Mesozooplankton community structure and grazing impact in the region of the Subtropical Convergence south of Africa

E.A. Pakhomov and R. Perissinotto

Abstract. Mesozooplankton distribution and community structure in the region of the Subtropical Convergence (STC) south of Africa were investigated during the SAAMES III cruise in austral winter (June–July) 1993. Both the STC and an associated warm-core eddy (WCE) exhibited enhancements in zooplankton abundance, compared to the Subantarctic waters. Particularly, elevated zooplankton densities were found in the centre of the STC and in the region north of it as well as at the edge of the WCE. Copepods (mainly Pleuromamma abdominalis and Metridia lucens), euphausiids (Euphausia spinifera, E. similis and E. recurva), pteropods (Limaana spp.) and chaetognaths (Eukrohnia hamata and Sagitta spp.) dominated numerically and accounted for >60% of the mesozooplankton community. Both cluster and ordination analyses indicated the occurrence of two major plankton communities located north and south of the STC. These results confirm that the STC is one of the strongest regional zoogeographical barriers, but south of Africa, WCEs may represent the most important source of disturbance in the meso-/macroscale zonation of the zooplankton assemblages. The daily grazing impact of the epipelagic community was estimated to remove ~1-18% of phytoplankton standing stock and 20-165% of daily primary production. The highest rates of phytoplankton consumption were found in the centre of the STC and within the WCE, suggesting that the zooplankton assemblage transferred by the WCE may enhance substantially the mesoscale carbon flux in the Subantarctic zone south of Africa.

Introduction

The Subtropical Convergence (STC) is regarded as the northern boundary of the Southern Ocean, where Subtropical Surface Waters from the subtropical gyres meet Subantarctic Surface Waters (Lutjeharms et al., 1993). South of Africa, the STC represents the convergence of the Antarctic Circumpolar Current (ACC) and the Agulhas Retroflection Current (ARC) (Lutjeharms et al., 1993). Spatio-temporal interactions between these two systems cause the shedding of 8-12 warm-core eddies (WCEs) annually, which subsequently migrate either southeastwards or southwestwards (Lutjeharms and Gordon, 1987; Lutjeharms and Valentine, 1988; Duncombe Rae, 1991). The advection of these eddies contributes substantially to the meridional heat flux, thereby impacting on the physics and chemistry of the northern area of the Southern Ocean. This oceanographic interaction is relatively well described (Lutjeharms, 1988a, b; Lutjeharms and Valentine, 1988; Duncombe Rae, 1991). Our understanding of the biological processes in the STC region south of Africa is, however, still poor and requires attention.

Some evidence suggests that the STC may exhibit enhanced biological activity throughout the year (Allanson et al., 1981; Lutjeharms et al., 1985; Pakhomov et al., 1994) and feature a unique planktonic community (Barange et al., 1997). Recent studies have shown that WCEs can also impact significantly on the biology of the regions in which they occur (Wiebe and Youce, 1992). For example, WCEs have a large impact on the pelagic fauna of the north Atlantic (Craddock et al., 1992), and provide an excellent fishing ground for pelagic fish and squid in the...
North Pacific (Sugimoto and Tameishi, 1992). Eddies shed from the ARC contribute to the enhancement of primary production in the vicinity of the STC (Dower and Lucas, 1993) and are important for the transfer of phytoplankton assemblages to different water masses (Froneman et al., 1997). Finally, because of their close analogy to frontal features, eddies are ideal sites for process-oriented biogeographical studies (Johnson and van der Spoel, 1986). The main aims of this paper were to study the variations in the mesozooplankton community associated with the interaction of different water masses, and to estimate the grazing impact of this community on the phytoplankton of the STC region south of Africa and within a WCE shed from the ARC.

**Method**

**Zooplankton abundance and community structure**

Zooplankton samples were collected during the third cruise of the South African Antarctic Marine Ecosystem Study (SAAMES III), aboard the SA ‘Agulhas’ (Voyage 72), to the region of the STC in austral winter, 24 June–11 July 1993 (Figure 1). In addition to ad hoc tows, three 24 h stations were occupied in the middle, in the southern and in the northern vicinity of the STC, respectively. At each station, tows were made at regular intervals of ~3–4 h. Zooplankton were collected using a Bongo net with a mouth area of 0.5 m$^2$ and a mesh size of 0.3 mm. The net was fitted with a Universal Underwater Unit (U$^3$) which monitored depth and temperature continuously (Robertson et al., 1981). The volume filtered by the net was calculated using electronic flowmeter data. Towing speed varied between 1.5 and 3 knots, and the net was towed obliquely between 0 and 300 m. Samples were preserved in 4–6% buffered formalin and examined in the laboratory. Catches were sorted and analysed for taxonomic identification and numerical abundance. Zooplankton abundance was expressed as number of individuals per cubic metre.

