoral to abyssal zones. Both species are necrophages and predators and exhibit cannibalistic behavior. The composition of their diet is determined more by the availability of the food than by its type. Both species are adapted to long periods of starvation throughout the year (Dearborn 1967; Jażdżewski et al. 1982; Presler 1986; De Broyer et al. 2004; Janecki and Rakusa-Suszczewski 2005, 2006; Jażdżewska & Ściński 2017).

2.3. Starvation

The amphipod (*W. obesa*) and isopod (*G. antarcticus*) in this study were caught from Admiralty Bay using a grab dredge. Individuals with similar body weight were selected for experimental studies. The mean weight of the *W. obesa* was 0.38 ± 0.05 g, and the *G. antarcticus* 23 ± 5 g.

The experiment was carried out in open tanks. A constant ratio of sea water to crustacean biomass was used, at 10 dm$^3$ of water for every 100 ± 5 g of crustacean weight. The sea water was taken from Admiralty Bay and had an average salinity of 34.6 ± 0.4 PSU, pH 8.2 ± 0.1 and oxygenation of 98–100%. The average concentrations of the determined forms of nitrogen and phosphorus (as in point 2.4.) were as follows: 0.009 ± 0.005 mg N-NO$_2^-$ dm$^{-3}$, 0.362 ± 0.058 mg N-NO$_3^-$ dm$^{-3}$, 0.021 ± 0.007 mg N-NH$_4^+$ dm$^{-3}$, 0.580 ± 0.041 mg N dm$^{-3}$ for total nitrogen (TN), and 0.080 ± 0.015 mg P dm$^{-3}$ and 0.087 ± 0.014 mg P dm$^{-3}$ for total reactive phosphorus (TRP) and total phosphorus (TP), respectively. These values were determined in fresh sea water each time before the water changes in the tanks and were taken into account in the calculated values of nitrogen and phosphorus excretion by the crustaceans.

The water in the tanks was constantly aerated, and the temperature was kept at 0 ± 0.5°C (isothermal laboratory with an air temperature of 0 ± 0.5°C and a day/night lighting cycle of 6 h/18 h).

In the unfed crustaceans, the tank water was replaced with fresh water after 1, 2, 3, 4, 5, 10, 15, 25, 35, 45 days, and for *W. obesa* additionally after 55 and 65 days. Each 24 hours after the water change, the concentrations of individual forms of nitrogen and phosphorus were determined, and their excretion calculated in μmol N or P h$^{-1}$ 100 g$^{-1}$ of crustacean weight.

2.4. Water quality tests

The concentrations of N-NO$_2^-$, N-NO$_3^-$, N-NH$_4^+$, total nitrogen (TN), total reactive phosphorus (TRP) and total phosphorus (TP) in the seawater, were determined using standard colorimetric techniques recommended by Standard Methods (APHA 1999). The absorbance measurements were performed using a CARL ZEISS UV-VIS SPECOL-1100 spectro-photometer. Total organic nitrogen (TON) was calculated according to the formula TON = TN - TIN, where TIN is the sum of N-NO$_2^-$, N-NO$_3^-$ and N-NH$_4^+$. Total organic phosphorus (TOP) was calculated according to the formula TOP = TP - TRP. The pH of the water was also measured using a HI 9025 pH meter from HANNA Instruments (USA), the salinity with a FL197 conductometer from WTW GmbH (Germany), and the oxygenation of the water with an Oxi 197 oxygen meter from WTW GmbH (Germany).
2.5. Analysis of body chemical composition

Before starting each experiment, and also after 1, 2, 3, 4, 5 and 65 days for *W. obesa* and after 1, 3, 5 and 50 days for *G. antarcticus*, we analyzed the chemical composition of the crustaceans, i.e. the percentage content of:

- nitrogen and total protein – by Kjeldahl method (PN-A-04018: Az3: 2002),
- dry mass – by drying samples at 105°C for 12 hours (PN-A-86783: 1962),
- ash – by roasting samples at 550°C for 10 hours (PN-EN ISO 936: 2000).

2.6. Statistical analysis

The data obtained were subjected to statistical analysis involving 1-way analysis of variance (ANOVA) and Tukey HSD. The minimum significance level was set at 0.05. The analysis was performed using STATISTICA (ver. 13.3) for Windows (TIBCO Software Inc.).

