# Temporal patterns in the distribution, biomass and community structure of macrozooplankton and micronekton within Port Foster, Deception Island, Antarctica

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## Abstract

The pelagic community within the flooded caldera of Deception Island, Antarctica, was sampled with a 10-m$^2$ opening-closing MOCNESS trawl on five cruises between March 1999 and November 2000. Collections were made in 50 m strata from the surface to 150 m depth in an area with a bottom depth of 155–160 m. From March 1999 through February 2000 the pelagic community was dominated by krill, primarily *Euphausia crystallorophias* and *E. superba*, which made up > 94% of total pelagic biomass on a dry-weight basis. Community composition shifted during early 2000, and samples from May and November 2000 contained a more diverse assemblage and large numbers of cydippid ctenophores, comprising ca. 30–35% of pelagic biomass on a dry weight basis. *E. crystallorophias*, which made up nearly 85% of the pelagic biomass in November 1999, declined to 5.8% during November 2000. The change in composition was accompanied by displacement of the biomass mode to greater depths, due to the deeper occurrence and lack of diel vertical migration in ctenophores, compared to krill. Integrated water-column biomass increased substantially from 1999 to 2000, primarily because of elevated abundances of gelatinous zooplankton and the presence of significantly larger krill during 2000.
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## 1. Introduction

The Southern Ocean is characterized by extreme environmental conditions. Seasonal cycles in ice cover and light availability result in high temporal variability in primary production (Smith and Nelson, 1986; Arrigo et al., 1997, Smith et al., 2001), and all of these factors may impact the abundance and distribution of pelagic fauna (Daly and Macaulay, 1991; Quetin and Ross, 2001; Brierley et al., 2002). The ecology of Antarctic macrozooplankton and micronekton communities has been examined in a number of locations, but typical studies have focused on a single time of year (e.g., Hopkins and Torres, 1988; Lancraft

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et al., 1991; Hopkins et al., 1993; Kaufmann et al., 1995; Cabal et al., 2002), and relatively little has been published on variation in the composition and structure of Antarctic pelagic communities on time scales exceeding the duration of a single cruise.

Studies spanning one or more annual cycles have greatly enriched our understanding of the processes affecting Antarctic macrozooplankton/ micronekton communities on seasonal to inter-annual time scales (Daly and Macaulay, 1991; Loeb et al., 1997; Fisher et al., 2003). From these studies, much of the variability in community structure has been related to variation in physical and biological factors, particularly ice cover and primary production. Krill constitute dominant components of the pelagic community in many areas of the Antarctic and appear to be affected to a great extent by the physical environment (Hofmann et al., 2002). These animals are associated with the under-ice surface, especially in winter (O'Brien, 1987; Daly and Macaulay, 1991), but their abundance and distribution appear to vary in relation to life history and season (Daly and Macaulay, 1991; Sprong and Schalk, 1992). While krill have received substantial attention, the dynamics of other elements of the pelagic community are less well understood.

This study was carried out to examine the dynamics of Antarctic macrozooplankton and micronekton during multiple seasons at a single location: Port Foster, the drowned caldera of Deception Island. Deception Island is located at the southern end of the South Shetland Island chain, just west of the Antarctic Peninsula. Until now, macrozooplankton and micronekton in Port Foster had been examined only during the austral summer (Everson, 1987; Brinton and Townsend, 1991). In both these studies, the numerically dominant animal was the ice krill, *Euphausia crystallorophias*, a coastal and neritic species that typically occurred in schools and migrated vertically on a diel basis, with maximum densities deeper than 80 m during the day and between 20 and 40 m depth at night (Everson, 1987). Similar migration patterns were reported in ice-free waters to the east off Enderby Land. However, diel vertical migration was attenuated and krill were

observed near the surface both day and night in the presence of ice cover and ice-associated algae that are known to constitute a food source for krill species (O'Brien, 1987). Other components of the macrozooplankton and micronekton community in Port Foster included the euphausiids *Euphausia superba* and *Thysanoessa* sp., and the notothenioid fishes *Notothenia newnesi* and *Champsocephalus gunnari* (Everson, 1987).

Surveys along the Antarctic Peninsula during the winter revealed few ice algae, and *E. crystallorophias* and *E. superba* were not found directly under the ice. Instead, abundances of *E. crystallorophias* generally increased from the surface to the maximum sampling depth of 250 m, while *E. superba* was most abundant at 30 m depth, with no diel vertical migration noted in either species (Nordhausen, 1994). Food availability likely was influential in determining these distributions: *E. crystallorophias* has a diverse diet including both planktonic and benthic diatoms (Kittel and Ligowski, 1980) and may consume up to 96% of the daily primary production in some areas during the summer (Pakhomov and Perissinotto, 1996).

This study was conducted during a series of five cruises covering nearly two years as part of a multidisciplinary research program (the Erupt program; Smith et al., 2003a) at Deception Island. Samples were collected during several seasons between March 1999 and November 2000 to examine spatial and temporal variability in the biomass, species composition and vertical distribution of macrozooplankton and micronekton in Port Foster.

## 2. Methods

### 2.1. Sample collection and processing

The macrozooplankton/micronekton community in Port Foster was sampled during five cruises (Table 1) on the R/V *Laurence M. Gould*. On each cruise, macrozooplankton and micronekton were collected with a six-net MOCNESS trawl towed at an average speed of ca. 2 knots through the center of Port Foster (Fig. 1). Each net had a 10-m² mouth opening with 4-mm circular mesh in the

Table 1
Water column characteristics in the center of Port Foster for sampling periods between March 1999 and November 2000

| Dates | Surface | | Thermal structure of water column |
| | Temperature ($^{\circ}$C) | Salinity (psu) | |
| --- | --- | --- | --- |
| 2–7 March 1999 | 1.6 | 34.0 | Steady decline to 1.4$^{\circ}$C at 45 m then accelerated decline to $-1.6^{\circ}$C at 150 m. Thermocline 50–100 m |
| 3–9 November 1999 | $-1.0$ | 33.6 | Steady decline to $-1.6^{\circ}$C at 150 m |
| 11–22 February 2000 | 2.5 | 33.9 | Steady decline to $-1.1^{\circ}$C at 150 m |
| 23 May—2 June 2000 | 0.3 | 34.0 | Isothermal to 110 m then rapid decline to $-0.5^{\circ}$C at 150 m. Thermocline 110–150 m |
| 21–26 November 2000 | 0.5 | 34.0 | Rapid decline to $-0.8^{\circ}$C at 30 m then isothermal to 150 m. Thermocline 0–30 m |

body and 505-μm mesh cod ends (Wiebe et al., 1985). Sampling periods lasted 30 minutes, with six sampling periods in a canonical day, flanking local noon and local midnight: 1100–1130, 1200–1230, 1300–1330, 2300–2330, 0000–0030, and 0100–0130 h. Each sample covered a single 50 m depth stratum: 0–50, 50–100 or 100–150 m. Typically, one trawl deployment was conducted in a day, and each deployment sampled a single depth stratum during three half hour sampling periods. A tow consisted of dropping the trawl to the lower limit of a depth stratum, opening a new net before sampling upward through a particular depth stratum for half an hour, then closing the sampling net, lowering the trawl to the bottom of the same depth stratum, and repeating the same sampling process twice more. On average, the region of Port Foster through which the trawls were conducted had a bottom depth of 155–160 m.

After retrieval of the trawl, samples were sorted on ice to lowest identifiable taxon, counted, and transported on ice to a station that had been set up on Deception Island. This station was sheltered from the wind and equipped with a portable generator that provided power for fluorescent lights and an analytical balance. Sorted samples were blotted dry and weighed wet to the nearest 0.01 g. Wet weights were not determined for gelatinous zooplankton such as salps and ctenophores. Instead, displacement volume was measured to the nearest 0.1 ml using a graduated cylinder. After mass and displacement volume measurements were completed, all samples were returned to the ship for preservation in 3.7% buffered formalin.

In the case of crustaceans, particularly *Euphausia* species, total length also was measured for up to 50 individuals from each sample. Displacement volumes were converted to wet weights, assuming a conversion of 1.0 g ml$^{-1}$. For taxa that were extremely abundant, not all individuals were counted. Instead, 50 haphazardly selected individuals were counted and weighed or evaluated for displacement volume. Weight or displacement volume measurements also were made on the remaining, uncounted individuals, and the total number of individuals in the sample then was estimated for each individual taxon.

To compare biomass among taxa with strikingly different body composition (e.g., krill vs. ctenophores), we estimated dry weight using conversion factors based on empirical measurements and published by Lancraft et al. (1989, 1991). Wet weights were converted to dry weights using ratios of 3.66 for *Euphausia crystallorophias* and *E. superba*, 3.40 for mysids (based on *Thysanoessa macrura*), 10.32 for ctenophores (based on *Callianira antarctica*), and 6.65 for mixed micronekton/macrozooplankton.

