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Metabolism and biomass vertical distribution of zooplankton in the Bransfield Strait during the austral summer of 2000

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Abstract

The vertical distribution (0–550 m) of zooplankton biomass, and indices of respiration (electron transfer system [ETS]) and structural growth (aminoacyl-tRNA synthetases activity [AARS]), were studied in waters off the Antarctic Peninsula during the austral summer of 2000. The dominant species were the copepod *Metridia gerlachei* and the euphausiid *Euphausia superba*. We observed a vertical krill/copepod substitution in the water column. The zooplankton biomass in the layer at a depth of 200–500 m was of the same magnitude as the biomass in the layer at a depth of 0–200 m, indicating that biomass in the mesopelagic zone is an important fraction of the total zooplankton in Antarctic waters. The metabolic rates of the zooplankton community were sustained by less than 0.5% of the primary production in the area, suggesting that microplankton or small copepods are the main food source. Neither food availability nor predation seemed to control mesozooplankton biomass. The wide time lag between the abundance peak of the dominant copepod (*M. gerlachei*) and the phytoplankton bloom is suggested to be the main explanation for the low summer zooplankton biomass observed in these waters.

The Bransfield Strait is located between the South Shetland Islands and the Antarctic Peninsula. It presents high variability in both physical conditions (e.g., mesoscale eddies and fronts; Zhou et al. 2006) and primary production rates (Basterretxea & Arístegui 1999; Varela et al. 2002; Morán et al. 2006). It is also considered to be a highly productive region for all trophic levels (Huntley et al. 1990; Zhou et al. 1994). The studies of Antarctic zooplankton have focused on estimating the impact of these organisms on the development and evolution of primary production in areas affected by strong micro- or mesoscale plankton distribution patterns, or by the influence of eddies and frontal systems, which are characteristic features of the Southern Ocean. More recently, the influence of the physical environment on zooplankton species distribution, as well as their role in energy flow, has been studied using indices of physiological processes (Bergeron et al. 1985; Schalk 1990; Drits et al. 1993; Hernández-León et al. 1999; Hernández-León et al. 2000). However, not all the variability in zooplankton biomass is explained by physical changes.

Zooplankton biomass and abundance in the Bransfield Strait have been studied during the austral spring and summer seasons (Alcaraz et al. 1998; Hernández-León et al. 1999; Hernández-León et al. 2000; Cabal et al. 2002; Calbet et al. 2005), showing a great interannual variability. Previous studies (Hernández-León et al. 1999; Hernández-León et al. 2000; Calbet et al. 2005) have reported low mesozooplankton biomass around the Antarctic Peninsula. This is probably related to predation and/or food quality, rather than to food availability. Hernández-León et al. (2000) studied the distribution of mesozooplankton biomass and metabolism in the upper 200-m layer, showing low zooplankton biomass with a rather high growth rate. Yet, zooplankton consumed less than 10% of the primary production, and a top–down effect of krill on copepods in the area was suggested. In addition, an important fraction of the biomass in these waters was found in the mesopelagic zone (below 200-m depth), as was observed in previous works on Antarctic copepods (Lancraft et al. 1989; Lancraft et al. 1991; Lopez & Huntley 1995; Pakhomov et al. 1996; Lancraft et al.

2004) and euphausiids (Hernández-León, Portillo-Hahnefeld et al. 2001; Hernández-León & Montero 2006). However, most studies to date have been focused on the upper 200-m layer. The study of biomass and diel vertical migration of the deep-water mesozooplankton (200–550-m depth) could improve our understanding of the trophic web in this region of the Southern Ocean.

The main aim of this study is to give a first insight on zooplankton biomass and metabolic rates in relation to the vertical distribution over the 0–550-m water column. We used two enzymatic methods to obtain high-resolution estimates of respiration and growth at depth. The activity of the electron transfer system (ETS; Packard 1971) was used to assess the maximum potential respiration. The aminoacyl-tRNA synthetases activity (AARS; Yebra & Hernández-León 2004) was applied as an index of the in-situ growth rate. The combined use of these methods allowed us to simultaneously study in-situ respiration and growth rates of mixed zooplankton populations inhabiting mesopelagic depths, without the need for incubation or elaborate procedures. A recent discussion of the usefulness and advantages of these biochemical methods can be found in Båmstedt (2000), Ikeda et al. (2000), Hernández-León, Almeida et al. (2001, 2002), Yebra, Harris et al. (2005), Yebra et al. (2006) and Guerra (2006). Secondarily, we seek to investigate the importance of bottom–up and top–down controls on zooplankton biomass in the Bransfield Strait. Finally, despite the short austral summer nights, we studied the plankton dynamic in the water column by day and night in an attempt to look at diel vertical migration and carbon fluxes mediated by zooplankton in the region.

