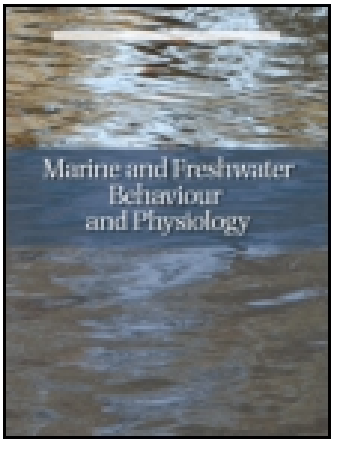

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Use of oxygen microsensors to measure the respiration rates of five dominant copepods and *Euphausia crystallorophias* furcilia from the Amundsen Sea, West Antarctica

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The individual respiration rates of five biomass-dominant copepods (*Calanoides acutus*, *Rhincalanus gigas*, *Metridia gerlachei*, *Calanus propinquus* and *Paraeuchaeta antarctica*), and *Euphausia crystallorophias* furcilia, from the Amundsen Sea, West Antarctica, were determined using a Clark-type oxygen microsensor affording high temporal resolution. Measurements were conducted on specimens collected from waters exhibiting a very narrow temperature range (−1.68 to −1.32 °C), at sites located between 71 and 75°S, during the summer (31 January–20 March 2012). A short incubation time (3 h) was sufficient to reveal significant declines in dissolved oxygen concentrations by 12–45%. The respiration rates of the copepods and *E. crystallorophias* furcilia were within the ranges of previously reported values. The respiration rates of relatively large-bodied species were rather low, whereas the smaller species generally exhibited higher respiration rates. The data show that this simple microsensor technique is a useful high-resolution non-invasive means of investigating the metabolism of zooplankton in the Southern Ocean. The method could be used in other situations when such information is required.

Keywords: respiration rate; oxygen microsensor; copepods; *Euphausia crystallorophias*; Amundsen Sea

Introduction

Copepods and euphausiids constitute > 70% of the total metazooplankton biomass in Antarctic waters (Mayzaud et al. 2002; Atkinson et al. 2012) where they play major roles in energy flow and biogeochemical cycles. Some of the organic carbon ingested by zooplankton is used for metabolic activities, and quantification of this carbon is of prime importance if we are to understand energy transfer and elemental cycling by the zooplankton of Antarctic ecosystems.

Oxygen consumption rates reflect the metabolic demands of copepods and euphausiids in different regions of the Southern Ocean, including the marginal ice zone, the pack-ice zone in the Antarctic Peninsula region and the Atlantic and Indian Ocean sectors (Table 1).

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Previous metabolic studies employed the Winkler titration method (Winkler 1888), polarographic oxygen electrodes (Clark 1956) or measurement of the activity of the electron transfer system (Packard 1971). Recently, oxygen microsensor technology has been used to measure a range of metabolic activities, including pericellular oxygen consumption by human cells (Pettersen et al. 2005), and the respiration of rotifers (Jensen et al. 2006), hydromedusae (Marshalonis & Pinckney 2007), benthic foraminifera (Geslin et al. 2011), midges (*Diptera*; *Chironomidae*) (Brodersen et al. 2008), oxygen consumption rates of copepod eggs (Nielsen et al. 2007) and copepod faecal pellets (Shek & Liu 2010). The technique should be applicable to determine the respiration rates of zooplankton; oxygen microsensors can be placed inside experimental bottles to monitor declines in oxygen concentration.

