F. Alonzo · P. Mayzaud · S. Razouls · P. Bocher
Y. Cherel

# Seasonal changes in biomass, growth rates and production of subantarctic calanoid copepods in the Bay of Morbihan, Kerguelen Islands

**Abstract** The present study addresses the ecology of two dominant copepod species in the Bay of Morbihan, Kerguelen Archipelago. The biomass of the herbivore *Drepanopus pectinatus* (from 2 mg m$^{-3}$ in winter up to 500 mg m$^{-3}$ in summer) is tightly coupled to seasonal changes in chlorophyll *a* concentration in the region, whereas the biomass of the predatory euchaetiid *Paraeuchaeta antarctica* increases during two distinct periods over the year: 250 mg m$^{-3}$ in early summer, with the recruitment of the annual generation, and 100 mg m$^{-3}$ in autumn, with the deposition of lipids as energy reserves in C5 stages and adults. The juvenile growth rates predicted by temperature-dependent models (0.09 day$^{-1}$) closely approximate those observed in *D. pectinatus* in summer, but are much greater than those observed in *P. antarctica* (from 0.001 to 0.04 day$^{-1}$ depending on developmental stages). This difference can be explained by the reproductive strategies and trophic positions of the two species and may also result from the dependence of larval growth on energy reserves in *P. antarctica*. The production rates are five- and tenfold greater in juvenile stages than in adults, respectively, for *D. pectinatus* and *P. antarctica*. The secondary production by *D. pectinatus* is insufficient to support *P. antarctica* during winter, when the predatory species probably shifts to alternate prey. In summer the predation by *P. antarctica* accounts for only a minor part of the mortality estimated for *D. pectinatus* (from 20% to 60% depending on the examined station). At two of the three stations examined in the Bay of Morbihan, the production of *P. antarctica* could potentially support the dietary requirements of planktivorous seabirds in the region (∼2,000 kg prey day$^{-1}$ for common diving petrels, *Pelecanoides urinatrix*, and ∼90 kg prey day$^{-1}$ for rockhopper penguins, *Eudyptes chysocome filholi*).

Present address: F. Alonzo
Observatoire Océanologique,
Océanographie Biochimique et Ecologie, LOBEPM ESA,
CNRS 7076, BP 28, 06230, Villefranche sur Mer, France

P. Mayzaud (✉)
Observatoire Océanologique,
Océanographie Biochimique et Ecologie,
LOBEPM ESA, CNRS 7076, BP 2806230,
Villefranche sur Mer, France

S. Razouls
Laboratoire Arago, Observatoire Océanologique,
URA-CNRS 117, 66630 , Banyuls Cedex, France

P. Bocher · Y. Cherel
Centre d'Etudes Biologiques de Chizé,
UPR-CNRS 1934, 79360, Villiers-en-Bois, France

P. Bocher
Laboratoire de Biologie et Environnement Marins,
EA 1220 de l'Université de La Rochelle,
17026, La Rochelle, France

F. Alonzo
IASOS—University of Tasmania,
GPO Box 252-77, 7001, Hobart, TAS, Australia

## Introduction

To date, relatively few studies have been carried out on the reproductive biology and ecology of copepods in subantarctic waters compared to high-latitude regions. However, the role of copepods in subpolar pelagic ecosystems is essential both quantitatively as the main component of the mesozooplankton and qualitatively as the major link of matter and energy between primary producers and large, carnivorous predators (Hopkins 1985; Falk-Petersen et al. 1990). In the subantarctic Kerguelen Islands (Fig. 1), the coastal mesozooplankton is dominated in summer by the endemic herbivorous copepod *Drepanopus pectinatus*, which produces four generations per year in the Bay of Morbihan and represents up to 99% of the abundance of the community (Razouls and Razouls 1988, 1990). In this extreme situation it is arguable that almost all the organic matter derived from the summer primary production is transferred to higher trophic levels via this single copepod species.
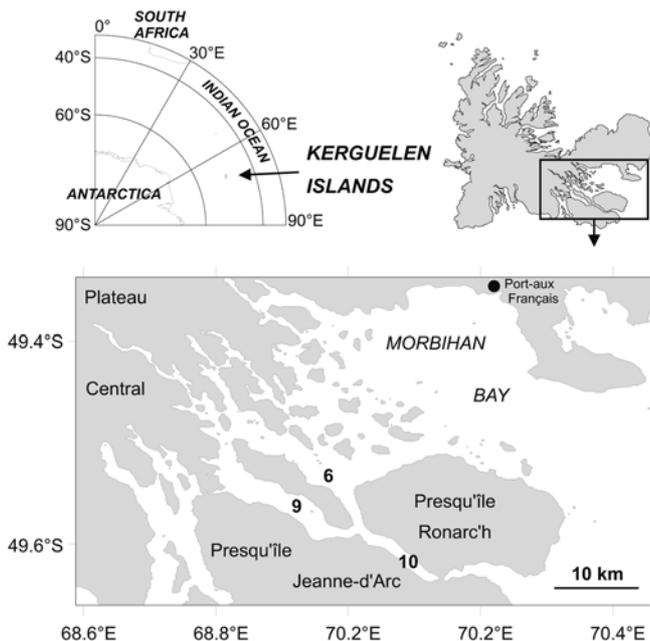
**Fig. 1** Location of the sampling stations ST6, ST9 and ST10 in the Bay of Morbihan

The large-bodied, carnivorous, euchaetiid *Paraeucheta antarctica*, whose geographic distribution extends into the high Antarctic (Park 1994), is abundant in the southwestern part of the Bay of Morbihan, where the species is recognized as a true breeding population in the sheltered fjords (Alonzo et al. 2000a). Given the size range of its prey (Yen 1991), the main food source for the species in the field is most likely to be *D. pectinatus*. The ability of *P. antarctica* to feed on *D. pectinatus* was demonstrated experimentally (Alonzo et al. 2000b), and the congeneric species *Drepanopus forcipatus* was a major component of the gut content of *P. antarctica* around South Georgia (Øresland and Ward 1993). The importance of *D. pectinatus* as a food item remains to be evaluated by assessing the potential of its secondary production to sustain the predatory euchaetiid species. At the next higher trophic level, *P. antarctica* has been described as an important component in the diet of the common diving petrel *Pelecanoides urinatrix* and the southern rockhopper penguin *Eudyptes chysocome filholi* (Tremblay and Cherel 2000; Bocher et al. 2000a, 2000b, 2002). The production of *P. antarctica* at various sampling stations has to be compared with the dietary demand of *P. urinatrix* and *Echysocome* to locate the potential foraging zones of the planktivorous seabird in the Bay of Morbihan.

Studies on the reproductive biology of *D. pectinatus* and *P. antarctica* were recently carried out in the Bay of Morbihan at Kerguelen (Alonzo et al. 2000a, 2000b, 2001). Both species are sac-spawners, i.e. adult females carry their eggs attached in an external mass. In both cases, reproductive strategies were based on the production of a small number of eggs with extended energy reserves. The individual energy budgets, including the energetic requirements for metabolism and reproduction, demonstrated the role of lipid storage acting as energy reserves for survival and reproduction when food availability is low. *D. pectinatus* and *P. antarctica* were adapted to the strong seasonal variability of environmental conditions, as shown by their ability to store large amounts of lipids (Sargent and Henderson 1986; Conover 1988). Furthermore, evaluating the relative involvement of reserves in the energy budget of the reproduction was essential for our understanding of zooplankton ecology, as it determines the degree of dependence of the egg production on immediate nutritional supply. The respective influence of temperature and food on the production of copepods still remains controversial, and production rates have been shown in recent works to depend on the reproductive modes of the species (Hunley and Lopez 1992; Huntley 1996; Kleppel et al. 1996; Hirst and Sheader 1997; Hirst and Lampitt 1998).

The present study reports the seasonal changes in biomass, weight-specific growth rates and secondary production of *P. antarctica* and *D. pectinatus* at three stations of the Bay of Morbihan, Kerguelen Islands. Energy budgets of populations were investigated to clarify the trophic link between the species. Estimated growth rates were compared to those predicted by various temperature-dependent models of copepod production, and used together with calculations of the predatory demand for planktivorous seabirds to assess the potential of each copepod species to support their respective predators.