Methods

Sampling

During the austral summer of 2000, from 24 January to 17 February, 10 stations were sampled on board the RV *BIO Hespérides* in the Bransfield Strait, Antarctic Peninsula (Fig. 1), using a Longhurst–Hardy Plankton Recorder (LHPR; 200-µm mesh net). The average day length was 20 h (06.00–02.00 h GMT), and darkness lasted for only 4 h (02.00–06.00 h GMT). Eight hauls were carried out by day (14.33–24.21 h GMT) and two hauls were carried out at night (03.56–04.39 h GMT), in order to study diel

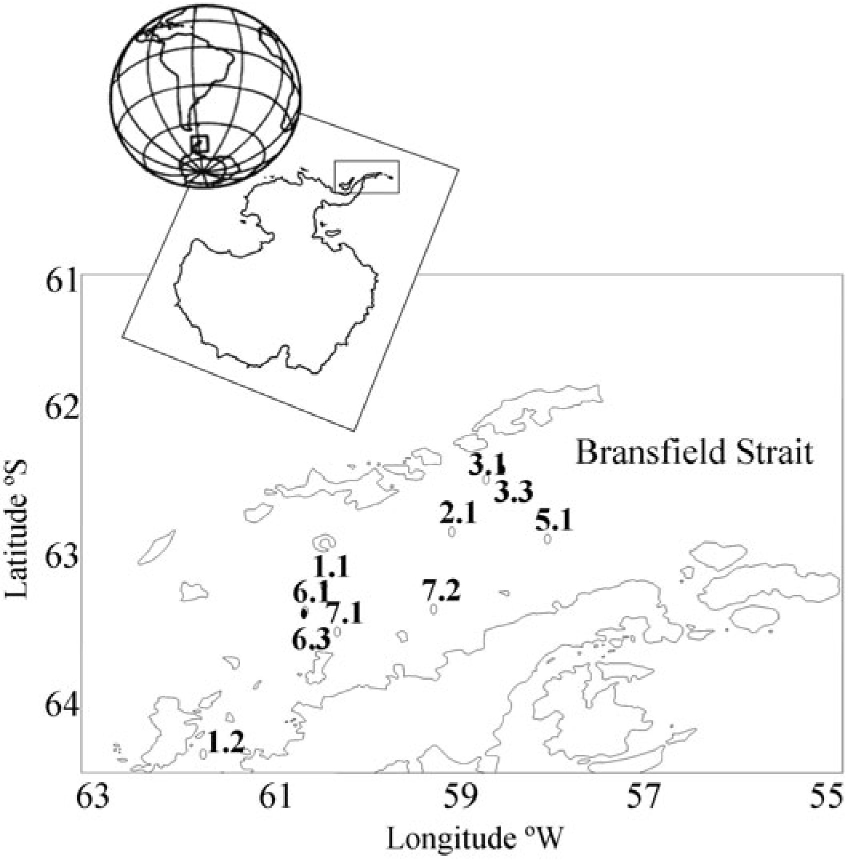

Fig. 1 Location of the Longhurst–Hardy Plankton Recorder net stations: ○, day; ●, night.

differences in biomass and metabolic profiles. Samples were collected from 550 to 0 m, at a speed of 3–4 knots. Each haul contained about 22 samples, corresponding to different layers, ranging from 13- to 24-m deep. A conductivity–temperature–depth (CTD) recorder was used to obtain high-resolution profiles of temperature, conductivity and fluorescence. On board, samples were split into two halves. One half was stored in liquid nitrogen at −196°C, for biochemical assays, and the other half was preserved in 4% formalin for presence/absence analyses of the two main groups found: euphausiids and copepods.

Biomass and metabolic rates

Frozen samples were homogenized with Tris-HCl buffer ($pH = 7.8$) before the assays. The protein content was measured using the folin dye method (Lowry et al. 1951), as modified for microanalysis by Rutter (1967). We transformed biomass, measured as protein content, to carbon, using published ratios: protein : dry weight (dw) = 0.192; carbon : dry weight = 0.40 (Postel et al. 2000).

The ETS activity was assayed using the method of Packard (1971), as modified by Gómez et al. (1996). ETS activity was corrected for the in-situ temperature at each depth using the Arrhenius equation with an activation energy of 15 kcal mol^{-1}, as given by Packard et al. (1975). AARS activity was measured using the method of Yebra & Hernández-León (2004), and was corrected for the in-situ temperature with an activation energy of 10.5 kcal mol^{-1} (Guerra 2006).

