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The role of zooplankton communities in carbon recycling in the Ocean: the case of the Southern Ocean

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Basin-scale carbon recycling estimates were obtained by combining high-resolution data on zooplankton taxonomic and functional composition with species-specific respiration rates. Datasets were collected in the Atlantic and Indian sectors of the Southern Ocean during four cruises covering spring, mid-summer, autumn and late winter between 1993 and 1998. Carbon recycling by Antarctic meso- and macrozooplankton represented a significant (44–62%) fraction of the primary production, which is at the higher end of previous estimates. Assessment based on detailed community structure appeared to be more realistic than previous estimates and showed that carbon dioxide recycling at the global scale is not a mere function of temperature and abundance of zooplankton. Both species and functional diversity influence current estimates at the community level through trophic type and developmental stage composition. In addition, a regional spatial heterogeneity linked to hydrodynamic features (frontal zones) is also important. The Southern Ocean zooplankton community respiration is assessed to be $\sim 0.6 \text{ GtC year}^{-1}$.

KEYWORDS: zooplankton community; carbon recycling; Southern Ocean

INTRODUCTION

Cycling of carbon in the upper ocean remains a key aspect in understanding the ability of the world ocean to buffer the atmospheric carbon dioxide (CO_2) increase and control the associated raise of pH. So far, the balance between

primary production and ecosystem respiration has been shown to be regulated mostly by photo- and microbial respiration (Rivkin and Legendre, 2001; Del Giorgio and Duarte, 2002). Although most models assume that over a year and large spatial domains primary production must be nearly balanced by plankton respiration, recent reviews

have suggested that large regional carbon deficits may exist (Del Giorgio *et al.*, 1997; Del Giorgio and Duarte, 2002). This, however, has been challenged using depth-integrated measurements of primary production and community respiration (Williams, 1998).

In almost all studies published thus far, the respiration of metazoan organisms (zooplankton and higher trophic levels) has been ignored. When considered, estimates of zooplankton and vertebrate respiration are derived using the assumption of a 10% physiological efficiency for each trophic level (Huntley *et al.*, 1991; Del Giorgio and Duarte, 2002). As a result, the contribution of zooplankton to the total plankton respiration was limited to 5%, hence representing a minor component in the oceanic carbon recycling. This view has also been challenged using a simple budget based on the assumption that density and temperature are the key controlling factors of respiratory rates (Hernandez-Leon and Ikeda, 2005). This yielded 3- to 8-fold higher mesozooplankton respiration than previously calculated (Hernandez-Leon and Ikeda, 2005).

The actual balance between autotrophy and heterotrophy at basin scales is of a prime importance to estimate the fate of CO₂ fixation by phytoplankton. The introduction of zooplankton as a potentially important contributor brings a new dimension to the problem. Indeed, microbial and primary production as well as photorespiration operate over similar spatio-temporal scales (Bequevort *et al.*, 1992; Rivkin and Legendre, 2001; Del Giorgio and Duarte, 2002) and result in a relative concordance between causes and effects. With zooplankton, respiration is controlled at least by population density and temperature, but differences in generation time could introduce space and time lag in response. It has been shown that the time needed to achieve population build-up varies from weeks to months (Steele, 1991) and maximum recycling does not generally match the time of maximum bloom carbon fixation due to delay in a maximum grazer recruitment. The migration abilities of the majority of zooplankton would further facilitate the transport of recycled carbon from the surface to the bottom of the photic zone or even deeper (Longhurst *et al.*, 1990). It is also believed that horizontal migration could result in an integration of trophic interactions and recycling over large areas. It appears that most budgets and models to a large extent have ignored major ecosystem features such as species diversity, size and trophic characteristics of zooplankton communities as controlling factors, although there is evidence that autotrophy and heterotrophy in ecosystems is related to the food web structure (Rivkin *et al.*, 1996; Gasol *et al.*, 1997; Pakhomov *et al.*, 2000; Pakhomov and Froneman, 2004).

The Southern Ocean may provide a promising polygon to allow reconstruction of mesozooplankton

respiration budgets at the basin scale because of the strong latitudinal gradient in zooplankton populations, its relatively high biomass and in some areas extended detailed work on the zooplankton community characteristics (e.g. Pakhomov *et al.*, 2000; Mayzaud *et al.*, 2002a, b; Pakhomov and Froneman, 2004). The main aims of this paper are 2-fold: first, to estimate the magnitude of the carbon recycling by Antarctic meso- and macrozooplankton using basin-scale zooplankton data; and second, to assess the effects of species and functional diversity on carbon cycling at the community level.

METHOD

Data on zooplankton composition and respiration were collected in the Atlantic and Indian sectors of the Southern Ocean during various cruises in the late 90s, i.e. ANTARES cruises in February–March 1994 (ANTARES 2, A2) and October 1995 (ANTARES 3, A3) along the 70° E longitude and SAAMES cruises in January–February 1993 and December 1997 to January 1998 along the 0° (SAAMES V70) and 6° E (SAAMES V86) longitude, respectively (Errhif, 1998; Errhif *et al.*, 1997; Pakhomov *et al.*, 2000; Mayzaud *et al.*, 2002a, b; Pakhomov and Froneman, 2004). Zooplankton were collected either with a 200 µm (ANTARES) or 300 µm (SAAMES) mesh net in the upper 300 m. The zooplankton data would thus represent a larger portion of the mesozooplankton assemblage. Zooplankton taxa were identified to the species level but, with the exception of copepods, combined into major taxonomic categories (ostracods, amphipods, euphausiids, pteropods, salps and chaetognaths) for the purpose of this study. More detailed definition at the species and copepodite stage level was retained for copepods, which dominated the planktonic communities. To achieve more realistic zooplankton community oxygen consumption rates, all groups were resolved according to their size (total length) and density was represented as abundance. Detailed information on the sampling protocols as well as zooplankton community structure and biomass can be found in Errhif (Errhif, 1998), Pakhomov *et al.* (Pakhomov *et al.*, 2000), Pakhomov and Froneman (Pakhomov and Froneman, 2004) and Mayzaud *et al.* (Mayzaud *et al.*, 2002a, b).

Respiration measurements

Detailed methods of the respiration rate measurements are presented in Mayzaud *et al.* (Mayzaud *et al.*, 2002a, b). Briefly, individuals were sorted to species and stage levels and kept in a cold room adjusted to seawater temperature ranging from 2 to 8°C. Animals were then placed in

experimental chambers filled with filtered and oxygenated (saturated) seawater. Animal density was kept to $\sim 400 \text{ ind}^{-1} \text{ L}^{-1}$ for the smaller species (*Oithona* or *Ctenocalanus*) and $20\text{--}40 \text{ ind}^{-1} \text{ L}^{-1}$ (3–6 per 150 mL) for larger copepod species (*Calanus propinquus* or *Rhincalanus gigas*). Control chambers without animals were used to monitor possible oxygen changes during incubations. Incubations were made under darkness for periods varying for $\sim 15\text{--}24 \text{ h}$ at $2\text{--}4^\circ\text{C}$ and 12 h at $6\text{--}8^\circ\text{C}$. Oxygen concentration was monitored using a Strathkelvin oxygen meter equipped with a Clark-type electrode. Experimental animals were preserved for length and/or weight measurements. Values of individual biomass of each species were obtained from both direct measurement or literature data (see Conover and Huntley, 1991). When specific dry weights were not available, values were computed from the relationship between size and weight for that species (Cohen and Lough, 1981; Uye, 1982; Kubjeweit, 1993; Webber and Roff, 1995).

