Reduced seasonality in elemental CHN composition of Antarctic marine benthic predators and scavengers

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ABSTRACT

At all but the lowest latitudes, photoperiod varies through the year, resulting in seasonal variation in coastal primary productivity. This leads to a pronounced seasonality in the physiology of most primary consumers, particularly in the seas around Antarctica, which are amongst the most seasonal on the planet. However, higher trophic levels have a more constant food supply and a recent study showed that a range of Antarctic benthic predators and scavengers had very little seasonal variation in physiology. This study investigated the seasonal signal in tissue elemental composition of these same five common benthic predators and scavengers: the gammarid amphipod *Paraceradocus miersii*; brittle star *Ophionotus* *victoriae*; nemertean *Parborlasia corrugatus*; nudibranch *Doris kerguelenensis* and tissues of the notothenioid fish *Harpagifer antarcticus*. Carbon (C), hydrogen (H) and nitrogen (N) content and C:N ratios were determined for five to seven time points during one year at Adelaide Island, Antarctic Peninsula. Whilst there were significant differences between species, only *P. miersii* exhibited seasonal differences, with significantly higher CHN content and C:N ratio in summer than in winter. In the other four species, elemental composition and C:N ratio were very stable throughout the year, supporting the assumption of homeostasis in ecological stoichiometry of benthic consumers and adding to the previously measured lack of seasonal physiological patterns. Recent disruption of the annual patterns of primary productivity, due to reduced occurrence of winter sea ice, may, therefore, not have an immediate impact on higher trophic levels.

Keywords: Proximate composition, Benthos, Carbon, Nitrogen, Polar

1. Introduction

In seasonal environments, factors such as temperature and food availability affect temporal variation in the physiology and energetics of marine animals. In many taxa, but particularly primary consumers, feeding and storage cycles become more intense with increasing latitude as the annual variation in photoperiod becomes more extreme (Clarke and Peck, 1991). As a consequence of this variation in photoperiod, Antarctic phytoplankton productivity is intensely seasonal, resulting in strong seasonal variability in primary consumer and detritivore feeding (Barnes and Clarke, 1995; Brockington, 2001), activity (Brockington, 2001; Morley et al., 2007), growth (Peck et al., 1997, 2000; Bowden et al., 2006), reproduction (Grange et al., 2004, 2007, 2011), metabolic costs (Morley et al., 2007) and body composition (Peck et al., 1987; Clarke and Peck, 1991; Brockington, 2001; Ahn et al., 2003; Norkko et al., 2005). Understanding the effect of reduced winter sea ice on the seasonal signals of temperature and primary productivity (Venables et al., 2013), and how these changes will affect temporal physiology, is therefore a vital component of predicting species response to climate change.

One recent investigation, however, found that at higher trophic levels, several benthic Antarctic predators and scavengers have mixed temporal, rather than seasonal, patterns of feeding, metabolism and excretion across the polar year (Obermüller et al., 2010). These secondary consumers have a more constant food supply and so they are thought to be less coupled to seasonal phytoplankton productivity, but it is unknown to what degree seasonal fluctuations in predator and prey physiology affect other aspects of their biology, including their proximate composition. Ecological stoichiometry is measured to investigate the relationships between the elemental composition of food, the elemental requirements of consumers and how these factors relate to key ecosystem processes (Sterner and Elser, 2002). Carbon (C), nitrogen (N) and phosphorus (P), together with hydrogen (H), oxygen (O) and sulphur (S) are major elemental components of all organisms. The C:N ratio provides an index of the carbohydrate and lipid to protein ratio as the composition of these compounds are stoichiometrically related to organic CHN contents (Gnaiger and Bitterlich, 1984; Anger and Harms, 1990). Lipids and carbohydrates do not contain nitrogen and so high C:N ratios indicate a high content of lipids and/or carbohydrates, whereas low C:N ratios reveal the opposite: a high protein content and thus low levels of lipid and/or carbohydrate. Tracking specific elements through food webs can provide information about ecosystem function at a variety of scales from differences between taxa, predator-prey interactions and seasonal variation in nutrient cycling, through to functional relationships within ecosystems (Elser and

Urabe, 1999; Reiners, 1986; Vanni, 2002). Resource and consumer elemental composition has been more intensively studied in aquatic pelagic systems and to a lesser extent in freshwater benthic systems (Anderson et al., 2004, 2005; Elser et al., 2007; Evans-White et al., 2005; Liess and Hillebrand, 2005). Such studies have found that C:N ratios of benthic grazers vary across species, taxa, and site, but to date few studies have focused on the elemental composition and ecological stoichiometry of benthic marine systems and organisms (Clarke, 2008; Weiss et al. 2009). One of these, a study of deep sea predatory benthic fish, found no seasonal variation in nutritional condition of three macrourid species (Drazen, 2002).

The aim of this study was to establish the elemental composition of a range of Antarctic benthic scavengers and predators to investigate whether their previously measured differences in temporal physiology and trophic strategies (Obermüller et al. 2010) leads to variation in C, H and N composition and C:N ratios, between species and across the year. The species used varied in dietary specialisation from the brittle star *Ophionotus victoriae* (Bell 1902) an opportunistic generalist (predator, scavenger, suspension and detritus feeder; Fratt and Dearborn 1984) to the gastropod *Doris kerguelenensis* (Bergh 1884), a highly specialised sponge consumer (Barnes and Bullough 1996; Wägele 1989). In between these were the amphipod *Paraceradocus miersii* (Pfeffer 1888) a scavenger (pers. obs.) and the nemertean *Parborlasia corrugatus* (McIntosh 1876) a predator and scavenger (Gibson 1983). Liver and muscle tissue, two of the major storage organs in notothenioid fish (Eastman and DeVries, 1981), were also sampled from the obligate predator *Harpagifer antarcticus* Nybelin 1947, a fish that consumes primarily amphipods and scale-worms (Wyanski and Targett, 1981; Casaux 1998).

2. Methods

2.1 Sampling

Between April 2007 and March 2008 five marine benthic species from the near shore habitats around Rothera Research Station, Adelaide Island, Antarctica (67°34'S, 68°07'W) were collected every 2-3 months by SCUBA divers from depths between 5 and 20 m. Sampling sites, collection depths and substratum types are summarised in Table 1 in Obermüller et al. (2010). Six individuals of each species were collected at each sampling time, between April and July 2007, after which it was increased to ten. We collected a similar size range of specimens at each sampling event and also tested for significant differences in animal mass in samples throughout the year. Specimens were transferred to a flow-through aquarium, where they were maintained for up to 4 days. Water temperatures in the aquarium were close to ambient, local, seawater temperatures, which ranged between -1.9 and +1.2°C over the study period. After wet mass (WM) had been measured, individuals were deep frozen as whole animal samples and stored at -80°C until analysis of elemental composition. The fish were killed, using prescribed UK Home Office schedule 1 methods, white trunk muscle and liver tissue were dissected, deep frozen and stored (muscle samples contained small residues of bones). Muscle and liver tissue were analysed separately to see if these tissues exhibit different patterns in proximate composition.