The community respiration rates (R; mg C m^{-2} h^{-1}) were assessed from specific ETS activities (µl O_2 mg $prot^{-1}$ h^{-1}) and integrated biomass (mg protein m^{-2}), assuming a respiratory quotient of 0.97 (Omori & Ikeda 1984) and a theoretical R : ETS ratio of 0.5 (Hernández-León & Gómez 1996; Ikeda et al. 2000). The community growth rates (nm PPi m^{-2} h^{-1}) were calculated from specific AARS activities (nm PPi mg $protein^{-1}$ h^{-1}) and integrated biomass (mg protein m^{-2}). We assessed the community potential ingestion (I; mg C m^{-2} h^{-1}) from respiration rates (R), assuming an assimilation and a gross growth efficiency of 70 and 30%, respectively, and applying the equation proposed by Ikeda & Motoda (1978): $I = 100\ R/(70 - 30) = 2.5\ R$.

Active flux

Protein content and ETS activity data were averaged at 25-m intervals to obtain day and night vertical distribution profiles. The biomass night profile was then subtracted from the biomass day profile to show daily changes. The day-minus-night protein profile was integrated to estimate migrant biomass (mg protein m^{-2}). The negative area values represent the migrant biomass that reached the euphotic layer at night (0–245-m depth).

To assess the respiratory flux (µl O_2 m^{-2} day^{-1}) of carbon to deep waters, positive values of the ETS (µl O_2 m^{-3} h^{-1}) day-minus-night profile were integrated and divided by the integrated biomass present in the same depth range (as in Yebra, Almeida et al. 2005). The specific ETS activity measured at depth (µl O_2 mg $protein^{-1}$ h^{-1}) was then multiplied by the migrant biomass (mg protein m^{-2}) to obtain the flux resulting from migrants' respiration located below 200-m depth during the day. For all calculations, we applied 4 h of darkness per day, and an R : ETS ratio of 0.5 (see above).

Results

Hydrology

We found no sea-ice cover during the sampling period. The water temperature ranged between 1 and 2°C at the surface, decreasing to −1°C at 500-m depth (Fig. 2). We observed occasional deep warm water masses at a depth of 200 m. Salinity ranged from 33.9 to 34.4 at the surface, but was similar below 100 m at all stations. The maximum of chlorophyll was observed at around 25-m depth, where values reached up to 14 mg Chl. *a* m^{-3}.

Zooplankton biomass

The most abundant organisms were the pelagic copepod *Metridia gerlachei* and the euphausiid *Euphausia superba*. *Calanoides acutus* and *Calanus propinquus* were also present, but were found only in low numbers. Visual assessments of the presence/absence of copepods and euphausiids showed that by day large euphausiids were in the surface waters (above 250-m depth), whereas smaller juveniles stayed at depth (500–550 m). *M. gerlachei* was located in a compact layer from 300 to 500 m depth. Occasional layers of salps (*Salpa thompsonii*) were also found around 100- and 300-m depths (Fig. 3a). Surprisingly, the biomass values by day were similar in both the 0–200-m and the 200–550-m layers ($t = -0.17$, $p = 0.86$; Table 1). At night, euphausiids were observed above 100 m and below 400 m, whereas copepods dominated the layer in between (150–400 m), and salps scarcely occurred above 100 m (Fig. 3b). During the night, the biomass was concentrated in the upper 200-m layer, increasing by twofold compared with daytime values ($t = 2.85$, $p < 0.01$; Table 1).

Metabolic indices

During the day, specific ETS activities decreased slightly from the surface down to 200 m, but presented higher

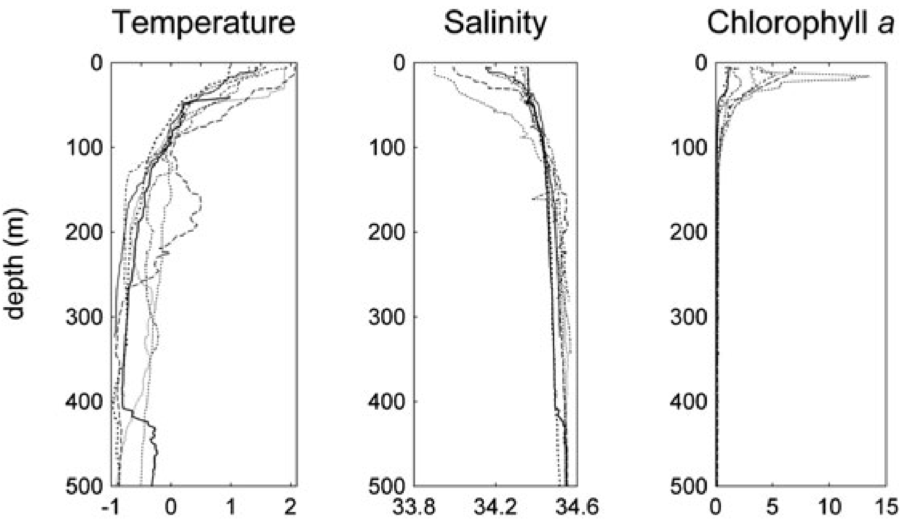

Fig. 2 Daytime conductivity–temperature–depth (CTD) vertical profiles of temperature (°C), salinity and chlorophyll *a* (mg Chl. *a* m^{-3}).

values at mesopelagic depths (200–550 m, $t = -2.81$, $p < 0.01$; Fig. 3a). In contrast, specific AARS activities were higher above 200 m (Fig. 3a), with an averaged specific AARS activity double that in the 200–550-m layer ($t = 3.83$, $p < 0.001$; Table 1).