The copepods *Calanoides acutus*, *Rhincalanus gigas*, *Metridia gerlachei*, *Calanus propinquus* and *Paraeuchaeta antarctica*, and the euphausiid *Euphausia crystallorophias*, are the dominant species in the Amundsen Sea, a poorly understood Antarctic ecosystem that has attracted increasing interest in recent years (Kaiser et al. 2009; Griffiths 2010). Copepods and *E. crystallorophias* constitute more than 80% of the total zooplankton biomass in the Amundsen Sea (Lee et al. 2013). Their distribution and production is affected by both sea-ice conditions and variations in food levels (Ducklow et al. 2007; Yager et al. 2012; Lee et al. 2013). In particular, polynya-associated distribution of *E. crystallorophias* (principally larval forms) has been documented in the Amundsen Sea during the summer, at which time the species generally increases in abundance and biomass because food concentrations are higher (Lee et al. 2013). Copepods living in the ice zone of the Antarctic are dependent on the spring ice-edge bloom for growth and completion of their life cycles (Kawall et al. 2001). Although copepods and euphausiids are numerically dominant in, and exert ecological impacts on, the Amundsen Sea, virtually no studies have explored the metabolism of these organisms (although distributional works have appeared) or how grazing by mesozooplankton impacts phytoplankton (Yager et al. 2012; Lee et al. 2013).

Our primary objectives in the present study were to determine the oxygen consumption rates of the major copepods and *E. crystallorophias* furcilia using an oxygen microsensor and to compare our results with those obtained using other methods in Antarctic marine ecosystems.

Materials and methods

Preparations for measuring the respiration rate

A multidisciplinary survey was conducted aboard the Korean icebreaker RV *Araon* in the Amundsen Sea, between 71 and 75°S, during the summer of 31 January–20 March 2012. To measure oxygen consumption rates, zooplankton specimens were collected with a Bongo net (of mesh apertures 330 and 500 μm) at three selected stations. The net was towed vertically within the upper 200 m of the water column (Table 2). We chose the numerically dominant species, *E. crystallorophias* furcilia and the major copepods, *C. acutus*, *R. gigas*, *M. gerlachei*, *C. propinquus* and *P. antarctica*. Undamaged adult females of each copepod species and furcilia of *E. crystallorophias* were immediately sorted and transferred into 2.6-L polycarbonate bottles where they were allowed to rest for ~3 h in 200 μm-prescreened natural seawater at ambient temperature. Live specimens chosen for experimentation were next placed in 300 mL polycarbonate bottles filled with 0.45 μm-prefiltered seawater at ambient temperature and starved for

Table 1. Dry weights and oxygen consumption rates for the major species of Antarctic waters. fem = females.

Species	Developmental stage	Dry weight (mg ind^{-1})	Oxygen consumption rate		References
			μL O_2 ind^{-1} h^{-1}	μL O_2 ind^{-1} mg dry wt^{-1} h^{-1}	
R. gigas	C6 (fem)	1.08 ± 0.18	0.44–0.94	0.47–0.78	(10), (11), (12)
C. acutus	C5	0.21–0.39	0.21–0.49	1.11–1.81	(7), (10), (12)
	C6 (fem)	0.49–0.69	0.10–0.76	0.20–1.33	(1), (7), (9), (11), (12)
C. propinquus	C5	0.69	0.47–0.78	0.68–1.13	(7), (12)
	C6 (fem)	0.73–2.50	0.51–1.30	0.20–0.98	(1), (2), (7), (8), (10), (11), (12)
M. gerlachei	C6 (fem)	0.21–0.27	0.21–0.32	0.49–1.14	(2), (9), (10), (11)
P. antarctica	C6 (fem)	5.71	2.57–3.83	0.16–0.45	(3), (6), (11), (12)
E. crystallorophias	Adult	5.95–50.38	3.16–37.60	0.17–0.36	(1), (4), (5)
E. superba	furcilia III	0.38 ± 0.03		0.73 ± 0.22	(13)
R. gigas	C6 (fem)	0.83 ± 0.02	0.19 ± 0.06	0.22 ± 0.07	This study
C. acutus	C6 (fem)	0.38 ± 0.03	0.28 ± 0.16	0.74 ± 0.42	This study
C. propinquus	C6 (fem)	0.80 ± 0.18	0.21 ± 0.03	0.26 ± 0.04	This study
M. gerlachei	C6 (fem)	0.27 ± 0.01	0.18 ± 0.06	0.68 ± 0.24	This study
P. antarctica	C6 (fem)	3.01 ± 0.61	0.77 ± 0.22	0.26 ± 0.07	This study
E. crystallorophias	furcilia	0.41 ± 0.04	0.45 ± 0.14	1.09 ± 0.64	This study