To compare plankton communities, the log$_{10}$ of Shannon–Weaver diversity indexes (Shannon and Weaver, 1949) was calculated for each assemblage. Nonmetric cluster analysis and multidimensional scaling were used in conjunction with the Bray–Curtis similarity index after log transformation [log$_{10}(x + 1)$] of the species abundance data. Significance levels and sources of difference between zooplankton communities were then tested using the similarity analysis programs ANOSIM and SIMPER of the Plymouth Routines In Multivariate Ecological Research (PRIMER; Clarke and Warwick, 1994) computer package, according to the procedure described by Field et al. (1982).

**Feeding ecology**

From each tow, individuals of the most abundant zooplankton species were taken for grazing studies. Animals for measurements of gut pigment content were sorted immediately after capture, placed in plastic centrifuge tubes (one adult euphausiid or 5–10 copepods per tube) with 5 ml of 100% methanol and stored at -20°C for ~12–24 h (Simard et al., 1985). After centrifugation (5000 r.p.m.), the pigment content of the methanol extract was measured with a Turner 111...
fluorometer, before and after acidification (Mackas and Bohrer, 1976). Pigment contents were expressed in terms of chlorophyll a equivalents per individual and calculated according to Strickland and Parsons (1968) as modified by Conover et al. (1986). When the Chl a/phaeopigment ratio of the gut content was >0.25, total pigment levels were corrected according to Baars and Helling (1985). Five to 10
replicate animals were used for the pigment extraction and measurement at each station or for each tow.

To estimate the gut evacuation rate \((k)\), freshly caught animals were gently placed into a 20 l plastic bucket filled with 0.2 \(\mu\)m filtered seawater to which non-fluorescent charcoal powder \((\leq 100 \mu\text{m}, \text{diameter})\) was added to keep the animals under continuous feeding conditions (Willason and Cox, 1987; Perissinotto, 1992; Perissinotto and Pakhomov, 1996). Containers with experimental animals were kept on deck at ambient temperature. The duration of these incubations ranged from 1 to 8 h and the decline in gut content was monitored at intervals of 5–20 min for the first hour and 0.5–2 h thereafter. The gut evacuation rate \((k, \text{h}^{-1})\) was derived from the slope of the regression of the natural logarithm of gut pigments versus time (Dam and Peterson, 1988).

Independent measurements of gut pigment loss were made to estimate the gut degradation efficiency. In each experiment, animals were first allowed to empty their gut of pigments for 24 h in filtered seawater with charcoal particles. One to 10 animals were then incubated for 1–2 h in 1 l bottles with naturally occurring phytoplankton concentrations. A two-compartment pigment budget approach was employed by comparing the decrease in pigment content in the grazing bottles with the increase in gut pigment levels of animals incubated in these bottles (Lopez et al., 1988; Mayzaud and Razouls, 1992; Perissinotto, 1992).

Daily ingestion rates \([I, \text{ng (pigm) ind}^{-1} \text{day}^{-1}]\) were estimated from the relationship (Wang and Conover, 1986; Perissinotto, 1992):

\[
I = k \frac{G}{(1 - b')}
\]

where \(G\) is an integrated value (over a 24 h period) of gut pigment contents [ng (pigm) ind\(^{-1}\)], \(k\) is the gut evacuation rate constant (h\(^{-1}\)) and \(b'\) is a non-dimensional index of the loss of pigment during digestion. As estimates of \(b'\) were not available for all species, an average value of 0.5 for this parameter, as derived from the literature (Mayzaud and Razouls, 1992; Perissinotto, 1992), was used when no direct measurements were made.

In order to estimate the community grazing impact, zooplankton abundance data were combined with individual ingestion rates. Ingestion rates were estimated at the 24 h stations (stations A, B and C) only. For the other stations, the average values of ingestion rates obtained from stations A, B and C were employed. To convert chlorophyll \(a\) concentration into autotrophic carbon \((C)\), the empirical equation obtained by Hewes et al. (1990), \(C = 80 \text{ Chl}^{0.6}\), was used. Areal chlorophyll \(a\) biomass and primary production rates in the euphotic zone (depth of 1% of surface irradiance) were obtained by trapezoidal integration (R.K. Laubscher, unpublished).

