*Limnol. Oceanogr.*, 49(3), 2004, 644–655


# Life cycle plasticity and differential growth and development in marine and lacustrine populations of an Antarctic copepod

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*Abstract*

We examined life cycle plasticity in two populations of the copepod *Paralabidocera antarctica*, one of which inhabits the coastal sea ice belt of Antarctica and the other of which has been isolated in a nearby saline lake for several thousand generations. Similarities in the life cycles of the two populations included long overwintering phases (>5 months) by late-stage nauplii, rapid development through the copepodid stages, and a short adult life span of 2–3 weeks. Adults appeared in late spring or early summer and spawned and died soon after. However, the life cycle of the lacustrine population was much less tightly regulated than at the marine site; animals were rarely found living within the lake ice, and synchrony in the developmental cycle was diminished. It is likely that a combination of factors, including ice hardness, a lack of predation threat, and a consistent food supply has freed the lacustrine population from the constraints imposed by living within the ice cover. Instantaneous growth rates calculated for the marine site showed a variable growth rate (0.04–0.14 $d^{-1}$). The lacustrine population in general had faster growth rates than the marine population (0.10–0.26 $d^{-1}$) and reached maturity at a smaller size. This is attributed, in part, to the higher environmental temperatures experienced by the lacustrine population.

The life history strategies of marine zooplankton are influenced by the physical and chemical environment they inhabit and by other biota in that environment. Because perturbations in physical and biological aspects of marine ecosystems are common on both temporal and spatial scales, plasticity in the life cycles of zooplankton can facilitate their continued exploitation of a habitat.

Copepods are an important component of most zooplankton assemblages, and factors that influence their growth and development will have a significant effect on secondary production and energy transfer through the marine food web. Although some species (e.g., *Oithona similis*) appear to be circumglobal in their distribution (Conover and Huntley 1991), others are restricted to narrower geographical ranges. Species with restricted distributions are constrained from inhabiting previously unoccupied environments by a combination of physical (e.g., temperature), chemical (e.g., salinity), and biological (e.g., predation) pressures. Elucidating the factors that control the life history strategies of copepods aids in understanding the distributions of these animals and allows us to predict how these species might be affected by environmental change.

Field studies aimed at investigating plasticity of zooplankton life cycles over long periods have two requirements. First, populations of zooplankton that have identifiable differences in strategies must be selected. Second, it must be clear that the same population is sampled regularly through time and that perceived changes do not originate from the sampling of different subpopulations. Environments in which species are largely segregated from the vagaries of water movement should provide ideal situations for longitudinal studies of copepod population dynamics.

The Antarctic copepod *Paralabidocera antarctica* (Calanoida: Acartiidae) fulfills these requirements. This species occurs in two distinct populations: it is an important component of the ice-associated biota of the sea ice of the East Antarctic coastline, where it reaches densities of up to 400,000 $m^{-2}$ (Tanimura et al. 1996; Swadling et al. 1997, 2000*a*), and it also occurs in three saline, marine-derived lakes in the ice-free Vestfold Hills (68°28′S, 78°10′E; Fig. 1) (Bayly 1978; Wright and Burton 1981; Bayly and Eslake 1989). In the marine environment, *P. antarctica* undergoes most of its development (NII–CIII) within the brine channel system of the sea ice cover, where it is cut off from water currents. Therefore, it is possible to sample a population repeatedly throughout its life cycle. The life cycle of *P. antarctica* is, on average, 1 yr long and includes a long overwintering period (>5 months) in the sea ice by the naupliar

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*Acknowledgements*

We thank the expeditioners at Davis Sta., Antarctica, particularly T. Newton, H. Cooley, and G. Watson, for assistance in the field. C. Blobel (Australian Bureau of Meteorology) provided additional sea ice thickness data, and J. Cox (Australian Antarctic Division) drew the map in Fig 1. L. Cromer kindly provided data on eggs in Ace Lake sediments.

This project was funded by an ARC Discovery grant (DP0209308), Australian Antarctic Science grants (691, 1328), the Ian Potter Foundation, and the University of Tasmania. The Australian Antarctic Division provided logistical support.

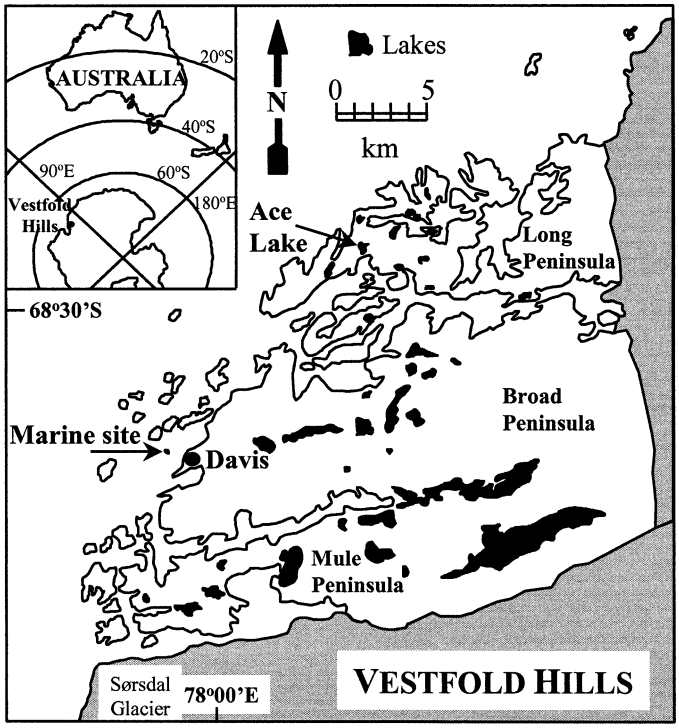


Fig. 1. Sampling locations at the marine site and Ace Lake, Vestfold Hills. The inset shows position of the Vestfold Hills in Antarctica.

stages and subsequent rapid development during late October and November through the copepodid stages to the adults (Tanimura et al. 1996). Adults spawn at the ice-water interface, and eggs are released into the water column in early to mid-December. Approximately 1 month after spawning, the first naupliar stage hatches and is incorporated into newly forming sea ice.

The lacustrine populations can also clearly be sampled consistently, because they are constrained within the lake basin and there is no recruitment from marine sources. The best-studied lacustrine population occurs in Ace Lake (Fig. 1) (Bayly and Burton 1987; Swadling and Gibson 2000). This lake was formed ~5,000 yr ago, when postglacial isostatic rebound trapped a pocket of seawater that was eventually cut off fully from the ocean (Zwartz et al. 1998). It has been shown that *P. antarctica* in Ace Lake reproduces annually (Swadling and Gibson 2000); therefore, this population has had ~5,000 generations to evolve independently of the marine population in an environment in which it has been largely free from predators and competitors. *P. antarctica* currently represents the highest trophic level in Ace Lake.

The co-occurrence of these two populations—lacustrine and marine—provides a prime opportunity to examine the extent of life cycle plasticity in an ice-associated copepod and to assess the role that abiotic and biotic factors play in influencing its reproduction and development. The ecologies of ice-associated herbivores are poorly understood, yet their role in biogeochemical cycling in the sea ice ecosystem must be significant. To provide information about the ecology of *P. antarctica,* in particular with regard to its degree of life cycle and behavioral plasticity, we compared the environmental distribution and the cohort development of marine and lacustrine populations over a 15-month period. Instantaneous daily growth rates were calculated, and the annual cycle of growth of each population was examined in light of the differences between the marine and lacustrine habitats.