During May and November 2000, many of the samples were very large, and there was insufficient time to sort each sample completely. In such situations, a subsample (typically 3–4 l) of the sample was sorted completely and processed as described previously. The remainder of the collection was measured volumetrically but not sorted;
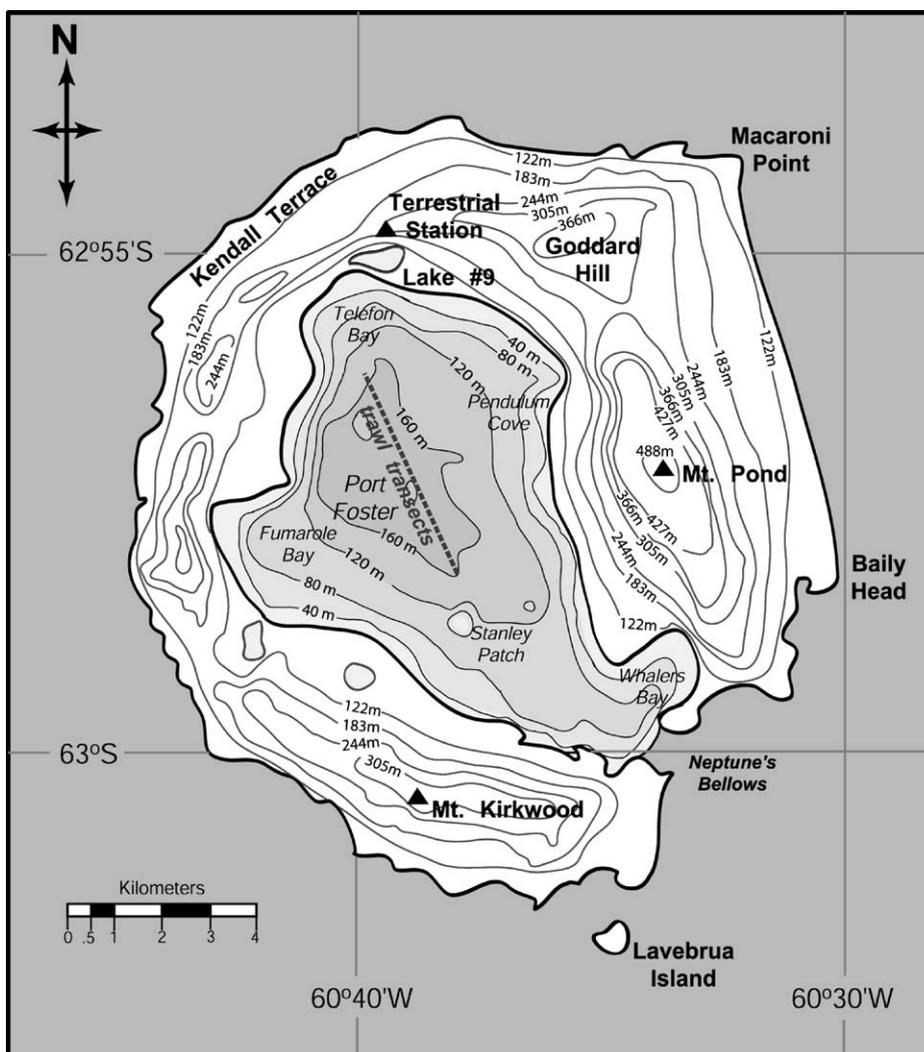
Fig. 1. Chart showing Deception Island and general locations of MOCNESS trawls through the central portion of Port Foster.

relative proportions of taxa in the sorted sub-sample were considered to be representative of the entire sample, and total abundances were estimated accordingly.

Copepods were collected in several of the samples, particularly during May 2000. However, opinions vary regarding the efficiency with which 4.0-mm mesh collects copepods (e.g., Hubold et al., 1988; Hosie et al., 1997). Because of the uncertainty associated with sampling bias, copepods were not included in this study. In general, copepods did not constitute a substantial fraction

of the fauna collected in this study, although it should be pointed out that the biomass of small copepods ($< 500 \mu m$) may be substantial (Cabal et al., 2002), and this size class likely was not sampled representatively by the MOCNESS trawl used in this study.

## 2.2. Statistical analysis

Estimates of abundance and biomass were compared between times of collection (day or night) within a single depth stratum and cruise

using a Mann–Whitney *U*-test. A Kruskal-Wallis non-parametric ANOVA was used to test for differences in biomass among cruises at a given depth and time (day or night). If significance was established by the Kruskal-Wallis test, an a posteriori Mann–Whitney *U*-test was used to determine where statistical significance occurred among the samples (Zar, 1999).

## 3. Results

### 3.1. Environmental characteristics

The structure of the water column varied substantially among cruises. Surface temperatures in March 1999 and 2000 were relatively warm, 1.6°C and 2.5°C, respectively (Table 1). A sharp thermocline was present in March 1999, May 2000 and November 2000; however, the depth of the thermocline varied from less than 0–30 m (November 2000) to 50–100 m (March 1999) to greater than 100 m (May 2000). No distinct thermocline was apparent in February 2000, although water temperature declined markedly from the surface to just above the sea floor. The water column in November 1999 was nearly isothermal, varying by only 0.5°C from the surface to 150 m depth (Table 1; Sturz et al., 2003).

Surface phytoplankton samples revealed elevated concentrations of chlorophyll *a* during February and November 2000 (Sturz et al., 2003). The phytoplankton assemblage during these bloom events was dominated by large chain-forming diatoms, particularly *Thalassiosira* spp. (February 2000, November 2000) and *Rhizosolenia* spp. (February 2000). By contrast, chlorophyll *a* concentrations in November 1999 and May 2000 were lower by two orders of magnitude. During these non-bloom periods, the phytoplankton community consisted mainly of solitary diatoms, primarily *Coscinodiscus* spp., with smaller numbers of chain-forming species.

### 3.2. Biomass

Biomass values for each taxon from each net tow were converted to dry weight and integrated over the upper 150 m of the water-column for each 30-min time period (e.g. 1100–1130, 1200–1230, etc.) on each cruise. Integrated water-column dry weight was consistently lower during the day than at night and significantly lower (Mann–Whitney *U*-test, $p < 0.05$) during all sampling periods except May 2000. The day-night discrepancy was most pronounced in November 1999, when the night-time mean ($\pm$ standard error) integrated dry weight was $24.8 \pm 5.50$ g m$^{-2}$, compared to $1.32 \pm 0.61$ g m$^{-2}$ during the day (Table 2, Fig. 2).

Integrated water-column dry weight also varied among sampling events in Port Foster, especially during the day. The highest daytime integrated dry-weight values were measured during 2000, with values exceeding 15 g m$^{-2}$ (Table 2, Fig. 2). By contrast, daytime integrated dry weight values from 1999 never exceeded 10 g m$^{-2}$. Differences in integrated dry weight were not statistically significant among sampling periods (Kruskal-Wallis ANOVA, $p > 0.05$; Fig. 2).

Krill (*Euphausia crystallorophias* and *E. superba*) constituted a major component of the epipelagic community in Port Foster during 1999 and 2000. These two species plus one or more cydippid ctenophore species, tentatively identified as belonging to the genus *Callianira* (G. Matsumoto, personal communication), made up >95% of the macrozooplankton/micronekton biomass during all five sampling events. Integrated night-time water-column biomass of *E. crystallorophias* peaked at $93.7 \pm 15.2$ g m$^{-2}$ in February 2000 then declined to $5.96 \pm 0.32$ g m$^{-2}$ in November 2000. *E. superba* exhibited a somewhat different temporal pattern, with a maximum night-time biomass of $58.8 \pm 6.54$ g m$^{-2}$ in November 2000, up from a minimum of $9.89 \pm 3.13$ g m$^{-2}$ in November 1999. *Callianira* spp. were virtually absent through most of 1999 but increased dramatically in abundance during 2000, reaching a maximum night-time integrated biomass of $102 \pm 10.0$ g m$^{-2}$ in November 2000. Integrated night-time biomass differences were significant among sampling periods for *E. crystallorophias* ($p = 0.037$) and *Callianira* spp. ($p = 0.021$) but not for *E. superba* ($p = 0.051$).

The mass of individual krill also was evaluated among sampling periods as a possible factor contributing to temporal variation in biomass.

Table 2

Estimates of biomass and dry weight for total macrozooplankton/micronekton and the dominant faunal taxa in Port Foster between March 1999 and November 2000

