Effects of the ice-edge bloom and season on the metabolism of copepods in the Weddell Sea, Antarctica

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Abstract

The metabolic responses of several species of Antarctic copepods to primary productivity and changes between seasons were investigated. To examine the influence of the spring ice-edge bloom on the metabolism of copepods, oxygen consumption rates were determined on specimens from three zones of widely different ice coverage and chlorophyll biomass: pack ice (pre-bloom), ice edge (bloom) and open water (post-bloom). Summer metabolic rates were compared with published winter rates. Field work was done in the Weddell Sea in the region of 60 °S, 36°W in late November and December 1993. Oxygen consumption rates were determined by placing individuals in syringe respirometers and monitoring the oxygen partial pressure for 10–20 hours. Higher metabolic rates were observed in the primarily herbivorous copepods, *Calanoides acutus*, *Rhincalanus gigas* and *Calanus propinquus* in regions of higher primary production: ice edge and open water. The carnivorous *Paraeuchaeta antarctica* showed a similar pattern. The omnivorous copepods *Metridia gerlachei* and *Gaetanus tenuispinus* showed no changes in metabolism between zones. Data on routine rates of copepods from the winter were available for *C. propinquus* and *P. antarctica*. In *P. antarctica*, rates were higher in the summer. *Calanus propinquus* showed a higher metabolic rate in the summer than in the winter, but the difference was not significant at the 0.05 level. It was concluded that copepods near the ice zone in the ice zone in the Antarctic rely on the spring ice-edge bloom for growth and completion of their life cycle.

Introduction

The Antarctic pelagial is a system with dynamic and predictable changes in the light regime and sea-ice coverage. When the Antarctic pack ice retreats during the austral spring, a meltwater lens is created in the euphotic zone, allowing primary producers and microheterotrophs to flourish. The physically stable, nutrient-rich environment at the ice edge acts as a culture vessel, leading to a period of high productivity that lasts around 60 days (Smith & Nelson, 1985; Nelson et al., 1987). During this period, as the ice progressively melts southward and the phytoplankton bloom moves with it, the zooplankton obtain much of their energy for growth and reproduction for the year.

Three different life history strategies exist within zooplankton and micronekton to deal with the highly pulsed Antarctic primary productivity (Torres et al., 1994b). Zooplanktonic organisms exhibit two of them. The first strategy (Type 1) is observed in the herbivorous species of copepods such as *Calanoides acutus* and *Rhincalanus gigas*. Both accumulate large quantities of lipids during the productive season and migrate to deep waters (Marin, 1988) to enter a state of true dormancy, or diapause, during winter months (Voronina, 1970; Schnack-Schiel et al., 1991; Pasternak et al., 1994). This process is also accompanied by cessation of feeding (Hopkins, 1985; Hopkins & Torres, 1988; Hagen et al., 1996), lowered metabolism (Hirche, 1984; Schnack-Schiel et al., 1991; Pasternak et al., 1994) and a slight utilization of the metabolic reserves (Drits et al., 1993; Donnelly et al., 1994). In the spring, those species migrate to the surface to capitalize on the spring bloom.

In the second strategy (Type 2), activity and metabolic rates are reduced after the summer (Quetin & Ross, 1991; Schnack-Schiel et al., 1991; Bathmann et al., 1993; Drits et al., 1993; Pasternak et al., 1994; Torres et al., 1994a) but no true dormancy is shown. The individuals may show marked depletion of metabolic reserves (Drits et al., 1993; Donnelly et al., 1994; Hagen et al., 1996) and part of the population often remains at the surface (Marin, 1988; Bathmann et al., 1993). This strategy has been observed in *Calanus propinquus* and *Paraeuchaeta antarctica*. No metabolic studies have been done on *Metridia gerlachei*, but it has been demonstrated that part of the population actively feeds on protozoans and crustaceans during the winter (Hopkins et al., 1993).

Species with different life history strategies would be expected to have different metabolic responses to the spring phytoplanktonic bloom. In species which are strongly herbivorous and diapause during the winter (Type 1), a profound change in metabolism would be expected. Examples of such species are *R. gigas* and *C. acutus*. In more omnivorous species, such as *C. propinquus* and *M. gerlachei,* a direct effect of the phytoplanktonic bloom would hypothetically be less evident.

The objective of the present research was to examine the degree to which the metabolism of Antarctic zooplankton was influenced by the spring ice-edge bloom. Metabolic rates were determined through direct measurements of oxygen consumption, with species from three regions in the seasonal ice zone with widely different conditions of primary productivity: ice edge (pre-bloom), within the bloom (ice edge) and open water (post-bloom). The focus of the study was on dominant species of copepods in the Weddell Sea. Metabolic rates were determined for each species within each sub-region of the marginal ice zone (see below), which allowed us to determine the effect of the phytoplankton bloom on the species' metabolism and to estimate its importance to their life history. Comparisons with rates from other seasons provided better understanding of their cycle throughout the year.

