Seasonal abundance of copepod assemblages and grazing pressure in the Kerguelen Island area (Southern Ocean)

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Abstract. A long-term survey of the monthly variations of the copepod assemblages was carried out off Kerguelen Island (Kerfix Station) from February 1992 through to January 1995. Copepods were clearly dominant in the mesozooplankton (>90% of the total), with population abundances ranging from <100 individuals m^{-3} in winter to 700 individuals m^{-3} in summer. *Calanus simillimus*, *Rhincalanus gigas*, *Metridia lucens*, *Oithona frigida*, *Oithona similis* and *Calanoides acutus* were the most abundant species. From mid-1993, incubation experiments were performed with copepods in order to estimate the grazing pressure on the phytoplankton standing stock. In addition, estimations of their metabolic cost (oxygen comsumption) were also made. All experimental measurements were made using four size groups (Gr) defined by the cephalothorax length of the copepods. These are: Gr I, 0.2–1.1 mm; Gr II, 1.2–2.5 mm; Gr III, 2.6–3.3 mm; Gr IV, 3.7–6.5 mm. The average grazing rates ranged between 0.7 and 2.2 ng of chlorophyll (Chl) a copepod^{-1} day^{-1}, according to the size class of the individuals. For the whole copepod assemblage, seasonal changes in the estimated grazing rate (27–1299 ng of Chl a m^{-3} day^{-1}) were due to changes in the abundance of the copepod species, not to apparent intrinsic seasonal trends in their physiological rates. The average ingestion reached a maximum level of 356 ng Chl a day^{-1} m^{-3} (or 38 μg C day^{-1} m^{-3}), representing 0.12% of the mean phytoplankton standing stock. In the summer period, up to 2% of the primary production was consumed, but the carbon needs, expressed by the respiratory metabolism, showed a slight discrepancy with the contribution of phytoplankton: the carbon required for the resting metabolism alone (94 μg C day^{-1} m^{-3}) representing ~0.31% of the algal standing stock. In summer, this metabolism could have been equivalent to 13% of the primary production. These results strongly suggest that the food of the mesozooplanktonic copepods off the Kerguelen Islands must include a large proportion of non-phytoplankton material.

Introduction

This study is part of the larger program KERFIX within the framework of JGOFS. KERFIX was designed to estimate the flux of carbon in the Indian sector of the Southern Ocean and to understand the mechanisms governing it (Jeandel *et al.*, 1998). Its aim was to determine the seasonal changes in physical, chemical and biological parameters.

Despite high nutrient concentrations, primary production in the open ocean zone of the Southern Ocean is known to be low, especially in the subantarctic sector (Jacques and Minas, 1981). Among several reasons that have been put forward to explain this paradox, mesozooplankton grazing on phytoplankton might be an important contributor (Hopkins, 1985). This is somewhat in contrast with high-chlorophyll (Chl) environments, where copepods are unable to control the phytoplankton biomass (Granéli *et al.*, 1993). Historically, the most relevant data on the phytoplankton–zooplankton trophic relationships in the Southern Ocean were obtained from oceanographic cruises, and were discountinuous in space and time (Schnack *et al.*, 1985; Drits *et al.*, 1993; Atkinson, 1994; Lopez and Huntley, 1995). A few studies have been conducted in the subantarctic sectors around the Prince Edward Archipelago (Perissinotto, 1992) or in the mixing zone

of the Antarctic Polar Frontal Zone (Atkinson, 1996) and most of them dealt with the physiological rates of definite species of copepods (*Calanoides acutus, Rhincalanus gigas* or *Metridia gerlachei*). However, for the Indian sector, this information is still scarce (Bedo *et al.*, 1995; Tirelli *et al.*, 1997).

The program KERFIX provided the first opportunity to investigate the seasonal variations in the open oceanic zone of the Indian sector of the Southern Ocean where low Chl conditions prevail (Jacques and Fukuchi, 1994; Fiala *et al.*, 1998). The present study was designed to examine the changes in the whole copepod assemblage and to document the phytoplankton standing stock–copepod relationships on an annual time scale.

To avoid gaps due to seasonality in the species or stage composition of the copepod community, copepod abundances and the physiological rates were estimated using a subdivision in size classes of animals.

Three major questions were investigated. (i) What is the grazing pressure due to the mesozooplanktonic copepod assemblages in the subantarctic, low-Chl region? (ii) Are the metabolic needs of these assemblages fulfilled? (iii) What is the proportion of the total phytoplankton biomass involved in these processes?