| | Mar. 1999 | | Nov. 1999 | | Feb. 2000 | | May 2000 | | Nov. 2000 | |
|---|---|---|---|---|---|---|---|---|---|---|
| | Day | Night | Day | Night | Day | Night | Day | Night | Day | Night |
| **Biomass** | | | | | | | | | | |
| 0–50 m | 162±116 | 283±67.6 | 10.2±6.30 | 216±112 | 59.0±7.14 | 458±124 | 0.90±0.16 | 80.0±72.3 | 30.7±1.81 | 325±55.1 |
| 50–100 m | 23.1±15.9 | 340±33.1 | 5.69±3.11 | 298±62.4 | 383±72.5 | 261±47.8 | 35.6±10.1 | 26.3±15.9 | 400±56.1 | 160±10.4 |
| 100–150 m | 71.6 | 28.3±8.00 | 16.6±8.17 | 89.3±40.6 | 64.0±9.42 | 225±54.9 | 919±91.2 | 947±57.0 | 553±27.2 | 645±66.8 |
| 0–150 m | 35.0±17.5 | 97.8±10.9 | 4.88±2.22 | 90.5±20.1 | 75.9±11.1 | 142±17.5 | 143±12.2 | 158±15.3 | 148±5.92 | 169±15.7 |
| **Dry Weight** | | | | | | | | | | |
| 0–50 m | 44.1±31.7 | 77.3±18.5 | 2.78±1.72 | 59.0±30.5 | 15.6±2.01 | 125±33.8 | 0.12±0.02 | 15.6±14.7 | 6.34±1.03 | 86.0±14.5 |
| 50–100 m | 6.05±2.56 | 93.3±8.99 | 1.53±0.86 | 81.6±17.2 | 105±19.8 | 71.4±13.1 | 6.16±2.17 | 5.03±2.98 | 43.5±6.10 | 28.7±2.20 |
| 100–150 m | 18.2±6.09 | 6.68±2.18 | 4.49±2.23 | 24.6±11.1 | 17.3±2.27 | 60.3±13.9 | 167±5.94 | 166±32.9 | 59.8±2.56 | 72.1±6.35 |
| 0–150 m | 9.34±4.74 | 26.6±2.95 | 1.32±0.61 | 24.8±5.50 | 20.6±3.05 | 38.4±4.96 | 26.0±0.82 | 27.9±4.35 | 16.4±0.74 | 28.0±2.67 |
| *E. crystallorophias* | | | | | | | | | | |
| 0–50 m | 0±0 | 233±64.9 | 2.42±2.32 | 181±94.4 | 53.4±7.68 | 272±79.6 | 0.01±0.02 | 27.5±27.2 | 5.60±2.01 | 38.5±2.25 |
| 50–100 m | 21.0±9.6 | 252±51.9 | 5.41±3.15 | 255±51.6 | 303±73.1 | 181±43.6 | 15.1±8.98 | 6.69±4.00 | 8.52±0.11 | 0.83±0.13 |
| 100–150 m | 29.4 | 5.65±2.80 | 14.3±7.79 | 74.3±37.1 | 10.6±2.02 | 172±37.1 | 215±47.4 | 277±76.5 | 1.43±0.22 | 0.42±0.13 |
| 0–150 m | 6.09±2.66 | 73.6±6.96 | 3.31±1.96 | 76.5±16.9 | 55.0±12.3 | 93.7±15.2 | 34.6±7.35 | 46.7±10.5 | 2.33±0.09 | 5.96±0.56 |
| *E. superba* | | | | | | | | | | |
| 0–50 m | 160±116 | 49.3±9.16 | 7.75±7.06 | 34.7±17.4 | 1.60±0.33 | 182±58.1 | 0±0 | 15.7±15.4 | 12.6±5.90 | 270±50.6 |
| 50–100 m | 0.01±0.01 | 70.1±24.4 | 0.04±0.03 | 30.0±6.96 | 77.6±0.73 | 77.0±4.33 | 0.03±0.03 | 6.69±4.00 | 13.4±5.96 | 70.1±7.96 |
| 100–150 m | 33.5 | 3.00±1.60 | 0.69±0.35 | 1.26±0.64 | 37.0±6.11 | 34.1±10.4 | 227±59.6 | 134±90.9 | 27.4±2.78 | 52.3±2.09 |
| 0–150 m | 27.3±18.2 | 18.4±4.55 | 1.27±1.06 | 9.89±3.13 | 17.4±1.01 | 43.9±7.43 | 34.0±8.94 | 23.4±12.2 | 8.01±1.10 | 58.8±11.3 |
| *Callianira* spp. | | | | | | | | | | |
| 0–50 m | 0±0 | 0±0 | 0±0 | 0±0 | 0±0 | 0±0 | 0.35±0.09 | 33.3±27.2 | 9.68±2.67 | 13.9±8.44 |
| 50–100 m | 0±0 | 0±0 | 0±0 | 0±0 | 0.18±0.18 | 0±0 | 19.7±10.6 | 10.7±7.61 | 369±51.3 | 75.6±8.81 |
| 100–150 m | 4.78 | 7.04±5.37 | 0±0 | 0±0 | 1.88±1.68 | 0.76±0.44 | 471±118 | 521±144 | 515±27.3 | 590±67.9 |
| 0–150 m | 0.48±0.28 | 1.06±0.81 | 0±0 | 0±0 | 0.31±0.28 | 0.11±0.07 | 73.7±17.4 | 84.7±24.9 | 134±4.82 | 102±17.3 |

Values are presented as mean ± standard error for three tows in each depth stratum and time period, except for 100–150 m during the day in March 1999, when only two tows were carried out. Units are g wet weight $1000\,m^{-3}$ or g dry weight $1000\,m^{-3}$ for estimates within 50 m depth strata and g wet weight $m^{-2}$ or g dry weight $m^{-2}$ for integrated water column estimates (0–150 m).

The smallest individuals of both *Euphausia crystallorophias* and *E. superba* were collected during November 1999, while the largest individuals of both species were obtained in May 2000 (Fig. 3). This temporal variation was statistically significant (Kruskal-Wallis ANOVA, $p < 0.001$) for both species. Given the large size and substantial mobility of krill, a diel difference in the body size of individuals captured by the MOCNESS trawl would not have been surprising. However, no significant day-night differences in body mass were detected for either species (Mann–Whitney *U*-test, $p > 0.05$), except for *E. superba* collected in November 2000 ($p = 0.015$).

During May and November 2000 a large number of juvenile *Euphausia crystallorophias* were collected. These animals were substantially smaller than the adults (May 2000: mean ± standard error of total length $= 10.2 \pm 0.03$ mm, $N = 799$ measurements for juveniles vs. $35.0 \pm 0.09$ mm, $N = 637$ measurements for adults; November 2000: $11.4 \pm 0.04$ mm, $N = 899$ measurements for juveniles vs. $34.0 \pm 0.14$ mm, $N = 816$ measurements for adults; Fig. 4) and were not present in samples between March 1999 and February 2000. The increase in mean total body length between May and November 2000 was statistically significant (Mann–Whitney *U*-test, $p < 0.001$).

Krill body length displayed temporal trends in both *Euphausia crystallorophias* and *E. superba*. Mean body length of *E. crystallorophias* shifted from $34.0 \pm 0.12$ mm in March 1999 to $28.2 \pm 0.09$ mm in November 1999, and a similar albeit much less pronounced change was observed in 2000, with total length increasing between
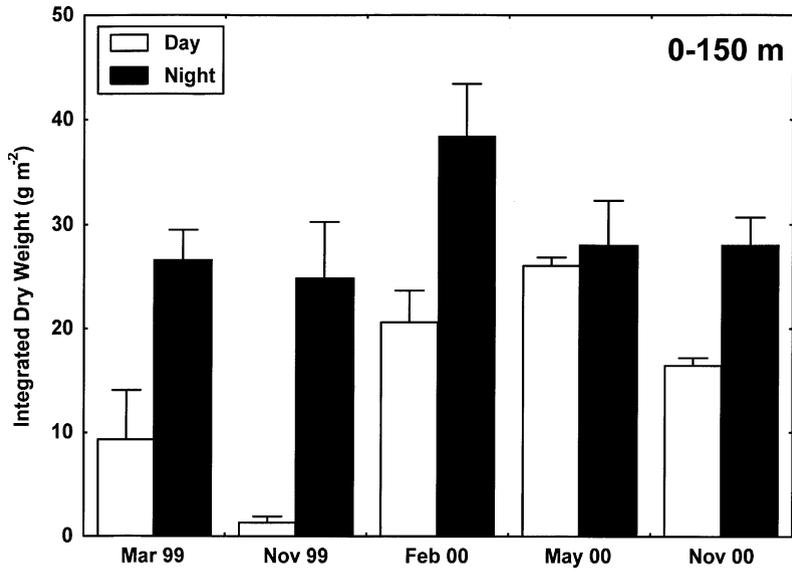
Fig. 2. Mean ($\pm$1 standard error) biomass of macrozooplankton/micronekton integrated over the upper 150 m of the water-column in Port Foster. Variations in integrated dry weight among cruises are not statistically significant.
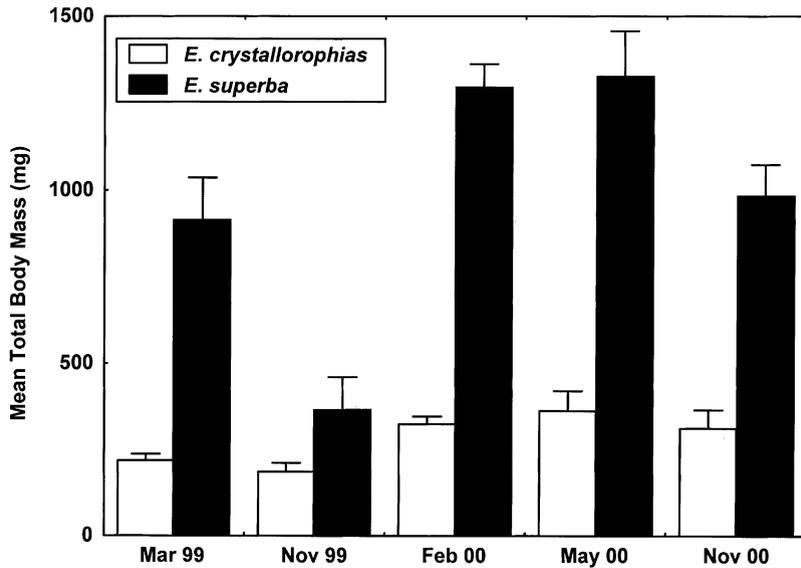


Fig. 3. Mean total body mass ($\pm$1 standard error) of *Euphausia crystallorophias* and *E. superba* collected in Port Foster. Mean body mass varied significantly among sampling periods for both species (Kruskal-Wallis ANOVA, $p < 0.001$ for both species).