In total, direct measurements were obtained for 13 different species including *Calanoides acutus*, *C. propinquus*, *Calanus*

simillimus, *Candacia maxima*, *Clausocalanus laticeps*, *Ctenocalanus citer*, *Euchirella rostromagna*, *Metridia lucens*, *Oncaea antarctica*, *Pareuchaeta antarctica*, *Pareuchaeta* spp., *Pleuromamma robusta* and *Rhincalanus gigas*. Usually, three different copepodite stages were considered (from copepodite 4 (C4) to adult). Measurements were made in triplicate. Mean values for all species and stages were used to compute the regression between dry weight and respiratory rates. The resulting relationship as a function of dry weight was

$$\begin{aligned} \log \text{Resp} (\mu\text{LO}_2 \text{ ind}^{-1} \text{ day}^{-1}) \\ = 0.78 \pm 0.018 \log \text{DW} + 1.28 \pm 0.016 \\ (R^2 = 0.988). \end{aligned}$$

This relationship was used in the copepod budget computation. For other groups, published length–dry weight and respiration–dry weight relationships were used (Table I). When needed, corrections for temperature difference between measurements and *in situ* were made assuming a Q_{10} of 2 (Hochachka and Somero, 1984).

Table I: Allometric relationships in Antarctic zooplankton taxonomic groups

Taxonomic group	Parameters	Allometric relationship	References
Ostracoda	Length/weight (mm)/(mg) Respiration/weight ($\mu\text{LO}_2 \text{ ind}^{-1} \text{ h}^{-1}$)/(mg)	$\log \text{DW} = 1.65 \log(L) + 1.93$ $\log R = 0.79 \log \text{DW} - 2.89$	Shmeleva (1965) Kaeriyama and Ikeda (2004)
Pteropoda			
<i>Clione</i> sp.	Length/weight (mm)/(μg) Respiration/weight ($\mu\text{LO}_2 \text{ ind}^{-1} \text{ day}^{-1}$)/(mg)	$\log \text{DW} = 2.109 \log(L) - 1.744$ $\log R = 0.703 \log \text{DW} - 0.882$	Conover and Lalli (1972) Conover and Lalli (1974)
<i>Limacina</i> sp.	Length/weight (mm)/(mg) Respiration/weight ($\mu\text{LO}_2 \text{ ind}^{-1} \text{ day}^{-1}$)/(mg)	$\log \text{DW} = 3.538 \log(L) - 1.575$ $\log R = 0.846 \log \text{DW} + 0.346$	Conover and Lalli (1972) Ikeda and Hing-Fay (1981)
Polychaeta	Length/weight (mm)/(mg) Respiration/weight ($\mu\text{LO}_2 \text{ ind}^{-1} \text{ day}^{-1}$)/(mg)	$\log \text{DW} = 1.8199 \log(L) - 2.175$ $\log R = 0.879 \log \text{DW} + 1.175$	Mizdalski (1988) Ikeda and Hing-Fay, (1981) Ikeda and Mitchell, (1982) Hirche (1984)
Amphipoda			
Hyperidae	Length/weight Respiration/weight ($\mu\text{LO}_2 \text{ ind}^{-1} \text{ h}^{-1}$)/(mg)	$\log \text{DW} = 2.969 \log(L) + 2.589$ $\log R = 0.502 \log \text{DW} + 0.418$	Mayzaud (unpublished data) Ikeda and Mitchell (1982) Donnelly <i>et al.</i> (2004)
Euphausiacea			
<i>Euphausia superba</i>	Length/weight Respiration/weight ($\mu\text{LO}_2 \text{ ind}^{-1} \text{ h}^{-1}$)/(mg)	$\log \text{WW} = 3.389 \log(L) - 2.413$ $\log R = 0.969 \log \text{WW} - 0.955$	Farber-Lorda (1994) Ikeda and Mitchell, (1982)
Larval krill	Respiration ($\mu\text{LO}_2 \text{ ind}^{-1} \text{ day}^{-1}$)	Value per stage	Ikeda (1981)
<i>Thysanoessa</i>			
Juveniles	Length/weight Respiration/weight ($\mu\text{LO}_2 \text{ ind}^{-1} \text{ h}^{-1}$)/(mg)	$\log \text{WW} = 2.83 \log(L) - 1.72$ $\log R = 1.369 \log \text{DW} + 0.799$	Mayzaud <i>et al.</i> (2003) ^a Ikeda and Hing-Fay, (1981)
Salpidae			
<i>Salpa thompsoni</i>	Length/weight (mm)/(mg) Respiration/weight ($\mu\text{LO}_2 \text{ ind}^{-1} \text{ h}^{-1}$)/(mg)	$\log \text{DW} = 2.204 \log(L) - 1.223$ $\log R = 0.736 \log \text{DW} - 0.442$	Huntley <i>et al.</i> (1989) Ikeda and Mitchell (1982)
Chaetognatha			
<i>Eukrohnia hamata</i>	Length/weight (mm)/(mg)	$\log \text{DW} = 4.063 \log(L) - 5.345$	Mizdalski (1988)
<i>Sagitta gazellae</i>	Length/weight (mm)/(mg) Respiration/weight ($\mu\text{LO}_2 \text{ ind}^{-1} \text{ h}^{-1}$)/(mg)	$\log \text{DW} = 3.566 \log(L) - 5.074$ $\log R = 0.885 \log \text{WW} - 2.00$	Mizdalski (1988) ^b
<i>Sagitta marri</i>	Length/weight (mm)/(mg)	$\log \text{DW} = 3.466 \log(L) - 4.448$	Ikeda and Kirkwood (1989)
<i>Sagitta elegans</i>	Respiration/weight ($\mu\text{LO}_2 \text{ ind}^{-1} \text{ h}^{-1}$)/(mg)	$\log R = 0.868 \log \text{DW} - 0.391$	Mizdalski (1988) Welch <i>et al.</i> (1996)

^a*Thysanoessa* conversion from WW to DW assumes 75% water content.

^b*S. gazellae* conversion WW to DW assumes 92% water content.