At night, the specific ETS remained variable, with peaks at 25- and 225-m depths. Specific AARS activity peaks were also higher in the upper 250-m layer (Fig. 3b). The upward diel migration was accompanied by a 60% increase in averaged specific ETS activity in the upper 200 m ($t = -2.78$, $p < 0.01$), and a slight but not significant ($t = 0.93$, $p = 0.35$) 15% decrease between 200 and 550 m. The specific AARS activity remained constant in shallow waters ($t = 0.42$, $p = 0.67$) and increased, although not significantly ($t = -1.77$, $p = 0.079$), by 46% in the mesopelagic zone at night (Table 1).

Community rates and active flux

Considering the whole water column, we observed a small increase in specific ETS and AARS activities by night (13% and 9%, respectively; Table 1). However, as the biomass also increased at night, the respiration rate of the community was 1.7 times higher during the night (0.20 mg C m^{-2} h^{-1}) compared to daytime (0.12 mg C m^{-2} h^{-1}). The community growth rate was also 50% higher by night (360.6 nm PPi m^{-2} h^{-1}) than by day (241.8 nm PPi m^{-2} h^{-1}). The mean community respiration (over 0–550 m) was 1.74 mg C m^{-2} day^{-1}, and the community ingestion (0–550 m) assessed from respiration was 4.35 mg C m^{-2} day^{-1}.

From the day-minus-night biomass differences observed in the upper 250 m (Fig. 4a) we obtained a daily migrant biomass of 92.3 mg protein m^{-2}. The integrated total ETS activity diel difference (Fig. 4b) was 187.8 µl O_2 m^{-2} h^{-1}, and we estimated an active flux to deep waters of 10.2 µg C m^{-2} d^{-1}.

Discussion

Relationship between biomass vertical distribution and enzyme activities

The Antarctic Peninsula is a region of low zooplankton biomass in comparison with other Antarctic areas (Atkinson et al. 1997; Ward et al. 1997; Ward et al. 2004). The summer zooplankton biomass in the Bransfield Strait has high interannual variability, ranging from 35 up to 1039 mg C m^{-2} (Table 2). The highest biomass record corresponds to a summer when the salp *S. thompsonii* was the most abundant zooplankton species (Alcaraz et al. 1998). This species can have a widespread oceanic distribution further north and east of the study area (Hosie 1994). However, they were scarcely found during our study, and were mainly associated with relatively warmer waters. Instead, zooplankton was dominated by crustaceans, and the biomass values we observed were within the lower range of the previous values reported in the area (Table 2).

The patterns of zooplankton vertical distribution described for Antarctic waters coincide with our observations in the Bransfield Strait. These studies show a surface layer dominated by krill, and a wide layer of smaller organisms below 200-m depth (Pakhomov et al. 1994; Murray et al. 1995; Weeks et al. 1995; Hernández-León, Portillo-Hahnefeld et al. 2001). During our sampling,

