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Importance of diatoms for *Oithona* in Antarctic waters

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ABSTRACT

Fatty acid biomarker analysis of the Cyclopoid copepods *Oithona similis* and *Oithona frigida* sampled from the Southern Ocean during the austral summer has indicated differences in diet between the two species. *Oithona similis* contained higher proportions of protozoan and bacterial fatty acids markers, indicative of microbial foodwebs involved in the recycling of detrital material and faecal pellets. In contrast, the fatty acid composition of *O. frigida* was characterized by a strong diatom signature. Despite these species-specific differences, the fatty acid biomarker composition of both species at each of the stations sampled, primarily reflected the species composition of the microplankton in their environment. Comparison of an index of fatty acid composition with nutritional condition indicated that those CV and female *O. similis* containing the highest levels of diatom biomarkers fatty acids were in the best condition. These findings suggest that diatoms are more important for *Oithona* spp. in the Southern Ocean than for other oceanic regions and are consistent view that *O. similis* is an integral component of food webs associated with the recycling of detrital aggregates and faecal material.

INTRODUCTION

The importance of smaller species of zooplankton and particularly *Oithona similis* has been increasingly realized (Paffenhöfer 1993, Gallienne and Robins 2001, Dubischar et al. 2002). *Oithona similis* is globally distributed, is often the dominant component of plankton communities and has been demonstrated to be an important link between microbial food webs and higher trophic levels (Nielsen and Sabatini 1996). *O. similis* is also likely to benefit from increasing sea temperatures, particularly in high latitudes, where reduced ice cover is predicted to increase the prevalence of microbial, recycling based ecosystems (Hansen et al. 2003).

Studies of the diet of *Oithona* are not numerous, but this genus is thought to prefer motile prey and in particular protozoans, although diatoms and flagellates are also ingested in smaller amounts (Atkinson 1995, Lonsdale et al. 2000, Castellani et al. 2005, 2008). Initially it was suggested that *Oithona* recycles detrital aggregates (Lampitt and Gamble 1982) and faecal pellets (coprophagy, González and Smetacek 1994) and this was supported by numerous direct and indirect observations (Smetacek 1980, Lampitt et al. 1990, Kiørboe and Visser 1999, Gonzalez et al. 2000, Wexels Riser et al. 2001, Svensen and Nejstgaard 2003). However, more recent experimental evidence has established that *Oithona* does not readily ingest faecal pellets (Reigstad et al. 2005) and protozoans have now been identified as key players in this process (Poulsen and Iversen 2008).

Lipids are often used to study food web interactions with specific fatty acids diagnostic of major microplankton taxa and can be traced through food webs (Stevens et al. 2004, Stowasser et al. 2009). 16:1(n-7), 16:4(n-1) and 20:5(n-3) are often used as biomarkers for diatoms; 22:6(n-3) and 18:4(n-3) for flagellates; and 15:0, iso15:0, anteiso15:0, 17:0 and iso17:0 for bacteria (Stevens et al. 2004). Although fatty acid biomarkers in many species of marine zooplankton have been well studied, analyses of *Oithona* have been limited, possibly owing to the small size of these copepods and the need for considerable numbers of individuals per analysis. Kattner et al. (2003) provided initial fatty acid biomarker analyses of *O. similis* and other small copepod species from Antarctic waters. More recently, Lischka and Hagen (2007) provided a more detailed seasonal analysis of this species from Arctic waters. Both these studies showed that *O. similis* has an omnivorous diet with a prevalence of biomarkers characteristic of motile prey. Additionally, these studies also provided lipid biomarker evidence for the ingestion of detrital aggregates and faecal pellets by *O. similis*.

Here we utilise fatty acid biomarker analysis to compare the diet of *O. similis* with its larger, but less well studied congener, *Oithona frigida*. Collectively, both species are among the numerically dominant zooplankton in Antarctic waters, the former being widely distributed (Metz 1996, Ward and Hirst 2007) whereas the latter appears particularly abundant near the Polar Front (Dubischaar et al. 2002). We collected *Oithona* from the Scotia Sea in the Atlantic sector of the Southern Ocean. The Scotia Sea is bounded by the Scotia Ridge where primary productivity is generally high and surface chlorophyll *a* levels can exceed 20 µg L^{-1}. (Atkinson et al. 2001). These intense blooms can persist for months and are typically dominated by large diatoms (Korb et al. 2008). By contrast, primary production in the central Scotia Sea is much lower, with surface chlorophyll *a* concentrations typically not exceeding 0.5 µgL^{-1} and where flagellates and microzooplankon comprise a substantial proportion of the microplankton standing stock (Korb et al. 2005).

We sampled *Oithona* from a number of sites across the Scotia Sea characterised by distinctly different production and microplankton communities with the aim of understanding how the food environment of *Oithona* was linked to both their nutritional condition and abundance. Given the small size of both species (prosome length of 500 µm and 700 µm for *O. similis* and *O. frigida* respectively), fatty acid biomarkers were analysed using a highly sensitive technique, involving the preparation of pentafluorobenzyl ester of the fatty acids, which were then detected by electron capture detector (ECD). This method is described in detail.

METHOD

Sample collection

Samples were collected from six stations during cruise JR177 of the RRS James Clark Ross to the Scotia Sea sector of the Southern Ocean during January and February 2007 (Fig. 1). At each station and immediately prior to zooplankton net hauls, vertical profiles of temperature and fluorescence were determined using a SeaBird 911+CTD equipped with a 12 position carousel water sampler and 10 L Niskin bottles (Table I). Seawater was collected from the fluorescence maxima and 3.2 L aliquots were filtered onto 47 mm ashed GF/F filters and samples stored in chloroform:methanol (2:1 v/v) at -80ºC until analysis. All zooplankton samples were collected using vertical net hauls from 400 m to the surface and conducted at dawn (approx. 04:00 local time). Nets were hauled at ~0.22 ms^{-1}. Zooplankton samples for the determination of abundances of the various developmental stages of the target copepod

species were collected using paired 53µm mesh bongo nets and preserved in buffered formaldehyde (4 % w/v). These samples were analysed in the UK using a binocular microscope at 60X magnification. Counts were made of all copepodid stages of *O. similis* and O. *frigida* (CI-CVI) and nauplii of *O. similis*. Nauplii of *O. frigida* were extremely rare and not counted. Also counted were the total numbers of egg sacs of *O. similis* in each haul, both those attached to females and detached and floating free in the sample and eggs female^{-1} determined. Egg sacs of *O. frigida*, which are easily distinguishable from those of *O similis* (Ward and Hirst 2007) were extremely rare and not counted.

Additional net hauls were made for the collection of animals for biochemical analyses. For carbon and nitrogen determinations of female copepods from selected stations, samples of 400-500 *O. similis* and 100-340 *O. frigida*, depending on availability, were sorted into a glass cavity well which enabled a final check of the sample identity and contaminating material, i.e. non target copepod species and microplankton material was removed. Purified samples of *Oithona* were then pipetted onto ashed GF/F filters (25 mm) and subjected to gentle vacuum to remove excess water. For fatty acid analysis, replicates containing 20 copepods were sorted onboard before preservation in 500 µl of chloroform:methanol (2:1 v/v) at -80ºC.

Microplankton species composition was determined on samples collected from 20 m depth and preserved in 1-2% Lugol solution in 250 ml brown glass bottles. In the laboratory, 50 ml subsamples were settled for 20-24 hours in Hydro-Bios setting chambers (Duncan and Associates, UK) and cell enumeration followed Hasle (1978). Microplankton carbon (µgC L^{-1}) was estimated from cell measurements following Poulton et al. (2007). No attempt was made to enumerate cell sizes of < 5 µm since these counts are unreliable using inverted microscopy (Poulton et al. 2007). For full details of cell counting and biomass estimate procedures, see Korb et al. (2010).

Biochemical analysis

Carbon and nitrogen analyses were conducted on both species of *Oithona* from selected sites, where both the numbers of copepods and time permitted the collection of the substantial numbers of animals required for these analyses. Carbon and nitrogen analyses of female copepods were performed on samples dried for 24 hours at room temperature in a vacuum dessicator before analysis in a CE-440 elemental analyser (Exeter Analytical Inc).