Method

Study sites

The JGOFS time series station Kerfix (50°40'S, 68°25'E) is situated ~60 miles southwest of the Kerguelen Islands (Figure 1). The frequent heavy weather conditions at this site did not allow the collection of enough healthy copepods to conduct process studies to estimate their grazing rates and carbon requirements. Another site, Bio-Station (49°43'S, 70°56'E), located 15 miles east of Kerguelen Island, was chosen as a more convenient location for a survey on annual biological processes for several reasons. (i) Like Kerfix Station, Bio-Station is located in the open ocean, far enough from the coast to be free of terrestrial influences and close enough for the mesozooplankton to be kept alive until the return to the laboratory, regardless of meteorological conditions. (ii) Both stations are situated in the same geographic area, close to the Polar Front, whose position is known to vary spatially and temporally (Park and Gamberoni, 1997; Park *et al.*, 1998). (iii) The hydrobiological parameters, surface water temperature, Chl *a* content, numerical abundance and species composition of the mesozooplankton community, recorded at Bio-Station, were typically of subantarctic origin and consistent with those observed at Kerfix Station (personal data). (iv) The floristic compositions of the phytoplankton assemblages were observed to be similar on a large latitudinal scale in this zone (Jacques *et al.*, 1979). For these reasons, we hypothesized that the phytoplankton assemblages were similar at Kerfix and Bio-Station.

These two sites were visited every month from February 1992 to January 1995 (Kerfix Station) and from May 1993 to January 1995 (Bio-Station).
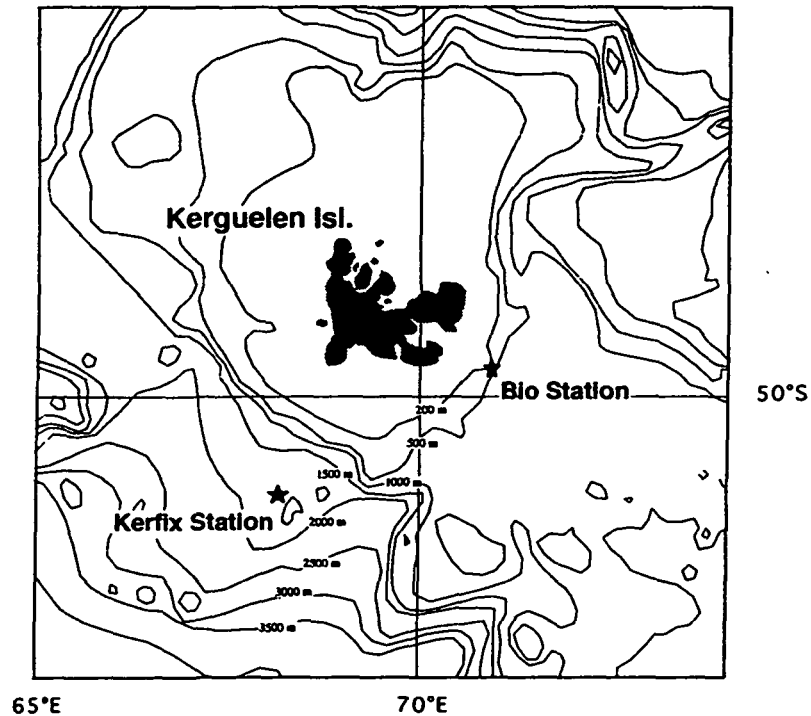
Fig. 1. Location of the sampling stations around the Kerguelen Archipelago.

Sampling

Because of the meteorological conditions described above, several failures in the zooplankton sampling program occurred, so that only the mean numbers of copepods per month were used in the analysis. At both sites, mesozooplankton were collected by vertical hauls (300 m–surface) using a Bongo frame fitted with 0.2-mm-mesh nets. At Kerfix Station, both samples were preserved, either in a 5% buffered formalin–water solution for identification and counting, or dried for later biomass measurements. At Bio-Station, one sample was preserved as a control, while the other was poured into a 20 l jar filled with natural sea water and brought to the laboratory to sort live copepods. Temperature and Chl a measurements were taken simultaneously in the surface layer (1 m depth). The natural sea water used for the experiments was collected from 1 m depth, sieved on a 200 µm gauze and maintained at 3–5°C first on board and later in a cold room in the laboratory.