February and May then shrinking in November (Fig. 4). This temporal pattern is mirrored in *E. superba*, with mean body length decreasing dramatically from $50.5 \pm 0.16$ mm in March 1999 to $34.6 \pm 0.24$ mm in November 1999 (Fig. 5). A similar but far less severe decline in body size apparently occurred during the winter of 2000. No distinct recruitment events were observed for
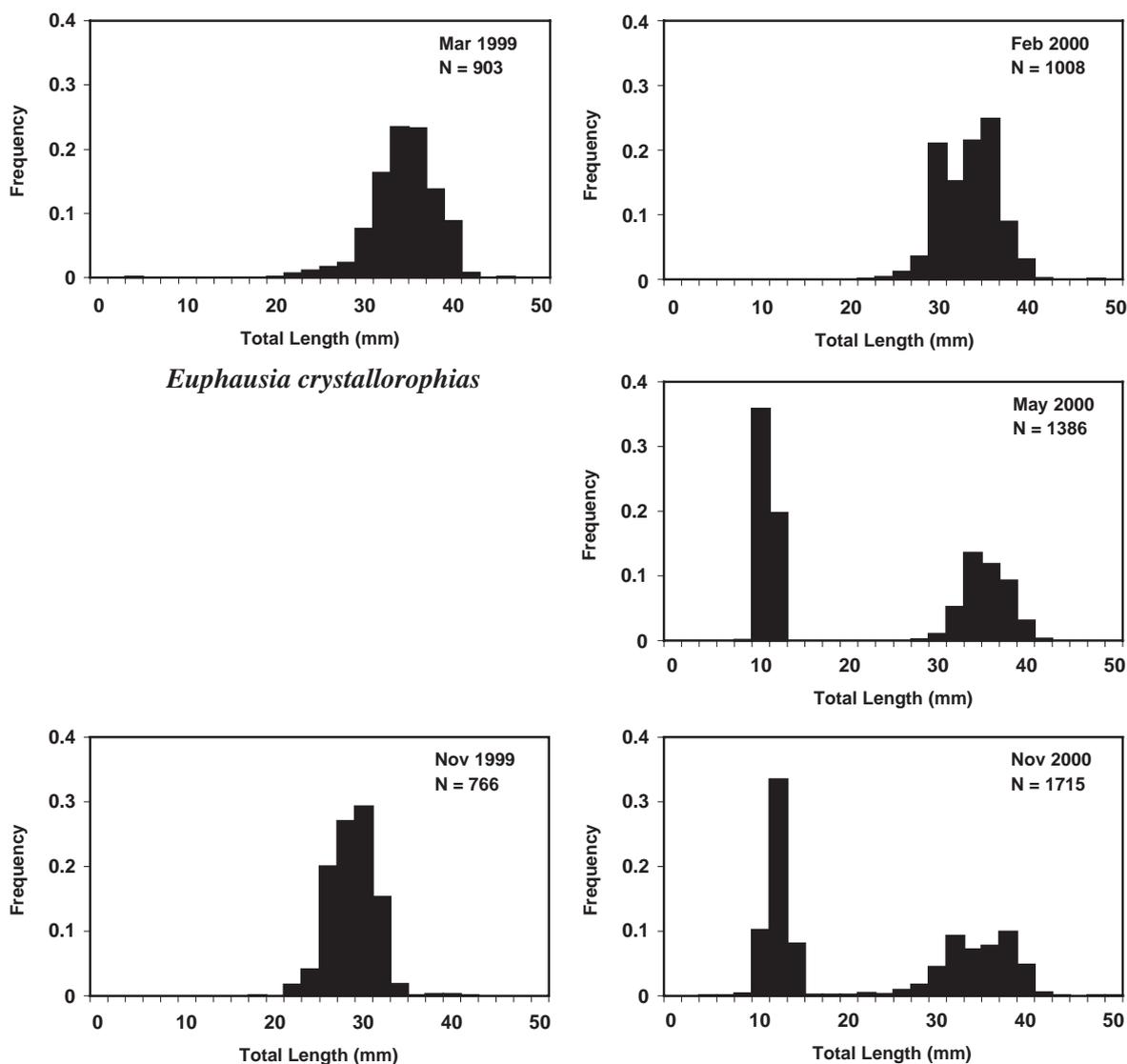
*Euphausia crystallorophias*

Fig. 4. Size distributions of *Euphausia crystallorophias* collected in Port Foster between March 1999 and November 2000. Individuals from the smaller size class were identified as juveniles (A. Townsend, personal communication) and were absent from collections made between March 1999 and February 2000.

*E. superba* during the time period covered by the Erupt sampling program.

The displacement volume of individual ctenophores also varied with time. Individuals collected during May 2000 averaged $3.54 \pm 0.50$ ml in volume (mean ± standard error), compared to $18.3 \pm 0.89$ ml during November 2000. This difference was statistically significant (Mann–Whitney $U$-test, $p < 0.001$). It is not clear whether this size difference reflects a change in body size between winter and summer or a shift from a smaller to a larger species of *Callianira*.

### 3.3. Species composition

The majority of the macrozooplankton/micronekton assemblage in Port Foster during the time period covered by this study consisted of the three
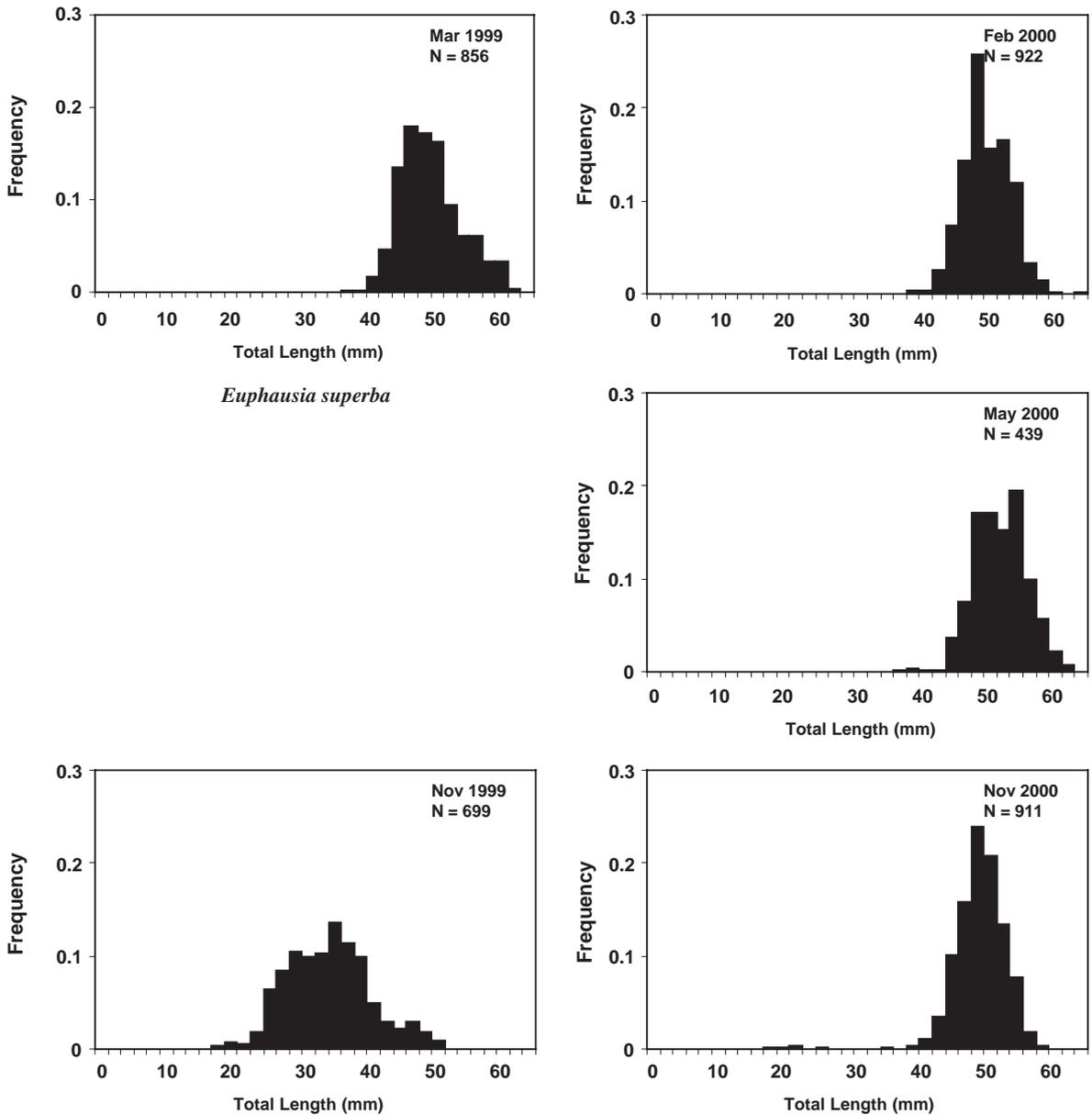
Fig. 5. Size distributions of *Euphausia superba* collected in Port Foster between March 1999 and November 2000. Note shift in population mode toward smaller animals in November 1999 compared to March 1999. A similar but less pronounced shift was apparent in 2000.

taxa mentioned previously: *Callianira* spp., *Euphausia crystallorophias*, and *E. superba*, as well as two unidentified species of Mysidacea. These four taxa made up 98.6–99.9% of the macrozooplankton/micronekton integrated dry weight at night