## Materials and methods

### Sample collection and treatment

The field sampling was carried out in the Bay of Morbihan aboard the R.V. "La Curieuse" from January 1996 to December 1996 as a part of an integrative scientific program on zooplankton and its predators ("Programme IOZ: Interactions Oiseaux-Zooplancton"). Zooplankton was collected at night every month at three stations (ST6, ST9 and ST10) located in the sheltered fjords of the southwestern part of the bay (Fig. 1). At each station, zooplankton was collected with a WP-2 net (1 m²; 200 μm mesh aperture) towed vertically. Hauls were performed from near the bottom (140 m at ST6; 80 m at ST9 and ST10) to the surface. Zooplankton were fixed immediately in 10% neutralized formaldehyde made up with seawater.

### Biomass

*Paraeucheta antarctica* and *Drepanopus pectinatus* were sorted from subsamples (Motoda box) to determine their relative total biomass in the community. The remaining unsorted fraction was weighed to evaluate the total biomass (mg m$^{-3}$) of zooplankton. All fractions were rinsed with 4.5% ammonium formate, dried at 60°C for 2 days and weighed.

### Biomass composition of *P. antarctica*

At each station, the seasonal composition of the population was investigated. All stages from C1 to adult were counted with males and females being identified for C4, C5 and adult stages. Seasonal changes in body dry weight of the various juvenile and adult stages at ST6 over the same year were reported in a previous study

**Table 1** *Paraeuchaeta antarctica*. Dry body weight of juvenile and adult stages and egg-production rate (total number of eggs produced per female during each time interval). Dry weight per egg: 17.4 $\mu$g egg$^{-1}$. Dry body weight of C3: 0.54 mg copepod$^{-1}$. Number of samples: 3 triplicates of 5 adult females; 3 triplicates of 10 other stages

| Date | Body weight (DW mg copepod$^{-1}$) | | | | | Egg production |
|------|------|----------|------------|-----------|--------------|----------------|
| | C4 | C5 male | Adult male | C5 female | Adult female | |
| 23 Jan 1996 | – | 1.83 | – | 2.44 | 5.26 | 2.1 |
| 16 Feb 1996 | – | 2.32 | – | 3.20 | 5.65 | 4.6 |
| 23 Apr 1996 | – | 2.40 | – | 3.18 | 5.20 | 0.8 |
| 2 Jun 1996 | – | 2.60 | 2.27 | 3.15 | 6.45 | 2.7 |
| 29 Jul 1996 | – | 2.22 | 2.07 | – | 4.08 | 38.5 |
| 27 Aug 1996 | – | – | 1.90 | – | 5.46 | 44.0 |
| 26 Sep 1996 | – | – | 1.71 | – | 4.33 | 28.9 |
| 27 Oct 1996 | – | – | – | – | 3.21 | 22.1 |
| 11 Nov 1996 | – | – | – | – | 3.98 | 9.1 |
| 25 Nov 1996 | 1.68 | – | – | – | 4.75 | 9.1 |
| 6 Dec 1996 | 2.11 | – | – | 2.43 | 5.78 | 13.3 |

(Table 1; Alonzo et al. 2000a) and were used to calculate the proportion of biomass associated with each developmental stage. At a given time, the relative biomass $b_i$ of stage $i$ (mg mg$^{-1}$ of *P. antarctica*) was calculated using the following equation:

$$b_i = \frac{p_i \cdot w_i}{\sum_j p_j \cdot w_j} \tag{1}$$

where $p_i$ and $p_j$ are the proportions of copepods and $w_i$ and $w_j$ the body dry weights (DW, mg copepod$^{-1}$) at stages $i$ and $j$. The absolute biomass $B_i$ of stage $i$ (mg m$^{-3}$) was then obtained from:

$$B_i = b_i \cdot B_{\text{tot}} \tag{2}$$

where $B_{\text{tot}}$ is the total biomass of *P. antarctica* (mg m$^{-3}$).

### Biomass of adult female and juvenile *D. pectinatus*

To calculate the production associated with juvenile growth and with reproduction of adult females, the proportion of the biomass represented by adult female and juvenile stages was required. The abundance of adult females $n_{\text{AF}}$ (copepods m$^{-3}$) was counted from subsamples (Motoda box) and their body dry weight $w_{\text{AF}}$ (mg copepod$^{-1}$) measured using triplicates of ten copepods. Biomasses of adult females $B_{\text{AF}}$ and of juveniles $B_{\text{juv}}$ (mg m$^{-3}$) were calculated using:

$$B_{\text{AF}} = n_{\text{AF}} \cdot w_{\text{AF}} \tag{3}$$

$$B_{\text{juv}} = B_{\text{tot}} - B_{\text{AF}} \tag{4}$$

where $B_{\text{tot}}$ is the total biomass of *D. pectinatus* (mg m$^{-3}$).

### Growth rates of juvenile stages

Previous studies provided the weights of eggs for *D. pectinatus* and *P. antarctica* (Alonzo et al. 2000a, 2001), and permitted evaluation of juvenile weight-specific growth rates.

In *D. pectinatus*, $g_{\text{juv}}$(day$^{-1}$) was calculated for each generation using the following equation:

$$g_{\text{juv}} = \frac{\ln\left(\frac{w_{\text{AF}}}{w_{\text{E}}}\right)}{\tau} \tag{5}$$

where $w_{\text{AF}}$ and $w_{\text{E}}$ are the dry weight of the adult female and of the egg, respectively, and $\tau$ is the generation time calculated from the development times observed by Razouls and Razouls (1990).

Whereas multigenerational *D. pectinatus* produces overlapping generations, *P. antarctica* produces clearly distinct annual generations, which make possible detailed stage-specific calculation of growth rates. Growth rates (day$^{-1}$) were therefore calculated during three distinct periods of development, from egg to stage C4, from C4 to C5 and from C5 to adult with the following equation:

$$g_i = \frac{\ln\left(\frac{w_f}{w_i}\right)}{t} \tag{6}$$

where $w_i$ and $w_f$ are the body dry weight of the initial stage $i$ and final stage $f$, and $t$ is the time lapse (days) between the dates when their respective maximum biomass was observed in the field.

### Production rates of adult females

In our study, the production of adult stages concerned exclusively the egg production of the females. The increase in body weight associated with the storage of energy reserves was already taken into account in the calculation of the growth rates of C5. Therefore, the production rate $g_{\text{AF}}$ of adult females (day$^{-1}$) was calculated using the equation:

$$g_{\text{AF}} = \frac{1 + f \cdot \frac{w_{\text{E}}}{w_{\text{AF}}}}{t} \tag{7}$$

where $f$ is the mean number of eggs produced by a female during time $t$ (days), and $w_{\text{E}}$ and $w_{\text{AF}}$ the dry weights of the egg and of the adult female, respectively. In *P. antarctica*, $f$ previously had been determined in the field for the seasonal cycle (Table 1; Alonzo et al. 2000b). In *D. pectinatus*, adult females tended to lose their eggs during capture, and $f$ was investigated in experimental conditions using various food situations (Alonzo et al. 2001). Depending on feeding conditions (starvation, low or abundant food supply), females of 27.3 $\mu$g DW produced 12.0 eggs sac$^{-1}$, whereas females of 56.6 $\mu$g DW produced 19.4 eggs sac$^{-1}$. The extrapolation of the observed experimental rates of egg production to the natural situation was therefore based on the level of energy storage observed in females from the field.

### Copepod production

In *D. pectinatus*, the production $P$ (mg m$^{-3}$ day$^{-1}$) was calculated using:

$$P = g_{\text{juv}} \cdot B_{\text{juv}} + g_{\text{AF}} \cdot B_{\text{AF}} \tag{8}$$

where $B_{\text{juv}}$ and $B_{\text{AF}}$ are the biomass (mg m$^{-3}$) of juveniles and adult females, respectively, and $g_{\text{juv}}$ and $g_{\text{AF}}$ their respective weight-specific growth rates (day$^{-1}$) as calculated above.