Transformation of respiration from oxygen to CO₂ was performed in two steps:

$$\text{Resp}_{\text{tot}}(\text{mgC m}^{-2} \text{ day}^{-1}) = \frac{\text{Resp}(\text{mL O}_2 \text{ m}^{-2} \text{ day}^{-1}) \times RQ \times 12}{22.4},$$

$$\text{Resp}_{\text{tot}}(\text{mmol CO}_2 \text{ m}^{-2} \text{ day}^{-1}) = \frac{\text{Resp}_{\text{tot}}(\text{mgC m}^{-2} \text{ day}^{-1})}{12}.$$

Biological diversity

For the species diversity assessment three indices were employed: (i) species richness (D_{Mn} , Whittaker, 1977) as a number of species with a contribution to the CO₂ respiration larger than 0.01 mol m⁻² day⁻¹, (ii) Shannon diversity index H' (Pielou, 1969) and (iii) Pielou evenness measure J' (Pielou, 1969, 1975). When indices were calculated, in addition to species level, various growth stages of key species and size classes of taxonomic groups were included to achieve maximum functional diversity. This was justified because the database illustrated snapshots at different periods where spatial heterogeneity exceeded short-term seasonal changes.

Statistical analyses

A multifactorial approach with multiple correspondence analysis (MCA) was employed to identify major factors controlling changes in population densities during all four cruises. MCA is an ordination method concerned with multivariate sampling of categorical variables, widely used for the analysis of ecological data (Gower, 1987). Contrary to other ordination methods, MCA describes at minima the total inertia of a multidimensional data set with fewer dimensions or axes. This represents the best integration of the information contained in the data set. Among inertia methods, MCA is concerned with contingency tables of categorical variables and uses χ^2 distances.

The original data set comprised 94 cases (total samples) described by 11 variables. The variables represent a full description of the functional groups and the associated sampling (date, latitude). All variables were disjointed and coded to transform into categorical variables, as shown in Table II. The biological variables (taxonomic categories) were considered as “active” and used in the calculation of the factorial axes. The other variables, which are descriptive, were projected as “supplementary” variables into the space defined by the axes.

The informative value of an “active” modality was expressed by its contribution to the axes and planes and its correlation with them. Computation was made using SPAD 5.5 software.

The relationships between changes in the zooplankton structure, CO₂ respiration rates and diversity were assessed by cluster analysis using the Bray and Curtis similarity index and un-weighted pair group average linkage (Pielou, 1984). Computation was made using the Primer 6 software package (Clarke and Gorley, 2006). Differences between trophic types was tested by ANOVA multiple comparison using the Statgraphics XVI software.

To evaluate the relative influence of the different population descriptors controlling community respiration, a hierarchical classification using the similarity index of Bray and Curtis (Pielou, 1984) was used on the entire data set. Respiration rates (CO₂ production) of both copepods and total populations with (i) the number of species in each taxonomic group (S) and (ii) the individual density in each taxonomic group (N) and three biodiversity indices: Shannon (H'), Evenness (J') and Equity (E) were compared.

RESULTS

Spatial changes in the zooplankton structure

Pooling all data on zooplankton abundance illustrated the global trend common to the Indian basin of the Southern Ocean and adjacent waters. A general north–south decrease in zooplankton abundance appeared to be the dominant feature (Axis 1, Level 1 versus Level 3), and was independent of the season and geographic location of sampling, with maximum values observed at the Polar Front Zone (PFZ, Fig. 1). The second axis is representative of the non-crustacean groups with a gradient between medium densities of polychaetes, salps and pteropods (level 2) and the high densities of polychaetes and pteropods (level 3). This was largely associated with differences between the late winter ANTARES 3 cruise and early autumn SAAMES V86 cruise. Axis 2 also singled out the frontal structures with latitude level of 5–8 (Antarctic Divergence, AD and Subtropical Front, STF, Table II).

The relationship between spatial changes in densities and north–south latitudinal gradient is illustrated by plotting the contribution on the first axis versus latitude (Fig. 2). During at least three voyages, the clear gradient from maximum zooplankton abundance in the PFZ (45° S) to minimal zooplankton abundance at the Continental shelf area (70° S) was only interrupted by two hot spots in zooplankton density associated with the Winter Ice Edge (WIE) ~57° S and the AD ~65° S (Fig. 3A, C and D).

Table II: Coding of taxonomic group and sampling conditions into categorical variables

Variables	Level	Code	Range	Number
Date (months)	1	Date 1	October	14
	2	Date 2	January	64
	3	Date 3	February–March	16
Latitude (°S)	1	Lat 1	45° < lat < 51°	20
	2	Lat 2	51° < lat < 57°	39
	3	Lat 3	60° < lat < 66°	22
	4	Lat 4	>66°	2
	5	Lat 5	AD	2
	6	Lat 6	STF	1
	7	Lat 7	APF	2
	8	Lat 8	WIE	6
Temperature (°C)	1	Temp 1	4–7°C	7
	2	Temp 2	2–4°C	25
	3	Temp 3	–2 to 2°C	58
Copepoda (ind m ⁻²)	1	V Cop 1	0–12 000	32
	2	V Cop 2	12 000–39 000	32
	3	V Cop 3	>39 000	30
Amphipoda (ind m ⁻²)	1	Vamph 1	0	36
	2	Vamph 2	1–68	29
	3	Vamph 3	>68	29
Chaetognatha (ind m ⁻²)	1	Vchae 1	<650	32
	2	Vchae 2	650–1500	32
	3	Vchae 3	>1500	30
Ostracoda (ind m ⁻²)	1	Vost 1	0–160	31
	2	Vost 2	160–710	32
	3	Vost 3	>710	31
Euphausiidea (ind m ⁻²)	1	Veuph 1	0–160	29
	2	Veuph 2	160–550	33
	3	Veuph 3	>550	32
Pteropoda (ind m ⁻²)	1	Vptero 1	0–7	32
	2	Vptero 2	8–150	30
	3	Vptero 3	>150	32
Polychaeta (ind m ⁻²)	1	Vtomo 1	0	31
	2	Vtomo 2	1–80	31
	3	Vtomo 3	>80	32
Salpidae (ind m ⁻²)	1	Vsalp 1	0	48
	2	Vsalp 2	1–65	23
	3	Vsalp 3	>65	23
Non-cop total (ind m ⁻²)	1	Vncop 1	0–1900	32
	2	Vncop 2	1901–4000	31
	3	Vncop 3	>4000	33

Only late winter cruise (A3) showed an opposite pattern in abundance distribution although it ended at the northern part of the Seasonal Ice Zone (SIZ, Fig. 3B). The lack of relationship with either date or cruise (longitude) confirmed that irrespective of the season or the area considered, the dominant factor is the latitudinal spatial heterogeneity.

In terms of taxonomic diversity, 10–15 species of copepods made up the bulk of the abundance and the respiratory activity (Table III) followed in decreasing order by species of ostracods, euphausiids, salps, amphipods and chaetognaths. The change in population density is not the only potential driver of community metabolism and from north to south a strong change in diversity as expressed by the Shannon index was also observed (Fig. 3). Although population densities showed a decreasing trend from the Polar Front and open ocean zones to

the Antarctic shelf in all summer cruises and the opposite in late winter, diversity appeared to vary in somewhat the opposite way suggesting that hot spots of biomass corresponded to communities of lower diversity (Fig. 3). Hence, besides zooplankton biomass, the spatial heterogeneity should also be included in species assemblage changes.