(1) Ikeda & Fay 1981 (2) Ikeda & Mitchell 1982 (3) Hirche 1984 (4) Ikeda & Bruce 1986 (5) Ikeda & Kirkwood 1989 (6) Yen 1991 (7) Schnack-Schiel et al. 1991 (8) Drits et al. 1993 (9) Chaolun et al. 2001 (10) Ikeda et al. 2001 (11) Kawall et al. 2001 (12) Mayzaud et al. 2002 (13) Meyer et al. 2002.

Table 2. Surface seawater temperature (Temp), salinity (Sal), chlorophyll *a* concentration (Chl *a*), sea ice extent and species collected at each sampling sites in the Amundsen Sea.

Latitude	Longitude	Sampling site	Collected species	Temp (°C)	Sal (psu)	Chl *a* ($\mu g\ L^{-1}$)	Sea ice concentration
71.58°S	133.99°W	39	*R. gigas* *C. propinquus*	−1.32	33.35	0.35	0%
72.85°S	116.50°W	7	*C. acutus* *M. gerlachei* *P. antarctica*	−1.68	33.58	3.41	50%
74.37°S	104.99°W	87	*E. crystallorophias* furcilia	−1.44	33.80	2.33	0%

12 h. We placed individual animals in each experimental chamber and prepared two or three replicates of each species to examine individual variation in respiration. Control chambers containing only 0.45 µm-prefiltered seawater (thus animal-free) were prepared alongside the experimental chambers. All chambers were dark-incubated for up to 12 h in a water bath at 0 ± 0.1 °C.

Experimental set-up

Respiration rate was monitored using a Micro-respiration system (a four-channel multimeter, Unisense A/S, Aarhus, Denmark), which allows continuous recording of dissolved oxygen (DO) concentration; the time interval between consecutive measurements is 10 s. DO levels were measured using Clark-type oxygen microelectrodes (Revsbech 1989), in which a 500 µm diameter tip was connected to a picoammeter. Microelectrodes were calibrated using 0% DO (achieved by bubbling with nitrogen) and 100% DO (achieved by bubbling with air) as endpoints. The respiration chambers were placed on a submerged rack in a temperature-controlled water bath. Both the control and experimental chambers were equipped with glass-coated mini-magnetic stirrers rotating at 500 rpm to prevent development of an oxygen gradient. Each chamber had capillary pores allowing insertion of the oxygen microsensor. The pore size of the chamber was sufficiently small to ensure that gas–liquid exchange was minimised. Animals were protected from impact with the stirrers by inclusion of acid-proof stainless-steel mesh dividers (with 200 µm pores) resting on glass cylinders. Individual stirrer heads were located in the rack directly beneath the chambers and did not emit heat. Moreover, magnet rotation did not affect the animals' swimming or position in the chamber. Each individual was placed in a 4 mL BOD-style glass micro-respiration chamber (inner diameter ~15 mm, height 33 mm) filled with 0.45 µm-prefiltered seawater at 0 °C and 33.2 psu, and transferred to a dark room. The animals were allowed to settle down for 10 min following transfer into the chambers, until the oxygen readings stabilised, after which the oxygen consumption rate was calculated as the linear slope of the DO concentration plotted against time for the next several hours. The use of short incubation times minimised the problem of oxygen depletion at the end of incubation. At the end of each experiment, the dry weight of each animal was measured on a microbalance (MC5; Sartorius AG, Göttingen, Germany) after drying at 60 °C for 24–48 h. The oxygen consumption rate and the weight-specific respiration rate (WSRR) were expressed in µL O_2 ind^{-1} and µL O_2 mg dry $wt^{-1}\,h^{-1}$, respectively. The experimental animals were examined for injuries during identification and discarded if injuries were present. All experiments were run at an identical temperature (0 ± 0.1 °C) (Figure 1).

