Plankton trophodynamics at the subtropical convergence, Southern Ocean

NICOLE B. RICHOUX* AND P. WILLIAM FRONEMAN
DEPARTMENT OF ZOOLOGY AND ENTOMOLOGY, RHODES UNIVERSITY, GRAHAMSTOWN 6140, SOUTH AFRICA

*CORRESPONDING AUTHOR: n.richoux@ru.ac.za

Received March 29, 2009; accepted in principle May 23, 2009; accepted for publication June 10, 2009; published online 3 July, 2009

Stable isotope signatures ($\delta^{13}C$, $\delta^{15}N$) in zooplankton tissues and particulate organic matter (POM) were determined to assess regional differences in the trophodynamics of zooplankton communities between 38 and 43°S, where the cool nutrient-rich subantarctic waters of the Southern Ocean meet the warm nutrient-poor subtropical waters of the southwest Indian Ocean at the subtropical convergence (STC). Significantly enriched values of $\delta^{15}N$ were noted in populations of all major zooplankton groups inhabiting the warm and saline water mass north of the STC (maximum surface temperature 21°C), including the euphausiids, salps, amphipods, copepods, ostracods, pyrosomes, pteropods and chaetognaths, compared with those in the cool, less saline southern water mass (minimum surface temperature 11°C). Similar patterns of $\delta^{15}N$ in POM collected throughout the region suggest that the large changes in zooplankton $\delta^{15}N$ values across the frontal region are driven by variations in the phytoplankton communities. The differing trophodynamics in communities north and south of the STC provide compelling evidence of distinct bottom-up effects on planktonic food webs which have important implications in the determination of trophic positions and motility of plankton and higher consumers using $\delta^{15}N$ signatures. Although expected, similar latitudinal variations in $\delta^{13}C$ signatures were not found.

INTRODUCTION

The subtropical convergence (STC) is one of the major oceanic fronts and represents the northern border of the Southern Ocean (Longhurst, 1998). In this zone, the cool nutrient-rich subantarctic water mass meets and mixes with the warm nutrient-poor subtropical water mass, resulting in strong latitudinal gradients in the physical parameters (Longhurst, 1998). South of Africa, the STC is strongly defined and highly dynamic, its location determined by the position of the retroreflection of the Agulhas Current and the Agulhas Return Current (Longhurst, 1998; Lutjeharms, 2006). Despite being an area of strong downwelling, this convergence zone is characterized by elevated biological activity and is thought to play an important role in atmospheric carbon sequestration (Llido et al., 2005). Furthermore, nitrate concentrations form sharp gradients from <0.1 μM L⁻¹ north of the STC to 27 μM L⁻¹ in the south (Lutjeharms et al., 1985; Altabet and Francois, 1994), with low iron availability representing the proximal control on phytoplankton production in the Southern Ocean (Takeda, 1998). In seeming contrast to the macronutrient gradients (apart from silicate), enhanced chlorophyll biomass is routinely observed at or just north of the STC (Lutjeharms et al., 1985), probably induced by the increased vertical stratification and stability created by the passage of the colder, nutrient-rich subantarctic water sliding below the subtropical water (Lutjeharms et al., 1985; Weeks and Shillington, 1996). The enhanced productivity occurs in intermittent pulses primarily in spring and summer (Llido et al., 2005), and the combination of hydrological, physical and biogeochemical processes occurring within this region creates a unique biological habitat and
planktonic community (Barange et al., 1998; Longhurst, 1998). In addition to the enhanced biological production measured north of the STC, phytoplankton are continuously advected into the region with the converging currents, thus further amplifying the chlorophyll biomass (Lutjeharms et al., 1985). Although the STC is considered as a biogeographical boundary to many organisms (Barange et al., 1998 and references therein; Longhurst, 1998) and an important contributor to total annual production in the Southern Ocean (Lutjeharms et al., 1985), the trophic ecology and energetics of the resident plankton remain poorly understood (Pakhomov and Perissinotto, 1997). Regions of the STC not in close proximity of continents or islands are particularly undersampled with respect to planktonic food webs.

Trophic relationships are notoriously difficult to decipher in aquatic environments (Jacob et al., 2006). Organisms of interest are typically very small, remote and/or behaviorally complex, and planktonic species in particular can exhibit a high degree of feeding plasticity in response to spatial and temporal variability in the nature and availability of food (Mayzaud et al., 2002). Furthermore, grazing and biochemical studies have provided ample evidence for the importance of omnivory in planktonic food webs (Pakhomov and Perissinotto, 1997; Stevens et al., 2004), whereas traditional gut pigment techniques are not capable of resolving the contribution from non-photosynthetic food sources (Mayzaud et al., 2002). As a result, the use of techniques such as stable isotope ratios and fatty acid profiles are increasingly being utilized in ecological studies (Petursdottir et al., 2008). These tools provide a time-integrated perspective of the assimilated feeding history of an organism or population (Michener and Schell, 1994). The premise of carbon isotope tracers is that primary producers fractionate their carbon sources of \(^{13}\text{C} \) and \(^{12}\text{C} \) to differing degrees (preferentially fix the lighter isotope), and the degree of fractionation of this ratio from producers to consumers is small (<1‰ relative to diet; Fry and Sherr, 1984). As a result, \(^{13}\text{C} / ^{12}\text{C} \) ratios are used to match consumers with their diet (Fry and Sherr, 1984; Michener and Schell, 1994), and primary producers with their nutrient sources or with specific water masses (Goericke and Fry, 1994).