Changes in CO₂ respiration rates

Daily depth-integrated CO₂ production (Fig. 4) only loosely followed changes in biomass (Fig. 3) with values ranging from 0.1 to 29 mmol m⁻². Regions of high density at the Antarctic Polar Front (APF), WIE and AD corresponded to a maximum CO₂ production by the zooplankton community with many locations nevertheless failing to show a strong correspondence between abundance

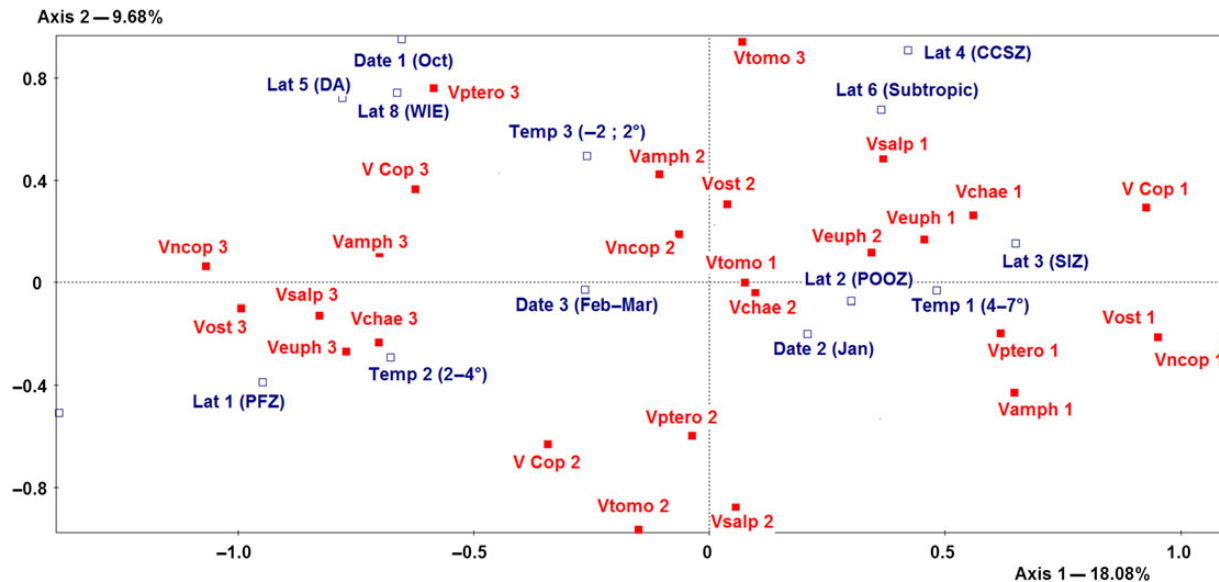


Fig. 1. Multiple correspondence analysis (MFC) of population densities for the Indian basin of the Southern Ocean and adjacent waters. The figure shows the ordination of variables in the plane of Axis 1 and 2 (27.8% of the total inertia). For coding of active (filled squares) and supplementary variables (empty squares) see Table II. Level 1—blue; Levels 2 and 3—red.

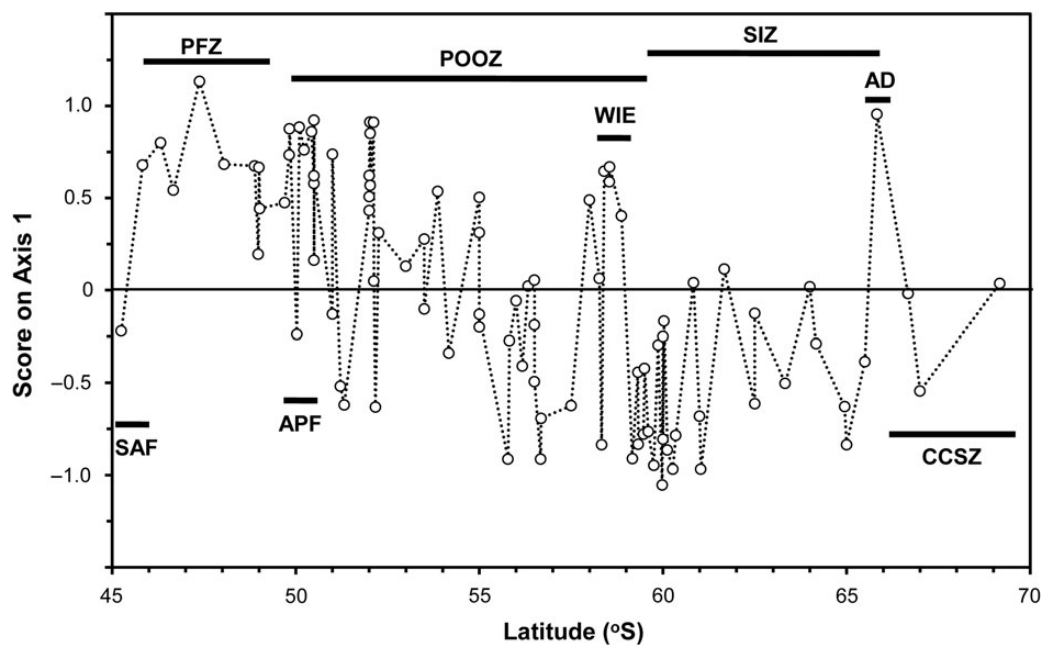


Fig. 2. Projection of factor scores from MFC on Axis 1 to illustrate the relationship between spatial changes and latitudinal gradient. SAF, Subantarctic Front; APF, Antarctic Polar Front; WIE, Winter Ice Edge; AD, Antarctic Divergence; CCSZ, Coastal and Continental Shelf Zone; PFZ, Polar Front Zone; POOZ, Permanent Open Ocean Zone; SIZ, Seasonal Ice Zone.

and the metabolic output. A clear influence of the season and/or cruise was evident from latitudinal profiles (Fig. 4). The lower variability ($0.1\text{--}9.3 \text{ mmol CO}_2 \text{ m}^{-2} \text{ day}^{-1}$) was recorded in spring, early autumn and late winter during the ANTARES (A2 and A3) and SAAMES V86 cruises (Fig. 4A, B and D), while maximum range

($1.2\text{--}29.2 \text{ mmol CO}_2 \text{ m}^{-2} \text{ day}^{-1}$) was observed during mid-summer SAAMES V70 voyage (Fig. 4C).