Sample treatment

The main species and stages of copepods were counted in the preserved samples from Kerfix Station only. For each month, the copepods counts were gathered according to four size groups defined below in the biological experiments.

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Experiments

The picking of live copepods for grazing or respiration measurements was done within a few hours after capture at Bio-Station. All incubations used natural unfiltered sea water and were carried out under conditions as close as possible to those prevailing *in situ*. The Chl profiles obtained at Kerfix Station showed that surface Chl *a* levels at Bio-Station approximated the mean levels encountered by the zooplankton in the mixed layer (Fiala *et al.*, 1998). Schnack-Schiel *et al.* (1991) and Bathmann *et al.* (1993) have shown that some copepods apparently do not feed in poor conditions of Chl *a* (<1 µg l⁻¹), so during the winter experiments, natural sea water was sometimes slightly enriched with net-collected phytoplankton, but never beyond local highest concentrations (Table I). Before experiments began, 7 l of natural culture medium were prepared either with or without phytoplankton added.

Live copepods were rapidly sorted by eye, on the basis of body size and/or species. Four batches were prepared with 50–150 animals sorted according to their individual size as follows: Group (Gr) I, *Oithona* spp. and small juveniles of several calanoids; Gr II, *Calanus simillimus* copepodite stages and *Metridia* spp.; Gr III, *C.simillimus* adult and *Calanoides acutus* young copepodite stages; Gr IV, copepodites V and adults of *R.gigas*, and *C.acutus*. All copepods were allowed to acclimate for 24 h under controlled conditions (darkness and *in situ* temperature). Each batch of sorted copepods was then transferred to 1 l bottles, filled with natural culture medium. Bottles were set up on a rotating plankton wheel for ~24 h. A control jar without copepods was included in each experiment. Chl *a* was measured at the start (control) and at the end of each experiment from duplicate aliquots of the control and of each experimental jar, using a Turner Designs fluorometer (Strickland and Parsons, 1968).

The question of selective grazing was not considered, but the incubation experiments in natural sea water respected the feeding effort of copepods on each food item.

The clearance rate was calculated according to the equation of Frost (1972): $F = V \times g/N$ (F is in ml h⁻¹ animal⁻¹), where V is the volume of the experimental jar in milliliters, g is the grazing coefficient $= \log C_o - \log C_t/t$, where C_o and C_t are the Chl *a* concentrations in µg l⁻¹ at the start and at the end of incubation, respectively, $t = 24$ h is the duration of the experiment and N is the number of copepods in the experimental bottle.

After each experiment, copepods were killed with a drop of 5% formaldehyde and preserved to check the identification and to measure the cephalothorax length (CL). The lengths of copepods within the four size groups in experimental batches were: Gr I, 0.2–1.1 mm CL; Gr II, 1.2–2.5 mm CL; Gr III, 2.6–3.3 mm CL; Gr IV, 3.7–6.5 mm CL. Immediately after counting, the copepods in each batch were rinsed and transferred to pre-weighed pans, dried at 60°C and weighed using a Cahn electrobalance. The dry weight of animals was used to standardize the filtration and respiratory rates.

Copepod assemblages and grazing pressure in Kerguelen Island

Table I. Environmental parameters at Bio- and Kerfix stations. Water temperature; initial Chl a concentration in the experiments, compared with Chl a content in situ; mean copepod abundances

Month	Temperature (°C)		Chl a (µg l⁻¹)			Copepods m⁻³		
	Bio-Station surface	Kerfix mixed layer	Incubation	Bio-Station surface	Kerfix mixed layer	Kerfix Mean	SD	N
I	3.4	3.19	0.69	0.79	0.40	742	2	2
II	4.5	3.67	0.42	0.44	0.28	167	11	2
III	4.3	4.09	0.28	0.70	0.20	155	216	2
IV	3	3.70	0.75	0.40	0.16	110	50	3
V	2.85	3.42	1.78	0.29	0.16	103	31	2
VI	2.55	2.77	0.28	0.20	0.14	168	166	2
VII	2.15	2.34	0.62	0.23	0.20	36		1
VIII	1.95	1.80	1.03	0.24	0.24	23	24	2
IX	1.4	1.65	0.34	0.36	0.28	137		1
X	1.5	1.71	0.70	0.64	0.33	149		1
XI	1.8	1.88	1.88	1.50	0.55	395		1
XII	2.15	2.84	1.19	1.16	0.62	247	315	2

N, number of samples.