Similarly, \(^{15}\text{N} / ^{14}\text{N} \) ratios in consumers differ from their diet by ~3–4‰, typically from fractionation during assimilation and protein synthesis in addition to preferential excretion of the lighter endogenous isotope (Minagawa and Wada, 1984). Therefore, \(^{15}\text{N} \) is a useful indicator for the trophic level of a consumer population.

Particulate organic matter (POM) in the southern hemisphere shows latitudinal gradients in \(^{13}\text{C} \) and \(^{15}\text{N} \), with pronounced changes reported to occur across the STC (Altabet and Francois, 1994; Goericke and Fry, 1994). Francois et al. (Francois et al., 1993) found a distinct gradient in \(^{13}\text{C}_{\text{POM}} \) in a transect crossing the STC near 68°E, with depleted values associated with the cold southern and \([\text{CO}_2\text{aq}]\)-rich water mass relative to more enriched values in the warm northern and low \([\text{CO}_2\text{aq}] \) water mass. Gradients or regional differences in \(^{13}\text{C} \) or \(^{15}\text{N} \) imply that phytoplankton growth and nutrient supply are important factors in structuring isotopic regimes in the marine environment (Altabet and Francois, 1994; Schell et al., 1998). Consumers of POM in any given region are ultimately affected by the \(^{15}\text{N} \) of primary producers and their physiological status (Minagawa and Wada, 1984).

As global climate change has the potential to cause major shifts in the location, strength and physical and biological properties of the STC (Bargagli, 2005), it is important that we determine the potential effects of such changes on the biological communities of the region. Any changes in the food quality or availability for the dominant species or in the trophic relationships among producers and consumers may have implications for top consumers such as fish, birds and mammals and the assessment of their diets using stable isotopes. As such, the aim of this study was to determine whether the strong latitudinal variability in physico-chemical parameters across the convergence zone influences the isotopic composition in the planktonic component at the STC southeast of Africa. We hypothesized that communities inhabiting the nutrient-poor but more productive northern water mass in the subtropical zone would have food webs isotopically enriched in both \(^{13}\text{C} \) and \(^{15}\text{N} \) relative to those in the high nutrient/low productivity southern water mass. Successful characterization of food webs in the STC will provide an excellent framework for future studies in Southern Ocean trophic ecology and will facilitate the assessment of trophic levels and habitat usage of consumers.

**METHOD**

**Sample collection**

Biological and physical data were collected from aboard the S.A. Agulhas during Voyage 135 from Cape Town, South Africa, to the Prince Edward Islands in April 2007. Six transects across the STC were completed between 38 and 43°S, and 38 and 42°E (Fig. 1). Physical data were collected by a research team from the University of Cape Town and will be documented in more detail elsewhere. Briefly, vertical profiles of salinity
and temperature were sampled to a depth of 1500 m at 48 stations using a Seabird SBE 9/11. Dissolved oxygen and macronutrient concentrations (nitrate, nitrite, silicate and phosphate) were determined using titration and standard colorimetric analyses, respectively, from water samples collected in Niskin bottles at 10 depths between 25 and 1500 m at all 48 stations. Total chlorophyll a (Chl a) concentrations were determined from water samples collected in Niskin bottles between 25 and 150 m at all 48 stations, and size-fractionated Chl a (>20, 2–20 and <2 μm) concentrations were determined from hand-collected surface water. All Chl a extractions and concentration measurements were completed onboard the ship using 90% acetone and a standard fluorometric procedure, respectively (Parsons et al., 1984; Turner 10AU fluorometer). Aliquots of 2–4.4 L of surface water (for the determination of POM isotopic ratios) were pre-screened through a 200 μm nitex mesh, filtered onto pre-ignited GF/F Whatman glass fiber filters (47 mm filters; <5 bar vacuum) and immediately frozen. Zooplankton were collected from 200 m (night) or 300 m (day) to surface using a Bongo net (200 μm mesh) fitted with flow and depth meters. Zooplankton samples were roughly sorted, transferred to bottles and frozen for the duration of the voyage.

Sample treatment

Upon return to the laboratory, frozen plankton samples were defrosted, sorted and measured on ice under a dissecting microscope. Several hundreds of the smallest organisms (e.g. copepods) were pooled per sample to obtain an adequate signal, whereas larger animals were processed as individuals. Euphausiids, amphipods and tunicates were identified to species using taxonomic keys (Baker et al., 1990; Esnal, 1999; Esnal and Daponte, 1999; Gibbons et al., 1999; Vinogradov, 1999), whereas most other taxa were placed into broad taxonomic groupings. One additional category of euphausiid furcilia was created from surplus animals in abundant samples from the north. Copepods were sorted into two categories based on size: large (>3 mm length) or small (<3 mm length). Small zooplankters were vacuum filtered onto GF/C filters. All filters and animal samples were visually inspected for contaminant material, placed in pre-ignited foil envelopes, lyophilized for 24 h and either shredded into small pieces (filters) or homogenized using a mortar and pestle (animals). A portion of the crustacean (all species), gastropod and water samples was treated with 1 M L⁻¹ HCL to eliminate carbonates, rinsed with distilled water, dried and re-homogenized. The only group to show significant differences in δ¹³C before and after acidification were the pteropods; therefore, data from acidified pteropod samples were used for the δ¹³C measurements.