2.2 Sample treatment and elemental analysis

All equipment was washed, dried and cleaned with acetone between samples to minimise contamination. Samples were dried to constant mass in an oven at 60˚C, and then homogenised using a Waring blender and ground to fine powder using a mortar and pestle. Total C, H and N were measured on sub-samples in a CHN analyser Model CE 440 (Exeter Analytical, Inc., Massachusetts, USA). Sample weights used for analysis typically ranged between 1 – 2 mg dry mass (DM). Most samples were run once, but duplicate measurements for random samples were carried out to control assay quality and ensure reproducibility. Fish liver samples, however, were measured in duplicates, and if necessary in triplicate, due to higher variability of values obtained. All runs were carried out with sample blanks (empty tin sample vials), an organic blank (benzoic acid) for nitrogen zeros, and acetanilide standards (quantities dependent on sample size). CHN data are expressed as percentage of DM (mean ± standard deviation SD).

In addition, brittle star and amphipod dry tissue was tested for the percentage of the inorganic carbon fraction retained in ashed tissue. This can form a significant part of total C in whole body samples due to the species' $CaCO_3$ skeleton (brittle stars) or other inorganic carbon content and, if not corrected for, can lead to overestimation of organic C content. The bone content of *H. antarcticus* muscle was negligible. Clarke (2008), who analysed six Antarctic invertebrate species for their organic and inorganic C content, found that the inorganic fraction was very low and insignificant in nemertean worms, molluscs (limpets without shell), polychaetes, and echinoderms, with the exception of the cushion star. We therefore did not correct CHN data in fish, nemertean worms, and nudibranchs (data expressed as percentage of dry mass) where effectively all C and N is retained in the organic fraction but only corrected elemental composition in brittle stars and the amphipod, *P. meirsii*. Despite this correction, the carapace of *P. meirsii* is made of chitin, which is organic, and the CHN content of its skeleton was therefore included in the organic component. After correction C:N ratios are expressed on a molar basis. Samples (0.5 g of dry powder) were ignited in a muffle furnace at 500°C for 1000 min. Thereafter, 2 – 3 mg of the ashed samples were analysed for total inorganic CHN content. Corrected CHN data are expressed as percentage of organic mass (mean ± standard deviation SD). The inorganic fractions amounted to 7.1 ± 0.2 %C, 0.07 ± 0.00 %H, and 0.04 ± 0.00 in *O. victoriae* and 2.8 ± 0.1 %C, 0.03 ± 0.00 %H, and 0.04 ± 0.00 %N in *P. miersii* (Table 1).

2.3 Animal morphometrics

Dry mass (DM) and water content for each species were calculated from the WM and DM measured in a separate set of experimental specimens (n = 12 – 17 per species) collected at the same time as all the CHN samples. Whole animal DM was measured after drying to a constant mass at 60°C. For each species WM was plotted against DM and the equations from these regressions were used to calculate DM estimates for those specimens analysed for CHN content. Ash mass (AM) was obtained after ignition in a muffle furnace at 500°C for 1000 min. AM was subtracted from DM to gain AFDM. Total body length in fish, amphipods, and nudibranchs as well as disc dimensions (diameter) in brittle stars were measured. The nemertean worms can contract and elongate their bodies significantly, naturally or in response to external stimuli (Gibson, 1983). Therefore, no length measurements were taken for the worms and measurements in nudibranchs should be regarded as estimates rather than true body length, as they also exhibit a significant degree of contraction and variation in body water content, but to a lesser extent than in nemerteans.

2.4 Statistical analysis

All data are expressed as mean ± standard deviation (SD). Statistical analysis was carried out using Minitab version 15.1 (Minitab, Pennsylvania State University, USA). Normally distributed data, tested with Ryan-Joiner similar to Shapiro-Wilk test, were analysed for seasonal differences (summer vs. winter) within species using one-way ANOVA together with a Tukey's multiple comparison test. Summer in the present study was categorised as November to May and winter from June to October, based on photoperiod, temperature and primary productivity (see Obermüller et al., 2010). If data could not be transformed to gain a normal distribution, the nonparametric Kruskal-Wallis test was used to test for seasonal differences. Differences between species were tested using pairwise nonparametric Kruskal-Wallis tests with a Bonferroni adjustment for ties (p_{adj}). In this cross-species comparison, data from summer and winter were tested together in all species except *P. miersii*.

3. Results

3.1 Mass and water content

WM and DM estimates of specimens analysed for CHN did not vary significantly between seasons in any of the species investigated (ESM Table 1). *Parborlasia corrugatus* had the highest water content of all the study species, 89.6 to 92.1%. The lowest water content was measured in *Ophionotus victoriae*, 59.6 to 60.7%. The water content of *Harpagifer antarcticus* (both muscle and liver), *Paraceradocus miersii* and *Doris kerguelenensis* ranged between 73.9 and 83.3%.

3.2 CHN content

Of all the species investigated only *P. miersii* exhibited significant seasonal differences in CHN content. %C (ANOVA: F = 11.63, p = 0.001, Fig. 1), %H (ANOVA: F = 7.83, p = 0.007, Table 2), and %N (ANOVA: F = 11.20, p = 0.002, Fig. 2) were significantly higher in summer (60.41 ± 17.83 %C; 8.20 ± 1.42 %H; 12.57 ± 2.37 %N) than in winter (44.80 ± 7.19 %C; 7.07 ± 1.04 %H; 10.40 ± 1.58 %N). For comparisons of elemental composition between species, seasonal values were pooled in each species except in *P. miersii* where summer and winter data were tested separately. Elemental composition was significantly different between species (Kruskal-Wallis test; for %C: H = 166.40, p < 0.001; for %H: H = 178.04, p < 0.001; for %N: H = 156.51, p < 0.001). *D. kerguelenensis* had the lowest CHN contents of all investigated species ($p < p_{adj}$ 0.0024; Fig. 1, Fig. 2, Table 2). CHN values measured in *P. corrugatus* and *O. victoriae* (47.32 ± 2.14 %C, 7.51 ± 0.73 %H, and 10.82 ± 0.96 %N) were higher than in *D. kerguelenensis* but lower than those recorded in *P. miersii* (summer) (Fig. 1, Fig. 2, Tables 1 and 2). *H. antarcticus* muscle tissue had significantly lower %C and %H but significantly higher %N than liver tissue ($p < p_{adj}$ 0.0024) (Fig. 1, Fig. 2, Table 2).