(Table 3). The other pelagic fauna identified from these samples included hyperiid and lysianassoid amphipods, pelagic isopods, larval and juvenile fishes, pelagic polychaetes, chaetognaths, pteropods, salps and siphonophores. Species richness
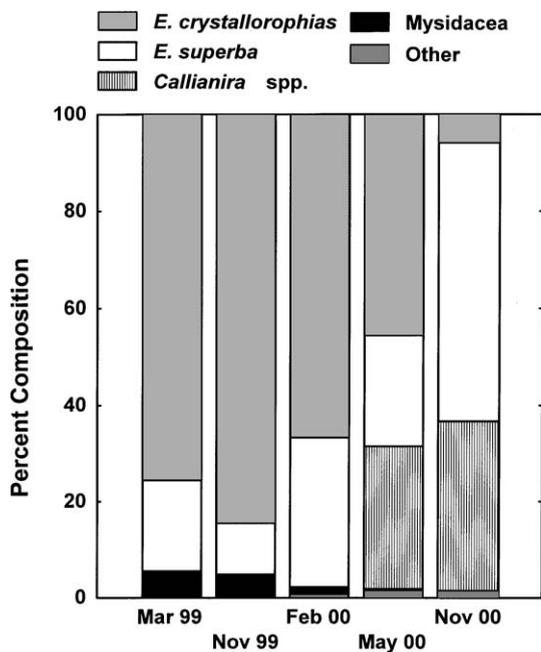
Table 3
Percent composition of the macrozooplankton/micronekton community in Port Foster based on integrated water column dry weight between March 1999 and November 2000

| TAXON | Mar. 1999 | Nov. 1999 | Feb. 2000 | May 2000 | Nov. 2000 |
|---|---|---|---|---|---|
| *Euphausia crystallorophias* | 75.7% | 84.4% | 66.6% | 45.7% | 5.82% |
| *Euphausia superba* | 18.9% | 10.9% | 31.2% | 22.9% | 57.4% |
| *Callianira* spp. | 0.39% | 0.00% | 0.03% | 29.4% | 35.2% |
| Mysidacea spp. | 4.92% | 4.63% | 1.34% | 0.66% | 0.20% |
| Other | 0.17% | 0.09% | 0.84% | 1.36% | 1.40% |

Data presented are from night trawls only.



Fig. 6. Percent composition of the macrozooplankton/micronekton community in Port Foster based on integrated water-column dry weight between March 1999 and November 2000. Data presented are from night trawls only.

varied over time: 16 and 17 species were identified from the samples collected in March and November 1999, respectively, compared to 29 and 25 species in May and November 2000.

Temporal variability in species composition of the macrozooplankton/micronekton was readily apparent during the period covered by this study. In 1999 and early 2000, krill dominated the community, making up 94.5–97.8% of the integrated dry weight at night (Table 3, Fig. 6). The dominant species was *Euphausia crystallorophias*, which comprised 66.6–84.4% of the total community dry weight, reaching a peak in November 1999. Its congener, *E. superba*, was less abundant, ranging from 10.9–31.2% of community dry weight through February 2000. Mysids also were abundant during 1999 and constituted 4.63–4.92% of community biomass (Table 3).

Community composition changed dramatically in early 2000. Between February and May, the population of cydippid ctenophores (*Callianira* spp.) increased from 0.03% to 29.4% of integrated night-time dry weight, rising still higher to 35.2% in November 2000. This dramatic increase in the biomass of ctenophores was accompanied by sharp declines in the proportion of *E. crystallorophias* and mysids and a striking increase in the relative contribution of *E. superba*. The contribution of mysids dropped to 0.20% of total integrated night-time dry weight in November 2000, and *E. crystallorophias*, which constituted 84.4% of integrated dry weight in November 1999, amounted to just 5.82% in November 2000. The proportion of *Euphausia superba* increased from 10.9% in November 1999 to 31.2% in February 2000 and 57.4% in November 2000 (Table 3).

### 3.4. Vertical distribution

The vertical distribution of macrozooplankton/micronekton biomass in Port Foster was not homogeneous during this study. A fairly even distribution of dry weight among the three strata sampled was observed only once, during night tows in February 2000 (Fig. 7). In contrast, the most extreme example of a vertically skewed
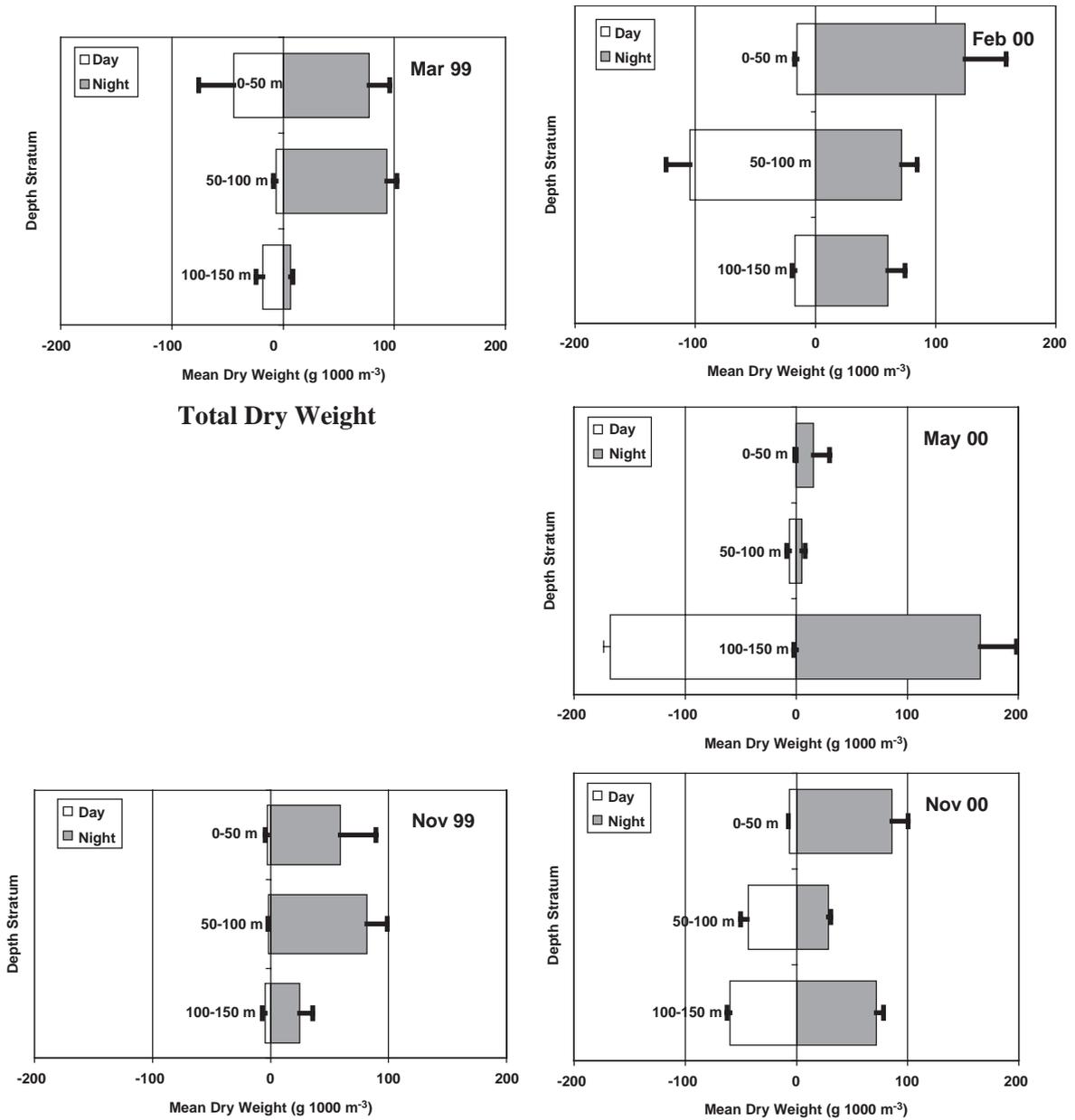
Fig. 7. Total dry weight of macrozooplankton and micronekton in each of three 50 m depth strata. Values are means of three net tows for each stratum, and error bars represent one standard error.

biomass distribution was apparent during the day in May 2000, when over 96% of the collected biomass was located 100–150 m below the surface. The skewed depth distribution in May 2000 was due in large part to the presence of high densities of *Callianira* between 100 and 150 m (Fig. 8).