Samples were analyzed at the Stable Light Isotope Laboratory in the Archaeology Department, University of Cape Town, on a Thermo Finnigan Delta XP Plus mass spectrometer interfaced with a Conflo III device to a Thermo Flash EA 1112 elemental analyzer. Results for carbon and nitrogen are reported relative to v-PDB and atmospheric N₂ respectively. The raw data were corrected using standards of known isotopic composition (sucrose, lentil and valine) and then normalized against the international standards. The analytical precision of the instruments was within ±0.2‰ (1 standard deviation). Isotope ratios are expressed in the δ notation:

\[ \delta(^{13}C) = \left( \frac{R_{\text{sample}}}{R_{\text{standard}}} - 1 \right) \times 1000 \]

where \( \delta(^{13}C) \) is \( ^{13}C \) or \( ^{15}N \) and \( R_{\text{sample}} \) and \( R_{\text{standard}} \) are the \( ^{13}C/^{12}C \) or \( ^{15}N/^{14}N \) ratios of the sample and standard, respectively.

Calculations and statistics

Given that our samples were not subjected to lipid extraction, we used a model from Post et al. (Post et al., 2007): \( \delta^{13}C_{\text{normalized}} = \delta^{13}C_{\text{untreated}} - 3.32 + 0.99 \times (\text{C:N}) \), derived from aquatic organisms to normalize \( \delta^{13}C \) values in all animal samples. These authors found C:N ratio to be a successful predictor of animal total lipid content, and lipid content an appropriate predictor of the difference in \( \delta^{13}C \) between lipid-extracted and untreated samples. As such, this equation provided \( \delta^{13}C \) values normalized for variable lipid content.
among individuals, results that would be comparable to the $\delta^{15}\text{C}$ signatures obtained had lipids been extracted (Post et al., 2007).

A consumer has a trophic position defined by the relative proportions of different prey in its diet. To calculate trophic positions of consumers, we followed the method outlined in Vander Zanden and Rasmussen (Vander Zanden and Rasmussen, 1999):

$$\text{Trophic position}_{\text{consumer}} = 2 + \left(\frac{\delta^{15}\text{N}_{\text{consumer}} - \delta^{15}\text{N}_{\text{salps}}}{\Delta \delta^{15}\text{N}}\right)^{-1},$$

where $\delta^{15}\text{N}_{\text{consumer}}$ is the $\delta^{15}\text{N}$ value for a given consumer, $\delta^{15}\text{N}_{\text{salps}}$ represents the reference baseline value at trophic position 2 within our food web and $\Delta \delta^{15}\text{N}$ is the mean trophic fractionation of 3.4‰ between adjacent trophic levels. As $\delta^{15}\text{N}$ of POM did not represent a pure phytoplankton signature in our study, salps were used as the baseline of the food web and assigned a trophic level of 2 (primary consumer position). A trophic level for each sample/individual was derived using this method, allowing for calculations of mean and standard deviation per sample type.

For the majority of species or sample types, we did not collect a sufficient number of individuals to include replicate samples from every location on our transect grid. As a result, similar sample types collected from each region (north, south and middle) represented replicate samples from that region, and the precise sample location was not included in subsequent statistical analyses. Stable isotope data were statistically analyzed with general linear models (GLMs) and standard linear regressions using Systat 12 and SigmaPlot 10, respectively. Residual analysis was completed with each model to ensure that the assumption of independent error terms was met. Although the terminology “explatory variable” is used to describe the variables tested in the models, significant results do not imply causative relationships.

**RESULTS**

**Physical data**

Sea surface temperature clearly identified the STC between 41 and 42°S (Fig. 1). Sample sites north of the STC were defined as those $\geq 35.1$ psu and $\geq 17°C$, south of the STC as those $\leq 34.4$ psu and $\leq 12°C$, and the “middle” zone of transition was demarcated by the region of 34.8 psu between 13 and 16°C. These three broad geographic zones of the STC (north, middle and south) were used in all figures to aid interpretation only, whereas salinity and temperature data were included in statistical models as continuous variables so that changes in these physical variables were used to represent the different physical properties from north to south. The sharp transition zone of the STC was expressed clearly to 200 m depth (Froneman et al., 2007). Surface oxygen varied between the northern subtropical $\left(\sim 5\text{ mL L}^{-1}\right)$ and the southern subantarctic $\left(\geq 6.8\text{ mL L}^{-1}\right)$ water masses. A companion study showed that total surface Chl a concentrations ranged between 0.03 and 0.42 $\mu$g L$^{-1}$ and were dominated by the picophytoplankton (Daly and Froneman, in press). Chl a values integrated from 0 to 150 m depth ranged from 12.8 to 40.1 mg m$^{-2}$, although they did not change significantly with temperature and salinity (Froneman et al., 2007). Of the four nutrients measured (nitrite, nitrate, silicate and phosphate), nitrate concentrations in the top 150 m showed distinct increases from north to south of the STC (Fig. 2A), whereas significant changes were not observed at depths down to 1500 m (Fig. 2B).

**Fig. 2.** Nutrient concentrations ($\mu$M L$^{-1}$) from the first transect of the research cruise; (A) depth-integrated mean $\pm$ SD of five measurements taken between 25 and 150 m depth; (B) depth-integrated mean $\pm$ SD of five measurements taken between 500 and 1500 m depth (nutrient concentrations along the remaining five transects showed similar patterns and are not shown). Arrows depict the middle site along the transect. Nitrite=$\text{NO}_2^-$, nitrate=$\text{NO}_3^-$, silicate=$\text{SiO}_4^{4-}$, and phosphate=$\text{PO}_4^{3-}$. 