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Ingestion rates

The ingestion rate was calculated individually as the product of the experimental clearance rate per animal and the *in situ* Chl *a* concentration. Assuming that the phytoplankton assemblages were similar at Kerfix and Bio-Station, the values of the Chl *a* concentration in the 0–100 m mixed layer recorded at Kerfix Station were used in these calculations. Rates were expressed as ng Chl *a* ingested animal^{-1}.

The carbon content equivalent to Chl *a* was calculated using the ratio C:Chl *a* = 106. This value was established from analysis of particulate organic carbon and Chl in the Kerfix area during the Antares 3 cruise (Bentaleb *et al.*, 1997) and is in accordance with those of Hewes *et al.* (1990).

Community grazing rates

The individual grazing rates were estimated and the mean ingestion rate of each size group was calculated. The monthly grazing impact of the copepod community was determined in two steps: (i) multiplying the mean ingestion rate per copepod of each size group by the number of copepods in this group per cubic meter; (ii) adding the results of the four size groups together.

Estimation of metabolic requirements

For the experiments on oxygen consumption, copepods were sorted as previously described and allowed to acclimate in filtered sea water. After 24 h acclimation to laboratory conditions (dark and *in situ* temperature), animals were incubated in experimental vessels filled with filtered sea water. The volume capacity of the respiratory vessels was 50, 125 or 250 ml and the number of copepods added to each vessel was chosen according to their size (from 1 animal per 2 ml for small ones, to 1 animal per 8 ml for large ones). They were maintained in the incubation vessels under controlled conditions for ~17 h. The dissolved oxygen was measured using a Clark electrode and a Strathkelvin oxymeter at 10°C. The O_2 requirements were estimated from the differences in dissolved oxygen content between the control and the incubation vessels, and were expressed in µl O_2 ind.$^{-1}$ h^{-1}. The equivalent carbon demand for respiration was calculated using a respiratory quotient value (RQ) of 1.

Also, mean respiration rates were calculated for all four size groups of copepods. The monthly estimations of their metabolic requirements were estimated by multiplying the mean respiration rate per copepod of each size group by the number of copepods in this group per cubic meter, and then adding the results together.

Results

The environment (Table I)

The seasonal changes in hydrological parameters, temperature and Chl *a* content were well marked and similar throughout the study area. At Kerfix, the

temperature ranged between 1.6 and 1.8°C from September to November, and between 3.4 and 4.3°C in January–March (Park *et al.*, 1997). At Bio-Station, the temperatures followed the same annual cycle, in the same range of values: 1.4–2 and 3.4–4.3°C in winter and summer, respectively.

The Chl *a* concentration measured at Kerfix Station in the 0–100 m mixed layer oscillated between minimum values of 0.14–0.16 µg l^{-1} in April–June and maximum values of 0.4–0.55 µg l^{-1} in November–January (Fiala *et al.*, 1998). During the same periods, the concentrations of Chl *a* at Bio-Station were ~0.20 and 0.8–1.5 µg l^{-1}, respectively.

Copepod abundance

At Kerfix, copepods (0.2–8 mm length) were the most numerous taxon of the mesozooplankton, with an overall average of 202 ind. m^{-3}. Other crustaceans, especially euphausiids, ostracods, chaetognaths and molluscs, accounted for only 3–4% of the total. More than 81% of the copepod stock was made up by adults of small species, essentially *Oithona frigida* and *Oithona similis*, and early juvenile stages of abundant species such as *Calanus simillimus*, *R.gigas* and *Calanoides acutus*. Late copepodite stages and adults of these species represented an average of 10, 2 and 1% of the total number of copepods, respectively, with other species contributing <1%. According to the size groups defined from the biological rate experiments, the species were numbered as follows: Gr I, *Oithona* spp., juveniles of several calanoids, or adults of small species such as *Ctenocalanus citer*; Gr II, *Calanus simillimus* copepodites IV–V, *Métridia* spp.; Gr III, *C.simillimus* adults, *Calanoides acutus* juveniles; Gr IV, copepodite V and adults of *R.gigas* and *C.acutus*. These species dominated the mesozooplanktonic assemblages (Figure 2) at both Kerfix and Bio-Station.

The copepod abundance showed a strong seasonal pattern of variation, with a maximum in January (≥700 m^{-3}), followed by a decrease from February to June (~150 ind. m^{-3}), to a minimum in July and August (<100 ind. m^{-3}). During austral spring, i.e. September–December, copepod numbers increased again to 400 ind. m^{-3} (Table I).