## Materials and methods

The marine site was situated ~1 km offshore from the Vestfold Hills, East Antarctica (Fig. 1) and had a water depth of 23 m. Access to the site for most of the study was over the fast ice, although, when open water was present, the site was accessed using a small boat. The physical and chemical characteristics of the inshore system near the marine site are detailed in Gibson and Trull (1999). Ace Lake (Fig. 1) is a stratified, marine-derived lake, with oxygenated water present to 12 m (*see* Rankin et al. 1999 for a review of the physical and chemical characteristics of the lake). Ice cover on the lake, which reaches a maximum thickness ~2 m, persists for at least 11 months each year. During the present study, the marine site was sampled 35 times between 15 December 1993 and 27 February 1995, and Ace Lake was sampled 15 times between 20 April 1994 and 13 March 1995.

*Environmental sampling*—During the periods when the sites were covered by ice, the underlying water column was reached by drilling holes through the ice with a 200-mm-diameter motorized auger. The ice itself was sampled using a 76-mm-diameter SIPRE corer. Ice thickness and snow depth were recorded on each sampling date.

Water temperature and conductivity were measured at 2, 10, and 20 m at the marine site and at 2, 5, and 10 m in Ace Lake using a Platypus Submersible Data Logger (Platypus Engineering). Salinity was calculated from conductivity using the equation of Fofonoff and Millard (1983). The bulk salinity of the ice was measured, after melting, on undiluted cores using a hand-held refractometer (±1). The chlorophyll *a* concentration in the water column and ice cover at both sites was measured, to estimate phytoplankton biomass. Water samples were collected from five depths (2, 5, 10, 15, and 20 m) at the marine site and from three depths (2, 5, and 10 m) at Ace Lake using a 2-liter polycarbonate Kemmerer bottle. Known volumes of the samples were filtered onto Whatman GF/F glass-fiber filters and frozen until analysis. Known volumes of the melted ice cores were processed in the same manner. Photosynthetic pigments were extracted from the samples with 90% (vol/vol) aqueous acetone, and Chl *a* concentrations were determined using the spectrophotometric method of Parsons et al. (1984).

*Biological sampling—P. antarctica* were collected from the water column by four independent tows of an umbrella net of 100-$\mu$m mesh (Kirkwood and Burton 1987). At the marine site, the net was towed vertically from 20-m depth (volume filtered, 1.6 $m^3$) and at Ace Lake from 10-m depth (volume filtered, 0.8 $m^3$). Each replicate tow was preserved in 10% borax-buffered formaldehyde. *P. antarctica* in the

Table 1. Mean carbon dry weight (SD) and length (range) of developmental stages of *Paralabidocera antarctica* at the marine site. The dates in 1994 when each stage was collected for dry weight (DW) measurements are also shown. *g* was calculated using the equation of Hirst and Lampitt (1998) for a water temperature of −1°C. *n* = number of samples

| Stage | Length (mm) | Dry weight ($\mu$gC) | *n* | Sampling dates for DW | *g* ($d^{-1}$) |
|---|---|---|---|---|---|
| Egg | 0.09–0.1 | 0.22 | 2 | 27 Feb | |
| NI | 0.12–0.14 | 0.21 | 2 | 15 Feb | |
| NII | 0.17–0.18 | 0.42 (0.16) | 3 | 2 Mar | |
| NIII | 0.20–0.23 | 0.81 (0.28) | 3 | 9 May | |
| NIV | 0.24–0.28 | 1.08 (0.25) | 3 | 9 May | |
| NV | 0.26–0.33 | 1.36 (0.30) | 4 | 9 Jun, 8 Sep | |
| NVI | 0.35–0.42 | 1.45 (0.26) | 3 | 9 Jun, 8 Sep | |
| CI | 0.50–0.59 | 1.66 | 2 | 21 Oct | 0.19 |
| CII | 0.60–0.78 | 1.77 | 2 | 21 Oct | 0.18 |
| CIII | 0.70–0.97 | 2.18 (0.37) | 3 | 21 Oct, 4 Nov | 0.17 |
| CIV | 0.89–1.23 | 2.65 (0.39) | 3 | 4 Nov | 0.16 |
| CV ♀ | 1.34–1.57 | 10.2 | 2 | 14 Dec | 0.11 |
| CV ♂ | 1.03–1.34 | 5.19 | 1 | 19 Nov | 0.13 |
| CVI ♀ | 1.66–2.05 | 16.9 (1.68) | 8 | 15–28 Dec | 0.05 |
| CVI ♂ | 1.36–1.77 | 8.58 (1.06) | 7 | 14–28 Dec | 0.07 |

sea or lake ice were obtained by collecting four replicate ice cores that were then wrapped in opaque black plastic and transported to the laboratory, where they were melted in GF/F (Whatman) filtered lake or seawater (dilution factor, 1 : 4 ice : water) in the dark. The temperature was maintained at <4°C during this procedure. The ice cores were not sectioned vertically, but subsequent studies have shown that >99% of the copepod population was present in the bottom 10 cm of fast ice in the region (Swadling et al. 2000*a*). *P. antarctica* were filtered from the melted core samples onto a 53-$\mu$m mesh sieve and preserved as described above. The animals from both the water column and the ice cover samples were sorted into developmental stages (including sex for stages CV and CVI), with reference to the taxonomic description of Tanimura (1992). When abundances were very high, the samples were split, and at least 1,000 specimens were examined in the subsamples. Standing stocks of copepods from the ice cores were calculated directly from the area of the cores, and those in the water column were calculated from abundance data per cubic meter, under the assumption of a 23-m water column at the marine site and a 12-m water column in Ace Lake.

During the period of open water in the 1993–1994 summer, several attempts were made to collect eggs of *P. antarctica* from the marine site. Bottom sediments were sampled with a small Ekman grab, the water column was sampled with the umbrella net, and pieces of thin, newly formed sea ice were collected and melted in the laboratory. Eggs from the lacustrine population were recovered from sediment cores taken with an impact corer during November 1994.

Additional animals were collected on several sampling dates (*see Tables 1, 2*) for the determination of biomass. Ten to 300 individuals of each developmental stage (depending on size) were sorted, rinsed in filtered seawater followed by 300 $\mu$l distilled water (Böttger and Schnack 1986), and their wet weight measured using a Mettler microbalance. The specimens were then dried at 60°C until constant mass was attained. Only animals that appeared to be intact when examined under a stereomicroscope were used. A factor of 30% was assumed for the loss in mass due to preservation in formaldehyde (Böttger and Schnack 1986). Carbon weight was assumed to be 40% of dry mass (Postel et al. 2000). Lengths of up to 20 animals of each stage were measured using an ocular micrometer, which was calibrated against a stage micrometer (±0.01 mm).