3. Results

3.1. Excretion of nitrogen

The tested *W. obesa* excreted significantly (P < 0.05) more nitrogen than *G. antarcticus* (Table I). For example, the mean TN excretions calculated for the entire starvation period in µmol N h⁻¹ 100 g⁻¹ were 1.760 for *W. obesa* and 1.127 for *G. antarcticus*. Generally, ammoniacal nitrogen dominated in the nitrogen pool and on average it accounted for 76% and 67% of TN, respectively, for *W. obesa* and *G. antarcticus*. At the same time, *W. obesa*, compared to *G. antarcticus*, excreted more (P < 0.05) ammoniacal nitrogen (1.5x), inorganic nitrogen (1.4x) and organic nitrogen (2.8x). In contrast, significantly higher (P < 0.05) values of nitrates (approx. 4.6x) and nitrates (approx. 2.9x) were recorded for *G. antarcticus* than for *W. obesa* (Table I). However, these were low values and, in total, did not exceed 30% TN for *G. antarcticus* or 15% TN for *W. obesa* (Appendix 1).

Starvation was associated with a tendency for a decrease in excreted N-NH₄⁺, TON, TN and TN, from maximum values in the first day down to a relatively constant level after about 10–15 days of starvation (Figure 2; Appendix 2). For example (in µmol N h⁻¹ 100 g⁻¹) for N-NH₄⁺ from 3.687 to ca. 0.567 for *W. obesa*, and from 1.336 to ca. 0.579 for *G. antarcticus* (Figure 2). During this time, excretions (in µmol N h⁻¹ 100 g⁻¹) of TN, TIN and TON decreased to 0.732, 0.626 and 0.106 for *W. obesa*, and to 0.931, 0.808 and 0.125 for *G. antarcticus* (Figure 2; Appendix 2). These trends can be described by exponential functions and the following formulas were determined for the excretion of TN by *W. obesa* and *G. antarcticus*: \( TN_{W0} = 4.659^{0.2006x} \) and \( TN_{GA} = 1.5571^{0.063x} \) (Figure 2).

The oxidized forms of nitrogen did not show similar trends of changes to the other forms of nitrogen (Figure 3). In the case of N-NO₂ there was a generally weak tendency of the value increase with time (a particularly clear increase was noted after the 15th day of *G. antarcticus* starvation and the 35th day of *W. obesa* starvation). On the other hand, sine wave variability was demonstrated for N-NO₃ with a minimum between 4 and 15 days of starvation for *G. antarcticus* and 5–25 days of starvation for *W. obesa* (Figure 3).

3.2. Excretion of phosphorus

Overall, the excretion of phosphorus by the tested crustaceans was lower than that of nitrogen. For example, TP excretions averaged 0.046 µmol P h⁻¹ 100 g⁻¹ for *G. antarcticus* and 0.017 µmol P h⁻¹ 100 g⁻¹ for *W. obesa* (Table I). At the same time, TRP was more prevalent than TOP and on average was 72% of TP (for *G. antarcticus*) and 65% of TP (for *W. obesa*). Phosphorus excretion was higher (P < 0.05) in *G. antarcticus* compared to *W. obesa* (average 2.9 times higher for TRP, 2.2 times higher for TOP and 2.7 times higher for TP – taking into account the mean values given in Table I). Nevertheless, the calculated Redfield ratio (TIN:TRP) was higher (P < 0.05) for *W. obesa* than for *G. antarcticus* (mean values 138 and 31, respectively) (Table I).

After the first 2 days of starvation, *G. antarcticus* decreased in TP excretion (approx. 1.6x) from 0.062 to 0.067 µmol P h⁻¹ 100 g⁻¹ to an average level of approx. 0.041 µmol P h⁻¹ 100 g⁻¹ in the remaining days of the experiment (Figure 4). At the same time, in these time intervals there was also an approximate 3x reduction in TOP excretion, from 0.023 to 0.036 µmol P h⁻¹ 100 g⁻¹ to an average of 0.01 µmol P h⁻¹ 100 g⁻¹ (Appendix 2). In the case of TRP, there was a slightly reduced excretion from an average level of 0.036 µmol P h⁻¹ 100 g⁻¹ in the first two days to approx. 0.028 µmol P h⁻¹ 100 g⁻¹ between 25 and 45 days (Figure 4).