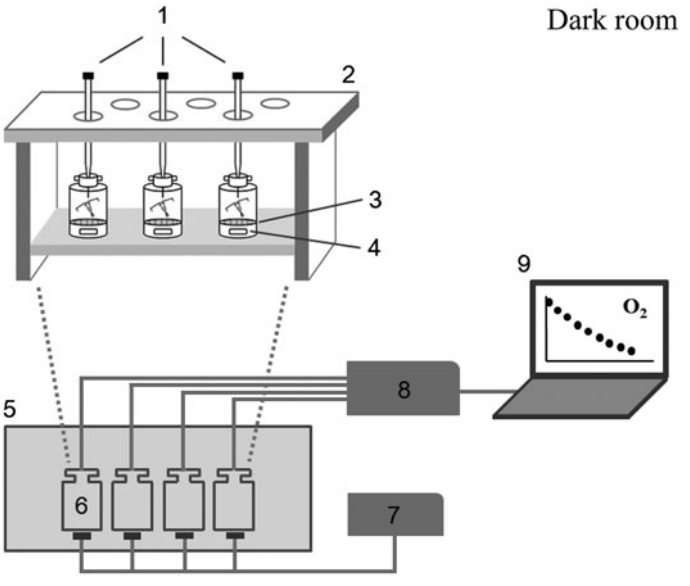

Figure 1. Experimental set-up for measurement of DO concentration using an oxygen microsensor: (1) the oxygen microsensor, (2) the rack, (3) the 200 μm mesh, (4) the stirrer magnet, (5) the incubation bath, (6) the miniaturised BOD chamber, (7) the stirrer controller, (8) the four-channel multimeter and (9) the computer.

Results

Variations in surface seawater temperature (−1.68 to −1.32 °C) and salinity (33.35–33.80 psu) were small, whereas chlorophyll *a* concentrations varied substantially, being relatively high in the Amundsen polynya (St. 7) and Pine Island polynya (St. 87). The extent of sea ice was ~50% at St. 7 and 0% at the other two stations (Table 2).

Variations in the dry weights of experimental *M. gerlachei* were minimal. The dry weight variations among *R. gigas*, *C. acutus* and *E. crystallorophias* furcilia were moderate, whereas those between *C. propinquus* and *P. antarctica* were relatively large (the standard deviations were up to 20% of the means) (Table 1).

The DO concentrations in experimental chambers decreased rapidly, whereas those in control chambers (without animals) remained constant. A short incubation time (3 h) was sufficient to reveal a significant decline in DO concentrations; the falls were 55–88%. The times required for a decline to 80% of the initial (saturated) concentration were 1.5 h for *P. antarctica*, 2.8 h for *C. acutus* and 4.1 h for *M. gerlachei*. For *R. gigas* and *C. propinquus*, the times were 5.8 and 5.3 h, respectively. The figure for *E. crystallorophias* furcilia was 2.5 h (Figure 2).

The WSRR of *R. gigas* was the lowest (0.22 ± 0.07 μL O_2 mg dry wt^{-1} h^{-1}) of all species tested. The values for *C. propinquus* and *P. antarctica* were similar at 0.26 ± 0.04 and 0.26 ± 0.07 μL O_2 mg dry wt^{-1} h^{-1}, respectively. The WSRRs of *M. gerlachei* and *C. acutus* (of lower dry weight) were relatively high. The WSRR of *E. crystallorophias* furcilia was the highest at 1.09 ± 0.64 μL O_2 mg dry wt^{-1} h^{-1} (Table 1).

Overall, the oxygen consumption rates and WSRRs of copepods and *E. crystallorophias* furcilia determined in the present study were slightly lower than those obtained in previous studies on zooplankton from the Southern Ocean (Table 1). The WSRR of

C. acutus measured in the present study, 0.74 ± 0.42 µL O_2 mg dry wt^{-1} h^{-1}, was in the range of previously published data, whereas the values of other species were lower than those previously reported.