---

1062
Particulate organic matter

Effects of several explanatory variables on the response variables $\delta^{15}$C$_{\text{POM}}$ and $\delta^{15}$N$_{\text{POM}}$ were tested using exploratory GLMs: mean seawater nitrate concentration (25–150 m), surface salinity, surface temperature, integrated Chl $a$ biomass (surface to 150 m), acid/no acid treatment, C:N ratio, mean seawater oxygen concentration (surface to 150 m) and $\delta^{15}$N$_{\text{POM}}$ or $\delta^{13}$C$_{\text{POM}}$. All potential explanatory variables showed no significant influence on the dependent variable $\delta^{15}$N$_{\text{POM}}$ ($P > 0.05$), with the sole exception of nitrate concentration ($F = 10.07, R^2 = 0.75, P < 0.05$). An exponential model was fitted to this smaller data set (nitrate concentrations and $\delta^{15}$N$_{\text{POM}}$) to further describe the relationship between the two variables, and the elevated nitrate concentrations and $\delta^{15}$N-depleted signatures associated with seawater POM south of the STC separated clearly from the $\delta^{15}$N-enriched POM signatures associated with northern seawater (Fig. 3; outlier at 3.5 $\mu$M L$^{-1}$ included in the analysis). All potential explanatory variables showed no significant effect on the dependent variable $\delta^{13}$C$_{\text{POM}}$ ($P > 0.05$), with the exception of C:N ratio ($F = 10.87, R^2 = 0.76, P < 0.001$; Fig. 4). No distinctions of $\delta^{13}$C$_{\text{POM}}$ signatures were apparent between northern and southern regions.

Euphausiids

Nine species of euphausiid were analyzed, seven of them found both north and south of the STC (Table I; Fig. 5). Effects of several explanatory variables on the response variables $\delta^{15}$C$_{\text{euphausiid}}$ and $\delta^{15}$N$_{\text{euphausiid}}$ were tested with exploratory GLMs: surface salinity, surface temperature, integrated Chl $a$ biomass (surface to 150 m), body length (mm), species, acid/no acid treatment, C:N ratio, $\delta^{15}$N$_{\text{POM}}$, and $\delta^{15}$N$_{\text{euphausiid}}$ or $\delta^{13}$C$_{\text{euphausiid}}$. The final models used to explain 77 and 54% of the variability in $\delta^{15}$N and $\delta^{13}$C, respectively, in euphausiids were:

$$\delta^{15}\text{N}_{\text{euphausiid}} = \beta_0 + \beta_1(\text{salinity}) + \beta_2(\text{length}) + \beta_3(\delta^{15}\text{C}_{\text{euphausiid}} \times \text{salinity}) + \beta_4(\delta^{15}\text{C}_{\text{euphausiid}} \times \text{length}) + \epsilon$$

(1)

$$\delta^{13}\text{C}_{\text{euphausiid}} = \beta_0 + \beta_1(\text{length}) + \beta_2(\delta^{15}\text{N}_{\text{euphausiid}}) + \beta_3(\text{salinity} \times \text{length}) + \epsilon$$

(2)

where $\delta^{15}$N$_{\text{euphausiid}}$ and $\delta^{13}$C$_{\text{euphausiid}}$ are dependent variables; $\beta_0$, the grand mean of population; $\beta_1$–$\beta_3$, true means due to explanatory variables salinity, body length, $\delta^{15}$C$_{\text{euphausiid}}$, $\delta^{15}$N$_{\text{euphausiid}}$ and interactions; and $\epsilon$ the error component. All explanatory variables in both models were significant at $P < 0.05$ ($\delta^{15}$N$_{\text{euphausiid}}$ $F = 45.35, R^2 = 0.77$; $\delta^{13}$C$_{\text{euphausiid}}$ $F = 15.65, R^2 = 0.54$), whereas all other potential explanatory variables were removed as insignificant ($P > 0.05$). These results from GLM (1) clearly showed that region (north versus south), as well as treatment, species and C:N ratio, contributed significantly to the variation in $\delta^{15}$N$_{\text{euphausiid}}$ in addition to the two interaction terms. In contrast, the results from GLM (2) showed that only body size, $\delta^{15}$N$_{\text{euphausiid}}$ and one interaction term contributed to the variation in $\delta^{13}$C$_{\text{euphausiid}}$. 

Fig. 3. POM. Signatures of $\delta^{15}$N ($\%o$) relative to depth-integrated mean nitrate concentration ($\mu$M L$^{-1}$) in seawater from 25 to 150 m depth. The curve represents the exponential relationship between the two variables, and transformation using ln(nitrate concentration) did not produce a linear relationship between the two variables.

Fig. 4. POM. Signatures of $\delta^{13}$C ($\%o$) relative to C:N ratio (linear regression).
Therefore no regional differences (i.e. north versus south) were apparent.

The influential explanatory variables from GLMs (1) and (2) were examined further using graphics and regressions to explore the nature of the associations. A clear separation of the euphausiid communities from north to south was related to changes in salinity, whereas carbon signatures showed no significant correlations with any physical properties of the seawater (Figs 4–6). Euphausiid δ15N and δ13C positively and linearly correlated with each other in the north and the middle region falling somewhere between (mean 6.8 ± 1.9‰; Table I, Figs 3, 5 and 6).