Given the small size of *Oithona*, fatty acids were determined using a highly sensitive technique that involves converting the fatty acids to Pentafluorobenzyl (PFB) esters and

detecting the fluoride with an Electron Capture Detector (ECD). After the addition of an internal fatty acid standard (23:0), the sample was phase separated using 0.88 % (w/v) KCl and total lipid extracted following Folch et al. (1957). Total lipid was initially saponified using 100 µL 1M KOH in ethanol (5:95 v/v) then acidified using 0.6M HCl to produce free fatty acids. After the addition of water (250 µL), free fatty acids were extracted using 2 x 250 µL diethylether. After drying under a stream of nitrogen, free fatty acids were converted to PFB esters by reacting with 140 µL of acetonitrile:diisopropylamine/ PFB bromide (1000:10:1 v/v/v) at 60 ºC for 30 minutes. PFB esters of the fatty acids were purified using thin layer chromatography (TLC, Pond et al. 2008) and analyzed using a Trace 2000 GC (Thermo) equipped with a Restek Stabilwax column (30 m x 0.32 mm) and an electron capture detector (ECD). Hydrogen was used as the carrier gas and nitrogen as the ionizing gas for the ECD. The output from the ECD (mol %) was converted to weight % to be consistent with most other studies of marine zooplankton. Fatty acids were identified by comparison with a standard mixture (Marinol) and by GC-MS following Pond et al. (1998).

Condition factor

Condition factor (CF), involving mass of carbon or nitrogen per unit volume has previously been used as a measure of a copepods nutritional status (Campbell et al. 2001). Here we use total fatty acid as a measure of nutritional condition in *O. similis.* Insufficient data was available to perform a similar analysis on *O. frigida.*

$$CF = TfaL^{-3}$$

where Tfa = total fatty acid (µg) and L = prosome length (µm).

Statistical Analysis

Linear regressions were used to determine the relationship between food availability (estimated carbon biomass) and abundances of the different developmental stages of *Oithona*. Linear regression was also used to investigate the relationship between condition of *O. similis* and an 'index' of fatty acid composition. This index was derived from a principal component analysis (PCA, see below) of the *Oithona* fatty acid data. The first principal component (PC1) is effectively a fatty acid biomarker spectrum ranging from diatom dominated to microzooplankton + bacteria + detritus dominated signatures.

To investigate differences in the fatty acid composition between the different developmental stages and species of *Oithona*, Principal component analysis (PCA) was conducted on the percentage contributions of fatty acids for each sample. Variables included in the analyses were either correlated with the first two principal components, or were included on the basis that they are recognised biomarkers. (Meglen 1992). Principal components were generated from a correlation matrix of the percentage contributions of fatty acids for each species, stage and site. Graphical representation of scores derived from the PCA analysis indicate relationships among samples. All statistical analyses were conducted using MINITAB 15 statistical software.

RESULTS

The environment

Values of sea temperature, integrated from the surface to 100m, exhibited a general latitudinal gradient with lowest values of 0.85 °C at station Su 5 and increasing to 2.97 °C at Su 9 (Fig. 1, Table I). Integrated chlorophyll *a* values ranged from 0.21 µg L^{-1} at Su 5 to 1.46 µg L^{-1} at Su 9. Integrated sea temperature and chlorophyll *a* values were correlated (Chl *a* = -0.466 + 0.545 sea temp., P = 0.030, F = 10.93).

Microplankton

Percent composition of the major taxonomic groups of microplankton was determined from estimates of microplankton biomass (µgC L^{-1}) and striking differences were evident between stations (Fig. 2a). Microplankton composition varied between Su 11, which was dominated by dinoflagellates (87 %) to Su 9, which was dominated by diatoms (92%, Fig. 2a). Proportions of ciliates were most abundant at Su 6 comprising 6 % of total microplankton. Since cell sizes of <5 µm were not counted, most naked flagellates were not included in the counts and only low levels were detected (Fig. 2b). Dinoflagellates comprised mostly 20-40 µm naked dinoflagellates, whilst diatoms were more diverse and dominated by *Thalassiothrix antarctica*, *Eucampia anatarctica*, *Odontella* sp, *Chaetoceros* sp. and *Coscinodiscus* sp. Ciliates were mostly *Strombidium* sp. See Korb et al. (2010) for full details on microplankton species composition. Total amounts of microplankton varied substantially between sites, ranging from 116 µg C L^{-1} at Su 9 to 8 µg C L^{-1} at Su 6 (Fig 2b). Levels of microplankton carbon were highest at the three sites where the microplankton community was dominated by diatoms (Fig 2b).

Fatty acid composition of microplankton at the sites was consistent with the microscopic analysis with the highest proportions of the dinoflagellate biomarkers 18:4(n-3), 18:5(n-3) and 22:6(n-3) at Su 11, whilst diatom markers 16:1(n-7), 16:4(n-1) and 20:5(n-3) were most abundant at the diatom dominated sites (Su 7-Su 9, Fig 2a, Table II).

Oithona abundance

Depth integrated abundances of *O. similis* copepodids and nauplii a exhibited a similar pattern between sites with highest abundances of all developmental stages present at Su 7 (Fig 3 a, b). Abundances of both developmental stages of *O. similis* were positively correlated with food availability (estimated carbon biomass) at the sites (*O. similis*, copepodids = 13 + 8.85 POC, p =0.001, F = 15.87; nauplii = 208 + 7.68 POC, P =0.001, F = 17.29). For *O. similis*, eggs female^{-1} was also correlated with food availability (eggs female^{-1} = 11.0 + 0.0852 POC, P = 0.026, F = 5.87). *O. frigida* was comparatively scarce with copepodids comprising mostly adult females. Younger stages were either rare, or absent from the net hauls (Fig. 3d). In contrast with *O. similis*, no relationship was found between the abundance of *O. frigida* copepodids and POC (*O. frigida* copepodids = 25.14 - 0.0230 POC, P = 0.795, F = 0.07).

Oithona biochemical composition

Maximum levels of carbon in female *O. similis* (1.62 µg copepod^{-1}, Su 8) were almost 3 times lower than the maximum levels found in female *O. frigida* (4.33 µg copepod^{-1}, Su 9, Fig. 4). Similar comparison of the levels of nitrogen indicated that *O. frigida* only contained 1.4 times more nitrogen than *O. similis* (Fig 4). This was reflected in differences in the overall mean C:N atom ratios which were 5.6 and 10.9 for *O. similis* and *O. frigida* respectively

With a few exceptions, the levels of total fatty acids in the two species and different developmental stages of *Oithona* tended to be quite similar between the six sites and were not correlated with food availability (POC, Fig. 5). Levels of total fatty acids in female *O. similis* were lower than those found in CV's (with the exception of Su 9) and tended to be more variable (Fig. 5). Less data are available for *O. frigida*, which reflects their low abundance at the sites, but it is clear that their levels of total fatty acids are typically 2-3 times higher than those in *O. similis* (Fig 5).

Mean fatty acid compositions for CV and female *O. similis* and female *O. frigida* are given in Table III. Overall, the mean fatty acid compositions of the different developmental stages and species were similar although *O. frigida* did contain higher levels of 16:1(n-7, 18:1(n-7) and 16:4(n-1) compared with *O. similis* (Table III). Highest proportions of 18:1(n-9) were found for CV *O. similis* (15.6%, Table III). Principal component analysis (PCA) of the fatty acid comprising 41 samples of *Oithona* indicated a broad separation of *O. frigida* and *O. similis* with the first two principal components accounting for 57% or the variability within the dataset. The score plot indicated that the diatoms biomarker fatty acids 16:1(n-7), 18:1(n-7) and 16:4(n-1) were key variables distinguishing *O. frigida* from *O. similis* for which the bacterial biomarkers 15:0, iso15:0, anteiso15:0, 17:0 and iso17:0 and the flagellate marker 22:6(n-3) were characteristic (Fig. 6a, b). Three samples of *O. frigida* were grouped with the cluster for *O. similis* and it is notable that two of these samples contained both low levels of total fatty acid and diatom biomarkers.

Since the identification of patterns between development stage and sites is not immediately apparent in Fig 6, site specific PCA's were conducted and all showed a similar pattern. The best example of this is provided by Su 8, for which most data are available (Fig. 7a,b). Again it is apparent that diatom biomarkers separate *O. frigida* from *O. similis* for which bacterial and flagellates biomarkers are key variables with the first two principal components accounting for 80.2% of the variability within the dataset (Fig 7a, b). Notably, CV and female *O. similis* are separated by PC2 and this separation is driven by the higher amounts of the storage reserve fatty acids 18:1(n-9) and 20:1(n-9) in the CV's (Fig 7b).