Results

Zooplankton distribution

Marked changes in mesozooplankton abundance were found across the STC. Along the transect, the main peak in zooplankton abundance (up to 91.4 ind. m\(^{-3}\))
was recorded in the centre of the STC (Figure 2). Generally, average zooplankton abundances decreased across the STC from north to south and then increased again within the WCE. Here, the most elevated mesozooplankton densities were found towards the edge of the eddy (Figure 2).

Cluster and ordination analyses, composition and abundance

Results of the hierarchical cluster analysis show the presence of two major groups of stations (Figure 3A). This separation is associated with the position of the STC. Each of these groups can be further subdivided into two smaller clusters of stations. The one-way ANOVA similarity test clearly shows significant differences between all four groups identified ($P < 0.001$).

Group 1a was comprised of stations situated inside the WCE. The zooplankton community of this group was characterized by the dominance of three copepod taxa, *Pleuromamma abdominalis*, *Clausocalanus* spp. and *Metridia lucens*, which accounted for ~70% of the total zooplankton abundance (Table I). Group 1b included only stations north of the STC. *Clausocalanus* spp., ostracods, *P. abdominalis*, chaetognaths and *Limacina* spp. were the most abundant taxa in this area (Table I). Groups 2a and 2b comprised stations situated south of the STC, in Subantarctic waters (Figures 1 and 3A). All stations of group 2a were

![Fig. 2. Spatial distribution of mesozooplankton abundance in the Subtropical Convergence region south of Africa during June-July 1993. Stations are arranged latitudinally and their code numbers correspond to those in Figure 1. Daytime and night-time levels were multiplied by average ratios calculated from the 24 h stations to derive daily averaged rates. WCE, warm-core eddy.](https://academic.oup.com/plankt/article-abstract/19/6/675/1521381)
Fig. 3. Results of the cluster (A) and ordination (B) analyses of the zooplankton community structure in the region of the Subtropical Convergence south of Africa during June–July 1993 (SAAMES III). STC, Subtropical Convergence; WCE, warm-core eddy.
### Table I. Zooplankton species composition and abundance during the SAAMES III cruise to the region of the Subtropical Convergence in austral winter 1993. Only species contributing ≥1% to the total abundance are listed