The role of zooplankton in carbon cycling varied with the level of primary production and the season considered (Table IV). It was negligible during the spring maximum production with only 3–11% of primary

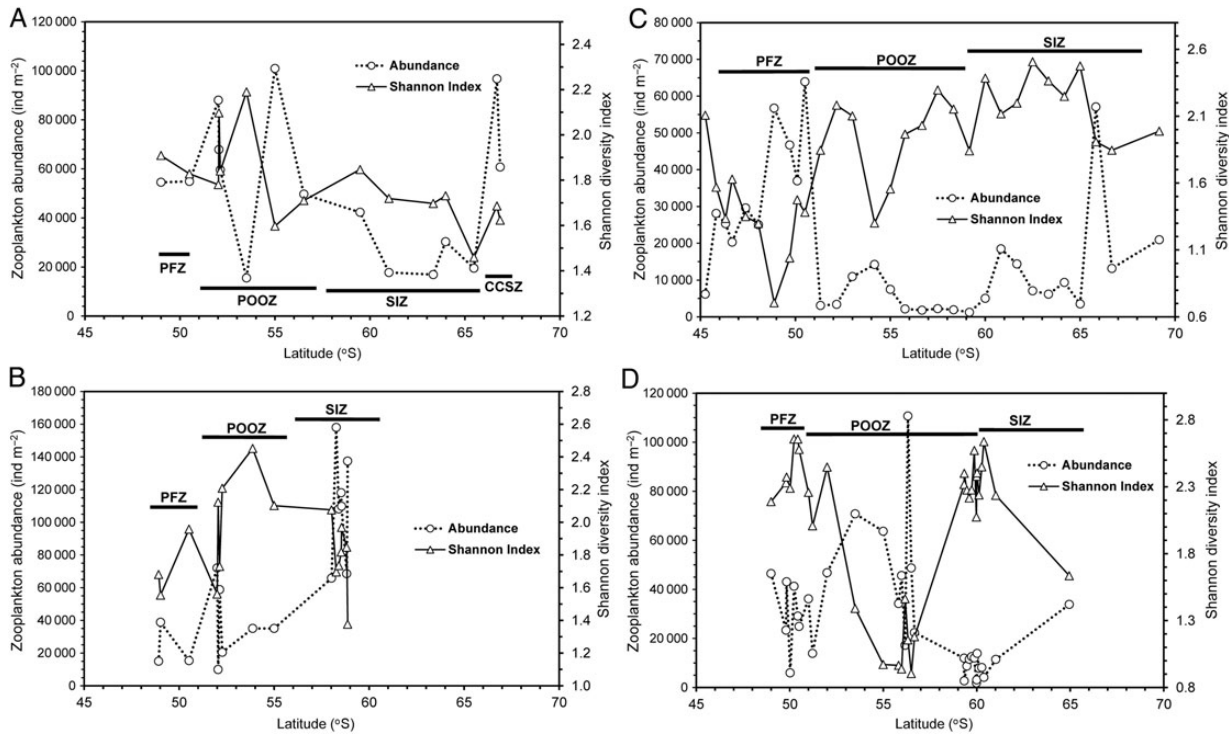


Fig. 3. Changes in zooplankton densities and Shannon index (H') for each cruise in relation to the north–south gradient. (A) ANTARES 2 (A2), February–March 1994, 70° E; (B) ANTARES 3 (A3), October 1995, 70° E; (C) SAAMES V70, January–February 1993, 0° E; (D) SAAMES V86, December 1997–January 1998, 6° E. Polar Front Zone, POOZ, Permanent Open Ocean Zone; SIZ, Seasonal Ice Zone; CCSZ, Coastal and Continental Shelf Zone.

Table III: Copepod species diversity constitutive of the zooplankton communities recorded during the four Antarctic cruises

ANTARES 2	ANTARES 3	SAAMES V70	SAAMES V86
<i>Calanoides acutus</i>	<i>C. acutus</i>	<i>C. acutus</i>	<i>C. acutus</i>
<i>Calanus propinquus</i>	<i>C. propinquus</i>	<i>C. simillimus</i>	<i>C. simillimus</i>
<i>Calanus simillimus</i>	<i>C. simillimus</i>	<i>C. propinquus</i>	<i>C. propinquus</i>
<i>Rhincalanus gigas</i>	<i>Drepanopus pectinatus</i>	<i>R. gigas</i>	<i>R. gigas</i>
<i>Metridia lucens</i>	<i>R. gigas</i>	<i>Metridia</i> spp.	<i>M. gerlachei</i>
<i>M. gerlachei</i>	<i>M. lucens</i>	<i>C. laticeps</i>	<i>M. lucens</i>
<i>Clausocalanus laticeps</i>	<i>M. gerlachei</i>	<i>Ctenocalanus</i> spp.	<i>Clausocalanus breviceps</i>
<i>Ctenocalanus citer</i>	<i>C. laticeps</i>	<i>Paraeuchaeta</i> spp.	<i>Ctenocalanus</i> spp.
<i>Paraeuchaeta</i> spp.	<i>C. citer</i>	<i>Oithona</i> spp.	<i>Paraeuchaeta</i> spp.
<i>Oithona frigida</i>	<i>Paraeuchaeta</i> spp.	<i>Oncaea</i> spp.	<i>O. similis</i>
<i>O. similis</i>	<i>O. frigida</i>	<i>Scolecithricella</i> spp.	<i>O. frigida</i>
<i>Oncaea antarctica</i>	<i>O. similis</i>	<i>E. rostromagna</i>	<i>Oncaea</i> spp.
<i>Microcalanus pigmaeus</i>	<i>O. antarctica</i>	<i>Candacia</i> sp.	<i>Scolecithricella</i> spp.
<i>Scolecithricella minor</i>	<i>M. pigmaeus</i>		<i>E. rostromagna</i>
<i>Pleuromamma robusta</i>	<i>S. minor</i>		<i>Microcalanus</i> spp.
<i>Euchirella rostromagna</i>	<i>P. robusta</i>		<i>Candacia</i> sp.
	<i>E. rostromagna</i>		<i>Heterorabdus austrinus</i>
			<i>Pleuromamma abdominalis</i>

production respired. However, outside maximum production periods zooplankton recycling could account for ~30% to over 100% of daily primary production respired. Maximum recycling also coincided with high zooplankton densities in January–February. Indeed, the

highest values were clearly associated with frontal zones (zooplankton density hotspots) and the PFZ.

The cluster analysis was performed to evaluate potential relationships between density (abundance), respiration and diversity (Fig. 5). The analysis effectively linked