### Other fauna

In addition to the nine euphausiids, three species of amphipod and a variety of broad taxon groups were analysed (Table I). This list of plankton is by no means a complete account of the taxa found in the STC region, but represents those organisms selected for the purposes of stable isotope analysis. The chaetognath group was composed primarily of Eukrohnia hamata, Sagitta gazellae and S. zeletis. The large size class of copepods was comprised primarily of Calanus simillimus and Pseudocalanus abdominalis, and the small size class composed of Clausocalanus brevicarpus and Oncella conifera. In situ ingestion rates (determined using a gut pigment method) for these copepod species inhabiting the STC during a companion study indicated similar feeding habits among species within each size class (Daly and Froneman, in press). The pteropod group was dominated by Lamacra retroversa but included numerous larger specimens from the genera Clione and Caecolina [for a more complete account of meso- and macrozooplankton].
species collected during the cruise refer to Sterley (Sterley, 2008) and Daly and Froneman (Daly and Froneman, in press).

All taxa showed significant enrichment in $\delta^{15}N$ in the north relative to the south, with samples taken from the middle region often having intermediate values (Table I; Fig. 7). Mean differences of $\delta^{15}N$ from north to south within each species or taxonomic group ranged from 1.1‰ in the amphipod *Themisto gaudichaudii* to 6.3‰ in the ostracods. In contrast, no detectable trend from north to south was observed in $\delta^{13}C$ of plankton (Table I; Fig. 8). Exploratory GLMs were fitted to $\delta^{13}C$ and $\delta^{15}N$ signatures of amphipods and copepods using the potential explanatory variables listed for the euphausiids. Significant terms in the $\delta^{15}N_{amphipod}$ model included salinity, $\delta^{13}C_{amphipod}$, body length and species [$F$ (for the four terms, respectively) = 38.8, 8.3, 14.0, 7.8, 5.2, $R^2 = 0.85$, $P < 0.01$]. Significant terms in the $\delta^{13}C_{amphipod}$ model included only salinity and $\delta^{15}N_{amphipod}$ [$F = 7.5, 32$, $R^2 = 0.57$, $P < 0.01$]. Similar influential explanatory variables were identified in a $\delta^{15}N_{copepod}$ GLM (salinity, temperature, $\delta^{13}C_{copepod}$ and body length; $F = 51.1, 30$, $R^2 = 0.87$, $P < 0.01$) and a $\delta^{13}C_{copepod}$ GLM (salinity, $\delta^{15}N_{copepod}$ and temperature; $F = 18.5, 31$, $R^2 = 0.64$, $P < 0.01$).

**Food webs**

Distinct trophic niches were not apparent among the taxa analysed. Rather, $\delta^{15}N$ signatures depicted a trophic continuum both north and south of the STC, although not necessarily in the same order of enrichment in the separate water masses (Fig. 7). Euphausiids, decapods, mysids, myctophids and chaetognaths generally occupied higher trophic positions than the jellyfish, amphipods, pyrosomes, pteropods, ostracods, copepods and salps (Fig. 7; Table II). POM did not represent the lowest trophic level according to $\delta^{15}N$ signatures, presumably owing to its complex composition. Signatures of $\delta^{13}C$ depicted POM as the most distinct grouping, whereas the faunal groups were remarkably similar to one another both within and between the north and south water masses (Fig. 8).

The trophic structures of the euphausiid communities remained markedly similar north and south of the STC,
with *Euphausia similis armata*, *E. spinifera*, *E. longirostris* and *Stylocheiron abbreviatum* maintaining a trophic position of ~3.8 on both sides of the margin, and *Nematocelis megalops* and *Thysanoessa longicaudata* maintaining slightly lower trophic positions of ~3.6 and 3.2, respectively (Fig. 5; Table II). However, the trophic position of *Euphausia similis* varied slightly with region (3.5 in the north and 3.1 in the south). The remaining three euphausiid species/groups, *E. recurva*, *Thysanopoda pectinata* and the pooled euphausiid furcilia, were collected only in the north. The increase in $\delta^{15}N_{euphausid}$ with $\delta^{13}C_{euphausid}$ was not unexpected, as both signatures show significant increases with body size (Fig. 6) and stepwise trophic enrichment with increased omnivory tends to occur simultaneously in the two parameters (Michener and Schell, 1994).

Of the remaining fauna, the chaetognaths (as well as some unidentified large mysids) also shared the highest trophic position in the dataset (up to 4.2). Interestingly, the chaetognaths increased by an entire trophic position from south to north (2.7 to 3.8), although the standard deviation for the southern group was large and the northern value is probably more representative of the typically carnivorous habits of chaetognaths. Other groups having trophic positions suggesting some carnivorous feeding include the jellyfish (maximum position 3.5), the myctophid larvae (3.1–3.4), the sergestoid and penaeidean shrimps...
(3.3–3.5), the small mysids Siriella thompsoni (3.0), and the amphipods Vibilia armata, Themisto gaudichaudii and Phronima sedentaria (2.2–3.0). The large copepods also occupied a trophic position of ~3.2, indicating an omnivorous diet, whereas the small copepods were herbivorous with positions between 2 and 2.7. The pyrosomes, ostracods, pteropods and salps occupied the lowest positions (as low as 1.8).