For comparison, uncorrected CHN values for *O. victoriae* and *P. miersii* are listed in ESM Table 2.

3.3 C:N ratios (molar ratios)

Only *P. miersii* exhibited significant seasonal differences in C:N ratios with higher values in summer (5.52 ± 0.74) than in winter (5.03 ± 0.29; ANOVA, F = 5.89, p = 0.019) (Fig. 3, ESM Table 3). C:N ratios also varied significantly between species (Kruskal-Wallis test, H = 178.58, p < 0.001). *P. corrugatus* had the lowest C:N ratios (annual mean 4.24 ± 0.15) measured in whole animal samples of the investigated invertebrate species. The overall range in C:N ratio in whole animal samples (corrected for inorganic carbon in *O. victoriae* and *P.*

miersii) was 4.2 – 5.9. C:N ratios measured in *H. antarcticus* muscle tissue were significantly lower (annual mean 4.21 ± 0.23) than in liver tissue, which revealed the highest C:N ratios of all investigated samples and species (annual mean 7.48 ± 0.40; Fig. 3; ESM Table 3).

3.4 Animal morphometrics

Animal morphometrics were determined in a separate set of experimental specimens of the same five species (ESM Table 4). Although smaller *O. victoriae* were collected for morphometrics in winter than summer (ESM Table 4) there was no difference in water content in winter (62.9 ± 0.5%) compared to summer (63.6 ± 0.3%) (ANOVA, F = 2.12. p = 0.21).

4. Discussion

Whilst there was significant variation in the CHN content and C:N ratios between species, four out of five of the Antarctic predators and scavengers, *Ophionotus victoriae*, *Parborlasia corrugates*, *Doris kerguelenensis* and isolated muscle and liver of *Harpagifer antarcticus*, studied here, had very stable elemental composition throughout the year. Only *Paraceradocus miersii* showed significant seasonal differences between summer and winter.

4.1 Comparisons across taxa

The C:N ratio ranged from 4.2 – 5.9 in whole animal samples of invertebrate species and muscle and liver samples of an Antarctic fish analysed in the present study (annual means). This was similar to the range of 4.2 – 6.7 measured by Clarke (2008) for 3 Antarctic marine benthic primary consumers (the holuthurian *Heterocucumis steineni*, the polychaete *Thelepus cincinnatus* and the limpet *Nacella concinna*), 1 deposit feeder (the polychaete *Flabelligera mundata*), 1 omnivore (the asteroid *Odontaster validus*) and 1 predator (*P. corrugatus*). However, the %C and %N values reported here were at the lower end of literature values for other Antarctic marine benthic invertebrates (Fig. 4; Clarke, 2008).

Whilst elemental composition varies significantly between taxonomic groups, less significant variation is found between species within the same taxa (Cross et al., 2005; Evans-White et al., 2005; Liess and Hillebrand, 2005). Phylogenetic constraints on the relative allocation of structural body constituents such as calcareous shells, chitinous exoskeletons or phosphorous-rich bones are important in constraining elemental composition within taxa (see Frost et al., 2003; Cross et al., 2003, 2005; Evans-White et al., 2005; Liess and Hillebrand, 2005). *O. victoriae* was conspicuous in having a higher proportion of skeleton than the other species studied here. However, once corrected for the inorganic elemental composition of this skeleton, its organic CHN content was comparable to that of other Antarctic species (Fig. 4).

Elemental stoichiometry also reflects dietary composition and different ‘functional feeding groups’ of benthic macro-invertebrates often have significantly different CHN contents. Predators usually have higher levels of N (and thus lower C:N ratios) than herbivores and detritivores (e.g. grazers, filter feeders and others termed as scrapers, shredders and collectors; Evans-White et al., 2005). Here, the obligate predator *P. corrugatus* had the lowest C:N ratios of all invertebrate species sampled in this study indicating its highly protein-rich diet (Obermüller et al., 2010). In contrast, *D. kerguelenensis,* which is also an obligate predator, had very low percentages of C and N. *D. kerguelenensis* has a highly specialised diet of hexactinellid and demosponges (Barnes and Bullough, 1996; Wägele,

1989) and their tissues match the very low C and N composition of their sponge prey (pers. obs. S. Morley). The surface grazing limpet *N. concinna* measured by Clarke (2008; Fig. 4), surprisingly, had C and N percentages more similar to the carnivore *P. corrugatus* and the omnivore *O. validus* than to the herbivore *H. steineni*. This might also have been caused by the high protein content in the limpets' diet (25.4% protein; Whitaker and Richardson, 1980). Grouping taxa by mode of feeding and not by the actual food consumed, therefore misses possible differences in diet within trophic guilds that can markedly affect proximate composition (Cross et al., 2005; Evans-White et al., 2005).

4.2 Temporal variation in proximate composition

Many of the differences in proximate composition between the current study and that of Clarke et al. (2008) may, in part, be explained by differences between seasons and years. The Western Antarctic Peninsula has strong seasonal and inter-annual variation in temperature and primary productivity (Clarke et al., 2008; Venables et al., 2013) which are known to have marked effects on the physiology of both primary and secondary consumers (Clarke and Peck, 1991; Morley et al., 2012). Some primary consumer mollusc species have elemental compositions which vary with the seasonal nutrient content of their food source (Cross et al., 2003). For example, seasonal differences in elemental composition (%C, %N) and C:N ratio in *Mytilus edulis* from Oostershelde, a temperate North Sea region, had values that were generally low during spring and summer and high for the rest of the year (Smaal and Vonck, 1997). Strong seasonal patterns and changes in weight and tissue composition are typical for mussels from temperate regions and are driven by changes in food availability and quality in relation to metabolic requirements (e.g. during reproductive activity; Hawkins and Bayne, 1992; Hawkins et al., 1985).