In *W. obesa*, the variability of phosphorus excretion was sinusoidal, with two maxima at 3–5 and 45–55 days of starvation; during this time the mean excretions (in µmol P h⁻¹ 100 g⁻¹) of TP, TRP and TOP were respectively 0.024, 0.016 and 0.009 and...
Table I. Ranges of nitrogen and phosphorus excretion (in μmol N or P h⁻¹ 100 g⁻¹) during experimental starvation *G. antarcticus* (GA) and *W. obsa* (WO); the shares (in %) of ammoniacal nitrogen in total nitrogen (TN) and in total inorganic nitrogen (TIN) and total reacting phosphorus (TRP) in total phosphorus (TP) and the Redfield ratio (TIN:TRP) and summary of one-way ANOVA results (*F* and *P*); (TON - total organic nitrogen; TOP - total organic phosphorus).

|       | N-NO₂⁻ | N-NO₃⁻ | N-NH₄⁺ | TIN | TON | TN | TRP | TOP | TP | N-NH₄⁺ in TN | N-NH₄⁺ in TIN | TRP in TP | TIN:TRP |
|-------|---------|---------|---------|-----|-----|----|-----|-----|----|-------------|--------------|------------|----------|
|       | μmol N h⁻¹ 100 g⁻¹ | μmol P h⁻¹ 100 g⁻¹ | %     | %   | %   |    |     |     |    |             |              |            |          |
| **GA** | Minimum | 0.027   | 0.121  | 0.418 | 0.586 | 0.022 | 0.682 | 0.024 | 0.006 | 0.031 | 58 | 67 | 45 | 17 |
|       | Maximum | 0.076   | 0.263  | 1.336 | 1.550 | 0.289 | 1.839 | 0.041 | 0.036 | 0.070 | 81 | 87 | 84 | 48 |
|       | Average | 0.046   | 0.173  | 0.766 | 0.984 | 0.141 | 1.127 | 0.032 | 0.013 | 0.046 | 67 | 77 | 72 | 31 |
|       | SD      | 0.014   | 0.038  | 0.236 | 0.239 | 0.060 | 0.275 | 0.004 | 0.009 | 0.006 | 7  | 6  | 11 | 8  |
| **WO** | Minimum | 0.002   | 0.017  | 0.406 | 0.489 | 0.033 | 0.564 | 0.004 | 0.002 | 0.006 | 69 | 82 | 45 | 40 |
|       | Maximum | 0.021   | 0.114  | 3.687 | 3.816 | 1.525 | 5.286 | 0.023 | 0.014 | 0.033 | 88 | 98 | 85 | 562 |
|       | Average | 0.010   | 0.060  | 1.297 | 1.367 | 0.393 | 1.760 | 0.011 | 0.006 | 0.017 | 76 | 93 | 65 | 138 |
|       | SD      | 0.005   | 0.026  | 1.125 | 1.140 | 0.462 | 1.596 | 0.005 | 0.003 | 0.007 | 5  | 5  | 9  | 126 |

ANOVA

| F    | 7.05 | 2.19 | 22.63 | 22.75 | 59.47 | 33.78 | 1.23 | 9.87 | 2.72 | 1.67 | 1.98 | 1.56 | 238.2 |
| P    | 0.000 | 0.000 | 0.014 | 0.077 | 0.004 | 0.035 | 0.000 | 0.000 | 0.000 | 0.000 | 0.000 | 0.001 | 0.001 |

a,b Different indexes in columns - values significantly different (ANOVA and Tukey HSD, *p* < 0.05).
were 1.8x, 2x and 1.5x higher than the minima (Figure 4; Appendix 2).

The variation in phosphorus excretion can be described by a polynomial and, for example, the following formulas were determined for total phosphorus excretion by *W. obesa* and *G. antarcticus*: 

\[
\text{TP}_{\text{WO}} = 0.0143 - 0.0009 + 5.1134 - 5x^2 \\
\text{TP}_{\text{GA}} = 0.0708 - 0.008x + 0.0005x^2
\]

(Figure 4).

3.3. Effects of starvation on metabolism

Weeks of starvation had different effects on the content of dry matter, nitrogen, protein and ash in both *W. obesa* and *G. antarcticus* (Table II).