Fatty acid biomarker ratios

Ratios of diatom to flagellate biomarker fatty acids, i.e 20:5(n-3)/22:6(n-3) and 16:1(n-7)/18:4(n-3) can be a good indicator of diet in marine zooplankton (Fig. 8, 9). Low ratios on both the x and y axes indicate diatom dominance in the diet, whilst higher values indicate that protozoans are more important in the diet. Comparison of these ratios in the microplankton and *Oithona* at each site is presented in Fig.8. Values for *Oithona* are between ratios determined for the flagellate and diatom dominated sites which is consistent with a mixed diet, albeit with a dominance of flagellates and protozoans (Fig. 8). A more detailed plot of the diatom/flagellate biomarker ratios in *Oithona* grouped copepods according to site rather than species or stage (Fig. 9). This suggests that although there are clear differences in the fatty acid profiles of the two species, the microplanktonic food environment is also a key determinant of the fatty acid composition of these species (Fig. 9).

Condition factor

To investigate if diet and therefore fatty acid composition of *O. similis* was related to nutritional condition we compared the scores from PC1 of Fig. 6a with a measure of condition, i.e. the concentration of total fatty acid in each unit volume of copepod. Condition factor for each copepod was determined from body volume estimates derived from prosome lengths following Campbell et al. (2001, Table IV). Regression analysis indicated a significant relationship between fatty acid composition and fatty acid content in the *O. similis* samples. (Fig. 10, CF = 3.99 - 0.561 PC1, p = 0.000, F = 29.91). Insufficient data was available to perform a similar analysis on *O. frigida*.

DISCUSSION

The life history traits of *Oithona* spp. from high latitudes differ from those of most calanoids from similar environments, in that they actively feed and reproduce throughout the year, albeit at lower rates in winter compared to the warmer months. They also exhibit extended female longevity and comparatively low respiration and ingestion rates (Paffenhöfer 1993, Castellani et al. 2005). Oithonidae are clearly a very successful group exhibiting considerable dietary plasticity, being capable of carnivory (Lampitt 1978), omnivory including a wide range of microplankton taxa but particularly protozoans (Atkinson 1996, Lonsdale et al. 2000) and also coprophagy (González and Smetacek 1994).

Food available to *Oithona* in the Scotia Sea varied considerably between stations with microplankton species composition, ranging from diatom dominated to dinoflagellate dominated communities and this reflected the oceanographic conditions, nutrient supply and food web structure at each site (Korb et. al. 2010). Korb et al. 2010 has previously catagorised stations Su 5 and Su 6 as a high nutrient low chlorophyll region (HNLC) with low primary production and a dominance of heterotrophic dinoflagellates**.** The region to the south west of South Georgia (Su 7) supported moderate production with a shift towards diatom dominated communities, whilst the north west of South Georgia (Su 8, Su 9) is a region that supports large blooms of sustained primary production again dominated by diatoms (Korb et al. 2010). Su 11, which was not reported on by Korb et al. (2010) was located on the South Georgia Shelf and was in a post bloom situation supporting low microplankton biomass and being dominated by heterotrophic dinoflagellates.

At each station in the current study, the fatty acid composition of both species of *Oithona* reflected that of the microplankton in their environment. These findings are consistent with the view that *Oithona* ingests motile prey, but also highlights the importance of diatoms in the diet of both species. The catholic nature of their diet has also been remarked upon by Hopkins (1985, 1987) and Hopkins and Torres (1989). The fatty acid composition of *O. frigida* with comparatively high levels of 16:1(n-7), 18:1(n-7) and 16:4(n-1) indicates a greater contribution of diatoms in its diet compared with *O. similis*. 18:1(n-7) is not generally considered a biomarker for diatoms but most zooplankton are able to elongate this fatty acid from the diatom derived 16:1(n-7) (Hirche et. al. 2003). The elevated levels of diatom biomarkers in *O. frigida* are consistent with the anatomy of this species. *O. frigida* is larger than *O. similis* with a prosome length of approximately 700 µm compared with 500 µm for *O. similis*. *Oithona frigida* also possesses substantial and robust maxillipeds relative to those of *O.similis*, and it is entirely feasible that these adaptations facilitate the ingestion and processing of diatoms, since the frustules of this group can be extremely robust and require considerable force to break (Hamm et al. 2003; Smetacek et al. 2004). Enlarged maxillipeds are also typical of carnivory, a feeding mode that some species of *Oithona* are known to adopt (Lampitt 1978). However the fatty acid data for *O. frigida* in the current and other studies (Kattner et al. 2003; Lischka and Hagen 2007) do not indicate that carnivory is important. It should be noted that the current research was conducted during summer and that no information is currently available regarding the feeding habits of *O. frigida* during winter, a season when the abundance of its microplanktonic prey is low. Further feeding studies, including stomach content analyses over a seasonal cycle could help to resolve this issue.

Oithona contrasts with most species of marine zooplankton since the levels of the flagellate-protozoan marker 22:6(n-3) generally exceed that of 20:5(n-3), a biomarker characteristic of diatoms (Lischka and Hagen 2007 and this study). This undoubtedly reflects the high levels of 22:6(n-3) in the diet of *Oithona* given their preference for motile prey which contain comparatively high levels of this fatty acid. However, since 22:6(n-3) serves critical neurological functions in many organisms, high levels of this fatty acid in *Oithona* could potentially be related to energy efficient transfer of nerve impulses which either facilitates a fast escape response and/or the capture of prey particles (Scott et al. 2002; Waggett and Buskey 2008; Kiørboe et al. 2010).

Ratios of fatty acid biomarkers are often used to study diets of marine plankton. Schmidt et al. (2006) plotted the ratios of 20:5(n-3)/22:6(n-3) and 16:1(n-7)/18:4(n-3) to

study the relative importance of diatoms and flagellates in the diet of Antarctic krill. 20:5(n-3) and 16:1(n-7) are biomarkers for diatoms whilst 22:6(n-3) and 18:4(n-3) are biomarkers for protozoans and flagellates. Previous studies on marine zooplankton have also indicated a relationship between fatty acid profiles and the levels of total lipid, an index of condition (Schmidt et al. 2006). Here we have adopted a slightly different approach by plotting the data from the overall PCA analysis (PC1) which is effectively an index of fatty acid composition, and the levels of total fatty acids in the same samples. Given that the loadings on PC1 are effectively a spectrum of diatom dominated (- loading) to flagellate and protozoan dominated (+ loading) fatty acid profiles, it can be concluded that those copepods inhabiting environments where diatoms are abundant are in the best condition. Initially this seems to be at odds with the view that *Oithona* preferentially ingest flagellates and protozoans (Atkinson 1996). However, environments where diatoms are abundant are generally hotspots of secondary production with elevated abundances of all types of microplankton taxa, particularly protozoans, (Verity 1986; Brussard et al. 1996; Boyd et al. 2000) and are also favourable environments for zooplankton growth and development (Pond et al. 2005; Ward et al. 2007). It is equally possible that the *Oithona* population inhabiting the Southern Ocean have a greater preference for diatoms than those in other oceanic regions, especially given the abundance and importance of diatoms in the Southern Ocean food web (Smetacek et al. 2004).

Given the close relationship between food availability and the population of *O. similis*, this species is clearly able to rapidly exploit increases in food availability. This finding is consistent with Ward and Hirst (2007) who investigated the effect of chlorophyll *a* concentrations, a proxy for food availability and sea temperature on the abundances of *O. similis* in the Scotia Sea. Abundances of all developmental stages of *O. similis* were correlated with both temperature and chlorophyll *a* concentrations (Ward and Hirst 2007). These findings contrast with the situation for *O. frigida* for which no similar relationship has been established and whose lifecycle remains largely undescribed. C:N atomic ratios of *O. similis* and *O. frigida* were within the range reported for other species of marine copepod (Båmstedt 1986), although *O. frigida* with a mean C:N value of 10.9 contained proportionally more carbon that *O. similis* with a C:N value of 5.6. A higher C:N ratio in female *O. frigida* compared with *O. similis* could be attributable to lower fecundity rates in the former during the current study. Eggs of marine copepods are typically rich in lipid and the production of eggs can deplete maternal lipid reserves (Mayor et al., 2009)

The potential role of *O. similis* in recycling detrital and faecal material in the world's oceans has been debated for nearly two decades, with much direct and indirect evidence providing support for this hypothesis (González and Smetacek 1994; Kiørboe and Visser 1999; Svensen and Nejstgaard 2003). More recent evidence has established that although copepods do ingest and recycle faecal pellets, the dominant organisms responsible for the degradation and retention of this material in surface waters are protozoans, particularly heterotrophic dinoflagellates (Poulsen and Iversen 2008). In the current study, key fatty acids distinguishing *O. similis* from *O. frigida* were the bacterial biomarkers 15:0, i15:0, a15:0, 17:0 and i17:0. Since both detrital material and faecal pellets are rapidly colonised by bacteria (Hansen et al. 1996), bacterial markers in *O. similis* are most likely derived indirectly from the ingestion of heterotrophic dinoflagellates. *O. similis* readily ingest dinoflagellates and these were major components of the microplankton community at the more southerly and northerly sites.