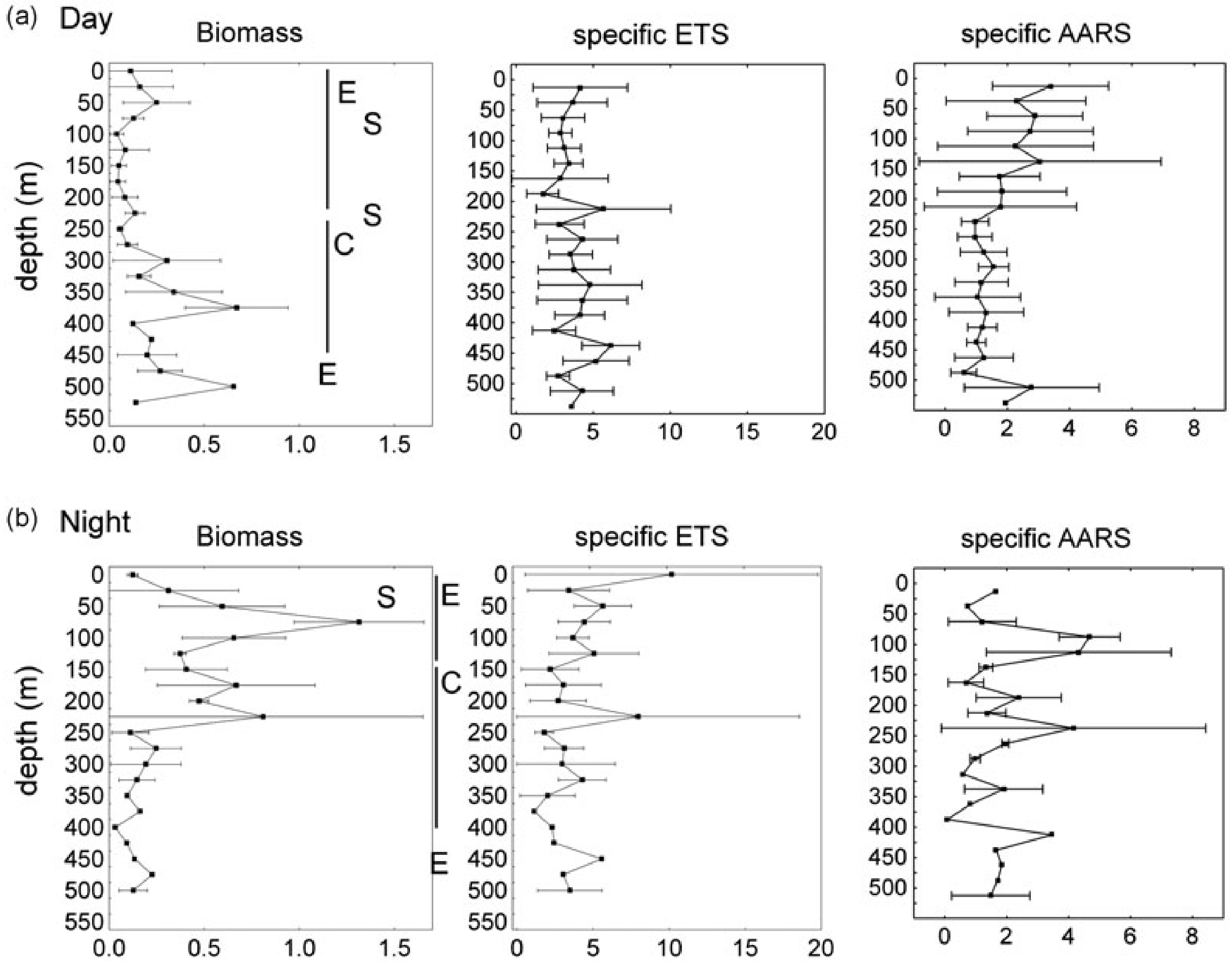

Fig. 3 (a) Day and (b) night averaged vertical profiles (±SD) of biomass (mg protein m^{-3}), specific electron transfer system (ETS) activity (µl O_2 mg protein^{-1} h^{-1}) and specific aminoacyl-tRNA synthetases (AARS) activity (nm PPi mg protein^{-1} h^{-1}). Biomass plots show the general vertical distribution of euphausiids (E), copepods (C) and salps (S).

euphausiids (*E. superba*) were concentrated above 200 m and around 550-m depth. The copepod *M. gerlachei* was found in the 300–500-m layer, as previously observed (Schnack-Schiel & Mújica 1994; Lopez & Huntley 1995; Hernández-León, Portillo-Hahnefeld et al. 2001), and was the dominant copepod species during our sampling. This agrees with Pakhomov et al. (2000), who observed that this copepod could make up 40–95% of the total abundance in the absence of krill swarms. Despite the reduced krill presence below 200-m depth, the biomass in the mesopelagic zone was similar to that in upper waters. This is in agreement with studies showing that copepods could represent more than 50% of the total biomass in Antarctic waters (Boysen-Ennen et al. 1991; Conover & Huntley 1991; Pakhomov et al. 2000).

The vertical distribution of ETS activities was related to biomass concentrations. The highest specific respiration rates (ETS activities) were found below 200 m, and were mainly related to copepod populations. Because of the inverse allometric relationship between size and metabolism (Ikeda 1985), copepods would show a higher metabolism than euphausiids, thereby explaining the observed tendency of specific respiration rates to increase with depth. Specific ETS activity increases in relation to high biomass values were previously observed in the Weddell Sea (Jacques & Panouse 1991; Schnack-Shiel & Mújica 1994). The night-time increase in biomass from 0 to 200 m also corresponded to higher values of specific ETS, and suggests that higher ingestion rates occur at night. Enhanced feeding at night has been previously observed in Antarctic waters. Atkinson et al. (1996) observed higher grazing rates of copepods, and Hernández-León, Portillo-Hahnefeld et al. (2001) found higher gut fullness of Antarctic krill at night. Opposite to

Table 1 Zooplankton biomass (mg protein m^{-3}, except where otherwise noted), specific electron transfer system (ETS; μl O$_2$ mg protein^{-1} h^{-1}) and specific aminoacyl-tRNA synthetases (AARS; nm PPi mg protein^{-1} h^{-1}) activities. Potential respiration (mg C m^{-2} h^{-1}) and ingestion (mg C m^{-2} h^{-1}) rates calculated from specific ETS activities and biomass. Growth rates (nm PPi m^{-2} h^{-1}) calculated from specific AARS activities and biomass (see Methods) for depths of 0–200, 200–550 and 0–550 m in the Bransfield Strait.