The content of nitrogen and protein in both decreased in the first starvation period, reaching minimum values on the 3rd and 5th day, for *W. obesa* and *G.
antarcticus, respectively. After 65 days of starvation, the content of these indices in W. obesa was significantly higher \((p < 0.01)\) compared to the first 5 days of starvation. In contrast, the nitrogen and protein content in G. antarcticus after 50 days of starvation was significantly higher \((p < 0.01)\) than on the 5th day of starvation, but was still lower than before starvation (Table II).

Dry matter content in W. obesa, after the period of initial stability, decreased highly statistically significantly \((p < 0.01)\) on the 3rd day of starvation, and reached a minimum on the 4th day. Thereafter, an increase in dry matter content was recorded up to a maximum on day 65 of starvation. On the other hand, in G. antarcticus, dry matter content showed a clear decreasing trend from the 5th day of starvation, and then a highly significant \((p < 0.01)\) increase in the value on the 50th day in relation to the minimum value (Table II).

The ash content in both tested species gradually increased until the 5th day of starvation, and then decreased significantly \((p < 0.01)\) in the last days of the experiment. Nevertheless, the ash content was significantly higher at that time than before starving the crustaceans (Table II).
4. **Discussion**

4.1. **Excretion of N and P**

In general, the amounts of N and P excreted by the tested invertebrates were similar to previous studies, which also showed a high share of ammonium nitrogen in total nitrogen (e.g. Robertson et al. 2001; Obermüller et al. 2010). The reduced form of nitrogen also prevailed over the oxidized forms of nitrogen, as in the research on N and P excretion by Antarctic fish by Stepanowska and Nędzarek (2020). At the same time, the maximum values of ammoniacal nitrogen recorded in the first 2 days of the experiment corresponded to the excretions observed in fed animals (e.g. Boyce 1999; Robertson et al. 2001; Obermüller et al. 2010).

According to Boyce (1999), organic nitrogen, defined by the concentration of urea, constitutes 10–20% of total nitrogen excreted by Antarctic marine organisms. In our research, we also showed...
Table II. Changes in the chemical composition (in %) of *W. obesa* (WO) and *G. antarcticus* (GA) during starvation (x ± SD).

| Chemical composition | Day of starvation |
|----------------------|-------------------|
|                      | 0                 | 1                 | 2                 | 3                 | 4                 | 5                 | 65                |
| **WO**               |                   |                   |                   |                   |                   |                   |                   |
| Dry matter           | 23.75 ± 0.17<sup>b</sup> | 23.60 ± 0.31<sup>b</sup> | 23.71 ± 0.27<sup>b</sup> | 21.81 ± 0.09<sup>a</sup> | 22.43 ± 0.14<sup>a</sup> | 23.62 ± 0.27<sup>c</sup> | 28.64 ± 0.39<sup>a</sup> |
| Protein              | 8.15 ± 0.16<sup>a</sup> | 7.13 ± 0.03<sup>c</sup> | 6.68 ± 0.07<sup>b</sup> | 5.80 ± 0.17<sup>a</sup> | 5.95 ± 0.12<sup>a</sup> | 6.25 ± 0.13<sup>b</sup> | 9.93 ± 0.64<sup>ab</sup> |
| N                    | 1.30 ± 0.03<sup>c</sup> | 1.14 ± 0.01<sup>c</sup> | 1.07 ± 0.01<sup>b</sup> | 0.93 ± 0.03<sup>a</sup> | 0.95 ± 0.02<sup>a</sup> | 1.00 ± 0.02<sup>b</sup> | 1.59 ± 0.10<sup>c</sup> |
| Ash                  | 9.16 ± 0.29<sup>d</sup> | 10.47 ± 0.47<sup>c</sup> | 10.80 ± 0.28<sup>c</sup> | 10.70 ± 0.12<sup>c</sup> | 11.45 ± 0.12<sup>d</sup> | 11.63 ± 0.35<sup>c</sup> | 9.36 ± 0.13<sup>d</sup> |
| **GA**               |                   |                   |                   |                   |                   |                   |                   |
| Dry matter           | 22.12 ± 0.16<sup>d</sup> | 21.15 ± 0.20<sup>c</sup> | 17.82 ± 0.19<sup>b</sup> | 14.61 ± 0.04<sup>c</sup> | 20.34 ± 0.71<sup>c</sup> |                   |                   |
| Protein              | 13.86 ± 0.18<sup>d</sup> | 12.98 ± 0.02<sup>c</sup> | 10.37 ± 0.09<sup>b</sup> | 8.94 ± 0.19<sup>a</sup> | 13.20 ± 0.31<sup>c</sup> |                   |                   |
| N                    | 2.22 ± 0.03<sup>c</sup> | 2.08 ± 0.01<sup>c</sup> | 1.66 ± 0.02<sup>b</sup> | 1.43 ± 0.03<sup>b</sup> | 2.11 ± 0.05<sup>c</sup> |                   |                   |
| Ash                  | 2.27 ± 0.02<sup>d</sup> | 2.66 ± 0.06<sup>b</sup> | 3.18 ± 0.07<sup>d</sup> | 3.21 ± 0.02<sup>d</sup> | 2.83 ± 0.06<sup>c</sup> |                   |                   |