Distinct day-night differences in the vertical distribution of macrozooplankton and micronekton were evident in all sampling periods.
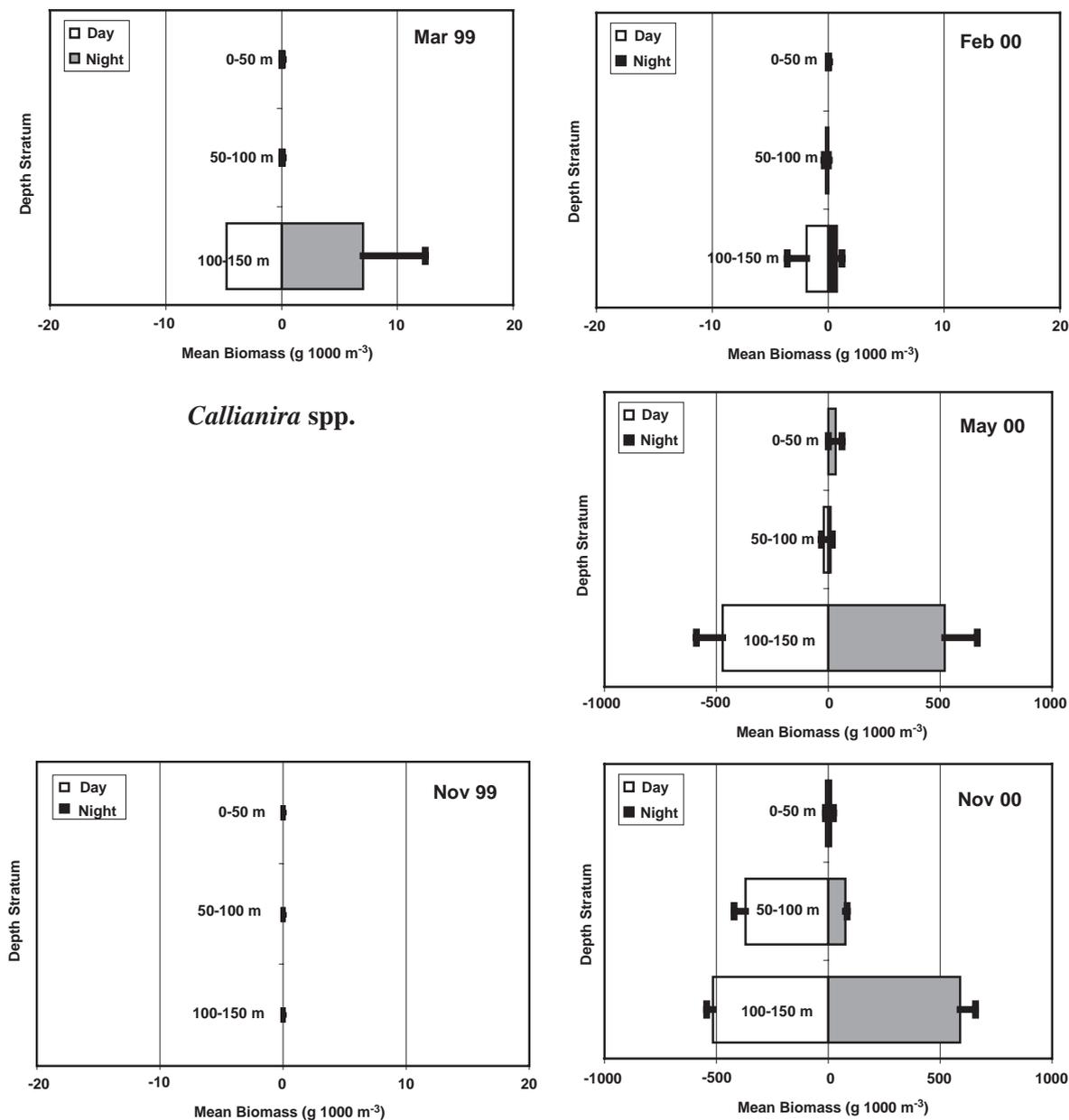
Fig. 8. Biomass of *Callianira* spp. in each of three 50 m depth strata. Values are means of three net tows for each stratum, and error bars represent one standard error. Note differences in horizontal axis scales among time periods.

Generally, a greater proportion of the community was present in surface waters at night compared to the daytime (Fig. 7). Diel differences in the vertical distribution of macrozooplankton and micronekton were most evident in *Euphausia crystalloro-* *phias* (Fig. 9) and *E. superba* (Fig. 10). The biomass distribution of both of these species apparently shifted toward surface waters at night. However, integrated daytime biomass of *Euphausia* species was consistently lower than night totals,
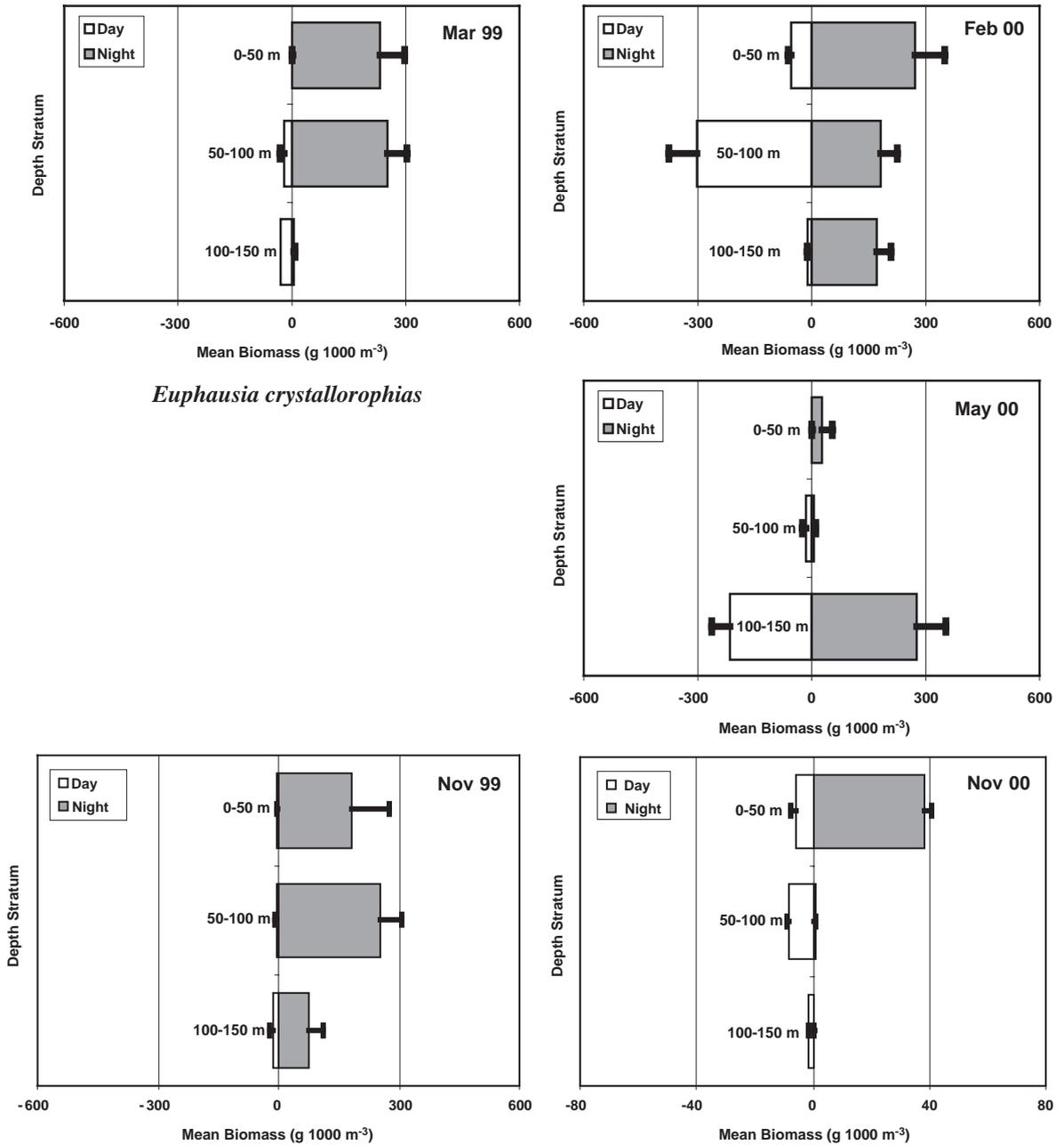
Fig. 9. Biomass of *Euphausia crystallorophias* in each of three 50 m depth strata. Values are means of three net tows for each stratum, and error bars represent one standard error. Note differences in horizontal axis scales among time periods.

perhaps indicating greater net avoidance by both species during the day. Diel differences in depth distribution were less evident in both species of *Euphausia* during May 2000 and never