The protozoan and bacterial biomarkers in *O. similis* are consistent with this species being integral to recycling food webs, either directly by ingestion of faecal-detrital material or indirectly, by the ingestion of coprophageous protozoans (Poulsen and Iversen 2008). Whilst the biomarker composition and morphological characteristics of *O. frigida* suggests this copepod is well adapted to ingesting diatoms, the nutritional condition of *O. similis* was also linked to the levels of diatoms in its diet and indicates the greater importance of diatoms for *Oithona* in Antarctic waters, compared to other oceanic regions.

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List of figures

Fig. 1. Locations of the six sampling sites. Major oceanographic boundaries indicated are APF, Antarctic Polar Front; SACCF, Southern Antarctic Circumpolar Current Front; SB, Southern Boundary.

Fig. 2. (a) Microplankton percent composition calculated from estimates of carbon biomass derived from microscopy and (b) estimated carbon biomass ($\mu g\ L^{-1}$) at the six study sites.

Fig. 3 Abundances of different developmental stages of *Oithona*. Abundances are values integrated over 400 m water depth. Note that although nets hauls were conducted from 400 m, 95 to 98% of all developmental stages occupied the upper 100 m, Ward unpublished).

Fig. 4 Carbon and nitrogen contents of *Oithona* at selected sites (n=1). (Mean C:N atom ratios for; *Oithona similis* = 5.6, *Oithona frigida* 10.9).

Fig. 5 Total fatty acid contents of *Oithona* sp. at the six study sites.

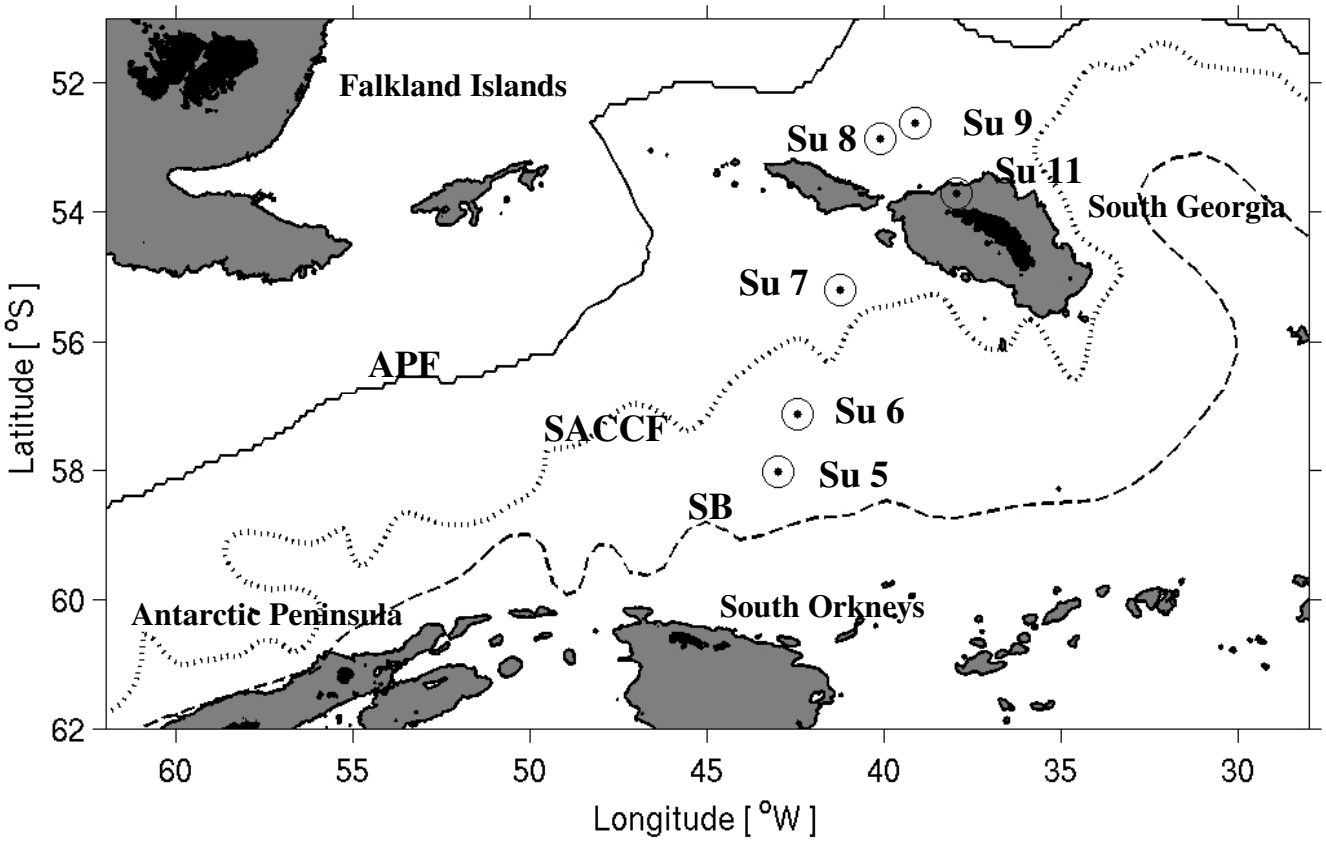
Fig. 6 Principal component analysis of fatty acid composition (percentage data) for female and CV *Oithona similis* and female *Oithona frigida* (a) Score plot. Number denotes station followed by code for species. os v = *O. similis* CV, os f = *O. similis* female, of f = *O. frigida* female (b) loading plot indicating the importance of each fatty acid for determining the scores for the different species and maturity stages plotted in Fig 6a.

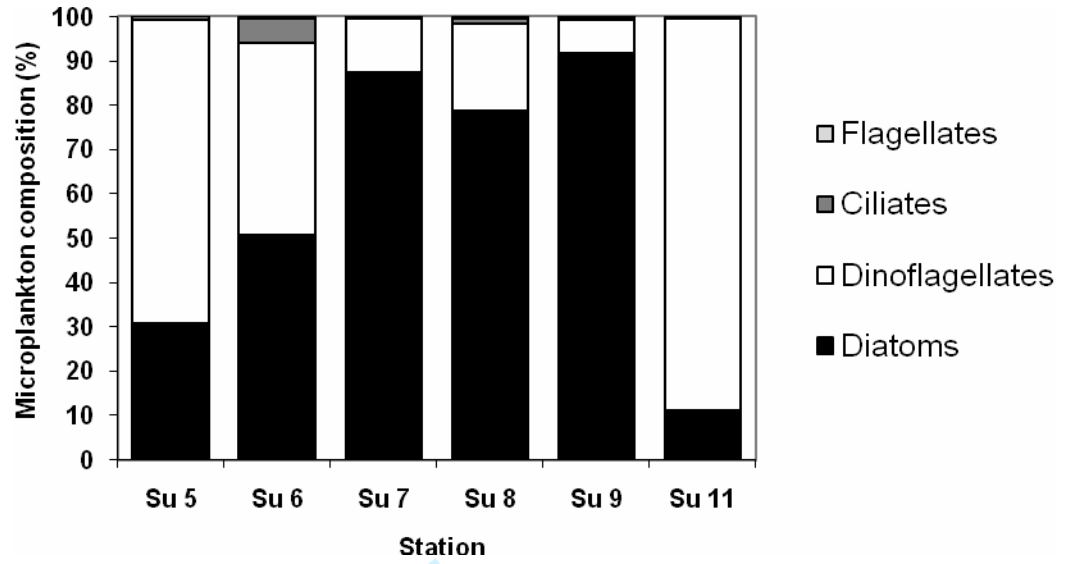
Fig. 7 Principal component analysis of fatty acid data for *Oithona similis* female and CV and female *Oithona frigida* at station Su 8.