In *P. antarctica*, the production $P$ (mg m$^{-3}$ day$^{-1}$) was calculated from:

$$P = \sum_i g_i \cdot B_i + g_{\text{AF}} \cdot B_{\text{AF}} \tag{9}$$

where $B_i$ and $B_{\text{AF}}$ are the biomass (mg m$^{-3}$) of stage $i$ and adult females, respectively, and $g_i$ and $g_{\text{AF}}$ their respective weight-specific growth rates (day$^{-1}$) as calculated above.

## Mortality

Mortality constitutes the fraction of a population which is potentially available as a food source to its predators. The mean mortality $\bar{M}b$ (mg m$^{-3}$ day$^{-1}$) of *P. antarctica* over a time period $t$ (days) was calculated using the mean production $\bar{P}$ (mg m$^{-3}$ day$^{-1}$) and the biomass $B_{tot}$ (mg m$^{-3}$) according the following equation (Crisp 1971):

$$\Delta B_{tot} = (\bar{P} - \bar{M}b) \cdot t \text{ and } \bar{M}b = \bar{P} - \frac{\Delta B_{tot}}{t} \tag{10}$$

The equation assumes that changes in biomass associated with advection are negligible compared to production and mortality rates. Such an assumption is applicable to *D. pectinatus* and *P. antarctica* in Kerguelen as both species are present in great biomass in the Bay of Morbihan, but are absent from the continental shelf and the open ocean. Therefore, given that:

$$\bar{P} = \sum_i g_i \cdot \bar{B}_i \tag{11}$$

where $\bar{B}_i$ is the mean biomass, and assuming an exponential variation of biomass between $t_1$ and $t_2$:

$$\bar{M}b = \sum_i g_i \cdot \frac{(B_{i2} - B_{i1})}{\ln(B_{i2}/B_{i1})} - \frac{B_{tot2} - B_{tot1}}{t_2 - t_1} \tag{12}$$

$B_{i1}$ and $B_{i2}$ being the biomass of stage $i$ at time $t_1$ and $t_2$, respectively.

## Respiration of *P. antarctica*

The respiration of *P. antarctica* was investigated as the energy cost associated with body maintenance. The mean respiration of the population $\bar{R}_{tot}$ ($\mu$l O$_2$ m$^{-3}$ day$^{-1}$) was given by:

$$\bar{R}_{tot} = \sum \frac{\bar{B}_i}{w_i} \cdot R_i \tag{13}$$

where $R_i$ is the respiration of a copepod ($\mu$l O$_2$ day$^{-1}$ copepod$^{-1}$) of body weight $w_i$ (mg copepod$^{-1}$) and mean biomass $\bar{B}_i$. $R_i$ was calculated using the allometric relationship established for marine zooplankton (Ikeda 1974):

$$\log_{10} R = (0.8918 - 0.01089T) \cdot \log_{10} W + (0.02438T - 0.1838) \tag{14}$$

where $R$ is the respiration ($\mu$l O$_2$ animal$^{-1}$ h$^{-1}$), $W$ the dry weight (mg animal$^{-1}$) and $T$ the temperature (°C).

## Energy requirements and supply

The potential of *D. pectinatus* to support *P. antarctica* was assessed by comparing the energy requirements of the feeding stages of the predatory, carnivorous species to the energy supplied via mortality of its prey. Converting amounts of O$_2$, protein and lipids into energy was performed using the equivalents of 19.38 J ml$^{-1}$ O$_2$ (Båmstedt 1979), 39.5 J mg$^{-1}$ lipids and 23.6 J mg$^{-1}$ protein (Winberg 1971).

Energy demand of *P. antarctica* included respiration (as an energy demand for body maintenance), growth and production of eggs. Respiration of adult males was not taken into account as they do not feed, and survive using their intrinsic energy reserves only (Yen 1991). The energy required by the population for its production was estimated assuming copepod dry weight was composed of 50% lipids and 50% protein (Alonzo et al. 2000a). The total requirement of *P. antarctica* was corrected assuming the energy reserves of adult females provided 50% of their energy demand from June to October (Alonzo et al. 2000b). A factor of 1.25 was added to adjust for an assimilation rate of 80%. The potential energy supplied by the mortality of *D. pectinatus* was estimated assuming the dry weight of prey was composed of 20% lipids and 80% protein (Alonzo et al. 2001).

## Predation on *P. antarctica* by seabirds

The diet of six seabird species breeding in the Bay of Morbihan was investigated during the summer months as a part of the IOZ program. Two of the six species, the common diving petrel and the southern rockhopper penguin, preyed significantly on *P. antarctica* during the chick-rearing period. *D. pectinatus* was too small, and accounted for an insignificant proportion by mass of the birds' diet (Bocher et al. 2000a; Cherel et al. 2002a, 2002b). The biomass of copepods preyed on (Pb) by common diving petrels and rockhopper penguins in January–February 1996 (kg day$^{-1}$) was calculated using the data in Table 2 with the following equation:

$$\text{Pb} = \frac{N_{pair} \cdot f_{feeding}}{p_{chick}} \cdot \sum_i n_i \cdot w_i \tag{15}$$

where $N_{pair}$ is the number of breeding pairs in the bay, $f_{feeding}$ is the frequency of chick feeding (day$^{-1}$), $p_{chick}$ is the proportion of gathered energy by adult birds which is delivered to the chick, $n_i$ is the number of prey at stage $i$ per chick stomach content and $w_i$ is the body dry weight of stage $i$ (mg copepod$^{-1}$). The biomass that has been preyed on was compared with the mortality in biomass of *P. antarctica*.

**Table 2** *Pelecanoides urinatrix, Eudyptes chysocome filholi*. Abundance and foraging characteristics of planktivorous seabirds during the chick-rearing period in the Bay of Morbihan

| Description | Symbol | Common diving petrels | Rockhopper penguins |
|---|---|---|---|
| Estimated breeding populations (pairs) | $N_{pair}$ | 250,000[a] | 5,000[a] |
| Number of *Paraeuchaeta antarctica* per chick food sample | $n_i$ | 454[b] | 360[c] |
| Chick feeding frequency (number of meals per day) | $f_{feeding}$ | 1.0[b] | 1.4[d] |
| Percent of adult gathered energy delivered to chick | $p_{chick}$ | 16[e] | 16[e] |
| Selected prey | – | No[c] | Adult females[c] |
| Mean maximum dive depths (m) | – | 33[b] | 70[c] |

[a]Weimerskirch et al. (1989); about a third of the Kerguelen population of common diving petrels (500,000–1,000,000 pairs) is assumed to breed in the Bay of Morbihan

[b]Bocher et al. (2000a)

[c]Authors' unpublished data

[d]Rockhopper penguin chicks are fed daily by the females during the brooding period (about 25 days). They are fed by the two adults during the crèche stage (about 45 days), which is marked by slightly longer foragingtrips. We therefore estimated the feeding frequency for the whole chick-rearing period (about 70 days; Stahl et al. 1985) to average 1.4 meals day$^{-1}$ (0.7 meals day$^{-1}$ adult$^{-1}$)

[e]Roby and Ricklefs (1986) for common diving petrels; sinceno value was available for rockhopper penguins, we assumed a similar ratio asthat for diving petrels