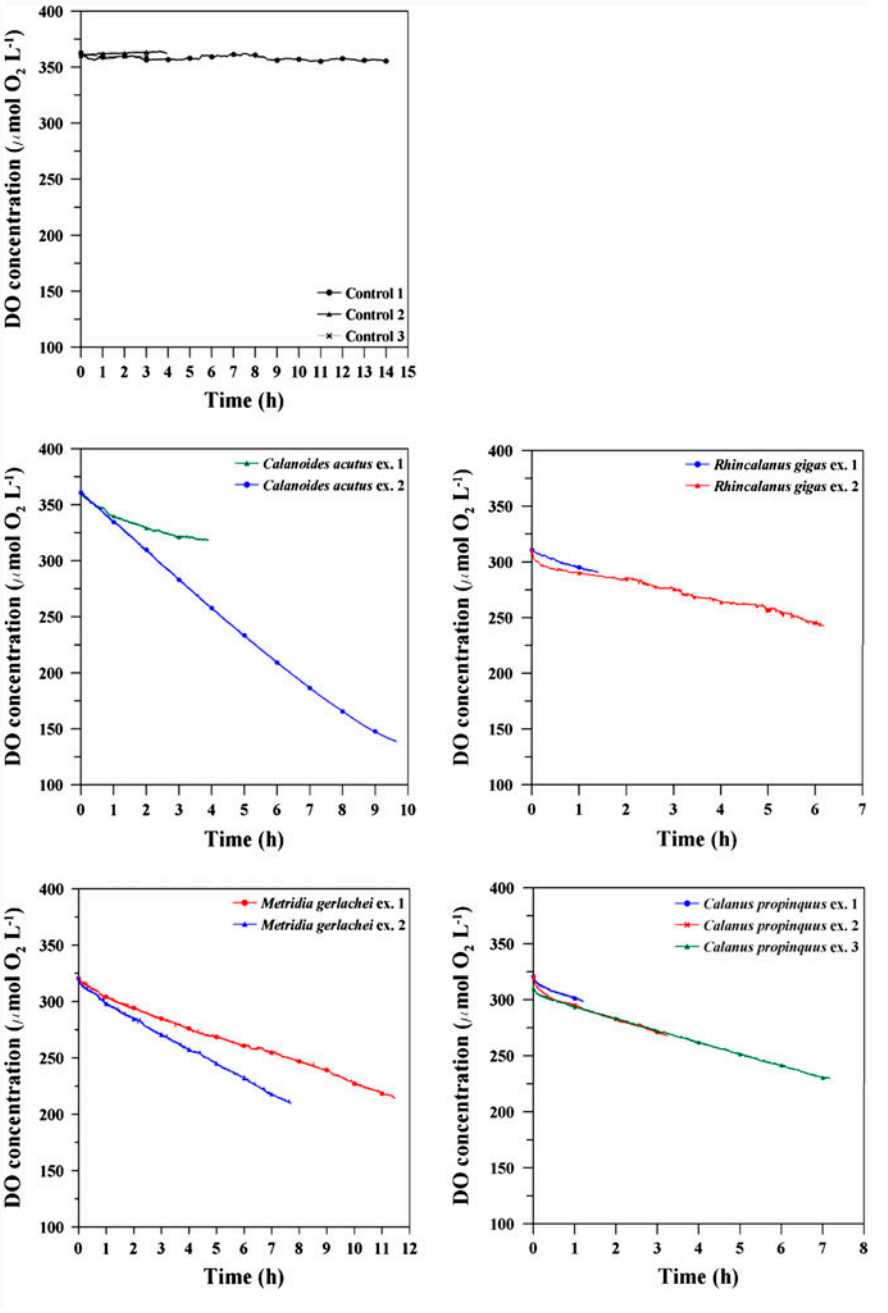

Figure 2. (Colour online) Time-dependent changes in oxygen concentration in chambers in which copepods and *Euphausia crystallorophias* were respiring.