The abundance data for each stage on each sampling date were used to describe the cohort development of *P. antarctica*, and combined with the stage-specific weight data to

Table 2. Mean carbon dry weight (SD) and length (range) of developmental stages of *Paralabidocera antarctica* at Ace Lake. The dates in 1994 when each stage was collected for dry weight (DW) measurements are also shown. *g* was calculated using the equation of Hirst and Lampitt (1998) for water temperatures of −0.5°C and 10°C. ND, Not determined. *n* = number of samples.

| Stage | Length (mm) | Dry weight ($\mu$gC) | *n* | Sampling dates for DW | *g* ($d^{-1}$) | |
|---|---|---|---|---|---|---|
| | | | | | −0.5°C | 10°C |
| Egg | 0.09–0.10 | ND | | | | |
| NI | 0.12–0.14 | 0.20 (0.09) | 3 | 22 May | | |
| NII | 0.16–0.18 | 0.38 (0.21) | 3 | 22 May | | |
| NIII | 0.19–0.20 | 0.59 (0.07) | 3 | 22 May | | |
| NIV | 0.20–0.23 | 0.97 (0.05) | 3 | 22 Jul | | |
| NV | 0.22–0.25 | 1.23 (0.04) | 3 | 22 Jul | | |
| NVI | 0.27–0.34 | 1.37 (0.13) | 3 | 22 Jul | | |
| CI | 0.47–0.50 | 1.42 (0.06) | 6 | 22 Jul, 23 Aug | 0.20 | 0.26 |
| CII | 0.53–0.59 | 1.57 (0.09) | 3 | 21 Sep, 12 Oct | 0.20 | 0.26 |
| CIII | 0.68–0.74 | 1.99 (0.04) | 3 | 23 Nov, 23 Dec | 0.18 | 0.24 |
| CIV | 0.69–0.84 | 2.43 (0.05) | 5 | 12 Oct, 26 Oct, 23 Nov | 0.17 | 0.23 |
| CV ♀ | 0.89–1.05 | 3.28 (0.16) | 4 | 10 Nov | 0.16 | 0.21 |
| CF ♂ | 0.88–0.99 | 2.95 (0.12) | 3 | 10 Nov | 0.16 | 0.21 |
| CVI ♀ | 1.09–1.24 | 6.78 (0.57) | 6 | 10 Nov, 23 Nov, 10 Dec, 23 Dec | 0.08 | 0.08 |
| CVI ♂ | 1.02–1.09 | 4.96 (0.35) | 5 | 10 Nov, 23 Nov, 10 Dec | 0.10 | 0.10 |

calculate the biomass of each population on each date. The logarithm of the mean individual dry weight was plotted against time for the period of juvenile (somatic) growth and a monotonic spline curve describing the shape of this relationship fitted (Wood 1994). From this curve, the instantaneous daily growth rate was estimated by the slope (first derivative) of the curve, which varied with time. The smoothness of the splines was estimated by cross-validation in all cases. All data analyses were conducted using the *R* statistical system (Ihaka and Gentleman 1996). Because the cohort structure of the lacustrine population could not be distinguished clearly (*see ''Results'' and ''Discussion'' sections*), we were unable to apply the above method to estimating growth in that population. Therefore, to provide a basis of comparison with the marine population, we applied the global models for calculating weight-specific growth in marine planktonic copepods developed by Hirst and Lampitt (1998) to both the marine and lacustrine populations:

$$\log g = -0.6516 - 0.5244(\log BW) \quad (1)$$

$$\log g = 0.0111(T) - 0.2917(\log BW) - 0.6447 \quad (2)$$

where $g$ is the weight-specific growth ($d^{-1}$), $T$ is water temperature (°C), and $BW$ is the body weight ($\mu$g C individual$^{-1}$). We applied their models for broadcast spawners and considered adults (Eq. 1) and juveniles (Eq. 2) separately. For the juveniles, we determined growth for copepodids (stages CI–CV) only, because the nauplii of both populations have long periods of no growth. For the marine population, we assumed an environmental temperature of −1°C. However, for the lake population, it was possible that the copepods were experiencing a range of water temperatures of −0.5–10 °C as they developed (Bayly and Burton 1987; *see Fig. 2*). Because we did not know the primary locations of each stage in the water column while they developed, we calculated the growth rates at both temperature extremes, which would represent the upper and lower limits of their range.

During early January 1994, an egg production experiment was conducted in which five pairs of adult females of *P. antarctica* from the marine site were incubated for 5 days in each of two food treatments and their daily egg production monitored. The copepods were placed in 60-ml crystallizing dishes filled with seawater and algal suspensions. In one treatment, the incubation water included particles <200 $\mu$m in diameter, and, in the other, particles >200 $\mu$m. Attempts to measure in situ egg production rates of the lacustrine population proved to be unsuccessful.

## Results

*Growth and decay of ice cover*—When the marine site was first sampled in December 1993, the ice thickness was ~1.6 m. The ice broke out on 23 December 1993, and the site remained ice-free until the appearance of frazil crystals in late February 1994. The ice grew at a rate of ~1 cm d$^{-1}$ during March and April, thereafter growing more slowly until it reached maximum thickness (1.64 m) in November. It was blown out on 13 January 1995 after a period of strong wind. Snow cover on the ice fluctuated over a range of 0–280 mm.

The ice cover on Ace Lake was 0.85 m thick in April 1994, and it reached maximum thickness (1.80 m) in late October. It began to break up in late January 1995 and had disintegrated completely by 14 February 1995. There was a short period of open water before refreezing began. Consolidation of the ice cover was rapid, and it was again traversable by 10 March 1995. Snow cover was variable, ranging from 0–340 mm.

*Salinity and temperature*—The bulk salinity of the ice at the marine site ranged from 3–9 and averaged ~8 until July. In September, cold temperatures caused brine to be excluded from the ice matrix, and salinity fell to 3. The ice was hard and opaque throughout autumn and winter, then became softer, with larger brine channels, in late spring. The temperature and salinity of the water column followed a seasonal cycle (Fig. 2A,C) that is typical for inshore Antarctic sites (Gibson and Trull 1999). The maximum water temperatures recorded during the 1993–1994 and 1994–1995 summers were at 2 m and were 0.04°C and 1.39°C respectively. Salinity was lowest during summer (~32.5), when freshwater from melting ice diluted the surface waters. It increased steadily throughout winter to a maximum in October (34.2).

In Ace Lake, the bulk salinity of the ice cover was low, reaching no more than 3. There was a gradual decrease from May to September, as air temperatures dropped, and an increase during October as air temperatures gradually increased. The general appearance of the ice was much harder and clearer than that at the marine site. There was considerable stratification of both the salinity and temperature of the water column in the lake (Fig. 2B,D; *see also* Gibson 1999 for detailed vertical profiles). The salinity varied from 7 at 2 m to 30 at 10 m. The temperature was at a minimum of slightly below 0°C at 2 m in winter, and a maximum of 10°C was recorded at 10 m during late summer.

*Chl* a—A single major peak in Chl *a* occurred in the water column at the marine site in late January 1994 (Fig. 2E), after which the concentration dropped rapidly to low winter background levels (<0.5 $\mu$g L$^{-1}$). Mild stratification occurred on occasions, with higher Chl *a* concentrations in the top 2 m (Gibson et al. 1997; Gibson 1998). After a gradual rise in Chl *a* that began in late October, three peaks of similar magnitude were observed during the 1994–1995 summer that were interspersed with periods of relatively low Chl *a* (<2 $\mu$g L$^{-1}$). There were measurable quantities of Chl *a* present throughout the winter in the sea ice (Fig. 2E). A peak in ice Chl *a* occurred in early May, and then the concentration declined until July before gradually increasing to a maximum on 4 November.

