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Metabolism of Antarctic micronektonic crustacea across a summer ice-edge bloom: respiration, composition, and enzymatic activity

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Abstract

The Antarctic marginal ice zone is an important oceanic front separating the pack-ice and open-water environments. During summer, the retreating pack ice creates a meltwater lens in the euphotic zone, allowing primary producers and microheterotrophs to flourish in a discrete bloom just seaward of the retreating ice edge that lasts about 60 days. The purpose of the present study was to see if the ice-edge bloom had a discernible effect on the metabolism and physiological condition of Antarctic micronekton similar to that observed in zooplankton species. We also wished to assess the importance of the summer season to species' life cycles. Two major data sets were collected on 25 species in the following taxonomic groups: amphipods, cephalopods, decapods, euphausiids, isopods, mysids, ostracods, and polychaetes. The first data set described the metabolic rates of individuals in areas of the marginal ice zone with widely different levels of chlorophyll biomass to investigate the effect of the ice-edge bloom on metabolism. Additionally, summer metabolic rates were compared with data from other seasons. The second data set detailed the levels of protein, water, ash, RNA and DNA, and the activities of metabolic enzymes (citrate synthase and malate dehydrogenase) to examine the efficacy of biochemical indices as predictive tools for metabolism. Results suggested that the mobility of the micronektonic species eliminated most direct effects of the bloom on metabolism. Individuals captured in very different productivity regimes showed few significant differences in the metabolic indicators listed above. Isolated cases of changes in body composition and enzyme activity, however, implied that longer-term effects of the bloom may be exhibited. Seasonal increases in metabolism from winter to summer were observed in the euphausiids *Euphausia superba, E. triacantha*, and *Thysanoessa macrura* and the amphipod *Vibilia stebbingi*. It was concluded that the seasonal shifts were indicative of a "type 2" or compromise overwintering strategy whereby metabolism drops without an accompanying dormant state. Protein content and MDH activity were found to be the best predictors of respiration rate, while nucleic acid measures only correlated with respiration in immature specimens.

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1. Introduction

The Antarctic marginal ice zone (MIZ) is an important oceanic front separating the pack-ice and open-water environments. When sea ice melts in the summer, a low-density meltwater lens is formed over the higher-salinity seawater below, creating a physically stable and nutrient-rich layer seaward of the ice edge. The summer increase in insolation and penetration of light into the layer creates optimal conditions for phytoplankton growth (Sakshaug and Skjoldal, 1989). The resulting ice-edge bloom contributes about 40% of the total annual production in the Southern Ocean (Smith and Sakshaug, 1990). However, it is ephemeral, lasting for approximately 60 days as a rolling wave of high production following the retreating ice edge (Smith and Nelson, 1985). During this period, as the ice progressively melts southward and the phytoplankton bloom moves with it, herbivorous species obtain much of their energy for growth and reproduction for the year.

The short, highly pulsed period of maximum production and the months of extremely low productivity that follow it pose a challenge to longer-lived consumer species with generation times of a year or more. Three types of overwintering strategies were proposed for Antarctic zooplankton and micronekton by Torres et al. (1994b). Type 1, exhibited by some calanoid copepods, is characterized by accumulation of large lipid deposits accompanied by a depressed metabolism (diapause) and sinking of the population maximum to mesopelagic depths (400–1000 m). In the Type 2 strategy, activity and metabolic rates are reduced after the summer season (Quetin and Ross, 1991; Torres et al., 1994a), but no true dormancy is shown. The individuals may show depletion of metabolic reserves (Drits et al., 1993; Torres et al., 1994b) in addition to expanding their spectrum of food items (Daly, 1990; Huntley et al., 1994). The Type 2 strategy has been observed in *Euphausia superba* and hyperiid amphipods such as *Cyllopus lucasii* and *Vibilia stebbingi*. Type 3 is exhibited by decapods and gammarid amphipods, which are opportunistic feeders, and show no difference in metabolic rates or compositional attributes during the winter season.

The purpose of the present study was to see if the ice-edge bloom had a discernible effect on the metabolism and physiological condition of Antarctic micronekton, similar to that observed in zooplankton species (Geiger et al., 2001; Kawall et al., 2001). By definition, micronektonic species are capable of purposeful extended horizontal movement. Their ability to move in and out of areas of higher production might eliminate the obvious effects on metabolic processes. We also wished to assess the importance of the summer season on species' life cycles (cf. Meyer et al., 2002a, b; Atkinson et al., 2002). The following data sets on biomass-dominant micronektonic species were collected: (1) oxygen consumption rates in areas with widely different levels of primary productivity to investigate the effect of the ice-edge bloom, and in addition, providing summer metabolic data for comparison with data from other seasons; and (2) proximate composition (water, ash, protein, lipid, and chitin), RNA and DNA content, and the activities of intermediate metabolic enzymes citrate synthase (CS) and malate dehydrogenase (MDH) to examine the efficacy of biochemical indices as predictive tools for metabolism.

2. Methods

2.1. Collection of specimens

Field work was done in the Weddell Sea vic. 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 continuously monitoring chlorophyll biomass as in vivo fluorescence (Fig. 1). The first was a west–east transect within the marginal ice zone to examine variability within the core of the bloom. The second was a north–south transect to look at the north–south influence of the bloom. The transect was initiated north of the ice edge where in vivo fluorescence values had dropped to values well below those found in the bloom. From its most northerly point in open water, the transect

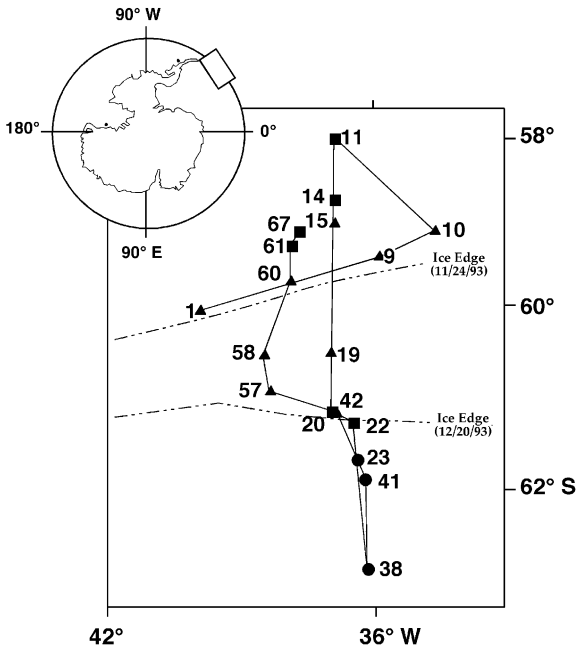

Fig. 1. Cruise track during November–December, 1993 within the MIZ in the northwest Weddell Sea. Station numbers shown depict the first and last for each area within the MIZ: (■) open water, (▲) ice edge, and (●) pack ice.

proceeded through the core of the bloom in the marginal ice zone into the pack ice until the fluorescence signal from the bloom was absent at the southern end. At that point, zonal occupations of 5–6 days were performed in each of three MIZ areas: pack ice, ice edge, and open water. The biological and physical framework of each region was provided by CTD/rosette casts, primary productivity measurements, and chlorophyll biomass determinations (see Kawall et al. (2001) for a more detailed description of the bloom and marginal ice-zone conditions).

Sampling was conducted with two nets, an obliquely towed Tucker trawl (9 m^2 mouth area) and a vertically deployed Plummet net (1 m^2 mouth area). Each net terminated in a blind codend, which maintained the animals in good condition for physiological studies. Specimens for respiration measurements were obtained predominantly from 0–200 m tows, while those frozen for biochemical assays were collected over 0–1000 m.

2.2. Respiratory measurements

On board, organisms were kept in buckets filled with cold (~0°C) sea water, and sorted for respirometry and biochemical assays. Oxygen consumption rates were determined by allowing individuals to deplete the oxygen in sealed, water-jacketed, lucite chambers filled with filtered (0.45 μm) sea water, at a controlled temperature of 0.5 °C. Chambers of different volumes (25–1340 ml) were used to accommodate different-sized specimens. Oxygen partial pressure (PO_2) was continuously monitored with Clark polarographic oxygen electrodes. Electrodes were calibrated before each experimental run with air- and nitrogen-saturated sea water. Data were recorded every minute for a period of 10–20 h using a computer-controlled data-logging system. A graph of oxygen partial pressure versus time was generated, allowing determination of the best slope representing the routine rate. The data acquired in the first hour were discarded because of the increased rates associated with handling stress. The lowest and highest respiratory rates observed for each run were designated the minimum and maximum rates. To control for possible O_2 consumption by microorganisms, one respirometer was kept without a specimen and oxygen partial pressure recorded as in the experimental chambers. No decrease in oxygen was observed in the control runs.

After respiratory measurements were taken, specimens were blotted dry, individually sealed in either plastic freezer bags or polypropylene vials, frozen in liquid nitrogen, and stored in a −80 °C freezer.

2.3. Biochemical assays

Identifications of species, sex, and developmental stage were verified in the laboratory. Individuals were then measured from the tip of the rostrum to the end of the telson (standard length (SL)), weighed (wet mass (WM)), and homogenized in deionized water with a glass tissue grinder followed by an Ultrasonic homogenizer. Dilutions (WM to water) varied from 1:9 in larger animals to 1:24 in smaller individuals. The homogenate was

kept cold (~0 °C) and aliquotted for the biochemical assays. Water content, dry mass (DM), ash-free dry mass (AFDM), and protein were measured using the methods of Donnelly et al. (1990). Lipids were extracted from aliquots using the methods of Bligh and Dyer (1959). Extracts were dried at 30 °C under a flow of nitrogen and total lipid content determined gravimetrically. Hexosamine (= chitin) was measured using the methods of Donnelly et al. (1994), with D-glucosamine hydrochloride as the standard. Nucleic acid (RNA, DNA) contents were measured fluorimetrically following the procedures of Bentle et al. (1981), with bakers' yeast RNA and calf thymus DNA used as standards. CS activities were determined using the methods of Torres and Somero (1988a). MDH activities were determined using the methods of Childress and Somero (1979), with 20 mM $MgCl_2$ being substituted for 20 mM $MgSO_4$.

2.4. Data

Respiratory rates are expressed as μl of oxygen consumed per individual ($\mu l\, O_2\, ind^{-1}\, h^{-1}$) and per milligram wet mass per hour ($\mu l\, O_2\, mg WM^{-1}\, h^{-1}$, $\dot{V}O_2$). Water content is expressed as percent of wet mass (%WM), and ash content as percent of dry mass (%DM). Protein, lipid and hexosamine are expressed as total content ($mg\, ind^{-1}$) and as a mass percent (%WM, %AFDM). Nucleic acids are expressed as total content ($mg\, ind^{-1}$) and as a ratio (RNA:DNA). Enzymatic activity is expressed as μmol of substrate converted to product per min per total WM (International Unit (IU) ind^{-1}) and as activity per gram wet mass ($IU\, g\, WM^{-1}$).