	Depth range (m)	Day		Night	
		Mean ± SD (number of samples)	Range	Mean ± SD (number of samples)	Range
Biomass	0–200	0.23 ± 0.61 (62)	0.001–4.68	0.54 ± 0.39 (21)	0.05–1.56
	200–550	0.24 ± 0.20 (59)	0.004–0.86	0.25 ± 0.32 (28)	0.03–1.71
Average	0–550	0.24 ± 0.46 (121)		0.37 ± 0.38 (49)	
Total	0–550	0.52/130.0* (121)		1.23/179.4* (49)	
Specific ETS	0–200	3.12 ± 2.03 (76)	0.04–10.86	4.99 ± 4.21 (21)	1.05–21.19
	200–550	4.23 ± 2.69 (83)	0.54–14.18	3.63 ± 3.63 (28)	0.51–20.10
Average	0–550	3.70 ± 2.45 (159)		4.20 ± 3.90 (49)	
Specific AARS	0–200	2.49 ± 2.28 (62)	0.11–11.36	2.23 ± 2.00 (18)	0.03–7.33
	200–550	1.26 ± 1.70 (65)	0.08–7.87	1.84 ± 1.83 (24)	0.07–9.28
Average	0–550	1.86 ± 1.90 (127)		2.01 ± 1.89 (42)	
Potential respiration	0–200	0.037		0.140	
	200–550	0.092		0.083	
Average	0–550	0.065 ± 0.039		0.111 ± 0.041	
Potential ingestion	0–200	0.093		0.350	
	200–550	0.231		0.206	
Average	0–550	0.162 ± 0.197		0.278 ± 0.102	
Growth	0–200	114.54		240.84	
	200–550	105.84		161.00	
Average	0–550	110.19 ± 6.15		200.92 ± 56.46	

* mg protein m^{-2}.

respiration, the specific growth rates (AARS activity) during the day in the upper 200 m were higher than in the mesopelagic layer. This indicates higher specific growth rates in the euphotic zone, where primary production was concentrated. Also, specific AARS activities did not increase at night, which suggests that although feeding seemed to have a day–night cycle, the somatic growth of the populations remained constant in the upper waters.

Control of zooplankton biomass

One of the main unsolved questions in the region is which factors determine the low summer zooplankton biomass. We looked at zooplankton metabolic rates and food availability to discuss the importance of the bottom–up and top–down control of zooplankton populations. The community respiration in the 0–200-m layer (1.33 mg C m^{-2} day^{-1}) was similar to the summer 1993 estimates in the Bransfield Strait (1.5 mg C m^{-2} day^{-1}; Hernández-León et al. 2000). However, in summer 1994, the biomass was dominated by salps, and the zooplankton carbon losses due to respiration ranged from 10 to 50 mg C m^{-2} day^{-1} (Alcaraz et al. 1998). On the other hand, we found that respiration in the mesopelagic waters (200–550-m depth) was 30% higher than that in the euphotic zone (2.2 mg C m^{-2} day^{-1}). When comparing the average respiration rate of the whole 0–550-m water column (1.74 mg C m^{-2} day^{-1}) with the average primary production found in the area (2854.5 mg C m^{-2} day^{-1}; Agawin et al. unpubl. data; Table 2), we observe that the zooplankton daily respiration needs accounted for only 0.06% of phytoplankton production. This value is much lower than the 0.9 and 5.3% reported for crustacean zooplankton and salps, respectively, by Alcaraz et al. (1998). Likewise, the average community ingestion (0–550 m) derived from respiration represented only 0.15% of the primary production. Therefore, in our study, zooplankton metabolic requirements accounted for less than 0.3% of the photosynthetic production. This percentage is lower than that observed in previous studies (Atkinson & Shreeve 1995; Lopez & Huntley 1995; Alcaraz et al. 1998; Hernández-León et al. 1999; Hernández-León et al. 2000). However, it is important to note that the phytoplankton bloom in February 2000 was notably intense. The average chlorophyll *a* concentration varied from 3.16 ± 1.5 mg Chl. *a* m^{-3} (ranging from 0.38 to 16.75 mg Chl. *a* m^{-3}) in open water (Agustí et al. 2004) to 19 ± 5 mg Chl. *a* m^{-3} within the waters of Deception Island (Sturz et al. 2003). Also, the primary production rate was the highest recorded in the area that we know of (Table 2). The other important food source to consider for