In Ace Lake, Chl *a* concentrations in the oxygenated waters fluctuated between 0.8 and 1.6 $\mu$g L$^{-1}$ (Fig. 2F). There were no distinct seasonal trends, and stratification was minimal, with slightly higher concentrations recorded at 2 m. The concentration of Chl *a* in the lake ice was generally low and never reached >1.0 $\mu$g L$^{-1}$ (Fig. 2F). Maximum concentrations in the ice were recorded during August and September.

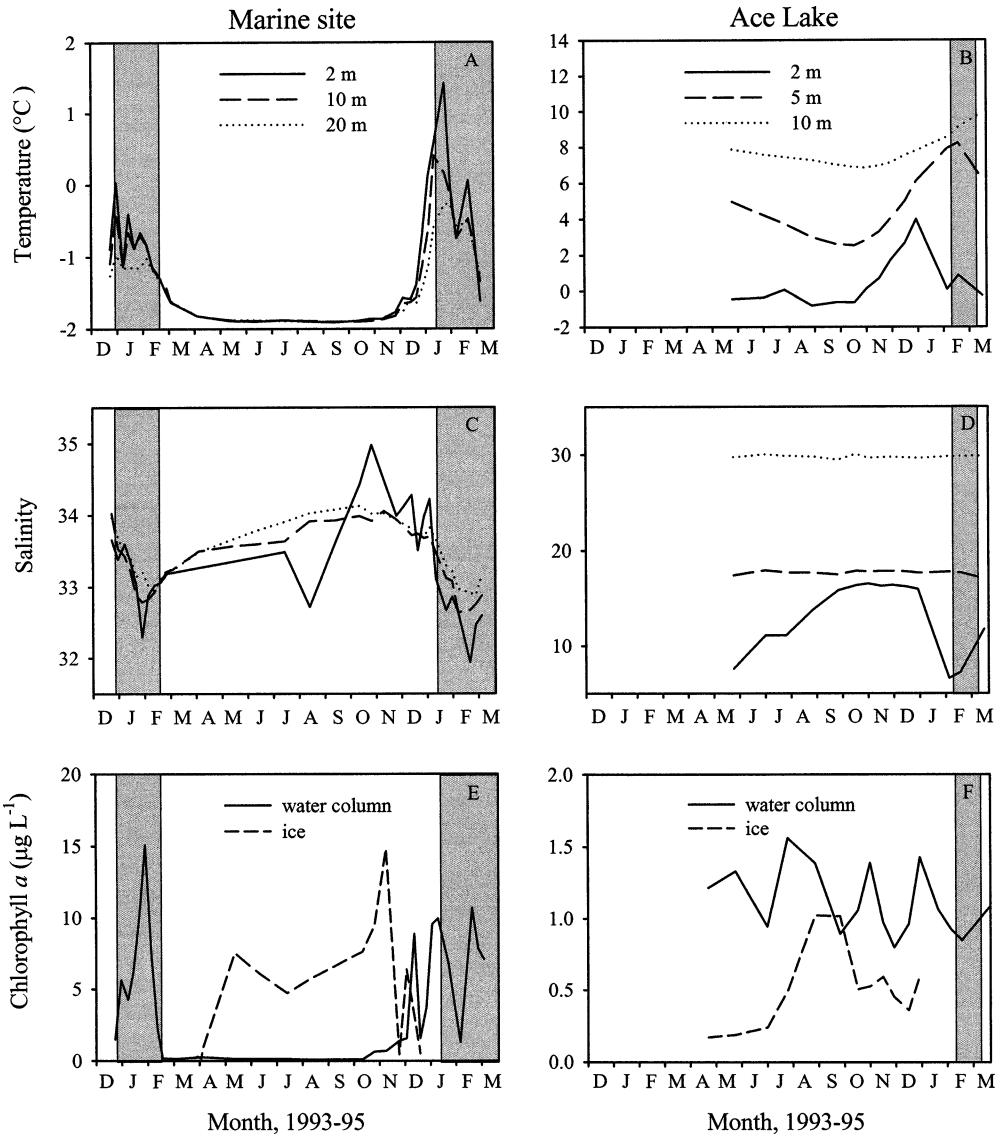


Fig. 2. (A, B) Water temperature, (C, D) water salinity, and (E, F) water and ice Chl *a* concentrations at the marine site and at Ace Lake during 1993–1995. Shaded areas represent periods of no sea ice cover.

*Abundance and distribution of* P. antarctica—The standing stock of *P. antarctica* in the water column at the marine site was highest in late February 1994, reaching a maximum of 53,200 m$^{-2}$ (Fig. 3A). In contrast, low numbers (<3,000 m$^{-2}$) were recorded from April to July, followed by an increase in August and September. Between May and July, >98% of the population was found in the sea ice (Fig. 3B), although this proportion dropped to 70% in October but returned to 97% immediately before the break-up of the sea ice. Within the sea ice, a maximum standing stock of 270,800 m$^{-2}$ was reached in May, and a minimum of 45,200 individuals m$^{-2}$ was seen in August (Fig. 3B).

In Ace Lake, the standing stock of *P. antarctica* in the water column was variable, ranging from ~60,000 individuals m$^{-2}$ on 28 June to a maximum of 340,000 individuals m$^{-2}$ on 26 October (Fig. 3C). Ice cores were examined regularly for the presence of *P. antarctica.* Two copepodites were observed in September, but, in all other lake ice samples, *P. antarctica* was absent.

*Cohort analysis of* P. antarctica—At the marine site, adult females were the dominant stage on 15 December 1993 (Fig. 4), and all of them possessed spermatophores. The population consisted mainly of adults until 19 January, although from 22 December to 19 January the total density was very low (<10 m$^{-3}$). No adults were found after 19 January. From late January to the end of February 1994, before the beginning of sea ice formation, the median stage was NI. In March and April, NII was the dominant stage in the water column, and nauplii had begun to colonize the newly formed sea ice. Nauplii then developed in the ice as far as NIV, at which stage they overwintered in the sea ice, with very few indi-

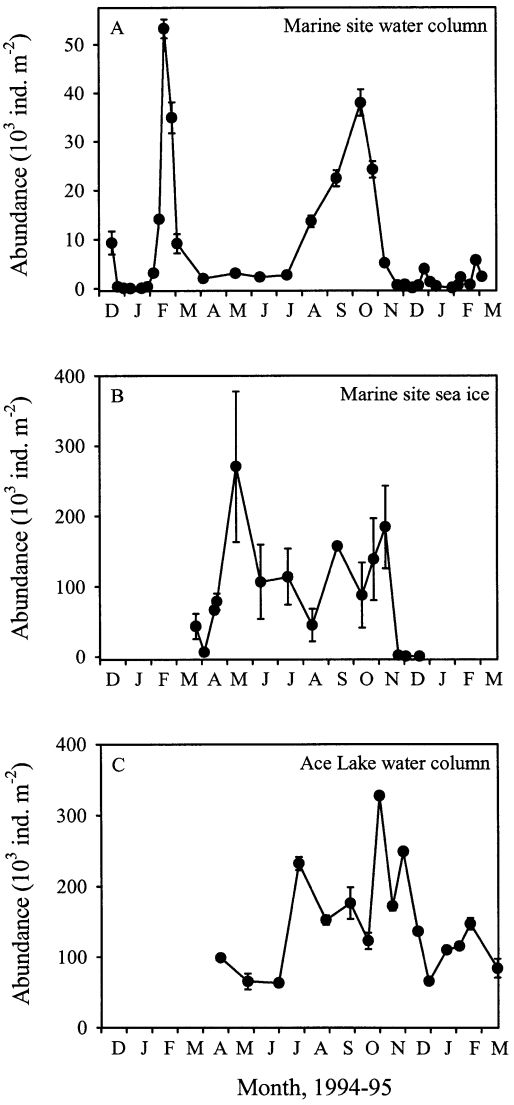


Fig. 3. *Paralabidocera antarctica.* Abundance (mean ±SE) in (A) the water column and (B) the sea ice at the marine site and in (C) the water column of Ace Lake.