Oxygen consumption rates and biochemical measures were grouped by size classes within each species. The size classes were created by halving each order of magnitude change in WM (as in Torres et al. (1994a)); i.e., size class 1: 0.0–4.9 mg, size class 2: 5.0–9.9 mg, size class 3: 10.0–49.0 mg, size class 4: 50.0–99.9 mg, size class 5: 100–499.9 mg, size class 6: 500–999.9 mg, and size class 7: 1000–4999.9 mg. All krill length measurements were from the tip of the rostrum to the end of the telson, slightly different from the total length used by Mauchline and Fisher (1969), but used several times previously in the literature (Fraser, 1936; Einarsson, 1945; Nemoto, 1957).

Data are reported as mean ± standard deviation. Means were tested for differences using one-way analysis of variance (ANOVA), and when variances were not homogeneous, a Kruskal–Wallis test (KW) was applied (Zar, 1974). Simple regressions were fitted using the least-squares method. Regressions were compared using analysis of covariance (ANCOVA). The level of significance for all statistical analyses was $p < 0.05$.

3. Results

3.1. Oxygen consumption rates

Routine, maximum and minimum oxygen consumption rates for 23 species are shown in Table 1. Mean $\dot{V}O_2$ ranged from 0.006 in the largest specimens of *Gigantocypris mulleri* to 0.403 in the smallest specimens of *C. lucasii*. Rates for all species fell into two general groups. Species in the first group with mean rates between 0.006 and 0.094 $\mu l\, O_2\, mg\, WM^{-1}\, h^{-1}$ included all the gammarid amphipods; the hyperiid amphipods *Hyperiella antarctica*, *Megalanceola remipes*, *M. stephenseni* and large *Primno macropa*; the cephalopod *Galiteuthis glacialis*; all the decapods except for the smallest size class of *Pasiphaea scotiae*; the mysid *Boreomysis rostrata*; the ostracod *G. mulleri*; and the polychaete *Tomopterus carpenteri*. Species in the second group with mean rates between 0.122 and 0.403 $\mu l\, O_2\, mg\, WM^{-1}\, h^{-1}$ included the hyperiid amphipods *C. lucasii*, *Hyperoche medusarum*, small *P. macropa*, and *V. stebbingi*; small *P. scotiae*; all the euphausiids; and the isopod *Anuropus australis*. All of the mesopelagic species examined (i.e. those with a minimum depth of occurrence > 200 m) fell into the first group, while those species with MDOs < 200 m had representatives in both groups. Mass-specific rates showed an inverse relationship with size in all species examined over multiple size classes. The ratios of maximum to routine rate and maximum to minimum rate were similar for all species, with

Table 1
Oxygen consumption rates for 23 species of invertebrate micronekton

Group					O_2 consumption rates ($\mu l\, O_2\, mg\, WM^{-1}\, h^{-1}$)			Conversions	
Species	MDO (*m*)	SC (*n*)	SL (mm) [range]	WM (mg)	Routine	Min	Max	DM	AFDM
Amphipods (Gammarid)									
Cyphocaris faueri	40	5 (1)	31.0	467.4	0.082	0.056	0.119	3.38	4.31
C. richardi	340	4 (1)	15.0	54.2	0.081	nd	nd	nd	nd
		5 (10)	25.1 [21.0–31.5]	287.0 (105.2)	0.067 (0.018)	0.034 (0.012)	0.110 (0.037)	4.64	5.99
		6 (3)	34.3 [31.0–36.0]	700.3 (48.0)	0.038 (0.009)	0.019 (0.008)	0.068 (0.030)	2.55	2.93
		7 (1)	40.0	1106.9	0.042	0.023	0.087	2.97	3.39
Cleonardo longipes	Nd	5 (1)	21.5	151.2	0.049	nd	nd	3.94	4.85
Parandania boecki	270	6 (1)	27.0	886.5	0.030	0.019	0.051	6.29	9.17
Amphipods (Hyperiid)									
Cyllopus lucasii	0	3 (1)	11.0	48.1	0.403	0.120	0.630	nd	nd
		4 (5)	13.0 [12.0–14.5]	89.6 (9.0)	0.230 (0.077)	0.123 (0.060)	0.376 (0.146)	5.53	7.08
		5 (10)	18.6 [17.5–22.0]	241.7 (30.0)	0.130 (0.031)	0.065 (0.026)	0.203 (0.054)	4.76	5.96
Hyperiella antarctica	0	4 (1)	11.0	67.2	0.067	0.027	0.126	nd	nd
Hyperoche medusarum	0	4 (1)	11.0	62.1	0.167	0.101	0.246	nd	nd
Megalanceola remipes	100	5 (1)	30.0	418.9	0.042	0.023	0.056	8.41	12.36
M. stephenseni	nd	7 (1)	42.0	4997.1	0.008	0.003	0.013	15.15	25.64
Primno macropa	0	3 (1)	9.5	36.0	0.266	nd	nd	nd	nd
		4 (1)	15.0	94.6	0.094	0.038	0.186	5.26	6.67
Vibilia stebbingi	0	3 (9)	10.7 [8.0–12.0]	38.6 (10.5)	0.321 (0.114)	0.202 (0.093)	0.555 (0.173)	nd	nd
		4 (8)	12.3 [11.0–13.5]	58.4 (5.7)	0.236 (0.051)	0.119 (0.032)	0.404 (0.107)	nd	nd
Cephalopods									
Galiteuthis glacialis	50	5 (2)	17.3[a] [16.0–18.5]	423.7 (70.4)	0.039 (0.003)	0.014 (0.008)	0.065 (0.0002)	13.94	17.93
		6 (6)	24.1[a] [22.0–29.0]	771.6 (135.5)	0.033 (0.009)	0.019 (0.006)	0.055 (0.012)	11.72	14.01
Decapods									
Gennadas kempi	500	7 (2)	52.5 [50.0–55.0]	1839.0 (387.8)	0.037 (0.001)	0.017 (0.008)	0.054 (0.010)	3.28	3.68
Nematocarcinus lanceopes	0	5 (3)	42.8 [38.0–46.0]	308.3 (23.3)	0.073 (0.040)	nd	nd	4.50	5.23
Pasiphaea scotiae	100	5 (2)	35.8 [33.0–38.5]	299.5 (110.4)	0.212 (0.189)	0.128 (0.139)	0.334 (0.249)	3.51	3.85
		6 (1)	47.0	725.5	0.052	0.015	0.096	2.67	2.90
		7 (3)	73.5 [67.0–81.0]	2927.8 (770.8)	0.034 (0.013)	0.018 (0.008)	0.057 (0.024)	3.06	3.31
		8 (1)	100.0	5421.9	0.028	0.019	0.037	2.78	2.98
Petalidium foliaceum	500	6 (1)	43.0	792.2	0.025	0.013	0.036	3.19	3.48
Euphausiids									
Euphausia superba	0	3 (16)	15.7 [12.0–18.0]	31.7 (9.4)	0.291 (0.078)	0.146 (0.084)	0.516 (0.140)	nd	nd
		4 (5)	21.3 [20.0–22.0]	81.2 (14.8)	0.239 (0.046)	0.132 (0.028)	0.375 (0.074)	4.44	5.12
		5 (8)	28.3 [26.0–36.5]	206.3 (114.5)	0.160 (0.018)	0.085 (0.014)	0.250 (0.042)	5.38	6.36
		6 (9)	42.9 [39.0–48.0]	742.0 (102.8)	0.122 (0.025)	0.071 (0.019)	0.177 (0.037)	5.57	6.73
		7 (23)	51.5 [49.0–58.0]	1403.0 (313.1)	0.130 (0.026)	0.086 (0.025)	0.183 (0.032)	4.62	5.42
E. triacantha	0	5 (2)	35.5 [35.0–36.0]	296.0 (3.6)	0.148 (0.022)	0.072 (0.025)	0.215 (0.046)	4.84	5.50
Thysanoessa macrura	100	3 (16)	16.6 [14.5–18.5]	35.7 (7.9)	0.234 (0.072)	0.092 (0.039)	0.415 (0.152)	3.55	4.23
		4 (7)	22.3 [19.0–24.0]	72.3 (14.3)	0.245 (0.069)	0.082 (0.037)	0.389 (0.203)	5.05	6.11
		5 (2)	28.0 [27.0–29.0]	164.4 (10.7)	0.188 (0.020)	0.118 (0.050)	0.337 (0.086)	3.31	3.64
Isopods									
Anuropus australis	100	6 (1)	23.0	528.0	0.214	0.134	0.251	4.51	5.68
Mysids									
Boreomysis rostrata	550	6 (1)	45.0	934.8	0.055	0.022	0.076	2.70	2.85
Ostracods									
Gigantocypris mulleri	500	5 (1)	10.0[b]	431.0	0.020	0.011	0.036	14.39	20.82
		6 (1)	13.0[b]	739.2	0.011	0.005	0.015	14.80	23.00
		7 (4)	17.0[b] [15.0–18.0]	1803.6 (458.8)	0.006 (0.002)	0.003 (0.001)	0.013 (0.007)	12.10	16.41

Table 1 (*continued*)

Group					O_2 consumption rates ($\mu l\, O_2\, mg\, WM^{-1}\, h^{-1}$)			Conversions	
Species	MDO (*m*)	SC (*n*)	SL (mm) [range]	WM (mg)	Routine	Min	Max	DM	AFDM
Polychaetes									
Tomopterus carpenteri	0	5 (3)	36.8 [33.0–39.0]	354.5 (55.5)	0.097 (0.015)	0.056 (0.022)	0.163 (0.015)	9.32	12.65
		6 (2)	47.0 [41.0–53.0]	788.3 (294.2)	0.060 (0.020)	0.030 (0.023)	0.091 (0.007)	8.26	10.71

Values are mean ± standard deviation. Multiply WM-specific rate by conversion factors to yield DM-specific or AFDM-specific rates. Minimum depth of occurrence (MDO) data from Lancraft et al., 1989, 1991). SC = sizeclass, *n* = number of replicates used in determining respiration rates, SL = standard length, WM = wet mass, DM = dry mass, AFDM = ash-free dry mass, nd = no data.

[a]values are mantle length.

[b]values are sphere diameter.

overall means of 1.57 ± 0.19 (range: 1.17–1.98) and 3.25 ± 0.88 (range: 1.88–4.96), respectively.