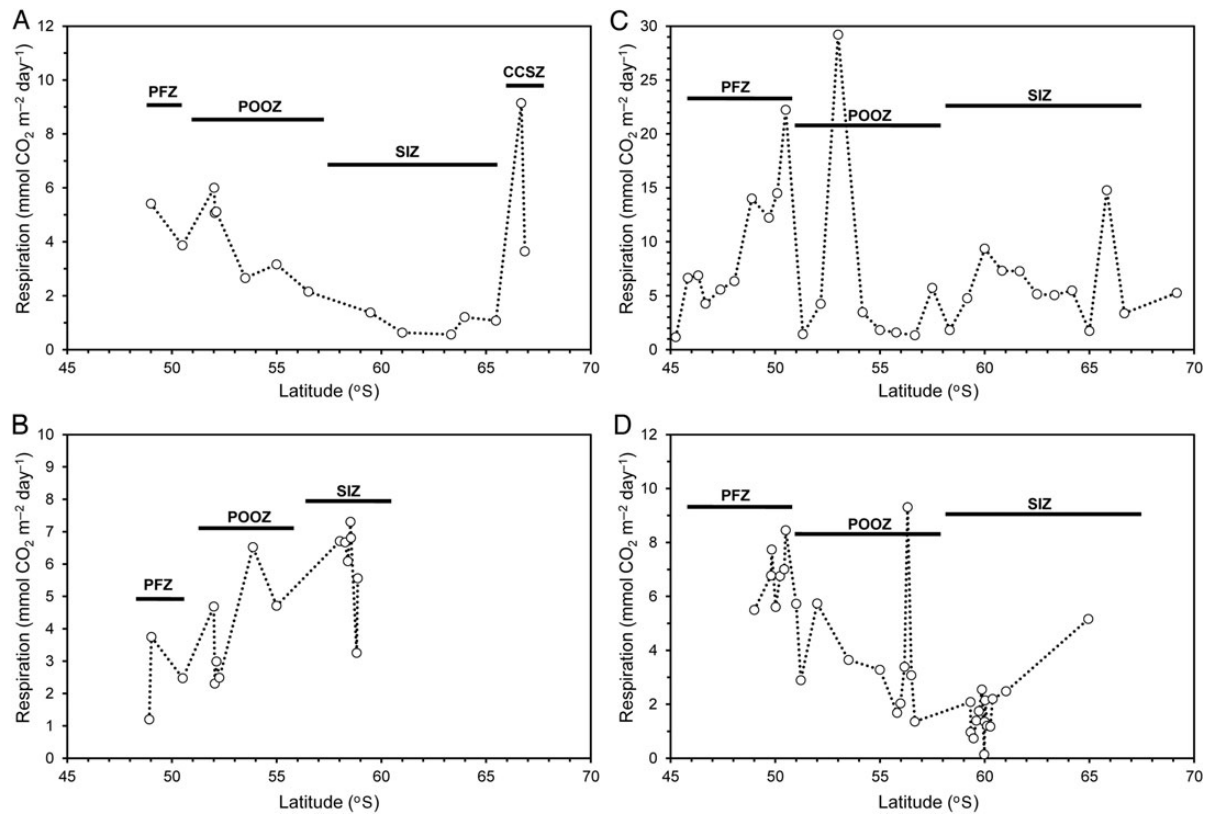


Fig. 4. Changes in total population CO₂ produced respiration rates for each cruise in relation to the north–south gradient. **(A)** ANTARES 2 (A2), February–March 1994, 70° E; **(B)** ANTARES 3 (A3), October 1995, 70° E; **(C)** SAAMES V70, January–February 1993, 0° E; **(D)** SAAMES V86, December 1997–January 1998, 6° E. Polar Front Zone, POOZ, Permanent Open Ocean Zone; SIZ, Seasonal Ice Zone; CCSZ, Coastal and Continental Shelf Zone.

Table IV: Zooplankton community respiration in relation to total measured primary production (¹⁴C based)

Cruise	Oceanic zone	Latitude (°S)	Period	Primary production	Respiration (mgC m ⁻² day ⁻¹)	Respiration % primary production
ANTARES 3	PFZ	48–50°	October	122.4	37.1 ± 10.8	30.5 ± 8.9
	POOZ	52–55°	–	123.2	47.4 ± 19.7	40.3 ± 19.8
	SIZ/WIE	58–59°	–	241.2	72.7 ± 16.2	30.1 ± 7.2
SAAMES V86	APF	49–51°	December–January	800.0	55.6 ± 13.7	6.9 ± 1.1
	WIE	56°30'	–	305.4	33.9	11.1
	SIE	60°30'	–	601.2	17.1 ± 8.8	2.8 ± 0.9
SAAMES V70	PFZ	46–48°	January–February	156.7	109.8 ± 7.3	96.9 ± 74.0
	APF	49–50°	–	217.5	234.2 ± 2.7	113.6 ± 37.4
	POOZ	51–59°	–	89.2	47.8 ± 31.2	53.3 ± 33.7
	SIZ	60–66°	–	197.5	49.7 ± 27.7	27.6 ± 16.5
ANTARES 2	PFZ	49–50°	February–March	104.2	55.7 ± 13.1	53.4 ± 12.6
	POOZ	52–56°	–	104.2	49.0 ± 17.1	47.1 ± 16.6
	SIZ	59–65°	–	106.7	11.6 ± 4.2	10.9 ± 4.0
	CCSZ	66–67°	–	106.1	77.3 ± 45.7	72.9 ± 43.1

PFZ, Polar Front Zone; POOZ, Permanent Open Ocean zone; WIE, Winter Ice Edge; SIE, Seasonal Ice Edge; SIZ, Seasonal Ice Zone; CCSZ, Continental Coastal Shelf Zone.

the zooplankton metabolic outputs to the diversity indices and to a lesser extent to the total number of species either in the community (S_{tot}) or in the copepod

subgroup (S_{cop}). The latter was expected because copepods dominated in terms of the species number. Interestingly, the community respiration was weakly

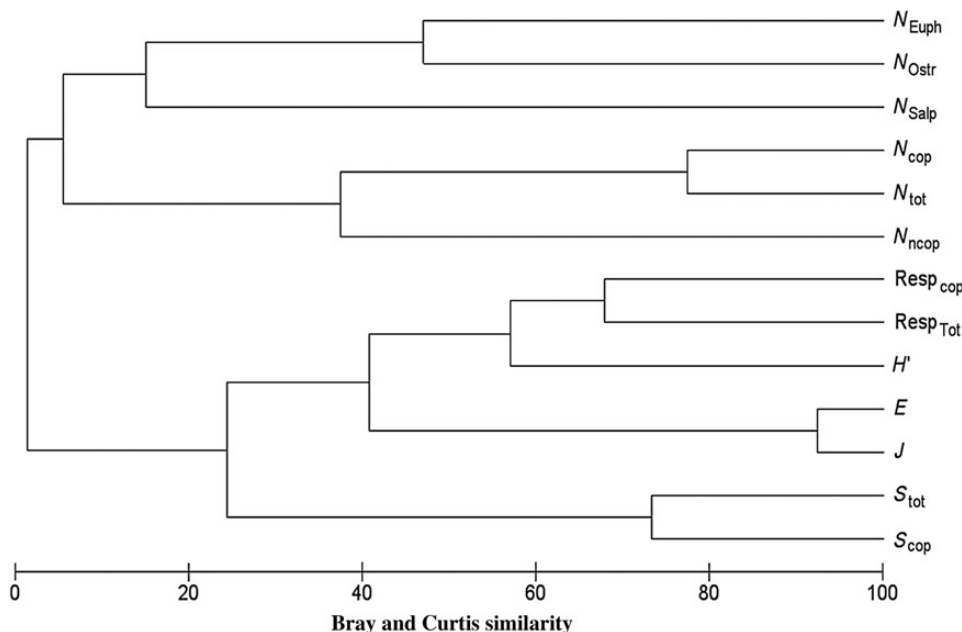


Fig. 5. Cluster analysis based on the Bray and Curtis similarity index on main taxa densities (N), total number of species (S) for copepod and total community, respiration rates of copepod ($Resp_{cop}$) and total population ($Resp_{tot}$) and diversity indices: H' (Shannon), E (Equity), J (Evenness).

related to the abundance descriptors (N) of total zooplankton community and/or various groups by composing a separate cluster association (Fig. 5). If salps are omitted from the analysis, all taxonomic groups cluster together in a separate cluster at a relatively high value of the Bray–Curtis index. A 3D plot of CO_2 respiration against both population densities and diversity (Shannon H' index) illustrated such complexity, because respiratory rates appeared to be both density and diversity-dependent (Fig. 6). The increase in CO_2 production did not, however, show a linear relationship with zooplankton density, but it was rather a unimodal distribution with the maximum respiration rates at the highest diversity and medium population density levels (Fig. 6).