## Results

### Structure and biomass of copepods

The biomass of *Drepanopus pectinatus* increased strongly in relation to primary production, with summer biomass up to 280 times greater than winter biomass (Figs. 2, 3). The biomass was mainly dominated by juveniles, except in late December at ST6 (adult females accounted for 85% of total biomass), from late November to late December at ST9 (75–89%) and mid-November at ST10 (58%), when the second annual generation (G2) was recruited. The concentration of chlorophyll *a* was greater at ST10 than at the other stations and increased
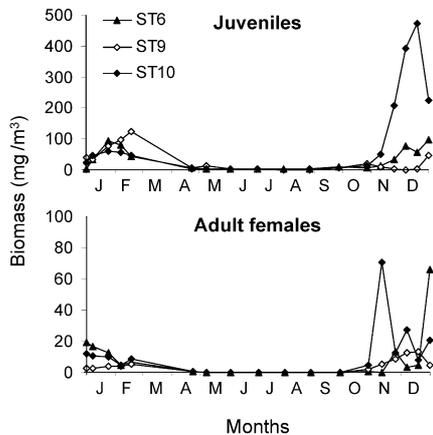
Fig. 2 *Drepanopus pectinatus*. Seasonal biomass of juveniles and adult females at three stations in the Bay of Morbihan
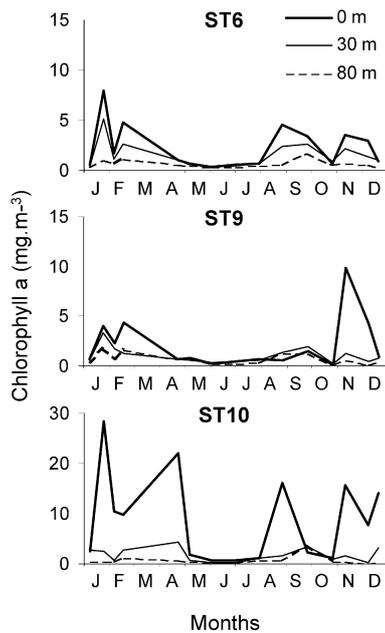
Fig. 3 Seasonal concentration in chlorophyll *a* in relation to depth at three stations of the Bay of Morbihan. Pigment concentration was measured as part of the IOZ program (authors' unpublished data)
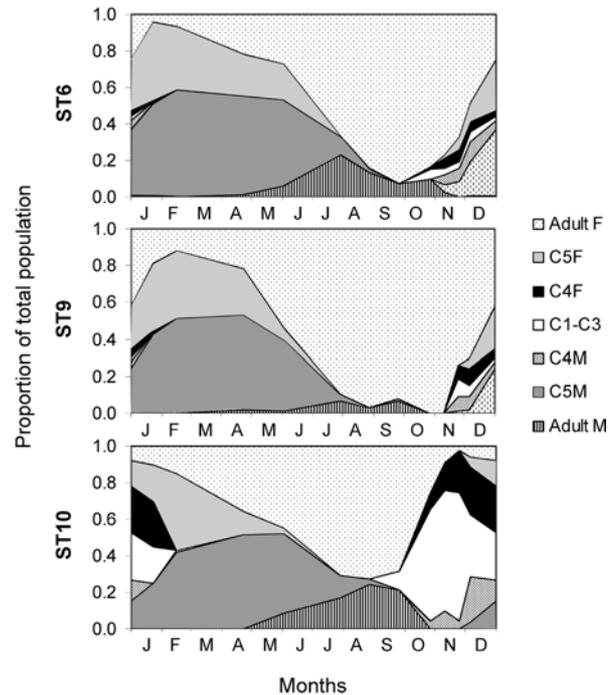
Fig. 4 *Paraeuchaeta antarctica*. Seasonal proportion of the various developmental stages at three stations in the Bay of Morbihan

as early as the end of August (Fig. 3). As a consequence, the peak biomass was much greater and occurred earlier at ST10 (mid-November to mid-December) than at ST6 (late January) and ST9 (mid-February).

In *Paraeuchaeta antarctica*, the population structure (Fig. 4) was similar among stations, being dominated by juvenile stages from December to June during the summer recruitment and growth of the annual generation, and by adult stages from July to November during the reproductive season. However, the proportion of stages C1–C4 was far greater at ST10 (up to 98% of the total abundance of late November) than at the two other stations (< 25% at the same date).

Two biomass maxima were observed over the course of the year at every station, and were generally greater at ST6 than at the other stations (Fig. 5): (1) a major mid-summer peak, associated with the growth of the annual generation and mainly composed of C5 stages; and (2) a peak from late autumn to winter, dominated by adult females with extended energy reserves at the end of the feeding season. At ST10 the juvenile peak occurred earlier (late spring) and was dominated by C4 stages, whereas the peak of C5 stages took place later (in autumn) than at the other stations.

### Growth rates

In *D. pectinatus* the juvenile growth rate varied strongly among generations (Table 3). A minimum value of 0.03 day⁻¹ was observed in the winter generation (G4),
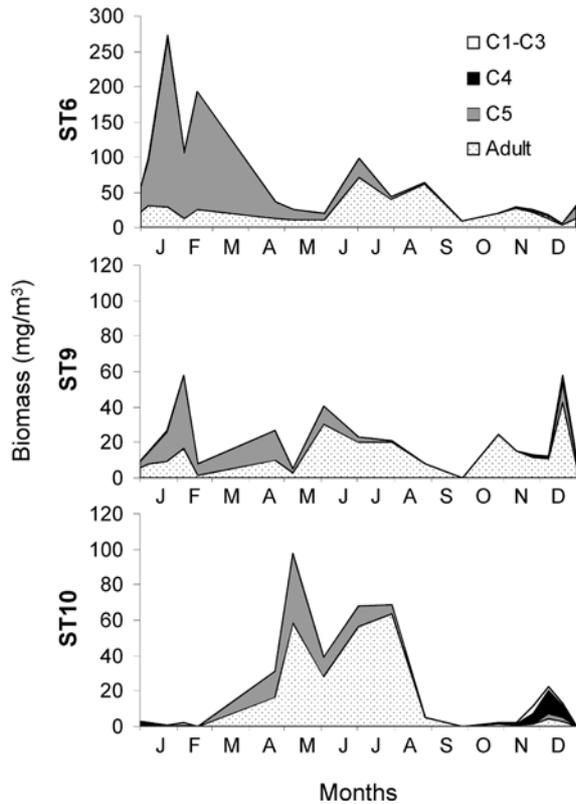
**Fig. 5** *Paraeuchaeta antarctica*. Seasonal biomass of the various developmental stages at three stations in the Bay of Morbihan

whereas greater growth rates were recorded from spring to autumn, with a maximum of 0.10 day$^{-1}$ in the summer generation (G2). A comparison of body dry weight of females between experimental conditions and the field (Table 3) was used to estimate that females produced on average 19.4 eggs brood$^{-1}$ in the spring generation (G1) (and in generation G2 of summer 1997) and 12.0 eggs brood$^{-1}$ in generations G2 and G3 of 1996. Production rates associated with adult reproduction were five to seven times smaller than juvenile growth rates with a maximum value of 0.020 day$^{-1}$ in the autumn generation (G3).

In *P. antarctica* juvenile growth rates varied in relation with development and sex, and were relatively consistent among stations (Table 4). A maximum of 0.03–0.04 day$^{-1}$ was observed during development from egg to C4 stage. Growth rates decreased at stage C4 and varied with sex: 0.001–0.005 day$^{-1}$ in C4 males and 0.003–0.010 day$^{-1}$ in C4 females. Growth rates varied from 0.005 to 0.009 day$^{-1}$ in C5 females, while no growth was observed in males between C5 and adult stages. Production rate of adult females was again much smaller than juvenile growth rates, with a maximum value of 0.005 day$^{-1}$ at the peak intensity of reproduction (end of August).