A total of 61 respiratory runs on *E. superba* of different sexes and developmental stages (Table 2a, b) allowed further investigation of metabolism in this species. Adults were defined as individuals with a total length greater than ~32 mm (Ikeda, 1985). Females carrying spermatophores or eggs were considered separately. As expected, the mean rate value for mass-specific oxygen consumption was significantly higher in immature specimens ($p < 0.003$); however, no differences in mean O_2 consumption rate were observed between any adult group ($p > 0.94$) (Table 2a). The slopes of the regression lines for respiration rate ($\mu l\, O_2\, ind^{-1}\, h^{-1}$, y) vs. WM (mg, x) were also found to be significantly different between immature and adult specimens ($p < 0.00001$) (Table 2b).

Six species were respired in sufficient numbers to allow comparison of metabolism between the different areas of the marginal ice zone (Table 3). No significant differences ($p > 0.40$) in mean VO_2 between areas were found for *Cyphocaris richardi*, *V. stebbingi*, *G. glacialis,* and *Thysanoessa macrura.* Significant differences in mean VO_2 were found between ice-pack and open-water areas in *C. lucasii* and between the ice-pack and edge areas in *E. superba*; however, these were due to differences in specimen size between areas for both these species. In *C. lucasii* there was a clear inverse pattern of decreasing WM and increasing VO_2 from ice-pack to edge to open water. In *E. superba* the size effect was less apparent. While mean WM values were similar between ice-pack and edge areas (647 vs. 616 mg), median values were not (719 vs. 153 mg), indicating a greater number of smaller specimens in the edge group. Examining only *E. superba* specimens greater than size class 3, there were no significant differences in mean VO_2 between areas ($p > 0.83$, mean VO_2 ice:edge:open = 0.150:0.139:0.137).

Regressions of routine rate ($\mu l\, O_2\, ind^{-1}\, h^{-1}$, y) vs. WM (mg, x) within each area for *C. richardi*, *C. lucasii*, *V. stebbingi*, *E. superba* and *T. macrura* were also compared. No significant differences ($p > 0.50$) in either the slope or intercept were found for any species. Consequently, data from all areas were combined to generate regressions of routine rate vs. WM for those species with data over a size range ($n \geqslant 5$, Table 4). Only *G. mulleri* showed no noticeable change in oxygen consumption rate with increased mass.

3.2. Biochemical measures

Twenty-five species were analyzed for water, ash, protein and nucleic acid content, and the activities of CS and MDH (Table 5). Lipid and hexosamine content were analyzed in 15 of the species, but only on a subsample of specimens. Measures of compositional components (water, ash, protein, lipid, hexosamine) showed a range of values, reflecting differences in species' body type and ecology. Seven species (*Parandania boecki*, *Megalanceola* spp., *G. glacialis*, *Gnathophausia*

Table 2
(a) Biochemical parameters and oxygen consumption rates for *E. superba*. Values are mean ± standard deviation. (b) Regressions ($y = ax^b$) of oxygen consumption and nucleic acids vs. WM, and protein vs. RNA content for *E. superba*

(a)

Sex/developmental stage	*n*	SL (mm) (range)	WM (mg)	Water (%WM)	Ash (%DM)	Protein (%WM)	Protein (%AFDM)	RNA:DNA	CS (IU g WM^{-1})	MDH (IU g WM^{-1})	O_2 consumption rates (μl O_2 mg WM^{-1} h^{-1})		
											Routine	Min	Max
Immature	29	19.0 (12–27)	65.6 (50.0)	81.3 (1.6)	15.5 (2.1)	8.0 (1.5)	59.4 (10.9)	2.09 (0.66)	2.19 (1.18)	31.00 (17.63)	0.253 (0.082)	0.130 (0.070)	0.434 (0.154)
♂	12	48.0 (32–53)	1139.5 (393.7)	78.3 (1.9)	16.1 (3.2)	9.1 (0.8)	50.3 (7.6)	2.65 (0.55)	2.92 (0.77)	99.20 (43.84)	0.126 (0.026)	0.088 (0.020)	0.179 (0.027)
♀	11	47.0 (39–51)	1007.3 (259.5)	80.5 (2.6)	17.4 (1.8)	10.0 (1.8)	62.3 (7.2)	2.45 (1.60)	1.82 (0.68)	83.57 (22.22)	0.121 (0.027)	0.072 (0.029)	0.176 (0.042)
♀ w/ spermatophore	7	46.1 (39–52)	970.0 (278.3)	83.3 (1.8)	17.5 (1.1)	9.3 (1.5)	66.9 (5.0)	2.55 (1.74)	1.92 (0.45)	68.19 (32.94)	0.143 (0.023)	0.078 (0.027)	0.204 (0.025)
♀ w/ eggs	7	54.7 (50–58)	1720.0 (363.1)	76.4 (1.5)	11.6 (1.5)	9.2 (1.6)	44.2 (8.2)	5.64 (1.91)	2.23 (0.87)	66.23 (13.43)	0.124 (0.022)	0.090 (0.013)	0.168 (0.028)

(b)

Stage	μl O_2 ind^{-1} h^{-1} vs. WM (mg)	RNA (mg) vs. WM (mg)	DNA (mg) vs. WM (mg)	RNA:DNA vs. WM (mg)	Protein (mg) vs. RNA (mg)
Immature (SC 3,4,5)	$y = 0.759x^{0.710\pm0.048}$ (0.89, 29, <0.0000)	$y = 0.015x^{0.907\pm0.062}$ (0.89, 29, <0.0000)	$y = 0.023x^{0.617\pm0.068}$ (0.75, 30, <0.0001)	$y = 0.472x^{0.362\pm0.074}$ (0.46, 30, <0.0001)	$y = 7.854x^{1.091\pm0.075}$ (0.89, 29, <0.0000)
Adult (SC 6,7)	$y = 0.086x^{1.053\pm0.111}$ (0.75, 32, <0.0001)	$y = 0.017x^{0.816\pm0.287}$ (0.20, 34, 0.0077)	$y = 0.014x^{0.701\pm0.200}$ (0.27, 35, 0.0013)	nc	nc

b values are slope ± standard error. Values in parentheses are: correlation coeficient (r^2), *n*, significance level (*p*). SC = sizeclass, nc = no correlation.

Table 3
Oxygen consumption rate and biochemical parameters for six micronekton species from different areas of the MIZ

Species	MIZ area	n	WM (mg)	O_2 consumption rate ($\mu lO_2 mg WM^{-1} h^{-1}$)	Water (%WM)	Ash (%DM)	Protein (%WM)	Protein (%AFDM)	CS ($IU g WM^{-1}$)	MDH ($IU g WM^{-1}$)	RNA:DNA
Cyphocaris richardi	Edge	7	220.8 (114.7)	0.065 (0.020)	81.2 (4.1)	31.0 (9.5)	5.4 (1.7)	39.0 (5.7)	0.99 (0.98)	9.16 (7.86)	3.49 (1.77)
	Open	9	511.9 (325.8)	0.057 (0.021)	66.7 (10.6)	16.7 (5.1)	8.4 (2.4)	31.1 (5.3)	1.67 (0.87)	13.57 (7.80)	4.23 (1.82)
Cyllopus lucasii	Ice	5	240.5 (30.9)	0.130 (0.035)	78.3 (4.6)	19.8 (4.2)	7.6 (0.6)	44.7 (7.6)	2.20 (0.57)	50.63 (4.53)	3.88 (3.38)
	Edge	6	192.4 (80.5)	0.173 (0.083)	80.2 (2.3)	20.2 (1.3)	7.1 (0.7)	45.7 (2.8)	2.82 (0.98)	53.81 (10.09)	3.13 (1.90)
	Open	5	111.2 (80.0)	0.213 (0.082)	80.8 (0.0)	23.6 (1.6)	7.7 (1.1)	51.4 (1.6)	3.50 (1.77)	55.39 (10.70)	4.31 (1.62)
Vibilia stebbingi	Edge	12	44.0 (12.6)	0.275 (0.107)	nd	nd	7.4 (1.8)	nd	1.26 (1.17)	50.98 (27.73)	16.03 (5.32)
	Open	6	56.6 (8.9)	0.297 (0.082)	nd	nd	7.8 (1.5)	nd	0.91 (1.44)	41.10 (33.99)	18.36 (9.22)
Galiteuthis glacialis	Ice	4	750.2 (255.3)	0.032 (0.013)	91.8 (0.4)	18.0 (1.1)	2.8 (0.2)	41.0 (2.1)	1.01 (0.16)	2.40 (0.80)	2.10 (0.20)
	Edge	5	737.6 (119.6)	0.035 (0.008)	91.5 (0.6)	15.1 (1.6)	3.1 (0.3)	42.1 (2.3)	1.09 (0.20)	2.81 (0.85)	1.72 (0.38)
	Open	3	681.3 (256.8)	0.036	91.9 (1.3)	17.3 (2.6)	2.9 (0.9)	42.4 (5.3)	1.09 (0.31)	4.36 (2.31)	2.53 (0.33)
Euphausia superba	Ice	18	647.3 (414.8)	0.146 (0.034)	82.7 (2.1)	17.3 (1.3)	9.0 (1.4)	63.6 (6.6)	2.36 (0.80)	55.46 (26.17)	2.79 (1.38)
	Edge	41	615.5 (698.0)	0.206 (0.062)	78.7 (2.4)	15.8 (3.0)	8.7 (1.3)	55.1 (12.1)	2.31 (0.80)	60.81 (34.61)	2.62 (2.12)
	Open	7	1376.6 (656.2)	0.137 (0.033)	77.8 (2.6)	12.7 (2.9)	8.9 (1.4)	45.5 (8.5)	1.85 (1.25)	73.03 (36.82)	2.73 (0.82)
Thysanoessa macrura	Ice	12	53.0 (24.8)	0.272 (0.083)	80.3	17.7	9.2 (1.0)	56.7	0.06 (0.01)	38.59 (14.74)	2.95 (1.25)
	Edge	14	41.3 (12.2)	0.210 (0.045)	78.6 (1.5)	16.8 (0.5)	9.8 (1.2)	53.0 (4.6)	0.39 (0.54)	37.83 (19.04)	2.16 (0.88)

Values are mean ± standard deviation.

gigas, *G. mulleri*, and *T. carpenteri*) had high water levels (84–93%WM). Except for *G. glacialis*, those species also tended to have the highest ash levels (23–41%DM). Protein ranged from 0.8 to 13.3%WM (19.0–61.4%AFDM) and was highest in euphausiids. Lipid ranged from 1.1 to 29.0%WM (15.2–86.1%AFDM) and, except for *Pasiphaea scotiae* and *G. mulleri*, was highest in deeper-living species. Hexosamine ranged from 0.6 to 2.6%WM (2.2–15.4%AFDM).