However, the only seasonal difference in the benthic predators and scavengers measured in the current study was between summer and winter *P. meirsii*. The fact that this study found few seasonal stoichometric differences may seem at odds with the extreme seasonality of photoperiod, ice cover and primary productivity. It does, however, likely indicate that the majority of benthic scavenger and predator species studied were able to buffer the demand and utilisation of carbon and nitrogen across the year as has been demonstrated in other benthic secondary consumers (Frost et al., 2003; Clarke, 2008). Seasonal food availability is much more consistent for predators and scavengers and only two of the five predators and scavengers in this study, *P. miersii* and *D. kerguelenensis*, have significantly reduced faecal production in winter, and all species exhibit some feeding, during the winter months (Obermüller et al., 2010). Several Antarctic predatory fish, both larvae (North and Ward, 1989) and adults (Targett et al., 1987; Montgomery et al., 1993; Gröhsler, 1994) are also known to feed during the winter period. Antarctic primary consumers have more seasonal feeding strategies. Some species cease feeding for several months in winter (Brockington et al., 2001), while a few others maintain feeding throughout the year (Barnes and Clarke, 1995). However, even in the latter, food quality and availability vary markedly from summer to winter (Clarke et al., 2008).

Benthic species generally expend less energy on locomotion than pelagic species, which often expend a large portion of their energy budget on moving through the water column (Clarke and Peck 1991 and references therein). This high energy requirement of pelagic zooplankton has been linked to the greater need for high energy lipid stores in pelagic compared to benthic species (Clarke and Peck, 1991). Even some Antarctic primary consumers, such as the limpet *N. concinna*, which lose weight in winter (Fraser et al., 2002), have no seasonal change in CHN content of tissues (Clarke, 2008). Their low energy benthic life-style may allow protein to fuel this limpets' metabolism year round (Fraser et al., 2002). Other Antarctic benthic primary consumers, including the brachiopod, *Liothyrellla uva*, have very low metabolic rates and utilise proteins to support metabolic requirements across the year (Peck, 1996; Peck et al., 1987). For the predatory and scavenger species in the current study, there were small seasonal differences in the O:N ratios of all but *P. meirsii*, which utilises a mixture of lipids and carbohydrates (O:N of 30 to 62) throughout the year (Obermüller et al., 2010). This seasonal variation in O:N ratios was not consistent, with *H. antarcticus* utilising less (O:N of 51-91 in summer and 24-48 in winter), but *O. victoriae* utilising more lipid (O:N of 30-230 in summer and 150-210 in winter), in winter than summer (Obermüller et al., 2010). Whilst CHN was only investigated in isolated tissues of *H. antarcticus,* fish liver and muscle are known sites of energy storage that can be mobilised during starvation and to fuel reproduction, particularly in migratory notothenioids (Fenaughty et al., 2008). In an extreme example of this, the occurrence of low condition factor, "axe handle" specimens of the Antarctic tooothfish, *Dissostichus mawsoni*, in the Ross Sea, was linked to energy mobilisation from muscles to fuel spawning migration and subsequent habitation of oligotrophic waters (Fenaughty et al., 2008). Any greater seasonal utilisation of lipid stores in *H. antarcticus* cannot have been sufficiently large to lead to a detectable change in tissue proximate composition between summer and winter.

Strong seasonal variation in primary production is characteristic of Antarctic shelf seas (e.g. Clarke et al., 2008) and this often leads to a matching temporal variation in reproductive cycles (e.g. Grange et al., 2004, 2007). Even if adult predators and scavengers do not directly rely on phytoplankton for food, the release of larvae is often timed to ensure a match between the feeding of planktonic larvae and the phytoplankton bloom (Cushing, 1990), or with food availability for newly settled juveniles (Bowden et al., 2006). The cycles of gonad production and gamete release would, therefore, be expected to result in temporal cycles of elemental composition as lipids increase and decrease through the spawning cycle. However, many Antarctic species develop eggs over 2 years with only a small proportion of the gonad spawned in any one year. For example as little as 34% of the Antarctic starfish, *Odontaster validus*, gonad is spawned annually (e.g. Grange et al., 2007). Whilst there is a large inter-annual variation in the amount of energy investigated into gonads; peak gonad index of *Ophionotus victoriae* only varied between 0.5 and 2% between years (Grange et al., 2004). This temporal variation may be too small a change to cause a detectable difference in C:N ratios.

As with the previously measured seasonal physiology, the CHN values, of these five benthic predators and scavengers, did not show a consistent seasonal pattern and were, in the main, very stable across the year. The expected immediate impact of loss of winter sea ice, and the resultant disruption of primary productivity on primary consumers, may, therefore, be buffered at higher trophic levels. However, over longer time scales, the reduced seasonal storage and energy saving mechanisms of predators and scavengers may make them more vulnerable to changes in the predictability of energy flow through the shallow water Antarctic ecosystem.

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Figure Captions

Fig. 1 Carbon concentration: Data expressed as percentage of dry mass (mean and standard error) except for *Ophionotus victoriae* and *Paraceradocus miersii*, where values were corrected for inorganic carbon fraction (thus expressed as percentage of ash free dry mass). Filled columns, summer samples: April-May 2007 and November 2007–March 2008) and open columns, winter samples: June-October 2007. Ha *Harpagifer antarcticus*. Different letters indicate that *P. miersii* had significantly higher percentage Carbon in summer than winter (ANOVA, F = 11.63, p = 001).

Fig. 2: Nitrogen concentration: Data expressed as percentage of dry mass (mean and standard error) except *Ophionotus victoriae* and *Paraceradocus miersii*, where values were corrected for inorganic hydrogen fraction (thus expressed as percentage of ash free dry mass). Filled columns, summer samples and open columns, winter samples (see Fig. 1). Ha *Harpagifer antarcticus*. Different letters indicate that *P. miersii* had significantly higher percentage Nitrogen in summer than winter (ANOVA, F = 11.20, p = 0.002).

Fig. 3: Molar C:N ratio. Data are calculated for constituencies in dry mass and shown as mean and standard error, except *O. victoriae* and *P. miersii*, where values were corrected for inorganic carbon and nitrogen fraction (thus calculated in ash free dry mass). Filled columns, summer samples and open columns, winter samples (see Fig. 1). Ha *Harpagifer antarcticus*. Different letters indicate that *P. miersii* had significantly higher C:N ratio in summer than winter (ANOVA, F = 5.89, p = 0.019).

Fig. 4: Relationship between carbon and nitrogen in four of the species examined in this study (filled symbols) in comparison with data from Clarke (2008; open symbols). Data shown as mean and standard error and expressed as percentage of ash free dry mass except *Parborlasia corrugatus* and *Doris kerguelenensis* samples from present study (expressed as percentage of dry mass as inorganic Carbon). Summer and winter samples pooled unless stated otherwise.