## Production

The production of *D. pectinatus* mainly occurred in summer in relation to primary production and was almost zero from April to November during the period of low food availability (Fig. 6). Increasing production was observed from mid-November and reached a maximum of about 10 mg m$^{-3}$ day$^{-1}$ at ST6 and ST9 at the end of December. Greater production was observed at ST10,

**Table 3** *Drepanopus pectinatus*. Production rates associated with juvenile growth and adult reproduction in the four annual generations. Generation period and generation time ($\tau$) were reported by Razouls and Razouls (1990). Dry weight per copepod and per egg (0.34 $\mu$g egg$^{-1}$) were reported by Alonzo et al. (2001) (*n.d.* not determined)

| Period | Temperature range (°C) | Generation time (days) | Dry weight ($\mu$g copepod$^{-1}$) | | $g$ (day$^{-1}$) | $g_E$ (day$^{-1}$) |
|---|---|---|---|---|---|---|
| | | | Mean | SD | | |
| Oct–Dec 1995 | 3.5–6.5 | G1 72 | 53.5 | 5.0 | 0.07 | 0.016 |
| Jan–Feb 1996 | 6.5 | G2 52 | 31.5 | 4.3 | 0.09 | 0.017 |
| Feb–Apr 1996 | 4.5–6.5 | G3 52 | 27.5 | 8.6 | 0.08 | 0.020 |
| Apr–Sep 1996 | 2.5–4.5 | G4 72[a] | 4.1[a] | 0.6 | 0.03[a] | n.d. |
| Oct–Dec 1996 | 3.0–7.0 | G1 72 | 59.4 | 5.4 | 0.07 | 0.015 |
| Jan–Feb 1997 | 7.0–8.0 | G2 52 | 54.5 | 3.5 | 0.10 | 0.016 |
| Feb–Apr 1997 | 5.5–7.0 | G3 52 | 29.4 | 3.3 | 0.09 | 0.018 |

[a]Data concern the development from egg to C3 only as the abundance of C4, C5 and adult stages was not sufficient for gravimetry

**Table 4** *Paraeuchaeta antarctica*. Development time and weight-specific growth rates of juvenile stages (*M* male; *F* female)

| Development | Development time (days) | | | Growth rate (day$^{-1}$) | | |
|---|---|---|---|---|---|---|
| | ST6 | ST9 | ST10 | ST6 | ST9 | ST10 |
| Egg to C4 | 134 | 171 | 131 | 0.036 | 0.028 | 0.037 |
| C4 to C5M | 41 | 49 | 152 | 0.005 | 0.004 | 0.001 |
| C4 to C5F | 41 | 49 | 152 | 0.010 | 0.008 | 0.003 |
| C5F to adult | 135 | 117 | 83 | 0.005 | 0.006 | 0.009 |

**Fig. 6** *Drepanopus pectinatus,*
*Paraeuchaeta antarctica.*
Seasonal production associated
with the growth of juveniles and
reproduction of adult females at
three stations in the Bay of
Morbihan
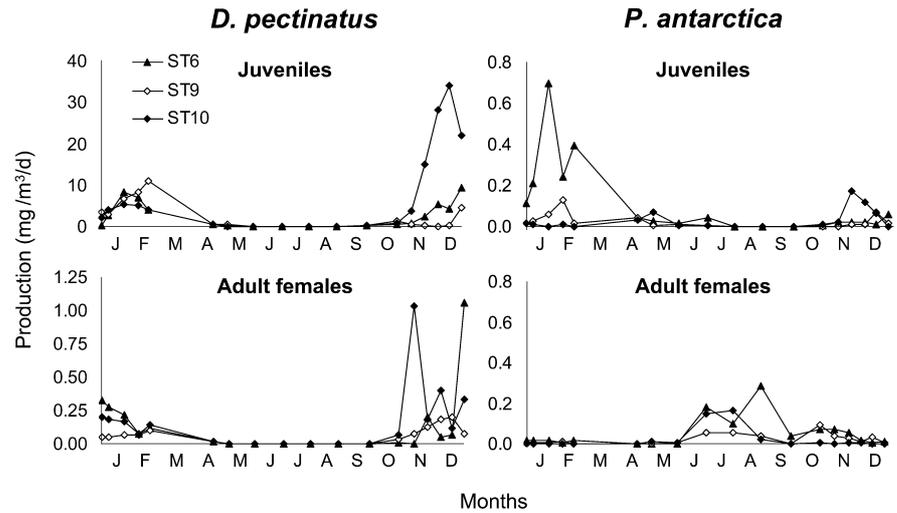


with values up to 34 mg m$^{-3}$ day$^{-1}$. The production of
adult females took place at the same period and re-
presented a minor part of the total production with values
10–30 times smaller than those associated with juvenile
growth. The production of *P. antarctica* remained low
over the course of the year with maximum values at ST6 of
0.7 mg m$^{-3}$ day$^{-1}$ in summer and of 0.3 mg m$^{-3}$ day$^{-1}$ in
winter (Fig. 6). Thus, seasonal variations were mainly
qualitative, and two peaks of production were observed:
(1) a major peak in summer, associated with the juvenile
growth, and (2) a peak in winter during the season of
reproduction. Production was generally smaller at ST9
and ST10 (maximum of 0.2 mg m$^{-3}$ day$^{-1}$) than at ST6.

## Mortality of *D. pectinatus*

As a result of the seasonal variability in biomass and
production of *D. pectinatus*, the mortality in biomass of
the population (Fig. 7) varied from zero in winter to up
to 10 mg m$^{-3}$ day$^{-1}$ in summer. The mortality was much
greater at ST10 than at the other stations, with a
calculated maximum of about 50 mg m$^{-3}$ day$^{-1}$ in
December (not shown on figure).

## Respiration of *P. antarctica*

Seasonal changes of respiration of *P. antarctica* followed
those observed in biomass and composition of the popu-
lation (Fig. 8). At ST6, respiration was about three times
lower in winter (1.5 ml O$_2$ m$^{-3}$ day$^{-1}$) than in summer
(5.2 ml O$_2$ m$^{-3}$ day$^{-1}$). Such strong changes were not
observed at ST9 and ST10 over the course of the year, with
values remaining below 1.6 ml O$_2$ m$^{-3}$ day$^{-1}$.

## Energy budget

On the one hand, the mortality in biomass of *D. pecti-*
*natus* was expressed in terms of energy. On the other

hand, the energy demand of the feeding stages of
*P. antarctica* was calculated including their requirements
for growth, reproduction and respiration. These two
components were compared at each station over a sea-
sonal cycle (Fig. 9). From October to April *P. antarctica*
could easily achieve its energy needs from *D. pectinatus*
mortality, owing to the great summer production of the
species. The energy supplied by the herbivore decreased
strongly around mid-April in association with the
recruitment of the winter generation (G4) and quickly
became insufficient to meet the demand of *P. antarctica*.
Therefore, a shift to an alternate prey was necessary
during winter to support the survival and reproduction
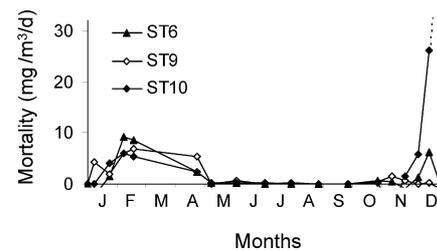of the predatory species. Due to the late summer peak of



**Fig. 7** *Drepanopus pectinatus.* Seasonal mortality in biomass of the
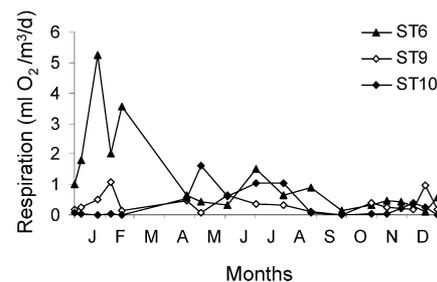total population at three stations in the Bay of Morbihan



**Fig. 8** *Paraeuchaeta antarctica.* Seasonal respiration of the total
population at three stations in the Bay of Morbihan

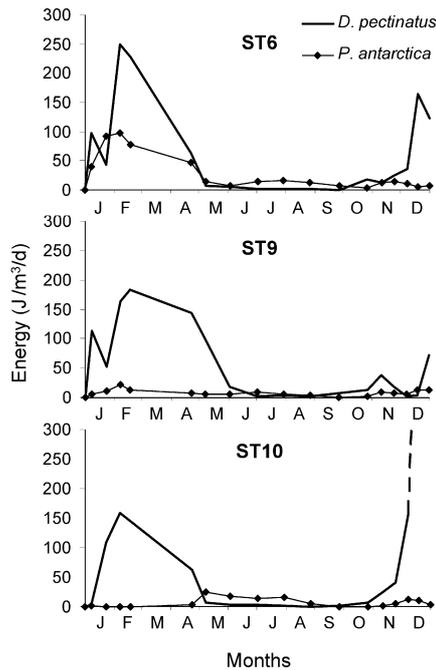**Fig. 9** *Drepanopus pectinatus, Paraeuchaeta antarctica.* Energy budget of a theoretical volume (1 m³) of seawater at three stations of the Bay of Morbihan. *D. pectinatus*: energy supplied by the mortality of the population; *P. antarctica*: energy demand associated with somatic growth, reproduction and respiration of the feeding stages (except adult males)

biomass of *D. pectinatus* at ST9, a short period of insufficient availability of this prey also occurred for *P. antarctica* in December at this station.