Mean values for RNA:DNA ratio ranged from 0.36 to 25.47. For *P. boecki*, *P. macropa* and *Themisto gaudichaudi*, the high ratio values may be related to reproduction. All the specimens of *P. boecki* and *P. macropa* were carrying eggs and the specimen of *T. gaudichaudi* had young in a brood pouch. Elevated ratio values were observed in other specimens that were without visible eggs or young: all *H. antarctica, H. medusarum*, *Megalanceola* spp., and *V. stebbingi*; and several *C. richardi*, *C. lucasii*, *P. scotiae*, *E. superba*, *T. macrura* and *T. carpenteri* specimens. A few specimens with eggs (3 *C. lucasii*, 2 *G. mulleri*) showed no elevation in RNA:DNA ratio.

Mass-specific enzyme activities exhibited both inter- and intraspecific variability. Activities were generally 1–2 orders of magnitude higher in MDH than CS, with mean values ranging from 0.06 to 5.31 for CS and from 0.77 to 88.76 for MDH.

Mass-related changes in biochemical measures were examineud in *C. richardi*, *C. lucasii*, *V. stebbingi*, *G. glacialis*, *P. scotiae*, *E. superba*, *T. macrura*, *G. mulleri* and *T. carpenteri* (Table 4). In all nine species, protein content scaled directly with WM. With the exception of *C. richardi*, no changes in relative composition (%WM, %AFDM) with mass (mg, m) were observed. In *Cyphocaris*, smaller specimens had higher water (%WM, w), ash (%DM, a), and protein (%AFDM, pr), as expressed by the following equations: $w = 194.44\,m^{-0.17\pm0.04}$, $r^2 = 0.60$, $p = 0.0005$; $a = 144.62\,m^{-0.44\pm0.05}$, $r^2 = 0.83$, $p < 0.0000$; $\mathrm{pr} = 60.17\,m^{-0.13\pm0.03}$, $r^2 = 0.57$, $p = 0.0008$. Limited data on lipid and hexosamine precluded statistical testing for any species. It is interesting to note, however, that the lower lipid shown for sizeclass 5 *C. richardi* was from a pregnant specimen whose eggs hatched prior to

Table 4
Regressions of oxygen consumption rate and biochemical parameters vs. WM, and protein vs. RNA content for nine species of micronekton

Species	Misc. parameter vs. WM (mg)									Protein (mg) vs. RNA (mg)
	$\mu l\, O_2\, ind^{-1}\, h^{-1}$	Protein (mg)	RNA (mg)	DNA (mg)	RNA:DNA	CS ($IU\, ind^{-1}$)	MDH ($IU\, ind^{-1}$)	CS ($IU\, gWM^{-1}$)	MDH ($IU\, gWM^{-1}$)	
Cyphocaris richardi	$y = 0.334x^{0.696\pm0.093}$ (0.81, 15, <0.0000)	$y = 0.020x^{1.211\pm0.124}$ (0.86, 17, <0.0000)	$y = 0.007x^{0.870\pm0.213}$ (0.53, 17, 0.0010)	$y = 0.002x^{0.825\pm0.179}$ (0.59, 17, 0.0003)	nc	$y = 0.0002x^{1.279\pm0.302}$ (0.54, 17, 0.0007)	$y = 0.001x^{1.310\pm0.287}$ (0.58, 17, 0.0003)	nc	nc	$Y = 21.259x^{0.792\pm0.192}$ (0.53, 17, 0.0009)
Cyllopus lucasi	$y = 2.457x^{0.460\pm0.118}$ (0.52, 16, 0.0016)	$y = 0.070x^{1.012\pm0.051}$ (0.97, 16, <0.0000)	$y = 0.010x^{0.864\pm0.255}$ (0.45, 16, 0.0045)	$y = 0.003x^{0.856\pm0.303}$ (0.36, 16, 0.0136)	nc	$y = 0.008x^{0.774\pm0.185}$ (0.57, 15, 0.0011)	$y = 0.055x^{0.992\pm0.079}$ (0.92, 15, <0.0001)	nc	nc	$Y = 13.217x^{0.536\pm0.159}$ (0.45, 16, 0.0045)
Vibilia stebbingi	$y = 1.976x^{0.477\pm0.211}$ (0.25, 17, 0.0391)	$y = 0.068x^{1.019\pm0.213}$ (0.59, 18, 0.0002)	nc	nc	nc	nc	$y = 0.022x^{1.15\pm0.563}$ (0.21, 18, 0.0579)	nc	nc	nc
Galiteuthis glacialis	$y = 0.323x^{0.650\pm0.293}$ (0.45, 8, 0.0685)	$y = 0.010x^{1.168\pm0.166}$ (0.83, 12, <0.0000)	$Y = 0.0002x^{1.345\pm0.256}$ (0.73, 12, 0.0004)	$y = 0.0002x^{1.194\pm0.251}$ (0.69, 12, 0.0008)	nc	$y = 0.0001x^{1.459\pm0.164}$ (0.89, 12, <0.0000)	$y = 0.00004x^{1.641\pm0.396}$ (0.63, 12, 0.0020)	$y = 0.051x^{0.459\pm0.165}$ (0.44, 12, 0.0193)	$y = 0.042x^{0.641\pm0.396}$ (0.21, 12, 0.1372)	$Y = 17.424x^{0.721\pm0.121}$ (0.78, 12, 0.0001)
Pasiphaea scotiae	$y = 0.730x^{0.612\pm0.123}$ (0.86, 6, 0.0075)	$y = 0.066x^{1.008\pm0.044}$ (0.99, 8, <0.0000)	$y = 0.004x^{0.850\pm0.098}$ (0.93, 8, 0.0001)	$y = 0.004x^{0.672\pm0.077}$ (0.94, 7, 0.0003)	$y = 0.599x^{0.262\pm0.062}$ (0.82, 6, 0.0130)	$y = 0.004x^{0.728\pm0.154}$ (0.79, 8, 0.0032)	$y = 0.021x^{0.993\pm0.062}$ (0.98, 8, <0.0000)	$y = 3.861x^{-0.272\pm0.154}$ (0.34, 8, 0.1271)	nc	$y = 50.470x^{1.096\pm0.140}$ (0.91, 8, 0.0002)
Euphausia superba	$y = 0.562x^{0.786\pm0.018}$ (0.97, 61, <0.0000)	$y = 0.062x^{1.059\pm0.012}$ (0.99, 66, <0.0000)	$y = 0.027x^{0.758\pm0.035}$ (0.88, 63, <0.0000)	$y = 0.021x^{0.648\pm0.027}$ (0.90, 65, <0.0000)	$y = 1.197x^{0.117\pm0.039}$ (0.12, 66, 0.0037)	$y = 0.001x^{1.065\pm0.054}$ (0.86, 62, <0.0000)	$y = 0.006x^{1.353\pm0.034}$ (0.96, 66, <0.0000)	nc	$y = 6.494x^{0.353\pm0.035}$ (0.62, 66, <0.0000)	$y = 10.676x^{1.228\pm0.062}$ (0.87, 63, <0.0000)
Thysanoessa macrura	$y = 0.298x^{0.927\pm0.106}$ (0.77, 25, <0.0000)	$y = 0.112x^{0.955\pm0.045}$ (0.94, 28, <0.0000)	$y = 0.004x^{1.081\pm0.176}$ (0.59, 28, <0.0001)	$y = 0.009x^{0.626\pm0.140}$ (0.43, 28, 0.0001)	$y = 0.416x^{0.454\pm0.158}$ (0.24, 28, 0.0079)	nc	$y = 0.015x^{1.203\pm0.208}$ (0.56, 28, <0.0001)	$y = 1.641x^{-0.695\pm0.371}$ (0.13, 26, 0.0732)	nc	$y = 9.052x^{0.487\pm0.098}$ (0.48, 28, <0.0001)
Gigantocypris mulleri	$y = 4.277x^{0.1097\pm0.080}$ (0.32, 6, 0.2442)	$y = 0.002x^{1.242\pm0.138}$ (0.95, 6, 0.0008)	$y = 0.0002x^{1.120\pm0.263}$ (0.82, 6, 0.0130)	$y = 0.001x^{0.857\pm0.333}$ (0.62, 6, 0.0616)	$y = 0.268x^{0.258\pm0.088}$ (0.68, 6, 0.0434)	nc	$y = 0.0001x^{1.428\pm0.378}$ (0.78, 6, 0.0195)	nc	nc	$y = 25.127x^{0.952\pm0.194}$ (0.86, 6, 0.0080)
Tomopteris carpenteri	$y = 3.256x^{0.397\pm0.224}$ (0.51, 5, 0.1743)	$y = 0.027x^{1.060\pm0.136}$ (0.94, 6, 0.0015)	nd	nd	nd	$y = 0.004x^{0.734\pm0.143}$ (0.87, 6, 0.0069)	$y = 0.002x^{1.115\pm0.422}$ (0.64, 6, 0.0573)	$y = 3.975x^{-0.266\pm0.143}$ (0.46, 6, 0.1369)	nc	nd

b values are slope ± standard error. Values in parentheses as in Table 2b. nc = no correlation, nd = not determined.