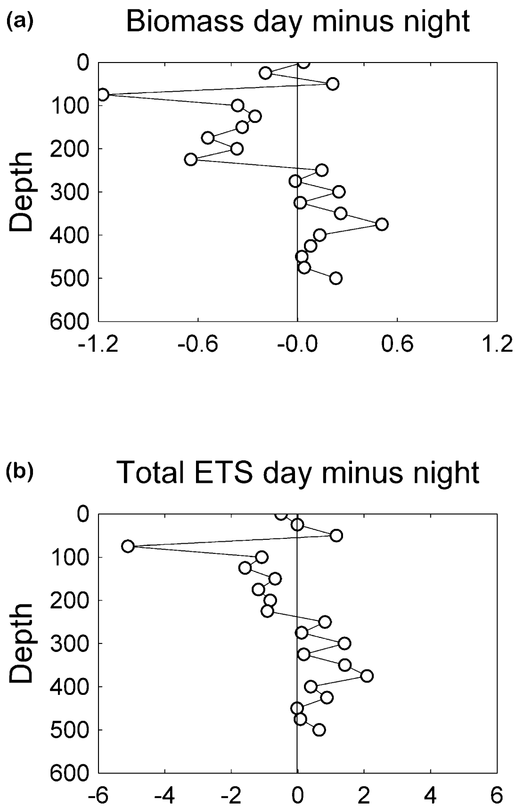

Fig. 4 Day-minus-night averaged value profiles of (a) biomass (mg protein m^{-3}) and (b) total electron transfer system activity (ETS; µl O$_2$ m^{-3} h^{-1}).

mesozooplankton is microplankton. *E. superba* is known to feed on ciliates as well as copepods (Price et al. 1988; Froneman et al. 1996; Atkinson & Snyder 1997; Perissinotto et al. 2000; Wickham & Berninger 2007). Likewise, *M. gerlachei* has shown preference for ciliates and other copepods over algae, in both austral autumn and winter (Atkinson 1996, 1998; Pasternak & Schnack-Schiel 2001; Wickham & Berninger 2007). Calbet et al. (2005) suggested that, in this region, the mesozooplankton was grazing on microplankton rather than on phytoplankton, and was therefore aiding the development of the phytoplankton bloom. Nevertheless, the net microplankton production found (76.36 mg C m^{-3} day^{-1}; Agustí et al. 2004) was much higher than the phytoplankton production (4.6 mg C m^{-3} day^{-1}; Agawin, unpubl. data), although it was similar to the value found in a previous study in the region (93.35 mg C m^{-3} day^{-1}; Arístegui et al. 1996). Therefore, the mesozooplankton metabolism during summer 2000 was not limited by phyto- or microplankton availability. Hence, as previously suggested (Hernández-León et al. 1999), we reject the bottom–up control hypothesis.

On the other hand, a top–down effect of krill on copepods has been suggested as the main factor controlling copepod abundance and development in the Bransfield Strait (Hernández-León et al. 1999; Hernández-León et al. 2000; Hernández-León, Portillo-Hahnefeld et al. 2001). This idea is supported by the inverse relationship of krill/non-krill zooplankton distribution observed here, and in other Antarctic areas, where high krill densities coincide with very low copepod abundances (Hosie 1994; Voronina et al. 1994; Atkinson et al. 1999). As mentioned above, krill is able to prey selectively on copepods (Price et al. 1988; Graneli et al. 1993; Atkinson & Snyder 1997), although their impact on copepods might be reduced in spring or summer, when phytoplankton concentrations are high. Hernández-León, Portillo-Hahnefeld et al. (2001) observed that during the austral summer of 1993 *E. superba* grazed on phytoplankton by day, but, despite the high primary production (Basterretxea & Arístegui 1999; Table 2), they switched to feed on *M. gerlachei* at night, when copepods migrated upwards. Our study reflected a similar scenario, with zooplankton biomass in the lower range and a high primary production. Hence, the low biomass found could be the result of predation pressure (top–down control). However, as a result of the short length of the summer night and the high phytoplankton concentrations available to krill during the bloom, their impact on copepods would be minimal. Thus, predation might not be the only cause for the low zooplankton biomass in the Bransfield Strait, and copepod life history might be an important factor to explain the low values found in summer. Ward et al. (2004) suggested that the low biomass found was probably linked to the higher latitude, lower temperatures and reduced production in comparison with areas further north. This combination could delay the development of zooplankton populations. This agrees with studies of *M. gerlachei* showing that their abundance peaks in autumn, i.e., March–May (Schnack-Schiel & Hagen 1994, 1995; Tucker & Burton 1990) or in early winter, i.e., June (King & LaCasella 2003). King & LaCasella (2003) found the biomass of *M. gerlachei* in the waters of Deception Island (Bransfield Strait) to be 1.7 mg dw m^{-3} during February 2000, which is similar to the biomass that we observed in open waters at that time (1.2 mg dw m^{-3}). Nevertheless, the biomass they found in June (31.4 mg dw m^{-3}) was 20 times greater, showing a four-month lag response of the copepod population to the phytoplankton bloom. This may be explained by their preference for microplankton and small copepods (i.e., *Oithona* spp.) as prey, the populations of which would peak after the phytoplankton bloom. Therefore, it is probable that the low zooplankton biomass found in summer is not caused by predation pressure either, but instead is the result of life-cycle

Table 2 Interannual variability of mesozooplankton biomass (ZPB; mg C m^{-2}) and average primary production (PP; mg C m^{-2} day^{-1}) in the Bransfield Strait.