Predation on *P. antarctica* by seabirds

The estimated total predation of *P. antarctica* during chick-rearing is reported in Table 5. During the chick-rearing period (January–February), the daily biomass of *P. antarctica* predated by planktivorous seabirds was

**Table 5** *Paraeuchaeta antarctica.* Impact of predation of planktivorous seabirds (*Pelecanoides urinatrix*, *Eudyptes chysocome filholi*) during the chick-rearing period (February) in the Bay of Morbihan. Maximum mortality in biomass occurred on 7 February 1996 at ST6 and 18 February 1996 at ST9 and ST10

| | Common diving petrels | Rockhopper penguins |
|---|---|---|
| Total daily predation | | |
| Abundance (millions of prey day⁻¹) | 709 | 16 |
| Biomass (kg day⁻¹) | 1,987 | 86 |
| Mortality, in biomass (mg m⁻³ day⁻¹) | | |
| ST6 | 12.3 | 1.5 |
| ST9 | 4.6 | 1.0 |
| ST10 | 0.2 | 0.0001 |
| Foraging area (km⁻²) | | |
| ST6 (140 m depth) | 1.1 | 0.4 |
| ST9 (80 m depth) | 5.5 | 0.6 |
| ST10 (80 m depth) | 150 | 9,450 |

evaluated at 2 tons of C5 and adult stages for the common diving petrels and at 86 kg of adult females for the rockhopper penguin. Considering the maximum mortality in biomass of *P. antarctica* in February, we calculated the foraging area of sea (km²) by which, over the water column, the copepod mortality meets the dietary needs of the planktivorous birds. At ST6 on 7 February 1996 and at ST9 on 18 February 1996, foraging areas of 1.1–5.5 km² and 0.4–0.6 km² were sufficient to balance the predatory demands of common diving petrels and rockhopper penguins, respectively. The two planktivorous seabirds could potentially achieve their dietary needs easily from *P. antarctica* at these stations. At ST10, the mortality of *P. antarctica* was at all times insufficient to support the predation of seabirds, with foraging areas of 150 km² and up to 9,450 km². Thus, this station was unlikely to be a foraging zone for planktivorous seabirds.

## Discussion

Comparison of production rates

In the present study, production rates associated with juvenile growth and adult reproduction were estimated for two sac-spawning species of copepod during an an-
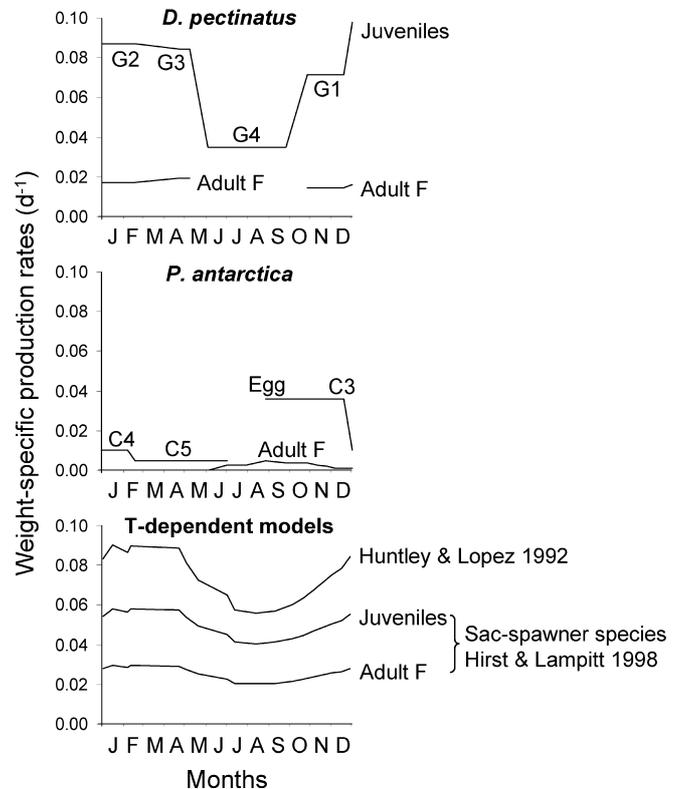


**Fig. 10** *Drepanopus pectinatus, Paraeuchaeta antarctica.* Juvenile and adult production rates during the course of 1 year in relation to generations (*D. pectinatus*) and development (*P. antarctica*), and production rates predicted from temperature (*T*) according to Huntley and Lopez (1992) and Hirst and Lampitt (1998)

nual cycle. Several models have been proposed in the literature to calculate the production rates of copepods from temperature (Huntley and Lopez 1992; Hirst and Sheader 1997; Hirst and Lampitt 1998). A comparison between observed growth rates and predicted values (Fig. 10) led to the conclusion that, for *Drepanopus pectinatus*, the simplified method of Huntley and Lopez (1992) for estimating secondary production was adequate for nearly all generations (except G4), since the estimated specific growth rate for generations G1–G3 was quite well approximated by the maximum weight-specific growth rate predicted by the authors' function of temperature (Fig. 10). Juvenile growth rates for *D. pectinatus* were underestimated by the equation that Hirst and Lampitt (1998) specifically established for sac-spawning species. Conversely, in *Paraeuchaeta antarctica*, this equation overestimated the actual juvenile weight-specific growth rates that we observed. The two copepods investigated in the present study illustrated that the distinction between free- and sac-spawning modes might not be sufficient to describe the diversity of situations.

In spite of a common mode of reproduction, different growth rates could be expected from the multi-generational species *D. pectinatus*, whose life cycle is based on four generations per year, and the annual species *P. antarctica*, which produces only one generation a year. Besides reproductive strategies, the differences might also be related to the distinct trophic positions occupied by the herbivorous *D. pectinatus* and the predatory *P. antarctica* in the food web. The biochemical composition also differed between the studied species, being dominated by protein in *D. pectinatus*, whereas lipids are the major component in *P. antarctica*, and might have an effect on growth. In *P. antarctica* a major decrease in growth rate occurred at stage C4, with production rates of stages C4 and C5 low and similar to that of adult females. This decrease has been interpreted

in the genus *Calanus* as an effect of the extended lipid biosynthesis occurring at the subadult and adult stages (Hirche 1996).

During development of *P. antarctica* from egg to C4, the dependence of growth of early stages on energy reserves might have a major influence on the estimation of growth rate. In fact, a low apparent growth might result from the existence of extended energy stores in the eggs (Fig. 11). A decrease in weight associated with respiration occurring between the egg and the first feeding stage could also be hypothesized. The correction would require: (1) the growth rate to be calculated only from the first feeding stage (C1 in the case of euchaetiid copepods after about 1 week of development) (Nicholls 1934), or (2) the functional fraction of the growing organism to be distinguished from its energy reserves, using a modification of the equation for juvenile growth rates:

$$g_{e-i} = \frac{\ln\left(\frac{w_i}{w_e \cdot (1-p_E)}\right)}{t_{e-i}} \qquad (16)$$

where $w_e$ and $w_i$ are the dry weight of egg and stage $i$, $p_E$ the proportion of energy reserves in the dry weight of egg and $t_{e-i}$ the development time to stage $i$ (days). Given the dry weight and the development time of C4, a mean growth rate of 0.05 day$^{-1}$, as predicted by the Hirst and Lampitt (1998) model, would imply an egg weight of 5 $\mu$g. This implies that $>70\%$ of the observed weight (17.4 $\mu$g egg$^{-1}$) could correspond to energy reserves.