Table Legends

Table 1: Elemental composition (C: carbon, H: hydrogen, N: nitrogen) in one Antarctic benthic fish (muscle and liver tissue) and four invertebrate species. All data expressed as percentage of dry mass (mean and standard deviation SD). %C, %H, and %N concentration in *Ophionotus victoriae* and *Paraceradocus miersii* were corrected for inorganic CHN fraction (*O. victoriae*: 7.1 ± 0.2 %C, 0.07 ± 0.00 %H, 0.04 ± 0.00 %N; *P. miersii*: 2.8 ± 0.1 %C, 0.03 ± 0.00 %H, 0.04 ± 0.00 %N). S = summer, W = winter (see Table 2).

Table 2: Hydrogen concentration in *Harpagifer antarcticus* muscle tissue, *H. antarcticus* liver tissue, *Ophionotus victoriae*, *Paraceradocus miersii*, *Parborlasia corrugatus* and *Doris kerguelenensis*. Data expressed as percentage of dry mass (mean and standard deviation SD) except *O. victoriae* and *P. miersii*, where values were corrected for inorganic hydrogen fraction (thus expressed as percentage of ash free dry mass). Inorganic H fraction negligible in other species. S: summer (April-May 2007 and November 2007–March 2008), W: winter (June-October 2007).

ESM Table 1: Wet mass (WM) measured in one Antarctic benthic fish, *Harpagifer antarcticus*, and four invertebrate species, *Ophionotus victoriae*, *Paraceradocus miersii*, *Parborlasia corrugatus* and *Doris kerguelenensis*, in those specimen used for CHN analysis (ESM Tables 2 and 3). Dry mass (DM) calculated for each species from the WM:DM relationship of individual data for the mean values shown in ESM Table 4 (Animal Morphometrics). WM was plotted against DM and regressions calculated. All data expressed as mean and SD. S: summer (April-May 2007 and November 2007–March 2008), W: winter (June-October 2007).

Species Month	**Season**	**N**	**WM** (g)	**DM** (g)	**% water**
H. antarcticus					
April 2007	S	12	11.65 ± 3.16	2.95 ± 0.83	74.7
June 2007	W	6	11.18 ± 3.42	2.82 ± 0.90	74.8
September 2007	W	10	10.40 ± 1.20	2.62 ± 0.32	74.8
November 2007	S	10	11.07 ± 2.33	2.79 ± 0.62	74.8
January 2008	S	10	9.85 ± 2.32	2.47 ± 0.61	74.9
Annual mean	S + W	48	10.84 ± 2.52	2.73 ± 0.67	74.8
O. victoriae					
May 2007	S	6	7.90 ± 2.22	3.17 ± 0.77	59.9
July 2007	W	6	7.47 ± 1.65	3.02 ± 0.57	59.6
September 2007	W	10	8.29 ± 1.30	3.30 ± 0.45	60.2
November 2007	S	10	8.12 ± 2.00	3.24 ± 0.70	60.1
January 2008	S	10	9.27 ± 1.49	3.64 ± 0.52	60.7
March 2008	S	10	8.69 ± 3.18	3.44 ± 1.10	60.4
Annual mean	S + W	52	8.38 ± 2.06	3.33 ± 0.71	60.3
P. miersii					
April 2007	S	6	0.63 ± 0.40	0.16 ± 0.12	74.6
June 2007	W	6	0.77 ± 0.40	0.20 ± 0.12	74.0
September 2007	W	10	0.51 ± 0.39	0.12 ± 0.12	76.5
November 2007	S	9	0.53 ± 0.35	0.13 ± 0.10	75.5
January 2008	S	11	0.83 ± 0.27	0.22 ± 0.08	73.5
February 2008	S	10	0.92 ± 0.34	0.24 ± 0.10	73.9
Annual mean	S + W	52	0.70 ± 0.37	0.18 ± 0.11	74.3
P. corrugatus					
April 2007	S	7	64.90 ± 28.01	5.58 ± 1.43	91.4
May 2007	S	6	89.24 ± 24.07	7.05 ± 4.01	92.1
July 2007	W	6	93.72 ± 32.51	7.80 ± 5.41	91.7
October 2007	W	10	84.99 ± 11.57	6.34 ± 1.93	92.5
December 2007	S	10	105.87 ± 29.67	9.82 ± 4.94	90.7
February 2008	S	10	124.46 ± 27.37	12.91 ± 4.56	89.6
March 2008	S	10	89.98 ± 33.03	7.17 ± 5.50	92.0
Annual mean	S + W	49	95.00 ± 31.14	8.41 ± 4.78	91.1
D. kerguelenensis					
June 2007	W	6	12.93 ± 2.95	2.24 ± 0.40	82.7

August 2007	W	6	13.12 ± 8.75	2.26 ± 1.18	82.8
December 2007	S	5	15.36 ± 8.50	2.57 ± 1.15	83.3
March 2008	S	5	13.82 ± 9.07	2.36 ± 1.23	82.9
Annual mean	S + W	22	13.73 ± 7.12	2.35 ± 0.96	82.9

ESM Table 2: Carbon, hydrogen and nitrogen concentration in *Ophionotus victoriae* and *Paraceradocus miersii* not corrected for the inorganic CHN fraction. Data expressed as percentage of organic mass (i.e. ash free dry mass, mean and standard deviation SD). S: summer, W: winter (see Table 2).

Species Month	**Season**	**n**	**%C** Mean ± SD	**%H** Mean ± SD	**%N** Mean ± SD
O. victoriae					
May 2007	S	6	21.76 ± 1.62	2.38 ± 0.31	3.34 ± 0.66
July 2007	W	6	21.78 ± 1.76	2.43 ± 0.27	3.59 ± 0.55
September 2007	W	10	23.24 ± 3.91	2.65 ± 0.53	3.62 ± 0.76
November 2007	S	10	22.03 ± 2.14	2.47 ± 0.30	3.50 ± 0.64
January 2008	S	10	25.28 ± 4.30	2.95 ± 0.88	4.15 ± 1.11
March 2008	S	10	20.90 ± 1.39	2.29 ± 0.16	3.26 ± 0.48
P. miersii					
April 2007	S	5	35.60 ± 5.95	4.86 ± 0.27	7.36 ± 1.14
June 2007	**W	7	32.50 ± 3.72	4.74 ± 0.57	6.70 ± 0.80
September 2007	**W	8	32.59 ± 5.81	4.71 ± 0.83	7.16 ± 1.24
November 2007	S	10	35.35 ± 6.58	4.90 ± 0.80	7.52 ± 1.21
January 2008	S	11	48.68 ± 13.65	5.85 ± 1.00	8.89 ± 1.65
February 2008	S	9	49.15 ± 10.41	5.84 ± 0.79	9.22 ± 1.53

**indicates significant seasonal difference: Summer significantly higher than winter data (months combined) for %C (F = 11.51, p = 0.001) and %N (F = 10.59, p = 0.020) (all ANOVA).