Clearance, ingestion and grazing rates

The range of initial Chl *a* concentration used in the experiments, from 0.10 to 1.88 µg l^{-1}, was selected in accordance with the *in situ* pigment level (Table I).

The average values of filtration rates ranged between 0.255 ml h^{-1} copepod^{-1} for Gr I to 0.08 ml h^{-1} copepod^{-1} for Gr IV (Table III).The pooled data of the 49 observations showed an allometric relationship between the weight-specific filtration rate and the size of animals (cephalothorax length expressed in millimeters): log F = 0.97 − 0.63 log L (r = −0.73). However, correlations were not observed between the Chl *a* concentration range used in the experiment (0.1–1.9 µg l^{-1} Chl *a*) and the filtration rates (Figure 3).

Ingestion rates were calculated for each experimental batch from the relationship: $F \times$ *in situ* Chl *a* (Table II). Considering the lack of clear seasonal trends
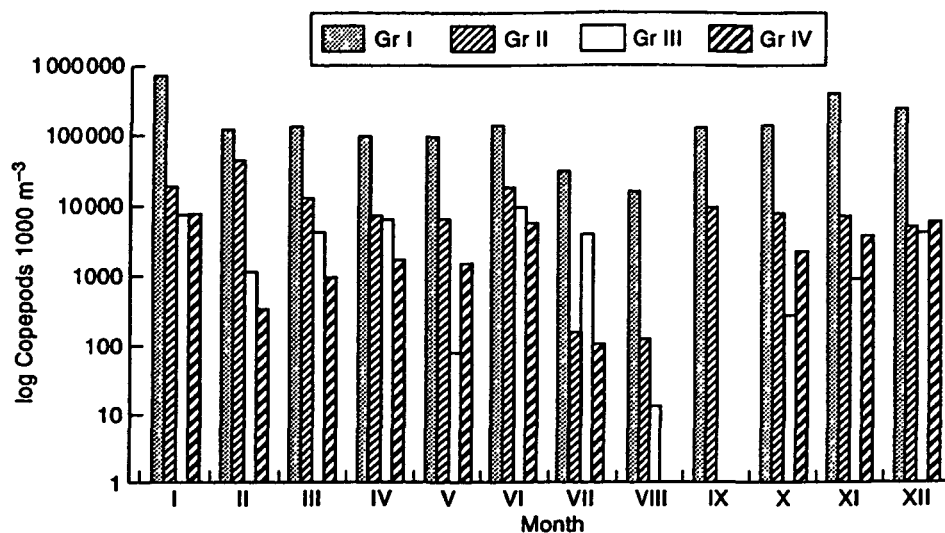
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Fig. 2. Monthly means of copepod abundances (January 1993–January 1995) at Kerfix.
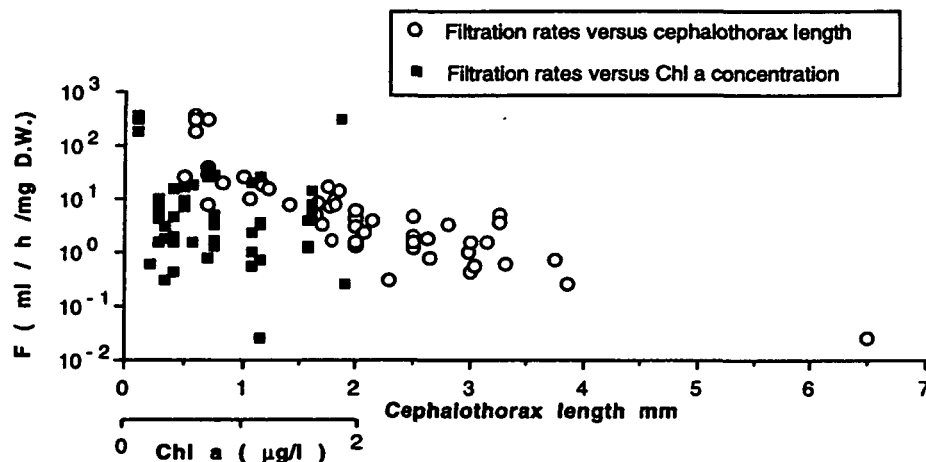

Fig. 3. Allometric relationship between weight-specific filtration rates and the size groups of copepods and filtration rates versus experimental Chl *a* concentration (May 1993–January 1995).