**DISCUSSION**

Signatures of $\delta^{13}$C in POM and zooplankton at the STC were significantly different from north to south. The primary source of the variation was related to the latitudinal gradient in nitrate concentrations, with the secondary influence of salinity being an indirect function of the different water masses on either side of the
boundary. Interestingly, much larger shifts from north to south were seen in some of the animal groups, such as the ostracods and small copepods (mean differences in δ^{13}N between north and south of up to 6.3‰, Table I). This finding emphasizes the benefits of using isotope signatures in primary consumer tissues to show a time-integrated perspective of changes in oceanic habitat, whereas POM values are instantaneous measures that indicate only very recent changes. Signatures of δ^{13}C in the plankton did not exhibit significant changes from north to south.

**Particulate organic matter**

Marine δ^{13}C_POM signatures typically range between −18 and −28‰ (Goericke et al., 1994), and all of our δ^{13}C_POM measurements (range −21.6 to −24.3‰) were well within this limit. Rau et al. (Rau et al., 1989) found more depleted values of δ^{13}C_POM to −35‰ south of the polar front, possibly owing to the elevated availability of CO_{2}(aq) in very cold water causing greater fractionation of δ^{13}C as algae fix dissolved inorganic carbon (DIC). More recent studies have provided evidence that seasonal and regional variations of phytoplankton δ^{13}C are frequently explained by changes in the isotopic composition of the DIC (Michener and Schell, 1994), or carbon fixation pathways used by the dominant species, ultimately influenced by light availability (Goericke et al., 1994). Any changes in these parameters at the scale of our STC study were clearly not sufficiently pronounced to cause regional effects on the phytoplankton or zooplankton, and δ^{13}C_POM did not show the marked spatial variations in δ^{13}C of particulate organic carbon in an eastern section of the STC (Francois et al., 1993). The significant negative relationship between C:N ratio and δ^{13}C_POM that we found may relate to variability in lipid content among samples or in the relative contribution of phytoplankton or bacterial degradation to the bulk POM (Minagawa et al., 2001), although this was clearly not a regional effect (Fig. 4).

In addition to all animal taxa analysed, significantly enriched δ^{15}N_POM values were found north of the STC (mean 5.5 ± 0.8‰) relative to south (mean 2.5 ± 0.9‰), clearly indicating that the source of the trend in consumers is a bottom-up phenomenon rather than an increase in omnivory in northern organisms. All values of δ^{15}N_POM were within the range typical of the Southern Ocean [reported range −7 to +6‰ (Wada et al., 1987; Rau et al., 1991)]. The most depleted
δ^{15} N_{POM} signatures have been measured in samples derived from very high latitudes and appear to be related to the low temperatures in polar regions (Altabet and Francois, 1994).

Although POM roughly approximated the primary food source for non-selective particle feeders at the STC, the δ^{15} N_{POM} signature was more enriched than that of some consumers (e.g. Themisto gaudichaudii and Salpa thompsoni, Fig. 7). Significant δ^{15}N-enrichment of POM relative to phytoplankton has also been reported in Alaskan regions (Goering et al., 1990). This enrichment was not unexpected, as bulk POM does not comprise phytoplankton alone, but rather a variety of components including bacteria and detritus. Furthermore, microbial occupation and degradation of particles tends to isotopically enrich organic material (del Giorgio and France, 1996). The detrital component of POM is thus likely to be enriched relative to phytoplankton, and selective pelagic grazers can exhibit more depleted isotopic signatures than that of bulk POM. As a result, POM did not represent a reliable measure of the baseline food source for selective feeders, and, since salps showed the most depleted δ^{15}N in the northern region, they were chosen as the representative food web baseline from which trophic positions of the other consumers were calculated.

The distinct isotopic signatures of POM that we found in water masses north and south of the STC were consistent with data derived by Altabet and Francois (Altabet and Francois, 1994), who documented enriched δ^{15}N_{POM} signatures in transects running from 55 to 30°S, with the most pronounced shift occurring at the STC. Because their latitudinal range was larger than ours, the most depleted δ^{15}N_{POM} values they measured in the south were ~ −4‰, and the most enriched in the north were ~ +7‰, resulting in an 11‰ range in δ^{15}N_{POM} from north to south (Altabet and Francois, 1994) rather than the smaller 3‰ difference that we recorded (Table I). The relationship they found between nitrate levels and δ^{15}N_{POM} was coincidental, as δ^{15}N_{POM} was a function of relative nitrate utilization by phytoplankton (Altabet and Francois, 1994). In our study region, the primary nitrogen source for phytoplankton was likely nitrate (Altabet and Francois, 1994), and since nitrates originating at depth for phytoplankton was likely nitrate (Altabet and Francois, 1994) rather than the smaller 3‰ difference in phytoplankton species composition or cell size is probably not influential factors on δ^{15}N_{POM}. Although phytoplankton species composition in the different water masses was not determined, any latitudinal differences in phytoplankton species composition at the STC would likely have produced variations in δ^{15}C_{POM}, arising from alterations in C fixation pathways, which we did not see.