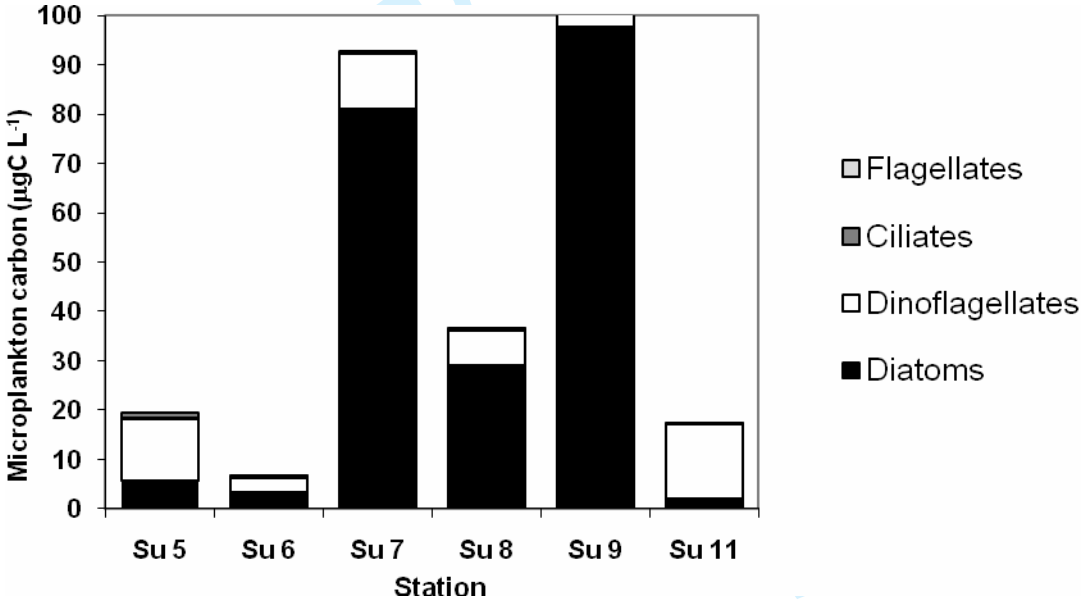
Fig. 8 Relationship between the ratios of diatom fatty acid biomarkers (20:5(n-3) and 16:1(n-7)) and those for flagellates (22:6(n-3) and 18:4(n-3)) for the microplankton and *Oithona* sp. fatty acids at the six stations.

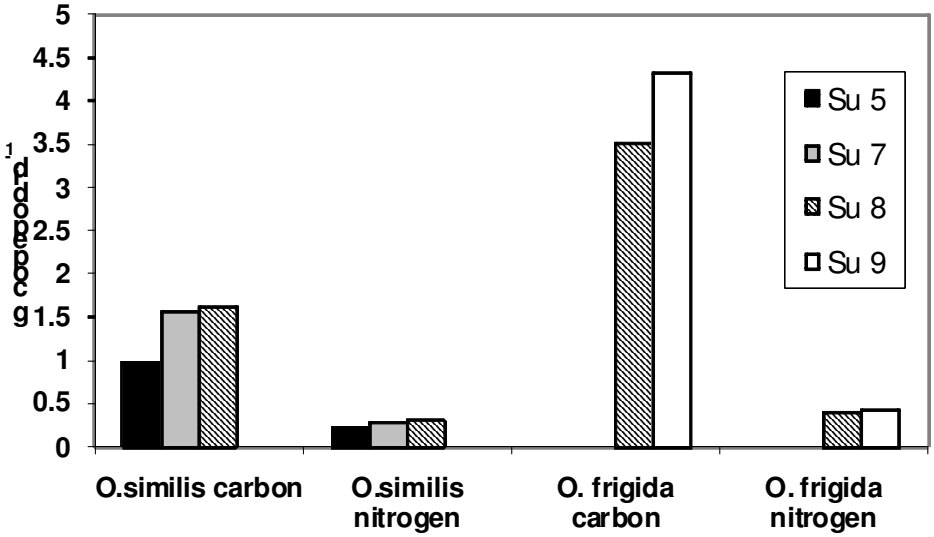
Fig. 9 Ratios of diatom to flagellate fatty acid biomarkers in *Oithona* sp.

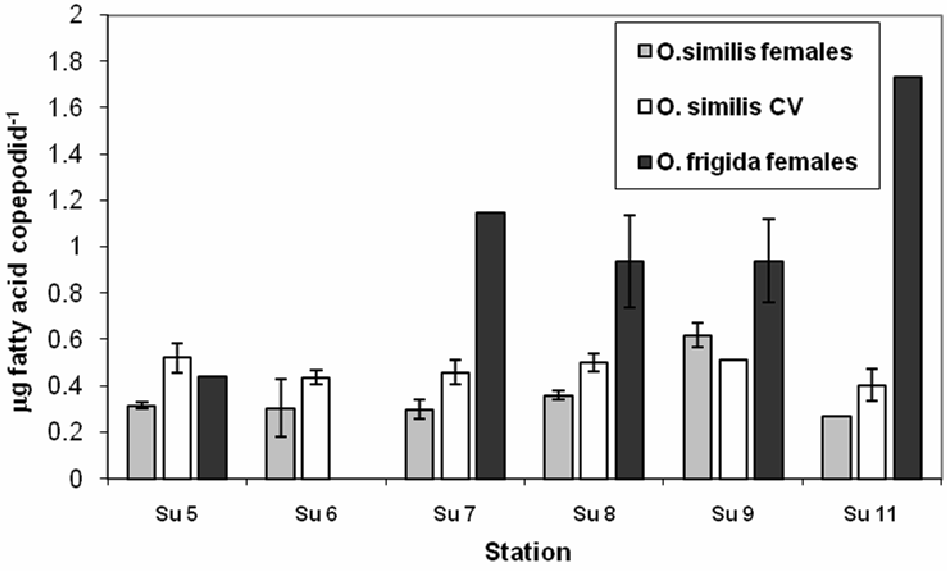
Fig. 10 Relationship between the condition factor (CF) *Oithona similis*. (where CF= WL-3, W = mass fatty acid copepod-1, L = prosome length) with an index of fatty acid composition (i.e. first principal component, PC1 of the *O. similis* fatty acid analysis, Fig. 6a).

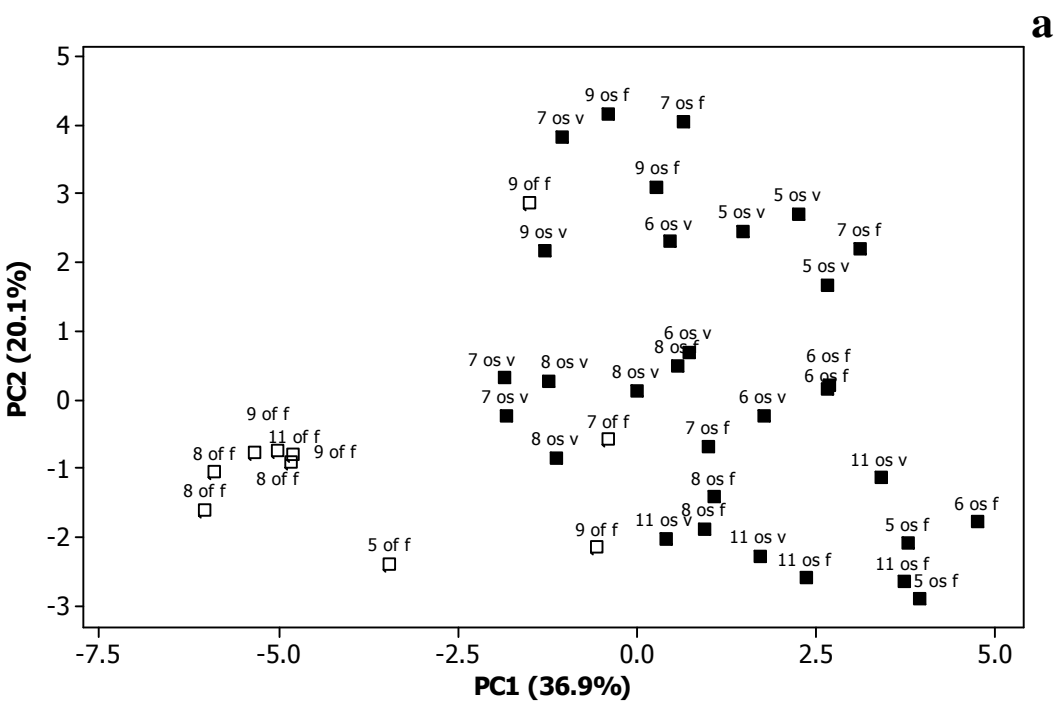

Falkland Islands
Su 8
Su 9
Su 11
South Georgia
Su 7
APF
SACCF
Su 6
Su 5
SB
Antarctic Peninsula
South Orkneys
Latitude [°S]
Longitude [°W]
52
54
56
58
60
62
60
55
50
45
40
35
30