<table>
<thead>
<tr>
<th>Group</th>
<th>No. of species</th>
<th>Shannon Index</th>
<th>Abundance ind. m⁻³ (± SD)</th>
<th>Species composition and % contribution</th>
<th>Zooplankton/micronekton species recorded only in this group</th>
</tr>
</thead>
<tbody>
<tr>
<td>1a</td>
<td>63</td>
<td>0.910</td>
<td>36.3 ± 27.7</td>
<td><em>Pleuromamma abdominalis</em> (45.0%), <em>Clausocalanus</em> spp. (13.3%), <em>Metridia lucens</em> (10.5%), <em>Chaetognatha</em> (5.3%), <em>Ostracoda</em> (3.8%), <em>Oithona</em> spp. (3.7%), <em>Euchaeta</em> spp. (2.3%), <em>Calocalanus</em> spp. (2.2%), <em>Lucicutia</em> spp. (2.0%), <em>Oncaea</em> spp. (1.9%), <em>Calanus australis</em> (1.4%), Appendicularia (1.3%), <em>Limacina</em> spp. (1.1%)</td>
<td><em>Eucalanus hyalinus</em>, <em>Themisto gaudichaudi</em>, <em>Doliolidae</em>, <em>Streetsia mindanaoni</em>, <em>Diacria trispinosa</em>, <em>Curvierina collumbelli</em>, <em>Gymnoscopelus bolini</em>, <em>Leptocephalus</em></td>
</tr>
<tr>
<td>1b</td>
<td>83</td>
<td>1.311</td>
<td>64.8 ± 22.2</td>
<td><em>Clausocalanus</em> spp. (15.2%), <em>Ostracoda</em> (12.4%), <em>Pleuromamma abdominalis</em> (8.7%), <em>Chaetognatha</em> (8.6%), <em>Lucicutia</em> spp. (6.3%), <em>Calocalanus</em> spp. (4.2%), <em>Oncaea</em> spp. (4.1%), <em>Calanus australis</em> (3.5%), <em>Euchaeta</em> spp. (3.3%), <em>Scolecitricella</em> spp. (3.0%), <em>Oithona</em> spp. (2.9%), Appendicularia (2.6%), <em>Ctenocalanus</em> spp. (1.7%), <em>Siphonophora</em> (1.5%), <em>Salpa</em> sp. (1.5%), <em>Limacina</em> spp. (1.2%), <em>Ostracoda</em> (1.0%)</td>
<td><em>Rhincalanus nasutus</em>, <em>Diphyes dispar</em>, <em>Thysanoessa pectuncula</em>, <em>Iasis zonaria</em>, <em>Diaphus taenini</em>, <em>D.indicus</em>, <em>Lampanyctus alatus</em>, <em>L.pussillus</em>, <em>L.australis</em>, <em>Lampadema pontex</em>, <em>Scopeplus multipunctatus</em>, <em>Bentosema suborbitalis</em>, <em>Symbolophorus hoops</em>, <em>Notolychnus valdivia</em></td>
</tr>
<tr>
<td>2a</td>
<td>60</td>
<td>0.686</td>
<td>81.9 ± 80.5</td>
<td><em>Pleuromamma abdominalis</em> (41.2%), <em>Metridia lucens</em> (31.5%), <em>Clausocalanus</em> spp. (16.6%), <em>Oncaea</em> spp. (1.3%), <em>Ostracoda</em> (1.0%), <em>Chaetognatha</em> (1.1%), <em>Euchaeta</em> spp. (1.0%)</td>
<td><em>Marrus</em> sp., <em>Cimbulia sibogae</em>, <em>Funchalia woodwardi</em>, <em>Hymenodora glacialis</em>, <em>Diaphus meadi</em>, <em>Hygeophum hudsoni</em>, <em>Symbolophorus evermann</em></td>
</tr>
<tr>
<td>2b</td>
<td>34</td>
<td>0.693</td>
<td>13.3 ± 7.8</td>
<td><em>Clausocalanus</em> spp. (54.9%), <em>Pleuromamma abdominalis</em> (21.8%), <em>Metridia lucens</em> (5.0%), <em>Chaetognatha</em> (4.5%), <em>Oithona</em> spp. (1.3%), <em>Scolecitricella</em> spp. (1.1%), <em>Calanus australis</em> (1.1%), <em>Ostracoda</em> (1.0%)</td>
<td></td>
</tr>
</tbody>
</table>
occupied during night-time, while group 2b included only stations where midday Bongo tows were carried out. Very similar zooplankton communities were identified within these two groups of stations. As for group 1a, three copepod taxa, *P. abdominalis*, *M. lucens* and *Clausocalanus* spp., formed the bulk of the total zooplankton abundance (Table I). Ordination analysis showed a very similar pattern and a closer relationship between groups 1a, 2a and 2b than was identified with the cluster analysis (Figure 3B).

The results of the similarity analysis (SIMPER) are presented in Table II. The highest average dissimilarity indexes (57–67%) were observed between the groups north (1b) and south (2a and 2b) of the STC. This was due to a drastic reduction in the number of subtropical species, e.g. Brachiura and Stomatopoda larvae, Phyllosoma (Palinuroidea), *Leptocephalus* sp. The lowest dissimilarities in zooplankton community structure (46–49%) were found between the group from the region north of the STC (1b) and that from the WCE (1a), as well as the group consisting of the night-time samples collected south of the STC (Table II).

Both species richness and diversity index were highest for the group of stations situated north of the STC (group 1b, Table I). The lowest number of species was found in samples from midday tows carried out south of the STC (group 2b). Although the species richness at stations within the WCE (group 1a) was similar to that observed at the stations south of the STC (groups 2a and 2b combined), the diversity index was substantially higher for group 1a compared to both 2a and 2b (Table I).

### Ingestion rates and grazing impact

Only the seven most abundant mesozooplankton taxa were considered in the estimation of community grazing impact (Table III). During the period of the investigation, these taxa together accounted for 40–90% of the total mesozooplankton abundance.