viduals in the water column. Most of the population had developed to naupliar stages NV and NVI by early October, and a few CI had appeared. In late October, the majority of the population was in the sea ice, with younger individuals found in the water column. We interpreted this as the occurrence of two cohorts. Most of the population formed a faster growing cohort mainly within the sea ice, coinciding with an increase in the biomass of ice algae. This cohort developed to stage CIII by 4 November, at which time the rest of the population, in the slower cohort in the water column, had shown little development. Between 4 and 19 November, the population shifted from the sea ice to the water column, and the progression of the two cohorts was indistinguishable. Very few CV males and females were observed. Adult males were the dominant stage from late December 1994 to early January 1995, but, from late January to the end of the study, stage NI accounted for at least 70% of the population.

Eggs were not found in the water column or the sea ice at the marine site. However, large numbers of eggs were present in the sediments: 430 eggs were recovered from ~145 g of wet sediment. These eggs were identical in size and appearance to those spawned by *P. antarctica* during the egg production experiments (see below).

The *P. antarctica* cohort in Ace Lake (Fig. 5) followed a developmental cycle similar to that described for the marine site from April to June 1994, although the cohort was broader. In Ace Lake, stage NI individuals were present throughout the year, with the result that the cohort structure became broader and flatter until mid-October, when the composition of the population was quite evenly spread between stages NI–CV. Adult females, most with spermatophores attached, were the dominant stage on 10 November. On 23 November, females with spermatophores were again more abundant than those without, whereas, on 10 December, the reverse was the case. By 23 December, females with spermatophores were again dominant. Copepodids remained common during December but were largely absent in January 1995. By late January, early naupliar stages dominated the population, although small numbers of copepodites persisted.

No eggs were recovered from the lake ice or the water column. Eggs from the sediment cores collected from Ace Lake were identical in size and appearance to those collected from *P. antarctica* during the egg production experiments (see below). A mean of 230 eggs was recovered from 1 g of wet sediment.

*Growth rates and egg production*—The dry weight of each individual developmental stage was lower at Ace Lake than at the marine site (Tables 1, 2), although this differential was marginal up to stage CIV and was greatest in the CV and adult stages. Adult females at the marine site were 2.5-fold heavier and 60% longer than females from Ace Lake.

Figure 6B shows the instantaneous daily growth rates for the marine site, calculated using the graphical method outlined above. Tables 1 and 2 give growth rates for both populations as determined from the equations of Hirst and Lampitt (1998).

At the marine site, the mean biomass per individual remained stable during the period of egg development to stage NI in January 1994, after which biomass increased quite rapidly until May, with growth rates of up to 0.06 $d^{-1}$ (Fig. 6B). Biomass then remained stable until October, and there was zero community growth. In October and November, the faster cohort, which made up the main body of the population within the sea ice, grew at rates up to 0.14 $d^{-1}$, which resulted in a significantly greater mean biomass than for the more slowly growing cohort. There was no clear trend in biomass over the year (Fig. 6A). The product of the instantaneous growth rate of the faster cohort and the geometric mean annual biomass of the marine population (9.1 mg C $m^{-2}$; Fig. 6C), summed over the year, yielded an estimate of annual secondary production by the *P. antarctica* population of 123 mg C $m^{-2}$ $yr^{-1}$.

The highest growth rate calculated for the marine population (0.14 $d^{-1}$) occurred when stages CII–IV dominated the population (Fig. 4). Thus, the highest growth rate determined directly from the field data was somewhat lower than the

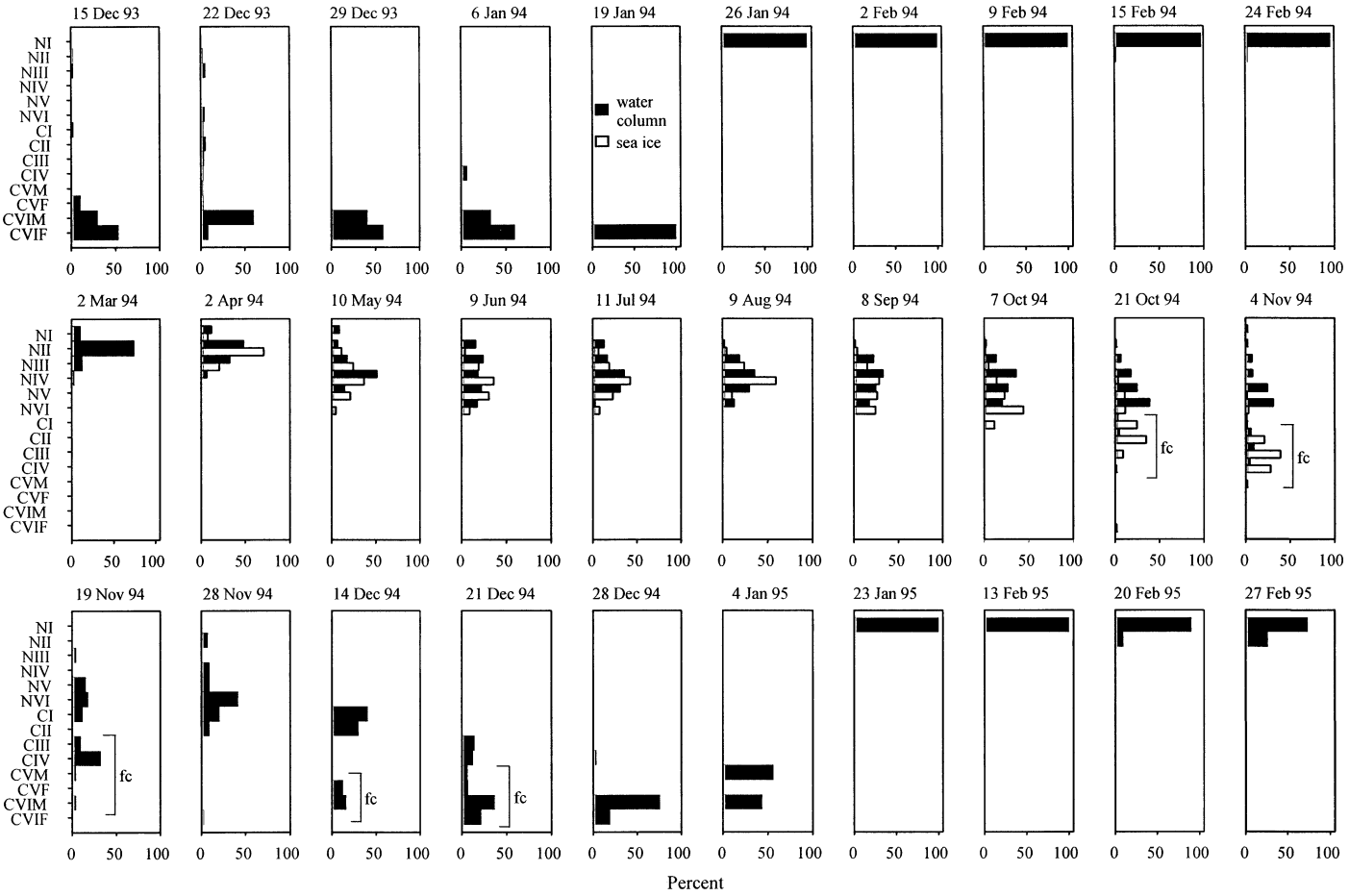


Fig. 4. *Paralabidocera antarctica.* Percentage composition of developmental stages in the water column and sea ice at the marine site, December 1993–February 1995. Brackets labeled ''fc'' denote the fast cohort.