Table 5
Biochemical parameters for 25 species of micronekton

Group Species	MDO (m)	SC (n)	WM (mg)	Water (%WM)	Ash (%DM)	Protein (%WM)	Protein (%AFDM)	Lipid (%WM)	Lipid (%AFDM)	Hexosamine (%WM)	Hexosamine (%AFDM)	RNA:DNA	CS (IU gWM^{-1})	MDH (IU gWM^{-1})
Amphipods (Gammarid)														
Cyphocaris faueri	40	5 (1)	467.4	70.4	21.6	6.5	28.0	12.8	55.2	2.6	11.0	2.54	0.51	18.73
C. richardi	340	4 (1)	54.2	nd	nd	7.5	nd	nd	nd	nd	nd	2.11	3.11	13.12
		5 (11)	275.5 (106.8)	79.0 (5.2)	26.4 (10.1)	5.8 (2.1)	37.3 (6.1)	8.6	49.8	1.3	7.3	4.27 (1.85)	0.95 (0.82)	8.14 (6.86)
		6 (4)	691.4 (43.1)	61.0 (4.7)	12.9 (0.7)	10.3 (1.6)	30.3 (1.4)	21.7 (4.0)	61.3 (5.9)	2.3 (0.4)	6.6 (0.4)	4.69 (0.56)	1.93 (0.68)	16.79 (10.61)
		7 (1)	1106.9	66.3	12.5	7.2	24.3	25.4	86.1	1.6	5.3	2.63	1.46	15.59
Cleonardo longipes	nd	5 (1)	151.2	74.6	18.9	9.3	45.3	nd	nd	nd	nd	1.63	0.60	0.77
Parandania boecki	270	6 (1)	886.5	84.1	31.4	4.6	42.6	5.6	51.3	1.0	8.9	6.41	0.13	5.17
Amphipods (Hyperiid)														
Cyllopus lucasii	0	3 (1)	48.1	nd	nd	9.0	nd	nd	nd	nd	nd	3.87	5.31	68.55
		4 (5)	89.6 (9.0)	82.5 (2.5)	21.5 (4.6)	7.0 (1.0)	50.3 (3.3)	nd	nd	nd	nd	3.44 (2.20)	3.08 (1.49)	49.06 (9.91)
		5 (10)	241.7 (30.0)	78.9 (3.2)	20.4 (2.9)	7.5 (0.5)	45.5 (5.6)	nd	nd	nd	nd	3.86 (2.41)	2.50 (0.85)	54.27 (6.68)
Hyperiella antarctica	0	3 (1)	11.2	nd	nd	10.2	nd	nd	nd	nd	nd	nd	0.59	nd
		4 (1)	67.2	nd	nd	2.8	nd	nd	nd	nd	nd	11.53	1.34	4.25
Hyperoche medusarum	0	4 (1)	62.1	nd	nd	8.0	nd	nd	nd	nd	nd	10.98	2.23	31.30
Megalanceola remipes	100	5 (1)	418.9	88.1	31.9	3.5	43.2	nd	nd	0.6	8.0	9.50	0.20	16.74
M. stephenseni	nd	7 (1)	4997.1	93.4	40.9	1.3	32.6	nd	nd	0.6	15.4	8.55	0.15	1.41
Primno macropa	0	3 (2)	33.5 (3.6)	nd	nd	4.8 (1.7)	nd	nd	nd	nd	nd	25.47 (6.8)	0.39 (0.16)	42.00 (5.39)
		4 (1)	94.6	81.0	21.1	6.3	nd	nd	nd	nd	nd	11.43	0.10	34.35
Themisto gaudichaudi	0	4 (1)	81.5	nd	nd	6.1	nd	nd	nd	nd	nd	5.19	0.18	31.07
Vibilia stebbingi	0	3 (9)	38.6 (10.5)	nd	nd	7.8 (1.8)	nd	nd	nd	nd	nd	15.06 (5.24)	1.42 (1.27)	48.62 (29.14)
		4 (9)	57.7 (5.7)	nd	nd	7.3 (1.7)	nd	nd	nd	nd	nd	18.45 (7.82)	0.87 (1.21)	46.75 (31.26)
Cephalopods														
Galiteuthis glacialis	50	5 (2)	423.7 (70.4)	92.8 (0.8)	18.3 (2.8)	2.3 (0.6)	39.0 (3.5)	2.4	37.0	nd	nd	2.15 (0.42)	0.77 (0.04)	2.70 (1.34)
		6 (10)	788.6 (136.1)	91.4 (0.5)	16.3 (1.9)	3.0 (0.3)	42.4 (2.7)	1.1 (0.2)	15.2 (3.7)	nd	nd	2.03 (0.47)	1.12 (0.16)	3.14 (1.51)
Decapods														
Gennadas kempi	500	7 (2)	1839.0 (387.8)	69.4 (1.1)	11.0 (0.2)	9.0 (0.4)	33.1 (2.8)	14.7 (2.4)	54.0 (6.7)	0.8 (0.2)	2.9 (0.7)	1.09 (0.09)	1.31 (1.19)	15.65 (16.33)
Nematocarcinus lanceopes	0	5 (4)	280.2 (59.6)	77.9 (1.7)	14.1 (1.9)	7.1 (1.0)	37.5 (1.9)	6.8 (0.9)	35.0 (3.0)	0.9 (0.0)	4.6 (0.5)	2.13 (0.38)	1.13 (0.19)	24.57 (5.78)
Pasiphaea scotiae	100	5 (2)	299.5 (110.4)	71.8 (1.8)	8.9 (0.6)	6.9 (0.1)	26.8 (1.5)	nd	nd	nd	nd	2.79 (0.30)	0.94 (0.13)	20.13 (1.09)
		6 (1)	725.5	62.6	7.8	8.0	23.1	29.0	84.2	1.3	3.7	2.79	0.87	22.27
		7 (3)	2927.8 (770.8)	67.2 (3.2)	7.6 (0.6)	6.4 (1.0)	21.1 (2.1)	22.1 (4.2)	69.3 (8.9)	1.0 (0.3)	3.2 (0.8)	5.13 (0.95)	0.28 (0.09)	17.30 (4.80)
		8 (2)	6724.0 (1841.2)	63.8 (1.2)	6.6 (0.3)(0.3)	7.9 (0.5)	23.5 (2.2)	24.2 (0.8)	71.7 (4.9)	1.2 (0.0)	3.6 (0.3)	4.95 (1.60)	0.58 (0.14)	22.70 (1.50)
Petalidium foliaceum	500	6 (1)	792.2	68.7	8.3	7.4	25.9	15.4	53.7	0.7	2.3	0.66	0.57	3.28

Euphausiids														
Euphausia superba	0	3 (17)	31.6 (9.1)	nd	nd	7.3 (1.1)	nd	nd	nd	nd	nd	1.87 (0.70)	1.86 (1.07)	22.14 (12.79)
		4 (5)	81.2 (14.8)	81.1 (3.1)	13.3 (0.1)	9.2 (0.8)	61.4 (23.2)	nd	nd	nd	nd	2.51 (0.57)	3.06 (1.01)	45.26 (10.73)
		5 (8)	206.3 (114.5)	81.1 (3.1)	15.8 (2.7)	9.0 (1.4)	57.1 (9.4)	nd	nd	nd	nd	2.85 (1.23)	2.41 (1.29)	46.96 (17.55)
		6 (9)	742.0 (102.8)	82.1 (2.4)	17.3 (1.4)	8.6 (1.2)	58.5 (5.4)	nd	nd	nd	nd	3.38 (1.31)	2.59 (0.73)	69.75 (33.73)
		7 (27)	1379.7 (299.2)	78.7 (2.5)	15.5 (3.3)	9.7 (1.4)	55.2 (12.2)	nd	nd	nd	nd	2.93 (1.98)	2.24 (0.86)	88.76 (34.03)
E. triacantha	0	5 (2)	296.0 (3.6)	79.4 (0.1)	12.0 (4.3)	9.9 (0.1)	54.6 (2.1)	nd	nd	nd	nd	1.44 (0.30)	1.35 (1.10)	35.73 (0.06)
Thysanoessa macrura	100	3 (18)	35.4 (7.5)	76.9	16.2	9.8	57.7	nd	nd	nd	nd	2.18 (0.92)	0.33 (0.51)	37.49 (18.69)
		4 (8)	71.9 (13.3)	79.8 (0.4)	17.3 (0.3)	9.0 (0.8)	52.7 (4.1)	nd	nd	nd	nd	3.31 (1.19)	0.07 (0.04)	39.74 (12.74)
		5 (2)	164.4 (10.7)	71.1	9.0	8.3 (0.3)	32.4	nd	nd	nd	nd	4.59 (0.68)	0.06 (0.00)	40.06 (18.42)
Isopods														
Anuropus australis	100	6 (1)	528.0	77.8	20.7	5.5	31.3	8.6	49.0	1.3	7.1	0.59	0.02	15.65
Mysids														
Boreomysis rostrata	550	6 (1)	934.8	63.0	5.1	13.3	37.9	20.9	59.5	0.8	2.2	1.06	1.54	36.69
Gnathophausia gigas	500	7 (1)	1274.1	84.8	28.9	2.8	25.7	6.2	57.7	0.8	7.8	0.36	0.02	7.48
Ostracods														
Gigantocypris mulleri	500	5 (1)	431.0	93.1	30.9	1.0	19.9	nd	nd	nd	nd	1.33	0.18	1.25
		6 (1)	739.2	93.3	35.1	0.8	19.0	nd	nd	nd	nd	1.41	0.03	0.91
		7 (4)	1803.6 (458.8)	91.7 (0.6)	25.7 (7.4)	1.3 (0.2)	21.1 (2.9)	1.5 (0.3)	24.9 (3.8)	0.6 (0.1)	10.7 (3.4)	1.87 (0.35)	0.18 (0.15)	2.75 (1.24)
Polychaetes														
Tomopterus carpenteri	0	4 (1)	55.2	nd	nd	4.0	nd	nd	nd	nd	nd	3.15	1.58	4.54
		5 (3)	354.5 (55.5)	89.5 (2.7)	28.5 (8.1)	3.4 (1.2)	45.1 (5.8)	1.5 (0.8)	19.0 (2.8)	nd	nd	10.65	0.77 (0.29)	3.44 (3.35)
		6 (2)	788.3 (294.2)	87.9 (0.9)	22.8 (2.3)	4.7 (0.0)	50.1 (2.7)	1.6	16.8	nd	nd	8.08	0.77 (0.11)	5.58 (0.46)

Values are mean ± standard deviation. MDO = minimum depth of occurrence, SC = sizeclass, n = number of specimens analyzed. nd = no data.

analysis. Nucleic acid content also scaled with WM but not as well or as uniformly as protein content, especially for *C. richardi*, *C. lucasii*, *V. stebbingi* and *T. macrura* where the correlations became weak or non-existent. Strong correlations between RNA:DNA ratio (y) and wm (m) were observed in *P. scotiae* (specimens <6 g), immature *E. superba* (sizeclasses <6, Table 2b) and *G. mulleri*. Species that showed a good correlation between RNA content and mass (*G. glacialis*, *P. scotiae*, *E. superba*, and *G. mulleri*) also showed a similarly strong relationship between protein and RNA content (Table 4). Total enzyme activity ($IU\,ind^{-1}$) also scaled with mass in most species, with MDH showing a better correlation to mass than CS in all but *G. glacialis* and *T. carpenteri*. Mass-specific enzyme activity ($IU\,g\,WM^{-1}$) only showed a correlation with mass in three instances: CS in *G. glacialis* and *T. macrura*; and MDH in *E. superba*.

Biochemical measures were further examined in *E. superba* with respect to sex/developmental stage (Table 2a, b). Within the adult groups, pregnant females had significantly higher mean WM ($p<0.014$) and RNA:DNA ratio ($p<0.003$), and lower mean ash (%DM, $p<0.004$) than males and non-pregnant females. Pregnant females also had significantly lower water (%WM, $p<0.003$) and protein (%AFDM, $p<0.0004$) than non-pregnant females (Table 2a). Mass-specific CS and MDH activities were not significantly different among adults ($p>0.30$). The regressions of protein content, total CS ($IU\,ind^{-1}$) and total MDH ($IU\,ind^{-1}$) vs. WM shown in Table 4 are generally unchanged when immature and adult *E. superba* are considered separately; however, the correlations of both RNA and DNA content with WM as well as that between protein content and RNA content become very weak or non-existent in adult specimens (Table 2b).