All zooplankton taxa investigated showed unimodal diel feeding rhythms, with a peak in gut pigment occurring generally during the night. In all cases, negative exponential models provided the best fit to the decline in gut pigment contents during gut evacuation experiments. Values obtained for the gut evacuation rate constant ranged from 0.619 to 5.224 h⁻¹ in copepods and in the subadult stages of euphausiids, and from 0.178 to 0.736 h⁻¹ in pteropods (*Limacina* spp.) and adult euphausiids (Table IV). Individual ingestion rates were highest for the euphausiids [218–1690 ng (pigm) ind⁻¹ day⁻¹] and lowest [43 ng (pigm) ind⁻¹ day⁻¹] for the small copepods of the genera *Microcalanus*, *Clausocalanus*, *Ctenocalanus* and *Calocalanus* (Table IV).
Table III. Numerical estimates (ind. m$^{-2}$) of the most abundant components of the mesozooplankton community at the primary production stations occupied in the Subtropical Convergence region south of Africa during austral winter 1993. All abundance values are integrated over a period of 24 h and a water column of 0–300 m depth.

<table>
<thead>
<tr>
<th>Taxon</th>
<th>Station number</th>
<th>35</th>
<th>43</th>
<th>49</th>
<th>55</th>
<th>67</th>
<th>79</th>
<th>A</th>
<th>B</th>
<th>C</th>
<th>121</th>
</tr>
</thead>
<tbody>
<tr>
<td>Rhincalanus spp.</td>
<td></td>
<td>-</td>
<td>85.6</td>
<td></td>
<td>-</td>
<td>-</td>
<td>9.8</td>
<td>50.1</td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>Calanus spp.</td>
<td></td>
<td>-</td>
<td>299.6</td>
<td>257.3</td>
<td>170.4</td>
<td>-</td>
<td>98.5</td>
<td>580.1</td>
<td>37.3</td>
<td>144.8</td>
<td>64.5</td>
</tr>
<tr>
<td>Pleuromamma spp.</td>
<td></td>
<td>127.0</td>
<td>2183.0</td>
<td>8563.4</td>
<td>10853.0</td>
<td>6675.7</td>
<td>2113.7</td>
<td>1423.2</td>
<td>9808.3</td>
<td>3027.9</td>
<td>1064.3</td>
</tr>
<tr>
<td>Metridia spp.</td>
<td></td>
<td>15.9</td>
<td>171.2</td>
<td>1160.3</td>
<td>1386.4</td>
<td>2678.3</td>
<td>-</td>
<td>8.1</td>
<td>8186.8</td>
<td>2884.3</td>
<td>354.8</td>
</tr>
<tr>
<td>Small copepods$^b$</td>
<td></td>
<td>1214.3</td>
<td>2354.2</td>
<td>2109.6</td>
<td>2725.9</td>
<td>3464.5</td>
<td>1517.4</td>
<td>2590.3</td>
<td>6766.9</td>
<td>819.5</td>
<td>3698.9</td>
</tr>
<tr>
<td>Euphausia spp., fucilia</td>
<td></td>
<td>15.9</td>
<td>128.4</td>
<td>77.2</td>
<td>56.8</td>
<td>38.1</td>
<td>39.4</td>
<td>521.8</td>
<td>414.5</td>
<td>74.5</td>
<td>43.0</td>
</tr>
<tr>
<td>Euphausia spp., subadults$^b$</td>
<td></td>
<td>-</td>
<td>-</td>
<td>32.2</td>
<td>-</td>
<td>12.8</td>
<td>9.9</td>
<td>7.7</td>
<td>17.1</td>
<td>20.0</td>
<td>2.2</td>
</tr>
<tr>
<td>Euphausia spp., adults$^b$</td>
<td></td>
<td>41.3</td>
<td>-</td>
<td>6.4</td>
<td>12.8</td>
<td>-</td>
<td>-</td>
<td>-</td>
<td>-</td>
<td>28.8</td>
<td>-</td>
</tr>
<tr>
<td>Limacina spp.</td>
<td></td>
<td>31.7</td>
<td>85.6</td>
<td>360.2</td>
<td>28.4</td>
<td>228.4</td>
<td>69.0</td>
<td>127.3</td>
<td>101.9</td>
<td>13.6</td>
<td>43.0</td>
</tr>
</tbody>
</table>

$^a$Including Microcalanus spp., Calocalanus spp., Ctenocalanus spp. and Clausocalanus spp.

$^b$Mainly a mixture of Euphausia spinifera and E.similis.
Table IV. Gut evacuation rate constant \((k, \text{h}^{-1})\), gut pigment degradation efficiency (pigments losses, %) and ingestion rates \([\text{ng (pigm) ind.}^{-1} \text{day}^{-1}]\) of selected mesozooplankton taxa during the three 24 h stations occupied in the Subtropical Convergence region south of Africa, austral winter 1993.