ESM Table 3: C:N ratio (mean and SD) in one Antarctic benthic fish and four invertebrate species (see Table 1). All data expressed on a molar basis and calculated for constituencies in dry mass. ^{c} indicates data corrected for inorganic carbon and nitrogen fraction (expressed as percentage of organic mass, i.e. ash free dry mass) in *O. victoriae* and *P. miersii*. S = summer, W = winter (see Table 2).

Species Month	**Season**	**n**	**C:N Mean ± SD**	
***H. antarcticus* Muscle tissue**				
April 2007	S	12	4.18 ± 0.25	
June 2007	W	6	4.27 ± 0.18	
September 2007	W	10	4.29 ± 0.32	
November 2007	S	10	4.17 ± 0.14	
January 2008	S	10	4.17 ± 0.22	
***H. antarcticus* Liver tissue**				
April 2007	S	12	7.75 ± 2.55	
June 2007	W	5	7.80 ± 0.69	
September 2007	W	10	7.17 ± 1.12	
November 2007	S	7	7.63 ± 1.65	
January 2008	S	8	6.81 ± 1.10	
O. victoriae				
May 2007	S	6	7.73 ± 0.90	^{c} 5.25 ± 0.53
July 2007	W	6	7.14 ± 0.60	^{c} 5.28 ± 0.94
September 2007	W	10	7.59 ± 0.87	^{c} 5.37 ± 1.30
November 2007	S	10	7.48 ± 0.97	^{c} 5.47 ± 1.98
January 2008	S	10	7.27 ± 0.86	^{c} 4.29 ± 0.77
March 2008	S	10	7.60 ± 1.00	^{c} 5.91 ± 1.38
P. miersii				
April 2007	S	6	5.45 ± 0.53	^{c} 5.04 ± 0.50
June 2007	W	7	5.66 ± 0.28	^{c} 5.20 ± 0.28**
September 2007	W	8	5.31 ± 0.18	^{c} 4.87 ± 0.20**
November 2007	S	10	5.47 ± 0.41	^{c} 5.05 ± 0.43
January 2008	S	11	6.28 ± 0.73	^{c} 5.93 ± 0.79
February 2008	S	9	6.20 ± 0.66	^{c} 5.86 ± 0.68
**indicates significant seasonal difference: C:N corrected for inorganic fraction significantly higher in summer than winter (months combined) (ANOVA, F = 5.89, p = 0.019).				
P. corrugatus				
April 2007	S	7	4.15 ± 0.11	
May 2007	S	6	4.20 ± 0.13	
July 2007	W	6	4.33 ± 0.15	
October 2007	W	10	4.22 ± 0.14	
December 2007	S	10	4.31 ± 0.14	
February 2008	S	10	4.29 ± 0.20	
March 2008	S	10	4.20 ± 0.13	

D. kerguelenensis			
June 2007	W	6	5.10 ± 0.17
August 2007	W	6	5.13 ± 0.19
December 2007	S	5	5.03 ± 0.13
March 2008	S	5	5.15 ± 0.17

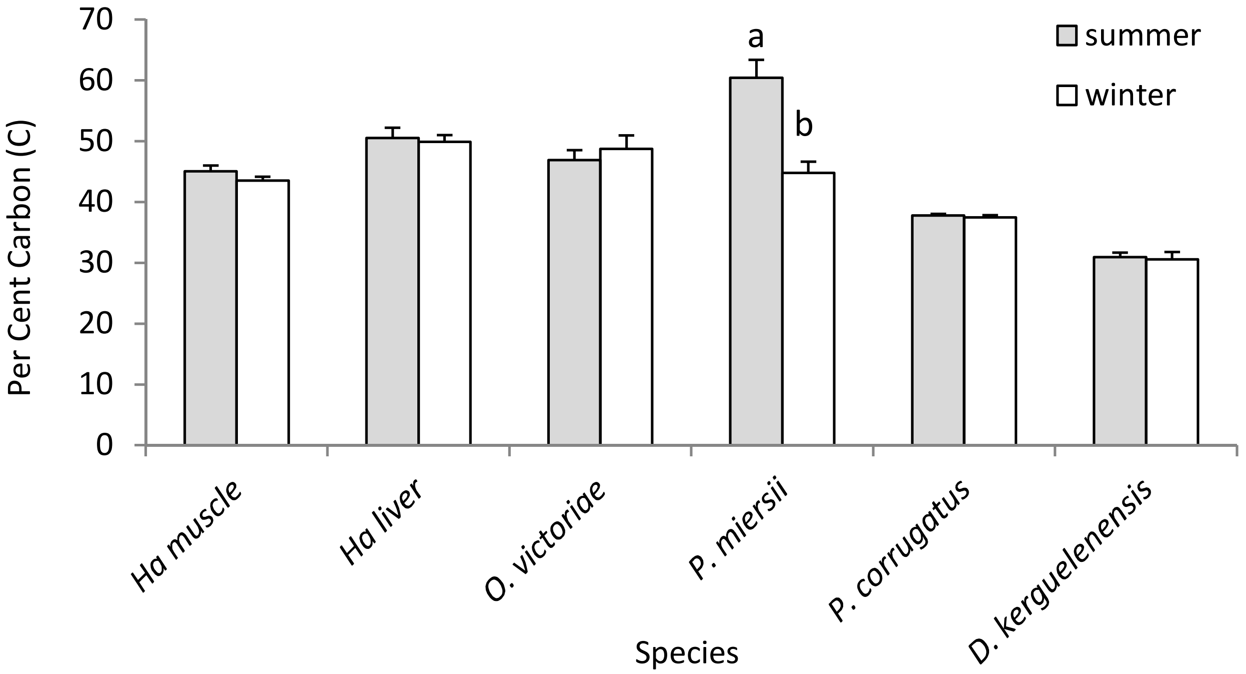
ESM Table 4: Animal Morphometrics: Wet mass (WM), dry mass (DM) and ash free dry mass (AFDM) in one Antarctic benthic fish and four invertebrate species (see Table 2). Total length (TL) measured in *Harpagifer antarcticus* and *Paraceradocus miersii* and *Doris kerguelenensis*. ^{d} Disc diameter measured in *Ophionotus victoriae*. No length measurements taken for *Parborlasia corrugatus*. All data expressed as mean and SD. Seas = Season, S = summer, W = winter (see Table 2).