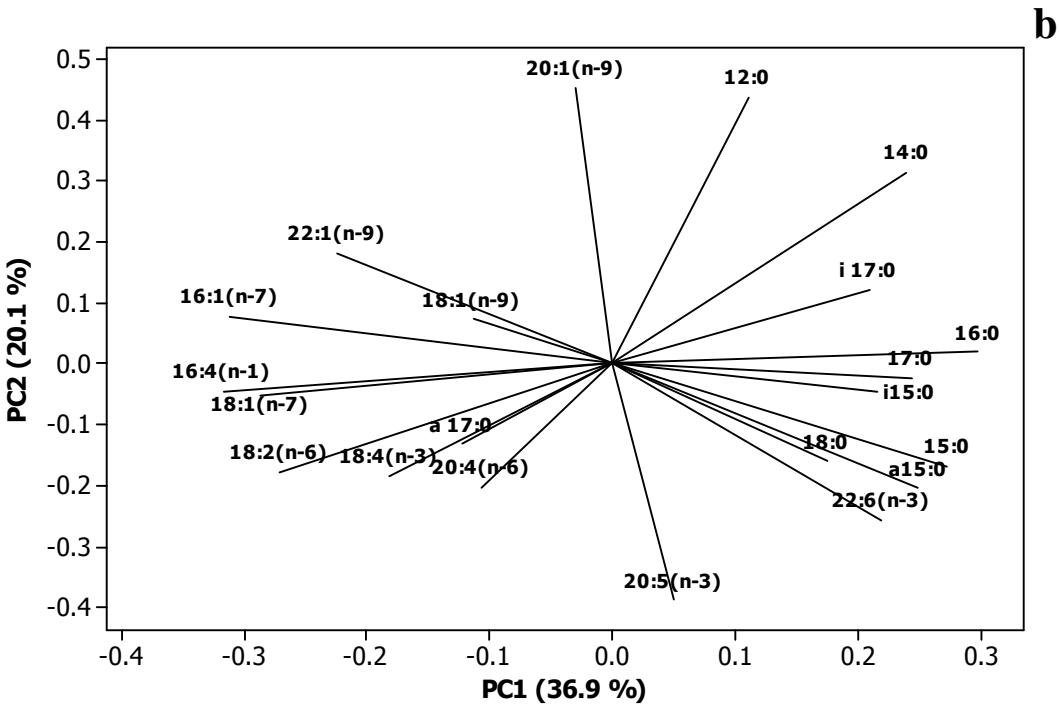

Microplankton composition (%)
100
90
80
70
60
50
40
30
20
10
0
Su 5
Su 6
Su 7
Su 8
Su 9
Su 11
Station
Flagellates
Ciliates
Dinoflagellates
Diatoms

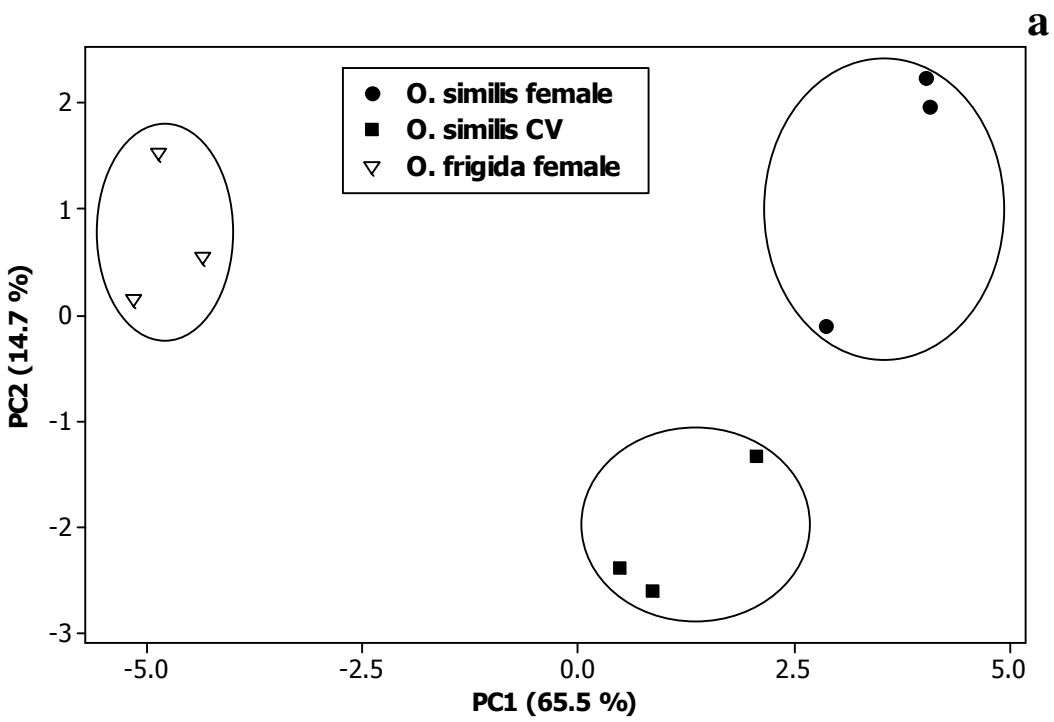

Microplankton carbon (µgC L-1)
100
90
80
70
60
50
40
30
20
10
0
Su 5
Su 6
Su 7
Su 8
Su 9
Su 11
Station
Flagellates
Ciliates
Dinoflagellates
Diatoms