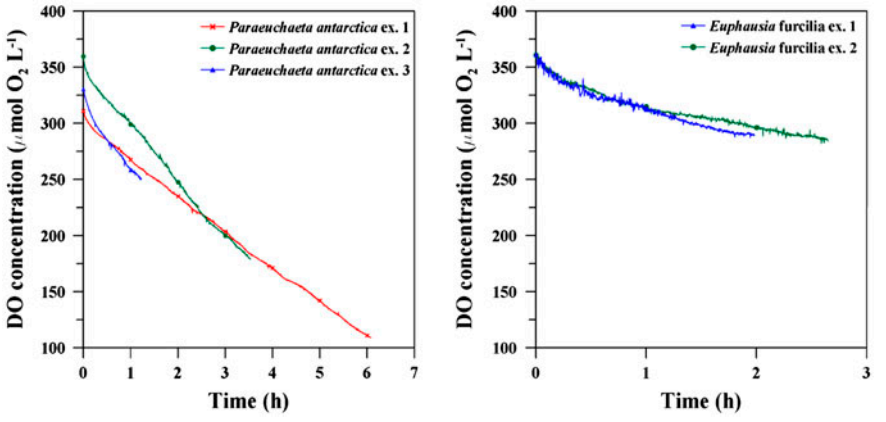

Figure 2. (*Continued*).

Discussion

Commencing in the 1980s, oxygen microsensors have been frequently used to study microbial activities including photosynthesis and respiration in microbial mats and on the undersurface of sea ice, and material flux through sediment–water interfaces (Revsbech et al. 1983; Revsbech & Jørgensen 1986; McMinn et al. 2000; Glud 2008; Geslin et al. 2011; Lee et al. 2012). Marshalonis and Pinckney (2007) estimated the respiration rates of hydromedusae using an oxygen microsensor identical to the one we employed. Shek and Liu (2010) monitored the oxygen consumption of faecal pellets of three species of copepod using an oxygen microsensor. In addition, several interesting field studies have used microsensors (Petterson et al. 2005; Jensen et al. 2006; Nielsen et al. 2007; Brodersen et al. 2008; Geslin et al. 2011). However, few published works on zooplankton metabolism have employed this technique.

Many factors can affect the measured respiration rates of zooplankton (Ikeda et al. 2000), and use of a microsensor can eliminate a significant proportion of problems. The density of animals relative to the volume of the experimental bottle can be crucial. The volumes of bottles and the numbers of specimens in each should be planned to minimise accumulation of excreta and to avoid oxygen depletion at the end of incubation (Ikeda et al. 2000). The Clark-type oxygen electrode (1956) has been successfully employed to examine the respiration of individual copepods and fish larvae as small as 2 mm unstirred electrodes (Ikeda et al. 2000). Our incubation chambers were relatively large (~4 mL), thus multiples of body lengths, allowing individual animals to swim both vertically and horizontally. Individual variability in oxygen consumption rates could be explored, as only a single animal was incubated in each experimental chamber. Any potential complications (e.g. death or injury during incubation) of interpretation caused by incubating multiple animals in a chamber could be avoided.

The length of incubation may be critical. Generally, the microsensor technique works well even when the incubation time is short. Longer incubation can distort respiration results (Köster & Paffenhöfer 2013). For example, defecation may be a significant source of error in oxygen-consumption measurements taken during long-term incubation, although starving the animals prior to experiments (as did we) can reduce such problems. Köster et al. (2008) and Köster and Paffenhöfer (2013) obtained significant results over a

short incubation time (only 6 h) using a fluorescence-based oxygen assay. In most oxygen consumption measurements on zooplankton living in oxygen-saturated environments, the oxygen saturation level should be no less than ~80% by the end of the incubation to safely avoid any effect of low oxygen (Ikeda et al. 2000). In our study, the DO concentrations were generally above 80% saturation ~2–3 h from the start of the experiment (but the figure was 55–66% for *P. antarctica*). Notably, the rate of oxygen consumption by all species was rather constant over an extended period to the point when the oxygen level was notably diminished, suggesting that the microsensor technique yields credible zooplankton oxygen-consumption rates over short incubation times. Furthermore, because such rates are retained over longer incubation periods, using data from later stages of incubation is possible in analysis.