Materials and methods

Collection of specimens

Field work was done in the Weddell Sea in the vicinity of 60 °S 36 °W in late November and December 1993. To assess the location and extent of the spring bloom within the study area, two transects were run while continually monitoring chlorophyll biomass as *in vivo* fluorescence (Fig. 1). The first was a west-east transect along the marginal ice zone, to examine variability within the core of the bloom (stations 1–9, between 40 ° and 35 °W). The second was a north-south transect, to verify the latitudinal extent of the bloom. The transect was initiated seaward from the bloom, in open water, where *in vivo* fluorescence was reduced to values well below those found in the bloom. From its most northerly point in open water, the transect proceeded through the bloom in the marginal ice zone, and into the pack ice until the fluorescence signal from the bloom was absent at the southern end. Zonal occupations of 5–6 days were then performed in each of the regions: pack ice, stations 23–41; ice edge, stations 42–57; and open water, stations 61–67. The biological and physical framework of each region was provided by CTD/rosette casts, primary productivity measurements, and chlorophyll biomass determinations.

Specimens were collected with a vertically towed, opening-closing plummet net (1 m^2 mouth area). The cod-end of this net was a 1 l jar, which returned the animals to the surface in excellent condition for physiological work. Tow depths were 0–200 m, 200–400 m and 0–400 m.

Respiratory measurements

Once on board, the sample was transferred from the collecting jar to a bucket filled with cold sea water (∼0 °C) and taken immediately to the laboratory. Small volumes of diluted sample were placed in petri dishes and specimens in good conditions were sorted under a stereoscope microscope and transferred without delay to the respirometers. A maximum lag time of 30 min occurred between the capture and the starting of measurement.

Oxygen consumption rates were determined by placing each individual in a sealed chamber filled with filtered sea water at a controlled temperature of 0.5 °C, and monitoring the decrease in oxygen partial pressure. Respirometers made of syringes were used to accommodate copepods and other zooplanktonic organisms <10 mm. Briefly, the 'needle' end of the 5 ml syringes was cut off and fitted with custom made Clarke microcathode electrodes that provided an airtight seal. The other end was sealed with the normal syringe plunger. This design created an adjustable sealed volume into which the animals were placed for
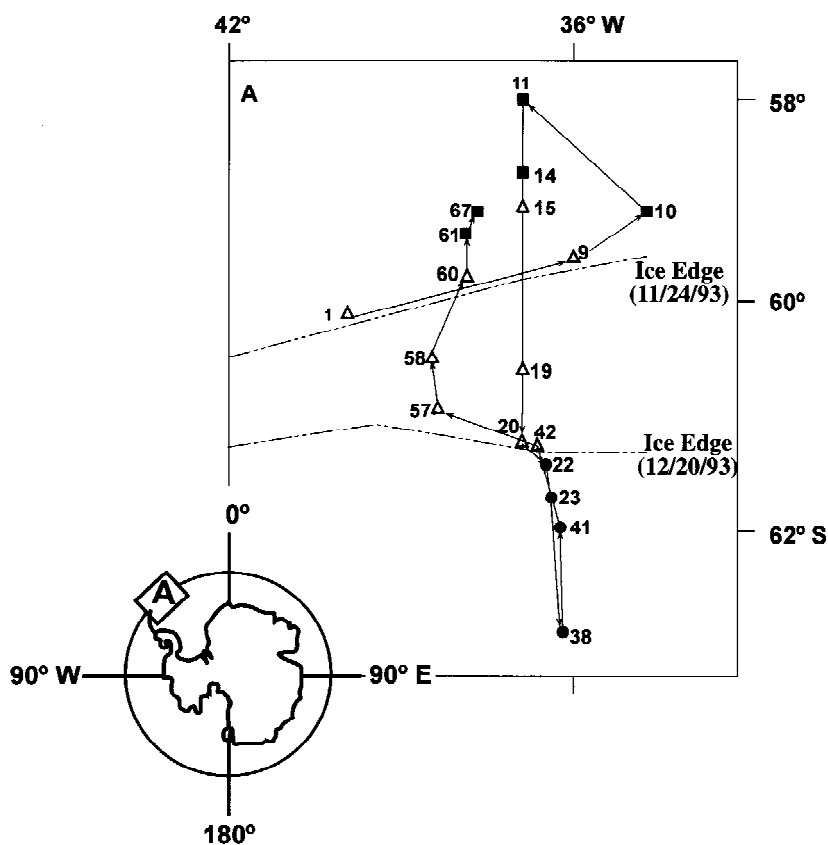
Figure 1. Cruise transect in the Weddell Sea. Some stations from each of the three regions are represented: (■) open water; (△) ice edge; (●) pack ice. Notice the position of the receding ice edge at the beginning and end of the cruise.

respiratory measurements. Volumes were, in most of the measurements, between 1.0 and 2.5 ml, and extremes were 0.4 and 4.8 ml. Oxygen was continuously monitored with the oxygen electrodes and data were recorded every minute, over a 10–20-h period, using a computer-controlled data logging system. Electrodes were calibrated before each experimental run with air- and nitrogen- saturated sea water. To calculate routine oxygen consumption rates, the difference in oxygen partial pressure was determined from 5 min averages at the beginning and end of every 30-min interval during the course of a run. The difference was multiplied by 2, to obtain the change per hour. The data acquired in the first hour were discarded because individuals showed high activity just after introduction into the respirometer, determining increased oxygen consumption rates. Every respiration run was printed as a graph of oxygen partial pressure *versus* time, allowing the detection of slope changes in the beggining of a run and the occurrence of a critical oxygen partial pressure (Pc). The respiration rates were estimated

in a range subsequent to the initial excitatory period, and above the Pc for the animal. The lowest and highest respiratory rates observed for each run were designated as minimum and maximum rates. To control for possible O_2 consumption by micro-organisms, one of the chambers was run without a specimen and the oxygen partial pressure was recorded during each suite of runs. No decrease in oxygen was observed in the control runs. After the respiration measurements, the specimens were blotted dry, individually sealed in polypropylene vials, and then frozen in liquid nitrogen. The animals were stored in a –80 °C freezer for later measurements of mass and for biochemical analysis.