and the fact that all the size groups of copepods were not sampled equally every month, ingestion rate data were expressed as the overall mean for each size group: Gr I, 0.073 ng h^{-1} copepod^{-1} (range 0.008–0.465); Gr II, 0.091 ng h^{-1} copepod^{-1} (range 0.007–1.112); Gr III, 0.071 ng h^{-1} copepod^{-1} (range 0.014–0. 315); Gr IV, 0.029 ng h^{-1} copepod^{-1} (range 0.009–0.053) (Table III). The monthly ingestion rates were calculated for the whole copepod community taking into account the densities of copepods in each of these groups (Table IV). The

Table II. Mean ingestion rates of copepods in the different size classes, Gr. Mean ± standard error

Month	Chl a (mg l⁻¹) in situ	Ingestion (ng Chl a h⁻¹ copepod⁻¹)			
		Gr I	Gr II	Gr III	Gr IV
I	0.4	0.064 (1)		0.087 ± 0.010 (3)	0.031 ± 0.022 (2)
II	0.28		0.037 ± 0.016 (3)	0.015 ± 0.001 (2)	
III	0.2	0.036 (1)	0.054 ± 0.010 (3)		
IV	0.16		0.020 ± 0.004 (2)		
V	0.16		0.029 ± 0.008 (3)	0.078 (1)	
VI	0.14	0.047 ± 0.015 (3)			
VII	0.2	0.012 ± 0.003 (3)	0.023 (1)		
VIII	0.24		0.075 ± 0.044 (8)		
IX	0.28		0.020 ± 0.013 (2)	0.031 (1)	
X	0.33	0.015 (1)		0.020 (1)	
XI	0.55	0.466 (1)			
XII	0.62	0.050 (1)	0.421 ± 0.489 (3)	0.135 ± 0.127 (3)	0.053 (1)

Numbers within parentheses = number of observations.

Table III. Mean values of filtration, grazing and respiration rates of copepods in the different size groups. Mean (± standard error). Ingestion rate: mean and range of values (min–max)

Copepods	Cephalothorax length (mm)	Mean filtration rate (ml h⁻¹ ind.⁻¹)	Mean ingestion rate (ng Chl a h⁻¹ ind.⁻¹)	N	Mean respiration rate (O_2 µl⁻¹ h⁻¹ ind.⁻¹)	N
Group I	0.2–1.1	0.226 ± 0.25	0.073 (0.008–0.465)	11	0.013 ± 0.005	4
Group II	1.2–2.4	0.357 ± 0.261	0.091 (0.007–1.112)	25	0.121 ± 0.035	15
Group III	2.6–3.3	0.195 ± 0.158	0.071 (0.014–0.315)	11	0.305 ± 0.145	5
Group IV	3.7–6.5	0.085 ± 0.072	0.029 (0.009–0.053)	3	0.555 ± 0.404	9

N, number of observations.

estimated average annual grazing pressure by the mesozooplanktonic copepods was 356 ng day^{-1} m^{-3} Chl a, with a minimum value of 27 ng day^{-1} m^{-3} in August and a maximum value of 1299 ng day^{-1} m^{-3} in January. In terms of carbon equivalents (assuming a ratio of C:Chl = 106), the mean annual amount of Chl a ingested corresponds to 1574 ng C h^{-1} m^{-3} or 38 μg C day^{-1} m^{-3} (Figure 4). This represents ~0.12% (range 0.1–0.3%) of the Chl a standing stock measured in the euphotic zone (Table I). During the cruise Antares 2 (February–early March 1994), the Kerfix Station was visited and the local daily primary production was estimated as 3 mg C m^{-3} (T.Caubert, personal communication). Assuming this as an average figure of the phytoplankton productivity during summer, a rough average of 2.4% of primary production would be grazed by the copepods in December and 4.6% in January.

Respiratory rates

The carbon requirements for the resting metabolism of copepods in each size group were derived from measurements of dissolved oxygen consumption (Figure 5). As previously noted for ingestion rate experiments, all the size groups of copepods were not present equally in each sample, so the data were pooled in order to obtain an overall mean of the respiratory rate for every size group. Table III synthesizes the mean oxygen consumption values: 0.013 μl h^{-1} ind.$^{-1}$ for Gr I, 0.121 for Gr II, 0.305 for Gr III and 0.555 for Gr IV.