<sup>a–e</sup>Different indexes in rows - values significantly different (ANOVA, Tukey HSD test, p < 0.05).
similar values - the share of TON in TN was on average 12.5% (for G. antarcticus) and 22% (for W. obesa).

The demonstrated differences in N and P excretion between the tested invertebrates are in line with the observations by Alves et al. (2010) and Balik et al. (2018). They showed that the excretion of N and P by various species, despite having similar functions in the ecosystem, can differ significantly due to differences in key functional characteristics, e.g. diet specialization, varying degrees of aggressiveness and cannibalism, metabolic rate, body size. More aggressive and cannibalistic species may consume more protein and, as a result, excrete more nitrogen. Smaller animals, due to their faster metabolism, should also generally have a higher nitrogen excretion rate. Balik et al. (2018) also emphasize that consumer-driven nutrient recycling is a complex interaction of ecology and physiology. The complexity of these interactions is also confirmed by the differences in nutrient excretion demonstrated in our study: higher N excretion by W. obesa (1.6x for TN) compared to G. antarcticus, and, on the contrary, P excretion was higher in G. antarcticus (2.7x for TP) than in W. obesa. Similar differences between N and P excrections depending on the weight of invertebrates were shown by Balik et al. (2018), arguing that organisms that are smaller but with a higher metabolism may have a higher requirement for P and thus excrete less P.

4.2. Effect of starvation on excretion

Numerous studies of the influence of starvation on the metabolism of marine organisms (e.g. Chapelle et al. 1994; Comoglio et al. 2005; Obermüller et al. 2010; Lehette et al. 2012; Stepanowska & Nędzarek 2020), and those carried out on benthic animals inhabiting the Antarctic sea (e.g. Robertson et al. 2001; Rakusa-Suszczewski et al. 2010; Janecki & Rakusa-Suszczewski 2004, 2005, 2006), have shown that their metabolism slows down over time, but that the pattern of metabolic response may be different. In the case of W. obesa, 10-day hunger reduces the metabolic rate by 36% and 30-day hunger by 66% compared to well-nourished individuals (Janecki & Rakusa-Suszczewski 2005). In contrast, the metabolism of G. antarcticus decreases by 30% after 14 days, and by 70% after 42 days of starvation (Janecki & Rakusa-Suszczewski 2006). This is accompanied by a decrease in N excretion, as was shown in this research for the example of ammoniacal nitrogen, TON and TN. Higher reduction of N excretion in W. obesa (<85%) than in G. antarcticus (<40%) can probably be explained by the higher metabolism of W. obesa (as postulated by, e.g. Balik et al. 2018) and higher resistance of G. antarcticus to food deficiency (Janecki & Rakusa-Suszczewski 2006).

In the case of phosphorus, the effect of starvation on the amount of its excretion was not as high as in the case of nitrogen. This observation is consistent with Obermüller et al. (2010). They argue that due to the differentiation of energy reactions depending on the availability and/or type of food, the same general relationships cannot be drawn for N and P excretion.

A more pronounced effect of starvation on P excretion was demonstrated in G. antarcticus (especially for TP, whose excretion after 10 days decreased by approx. 40% and remained at that level for the next 35 days). Presumably, this could be the result of the excretion of undigested food during the first 2 days of starvation, analogous to what was observed in starving Antarctic fish (Stepanowska & Nędzarek 2020).