rates calculated for these stages using the Hirst and Lampitt (1998) equations (0.16–0.18 $d^{-1}$; Table 1). On the basis of the equations, the growth rate was highest for stage CI and decreased steadily to stage CV before declining considerably in the adult stages. The average growth rates of the lacustrine population were slightly greater at both temperatures used in the model (−0.5°C, 0.16 $d^{-1}$; 10°C, 0.20 $d^{-1}$) than those for the marine population, although they showed similar trends through the developmental stages (Table 2).

Egg production was examined for adult females collected from the marine site only. Egg production was significantly greater in water that contained particles >200 $\mu$m than in water with particles <200 $\mu$m (two-way analysis of variance [ANOVA] with replication; $F_{1,4} = 45.7$; $P < 0.001$) (Fig. 7). Over the 5-day course of the experiment, egg production rates decreased significantly (two-way ANOVA with replication; $F_{1,4} = 79.0$; $P < 0.001$), from 69 to 12 eggs female$^{-1}$ $d^{-1}$ in the >200 $\mu$m treatment and from 44 to 4 eggs female$^{-1}$ $d^{-1}$ in the <200 $\mu$m treatment. The highest egg production rate measured (69 eggs female$^{-1}$ $d^{-1}$) corresponded to a dry-weight–specific egg production rate of 0.88 $d^{-1}$, as based on a mean measured egg dry weight of 0.216 $\mu$g.

## Discussion

*Comparison of life cycles*—Marine and lacustrine populations of *P. antarctica* each have an annual cycle, with eggs produced during summer and adults developing by the end of the year. This pattern is similar to that described by Tanimura et al. (1996) for a coastal population of *P. antarctica* near Syowa Station (69°00′S, 39°35′E). In the ocean, all stages of the life cycle are closely associated with the sea ice (Tanimura et al. 1996). Accordingly, the marine population within the sea ice was 2 orders of magnitude greater in abundance than that in the water column. In contrast, at Ace Lake the entire population remained in the water column, and, as a result, abundances within the water column were 10-fold greater at Ace Lake than at our marine site.

The lacustrine population of *P. antarctica* differed from the marine population in several important ways. First, dry-weight determinations revealed that the lacustrine animals were smaller and that this difference was most marked in the stage CV and adult copepods. This difference was first reported by Bayly (1978), who found that adults of the lacustrine population were ~60% of the length of the coastal specimens, which may be a consequence of the lacustrine

population living at higher temperatures, at lower salinity, and with less food available (*see below*). Second, even though lacustrine populations were most dense immediately under the ice (Bayly and Burton 1987), the ice itself is unavailable to the copepods, because it offers few brine channels as refugia. The salinity of the ice cover at the marine site was greater than that of Ace Lake, which resulted in greater porosity and a greater availability of habitat space (Eicken et al. 1991). Third, copepodites in Ace Lake matured to the adult stages ~1 month earlier than the marine population. Finally, the Ace Lake population has continuous recruitment, because early naupliar stages were present throughout the year.

*Recruitment and egg banks*—The mechanism by which *P. antarctica* continuously recruits in Ace Lake is unclear but might be attributable to an egg bank. Tanimura et al. (1996) reported that eggs are spawned at the ice-seawater interface during late summer, when the sea ice is at its thinnest, and then become incorporated into the ice. Hoshiai and Tanimura (1986) also reported a large number of unidentified eggs in sea ice cores collected near Syowa Station. However, in our collections, we were unable to establish the presence of *P. antarctica* eggs in the ice but instead found many eggs in the sediment at both the marine and lacustrine sites. At the marine site, the eggs persisted in the sediment for ~4 weeks before all had hatched (K.M.S. pers. obs.). The eggs of under-ice copepods can take an appreciable time to hatch, for example 19–20 d for *Pseudocalanus* (McLaren 1969), 20 d for *Tortanus discaudatus,* 14 d for *Eurytemora hirundoides* (McLaren et al. 1969), and 9 d for *Rhincalanus gigas* (Ward and Shreeve 1998). The period of 4 weeks is reasonable, therefore, as a time frame during which eggs of *P. antarctica* may persist. Although resting eggs are common in copepods of the family Acartiidae (Mauchline 1998), we were unable to confirm their existence in *P. antarctica.* Quiescent eggs of copepods may be induced by adverse environmental conditions and are often morphologically very similar to subitaneous (directly developing) eggs (Uye 1985).

Ace Lake is meromictic, with a pronounced oxycline at ~11 m (Rankin et al. 1999). However, a bank of *P. antarctica* eggs has been found to occur in the lake sediments, where densities can reach up to 600 eggs $g^{-1}$ of dry sediment (L. Cromer pers. comm.). The morphology of Ace Lake is essentially a simple basin, with the deepest, anoxic point near the middle of the lake. The proportion of oxygenated sediments that occur around the margin of the lake is ~75% of the total sediment area (Rankin et al. 1999). Therefore, it is possible that, although nauplii do not recruit from those eggs that fall to anoxic sediments, they recruit throughout the year from the oxygenated or partially oxygenated sediments. An alternative explanation for the continuous presence of early naupliar stages is that some individuals developed at a much slower rate or failed to develop past a certain stage. The low biomass of food in the lake (as evidenced by Chl *a* concentrations) might have been insufficient to support the growth of the entire cohort, thus inhibiting the development of a proportion of the population.