were apparent in *Callianira*, which were far more abundant below 50 m than in surface waters during all times when they were collected (Fig. 8).
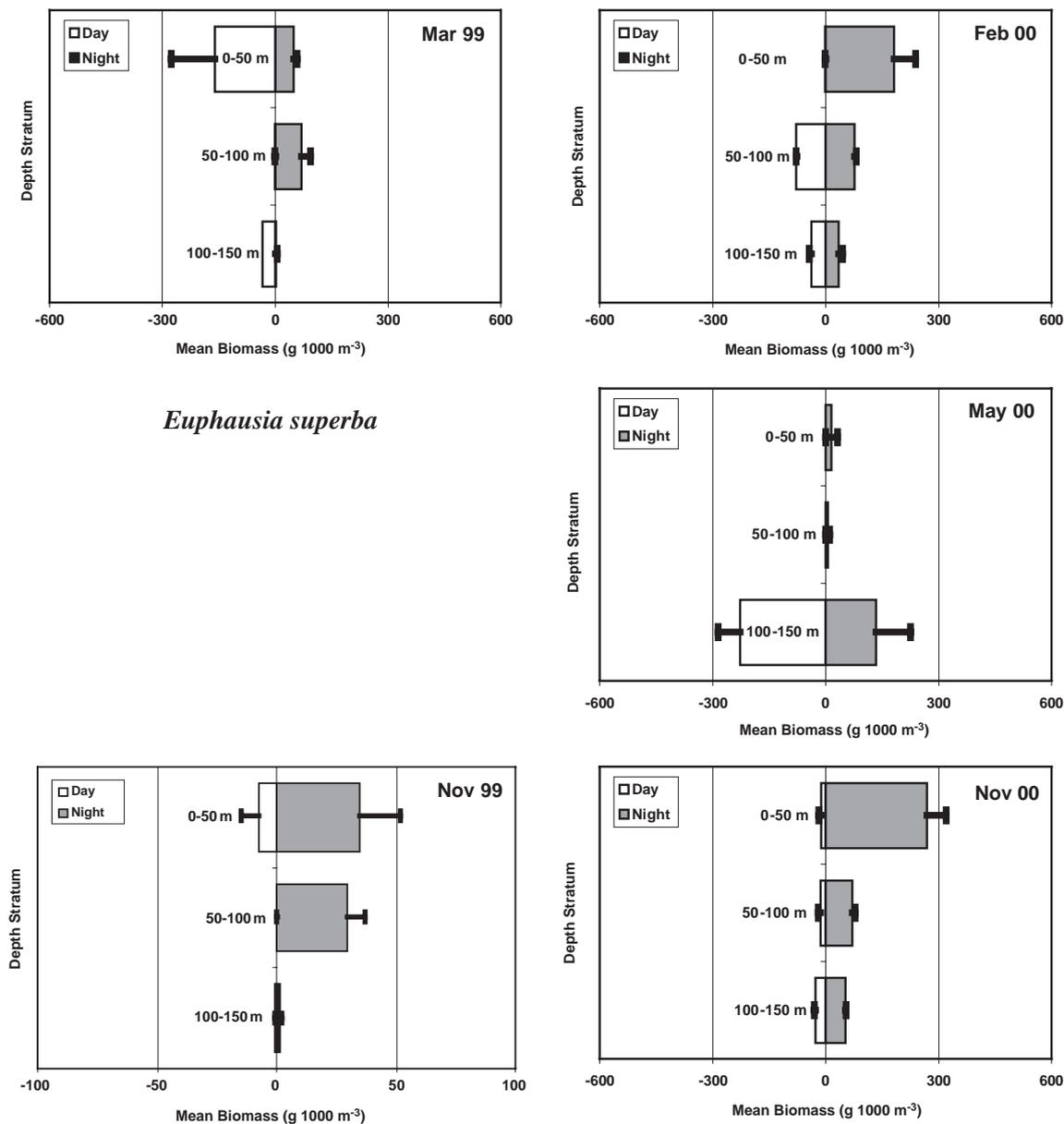
Fig. 10. Biomass of *Euphausia superba* in each of three 50 m depth strata. Values are means of three net tows for each stratum, and error bars represent one standard error. Note differences in horizontal axis scales among time periods.

## 4. Discussion

### 4.1. Biomass

Integrated water-column dry weight varied substantially within and among the five time periods sampled in this study. Diel differences within a sampling period (Fig. 2, Table 2) may have been the result of net avoidance, stimulated by visual or mechanical cues from the ship or the MOCNESS trawl system (Wiebe et al., 1982; Everson and Bone, 1986; Everson, 1987; O'Brien,

1987). Diel differences were most pronounced between March 1999 and February 2000, when the pelagic community was dominated by euphausiids (Figs. 2 and 6), and were far less apparent during May and November 2000, when ctenophores comprised ca. 30% or more of integrated dry weight. This pattern is consistent with numerous published observations of net avoidance, schooling behavior and escape responses by *Euphausia crystallorophias* (Everson, 1987; O'Brien, 1987; Pakhomov and Perissinotto, 1996) and *E. superba* (Hamner et al., 1983; Hamner, 1984; O'Brien, 1987; Hamner and Hamner, 2000).

Another possible explanation for the pronounced day-night difference in krill biomass is the occupation by krill of different regions of Port Foster on a diel basis. The aggregation of *Euphausia superba* near the sea floor in relatively deep water has been described (Gutt and Siegel, 1994), and it is conceivable that the distribution of *E. crystallorophias* and *E. superba* extended to the sea floor in Port Foster during the day. Although our sampling program did not include the bottom 5–10 m of the water column, near-bottom photographs were taken using a towed camera sled (Cranmer et al., 2003). No large aggregations of krill were observed in these photos; however, these transects were conducted along the center of Port Foster, and krill may have aggregated in other regions, e.g., along the sides of the caldera.

For the macrozooplankton/micronekton community in Port Foster, no temporal trend in night-time integrated dry weight was apparent (Fig. 2). The absence of a trend in community biomass over time is surprising, especially considering the pronounced seasonal and interannual changes in community composition (Fig. 3, Table 3) and food availability (Sturz et al., 2003), as well as the abundance of other components of the pelagic community in Port Foster (King and LaCasella, 2003). Conceivably, the lack of a temporal trend in community biomass could reflect the impact of predation or some other top-down regulatory process. Predation pressure on macrozooplankton and micronekton likely varied with time as a result of seasonal changes in the local populations of predators, including chinstrap penguins, whose abundance increased during periods of elevated

production (Kendall et al., 2003) that could have produced spring and summer biomass peaks.

Based on night tows, estimated biomass in the upper 150 m of Port Foster was comparable to values reported elsewhere in the Southern Ocean. During krill-dominated periods, night-time biomass ranged from 28.3 to 458 g wet weight $1000\,m^{-3}$ within 50 m depth strata and 90.5–142 g wet weight $m^{-2}$ integrated over the upper 150 m of the water column (Table 2). By comparison, Hunt et al. (2001) reported biomass values of approximately 50–60 g wet weight $1000\,m^{-3}$ for copepod- and krill-dominated communities in the upper 200–300 m of the water column near the Prince Edward Islands. Published estimates of pelagic biomass from open water in the Weddell Sea have ranged from 28.2 g wet weight $1000\,m^{-3}$ for a euphausiid-dominated assemblage in the upper 1000 m (Lancraft et al., 1989) to 482 g wet weight $1000\,m^{-3}$ for a community dominated by krill and salps in the surface 100 m (Fisher et al., 2003), with a number of estimates in between (Atkinson and Peck, 1988; Siegel et al., 1992).

Communities dominated by gelatinous zooplankton tend to exhibit higher biomass values compared to those in which crustaceans make up the bulk of the assemblage (Williams et al., 1986). In this study, night-time biomass ranged from 26.3 to 947 g wet weight $1000\,m^{-3}$ within 50 m depth strata and 158–169 g wet weight $m^{-2}$ integrated over the upper 150 m of the water-column during May and November 2000 when ctenophores comprised ca. 30% or more of the pelagic zooplankton community on a dry weight basis (Tables 2 and 3). Integrated water-column biomass estimates by Voronina et al. (1994) in the upper 200 m near the tip of the Antarctic Peninsula ranged from 58.5 to 498.1 g wet weight $m^{-2}$ for communities composed of 65% and 96% salps, respectively.

Biomass estimates for *Euphausia crystallorophias* also were within the range of published values. During 1999 and early 2000, when this species comprised 66.6–84.4% of total pelagic dry weight, night-time estimates ranged from 5.65 to 272 g wet weight $1000\,m^{-3}$ within 50 m depth strata and 73.6 to 93.7 g wet weight $m^{-2}$ for the upper 150 m of the water column (Table 2).

Assuming a mean wet weight of 240 mg per individual between March 1999 and February 2000 (Fig. 2), these biomass estimates correspond to approximately 23.5–1130 individuals $1000\,m^{-3}$ for 50 m strata or 307–390 individuals $m^{-2}$ for the upper 150 m. Everson (1987) surveyed *E. crystallorophias* in Port Foster during March 1985 at a time when the pelagic community was composed almost entirely of this species. His reported abundances of 4.69–23.50 individuals $m^{-3}$ in the upper 45–80 m of the water column are considerably higher than those obtained in this study. High abundances of *E. crystallorophias* also were measured by Pakhomov and Perissinotto (1996) in the upper 100–400 m of the Cooperation, Cosmonaut and Lazarev Seas. However, the majority of their net tows yielded biomass estimates similar to those obtained in Port Foster during 1999–2000. In closer proximity to Deception Island, Nordhausen (1994) collected *E. crystallorophias* in the Gerlache Strait at densities up to 83 individuals $m^{-2}$ over the upper 290 m of the water column in an area dominated by *E. superba*.

*Euphausia superba* biomass in Port Foster was similar to the range of values reported for coastal waters around Antarctica. Values of 0.2–54.5 g wet weight $m^{-2}$ have been recorded for the upper 100–250 m of the water column (Lancraft et al., 1989; multiple studies summarized in Voronina, 1998, and Siegel, 2000b) with towed nets similar to the MOCNESS trawl used in this study. These numbers correspond closely to the range of 1.27–58.8 g wet weight $m^{-2}$ reported here (Table 2). Excluding November 1999 when *E. superba* were much smaller than during the other four time periods (Fig. 3; Cullen et al., 2003), the mean weight for an individual of this species was approximately 1130 mg. Using this value for March 1999 and the three sampling periods in 2000, our biomass estimates are equivalent to a maximum density of roughly 239 individuals $1000\,m^{-3}$ for 50 m strata or 52.0 individuals $m^{-2}$ for the upper 150 m. By comparison, Loeb et al. (1997) described annual mean densities of 4.8–510.9 individuals $m^{-3}$ over 15 field seasons in the waters near Elephant Island, while Nordhausen (1994) reported much higher maximum abun-

dances of 810 individuals $m^{-2}$ in the upper 290 m of the Gerlache Strait.

Body size in *Euphausia crystallorophias* and *E. superba* varied substantially in Port Foster between March 1999 and November 2000. Adult krill collected during November 1999 were significantly smaller than in any other season (Fig. 3), mirroring the temporal trend in integrated dry weight (Fig. 2). Biochemical data for *E. superba* between November 1999 and November 2000 reflected a similar pattern and indicated that *E. superba* collected in November 1999 showed the effects of food deprivation during the previous winter (Cullen et al., 2003). Krill from November 2000 were much larger than those from the previous year, suggesting that the winter of 2000 may have been less severe in terms of food availability than 1999. This interpretation also is supported by the patterns in krill total length (Figs. 4 and 5), which illustrate a greater decline in body size during the winter of 1999 compared to 2000.