Dry weight and ash-free dry weight

Individual copepods were measured and weighed (wet mass) and then placed in pre-weighed aluminum foil pans and dried at 60 °C, for approximately 24 h, to a constant weight (dry mass). Samples were then com-

busted at 500 °C for 3 h and reweighed to determine ash weights and thus, the individuals' ash-free dry mass.

Data treatment

The respiratory rates were expressed in μl of oxygen consumed *per* milligram of wet mass in 1 h. Conversion factors were determined to enable the conversion of the wet-mass specific routine rates to dry mass and ash-free dry mass routine rates. Oxygen consumption rates were grouped by species, sex and size class. When sufficient data were available, comparisons were performed between seasons and between the three regions within the study area: pack ice, ice edge and open water.

Data are reported as mean ± standard deviation. Means were tested for differences using one-way analysis of variance (ANOVA). Least-significant-differences multiple range tests (MRT) were applied to determine which means were significantly different. When variances were not homogeneous, a Kruskal-Wallis test (KW) was applied. Simple regressions were fitted using the least-squares method. The statistical package Statgraphics Plus® (Manugistics Corporation) was used to perform all the tests. General level of significance adopted was $P < 0.05$. Probabilities between 0.05 and 0.1 are reported in the text.

Results

Characterization of the study area

Data from the North–South transect revealed that the study area showed a gradient in chlorophyll biomass spatially coherent with the density field. A well developed meltwater lens ($\Phi t = 27.3$) coincident with the maximum biomass (2.8 μg chlorophyll l^{-1}) was observed between 59° and 61° S within the marginal ice zone (Figs. 2 and 3).

Continuing south, the influence of surface meltwater was reduced and lower levels of chlorophyll were recorded. The end of the N–S transect coincided with station 23 at 62° S. We found low chlorophyll just after arriving within the pack ice (0.4 μg l^{-1}) and primary productivity was low relative to productivity at the ice edge. During the occupation in the pack-ice zone, integrated net primary production (0–50 m) increased from 250 mg C m^{-2} d^{-1} to 1000 mg C m^{-2} d^{-1} and chlorophyll biomass began to accumulate, characteristic of a developing bloom. The transect continued further south to station 38 at 63° S where low chlorophyll (0.4 μg l^{-1}) and a production of 500 mg C m^{-2} d^{-1} were observed. We then headed north to the zonal occupation within the core of the bloom. The stations in the core of the bloom, 47–57, averaged 3.5 μg chlorophyll l^{-1}; primary production was around 1000 mg C m^{-2} d^{-1}. Phytoplankton were observed occasionally in a light microscope, to verify that the growing cells were healthy and that the bloom was not past its peak and tending toward senescence. The open-water stations, 61–67, showed an average chlorophyll biomass of 1.7 μg chlorophyll l^{-1} (Fig. 3). Primary production was also intermediate, ranging from 500 to 750 mg C m^{-2} d^{-1}.

Overall trends

The overall average for routine metabolic rate of all copepods treated in the study, based on the mean of all individual determinations, was 0.131 ± 0.117 μl O_2 mg WM^{-1} h^{-1} (mean± SD) (Table 1). The species with lowest metabolism was *R. gigas*, with a routine rate of 0.063 μl O_2 mg WM^{-1} h^{-1}; *R. gigas* also showed the highest water content; 86.6% (Table 2). *Paraeuchaeta antarctica* showed a slightly higher rate, 0.068 μl O_2 mg WM^{-1} h^{-1}, followed by *Gaetanus tenuispinus*, 0.102 μl O_2 mg WM^{-1} h^{-1} and *Heterohabdus farrani*, 0.119 μl O_2 mg WM^{-1} h^{-1}. The routine rate of *C. acutus* was 0.129 μl O_2 mg WM^{-1} h^{-1}, closest to the global mean. *Calanoides acutus* also showed the lowest water content: 76.3%. *C. propinquus* showed a rate of 0.145 μl O_2 mg WM^{-1} h^{-1}; it also had an intermediate water level, 78.5%. *Metridia gerlachei*, the smallest of the seven copepods, showed the highest metabolic rate, 0.202 μl O_2 mg WM^{-1} h^{-1}, as well as a high water level, 82.2%. Maximum rates were approximately double the routine rates (1.92 ± 0.30, 7; mean ± SD, n). Ratios of maximum to minimum rates were higher and more variable (8.06 ± 6.37, 7).

Enough data on *C. propinquus* males were collected to test for differences in metabolic rates between sexes. No significant difference was observed (df= 35, *F*= 3.125, *P*= 0.55). *Rhincalanus gigas* also showed no differences between males and females (df= 35, *F*= 0.39, *P*= 0.54), nor did *P. antarctica* (df= 12, *F*= 0.94, *P*= 0.36).