<table>
<thead>
<tr>
<th>Taxon</th>
<th>Water T°C during experiments</th>
<th>Gut evacuation, (k) (h(^{-1}))</th>
<th>Pigment losses (%)</th>
<th>Ingestion rates</th>
</tr>
</thead>
<tbody>
<tr>
<td></td>
<td></td>
<td>mean (± SD)</td>
<td>min–max</td>
<td>mean (± SD)</td>
</tr>
<tr>
<td><em>Rhincalanus</em> spp.</td>
<td>19–20</td>
<td>1.438</td>
<td>–</td>
<td>–</td>
</tr>
<tr>
<td><em>Calanus</em> spp.</td>
<td>18–20</td>
<td>3.674 ± 2.191</td>
<td>2.124–5.224</td>
<td>70.4 ± 9.9</td>
</tr>
<tr>
<td><em>Pleuromamma</em> spp.</td>
<td>11–19</td>
<td>1.183 ± 0.694</td>
<td>0.692–1.673</td>
<td>1289 ± 0.440</td>
</tr>
<tr>
<td><em>Metridia</em> spp.</td>
<td>11–13</td>
<td>1.289 ± 0.440</td>
<td>0.978–1.700</td>
<td>104.8 ± 1.808</td>
</tr>
<tr>
<td>Small copepods</td>
<td>14–15</td>
<td>4.573</td>
<td>–</td>
<td>–</td>
</tr>
<tr>
<td><em>Euphausia</em> spp., furcilia</td>
<td>12–14</td>
<td>1.630</td>
<td>–</td>
<td>–</td>
</tr>
<tr>
<td><em>Euphausia</em> spp., subadults</td>
<td>12–19</td>
<td>1.626 ± 0.930</td>
<td>0.619–2.454</td>
<td>42.5 ± 31.7</td>
</tr>
<tr>
<td><em>Euphausia</em> spp., adults</td>
<td>12–19</td>
<td>0.408 ± 0.188</td>
<td>0.178–0.736</td>
<td>42.5 ± 31.7</td>
</tr>
<tr>
<td><em>Limacina</em> spp.</td>
<td>11–12</td>
<td>0.355</td>
<td>–</td>
<td>–</td>
</tr>
</tbody>
</table>
Table V. Phytoplankton biomass, production, zooplankton ingestion rates and grazing impact in the Subtropical Convergence region south of Africa during austral winter 1993

<table>
<thead>
<tr>
<th>Station no.</th>
<th>Phytoplankton biomass (mg Chla m$^{-2}$)</th>
<th>Primary production (mg C m$^{-2}$ day$^{-1}$)</th>
<th>Daily ingestion rates [mg (pigm) m$^{-2}$]</th>
<th>Daily grazing impact</th>
</tr>
</thead>
<tbody>
<tr>
<td></td>
<td></td>
<td></td>
<td>cop.</td>
<td>euph.</td>
</tr>
<tr>
<td>35</td>
<td>23.6</td>
<td>140.2</td>
<td>0.132</td>
<td>0.033</td>
</tr>
<tr>
<td>43</td>
<td>32.9</td>
<td>158.7</td>
<td>1.591</td>
<td>0.066</td>
</tr>
<tr>
<td>49</td>
<td>45.3</td>
<td>140.5</td>
<td>5.551</td>
<td>0.089</td>
</tr>
<tr>
<td>55</td>
<td>38.5</td>
<td>155.8</td>
<td>6.967</td>
<td>0.037</td>
</tr>
<tr>
<td>67</td>
<td>54.2</td>
<td>189.2</td>
<td>4.532</td>
<td>0.027</td>
</tr>
<tr>
<td>79</td>
<td>41.2</td>
<td>332.0</td>
<td>1.396</td>
<td>0.034</td>
</tr>
<tr>
<td>A</td>
<td>34.3</td>
<td>278.2</td>
<td>1.175</td>
<td>0.168</td>
</tr>
<tr>
<td>B</td>
<td>45.9</td>
<td>261.4</td>
<td>5.760</td>
<td>0.244</td>
</tr>
<tr>
<td>C</td>
<td>32.3</td>
<td>274.3</td>
<td>2.781</td>
<td>0.106</td>
</tr>
<tr>
<td>121</td>
<td>51.3</td>
<td>263.9</td>
<td>0.876</td>
<td>0.025</td>
</tr>
</tbody>
</table>
The daily grazing impact of the selected mesozooplankton taxa varied widely: from 0.8 to 18.2% of phytoplankton standing stock and from 20.4 to 165% of primary production (Table V). The highest zooplankton daily impact on phytoplankton (90-165% of primary production) was found in the centre of the STC and within the WCE in conjunction with high abundances of the calanoid copepods *P.* *abdominalis* and *M.* *lucens* (Table V).