The presence of juvenile *Euphausia crystallorophias* in Port Foster during May and November 2000 was consistent with results from previous studies. Siegel and Harm (1996) reported a well-defined population of juvenile *E. crystallorophias* with a modal length of 15 mm in the shelf region of the Bellingshausen Sea. Brinton and Townsend (1991) studied the development of *E. crystallorophias* in the Bransfield Strait region, including Deception Island, and reported spawning by *E. crystallorophias*, likely beginning in November. They collected juveniles 11–17 mm in length during December 1986 but did not sample during May, following the spawning period. The absence of this size class during 1999 may reflect a reduced and potentially inadequate food supply during 1999, compared to 2000. Evidence for this interpretation comes from greatly elevated chlorophyll *a* concentrations in Port Foster during November 2000 vs. November 1999 (Sturz et al., 2003).

It is unclear whether the lack of juveniles in Port Foster reflects the status of krill populations within Port Foster, in the Bransfield Strait or both. There has been some disagreement about whether Port Foster supports a self-sustaining population of krill or acquires them via exchange

from the Bransfield Strait. Everson (1987) reported distinct differences between frequency distributions of *Euphausia crystallorophias* in Port Foster and the Bransfield Strait, and concluded that Port Foster contained an isolated population of this species. Brinton and Townsend (1991) reached a different conclusion, based on observations of slight differences between *E. crystallorophias* in samples from Deception Island and the Bransfield Strait. If Everson's (1987) conclusions are valid, then the impact of poor recruitment during 1999 may have been restricted to Port Foster. However, if there was extensive exchange of animals between Port Foster and the Bransfield Strait, then the absence of juvenile *E. crystallorophias* in 1999 samples from Port Foster may have wider-reaching implications for populations in the region of the Antarctic Peninsula.

It is unclear whether the juveniles collected from Port Foster during November 2000 represented the same cohort sampled in May 2000; however, the increase in body length between May and November 2000 suggests the growth of a cohort during the winter (Fig. 4). Overwintering has been discussed (O'Brien, 1987; Daly and Macaulay, 1991) and the scenario that permits these juveniles to survive the winter has been tied to the presence of pack ice, which was not observed consistently in Port Foster during 2000 (Smith et al., 2003b). However, the size increase in *E. crystallorophias* between May and November was statistically significant and reflected an estimated length increase of 1.38 mm or 0.0075 mm day$^{-1}$. This estimate is an order of magnitude lower than the rate of 0.070–0.075 mm day$^{-1}$ reported by Pakhomov and Perissinotto (1996); however, they assumed growth for only 180 days per year, concentrated during the period of maximum food availability. Our results suggest that juvenile krill may undergo positive growth during the winter, but the circumstances that facilitate winter growth may not be ubiquitous in the Antarctic coastal marine environment, even during mild winters.

By contrast, krill appeared to shrink substantially during 1999 (Figs. 4 and 5). Assuming the krill collected in Port Foster during March 1999 belonged to the same cohort as those collected in November 1999, estimated shrinkage

rates from mean total length measurements were 0.023 mm day$^{-1}$ for *E. crystallorophias* and 0.065 mm day$^{-1}$ for *E. superba* between March and November 1999. These rates are comparable to laboratory measurements of 0.033 mm day$^{-1}$ for starved *E. superba* (Ikeda et al., 1985) and consistent with the idea that shrinkage may be a common mechanism by which krill manipulate their energetic requirements to cope with periods of scarce food resources (summarized in Nicol, 2000).

The shrinkage hypothesis may not explain the observed changes in length distribution of krill during 1999. An alternative is that smaller individuals collected in November belonged to a different cohort than the larger krill sampled in March. In this case, the smaller November animals should correspond to age classes approximately two years younger than those collected in March (2+ vs. 4+, respectively), based on mean length at age data from a variety of sources (summarized in Pakhomov, 2000; Siegel, 2000a). March 2000 size distributions would indicate a return to 4+ year old krill; however, a mechanism by which this transition might take place is unclear and seems less plausible than shrinkage as an explanation for our observations.

## 4.2. Species composition

The species composition of the macrozooplankton/micronekton assemblage in Port Foster changed dramatically between March 1999 and November 2000 (Fig. 5, Table 3). Southern Ocean pelagic ecosystems are known to shift between communities dominated by krill, particularly *Euphausia superba*, and those consisting primarily of gelatinous zooplankton, especially the salp *Salpa thompsoni* (e.g. Loeb et al., 1997; Kawaguchi et al., 1998; Pakhomov et al., 2002; Fisher et al., 2003). Closer to land, *E. crystallorophias* tends to replace *E. superba* as the dominant euphausiid (Hubold et al., 1988; Brinton and Townsend, 1991; Nordhausen, 1994), and this was evident in Port Foster during 1999 and 2000. However, to our knowledge this is one of the only reports of an Antarctic pelagic ecosystem being dominated by ctenophores (see Williams et al., 1986).

Ctenophores have been reported in large numbers elsewhere in the Antarctic. Two net tows conducted by Voronina et al. (1994) in the Atlantic sector of the Southern Ocean at approximately 62°S, 15°W, yielded ctenophores at 27.4% (Sta. 4104) and 40.3% (Sta. 4102) of the integrated biomass from 0–200 m. In both cases, integrated biomass was relatively low (23.7 and 22.0 g wet weight m$^{-2}$, respectively), with euphausiids comprising a substantial fraction of the pelagic community and salps absent or nearly so. Biomass values for these two samples ranged from 6.49–8.86 g wet weight m$^{-2}$ from 0–200 m. Large numbers of ctenophores also were collected by Voronina et al. (1994) near the tip of the Antarctic Peninsula. In this area, the integrated ctenophore biomass between 0 and 200 m was 17.13 g wet weight m$^{-2}$; however, this sample also contained large numbers of salps, and ctenophores made up only 3.5% of the total population biomass. Williams et al. (1986) collected large numbers of ctenophores near Prydz Bay, including one rectangular midwater net (RMT) trawl that yielded 85.8% ctenophores on a biomass basis.

Coincident with the decline in *Euphausia crystallorophias* abundance in Port Foster during 2000, densities of mysids also dropped by an order of magnitude (Fig. 5, Table 3). The same trend was not displayed by *E. superba*, which made up 57.4% of the pelagic community dry weight in November 2000, higher than at any other time during this study. Adult *E. superba* are larger than both *E. crystallorophias* (Fig. 3) and the mysid species collected in Port Foster, which should render *E. superba* less susceptible to predation by carnivorous ctenophores. Members of the genus *Callianira* are known to prey on euphausiids (Hofmann et al., 2002; G. Matsumoto, personal communication), and their predatory activities may have led to the shift in community structure observed between 1999 and 2000.

### 4.3. Vertical distribution

Temporal variation in the vertical distribution of macrozooplankton and micronekton in Port Foster occurred in concert with the shift in community composition from euphausiids to ctenophores. During 1999 and February 2000, the night-time biomass mode was at 50–100 m (March and November 1999) or 0–50 m (February 2000). However, during May and November 2000, the biomass mode was between 100 and 150 m both night and day (Fig. 6). This distributional pattern was due primarily but not entirely to the presence of abundant non-migratory ctenophores below 100 m (Fig. 5) and also was reflected in the vertical distribution of the copepod *Metridia gerlachei* in Port Foster during November 2000 (King and LaCasella, 2003).

Seasonal variation in the vertical migratory behavior of macrozooplankton and micronekton at Deception Island also was evident in recordings of acoustic backscatter made with an acoustic Doppler profiler (ADP). Canonical daily averages of backscatter showed seasonal variation in the depth distribution and daily movement patterns of acoustic scatterers (Lenn et al., 2003). Distinct diel differences in the distribution of scatterers were detected during the spring and fall. However, during April-June 2000 when *Callianira* were abundant below 100 m, a scattering layer was observed in the deeper part of Port Foster throughout the day and night. This layer generated a lower backscatter amplitude than similar records from krill-dominated periods, reflecting the weaker sound-scattering properties of ctenophores compared to krill (Lenn et al., 2003).

The vertical distribution of krill also exhibited seasonal variation. Diel vertical migration was conspicuous in both *Euphausia crystallorophias* and *E. superba* in March and November 1999 and 2000, but was noticeably absent in May 2000 (Figs. 8 and 9). During May 2000, the population mode of both euphausiid species remained below 100 m both day and night, in the same depth range as *Callianira*. This consistently deep distribution of krill apparently affected the geochemistry of Port Foster. Water-column profiles from the same time period showed a decline in concentrations of dissolved oxygen and increased concentrations of ammonia below 100 m (Sturz et al., 2003). This pattern was not evident during November 2000, when *Callianira* were abundant below 100 m but euphausiids exhibited diel vertical migration (Figs. 7–9).

The absence of migration in *Euphausia superba* during May 2000 also was reflected in the biochemistry of this species. Concentrations of both aerobic and anaerobic enzymes were reduced during May 2000, compared to time periods when diel vertical migration was observed (Cullen et al., 2003). A reduction in enzyme activity in this species might reflect a decrease in metabolic rates, facilitating overwintering of krill during times when food is relatively scarce.

## Acknowledgements

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