The metabolic requirements of the whole community were calculated using the mean respiration rate for each group mutiplied by the number of animals per cubic meter. This represented an average carbon equivalent amount of 148 μg C day^{-1} m^{-3} (range 231 μg in summer–11 μg in winter), i.e. 0.5% of the *in situ* phytoplankton carbon (Table IV).
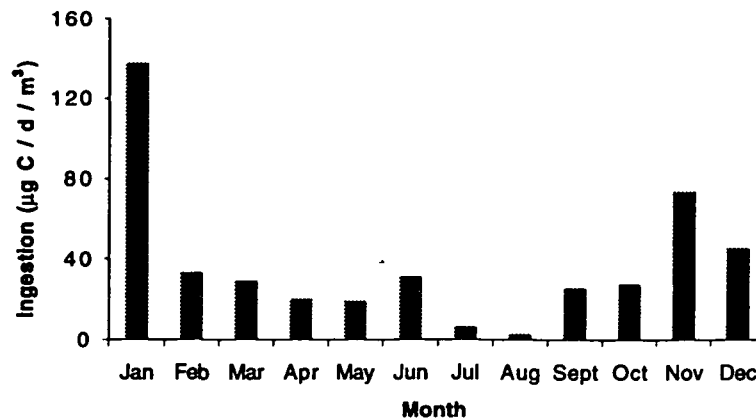

Fig. 4. Mean daily ingestion rates as C-Chl a equivalent per cubic meter for the whole copepod community.

Table IV. Overall estimation of the daily pigment and carbon equivalent requirements for the whole mesozooplankton copepod assemblages. Calculations were made taking into account the number of copepods in each of the four size groups

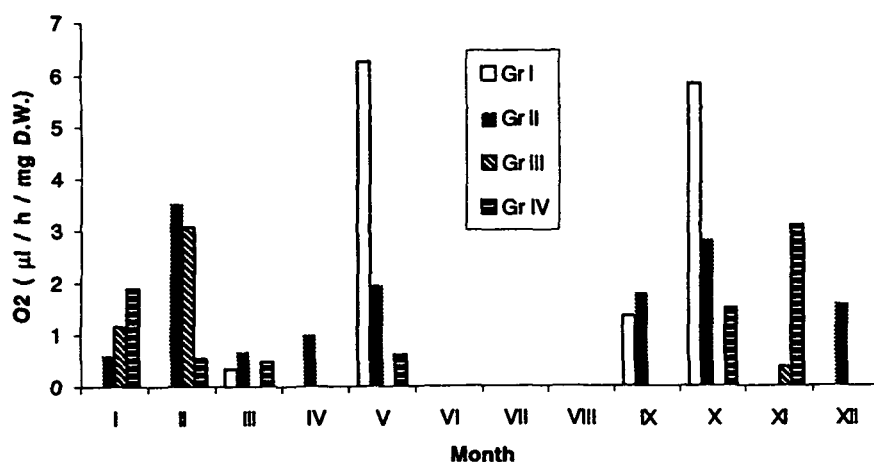| Month	Ingestion			Oxygen consumption		
	ng Chl a day^{-1} m^{-3}	µg carbon eq. day^{-1} m^{-3}	% C-Chl *situ*	µl O$_2$ day^{-1} m^{-3}	µg carbon eq. day^{-1} m^{-3}	% C-Chl *situ*
I	1299.1	137.7	0.32	431.1	230.9	0.54
II	312.5	33.1	0.11	183.4	98.2	0.33
III	276.	29.2	0.14	123.1	66.0	0.31
IV	193.7	20.5	0.12	118.05	63.2	0.37
V	182.6	19.3	0.11	69.4	37.2	0.22
VI	296.1	31.4	0.21	217.0	116.2	0.78
VII	62.4	6.6	0.03	46.5	24.9	0.12
VIII	27.4	2.9	0.01	20.7	11.1	0.04
IX	243.9	25.8	0.09	67.0	35.9	0.12
X	261.9	27.8	0.08	96.2	51.5	0.15
XI	691.3	73.3	0.13	194.5	104.2	0.18
XII	429.2	45.5	0.07	188.1	100.8	0.15

Fig. 5. Weight–specific oxygen consumption rates of copepods related to size (cephalothorax length).

Discussion

The aim of the work was to measure the potential impact of the copepod community on the phytoplankton biomass in a subantarctic area, known to be poor in Chl *a*. The specific structure of the copepod community, as well as the density of individuals, were found to be consistent with those observed in similar areas off Kerguelen Island (Semelkina, 1993; Ehrrif *et al.*, 1997), but were quite different from those of the Baie du Morbihan (Razouls *et al.*, 1996), thus reflecting the oceanic character of the sites under study.