Mean values of biochemical measures within different MIZ areas were examined in six species (Table 3). In *C. richardi*, water (%WM) and ash (%DM) levels were higher in the edge area but, as both these parameters scale with mass, the differences were a consequence of specimen size. No differences in any parameter between areas were observed for *C. lucasii*, *V. stebbingi* and *G. glacialis*. In *E. superba*, water level (%WM) was significantly higher in the ice than both the edge and open-water areas ($p<0.001$). Ash level (%DM) was not significantly different between ice and edge areas ($p=0.113$), but was significantly higher in the ice than open-water area ($p=0.0004$). For *E. superba*, individual values for water and ash levels varied only by 1–2% over the size range of specimens examined, and neither was found to scale with mass. In *T. macrura*, mass-specific CS activity ($IU\,g\,WM^{-1}$) was significantly higher in the edge than ice areas ($p=0.0004$). The high standard deviation associated with the mean in the edge sample is a consequence of three very high CS activities. If these three values are excluded from the comparison, mean mass-specific CS activity in the edge area (adjusted $x\pm$s.d. $=0.13\pm0.04$) is still significantly higher than in the ice area ($p=0.0012$).

3.3. Oxygen consumption vs. biochemical measures

The use of biochemical measures as predictors of metabolic rate was examined by regressing individual oxygen consumption rate ($\mu l\,O_2\,ind^{-1}\,h^{-1}$) against protein, RNA, and DNA content (mg); RNA:DNA ratio; and enzyme activity ($IU\,ind^{-1}$ and $IU\,g\,WM^{-1}$) individually for nine species analyzed over a size range ($n\geqslant5$) and also collectively for all 23 species in the data set (Table 6). Three species (*C. lucasii*, *G. glacialis*, and *G. mulleri*) showed only weak to moderate correlations of individual respiration rate with any biochemical parameter, five species (*C. richardi*, *P. scotiae*, *E. superba*, *T. macrura* and *T. carpenteri*) showed strong correlations between individual respiration rate and at least one parameter, and one species (*V. stebbingi*) failed to show any correlations. Protein content showed the best correlation in *C. richardi*, *P. scotiae*, *E. superba* and *T. macrura*, while MDH activity (total and mass-specific) showed the best correlation in *T. carpenteri*. For *E. superba*, a strong relationship between protein content and individual respiration rate was observed in both juveniles and adults. When all 23 species are considered collectively, protein content (mg) and total MDH activity

Table 6
Regressions of oxygen consumption rate vs. biochemical parameters for nine species of micronekton sampled over a size range

Species	$\mu l\, O_2\, ind^{-1}\, h^{-1}$ vs. :						
	Protein (mg)	RNA (mg)	DNA (mg)	CS ($IU\, ind^{-1}$)	MDH ($IU\, ind^{-1}$)	CS ($IU\, gWM^{-1}$)	MDH ($IU\, g\, WM^{-1}$)
Cyphocaris richardi	$y = 3.952x^{0.505\pm0.093}$ (0.69, 15, 0.0001)	$y = 18.903x^{0.456\pm0.114}$ (0.55, 15, 0.0014)	$y = 36.758x^{0.513\pm0.123}$ (0.57, 15, 0.0011)	$y = 26.511x^{0.354\pm0.105}$ (0.47, 15, 0.0050)	$y = 13.698x^{0.276\pm0.103}$ (0.35, 15, 0.0200)	nc	nc
Cyllopus lucasi	$y = 9.725x^{0.388\pm0.129}$ (0.39, 16, 0.0094)	$y = 26.944x^{0.292\pm0.107}$ (0.35, 16, 0.0162)	$y = 40.246x^{0.319\pm0.084}$ (0.51, 16, 0.0019)	nc	$y = 10.376x^{0.423\pm0.128}$ (0.45, 15, 0.0059)	nc	nc
Vibilia stebbingi	$y = 8.389x^{0.313\pm0.164}$ (0.19, 17, 0.0761)	nc	nc	nc	nc	nc	nc
Galiteuthis glacialis	$y = 5.328x^{0.485\pm0.218}$ (0.45, 8, 0.0677)	$y = 21.106x^{0.467\pm0.159}$ (0.59, 8, 0.0259)	$y = 27.277x^{0.406\pm0.180}$ (0.46, 8, 0.0653)	$y = 26.033x^{0.399\pm0.187}$ (0.43, 8, 0.0764)	nc	$y = 22.041x^{0.729\pm0.472}$ (0.28, 8, 0.1731)	nc
Pasiphaea scotiae	$y = 3.794x^{0.610\pm0.151}$ (0.80, 6, 0.0156)	$y = 45.516x^{0.545\pm0.210}$ (0.63, 6, 0.0603)	$y = 104.221x^{0.912\pm0.303}$ (0.75, 5, 0.0574)	$y = 79.980x^{0.530\pm0.312}$ (0.42, 6, 0.1652)	$y = 9.967x^{0.558\pm0.172}$ (0.73, 6, 0.0314)	$y = 45.265x^{-0.624\pm0.393}$ (0.39, 6, 0.1882)	nc
Euphausia superba (all)	$y = 4.509x^{0.738\pm0.019}$ (0.96, 61, <0.0000)	$y = 26.123x^{0.899\pm0.053}$ (0.84, 58, <0.0000)	$y = 61.957x^{1.109\pm0.051}$ (0.89, 60, <0.0000)	$y = 66.080x^{0.629\pm0.038}$ (0.83, 57, <0.0000)	$y = 11.357x^{0.555\pm0.020}$ (0.93, 61, <0.0000)	nc	$y = 0.250x^{1.366\pm0.146}$ (0.60, 61, <0.0000)
E. superba (immature)	$y = 5.213x^{0.628\pm0.050}$ (0.85, 29, <0.0000)	$y = 19.716x^{0.705\pm0.060}$ (0.84, 28, <0.0000)	$y = 42.659x^{0.902\pm0.101}$ (0.75, 29, <0.0000)	$y = 28.729x^{0.329\pm0.075}$ (0.42, 29, 0.0001)	$y = 11.242x^{0.430\pm0.045}$ (0.77, 29, <0.0000)	nc	$y = 1.875x^{0.604\pm0.166}$ (0.33, 29, 0.0011)
E. superba (adult)	$y = 2.107x^{0.905\pm0.106}$ (0.71, 32, <0.0000)	nc	$y = 106.309x^{0.443\pm0.153}$ (0.22, 31, 0.0074)	$y = 82.222x^{0.570\pm0.160}$ (0.33, 28, 0.0015)	$y = 21.928x^{0.421\pm0.103}$ (0.36, 32, 0.0003)	nc	nc
Thysanoessa macrura	$y = 2.792x^{0.904\pm0.119}$ (0.72, 25, <0.0000)	$y = 22.978x^{0.524\pm0.108}$ (0.51, 25, 0.0001)	$y = 53.933x^{0.686\pm0.200}$ (0.38, 25, 0.0023)	nc	$y = 8.514x^{0.489\pm0.087}$ (0.58, 25, <0.0001)	$y = 4.872x^{-0.348\pm0.113}$ (0.29, 25, 0.0053)	$y = 3.408x^{0.328\pm0.190}$ (0.11, 25, 0.0980)
Gigantocypris mulleri	$y = 7.249x^{0.096\pm0.060}$ (0.39, 6, 0.1839)	$y = 9.880x^{0.093\pm0.064}$ (0.35, 6, 0.2195)	$y = 10.468x^{0.101\pm0.074}$ (0.32, 6, 0.2423)	$y = 10.586x^{0.066\pm0.049}$ (0.31, 6, 0.2538)	$y = 8.762x^{0.073\pm0.048}$ (0.37, 6, 0.2028)	nc	nc
Tomopterus carpenteri	$y = 15.773x^{0.301\pm0.123}$ (0.67, 5, 0.0921)	nd	nd	$y = 58.522x^{0.428\pm0.097}$ (0.87, 5, 0.0217)	$y = 34.317x^{0.202\pm0.025}$ (0.96, 5, 0.0040)	$y = 47.367x^{0.783\pm0.388}$ (0.58, 5, 0.1368)	$y = 26.831x^{0.283\pm0.028}$ (0.97, 5, 0.0020)
All species[a]	$y = 4.391x^{0.652\pm0.025}$ (0.79, 179, <0.0000)	$y = 27.394x^{0.740\pm0.035}$ (0.73, 174, <0.0000)	$y = 52.016x^{0.578\pm0.037}$ (0.59, 175, <0.0000)	$y = 46.573x^{0.350\pm0.025}$ (0.53, 175, <0.0000)	$y = 10.789x^{0.525\pm0.021}$ (0.78, 178, <0.0000)	nc	$y = 9.301x^{0.317\pm0.063}$ (0.13, 178, <0.0000)

Regressions are also shown using individual values for all species in the data set. Values in parentheses as in Table 2b. nc = no correlation, nd = not determined.
[a]Individual values for all 23 species in the data set.

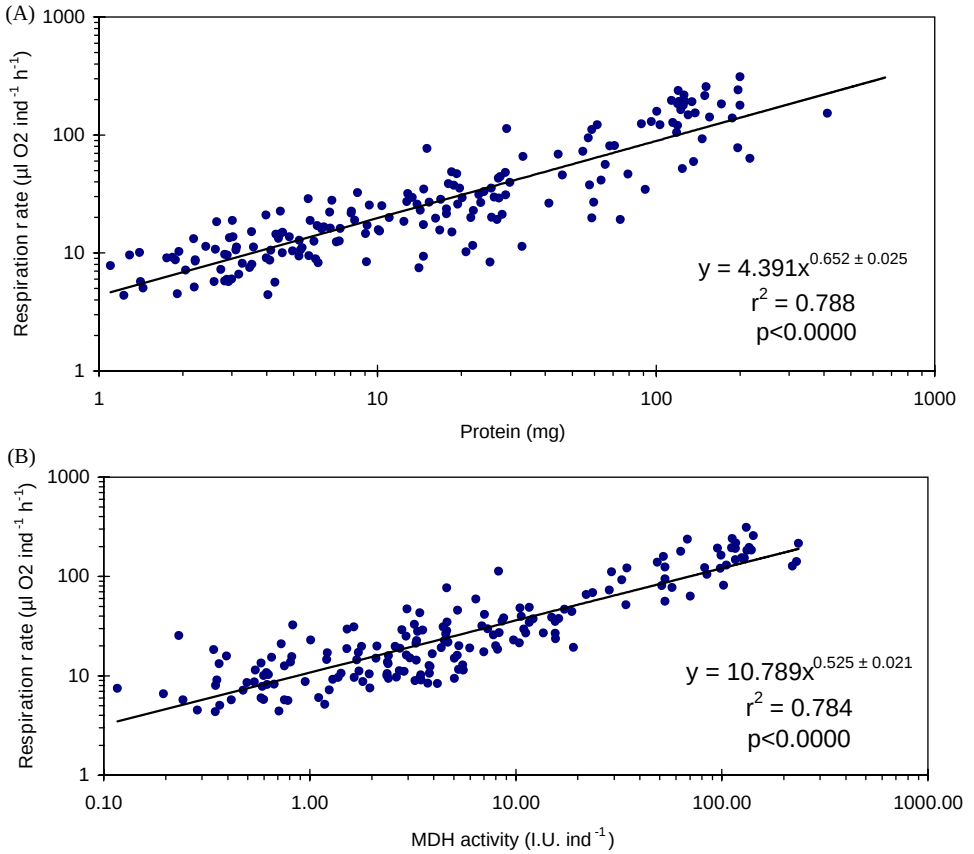

Fig. 2. Log–log plot of oxygen consumption rate ($\mu l\, O_2\, ind^{-1}\, h^{-1}$) vs. (A) protein content (mg) and (B) total MDH activity ($IU\, ind^{-1}$) using individual values ($n = 178$) for all species. b = slope ± standard error.