Depth	Date	ZPB	Reference	PP	Reference
0–200	12/1991	34.6*	Hernández-León et al. 1999	333	Basterretxea & Arístegui 1999
0–200	01/1993–02/1993	133.6*	Hernández-León et al. 2000	423–3913	Basterretxea & Arístegui 1999
0–200	01/1994	713–1039	Alcaraz et al. 1998	684–1396	Alcaraz et al. 1998
0–200	12/1995–02/1996	136–431	Cabal et al. 2002	14–176	Varela et al. 2002
0–43	02/1998	—	—	262–889	Morán et al. 2001
0–200	01/2000–02/2000	94.0–240.5	Present work	578–6911	Agawin unpubl. data
0–550		270.4–373.2			
0–200	01/2001–02/2001	9.3–179.3*	Catalán et al. 2008	—	—
0–250	12/2002	55	Calbet et al. 2005	23–451†	Morán et al. 2006

*Carbon calculated from dry weight (dw) applying a C : dw ratio of 0.4 for crustaceans (Postel et al. 2000) and 0.05 for salps (Schneider 1989).

†PP estimated from surface experiments, and assuming 15 h of light per day.

adaptation of the dominant copepod species to the production dynamics in the region.

Vertical migration and carbon fluxes

Biomass in the upper 200-m layer increased by twofold at night, corresponding to the upward migration of *M. gerlachei* (Park & Wormuth 1993; Lopez & Huntley 1995; Hernández-León, Portillo-Hahnefeld et al. 2001; King & LaCasella 2003). However, the integrated migrant biomass in the Bransfield Strait was low (192.0 mg C m^{-2}), compared with previous studies in the area (Voronina et al. 1994; Hernández-León et al. 2000), and was within the lower range (20–5200 mg C m^{-2}) of values found in Antarctica (Boysen-Ennen et al. 1991; Robins et al. 1995; Ward et al. 1995). The carbon flux due to migrant fauna respiration below 200-m depth (10.2 µg C m^{-2} day^{-1}) represented less than 0.01% of the averaged primary production measured in the area (2854.5 mg C m^{-2} day^{-1}; Agawin, unpubl. data). At the time of our sampling, Khim et al. (2007) were conducting a year-long study to determine carbon fluxes to depths of 960 and 1860 m in the Bransfield Strait. Most sediment particles (60–73%) were of lithogenic origin, followed by biogenic silica (20%) and organic carbon (3–5%). The organic carbon flux was similar at 960- and 1860-m depths (54.98 and 54.49 mg C m^{-2} day^{-1}, respectively). The authors suggested that this carbon was first coming from the diatom spring bloom (gravitational flux), and, later in summer, from zooplankton faecal pellets (active flux). In this sense, Anadón et al. (2002) observed summer carbon fluxes in the region ranging from 160 to 800 mg C m^{-2} day^{-1} at depths of 60–65 m. They calculated an average export flux from the euphotic zone of 294 ± 89 mg C m^{-2} day^{-1}, which represented 25.6% of the primary production (Varela et al. 2002), and suggested that the Bransfield Strait played an important role as a carbon sink area. On the other hand, Ebersbach & Trull (2008) observed export fluxes due to faecal pellets to be 50–60 mg C m^{-2} d^{-1} at 100-m depth. They concluded that the majority of export flux was processed through the heterotrophic food web, and was not a direct export of phytoplankton detritus. However, if that was the case in the Bransfield Strait, carbon fluxes would be high during autumn and early winter, when the biomass of copepods peaks. Instead, Khim et al. (2007) observed that more than 99% of the carbon flux for the year occurred between December and February. The extraordinarily minimal fluxes recorded during the rest of the year suggest important carbon recycling processes in the absence of phytoplankton blooms. Nevertheless, Serret et al. (2001) suggested that seasonal production and respiration uncoupling in the Bransfield Strait would increase the role of hydrodynamics (i.e., advection) in the trophic control of carbon export. Further research during the austral autumn and winter is needed to reveal the importance of microplankton, both as grazers and as prey, if we seek to assess the changes in carbon transport to the deep ocean through the year.

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