4.3. Potential importance of N and P excretion by crustaceans for autotrophs

Despite the fact that the waters of the Southern Ocean are generally rich in nutrients, high spatial variation in biomass and primary production is observed with the simultaneous seasonal succession of autotrophs and high dynamics of various forms of nitrogen available to them (Bode et al. 2002; Lehette et al. 2012). Contrary to nitrate nitrogen, the proportion of ammoniacal nitrogen dissolved in water in total nitrogen is relatively small, and according to Goeyens et al. (1998) averages 1.3–1.7% with a maximum at 7.5%. Thus, the available ammonium nitrogen may be a potential limiting factor in phytoplankton production (Priddle et al. 1995; Goeyens et al. 1998; Whitehouse et al. 1999). This takes place during the new production period (spring/early summer) when phytoplankton use up nitrate nitrogen. As the biomass grows, the phytoplankton nutrition changes to ammonium nitrogen and dissolved organic nitrogen (period of regenerated production) (Bode et al. 2002).

Based on this general outline of the complicated and not fully understood process of using biogenic salts by autotrophs, it can be assumed that metabolites excreted by benthic organisms may contribute significant N and P loads to primary production. This is indirectly confirmed by Sturz et al. (2003) who observed higher loads of biogenic salts in the bottom layer, the source of which, in addition to the microbial decomposition of sinking detritus, are metabolites excreted by animals staying near the
bottom. Therefore, in view of the naturally low concentration of ammoniacal nitrogen in the Southern Ocean, even a small inflow of ammoniacal nitrogen excreted by benthic animals may result in the enrichment of the ecosystem with available nitrogen in autotrophs (Bode et al. 2002). In general, the inflow of oxidized nitrogen forms into the environment (in these studies they accounted for approx. 20% TN; Appendix 2) may be of less importance for autotrophs. In the period of new production (see Bode et al. 2002) this nitrogen load may be supplemented by nitrates taken up by the phytoplankton in the spring time.

Relating these considerations to the Admiralty Bay ecosystem (considered a model for Antarctic studies), it should be pointed out that N and P concentrations in bay waters have increased in the bottom layer. Lipski (1987) recorded about 4.8 µmol dm⁻³ NO₃⁻N, about 0.03 µmol dm⁻³ NO₂⁻N and about 0.55 µmol dm⁻³ TRP in this layer. This increase in concentration also may be partly due to the excretion of N and P by zoobenthos. The total biomass of the benthic fauna inhabiting the entire bottom surface of Admiralty Bay was estimated at ca. 67,000 tonnes, the mean density at ca. 6500 individuals per m² (maximum densities can reach over 36,000 individuals per m²) (Jażdżewski et al. 1986). The mean wet weight of the zoobenthos is 700 g m⁻², with 500–900 g m⁻² falling within its 95% confidence limits (Jażdżewski et al. 1986; Jażdżewski & Siciński 1993). Based on these data, it is possible to estimate with some approximation the N and P loads that may be introduced into the ecosystem by the equivalent biomass of 700 g m⁻² of G. antarcticus or W. obesa, which are important zoobenthic species of Admiralty Bay (Siciński et al. 2011). Considering the average excretion of nitrate nitrogen and TRP by G. antarcticus and W. obesa, it can be estimated that these species can provide 1.21 and 0.4 µmol N h⁻¹ m⁻² and 0.22 and 0.08 µmol P h⁻¹ m⁻², respectively. Even if the calculated values are overestimated, the excretion of N and P by zoobenthos cannot be neglected in the balance of nutrients in this ecosystem because this source can influence primary production, among other things, by changing the N:P ratio.

Research by Redfield (1958) indicates that the nitrogen to phosphorus ratios in plankton (N: P = 16) and in ocean waters (N:P = 15) were similar, and reflect the phytoplankton demand for these nutrients. Klausmeier et al. (2004) argue, however, that the value of N:P = 16 should be viewed as a weighted average of the relative abundance of species, with various N:P ratios exceeding even 120. The relative abundance of species depends on the ecological conditions in which they grow and compete. At the same time, competitive equilibrium selects high N:P ratios, and exponential growth selects low N:P values. The N:P ratios in our research were higher (on average 2 times higher for G. antarcticus and 9 times higher for W. obesa) than postulated by Redfield (1958) for the standard for ocean waters. At the same time, high differences (P < 0.05) between the tested species (the maximum values of the TN:TRP ratio were 48 for G. antarcticus and 562 for W. obesa), perhaps, as concluded by Klausmeier et al. (2004), positively affect the competitive balance while maintaining high biodiversity. On the other hand, such an N:P ratio indicates that the primary production may be limited by the availability of phosphorus. As shown by Nędzarek (2008) in the waters of Admiralty Bay, primary production may be simultaneously limited by the availability of nitrogen and phosphorus (N: P = 12). However, in the light of a high inflow of ammoniacal nitrogen and organic nitrogen, this balance may be disturbed to the disadvantage of phosphorus. For example, Nędzarek et al. (2015), when examining the distribution of Antarctic fish remains, noted a 4 times greater available ammonia nitrogen for autotrophs compared to the value characteristic for Admiralty Bay water estimated by Nędzarek (2008), at 15%.