Calanoides acutus stage 5 copepodites (CV) showed higher respiration rates than adults (df= 34, *F*= 3.70, *P*= 0.06). No significant difference was observed

Table 1. Respiration rates of Antarctic calanoid copepods. All values are means ± standard deviation. Rates are expressed as $\mu l\ O_2\ mg\ WM^{-1}\ h^{-1}$. To convert the rates to dry mass (DM) or ash-free dry mass (AFDM) multiply the wet-mass-specific rate by the conversion factor (*conversion factors calculated with water and ash content from Donnelly et al., 1990). Max Rate: maximum rate; Min Rate: minimum rate

Species	n	Wet Mass (mg)	Routine Rate	Max Rate	Min Rate	Conversion DM	AFDM
Calanoides acutus	35	3.329±0.958	0.129±0.071	0.305±0.341	0.029±0.043	4.22	4.52
Calanus propinquus	44	4.718±1.423	0.145±0.086	0.266±0.153	0.053±0.049	4.65	5.08
Metridia gerlachei	42	1.409±0.806	0.202±0.071	0.422±0.219	0.074±0.098	5.62	6.42
Gaetanus tenuispinus	5	3.640±3.229	0.102±0.051	0.215±0.098	0.010±0.008	6.67	7.79*
Rhincalanus gigas	37	11.692±3.248	0.063±0.028	0.116±0.062	0.018±0.023	7.46	8.15
Paraeuchaeta antarctica	13	19.551±6.224	0.068±0.046	0.096±0.094	0.023±0.031	4.83	5.27*
Heterohabdus farrani	2	3.215±1.590	0.119±0.105	0.215±0.185	0.070±0.060	9.52	10.52*
Pooled data	178	6.150±2.454	0.131±0.117	0.267±0.207	0.043±0061		

Table 2. Water and ash content of calanoid copepods in the Weddell Sea. All values are mean (standard deviation, *n*). Water levels are expressed as percentage of wet mass. Ash content is expressed as percentage of dry mass. Data of winter and fall water content from Donnelly et al. (1990)

Species	Summer 93					Winter 88	Fall 86
	Water (% WM)	Ash (% DM)	Water (% WM)			Water (% WM)	
	All regions		Open water	Ice-edge	Pack-ice	All regions	
Calanoides acutus	76.3 (7.6,11)	6.7 (1.7)	68.3 (9.5, 3)	78.2 (4.3,6)	82.9 (2.3, 2)	84.2 (0.1)	86.0
Calanus propinquus	78.5 (2.9, 9)	8.5 (1.9)	77.2 (3.0, 3)	77.4 (0.9, 4)	82.9 (0.4, 2)	84.6 (0.7)	74.0
Metridia gerlachei	82.2 (3.3, 10)	12.5 (4.0)	79.5 (0.8, 3)	81.1 (2.1, 4)	86.3 (1.1, 3)	91.0	90.4
Rhincalanus gigas	86.6 (2.5, 11)	8.4 (1.2)	84.7 (2.5, 4)	87.1 (0.9, 5)	89.1 (0.1, 2)	91.0	–

Table 3. Routine metabolic rates of calanoid copepods in three regions in the Weddell Sea, and winter routine rates (J. J. Torres, data not published). All values are means (standard deviation, n). Means were tested for differences using ANOVA (between regions) or a '*t*-test' (between seasons). Significance: n.s.: not significant; ** $p < 0.05$, and * $p < 0.10$

| Species	Summer 1993 (regions)				Winter 1988	
	Pack-ice	Ice-edge	Open water	p (regions)	All regions	p (seasons)
Calanoides acutus	0.099 (0.064, 15)	0.131 (0.061, 12)	0.181 (0.067, 8)	**	–	
Calanus propinquus	0.076 (0.038, 7)	0.164 (0.096, 26)	0.144 (0.064, 11)	**	0.075 (0.025, 4)	*
Metridia gerlachei	0.214 (0.062, 12)	0.198 (0.076, 19)	0.194 (0.085, 11)	n.s.	–	
Gaetanus tenuispinus	–	0.101 (0.069, 3)	0.104 (0.021, 2)	n.s.	–	
Rhincalanus gigas	0.048 (0.020, 12)	0.070 (0.029, 7)	0.069 (0.029, 18)	*	–	
Paraeuchaeta antarctica	0.051 (0.032, 9)	0.091 (0.055, 3)	0.149 (–, 1)	*	0.055 (0.022, 14)	**
All copepods	0.102 (0.079, 55)	0.152 (0.086, 70)	0.132 (0.079, 53)	**	–	
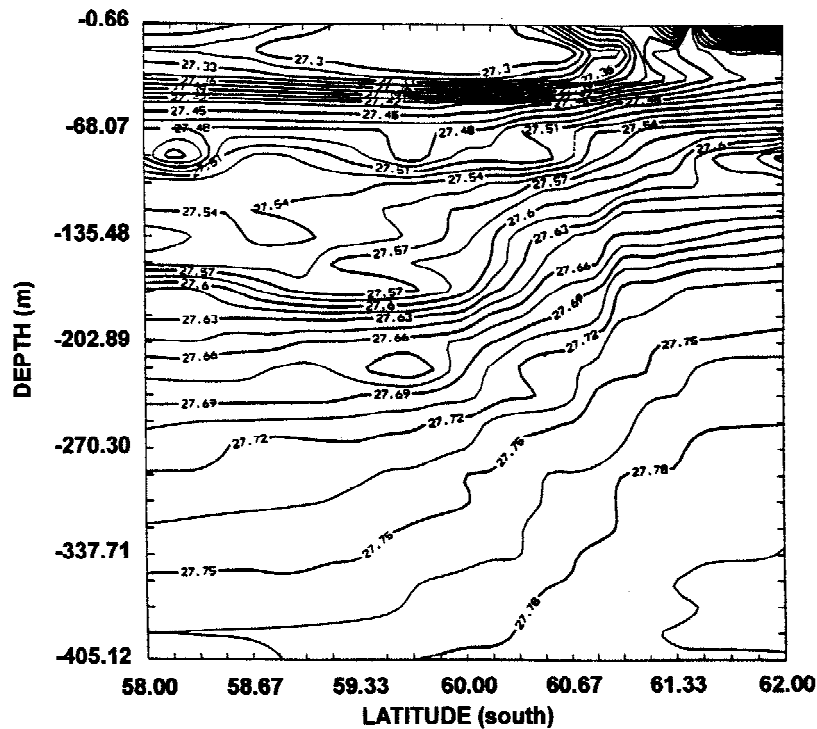
Figure 2. Contour plot of sigma-t for the initial North-South transect (unpublished data contributed by Gabriel A. Vargo, University of South Florida). Notice the meltwater lens at top center of figure.