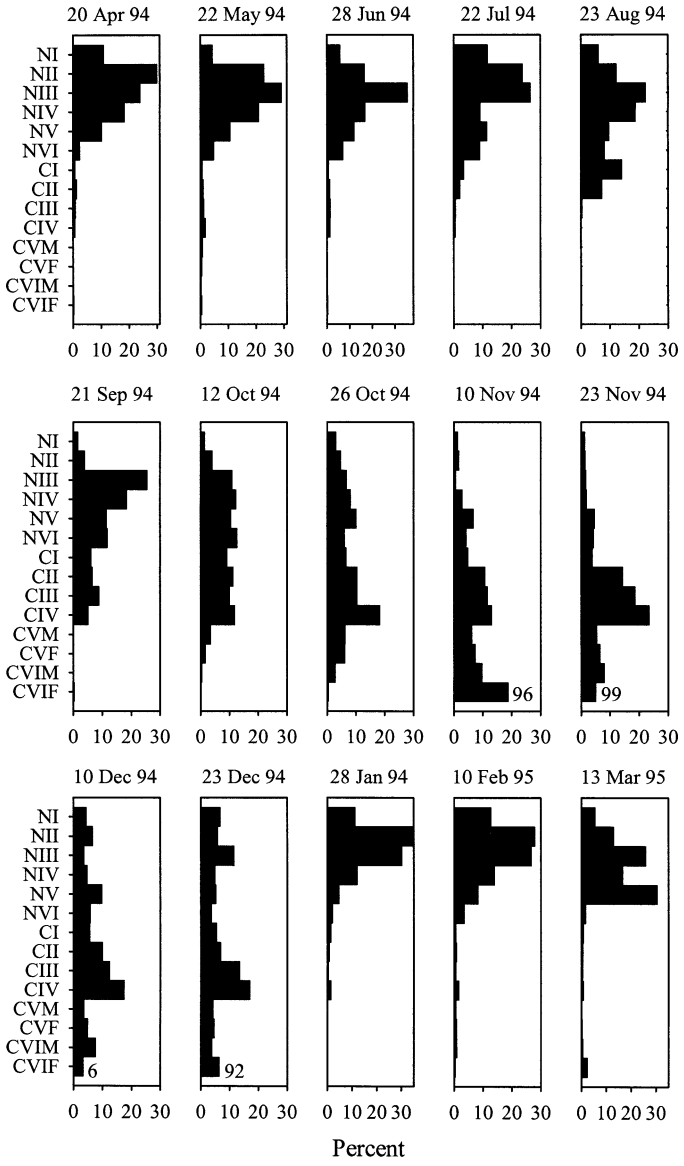


Fig. 5. *Paralabidocera antarctica.* Percentage composition of developmental stages in Ace Lake, April 1994–March 1995. Numbers on the graphs for November and December represent the percentage of females carrying spermatophores.

*Mortality*—In late December to mid-January, the marine and lacustrine populations of *P. antarctica* are synchronized by mass mortality. In early to mid-November, stage CIII and CIV copepodids leave the sea ice at the marine site, the time when the under-ice algal mat also started to slough off. These late-stage copepodids remain in close association with the bottom of the ice, where diatoms continue to grow. However, once out of the ice, the animals are more exposed to predation by the ice-fish *Pagothenia borchgrevinkii* (Hoshiai and Tanimura 1981; Hoshiai et al. 1991), as well as invertebrate predators. Abundances declined rapidly during this period (Fig. 3), although the effect of predation was confounded by the dispersal of the population through increased water mixing. In December, the population was dominated by spawning adults. Once egg production was complete, the

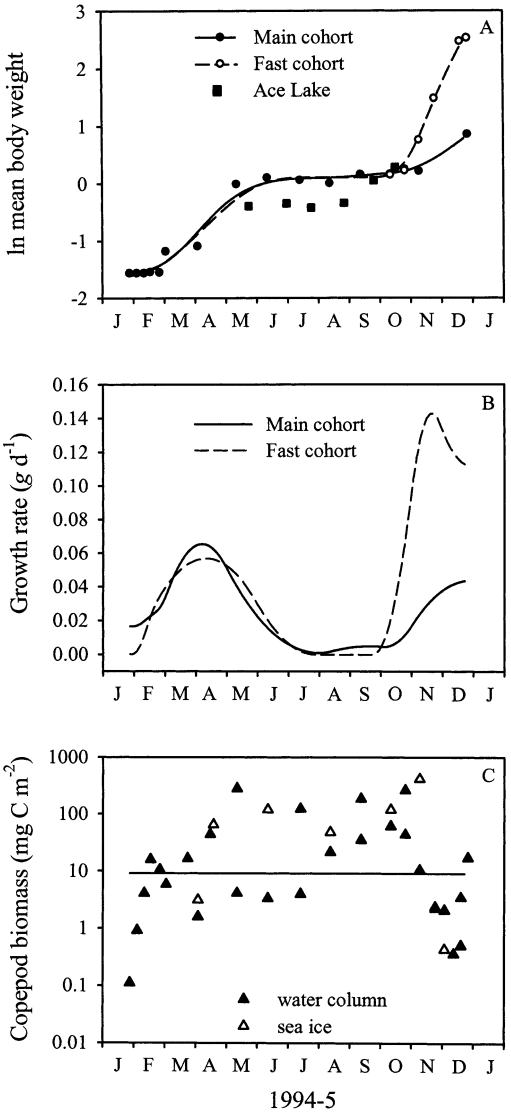


Fig. 6. *Paralabidocera antarctica.* (A) Annual cycle of mean individual biomass of cohorts sampled at the marine site and Ace Lake, (B) the corresponding instantaneous daily growth rates for the marine cohorts, and (C) biomass of the marine populations. The stippled line indicates the calculated geometric mean biomass (see text).

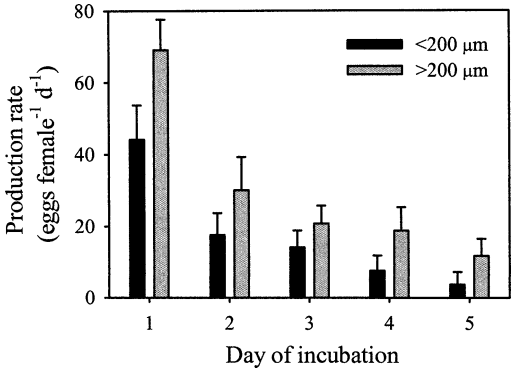


Fig. 7. *Paralabidocera antarctica.* Egg-production rates for females from the marine site, January 1995.

animals were in poor condition and disappeared rapidly from our samples. All adults vanished from the marine site over the 7-d period between 19 and 26 January, after which only NI stages were present. This period of high adult mortality was associated with the breakup of the ice and the development of early naupliar stages within the water column, before the new sea ice was colonized in March.

In the Ace Lake, high population mortality occurred before the breakup of the ice, and, in this environment, *P. antarctica* had no predators. In this population, it is not only the adult copepods that died in early January but all the copepodid stages. This mortality coincided with a period of rapid temperature increase in the lake water. In late December 1994, the minimum temperature in Ace Lake was 4°C, which may have stressed this population, although it is unclear why copepodids would have suffered more than nauplii. In the ocean, distributional data support the likelihood of a 3°C upper limit for this species, because the most northerly record of *P. antarctica* is 62°S (Zmijewska 1985), approximately the northern extreme of Antarctic Surface Water (maximum, 3°C). Bayly and Burton (1987) interpreted the vertical distribution of *P. antarctica* within Ace Lake on the basis of food, but a more parsimonious interpretation would be based on the temperature profile. On the date of Bayly and Burton's (1987) sampling, the distribution of the copepods matched that of cooler water and had a center of mass 1 m under the ice. It is uncertain whether the patterns we observed in Ace Lake, including the January mass mortality, also occur in the other lacustrine populations. One other study that examined the *P. antarctica* distribution in Ace Lake also observed the presence of most stages throughout the year and recorded a decline in abundance of nauplii and copepodites in late January (Bell and Laybourn-Parry 1999).

*Factors influencing body size*—The lacustrine population of *P. antarctica* was characterized by smaller body size than the marine population, particularly in the stage CV and adult copepods. It is not known what factors cause this reduction in body size of the lacustrine population, although likely causes include the warmer temperatures, lower food concentrations and variable salinities (6–30) experienced during their development. Dominant environmental influences on body size in other copepod species are variable and tend to involve a combination of causes. For example, growth rates of two large Antarctic copepods did not vary systematically with either temperature or food but did show negative relationships with silicate concentrations, which suggests a possible link with local primary production (Shreeve et al. 2002). A study on the temperate copepod *Tisbe holothuriae* showed that adult growth actually increased slightly with salinity but decreased greatly with temperature (Miliou 1996).