Chlorophyll concentrations are typically low in the STC region during austral autumn, with blooms occurring most frequently during austral spring (Llido et al., 2005). Chl a concentrations >1.0 µg L^{-1} occur north of the STC during bloom conditions, as demonstrated using satellite remote sensing and simulated models (Llido et al., 2005), and do not correspond with the enhanced nitrate concentrations consistently observed in the south. When they occur, blooms last from 8 to 60 days and the mean areal bloom extent ranges from 10 000 to 45 000 km². Such episodic events [Llido et al. (Llido et al., 2005) documented 263 bloom events in 1 year] are sure to have lasting effects on the planktonic food webs north of the STC and undoubtedly contribute to a unique biological and isotopic habitat that is distinguishable from the south (e.g. Barange et al., 1998). In this manner, residual effects of phytoplankton blooms can propagate through the entire planktonic food web so that the effects remain even during non-bloom periods. The episodic enhanced primary production north of the STC, despite continuously low nutrient levels, likely results from a unique combination of nutrients, temperature and water column stability, combined with the physical accumulation effect from converging currents that appear ideal for increased algal biomass and growth (Lutjeharms et al., 1983; Weeks and Shillington, 1996).

**Food webs**

Of the researchers who have measured isotopic signatures in consumers and POM, only some have found consumer signals to vary in concert with seasonal or regional changes in δ^{15}N_{POM} (e.g. Schell et al., 1998; Bode and Alvarez-Ossorio, 2004). At the STC, the differences in zooplankton δ^{15}N from north to south,
mirroring the regional variation in POM values, are remarkable considering that some of these pelagic organisms are highly mobile and do not appear geographically constrained by the presence of the STC boundary (Sterley, 2008). The distinct isotopic signatures of plankton in the two water masses suggest that individuals tend to remain with one water mass rather than cross the proximate physical margin, despite individuals of the same species inhabiting both northern and southern locations. Had there been extensive migrations, we would have expected individuals with more variable δ¹⁵N signatures representing an average of diet items removed from the more enriched northern region and more depleted southern region. Rather, it appears that the relative depletions and enrichments in the phytoplankton are preserved and passed directly on to the herbivores, detrivores and carnivores.

Rather than distinct, stepwise increases in trophic levels, we found a continuum of trophic positions among taxa consistent with the prevalence of generalist feeding and opportunistic omnivory in many aquatic food webs (e.g. France et al., 1998). Furthermore, different food web relationships were indicated by C and N isotopes. This type of discrepancy is not unexpected and has been recorded in other works (e.g. Goering et al., 1990). Fry and Quinones (Fry and Quinones, 1994) recommend that trophic positions not be calculated using δ¹³C, as fractionation of C sources is small (<1‰) from diet to consumer relative to errors in sampling. Furthermore, because fractionation steps of N sources are significantly larger (>3‰) between consumer and diet, there is generally greater confidence in δ¹⁵N as an indicator of trophic position even though the 3.4‰ per trophic level rule of thumb is not steadfast.

Even at the perspective of an individual organism, trophic position as indicated by δ¹⁵N is not necessarily constant, but varies with dietary state of a consumer (e.g. will differ if a consumer is metabolizing recently digested prey vs. stored reserves) and the ecosystem it inhabits. As we used the default fractionation value of 3.4‰ (which represents an average value based on an assortment of studies and organisms), our calculations would not account for the natural variation in trophic level enrichment among individuals, species and habitats. This natural variation in trophic level enrichment certainly contributed to the variation in calculated trophic positions for plankton both within and between regions. Nevertheless, the trophic position calculations for some of the taxa, the euphausiids in particular, were remarkably consistent both within and between the north and south water masses. The elevated trophic position (>3) occupied by all of the euphausiid species indicated a significant proportion of carnivory in this group (primary consumers would occupy a trophic position of 2 in our model), and coincided with the common finding of increased trophic fractionation and hence enrichment in δ¹⁵N with increasing body size (Fig 6; Fry and Quinones, 1994; France et al., 1998). This relatively elevated trophic position for euphausiids, as indicated by δ¹⁵N signatures, concurs with the dominance of heterotrophic prey found in the stomach contents of euphausiids collected during earlier research cruises in the Southern Ocean (Pakhomov et al., 1999). Euphausiids, along with chaetognaths, have consistently been categorized as the most important components of the carnivore populations in pelagic ecosystems within the Southern Ocean (e.g. Pakhomov et al., 1999 and references therein). Comparisons of our findings for Euphausia longirostris and Nematoscelis megalops with those from a study by Gurney et al. (Gurney et al., 2001) near the Prince Edward Islands, Southern Ocean, allow us valuable insights on the dietary plasticity of these euphausiids. Both species contained significant proportions of phytoplankton (particularly diatoms) in their guts and had δ¹⁵N values ~5‰ more enriched than those of a local herbivore, Calanus similimus (Gurney et al., 2001), a copepod that was also abundant in our STC study region. Nitrogen isotope signatures of the same euphausiid species from our study differed from the salp baseline by ~5.7, suggesting a relatively larger incidence of carnivory. These findings suggest an overall higher level of carnivory at the STC, consistent with the over-abundance of copepods available as food (Froneman et al., 2007; Daly and Froneman, in press) relative to the low phytoplankton biomass, particularly microplankton cells that would be large enough to allow direct consumption by euphausiids. Nitrogen isotope signatures of copepods at the STC, particularly the smaller size fractions (<3 mm length, trophic positions 2 to 2.7), confirmed their more herbivorous position in the trophic continuum. In contrast, δ¹⁵N of large copepods indicated substantial carnivory, as the calculated trophic position (~3.2) was elevated relative to the small forms (Table II).