Most of the usual procedures employed to estimate the grazing pressure of copepods are designed for single species and are inappropriate for the entire copepod communities. Subdividing copepods into size groups is an attempt to account for the seasonal changes in the community structure observed during the year survey, while considering the whole copepod assemblage.

Taking into account the similarity of the copepod assemblages—species composition and abundance levels—as well as that of the hydrological parameters (temperature, salinity) and biological characteristics (especially the Chl *a* concentration) at the two sites Bio-Station and Kerfix, we assumed that the biological indexes obtained for copepods at Bio-Station were applicable to any other site in the area, provided that the experimental conditions reflected those prevailing *in situ*. This could be a possible bias leading to an underestimation of the present results, but even if this hypothesis is not optimal, it should be a realistic estimation of a global carbon budget.

The results of the monthly surveys of filtration and ingestion rates suggest that mesozooplanktonic copepods could operate close to their minimum threshold of clearance and ingestion rates at the low Chl *a* concentration observed in the euphotic part of the water column. In all experiments, filtration rates were not clearly correlated to the range of experimental Chl *a* content, in contrast to what

might be expected, but, as pointed out by Paffenhöffer (1971) for young, small-sized stages of *Calanus helgolandicus*, we observed that small copepods filtered more actively than larger ones.

In parallel to this, the ingestion rates related to the filtration rate did not show any clear seasonal changes for any of the size groups. For this reason, the estimations of the amount of Chl *a* consumed by the whole copepod assemblage are in essence only dependent on the number of copepods in each size group. The overall values of ingestion shown here for copepods of Grs I and II (1.7–52 ng Chl *a* h^{-1} m^{-3}) are comparable to the values of 1–20 ng Chl h^{-1} m^{-3} observed for copepods of the same size from stations close to the frontal zone, SE off Kerguelen during Antares 2 cruise (Bedo *et al.*, 1995).

The levels of Chl *a* standing stock found to be grazed by the copepod community, <1%, are slightly lower than the 2.6% estimated for the copepod assemblages for the same zone during Antares 3 (Tirelli *et al.*, 1997) or the 3% at Prince Edward Archipelago in autumn (Perissinotto, 1992). In the Seasonal Ice Zone, Hopkins (1987) at MacMurdo and Atkinson (1994) near South Georgia report that 2% of the phytoplankton standing stock should be consumed by copepods. This suggests that phytoplankton are sufficient to sustain the copepod community even in the presence of very low food levels. From the extensive discussion of Ward *et al.* (1995), it appears that the grazing impact of mesozooplankton in Antarctic waters generally ranges from <1% to 55% of the local primary production. As pointed out by Morales *et al.* (1991), the low exploitation rate that results from the estimations of *in situ* grazing could be due to the dominance of small copepods. Swadling *et al.* (1997) evaluate at only 1–2% the part of the summer huge phytoplankton standing stock grazed especially by the small cyclopoids during the ice break-out.

The oxygen consumption values measured in the various size groups of copepods are in agreement with previous results available for the Antarctic area (Ikeda and Fay, 1981; Razouls and Razouls, 1982). However, the carbon equivalent calculations of the resting metabolism indicate slightly higher carbon requirements than the amounts of C-Chl *a* provided by grazing alone. This discrepancy confirms that copepod communities would not be strictly phytoplankton dependent and would be sustained by an alternative food item such as heterotrophic flagellates (Atkinson, 1996). A part of this difference may be explained by the large experimental range in the magnitude of the processes investigated. However, on the whole, the relative convergence of results indicates that mesozooplankton alone are not able to control the phytoplankton stock nor the primary production rates in the low Chl *a* level of the Antarctic. Also, the discrepancy between the phytoplankton concentration in the euphotic layer and the part eaten by the mesozooplankton confirms that the copepods alone are not the most prominent organisms involved in the control of phytoplankton relative to krill (Granéli *et al.*, 1993). However, as far as the carbon budget or carbon requirements are concerned, measurements of the metabolic requirements (respiratory rates) of size groups of copepod assemblages could be a reliable alternative method to ingestion rate measurements.

More detailed specific studies are needed with several methodologies in order

to improve the ecophysiological data on the alimentary regime of the copepod species and their developmental stages inhabiting high-latitude waters.

Acknowledgements

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