($IU\, ind^{-1}$) show the best correlation to individual respiration rate (Fig. 2).

4. Discussion

4.1. Effects of MIZ area

The absence of significant changes in oxygen consumption rate among specimens from different areas within the marginal ice zone implies that there is little short-term direct influence of the ice-edge bloom on metabolism for micronekton species or that the influence is masked by the mobility of the fauna. Higher levels of water and ash in *E. superba* in the pack-ice area and the higher level of CS activity in *T. macrura* in the ice-edge area suggest that longer-term effects of an individual's distribution with respect to the bloom may be exhibited by changes in proximate composition or metabolic potential. Data on zooplankton from the same cruise showed bloom-related changes in abundance and age structure (Burghart et al., 1999) as well as body compositon (Geiger et al., 2001) for the dominant copepod species, factors that could influence metabolism or chemical composition in micronekton species that were feeding on them. Of the six species examined across MIZ areas in this study, *C. richardi*, *C. lucasii*, *E. superba* and *T. macrura* are omnivorous (Hopkins, 1985; Hopkins and Torres, 1989; Daly, 1990). *V. stebbingi* is a

particulate feeder associated with salps (Madin and Harbison, 1977) and, based on dietary data for other Antarctic squids (Hopkins, 1985), *G. glacialis* is carnivorous. With the exception of *V. stebbingi*, all of the species are highly motile, can actively forage, and take a variety of prey. It is not surprising that physiological parameters for these species remain fairly uniform across the marginal ice zone.

4.2. Effects of season

Metabolic and/or compositional data for 17 of the species examined in this study are available from previous studies. Oxygen consumption rates from this study are similar to other reported summer values (Opalinski and Jazdzewski, 1978; Ikeda and Mitchell, 1982; Hirche, 1983, 1984; Ikeda and Bruce, 1986; Ikeda, 1988). For gammarids, decapods, mysids and ostracods, summer values for oxygen consumption rate were not significantly different from those measured in other seasons (Torres et al., 1994a). Consequently, metabolic data from all seasons were combined to generate regressions of respiration rate ($\mu l\, O_2\, ind^{-1}\, h^{-1}$) vs. WM (mg) for all species in these groups with $n \geqslant 6$ (Table 7). As was observed with the summer data, the giant ostracod *G. mulleri* continued to show no significant correlation ($p > 0.20$) of respiration with mass. Most compositional parameters for species in those groups were also similar between seasons (Clarke and Holmes, 1986; Torres et al., 1994b), the only noticeable exception being higher lipid levels in summer. Elevated summer lipid levels could reflect increases in storage depots during productive times, as well as being associated with egg production (Clarke and Holmes, 1986). The present data set included non-ovigerous females of *Gennadas kempi*, *B. rostatra* and *P. scotiae* (sizeclass 8), as well as ovigerous females of *C. richardi* and *G. mulleri*, so, for at least the latter two species, reproductive influences were important in the observed higher summer lipid levels.

For the hyperiid amphipods *C. lucasii* and *V. stebbingi,* mean respiration rates in summer are higher than those reported for fall and winter by Torres et al. (1994a). While both species show the same trend, differences in mean values are significant only for *V. stebbingi* (summer > winter, $p = 0.0002$; summer > fall, $p = 0.089$). Comparison of regressions of respiration rate ($\mu l\, O_2\, ind^{-1}\, h^{-1}$) vs. WM (mg) for *C. lucasii* between spring, summer, fall (combined) and winter show no significant difference in slopes ($p > 0.5$), but a significantly lower intercept in winter ($p < 0.5$) (Table 7). For *V. stebbingi*, the slope is significantly higher ($p < 0.005$) and the intercept significantly lower ($p < 0.001$) in winter compared to summer, fall combined (Table 7). In contrast, compositional values for the species are similar to winter values reported by Torres et al. (1994b). In that study, changes in proximate composition from fall to winter were attributed to combustion of body components, proposing that a lower salp biomass in the winter (Lancraft et al., 1991) argued against a fall–winter reproductive strategy. While no ovigerous specimens of *V. stebbingi* were observed in the present data set, there were several ovigerous *C. lucasii* specimens collected, indicating a summer reproductive effort.

For euphausiids, the present summer data complete the seasonal coverage on *E. superba* initiated by Torres et al. (1994a, b) and also allow for a summer–winter comparison in *T. macrura.* Mean summer respiration rates for both juvenile (sizeclass < 6) and adult (sizeclass > 5) *E. superba* are not significantly different than values for spring and fall ($p > 0.20$) but are significantly higher than winter rates ($p < 0.0001$). Comparison of the regressions of respiration ($\mu l\, O_2\, ind^{-1}\, h^{-1}$) vs. WM between spring, summer and fall show no significant differences in slope ($p > 0.25$) or intercept ($p > 0.50$). Comparison of the regressions for combined spring, summer, fall vs. winter show that, while the slopes are not significantly different ($p > 0.25$), the elevations of the lines are ($p < 0.001$) (Fig. 3). Consequently, the inclusion of summer respiration data only serves to further support the conclusion of Torres et al. (1994a) of a depressed winter metabolism in *E. superba.* The significant difference in regression slopes observed between juvenile and adult *E. superba* in the present data set is maintained when data from spring, summer, and fall are combined (Table 7). In juveniles, metabolism scales in a conventional way with mass

Table 7
Regression s of oxygen consumption rate ($\mu l\, O_2\, ind^{-1}\, h^{-1}$) vs. WM (mg) for eight species of micronekton

Species	All seasons	Spring–summer–fall seasons	Winter season
Cyphocaris richardi	$y = 0.157x^{0.848\pm0.075}$ (0.85, 24, <0.0000)		
Cyllopus lucasii		$y = 0.955x^{0.644\pm0.097}$ (0.62, 29, <0.0000)	$y = 0.470x^{0.728\pm0.171}$ (0.78, 7, 0.0081)
Vibilia stebbingi		$y = 2.698x^{0.362\pm0.239}$ (0.10, 23, 0.1441)	$y = 0.006x^{1.805\pm0.401}$ (0.74, 9, 0.0028)
Galiteuthis glacialis	$y = 0.578x^{0.614\pm0.125}$ (0.62, 17, 0.0002)		
Gennadas kempi	$y = 0.135x^{0.849\pm0.147}$ (0.89, 6, 0.0045)		
Pasiphaea scotiae	$y = 0.938x^{0.591\pm0.111}$ (0.70, 14, 0.0002)		
Euphausia superba			
All		$y = 0.497x^{0.805\pm0.019}$ (0.95, 88, <0.0000)	$y = 0.211x^{0.808\pm0.018}$ (0.97, 65, <0.0000)
Juvenile		$y = 0.646x^{0.739\pm0.039}$ (0.90, 42, <0.0000)	$y = 0.217x^{0.797\pm0.021}$ (0.97, 47, <0.0000)
Adult		$y = 0.214x^{0.929\pm0.117}$ (0.59, 46, <0.0000)	$y = 0.510x^{0.678\pm0.374}$ (0.17, 18, 0.0888)
Thysanoessa macrura		$y = 0.293x^{0.932\pm0.103}$ (0.77, 26, <0.0000)	$y = 0.309x^{0.824\pm0.075}$ (0.83, 26, <0.0000)

Regressions listed under "all seasons" for species that showed no significant differences in respiration between any season. Spring, fall, and winter data from Torres et al. (1994a). Values in parentheses as in Table 2b.

($b \approx 0.75$; Withers, 1992). In adults, the *b*-value is slightly higher ($b \approx 0.9$).

For *T. macrura*, mean respiration rates for sizeclasses 4 and 5 are significantly higher in summer than in winter ($p < 0.022$). Mean rates for sizeclass 3 are also higher in summer but not significantly so ($p = 0.22$). Comparison of the regressions of respiration ($\mu l\, O_2\, ind^{-1}\, h^{-1}$) vs. WM in *T. macrura* for summer and winter also shows no significant ($p > 0.10$) difference between slopes, but an unexpected higher intercept in the winter ($p < 0.001$). The higher winter intercept is a consequence of greater variability in respiration values among sizeclass 3 specimens and and the resultant lack of significant difference between seasons in this group. When just sizeclasses 4 and 5 are compared, the slopes remain similar ($p > 0.10$), but the winter intercept is significantly lower ($p < 0.001$). Thus, *T. macrura* also shows a winter metabolic depression, at least in the larger sizeclasses. Respiration rates ($\mu l\, O_2\, mg\, WM^{-1}\, h^{-1}$) for *E. triacantha* also appear higher in the summer vs. the winter, but data on similar-sized specimens are insufficient for statistical comparison.

Trends in water, ash, and protein levels among euphausiids are less consistent. For *E. superba,* summer and winter water levels are similar, both higher than fall values ($p < 0.001$), while ash levels are not significantly different in any season ($p > 0.30$). Protein levels (%WM) are similar in summer and winter, both lower than in fall ($p < 0.0001$). As %AFDM, fall and winter protein levels are the same, both are lower than in summer ($p < 0.005$). Limited sample size precludes statistical comparisons of compositional components for *T. macrura* and *E. triacantha*, but the general patterns for these species mirror that observed in *E. superba.* Lower %WM protein in summer merely reflects changes in water level, while higher %AFDM protein indicates actual increases in organic protein, suggesting increased growth during the productive season. Lipid and protein are the two main compositional components; when combusted, they are replaced by water. It is most likely that the high summer water contents and implied depletion of lipid reserves are a consequence of energy invested in reproduction. *T. macrura* reproduces in the spring (Nordhausen,

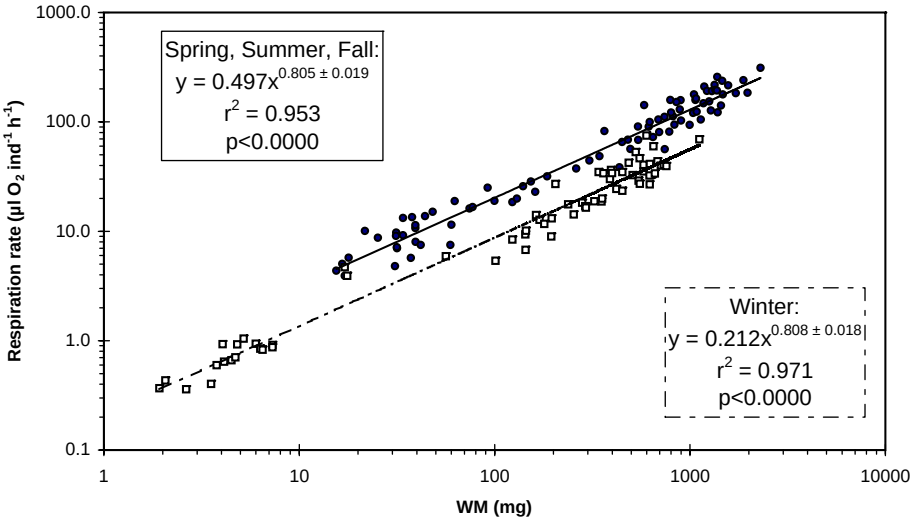

Fig. 3. Log–log plot of oxygen consumption rate ($\mu l\, O_2\, ind^{-1}\, h^{-1}$) vs. WM (mg) for *E. superba* between seasons. (●): combined spring, summer, and fall data; (□): winter data. b = slope ± standard error.