between routine rates of CV and adult *C. propinquus* (df= 43, *F*= 0.12, *P*= 0.74), nor in *R. gigas* (KW: 0.35).

Comparison between regions

Initially, the routine rates of six species of copepods were combined and tested for differences between the three regions. The average routine rate for all species was highest at the ice edge (0.152 μl O_2 mg WM^{-1} h^{-1}), followed by the open water (0.132 μl O_2 mg WM^{-1} h^1), with the lowest average in the pack ice (0.102 μl O_2 mg WM^{-1} h^{-1}). Differences were significant (df= 177, *F*= 5.93, *P*= 0.003) (Table 3 and Fig. 4). Notice in Figure 4 that the means of chlorophyll-*a* for the three regions track the overall pattern of metabolism of copepods.

For species taken individually, results were similar to the pooled data. In *C. acutus* the highest routine rate was observed in the open water region, followed by the ice-edge rate, with a low in the pack-ice region (df= 34, *F*= 4.42, *P*= 0.02; MRT: pack ice $\neq$ open water) (Fig. 5). *Rhincalanus gigas* showed a similar pattern as *C. acutus* (df= 36, *F*= 2.26, *P*= 0.09; MRT: pack ice $\neq$ open water) (Fig. 5). *Calanus propinquus* showed its lowest metabolism in the pack ice, with a peak

at the ice edge and decreasing slightly in open water. Differences were significant (KW: *P*=0.02; MRT ice edge $\neq$ pack ice) (Fig. 5). *Paraeuchaeta antarctica* also showed lower metabolic rates at the pack-ice region (df= 12, *F*= 2.85, *P*= 0.09) (Fig. 6). *Metridia gerlacheii* and *G. tenuispinus* did not show significant differences between the three regions (df= 41, *F*= 0.23, *P*= 0.79 and df= 4, *F*= 0.02, *P*= 0.99, respectively) (Fig. 6).

Seasonal comparison

Data on routine metabolic rates of copepods obtained in the 1988 winter season were available for *C. propinquus* and *P. antarctica* (J. J. Torres, data not published). For purposes of comparison, the summer rates used did not include data from the pack ice because the rates were significantly lower in the pack-ice region than at the ice edge and open water (Table 3). In *P. antarctica,* routine rates were significantly higher in the summer season (*t*-test: *P*=0.01, df=16). *Calanus propinquus* metabolism showed a higher mean metabolic rate in the summer than in the winter at the 0.07 level (*t*-test: *P*=0.07, df=39). Comparisons of winter rates with pack-ice summer rates were also performed
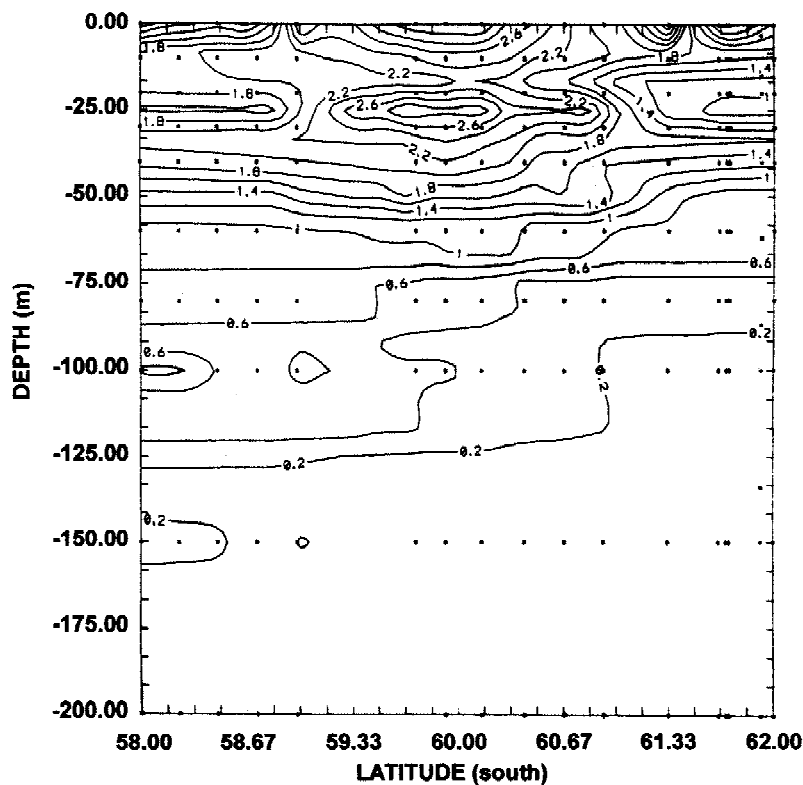
Figure 3. Contour plot of chlorophyll-*a* biomass (μg l^{-1}) for the initial North-South transect (unpublished data contributed by Gabriel A. Vargo, University of South Florida).