Stomach contents analysis of chaetognaths has confirmed the highly carnivorous feeding habits of this group (Sterley, 2008), thus further validating their elevated trophic position, particularly in the north (trophic position 3.8). Our findings for euphausiids and chaetognaths are not entirely consistent with other studies, as δ¹⁵N signatures recorded by Wada et al. (Wada et al., 1987) identified euphausiids as strict herbivores along with salps, but copepods and fish as strict carnivores occupying the highest trophic level in one pelagic food web in the Southern Ocean. They positioned the
chaetognaths and jellyfish at a level in between the strict herbivores and carnivores (Wada et al., 1987), whereas our data supported the assignment of a higher trophic position for both these groups (maximum trophic position for jellyfish 3.5). Jellyfish are commonly classified as carnivores in the Southern Ocean, in addition to amphipods, euphausiids, chaetognaths, siphonophores, decapods and fish (Pakhomov et al., 1999). Mysids are seldom mentioned in Southern Ocean food web studies owing to their low occurrence in the water column (Murano, 1999), although our results suggest that they are highly carnivorous like the decapod shrimps (trophic positions 3–4.2). The biomass and abundance associated with all the carnivorous groups varies substantially both spatially and temporally, but calculations of their predation impact have indicated that their feeding activities can represent a substantial contribution to C flux to depths in the open ocean (Pakhomov et al., 1999).

Nitrogen isotope signatures of all three amphipod species at the STC (trophic positions 2.2–3.0) indicated a level of carnivory somewhat lower than that of euphausiids. This trophic shift down relative to the euphausiids was also apparent in Themisto gaudichaudii near the Prince Edward Islands (Gurney et al., 2001), although heterotrophic prey dominated the stomach contents of this amphipod in South Georgia (Pakhomov and Perissinotto, 1996). Our results from the STC indicated overlapping trophic habits in the three amphipods analysed despite the small size of Vibilia armata relative to the others (V. armata <9 mm whereas P. sedentaria and T. gaudichaudii >11 mm length).

Few specimens of myctophid larvae were collected, but their δ¹⁵N values indicated carnivorous feeding habits consistent with previous studies (Pakhomov et al., 1996). In fact, myctophids were the dominate component of pelagic communities at the STC south of Africa (Barange et al., 1998), and this group may consume up to 40% of the annual secondary production in the Southern Ocean (Pakhomov et al., 1996). Future studies that combine gut contents and stable isotope techniques are needed to understand the variability in both myctophid and amphipod diets with time, space and life history.

In accordance with the literature on suspension or small particle feeders (Angel, 1999; Esnal and Daponte, 1999), the most δ¹⁵N-depleted and hence herbivorous consumers included the pyrosomes, ostracods, pteropods, and salps (trophic positions 1.8–2.8). Despite the varied composition of our pooled pteropod samples, which included specimens of Limacina retroversa, Clione spp. and Cavolinia spp., the δ¹⁵N pteropod signatures showed remarkably small within-region variability (Table I).

The salps and pyrosomes showed much larger within-region variability, and possible sources of this variability remain unclear. Together with the small copepods, these small particle feeders exhibited the greatest changes in δ¹⁵N from north to south (generally >5‰ difference; Table I), whereas consumers at higher trophic positions in the food web showed much smaller latitudinal variation (1–5‰ difference). This finding suggests that the regional differences in the biological component beginning with δ¹⁵NPOM signatures tend to attenuate with advancement in trophic level, perhaps to the extent that top consumers such as fish and birds would not reflect the significant regional distinctions shown in the zooplankton δ¹⁵N values shown here.

CONCLUSIONS

The results derived here suggest that, despite potential cross-frontal mixing from storms, eddies and meanders, the STC region southeast of South Africa represents a strong frontal boundary that manifests latitudinal variability not only at the level of physico-chemical, biogeochemical and hydrological parameters, but also in a biological manner in the form of stable nitrogen isotope ratios within the phytoplankton and zooplankton. These results provide important insights into how zooplankton communities take advantage of available resources in a unique region of the ocean, and in turn how their feeding activities may influence higher trophic levels. Our data have significantly increased our understanding of the STC as a region of isotopically distinct feeding habitats for planktonic consumers and the variability in trophodynamics within adjacent but isotopically distinct water masses. Future studies that incorporate samples from top predators will determine whether such distinctive bottom-up effects are discernible in these larger organisms. Our findings, encompassing the convergence region of the southwest Indian Ocean and the Southern Ocean where latitudinal gradients in physical and biogeochemical parameters are strong, may not apply to areas of the STC having weaker latitudinal gradients such as in the south Atlantic. Future studies should encompass regions of less intense convergence to determine whether similar latitudinal patterns in the food webs occur. Furthermore, the lack of any latitudinal δ¹³C gradient despite large differences in the physical properties of seawater occurring across the STC was a remarkable finding considering the significant changes in δ¹⁵N. It will be interesting to increase the temporal and spatial ranges in future studies to determine the seasonal dynamics at the STC and to determine at what scale...
variability in C isotope ratios begin to emerge in the biological components of the ecosystem.

ACKNOWLEDGEMENTS

We thank the officers and crew of the S.A. Agulhas and scientific personnel from Rhodes University and the University of Cape Town (UCT) for their assistance during sampling. Nutrient and oxygen data provided courtesy of the Oceanography team from UCT. Thanks also to I. Newton for processing the stable isotope samples and R. Daly for creating Fig. 1. Collection and analysis complied with the current laws in South Africa.

FUNDING

Funding was provided by the Department of Environmental Affairs and Tourism (DEAT) through the South African National Antarctic Program (SANAP) and administered by the National Research Foundation (NRF). Additional funds and facilities from Rhodes University and the University of Cape Town are appreciated.

REFERENCES