4.4. Effect of starvation on invertebrates

The seasonality of Antarctic marine ecosystems means that the relationship between nutrition and metabolism is of particular interest as many polar organisms must survive long periods without food, leading to multidirectional changes in their body chemistry (Clarke 1983, 1988; Ritar et al. 2003; Comoglio et al. 2005; Watts et al. 2014; Stepnowska & Nędzarek 2020), also shown in the subject’s amphipods and isopods. For example, a similar reduction in nitrogen and protein content in W. obesa starved for 64 days was observed by Chapelle et al. (1994).

Ritar et al. (2003) suggest that the utilization of metabolic reserves in crustaceans may proceed in an orderly fashion, from the oxidation of lipid reserves to protein catabolism and the subsequent breakdown of membrane phospholipids before death. Such a response pattern to hunger may explain the relatively low reduction of nitrogen and protein (partially also low phosphorus excrections) in the studied crustaceans.

It can also be assumed that the increase in protein content in W. obesa and G. antarcticus observed at the end of the long-term starvation resulted from
changes in the dry weight of crustaceans, and not the loss of tissue proteins. A similar phenomenon was observed by Friedrich and Stepanowska (2001) during a 12-week starvation of Cyprinus carpio. The increase in protein concentration with simultaneously changing percentage of dry matter content was observed already in the fourth week of C. carpio starvation. A similar phenomenon was also observed during the 52-day starvation of Antarctic fish Notothenia coriceps (Stepanowska et al. 2006).

The reported dry matter reduction in the crustaceans should be considered as the body’s natural response to hunger. Reduced food supply leading to hunger leads to the use of internal resources, resulting in a change in the weight of the whole body (McCue 2010). Various species, including marine crustaceans, can survive starvation for long periods (even >6 months) without marked changes in total body weight (Watts et al. 2014). As tissue reserves are used up during starvation, these organisms simultaneously take up water to maintain body volume (Comoglio et al. 2005). This mechanism could have influenced the obtained results (“apparent” increases) in the content of nitrogen, protein, ash and dry weight of the tested crustaceans after the end of the experiment.

5. Summary

The metabolic products excreted by the tested crustaceans may be a supplemental source of nitrogen and phosphorus for autotrophs. They generally contained more nitrogen than phosphorus. Ammoniacal nitrogen dominates the pool of nitrogen compounds and its excretion was higher in W. obesa than in G. antarcticus. TRP dominated in the pool of phosphorus compounds, and its excretion was higher in G. antarcticus than in W. obesa. Despite the low share of oxidized nitrogen forms in total nitrogen, they can supplement the nitrates taken up by phytoplankton in spring, during the new production period. High values of the Redfield coefficient significantly above 16 indicate that metabolites excreted by crustaceans may influence the direction of limiting the primary production by the availability of phosphorus.

The recorded decrease in excretion with the time of starvation is exponential for nitrogen and sinusoidal for phosphorus. The higher decrease in nitrogen excretion in W. obesa and in phosphorus in G. antarcticus may have been due to the differences in the metabolism of the studied species.

Despite the separate reactions of crustaceans to hunger, the greatest decreases in nitrogen and protein content in W. obesa and G. antarcticus occurred in the first days of starvation. On the other hand, the “apparent” increase in these body components after 65 and 50 days of starvation confirms the adaptation of amphipods and isopods to prolonged periods of hunger.

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No potential conflict of interest was reported by the author(s).

Supplementary material

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ORCID

A. Nędzarek @ http://orcid.org/0000-0002-6094-3647
K. Stepanowska @ http://orcid.org/0000-0003-2359-4844

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