Since an alternate source of variability could potentially be the trophic status of the species constituting the communities, different trophic types were defined. Trophic types were identified using the stable isotope definition given by Schmidt *et al.* (Schmidt *et al.*, 2003) for copepods and euphausiids and by conventional methods for pteropods (Lalli and Gilmer, 1989). Analysis of combined data revealed that herbivorous species displayed significantly higher respiration rates compared with omnivorous and carnivorous species (Table V). However, when cruises were considered separately, the higher rates of herbivores remained significant only for the late winter–early spring ANTARES 3 and mid-summer SAAMES V70 cruises. The lack of significance for the other two cruises may reflect an enhanced variability related to

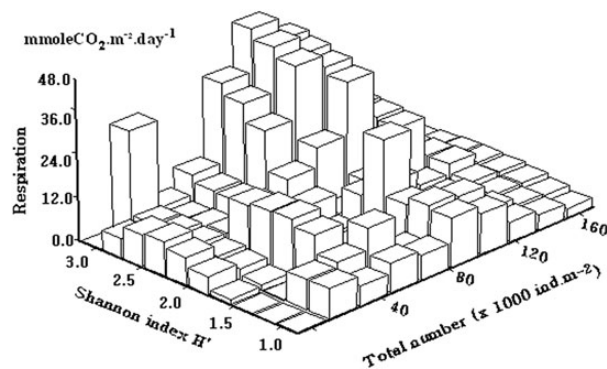


Fig. 6. 3D cubic smoothing spline bar plot of CO_2 respiration rates, population densities and Shannon index H' .

incomplete definition of the group's trophic status because ontogenic shifts in the diet were not considered.

DISCUSSION

Open ocean respiration as an estimation of CO_2 production remains largely limited to primary producers and to lesser extent to heterotrophic bacteria (see review by Del Giorgio and Duarte, 2002). The contribution of meso- and macrozooplankton is largely unknown and was extrapolated assuming that it represents 10% of the total community respiration (Del Giorgio and Duarte, 2002). Alternatively, the modelling exercise of the Southern Ocean ecosystem by Huntley *et al.* (Huntley *et al.*, 1991)

Table V: Results of the ANOVA multiple comparison test between trophic types for CO₂ respiration

Trophic type	N	Mean	Differences	F test	P
Pooled cruises					
Herbivores	110	4.39 ± 0.54	H versus O, C*	F _{2, 329} = 3.69	0.026
Omnivores	110	2.56 ± 0.54			
Carnivores	110	2.41 ± 0.54			
ANTARES 2					
Herbivores	16	2.01 ± 1.49	NS	F _{2, 47} = 0.76	0.47
Omnivores	16	3.65 ± 1.49			
Carnivores	16	1.07 ± 1.49			
ANTARES 3					
Herbivores	16	2.88 ± 0.26	H versus C*** O versus H*** C versus O, NS	F _{2,47} = 16.67	0.0001
Omnivores	16	0.82 ± 0.26			
Carnivores	16	1.41 ± 0.26			
SAAMES V70					
Herbivores	30	5.29 ± 0.76	H versus C** O versus H** C versus O, NS	F _{2, 89} = 6.48	0.002
Omnivores	30	1.72 ± 0.76			
Carnivores	30	2.22 ± 0.76			
SAAMES V86					
Herbivores	48	4.90 ± 1.03	NS	F _{2, 143} = 0.81	0.44
Omnivores	48	3.29 ± 1.03			
Carnivores	48	3.30 ± 1.03			

H, herbivores; O, omnivores; c, carnivores; N, number of cases. P value for the pair: * - <0.05; ** - <0.01; *** - <0.001.

concluded that zooplankton may consume as much as 95% and respire back ~34% of the total primary production. This constituted ~52% of total respiration of other model oxygen consuming compartments (Huntley *et al.*, 1991). Considering, that at a basin scale, primary consumer respiration may exceed primary production in many instances (Del Giorgio *et al.*, 1997; Duarte and Agusti, 1998; Harrison *et al.*, 2001), it becomes important to provide some real estimates of the larger size plankton respiration and ascertain the different sources of control.

The Southern Ocean is a unique habitat with a limited range of temperature changes both spatially and seasonally as well as predictable biological structure associated with the various frontal systems (Jacques and Treguer, 1986). The present study is focussed on the Atlantic and the Indian sectors of the Southern Ocean from the northern boundary of the Antarctic Ocean, PFZ, to the Coastal and Continental Shelf Zone (CCSZ) covering a significant part of the active biological season (late winter to autumn). The main feature of the Southern Ocean is the proportionally higher contribution of major frontal regions to the total plankton productivity (Allanson *et al.*, 1981; El Sayed, 1988; Laubscher *et al.*, 1993; Keith Moore and Abbott, 2000) and to the standing stocks of mesozooplankton and micronekton (Pakhomov *et al.*, 1994, 1999, 2000; Pakhomov and McQuaid, 1996). Hot spots of both increased primary production and zooplankton accumulation are also linked to the frontal regions associated with the WIE and AD (Cockcroft *et al.*, 1990; Pakhomov *et al.*, 2000). These features were evident during all seasons, all years and for all locations (longitude). This conclusion, however, should be

viewed with caution as it may directly be linked to the scale of the observation. Smaller east–west sampling scales could show different degrees of variability for the different taxa (Swadling *et al.*, 2010).

To our knowledge, only a few attempts have been made to date to quantify the CO₂ production aspect of plankton respiration either at individual or population levels (Raymont and Krishnaswamy, 1968; Rakusa-Suszczewski *et al.*, 1976; Kremer, 1977; Mayzaud *et al.*, 2005). Data obtained in the present study using oxygen consumed and the RQ values from Mayzaud *et al.* (Mayzaud *et al.*, 2005) agree with direct CO₂ estimates, e.g. 0.5–33 μLCO₂ ind⁻¹ day⁻¹, for copepods from the temperate Atlantic (Mayzaud *et al.*, 2005) compared with 0.5–40 μLCO₂ ind⁻¹ day⁻¹ for copepods from the present study. However, integrated estimates over the entire water column and at a basin scale have never been attempted and further comparison is difficult.