Other possible factors influencing oxygen consumption rates include starvation or feeding, which reduce or increase the rate, respectively. Associated specific dynamic action increases are attributable to the mechanical activity of eating and are a cost of growth (Kiørboe et al. 1985; Ikeda et al. 2000). Prolonged maintenance of wild zooplankton in the laboratory may change behaviour, swimming activity and nutritional conditions, all of which may affect metabolic rates (Ikeda et al. 2000). To avoid underestimating natural respiration rates, previous studies employed *in situ* incubation water to allow normal feeding. Metabolic rates are important in calculating the food intake needed to control biomass, although we measured oxygen consumption rates after 12 h of starvation. The slightly lower respiration rates of copepods and *E. crystallorophias* furcilia (compared to earlier data) that we recorded may be attributable to such starvation.

Environmental extremes in the Southern Ocean have caused development of a variety of survival strategies. Although many species co-exist in a similar environment, they differ in the length of the life cycle, the time and depth of maturation and reproduction, and the timing of seasonal vertical migration (Atkinson 1998; Atkinson et al. 2012). The life cycles of all species are well tuned to annual periodicities, although individual species exhibit quite different lifestyle strategies (Hagen & Schnack-Schiel 1996; Atkinson 1998; Atkinson et al. 2012). In the present study, we found that the relatively large herbivorous species *R. gigas*, the omnivorous *C. propinquus* and the carnivorous *P. antarctica* had low respiration rates. However, the smaller herbivorous *C. acutus*, the omnivorous *M. gerlachei* and *E. crystallorophias* furcilia had high metabolic rates. *R. gigas* and *C. propinquus* were living in an environment of low food level and little sea ice, whereas *P. antarctica*, *M. gerlachei* and *C. acutus* were in waters with a high food level and prominent sea ice. Kawall et al. (2001) explored the effect of the spring ice-edge bloom on the respiration rates of copepods living in three zones (pack ice, ice edge and open water) differing greatly in the extent of ice cover and chlorophyll biomass in the Weddell Sea in late November and December. *C. acutus*, *R. gigas* and *C. propinquus* exhibited high respiration rates in regions of higher primary production. *P. antarctica* showed a similar pattern, but the respiration rate of *M. gerlachei* did not differ greatly between zones. Among the species examined, differences in respiration rates were influenced principally by body size/weight. Environmental variation in sea-ice level and food supplies may also have influenced the interspecies variations in respiration rates that we noted. Overall, our data conform to the general pattern expected of pelagic zooplankton in polar oceans and other waters (Ikeda et al. 2000, 2001).

In summary, our results were similar to those recorded in previous studies on zooplankton from the Southern Ocean. Our short-term (several hours) microsensor measurements on individual animals representing the major zooplankton species of the Amundsen Sea showed that oxygen consumption rates were affected by body

size/weight, sea-ice concentration and food conditions, as is true for many cold water zooplankton of Antarctic waters. Use of the oxygen microsensor technique to measure zooplankton respiration affords many benefits. The technique is non-invasive, individual animals can be studied, the complications associated with lengthy incubation of experimental animals outside their natural habitat are avoided and the experimental procedure is much simpler than the traditional Winkler method. The chamber size can be adjusted to address confinement issues, especially when the respiration rates of groups of organisms are to be measured (e.g. to assess the effects of swarming behaviour on the respiration rate). Furthermore, the system allows continuous recording of DO concentration, with a minimal time interval (10 s) between consecutive measurements, which is particularly useful when tracking the time course is needed. Thus, the microsensor technique is a useful and powerful high-resolution means of investigating the metabolism of zooplankton in the Southern Ocean and elsewhere, and warrants further experimentation.

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