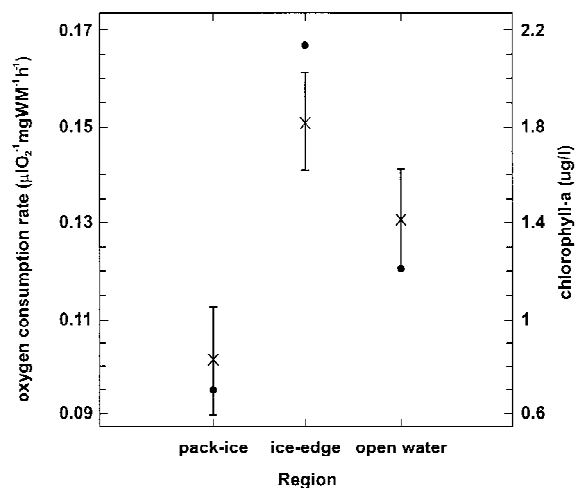*Figure 4.* Oxygen consumption rates of calanoid copepods (y left axis) and chlorophyll-*a* biomass (μg l^{-1}) (y right axis) in three different regions: pack ice, ice edge and open water. All values represent means $\pm$ standard errors. Closed circle: chlorophyll-*a*; cross and full line: oxygen consumption rate.

for both species. *Calanus propinquus* routine rates were not significantly different between winter and pack-ice summer rates (*t*-test: *P*= 0.35, df= 10), nor were the rates for *P. antarctica* (*t*-test: *P*=0.73, df=21).

Even not testing the data statistically, similarities in water content were observed between individuals captured in the pack ice and those captured in the winter season (Table 2). For all four biomass-dominant copepods, *C. acutus*, *C. propinquus*, *M. gerlachei* and *R. gigas*, water content were higher in the pack-ice region, and higher yet in the winter season.

Discussion

When comparing oxygen consumption rates of Antarctic copepods among different investigations, one should take into consideration the species' ontogenetic stage, area and period of study and technique used. For example, in the present study, *C. acutus* CVs showed slightly higher oxygen consumption rates than adult females. However, in *C. propinquus* and *R. gigas* no difference was observed between those
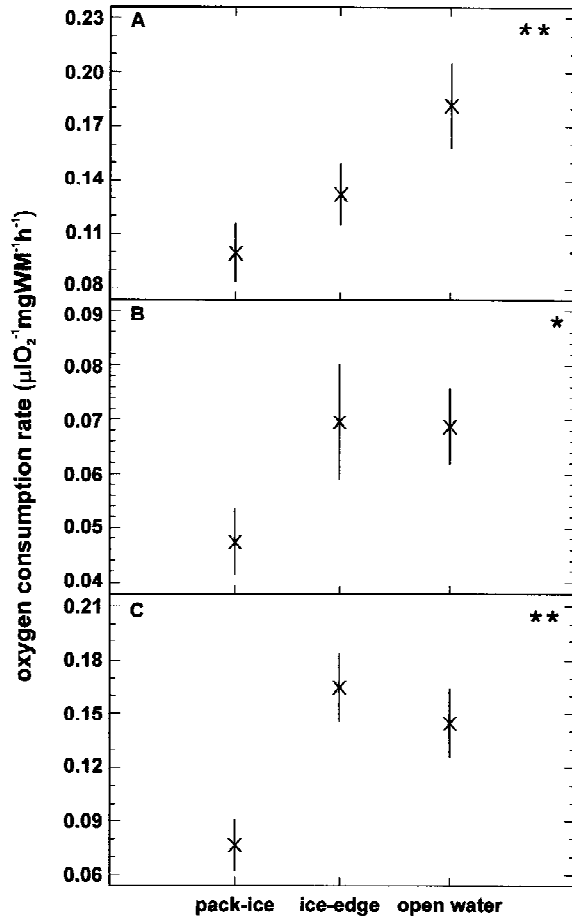
Figure 5. Routine oxygen consumption rates (μl O_2 mg WM^{-1} h^{-1}) of *Calanoides acutus* (A), *Rhincalanus gigas* (B), and *Calanus propinquus* (C) in the three zones: pack-ice, ice-edge and open water. Values are means $\pm$ standard errors. Means were tested for differences using ANOVA (** $p < 0.05$; * $p < 0.10$).