**Discussion**

**Community structure**

Fronts have important effects on pelagic organisms, from phytoplankton to nekton (Lutjeharms *et al.*, 1985; Olson, 1986; Laubscher *et al.*, 1993; Barange *et al.*, 1997). It is well documented that the STC represents a strong biogeographical barrier for many planktonic species (e.g. Deacon, 1982; Boden *et al.*, 1988; Pakhomov *et al.*, 1994; Froneman *et al.*, 1995). However, a biogeographical boundary in the open ocean cannot be expected to be very effective because animals will not exhibit dramatic responses to a physical parameter even when its gradient is sharp (Backus, 1986). Therefore, in regions where different communities come into contact, a transitional zone called an ecotone generally occurs (Pianka, 1988). The scale of ecotones may vary from metres to hundreds of kilometres and comprises specific biogeographical regions or provinces (Beklemishev, 1969; Backus, 1986). At any front, a particular ecosystem seems to develop which is distinct from those of the two adjacent water masses (Frontier, 1986). The nature of the STC as a convergence zone has recently led to the hypothesis that the local planktonic community may be unique (Barange *et al.*, 1997; Froneman *et al.*, 1997).

A convergence promotes the mechanical concentration of plankton from both sides of the front (Franks, 1992). Cross-frontal mixing processes can also bring about favourable conditions for phytoplankton blooms by enhancing the local nutrient availability (Laubscher *et al.*, 1993; Barange *et al.*, 1997). Despite the fact that four planktonic assemblages were identified in this study, there were no substantial differences in their species composition, suggesting that very intensive cross-frontal mixing processes occurred in both directions during the period of the investigation. The differences between the four assemblages were due to different proportions and densities of the same species rather than to their presence/absence in the various regions and due to a dramatic reduction in the abundance of larvae of subtropical species generally associated with the ARC. Indeed, there are some species which were found only in a specific water mass and not in the others (Table I). This, however, can probably be attributed to artifacts due to the low frequency of sampling employed during the investigation. This towing frequency does not seem to be adequate for studies of species distribution. It is well known that the unexpected presence of species in some areas may be due to a few expatriated specimens. Also, the absence of species in an area where they are expected to occur may reflect a poor collecting effort (Backus, 1986).

Although the biological community associated with the STC has no specific species composition, it exhibits a unique structure which is probably driven by
Mesozooplankton community structure

biological or and physical interactions occurring within the front. The high density of animals in this region (and consequently the complexity of the food web) can be partly explained by their mechanical concentration (Franks, 1992). As fronts are contact zones, special physical, chemical and biological phenomena may develop within the frontal region. These may have more influence on the ecological properties of the frontal area than the processes occurring within the two adjacent water masses themselves (Frontier, 1977, 1986). Turbulence is highly enhanced within convergence regions, increasing dramatically their 'co-variance' (Frontier, 1977, 1986). In such conditions, the spatial size of an individual ecological niche can decrease. For example, it has been shown that the individual niche size for Calanus finmarchicus in the Northern Atlantic has decreased from 0.99 in the open waters to 0.78 at the Polar Front (Zubova and Tomofeev, 1989). In other words, the turnover rate for any biological processes decreases and subsequently the living space of a single animal would be smaller within the front compared to that in adjacent waters. This, in turn, would allow for more animals to be accommodated per unit of space in the frontal area than in the adjacent areas. In this context, it must be pointed out that the 'supporting system' of this specific community, as hypothesized above, can only exist within the front.

During this study, species richness and mesozooplankton abundance generally decreased from north to south across the STC, but increased again within the WCE. A similar situation was also found for the macrozooplankton abundance (Pakhomov et al., 1994; Barange et al., 1997). From previous (Froneman et al., 1997) and these findings it is clear that WCEs play a key role in transferring biological communities from the STC, or north of it, to the Subantarctic zone, at least during the period of WCE formation. Results of the SIMPER analysis carried out in this study provide evidence for an enhancement in the zooplankton density within the WCE. These zooplankton originated from the community inhabiting the centre of the STC and north of it, and were advected by the WCE to the region south of the front (Table II). This could lead, therefore, to the transfer of portions of the rich and unique frontal community from the area where their 'supporting system' operates. Eddies can maintain a suitable environment for the survival and even reproduction of this community (Olson, 1986). At the same time, however, eddies become an effective transport mechanism only for those species which have the ability to exploit the eddy environment.