Growth rates of juvenile stages (except C4 and C5 in *P. antarctica*) were about four to five times larger than the production rate of adult females. The difference might be a result of *P. antarctica* and *D. pectinatus* reproductive strategies, as both species produce a small number of eggs, which yields low associated production rates (Alonzo et al. 2000a, 2001). The difference in

**Fig. 11** Calculation of juvenile growth rate, corrected by taking into account the proportion $p_E$ of energy reserves deposited in the egg (*hatched area*): correction of the egg weight or calculation of growth rate from the C1 stage only (considered here as the first stage showing apparent growth)
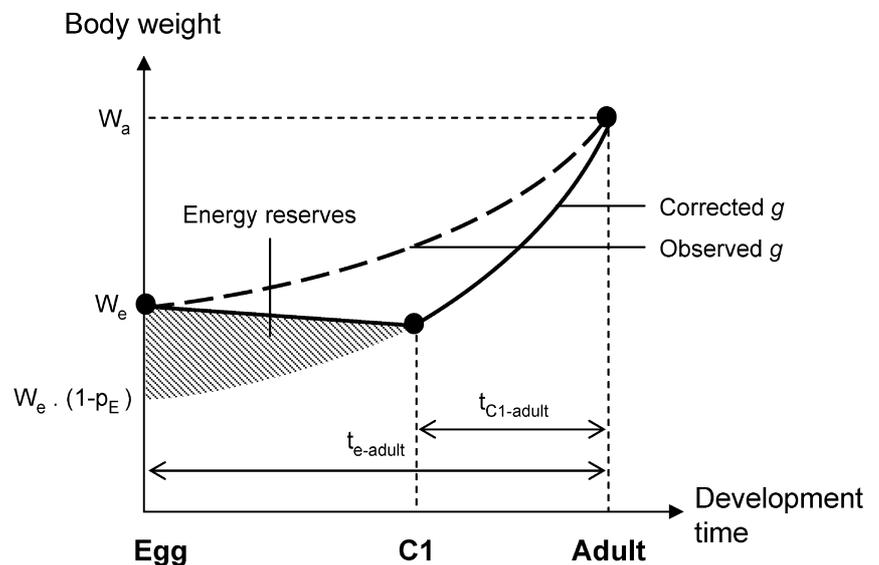
production rates between juveniles and adults was also predicted for sac-spawning copepods by Hirst and Lampitt ( 1998), and could be either intrinsic to the reproductive strategies of species or interpreted as an effect of food limitation in adults. A difference between production rates of juveniles (as somatic growth) and adults (as egg production) has often been described in copepods, more commonly in large species (Peterson 1986, 1988; Peterson et al. 1991; Richardson and Verheye 1999). These authors explained the difference as a consequence of the increasing effect of food limitation with the size of the copepods, which might also occur in Kerguelen, especially in *P. antarctica*. Indeed, a large difference in dry weight of adult females and brood size of the species was noted between Kerguelen Islands and South Georgia (Ward and Robins 1987; Alonzo et al. 2000a). This difference could either be the consequence of lower food availability for *P. antarctica* at Kerguelen than at South Georgia or result from differential predation pressure related to the size between the two regions.

### Source and availability of food for *P. antarctica*

This work is part of an ongoing study of the subantarctic ecosystem of the Kerguelen Islands. In the present study, we have attempted to model some aspects of the pelagic ecosystem of the Bay of Morbihan. The main result from the energy budget of the copepod community, including the energetic requirements of *P. antarctica* and the energy supplied by the mortality of *D. pectinatus*, was that the secondary production by *D. pectinatus* can support the needs of *P. antarctica* in summer and that the predatory species would need to shift to alternate prey in winter. The cyclopoid *Oithona* spp., which is part of the diet of *P. P. antarctica* at South Georgia and Crocker Passage (Øresland 1991; Øresland and Ward 1993), is likely to provide this alternate food source at Kerguelen. *Oithona* spp. (*O. frigida* and *O. similis*) were present in the Bay of Morbihan all year round (Razouls et al. 1995, 1996) and showed an abundance of 500–1,000 copepods m$^{-3}$ in winter (Razouls, unpublished data).

The role of *Oithona* and other small copepod species in marine pelagic ecosystems has been largely underestimated due to the selectivity of the conventional nets used in the study of mesozooplankton ecology (Gallienne and Robins 2001). These authors concluded that the use of a WP2 net with a 200 $\mu$m mesh might lead to the loss of a major fraction (up to 90%) of organisms between 200 and 800 $\mu$m in length. In our study, this fraction would include *Oithona* spp. and the young juvenile stages of *D. pectinatus*. Although the net failed at sampling the young stages of both copepod species the main conclusion of the study remains valid, since it is arguable that the missing small stages of *P. antarctica* (C1–C3) likely feed on smaller prey (nauplii and on the first copepodite stages of *D. pectinatus*) than those included in the present budget. Furthermore, Yen's (1991) results showed that 800 $\mu$m represented a suboptimal body length of prey for the large stages of *P. antarctica*, so that the main fraction of its food was taken into account in our budget.

### Copepod predators

The population of *D. pectinatus* could potentially easily support the predator *P. antarctica* in summer. Indeed, during this period the energy demand of the euchaetiid never exceeded 40%, 20% and 60% of the amount supplied by the mortality of *D. pectinatus*, respectively, at ST6, ST9 and ST10. Therefore, alternative trophic relationships remain to be investigated to explain the levels of mortality of *D. pectinatus* estimated in the Bay of Morbihan. The carnivorous, hyperiid amphipod *Themisto* g*audichaudii*, which is one of the most numerous species of macrozooplankton in the epipelagic zone of the Southern Ocean (de Broyer and Jazdzewski 1993; Pakhomov and McQuaid 1996; Vinogradov et al. 1996), is abundant in the waters of Kerguelen. Being a non-selective, opportunistic predator that feeds on the most abundant prey (Pakhomov and Perissinotto 1996; Froneman et al. 2000), the species is most likely responsible for a major part of the mortality of *D. pectinatus* (especially in the open part of the Bay of Morbihan, where *P. antarctica*is absent) and probably also feeds on the small developmental stages (larvae to C3) of *P. antarctica*.

Our study showed that the two planktivorous seabirds (common diving petrels and rockhopper penguins) could potentially achieve their dietary needs easily from the *P. antarctica* mortality estimated at ST6 on 7 February 1996 and at ST9 on 18 February 1996. One should note, however, the limitations of this approach, which was based on the assumed absence of advective import or export of biomass in the system. Such processes of advection must occur when the calculated production could not alone balance the variations of biomass, yielding negative values of mortality. The calculated production remained insufficient even when the observed growth rates were replaced by those predicted according to the Hirst and Lampitt ( 1998) model (data not shown). Furthermore, *P. antarctica* provided only a small, but significant, part of the food ingested by seabirds, accounting for 7.5% and 2.7% by mass (21.7% and 9.9% by number) of the diet of common diving petrels and rockhopper penguins, respectively, in February 1996, the major item being the amphipod *T. gaudichaudii* (Bocher et al. 2000a, 2000b, 2001, 2002; Tremblay and Cherel 2000).

This study is the first step toward a model of the subantarctic ecosystem of the Kerguelen Islands. The role of copepods in the pelagic food web and the relative importance of their predation by seabirds will be determined through the investigation of other components of the community: the small, cyclopoid copepod *Oithona*, as a winter food source of *P. antarctica* , and

the hyperiid amphipod *T. gaudichaudii* and larvae of fish (*Nothotenia*) (Koubbi 1992) as potential predators responsible for the mortality of *D. pectinatus* and *P. antarctica*.