Among the factors controlling integrated CO₂ production, temperature, population densities, seasonal and spatial heterogeneity (longitude and latitude) are known to affect rate measurements. Under present conditions, correspondence analyses showed that when the time and space scales are considered, temperature and longitude did not significantly affect the overall plankton CO₂ budget. Latitudinal variability dominated over the other factors and is usually linked to both population densities and population structure (Mayzaud *et al.*, 2002a, b). Besides, the basic assumption of a density-dependent control-linking process rates, such as grazing or respiration, and population density (Morales *et al.*, 1991; Perissinotto, 1992; Dam *et al.*, 1993; Ward *et al.*, 1995),

biodiversity has also been proposed as potentially an important factor (Irigoien *et al.*, 2004; Duffy and Stachowicz, 2006). Studies of relationships between biodiversity and ecosystem processes such as production, elemental cycling and trophic transfer have been the object of major concerns in both terrestrial and freshwater environments (Chapin *et al.*, 1997; Loreau *et al.*, 2001, 2002). This issue has, however, received little attention in the biological oceanography field although it has been the focus of some benthic ecology studies (Duarte, 2000; Emerson and Huxham, 2002; Duffy *et al.*, 2005). The study by Irigoien *et al.* (Irigoien *et al.*, 2004) partially filled this gap. This study, based on 12 different pelagic data sets concluded that diversity and biomass of zooplankton were linked through a unimodal function resulting from a balance between food limitations at low population level and selective predation at high population levels. In the present study, we also observed a complex relationship between CO₂ production and population densities and diversity (illustrated by the Shannon index) with a unimodal-type response at medium and high diversity. Relationships between diversity and ecosystem functioning are complex and there is a limited evidence that species assemblages in terrestrial ecosystems could be more productive (Tilman *et al.*, 2001; Cardinale *et al.*, 2006; Cadotte, 2013). It is thus possible that diversity–ecosystem functionality relationships are identical in both terrestrial and aquatic realms (see also Irigoien *et al.*, 2004).

Contribution of the total zooplankton respiration to our understanding of the global carbon cycle remains largely unknown although it appears to vary widely from <1% to >50% depending on the oceanic region, the level of productivity, depth and the estimation methodology (Packard and Williams, 1981; Joiris *et al.*, 1982). The actual budget of depth-integrated carbon recycled at a global ocean scale has only been attempted by Hernandez-Leon and Ikeda (Hernandez-Leon and Ikeda, 2005) and resulted in an estimate of some 13 GtC year⁻¹, with temperature and biomass being the primary mediating factors of carbon cycling. This estimate was >4-fold higher compared with the estimate of

3 GtC year⁻¹ computed by Del Giorgio and Duarte (Del Giorgio and Duarte, 2002).

At the world ocean scale from high latitude to the equator, temperature is indeed a key variable. However, since community respiration is a regional process, the spatial scale considered may result, at smaller scale, in a loss of information on the actual biological processes at work. If only the Southern Ocean is considered (Table VI), the estimates would be in excess of 0.8 and 0.23 GtC year⁻¹, respectively, for Hernandez-Leon and Ikeda (Hernandez-Leon and Ikeda, 2005) and Del Giorgio and Duarte (Del Giorgio and Duarte, 2002). In their paper, Hernandez-Leon and Ikeda (Hernandez-Leon and Ikeda, 2005) stressed that a better regional coverage of the Southern Ocean would increase the accuracy of the estimate. Assuming that the mean value during the different periods and locations is representative of average situations in the Southern Ocean our estimate of 0.6 GtC year⁻¹ falls right between the two previous estimates, though not statistically different from Hernandez-Leon and Ikeda (Hernandez-Leon and Ikeda, 2005) (Table VI). The strength of our approach is to take into account population and functional diversity and to include a great deal of the spatial heterogeneity along the longitudinal transects. It should be noted, however, that similar to all other similar studies, our values are likely to be an underestimate because the population abundance and biomass at both ends of the size spectrum are under sampled due to the use of standard nets (Galliène and Robins, 2001). This underestimation could, nevertheless, likely been compensated by the simplified assumption that all species remain active during the winter under the ice, which may overestimate the winter rate values. However, many copepod species (small cycloids and calanoids) remain active throughout winter continuing to grow and even reproducing (e.g. Atkinson, 1998; Daly, 2004; Meyer, 2012).

At such a regional scale, the amount of carbon respired can be converted into carbon ingested by the meso- and macrozooplankton. Using the trophodynamic relationships from Conover (Conover, 1978) and assuming 80%

Table VI: Epipelagic mesozooplankton carbon recycling through respiration for the Antarctic Ocean using specific respiration rates and population densities

Latitude range	Area ($\times 10^6$ km ²)	Time	Respiration (mgC m ⁻² day ⁻¹)	Global respiration (GtC year ⁻¹)	Reference
50–70 °S	43.9	October	38.30	0.61	This study
		January	28.70	0.46	This study
		January–February	98.60	0.73	This study
		February–March	32.71	0.52	This study
		Mean	49.60 \pm 24.5	0.58 \pm 0.10	This study
50–80 °S	41.05		52.80 \pm 9.71	0.80 \pm 0.20	Hernandez-Leon and Ikeda (2005)
50–70 °S				0.23 ^a	Del Giorgio and Duarte (2002)

^aValues computed using Hernandez-Leon and Ikeda (2005) ratio (0.08) of Antarctic to global ocean estimate.

assimilation efficiency to take into account the dominant feeding on heterotrophic protists, the ingestion (I) could be roughly calculated as: $I = 100R/(80 - 30)$. The calculated ingestion for the epipelagic zooplankton would then amount to $1.2 \text{ GtC year}^{-1}$. The comparison with global Antarctic primary production is difficult because of the absence of estimates at both seasonal and global scales. Here, we use two estimates: 2.7 and 1.95 GtC per annum, the first one based on extrapolating the data from Table IV (Mathot *et al.*, 1992; Laubscher *et al.*, 1993) and the second one recently obtained using remote sensing data (Arrigo *et al.*, 2008). Therefore, the Southern Ocean meso- and macrozooplankton ingestion may account for 44–62% of the regional primary production, a value quite close to the range computed by Hernandez-Leon and Ikeda (Hernandez-Leon and Ikeda, 2005).

In conclusion, carbon recycling by the Antarctic meso- and macrozooplankton has been ignored or underestimated in many studies. It represents a significant fraction of the primary production, larger than the values computed by Del Giorgio and Duarte (Del Giorgio and Duarte, 2002) but similar to the Hernandez-Leon and Ikeda (Hernandez-Leon and Ikeda, 2005) assessment. Our calculations based on the detailed community structure appear to be more realistic and show that CO_2 recycling at the global scale is not a mere function of temperature and density (abundance) of zooplankton. Both species and functional diversity influence the estimates at the community level with a contribution of a regional spatial heterogeneity linked to hydrodynamic features (frontal zones). The functional diversity further may influence carbon recycling estimates both through the trophic type and developmental stage composition.

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