1994) and *E. superba* from mid-November through April (Mauchline, 1980; Quetin et al., 1994).

Following the classification of metabolic strategies proposed by Torres et al. (1994b), summer oxygen consumption rates were higher in all species exhibiting a Type 2 overwintering strategy, while species with a Type 3 overwintering strategy did not show any changes in respiration rate during summer. An increased summer metabolism suggests that the animals are feeding, growing, and in some cases, accumulating energy stores for the winter.

4.3. Biochemical measures as predictors of respiration rate

The use of biochemical indices as predictive tools for growth (Buckley, 1980; Buckley et al., 1984; Mugiya and Oka, 1991; Brightman et al., 1997) and metabolism (Torres and Somero, 1988b; Clarke et al., 1984) is an idea that has been evolving since the early 1980s. The measurement of oxygen consumption rates of aquatic organisms is difficult and time consuming. Similarly, retrieving live animals in excellent condition for respirometry can be difficult, especially when studying animals from great depths or in delicate species such as gelatinous plankton (cf. Ikeda et al., 2000).

Since muscle tissue is the principal metabolizing body component, it is not surprising that oxygen consumption rate ($\mu l\, O_2\, ind^{-1}\, h^{-1}$) scales very strongly with protein content (mg). Furthermore, since protein content was found to scale directly with WM in every species examined , the nature of the respiration vs. protein relationship for a particular species depends mainly on the correlation between respiration rate and mass. For example, *C. richardi*, *P. scotiae*, *E. superba* and *T. macrura* showed strong correlations for both respiration vs. WM and protein vs. WM and, as a consequence, had good respiration vs. protein correlations. In contrast, *V. stebbingi* and *G. mulleri* showed no correlations between respiration and WM and also exhibited no respiration vs. protein correlations. The observation that protein content can be a good indicator of respiratory rate in pelagic organisms was first reported for pelagic crustaceans off Southern California by Childress and Nygaard (1974). Our findings indicate that this predictive relationship is present in Antarctic micronekton as well.

The usefulness of nucleic acids as predictors of respiration rate remains as long as these

components remain coupled to growth and increases in protein, as is the case in juveniles and individuals not generating major energy stores. Examples in the present data set are *G. glacialis*, *P. scotiae* and immmature *E. superba*. In all three species, RNA and DNA content as well as RNA:DNA ratio scaled positively with mass, indicating active growth, and, except in *G. glacialis*, these parameters also scaled positively with respiration rate ($\mu l\, O_2\, ind^{-1}\, h^{-1}$). The lack of correlation between respiration rate and RNA:DNA ratio in *G. glacialis* is likely a consequence of the limited size range of specimens examined and the resultant weak correlation between respiration rate and mass. The finding of elevated RNA:DNA ratios in ovigerous females is consistent with previous studies (Nakata et al., 1994; Saiz et al., 1998). That not all ovigerous specimens had higher relative RNA:DNA ratio values implies that the developmental stage of eggs may also influence measured values. In a study of the copepod *Calanus helgolandicus,* Biegala et al. (1999) found that gonad maturation also resulted in higher RNA:DNA ratios, which could explain the high ratio values observed in non-ovigerous specimens in this study. Furthermore, they found no change in protein content ($\mu g\, ind^{-1}$) during the same period, a finding consistent with the observed lack of correlation between protein and RNA in adult *E. superba* in the present study. Adult *E. superba* males show a weak but definite positive correlation between protein (y, mg) and RNA (x, mg) as expressed by the regression: $y = 35.171x^{0.647\pm0.302}$, $r^2 = 0.32$, $p = 0.057$, but adult females show no correlation at all ($r^2 = 0.02$, $p = 0.49$). Furthermore, the strong correlation observed in juveniles between protein content and RNA content improves when adult males are added to the regression ($y = 10.169x^{1.385\pm0.059}$, $r^2 = 0.94$, $n = 39$, $p < 0.0000$), but weakens when adult females are included instead ($y = 10.007x^{1.200\pm0.066}$, $r^2 = 0.87$, $n = 51$, $p < 0.0000$). Protein content continues to scale positively with WM in adult *E. superba*, but the correlation is stronger in males ($r^2 = 0.96$) than in females ($r^2 = 0.85$). The influence of reproductive activity on nucleic acid measures is also indicated in *C. richardi*, *C. lucasii* and *T. macrura*, all species exhibiting only weak correlations of RNA content vs. WM and protein content vs. RNA content. The very high RNA:DNA ratios found for *V. stebbingi* (8.9–24.0) suggest reproductive effects as well, but growth influences could also be a factor. Since *V. stebbiingi* feed directly on the particulate food collected by their host salp (Madin and Harbison, 1977), they are directly affected by phytoplankton concentrations. Thus RNA:DNA ratio values could be elevated in response to high food availability in the edge and open-water areas.

Mass-specific enzyme activity ($IU\, g\, WM^{-1}$) did not explain much of the variability in individual respiration rate ($\mu l\, O_2\, ind^{-1}\, h^{-1}$) when one was plotted against the other (Table 6). However, mass-specific activity did not scale strongly with mass in most species, and it initially appeared to contrast with that found for fish (Childress and Somero, 1979; Torres and Somero, 1988b). In the present study, entire specimens were homogenized rather than an excised muscle sample, as is normally done with fish. Homogenizing the entire specimen resulted in lower mass-specific enzyme activities but made the results more comparable with smaller species of Crustacea such as copepods, where excising the muscle would be impractical. A recent study (Cullen et al., 2003) using excised sections of abdominal muscle of *E. superba* gave CS activities approximately 5 times higher than those reported here.

Both CS and MDH catalyze reactions in the citric acid cycle serving as proxies for aerobic potential, but MDH also plays other roles; for example, shuttling electrons between the cytosol and mitochndrion, and as such might better represent overall metabolism (Lehninger, 1982). That *E. superba* was the only individual species to exhibit a strong correlation between mass-specific enzyme activity and mass (and consequently respiration rate) may be due to the combined influence of a large sample size, wide specimen size range, and high protein content (45–78%AFDM).

When all the species were considered using mean values for each sizeclass, MDH activity showed a significant positive correlation with respiration rate (Fig. 4). This illustrates a predictive capability of MDH activity for respiration

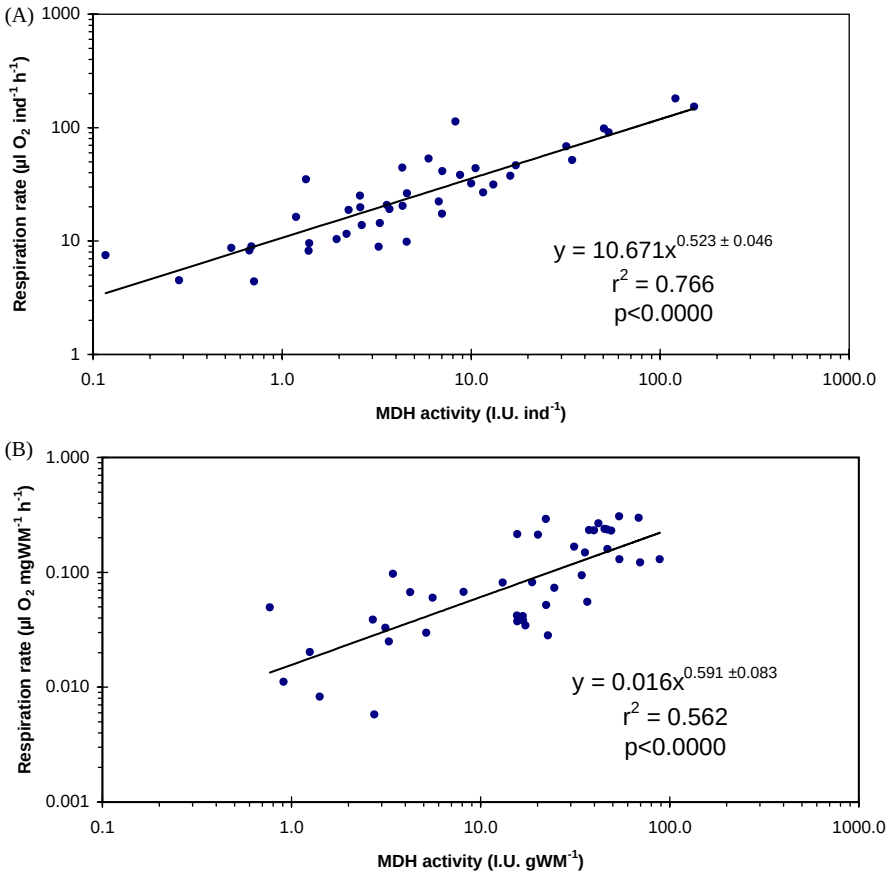

Fig. 4. (A) Log–log plot of individual oxygen consumption rate ($\mu l\, O_2\, ind^{-1}\, h^{-1}$) vs. total MDH activity ($IU\, ind^{-1}$) using sizeclass mean values ($n = 42$) for all species. b = slope ± standard error. (B) Log–log plot of mass-specific oxygen consumption rate ($\mu l\, O_2\, mg\, WM^{-1}\, h^{-1}$) vs. mass-specific MDH activity ($IU\, g\, WM^{-1}$) using sizeclass mean values ($n = 42$) for all species. b = slope ± standard error.

rate in invertebrate micronekton similar to what has been shown for pelagic fishes (Childress and Somero, 1979), making it and protein content the two most effective biochemical proxies for metabolic rate.

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