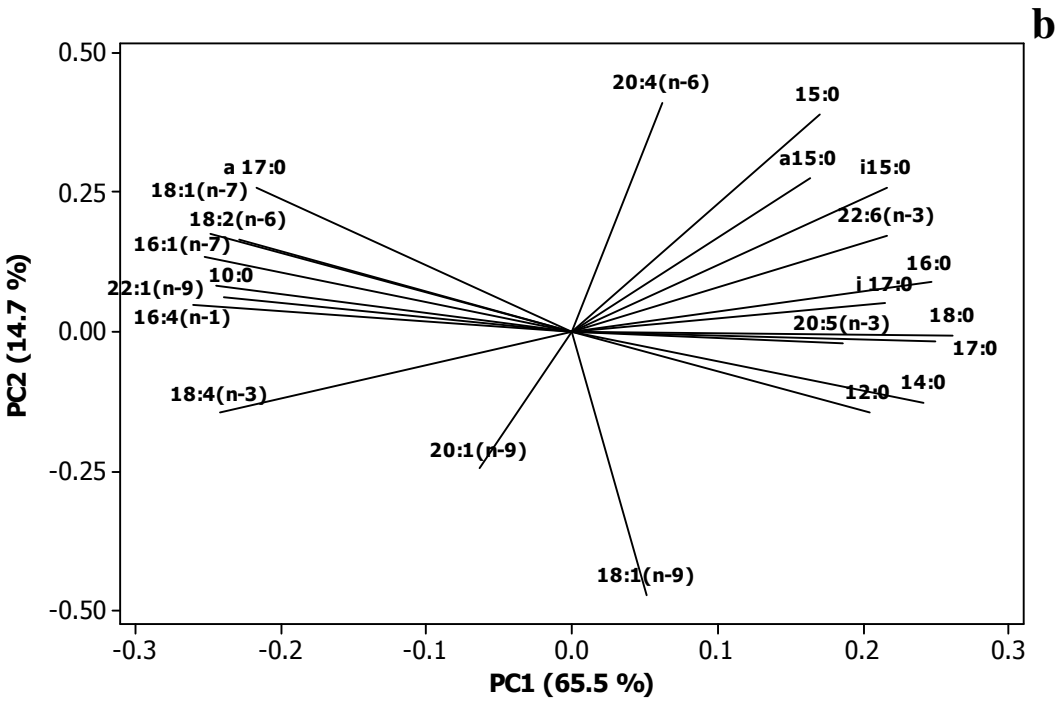


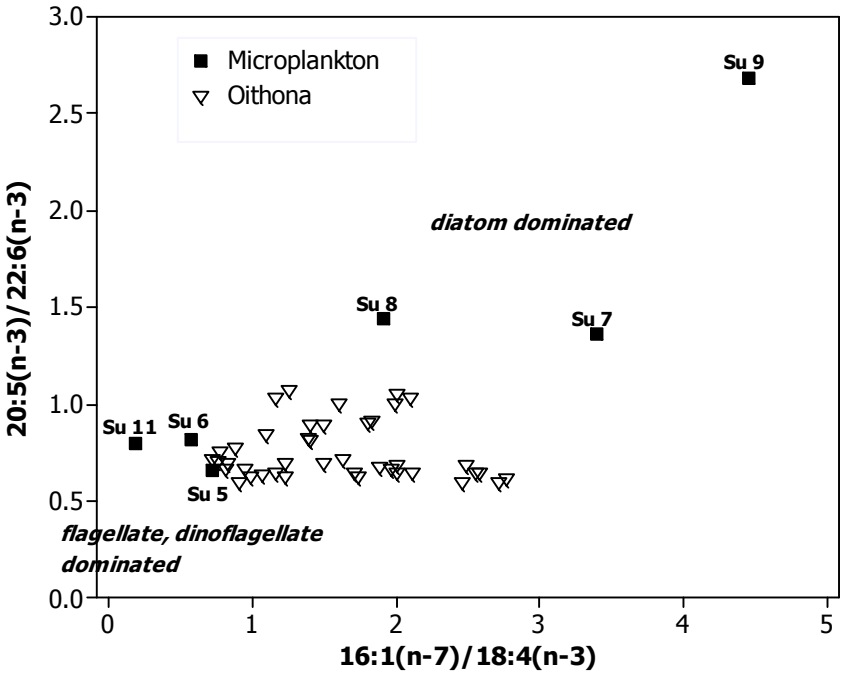


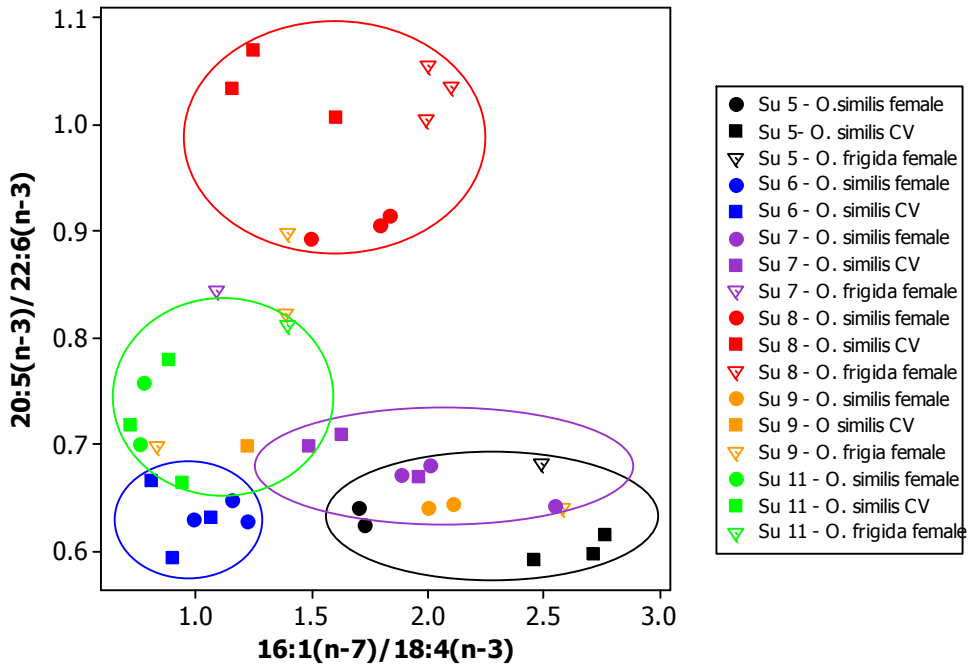

a
PC2 (20.1%)
PC1 (36.9%)
9 os f
7 os f
7 os v
9 os f
9 of f
5 os v
5 os v
9 os v
6 os v
7 os f
5 os v
6 os v
8 os f
7 os v
8 os v
8 os v
6 os f
6 os f
7 os v
6 os v
9 of f
11 of f
8 of f
9 of f
7 of f
8 os v
7 os f
11 os v
8 of f
8 of f
8 os f
6 os f
8 os f
11 os v
9 of f
5 os f
11 os v
11 os f
11 os f
5 os f
5 of f


b
PC2 (20.1 %)
PC1 (36.9 %)
20:1(n-9)
12:0
14:0
22:1(n-9)
i 17:0
16:1(n-7)
18:1(n-9)
16:0
17:0
16:4(n-1)
i15:0
18:1(n-7)
a 17:0
18:0
15:0
18:2(n-6)
18:4(n-3)
20:4(n-6)
a15:0
22:6(n-3)
20:5(n-3)


a
O. similis female
O. similis CV
O. frigida female
PC2 (14.7 %)
PC1 (65.5 %)
2
1
0
-1
-2
-3
-5.0
-2.5
0.0
2.5
5.0


b
20:4(n-6)
15:0
a15:0
i15:0
a 17:0
18:1(n-7)
18:2(n-6)
22:6(n-3)
16:1(n-7)
16:0
10:0
i 17:0
22:1(n-9)
16:4(n-1)
20:5(n-3)
18:0
17:0
18:4(n-3)
12:0
14:0
20:1(n-9)
18:1(n-9)
PC2 (14.7 %)
PC1 (65.5 %)
0.50
0.25
0.00
-0.25
-0.50
-0.3
-0.2
-0.1
0.0
0.1
0.2
0.3


Microplankton
Oithona
Su 9
Su 8
Su 7
Su 11
Su 6
Su 5
diatom dominated
flagellate, dinoflagellate dominated
20:5(n-3)/22:6(n-3)
16:1(n-7)/18:4(n-3)
0.0
0.5
1.0
1.5
2.0
2.5
3.0
0
1
2
3
4
5


1.1
1.0
0.9
0.8
0.7
0.6
20:5(n-3)/22:6(n-3)
1.0
1.5
2.0
2.5
3.0
16:1(n-7)/18:4(n-3)
Su 5 - O.similis female
Su 5- O. similis CV
Su 5 - O. frigida female
Su 6 - O. similis female
Su 6 - O. similis CV
Su 7 - O. similis female
Su 7 - O. similis CV
Su 7 - O. frigida female
Su 8 - O. similis female
Su 8 - O. similis CV
Su 8 - O. frigida female
Su 9 - O. similis female
Su 9 - O similis CV
Su 9 - O. frigia female
Su 11 - O. similis female
Su 11 - O. similis CV
Su 11 - O. frigida female

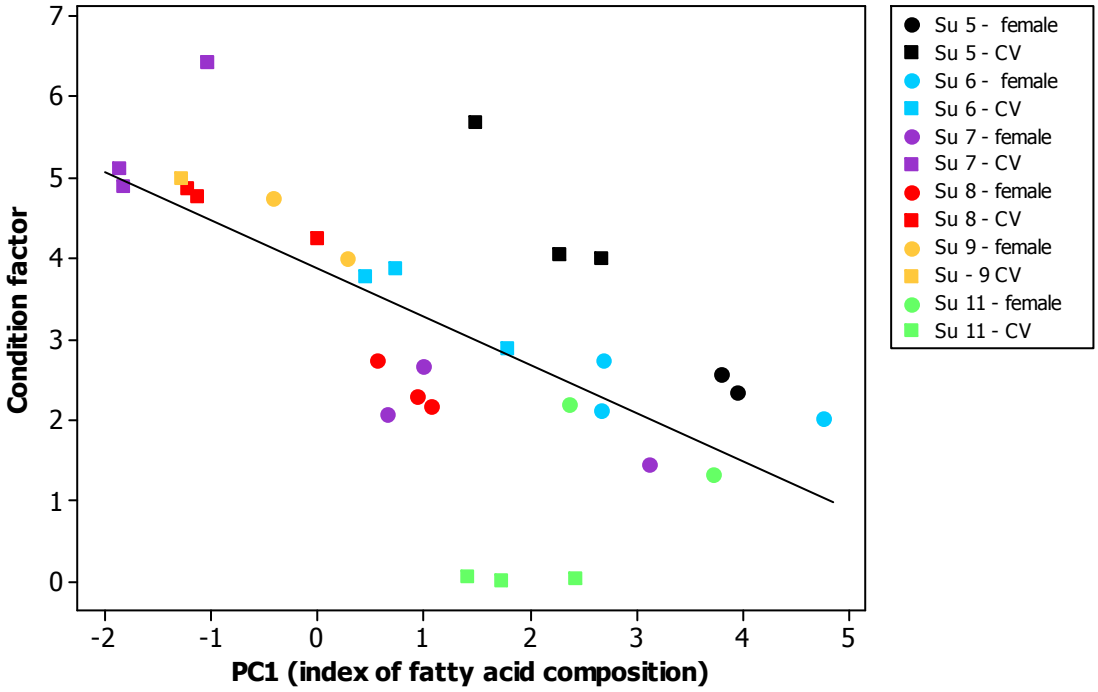

Condition factor
PC1 (index of fatty acid composition)
Su 5 - female
Su 5 - CV
Su 6 - female
Su 6 - CV
Su 7 - female
Su 7 - CV
Su 8 - female
Su 8 - CV
Su 9 - female
Su - 9 CV
Su 11 - female
Su 11 - CV