Overall, the phytoplankton biomass is substantially lower in Ace Lake, where the diet of *P. antarctica* is mostly cryptomonads (Swadling et al. 2000*b*), in contrast to the ice-associated pennate diatoms preferred by the coastal population (Watanabe et al. 1990). There is some evidence for an

ontogenetic shift in diet, because Hoshiai et al. (1987) were unable to identify diatoms in the gut contents of nauplii until stage NIV. This has been interpreted as nonfeeding by the earlier naupliar stages (Swadling et al. 2000*b*), but, in fact, the growth increments apparent in our weight data indicated that these nauplii do feed. Therefore, it is likely that the diets of early nauplii are composed of items such as flagellates (Swadling and Gibson 2000), which are not preserved by the process of preparation for scanning electron microscopy used by Hoshiai et al. (1987) to examine gut contents.

*Egg production*—*P. antarctica* egg-production rates at the marine site are high (up to 69 eggs female$^{-1}$ d$^{-1}$), in accordance with the universal strategy of polar copepods to assure high levels of fecundity at maturity (Conover and Huntley 1991). In terms of eggs produced per day, the egg-production rates of *P. antarctica* were in the midrange of those at temperatures $<6$°C, but the maximum specific egg production rate (0.88 d$^{-1}$) was an order of magnitude higher than has been previously recorded (*see table 45 in* Mauchline 1998). However, this may merely reflect a shortened, intensive period of egg production compared with other polar copepods. The drop-off in egg-production rates that we observed during the 5-d course of our experiment would support this interpretation. During, the 5 d of our experiment 150 eggs female$^{-1}$ were produced, but the actual fecundity was sure to be greater, because the females were sorted randomly from wild populations, and the stage of their reproductive life was therefore unknown. The differences that we observed between food treatments in our egg-production experiment most probably related to the greater abundance of large chain-forming diatoms in the $>200$ $\mu$m treatment.

*Growth rates and production*—The annual patterns of somatic growth rates that we calculated are similar to that predicted from modeling studies of *Calanus glacialis* for a biennial life cycle (Slagstad and Tande 1990), with environmental factors determining periods of zero growth alternating with periods of rapid growth. The unusual, and perhaps unique, feature of *P. antarctica* is that this copepod overwinters in the naupliar stages, whereas most polar calanoids overwinter as late-stage copepodids. In our study, the growth of early nauplii in the marine population was rapid (up to 0.06 d$^{-1}$), after which it slowed to zero during the winter residence of the nauplii within the brine channels of the sea ice. At the end of the winter, the bulk of the population was retained within the sea ice and developed faster than that within the water column. This period of cohort differentiation coincided with the maximal growth of ice algae. As the copepods reach the intermediate copepodid stages, somatic growth reached its maximum rate (0.14 d$^{-1}$), coinciding with a period in which the abundance of ice algae rapidly diminished, reflecting high grazing rates (*see below*). Our calculated growth rates are typical of those recorded for polar copepods (tables 12, 13 in Conover and Huntley 1991; table 55 in Mauchline 1998). Unfortunately, the period of most rapid growth through the copepodite stages was undersampled in the marine population, and the growth rates during this period could actually exceed our estimates. The utility of cohorts to estimate somatic growth rates is compromised when adults are present or when there is continuous recruitment. The presence of adults affected our estimates in the marine population and, in combination with continuous recruitment, prevented the estimation of growth of the lacustrine population from the field-collected data. However, our calculations of growth rates for each population based on the equations of Hirst and Lampitt (1998) showed reasonable agreement between populations and, perhaps more important, good agreement between the calculated rates and the estimates from field data for the marine population.

Our estimate of the annual somatic production of *P. antarctica* at the marine site, 123 mg C m$^{-2}$ yr$^{-1}$, although based on reliable estimates of growth rate, was compromised by a crude estimate of biomass. This number was low compared with estimates of annual secondary production by large polar copepods such as *C. glacialis* (8.4 g C m$^{-2}$ yr$^{-1}$; Slagstad and Tande 1990). The similar sized *Pseudocalanus minutus* achieved yearly rates of 341–496 mg C m$^{-2}$ yr$^{-1}$ during 1957 in Ogac Lake (McLaren 1969), which is approximately threefold higher than our yearly rate. Under the assumption of a specific egg-production rate of 0.88 d$^{-1}$, a biomass of adult females of 21.5 mg m$^{-2}$ (calculated from the December abundance of adult females) and a period of egg production of 14 d, the contribution of egg production by adult females to annual production could be as high as 265 mg C m$^{-2}$ yr$^{-1}$, which is more than twofold higher than annual somatic production by juvenile stages.

In Ace Lake, *P. antarctica* cleared 58–117% of primary production (Swadling and Gibson 2000). There are no comparable data for the coastal population, but the marked drop in Chl *a* concentration in the sea ice at the marine site in November (Fig. 2) coincided with the most rapid period of growth by *P. antarctica.* Under the assumption of similar weight-specific grazing rates within the marine population as those measured in the lacustrine population (60% body C d$^{-1}$) (Swadling and Gibson 2000), a population of $2 \times 10^5$ copepods m$^{-2}$ would be capable of grazing $\sim$100 mg C m$^{-2}$ d$^{-1}$. In contrast to the lacustrine population, it does not appear that the marine population is likely to have a significant effect on the production of ice algae (1200 mg C m$^{-2}$ d$^{-1}$ on 29 November 1993; Archer et al. 1996), and grazing by *P. antarctica* is not sufficient to account for the drop in Chl *a* values within the ice.

Habitat differences between the marine and lacustrine populations have caused corresponding changes in the biology of *P. antarctica.* In the marine population, our data support the life-cycle patterns previously documented by Tanimura et al. (1996) and show a year-long, synchronized cycle, with the nauplii overwintering in the sea ice. In contrast, although the Ace Lake population remained closely associated with the underside of the ice, its harder nature prevented the copepods residing within the ice cover itself. The presence of *P. antarctica* in the water column of Ace Lake throughout its life cycle indicates that this species is a facultative ice dweller and that the lower abundance within the water column of marine habitats is, at least in part, a consequence of substantial predation pressure in this environment. However, our study is the only one to date to have examined the annual population structure in detail within the

lacustrine populations, and we are therefore unsure how general our observations may be. Two aspects of the biology of the Ace Lake population merit further examination. First, the mechanism underlying the continual recruitment of nauplii to the population, and second, the mechanism underlying the mortality events witnessed in January.

The present study has indicated a strong degree of plasticity in both the reproductive behavior and the annual cycle of growth of *P. antarctica.* From this plasticity, it can be inferred that this species might be able to cope with future environmental change, in particular the predicted unpredictability in the timing of sea ice growth and decay and decreased extent of sea ice (e.g., Budd and Wu 1998), by its ability to complete its life cycle without entering the ice. This might give it a competitive advantage over other ice-associated species with less plastic life cycles.

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*Received: 8 July 2003*
*Amended: 18 November 2003*
*Accepted: 20 November 2003*