Within the Southern Hemisphere, the subtropical region south of Africa exhibits a maximum in heat flux (Olson et al., 1992). Here, WCEs are transported as anomalous water masses to the region south of the STC (Lutjeharms, 1988b). It is known that in the Gulf Stream area and within the South Atlantic, eddies may maintain their identity for many months and even years (Brown et al., 1986; Gordon et al., 1992). South of Africa, WCEs cool down as they drift off and are usually followed by new ones that are continuously generated in the region of the Agulhas Retroflection (Lutjeharms and Valentine, 1988). Sometimes, these eddies rapidly become indistinguishable from the surrounding environment, as a result of cooling through the ocean/atmosphere heat flux (Lutjeharms, 1988a,b). There is some evidence, however, suggesting that most WCEs may persist for at least 4–6 months and penetrate as far south as 45°S, thus reaching the Subantarctic Front.

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(Lutjeharms and Gordon, 1987; Lutjeharms and Valentine, 1988). It is obvious, therefore, that WCEs have a great impact on the physical, chemical and biological properties of the Subantarctic region south of Africa. Recent biogeographical studies conducted in the Atlantic sector of the Southern Ocean, along a transect from SANAE to Cape Town, have confirmed the role of the STC as a major biogeographical barrier in the Southern Ocean, but have also pointed out the biogeographical importance of the SAF (Froneman et al., 1995; Perissinotto et al., 1996). From a biogeographical point of view, this region is regarded as a Southern Temperate (or Southern Transitional) region (Backus, 1986), which persists throughout the Southern Ocean. The results of our study suggest that the region between the STC and the SAF can be considered as a true ecotone, at least in the region where important oceanographic features, such as the Agulhas Retroflection, occur.

**Grazing impact**

Results from numerous studies suggest that daily mesozooplankton grazing impact is generally <5% of the phytoplankton standing stock and <10% of primary production (Dam et al., 1993; Morales et al., 1993; Tsuda and Sugisaki, 1994; Atkinson and Shreeve, 1995; Atkinson, 1996). On the other hand, a few studies have shown that at higher latitudes mesozooplankton can consume most, if not all, of the phytoplankton production (Bathmann et al., 1990; Hansen et al., 1990; Ward et al., 1995). This can in general be attributed to the seasonality in the pelagic subsystem and also to the high degree of variability in the distribution of zooplankton and primary production levels in these regions. In winter, and in areas where low primary production levels or high zooplankton density occur, the grazing impact appears to be highest (Perissinotto, 1992; Landry et al., 1994; Ward et al., 1995).

The community ingestion rates estimated in this study are within the highest reported in the literature, indicating that phytoplankton removal in the region of the STC during winter is substantial. The lowest grazing rates (20–30% of primary production) were observed in Subantarctic waters (station 35), in the southern vicinity of the STC (stations 79 and 121) and at the northern edge of the STC (station A). The grazing impact at station A may, however, have been grossly underestimated because the seven species used for grazing studies there accounted for only ~40% of total abundance. Furthermore, the grazing rates of small salps (Table I) and large pyrosomes (Pyrosoma sp.) were not taken into consideration as no feeding measurements were carried out using these groups.

The highest impact on primary production was observed within the STC and the WCE (Table V). The highest grazing occurred in conjunction with high mesozooplankton standing stock and low primary production rates (Tables III and V). Grazing rates in excess of 100% of primary production were found in these regions, suggesting that grazers may have been food limited for the autotrophic food, at least during the period just after WCE formation. The deficit of phytoplankton food may, however, have been balanced by the consumption of large protozoans (Tsuda and Sugisaki, 1995; Ward et al., 1995; Atkinson, 1996). Indeed,
during this study, increases in mesozooplankton abundance closely co-varied with a dramatic decrease in microzooplankton density (Froneman and Perissinotto, 1996).

In conclusion, subtropical WCEs south of Africa can exist for a long time, they can migrate far south, rejoin the mainstream or be reinforced by boundary currents. Biologically, they are very important since they promote remarkable transfer of pelagic communities across the strong biogeographical barrier represented by the STC. Ecologically, WCEs may be responsible for the substantial alternation in mesoscale carbon flux within the Subantarctic zone between the STC and the SAF.

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E.A. Pakhomov and R. Perissinotto


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