Figure 6. Routine oxygen consumption rates (μl O_2 mg WM^{-1} h^{-1}) of *M. gerlachei* (A), *G. tenuispinus* (B), and *P. antarctica* (C) in the three zones: pack ice, ice edge, and open water. Values are means $\pm$ standard errors. Means were tested for differences using ANOVA (** $p < 0.05$; * $p < 0.10$).

two stages. Overall, the routine rates of adult females determined in the present study were in the same range as previously published data. The routine rate of *C. acutus* reported in this study, 0.544 μl O_2 mg DM^{-1} h^{-1}, was higher than the rates obtained by Ikeda & Hing Fay (1981), 0.398 μl O_2 mg DM^{-1} h^{-1}. Ikeda & Hing Fay (1981) used a direct measurement of respiration; however, the animals were maintained in an incubator for 2–6 weeks prior to measurement, which almost certainly reduced the metabolism because of starvation effects. The *C. acutus* routine rate obtained by Pasternak et al. (1994) was 0.204 μl O_2 mg DM^{-1} h^{-1} which is also lower than our result. Their experiments were performed in late summer, with animals from 500 to 1000 m, which were probably already descending into winter depths
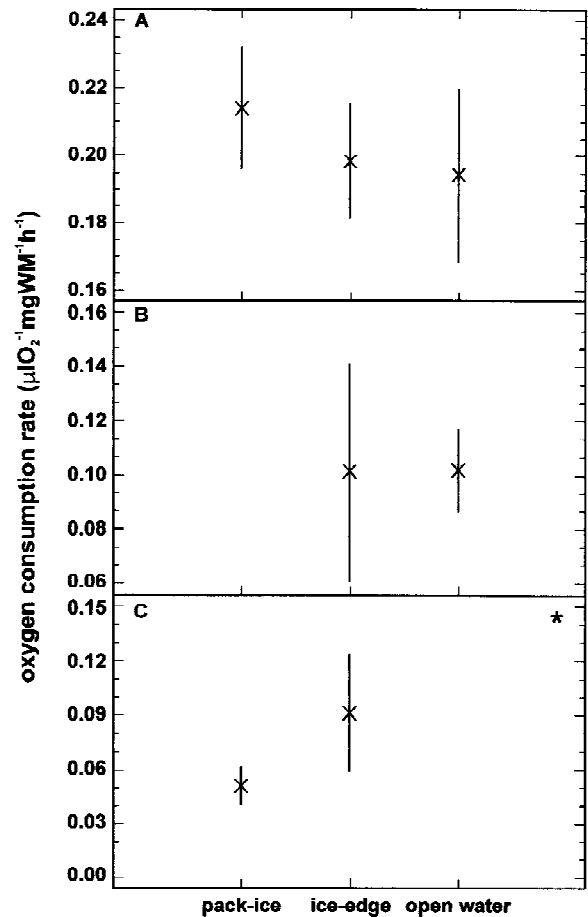
to diapause; consequently, a lower metabolism would be expected. The average summer routine metabolic rate for *R. gigas* in this study was 0.470 μl O_2 mg DM^{-1} h^{-1}; this is exactly the same rate as obtained by Rakusa-Suszczewski et al. (1976), measured with a Gilson respirometer in the winter. The routine metabolic rate of *C. propinquus* obtained, was 0.674 μl O_2 mg DM^{-1} h^{-1}; which was similar to the rate obtained by Drits et al. (1993), using electron transport system (ETS) activity in the fall (0.659 μl O_2 mg DM^{-1} h^{-1}). *Paraeuchaeta antarctica*, the largest of the copepods examined in the present study, also showed the lowest dry-mass specific respiration rate: 0.328 μl O_2 mg DM^{-1} h^{-1}. This rate is higher than that reported by Hirche (1984), 0.160 μl O_2 mg DM^{-1} h^{-1}, for

late summer. In contrast, *M. gerlachei,* which was the smallest copepod studied, also showed the highest dry-mass specific metabolic rate, 1.135 μl O_2 mg DM^{-1} h^{-1}. This rate agrees well with that reported by Ikeda & Mitchell (1982), 1.208 μl O_2 mg DM^{-1} h^{-1}. *Heterohabdus farrani*, a strictly carnivorous species, also showed a high metabolic rate, 1.133 μl O_2 mg DM^{-1} h^{-1}. *Gaetanus tenuispinus*, an omnivorous copepod, showed an intermediate rate of metabolism, 0.680 μl O_2 mg DM^{-1} h^{-1}.

Differences in the metabolic responses of the five dominant Antarctic calanoid copepods to the spring ice-edge phytoplankton bloom are attributable partially to differences in life histories, and partially to differences in their feeding preferences. The progressive occupation from south to north in the field study, described earlier, enabled us to see the copepods' life cycle in 'fast forward'. Life histories of copepods were intercepted progressively further along in the seasonal cycle, and their metabolism compared between pre-bloom conditions (pack-ice region), bloom (ice-edge region), and post-bloom conditions (open water).