Table I. Integrated temperature and chlorophyll *a* values for the six stations in the Scotia Sea. Data are integrated mean values generated from determinations of chlorophyll *a* and temperature from 10 m depth increments from 100 m to the surface).

Station	Date	Temperature (°C)	Chlorophyll *a* (µg L^{-1})
Su 5	19/01/08	0.85	0.21
Su 6	22/01/08	1.78	0.17
Su 7	25/01/08	2.54	1.10
Su 8	01/02/08	2.94	0.94
Su 9	04/02/08	2.97	1.46
Su 11	09/02/08	2.24	0.58

Table II. Fatty acid composition of microplankton sampled from the six stations in the Scotia Sea. Data presented as percent composition (n = 1).). Sat = saturated fatty acids, Mono = monounsaturated fatty acid, Diene = diunsaturated fatty acids, PUFA = polyunsaturated fatty acids, i.e. those containing 3 or more double bonds.

	Su 5	Su 6	Su 7	Su 8	Su 9	Su 11
14:0	6.4	3.6	9.2	6.5	9.5	5
i15:0	0.6	0.6	0.4	0.6	0.5	0.2
a15:0	0.2	0.2	0.2	0.4	0.2	0.2
15:0	0.9	1	0.7	0.8	0.5	0.6
16:0	12.7	14.9	14	9.6	9.5	8.5
16:1(n-7)	6.1	5.2	10.9	7.7	13.9	3.7
i17:0	0.2	0	0.2	0.5	0.3	0
16:2(n-4)	0.8	0.9	1.1	1.4	1.5	0.7
17:0	0.5	0.7	0.3	0.3	0.2	0.3
16:3(n-4)	0.4	0.5	0.8	0.8	0.9	0.5
16:4(n-3)	0.3	1.3	0.7	0.4	0.5	0.4
16:4(n-1)	0.3	0.5	4.3	4.3	7.7	1.9
18:0	4.5	9.6	4.3	3.5	2	4.3
18:1(n-9)	3.7	5.7	8.8	2.8	2.6	1.8
18:1(n-7)	1.5	1.3	1.5	1.8	1.3	0.8
18:1(n-5)	0.9	0.3	0	0.4	0.2	0.3
18:2(n-6)	2.4	1.8	2.7	1.5	1.7	1.4
18:3(n-6)	0.3	0.6	0.6	0.3	0.4	0.2
18:3(n-3)	3.4	2.9	0.9	0.9	0.6	3.5
18:4(n-3)	8.4	9.1	3.2	4	3.1	19.9
20:0	0.3	0.5	0.2	0.2	0.1	0.2
18:5(n-3)	12.5	10.3	5	4.1	3.2	14.1
20:4(n-6)	0.3	0.4	0.7	0.1	0.3	0.2
20:4(n-3)	0.4	0.4	0.8	0.4	0.9	0.6
20:5(n-3)	12.4	12.0	15.7	14.3	27.1	13.0
22:0	0.4	0.5	0.1	21.9	0.1	0.3
22:1(n-11)	0	0.1	0.2	0	0.3	0.3
22:1(n-9)	0.1	0.2	0.4	0.2	0.2	0.3
22:5(n-3)	0.5	0.4	0.5	0.2	0.6	0.4
22:6(n-3)	18.6	14.5	11.6	10.1	10.1	16.4
Sat	26.7	31.6	29.6	44.3	22.9	19.6
Mono	12.3	12.8	21.8	12.9	18.5	7.2
Diene	3.2	2.7	3.8	2.9	3.2	2.1
PUFA	57.8	52.9	44.8	39.9	55.4	71.1

Table III: Average fatty acid composition (%) of *Oithona similis* and *Oithona frigida* from the six stations. (n = number of samples, each containing 20 copepods. Mean values, SE = standard error). Sat = saturated fatty acids, Mono = monounsaturated fatty acid, Diene = diunsaturated fatty acids, PUFA = polyunsaturated fatty acids, i.e. those containing 3 or more double bonds.

	O. similis (female) n=15	(SE)	*O. similis* (CV) n=16	(SE)	*O. frigida* (female) n=10	(SE)
10:0	0.7	0.2	1.2	0.2	2.8	0.5
12:0	5.7	0.9	5.9	0.8	3.5	1.2
13:0	0.3	0.0	0.3	0.0	0.5	0.1
14:0	6.9	0.4	6.5	0.4	4.7	0.6
i15:0	0.7	0.0	0.5	0.0	0.5	0.1
a15:0	0.5	0.0	0.4	0.0	0.3	0.1
15:0	2.0	0.1	1.7	0.1	1.4	0.1
16:0	15.1	0.5	12.7	0.6	10.0	0.5
16:1(n-9)	1.7	0.2	1.4	0.2	1.2	0.2
16:1(n-7)	3.7	0.2	3.8	0.3	6.1	0.4
i17:0	1.0	0.1	0.9	0.1	0.5	0.1
a17:0	0.7	0.1	0.6	0.1	1.1	0.2
16:2(n-4)	0.5	0.1	0.4	0.0	0.9	0.2
17:0	1.2	0.1	1.0	0.1	0.7	0.1
16:3(n-4)	0.4	0.0	0.4	0.1	0.9	0.1
16:4(n-1)	0.3	0.1	0.4	0.1	1.6	0.3
18:0	5.2	0.5	4.2	0.4	3.2	0.5
18:1(n-9)	9.7	0.9	15.6	1.8	11.4	1.0
18:1(n-7)	2.0	0.1	1.8	0.1	5.3	0.7
18:1(n-5)	1.8	0.1	1.7	0.1	0.9	0.1
18:2(n-6)	2.1	0.1	2.2	0.1	3.2	0.2
18:3(n-6)	0.5	0.0	0.6	0.1	0.9	0.1
18:3(n-3)	0.7	0.1	0.8	0.1	1.0	0.1
18:4(n-3)	2.4	0.2	3.0	0.2	3.8	0.3
20:0	0.3	0.0	0.2	0.0	0.3	0.1
20:1(n-9)	1.2	0.2	1.5	0.2	1.2	0.2
20:4(n-6)	0.3	0.1	0.3	0.0	0.5	0.0
20:4(n-3)	1.4	0.1	2.0	0.2	2.5	0.3
20:5(n-3)	11.9	0.7	10.6	0.5	11.3	0.5
22:1(n-9)	0.2	0.0	0.2	0.0	0.3	0.0
22:5(n-3)	1.9	0.2	2.5	0.2	4.3	0.5
22:6(n-3)	17.0	1.1	14.6	0.7	13.5	0.6
Sat	40.3		36.2		29.4	
Mono	20.3		26.0		26.4	
Diene	2.6		2.6		4.1	
PUFA	36.9		35.2		40.2	

Table IV. Mean prosome length for CV and female *O. similis* (n=30).

	CV *O. similis*		**Female *O. similis***	
	Mean	(SE)	Mean	(SE)
Su 5	0.49	0.005	0.51	0.007
Su 6	0.50	0.005	0.53	0.008
Su 7	0.44	0.005	0.53	0.008
Su 8	0.48	0.005	0.53	0.005
Su 9	0.47	0.004	0.52	0.005
Su 11	0.48	0.004	0.54	0.009