Species Month	**Seas**	**n**	**WM** (g)	**DM** (g)	**AFDM** (g)	**TL** (mm)
H. antarcticus						
March 2007	S	15	18.70 ± 5.29	4.89 ± 1.25	4.06 ± 0.98	106.12 ± 9.47
June 2007	W	14	15.16 ± 7.22	4.03 ± 1.97	3.32 ± 1.58	98.10 ± 19.32
September 2007	W	15	12.73 ± 1.60	3.36 ± 0.44	2.76 ± 0.36	83.62 ± 3.49
November 2007	S	15	14.00 ± 2.38	3.64 ± 0.62	2.97 ± 0.50	85.18 ± 4.14
January 2008	S	17	13.70 ± 2.36	3.52 ± 0.61	2.90 ± 0.50	83.06 ± 6.30
O. victoriae						
February 2007	S	15	8.82 ± 1.27	3.21 ± 0.42	1.02 ± 0.75	^{d}30.13 ± 2.45
May 2007	S	15	8.26 ± 1.60	3.05 ± 0.60	1.05 ± 0.19	^{d}27.83 ± 1.92
July 2007	**W	15	6.24 ± 1.37	2.35 ± 0.48	0.75 ± 0.17	^{d}25.72 ± 2.70
September 2007	**W	15	7.54 ± 1.45	2.76 ± 0.49	0.94 ± 0.18	^{d}28.05 ± 2.54
November 2007	S	15	9.26 ± 2.29	3.29 ± 0.75	1.11 ± 0.28	^{d}29.20 ± 2.67
January 2008	S	15	8.58 ± 1.53	3.11 ± 0.58	0.97 ± 0.20	^{d}29.24 ± 1.66
March 2008	S	15	8.18 ± 1.08	3.02 ± 0.35	0.92 ± 0.13	^{d}28.82 ± 1.44
**indicates significant seasonal difference: Winter lower than summer WM (ANOVA, F=27.69, $p<0.001$), DM (ANOVA, F=26.55, $p<0.001$), AFDM (Kruskal-Wallis test, H=6.89, p=0.009), and Disc diameter (ANOVA, F=17.78, $p<0.001$).						
P. miersii						
February 2007	S	14	0.95 ± 0.24	0.29 ± 0.06	0.19 ± 0.04	40.52 ± 5.46
May 2007	S	15	0.83 ± 0.30	0.24 ± 0.09	0.16 ± 0.06	37.72 ± 6.12
June 2007	W	12	0.68 ± 0.30	0.20 ± 0.10	0.14 ± 0.06	34.22 ± 6.76
September 2007	W	15	0.89 ± 0.45	0.25 ± 0.12	0.17 ± 0.08	38.21 ± 7.96
November 2007	S	15	0.75 ± 0.24	0.21 ± 0.07	0.14 ± 0.05	36.06 ± 5.08
January 2008	S	15	1.18 ± 0.22	0.33 ± 0.06	0.21 ± 0.03	44.25 ± 3.14
February 2008	S	15	0.74 ± 0.19	0.21 ± 0.06	0.14 ± 0.04	36.63 ± 3.66

P. corrugatus	**Seas**	**n**	**WM** (g)	**DM** (g)	**AFDM** (g)	
March 2007	S	15	82.93 ± 24.32	9.78 ± 2.53	7.96 ± 2.15	
May 2007	S	14	97.23 ± 21.54	12.83 ± 3.15	10.44 ± 2.69	
July 2007	W	15	101.82 ± 29.70	12.30 ± 2.96	10.53 ± 2.69	
October 2007	W	15	94.52 ± 32.71	13.44 ± 4.50	11.12 ± 3.69	
December 2007	S	15	103.66 ± 26.14	13.88 ± 3.76	11.39 ± 3.14	
February 2008	S	16	108.37 ± 29.46	14.23 ± 3.81	11.59 ± 3.04	

D. kerguelenensis	**Seas**	**N**	**WM** (g)	**DM** (g)	**AFDM** (g)	**TL** (mm)
March 2007	S	13	14.75 ± 4.36	1.95 ± 0.53	1.33 ± 0.40	55.84 ± 5.22
June 2007	W	15	16.54 ± 10.79	2.33 ± 1.50	1.65 ± 1.14	58.15 ± 12.08