The herbivorous species *C. acutus*, *R. gigas* and *C. propinquus*, and the carnivorous *P. antarctica* showed lower metabolic rates in the pack-ice region and higher rates in the ice-edge and open-water regions. The lower metabolic rates in the pack ice were attributable to a starved, or poor nutritional condition because of the lower levels of food (phytoplankton) in this region. Reduced metabolic rates in starved animals have been demonstrated in several studies (Ikeda & Dixon,1982; Kiørboe et al., 1985; Torres et al., 1994a, 1996). These low rates can be related to a decrease in energy expenditure associated with feeding metabolism, activity, and growth. A comparison of the wet mass specific metabolic rates reported on this study with feeding rates in response to a spring bloom in the Bellingshausen Sea, obtained by Atkinson & Shreeve (1995), supports this statement. *Rhincalanus gigas* and *C. acutus* showed low metabolic and feeding rates. On the other hand, *C. propinquus* and *M. gerlachei* showed high metabolic and feeding rates.

Calanoides acutus overwinters in diapause between 400 and 1000 m (Andrews, 1966). In spring, copepodites return to surface waters to feed and reproduce, usually exerting a high grazing impact on phytoplankton stocks (Atkinson & Shreeve, 1995). Its reproduction is timed in a way that copepodites can capitalize on the bloom and the elevated post-bloom production, characteristic of the study area. This species accumulates lipid for times of low phytoplankton availability

(Clarke, 1984). In the present study, not only were metabolic rates higher in the ice edge and open water, but water levels were lower. Since water and lipid levels exhibit an inverse relationship (Donnelly et al., 1990), it is likely that as the bloom develops, *C. acutus* starts accumulating energy in the form of lipids. In contrast, animals in the pack ice were in poor nutritional condition. Lipid-poor adult females may represent specimens recently molted from the CV stages or recently spent females (Hagen, 1996).

Rhincalanus gigas, like *C. acutus*, is an herbivorous species that overwinters in diapause at depths of 400 – 1000 m (Voronina, 1970; Hopkins et al., 1993). However, unlike *C. acutus,* it apparently has a life cycle of more than 1 year, reproducing in late summer (Marin, 1988; Ward et al., 1997). The high water content observed in *R. gigas* (86.6%±2.5, Table 2) implies a low lipid storage (Donnelly et al., 1994) and agrees with its life history in two ways. First, it may not need large energy stores throughout the winter, since it shows depressed metabolism in this season and consequently does not have a high energy demand. Secondly, with reproduction delayed until late summer, it can rely on phytoplankton for energy to grow and later reproduce. Its summer metabolic rates were similar between open water and ice-edge regions, and in both regions these rates were higher than in the pack ice.

Calanus propinquus does not undergo a true diapause, like *C. acutus* and *R. gigas* (Hopkins et al., 1993). Part of its population remains in surface waters during the winter (Marin, 1988; Bathmann et al., 1993), although the species as a whole spreads out through the upper 1000 m. It is an opportunistic feeder during the winter (Hopkins et al., 1993). Like *C. acutus*, it reproduces in the spring and summer and developing copepodites can exploit the phytoplankton bloom. *Calanus propinquus* metabolism in the three regions of the study area (Fig. 5) showed the same pattern as that obtained for all the copepods and tracked the chlorophyll-*a* concentration (Fig. 4). The routine rate in the pack-ice region was approximately half that in the other two regions, and was not significantly different from the winter rates obtained by J. J. Torres in 1988 (Table 3). Even though *C. propinquus* can potentially rely on non-phytoplankton food sources during the winter, it shows a reduced metabolism at that season. Significant differences were observed among the metabolic rates in the three regions, and thus the bloom appears to be important also for adult *C. propinquus*. The pattern observed in *C. acutus*, with

water levels decreasing towards open water, was also observed in *C. propinquus*.

Paraeuchaeta antarctica is a large carnivorous copepod, yet has a high water content (Donnelly et al., 1990). It feeds year-round, primarily on copepods (Hopkins, 1985; Hopkins & Torres, 1989). Its lowered metabolism in the winter season and in the pack-ice region is puzzling. It has been suggested that *P. antarctica* has constantly high lipid levels (Clarke, 1984; Donnelly et al., 1990; Hagen, 1996) because the species is not strongly affected by the seasonal production cycle and does not use lipids as a primary energy depot (Hagen, 1996). However, because of the low metabolism in the animals from the pack-ice region, we believe that *P. antarctica* is affected by a shortage in food supply.

Metridia gerlachei is a small, omnivorous calanoid copepod that actively feeds in the winter (Hopkins et al., 1993). It shows a prolonged reproductive cycle, from late winter to late summer (Schnack-Schiel & Hagen, 1995). Given its life history, it is not surprising that *M. gerlachei* did not show a change in routine rates between regions. However, a decline in water content from the pack ice towards the open water region (Table 2) was observed, indicating that lipid was being accumulated during the season, in agreement with Hagen & Schnack-Schiel (1996).

The spring ice-edge bloom has a strong effect on the zooplankton community in the marginal ice zone in Antarctica. Not only primarily herbivorous species such as *C. acutus*, *R. gigas* and *C. propinquus*, but also carnivorous species such as *P. antarctica* showed higher metabolic rates in bloom (ice-edge) or post-bloom (open-water) conditions, than in the pre-bloom (pack ice). Even the omnivorous species, *M. gerlachei* and *G. tenuispinus*, which showed no change in metabolism, showed a decrease in water levels toward open water, indicating that they were accumulating energy and thus exploiting the increase in food supply. Thus, animals showing Type 1 and Type 2 overwintering strategies rely on the spring bloom for survival and completion of their life cycle.

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