## References

Alonzo F, Mayzaud P, Razouls S (2000a) Egg production, population structure and biochemical composition of the Subantarctic copepod *Paraeuchaeta antarctica* in the Kerguelen Archipelago. Mar Ecol Prog Ser 205:207–217

Alonzo F, Mayzaud P, Razouls S (2000b) Egg production dynamics, biochemical composition and hatching success of the subantarctic copepod *Paraeuchaeta antarctica*: laboratory studies. Mar Ecol Prog Ser 205:219–227

Alonzo F, Mayzaud P, Razouls S (2001) Egg production and energy storage in relation to feeding conditions in the subantarctic calanoid copepod *Drepanopus pectinatus*: an experimental study of reproductive strategy. Mar Ecol Prog Ser 209:231–242

Båmstedt U (1979) Reproductive bioenergetics within the summer and winter generations of *Euchaeta norvegica* (Copepoda). Mar Biol 54:135–142

Bocher P, Cherel Y, Hobson KA (2000a) Complete trophic segregation between South Georgian and common diving petrels during breeding at Iles Kerguelen. Mar Ecol Prog Ser 208:249–264

Bocher P, Labidoire B, Cherel Y (2000b) Maximum dive depths of common diving petrels ( *Pelecanoides urinatrix*) during the annual cycle at Mayes Island, Kerguelen. J Zool Lond 251:517–524

Bocher P, Cherel Y, Labat JP, Mayzaud P, Razouls S, Jouventin P (2001) Amphipod-based food web: *Themisto gaudichaudii* caught in nets and by seabirds in Kerguelen waters, southern Indian Ocean. Mar Ecol Prog Ser 223:261–276

Bocher P, Cherel Y, Alonzo F, Razouls S, Labat JP, Mayzaud P, Jouventin P (2002) Importance of the large copepod *Paraeuchaeta antarctica* (Giesbrecht, 1902) in coastal waters and the diet of seabirds at Kerguelen, Southern Ocean. J Plankton Res 24:1317–1333

Cherel Y, Bocher P, de Broyer C, Hobson KA (2002a) Food and feeding ecology of the sympatric thin-billed *Pachyptila belcheri* and Antarctic *P. desolata* prions at Iles Kerguelen. Mar Ecol Prog Ser 228:263–281

de Broyer C, Jazdzewski K (1993) Contribution to the marine biodiversity inventory. A checklist of the Amphipoda (Crustacea) of the Southern Ocean. Inst R Sci Nat Belg Doc Trav 73:1–154

Falk-Petersen S, Hopkins CCE, Sargent JR (1990) Trophic relationships in the pelagic arctic food web. In: Barnes M, Gibson RN (eds) Trophic relationships in the marine environment. Proc 24th Eur Mar Biol Symp. Aberdeen University Press, Aberdeen, pp 315–333

Froneman PW, Pakhomov EA, Treasure A (2000) Trophic importance of the hyperiid amphipod, *Themisto gaudichaudii*, in the Prince Edward Archipelago (Southern Ocean) ecosystem. Polar Biol 23:429–436

Gallienne CP, Robins DB (2001) Is *Oithona* the most important copepod in the world's oceans? J Plankton Res 23:1421–1432

Hirche HJ (1996) The reproductive biology of the marine copepod, *Calanus finmarchicus*: a review. Ophelia 44:111–128

Hirst AG, Lampitt RS (1998) Towards a global model of in situ weight-specific growth in marine planktonic copepods. Mar Biol 132:247–257

Hirst AG, Sheader M (1997) Are in situ weight-specific growth rates body-size independent in marine copepods? A re-analysis of the global syntheses and a new empirical model. Mar Ecol Prog Ser 154:155–165

Hopkins TL (1985) Food web of an antarctic midwater ecosystem. Mar Biol 89:197–212

Huntley M (1996) Temperature and copepod production in the sea: a reply. Am Nat 148:407–420

Huntley ME, Lopez MDG (1992) Temperature-dependent production of marine copepods: a global synthesis. Am Nat 140:201–242

Ikeda T (1974) Nutritional ecology of marine zooplankton. Mem Fac Fish Hokkaido Univ 22:1–97

Kleppel GS, Davis SD, Carter K (1996) Temperature and copepod growth in the sea: a comment on the temperature-dependent model of Huntley and Lopez. Am Nat 148:397–406

Koubbi P (1992) L'ichtyoplancton de la partie indienne de la province Kerguelienne (bassin de Crozet et plateau de Kerguelen): identification, distribution spatio-temporelle et stratégies de développement larvaire. PhD thesis, Université Paris VI, Paris

Nicholls AG (1934) The developmental stages of *Euchaeta norvegica* Boeck. Proc R Soc Edinb Sect B (Biol) 54:31–50

Øresland V (1991) Feeding of the carnivorous copepod *Euchaeta antarctica* in Antarctic waters. Mar Ecol Prog Ser 78:41–47

Øresland V, Ward P (1993) Summer and winter diet of four carnivorous copepod species around South Georgia. Mar Ecol Prog Ser 98:73–78

Pakhomov EA, McQuaid CD (1996) Distribution of surface zooplankton and seabirds across the Southern Ocean. Polar Biol 16:271–286

Pakhomov EA, Perissinotto R (1996) Trophodynamics of the hyperiid amphipod *Themisto gaudichaudii* in the South Georgia region during late austral summer. Mar Ecol Prog Ser 134:91–100

Park T (1994) Geographical distribution of bathypelagic genus *Paraeuchaeta* (Copepoda: Calanoida). Hydrobiologia 292/293:317–332

Peterson WT (1986) Development, growth and survivorship of the copepod *Calanus marshallae* in the laboratory. Mar Ecol Prog Ser 29:61–72

Peterson WT (1988) Rates of egg production by the copepod *Calanus marshallae* in the laboratory and in the sea off Oregon, U.S.A. Mar Ecol Prog Ser 47:229–237

Peterson WT, Tiselius P, Kiørboe T (1991) Copepod egg production, moulting and growth rates, and secondary production, in the Skagerrak in August 1988. J Plankton Res 13:131–154

Razouls S, Razouls C (1988) Seasonal size distribution of developmental stages of sub-antarctic copepod. Hydrobiologia 167/168:239–246

Razouls C, Razouls S (1990) Biological cycle of a population of subantarctic copepod, *Drepanopus pectinatus* (Clausocalanidae), Kerguelen Archipelago. Polar Biol 10:541–543

Razouls S, De Bovée F, Dellile D, Fiala M, Mayzaud P (1995) Temporal variability of bacteria, phyto- and zooplankton assemblages of the subantarctic Bay of Morbihan (Kerguelen Archipelago). In: Battaglia B, Valencia J, Walton DWH (eds) Antarctic communities: species, structure and survival. Cambridge University Press, Cambridge, pp 86–92

Razouls S, Koubbi P, Mayzaud P (1996) Spatio-temporal distribution of mesozooplankton in a sub-Antarctic coastal basin of the Kerguelen Archipelago (southern Indian Ocean). Polar Biol 16:581–587

Richardson J, Verheye HM (1999) Growth rates of copepods in the southern Benguela upwelling system: the interplay between body size and food. Limnol Oceangr 44:382–392

Roby DD, Ricklefs RE (1986) Energy expenditure in adult least auklets and diving petrels during the chick-rearing period. Physiol Zool 59:661–678

Sargent JR, Henderson RJ (1986) Lipids. In: Corner EDS, O'Hara SCM (eds) The biological chemistry of copepods. Clarendon, Oxford, pp 59–108

Stahl JC, Derenne P, Jouventin P, Mougin JL, Teulières L, Weimerskirch H (1985) Le cycle reproducteur des gorfous de l'archipel Crozet: *Eudyptes chrysolophus*, le gorfou macaroni et *Eudyptes chrysocome*, le gorfou sauteur. L'oiseau et RFO 55:27–43

Tremblay Y, Cherel Y (2000) Benthic and pelagic dives: a new foraging behaviour in rockhopper penguins. Mar Ecol Prog Ser 204:257–267

Vinogradov ME, Volkov AF, Semenova TN (1996) Hyperiid amphipods (Amphipoda, Hyperiidea) of the world oceans. Science, Lebannon

Ward P, Robins DB (1987) The reproductive biology of *Euchaeta antarctica* Giesbrecht (Copepoda: Calanoida) at South Georgia. J Exp Mar Biol Ecol 108:127–145

Weimerskirch H, Zotier R, Jouventin P (1989) The avifauna of the Kerguelen Islands. Emu 89:15–29

Winberg GG (1971) Methods for the estimation of production of aquatic animals. Academic, London

Yen J (1991) Predatory feeding behaviour of an Antarctic marine copepod, *Euchaeta antarctica*. Polar Res 10:433–442