August 2007	W	13	13.45 ± 10.96	1.88 ± 1.33	1.27 ± 0.93	54.60 ± 16.35
December 2007	S	15	13.11 ± 8.45	1.89 ± 1.10	1.30 ± 0.79	56.11 ± 14.35
March 2008	S	15	10.03 ± 7.84	1.44 ± 1.07	0.97 ± 0.76	48.27 ± 11.59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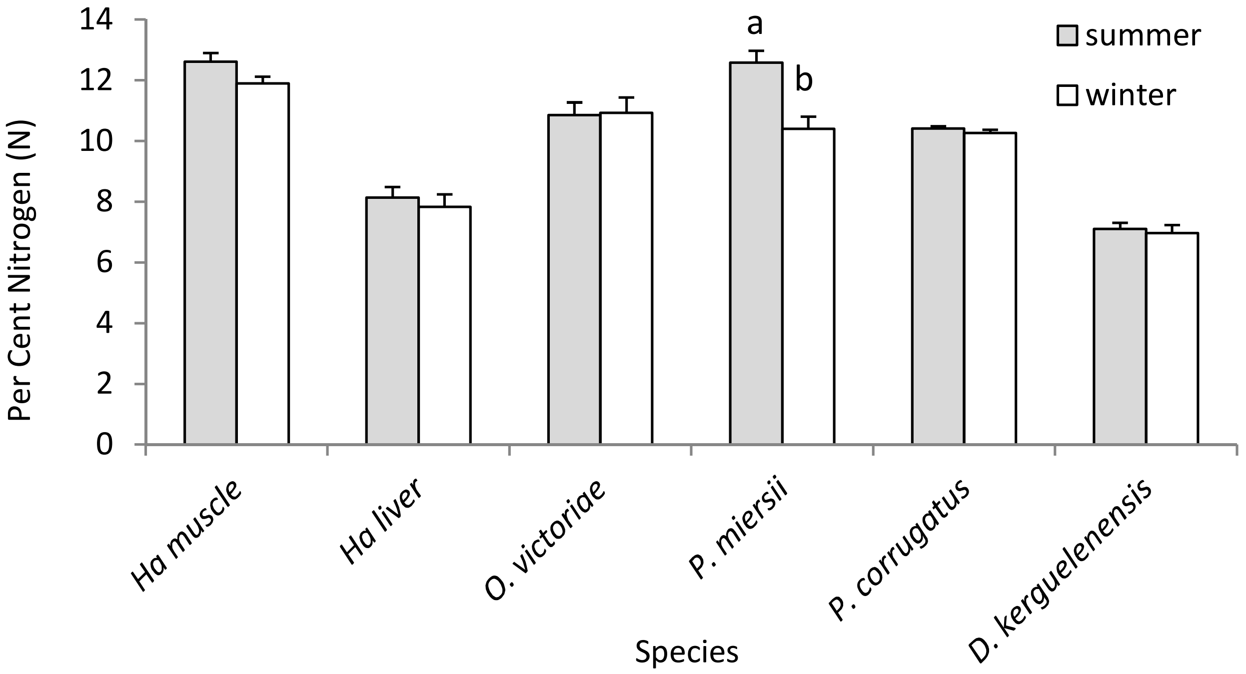
O. victoriae
P. miersii
P. corrugatus
D. kerguelenensis
Species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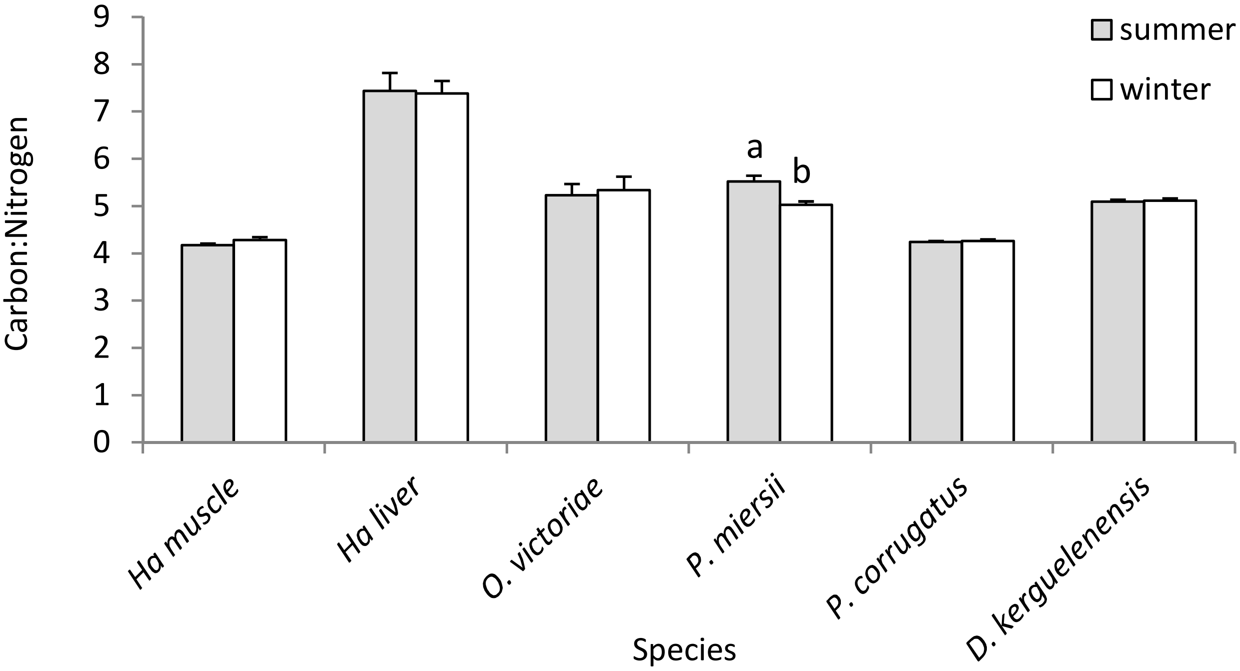
D. kerguelenensis
Species



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P. corrugatus
D. kerguelenensis
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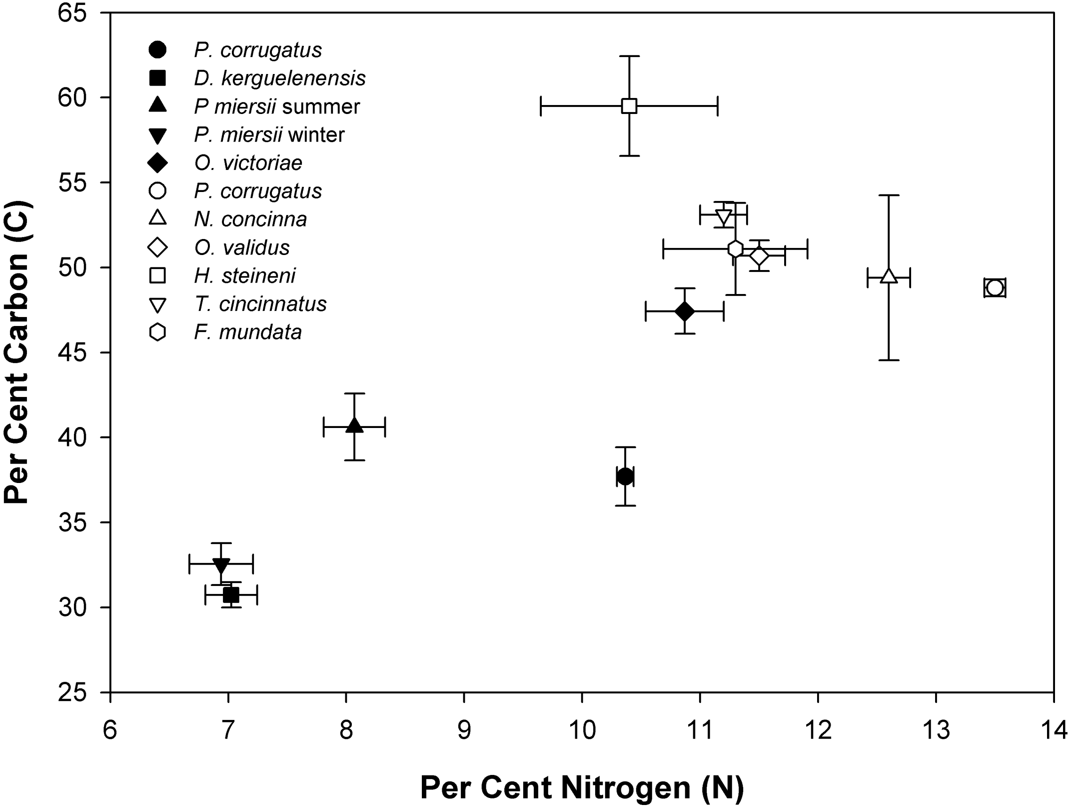

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Per Cent Carbon (C)
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Per Cent Nitrogen (N)
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■ D. kerguelenensis
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▼ P. miersii winter
◆ O. victoriae
○ P. corrugatus
△ N. concinna
◇ O. validus
□ H. steineni
▽ T. cincinnatus
⬡ F. mundata