INTRODUCTION

Recent scrutiny of the Antarctic pelagic ecosystem has uncovered a more complex system than the traditional trophic linkages (phytoplankton-krill-bird and mammal) originally thought to dominate (e.g. Hopkins 1985, Lancraft et al. 1989, Hopkins et al. 1993, Piatkowski et al. 1994, Voronina 1998). Many types of gelatinous zooplankton, including ctenophores, are now recognized as significant contributors to Antarctic marine ecosystem dynamics (Huntley et al. 1989, Pages & Kurbjeweit 1994, Pages et al. 1996, Pages

Furthermore, *Callianira* spp. made up 30 to 35% of the dry zooplankton biomass during early winter and spring of 2000 in the embayment of Deception Island, west of the Antarctic Peninsula (Kaufmann et al. 2003).

Ctenophores play an important role as predators in many ocean regions. Sporadic, dense blooms of ctenophores, driven by high fecundity and rapid growth rates (Reeve & Walter 23in th

2.5 knots. Due to heavy ice conditions in winter 2002, ctenophores and prey were mainly collected using a 1 m diameter Reeve net (333 µm mesh) with a 20 l non-filtering cod end. The Reeve net was deployed parallel to the water surface between 10 and 15 m depth off the stern, while the propellers were run at 15 to 25 % pitch to keep water circulating into the net, but with little forward ship movement or ice sweep-down into the net. This approach retrieved animals in exceptionally good condition. Ctenophores were immediately separated from the catch once on board and gently placed in a bucket of 0.1 µm filtered seawater at sea surface temperature (–1.8 to 0°C).

Ctenophores were also hand-collected in individual jars by SCUBA divers working in the upper 10 m of the water column under sea ice during winter 2001 and 2002. At the surface, jars were placed in buckets of seawater to prevent freezing and injury to

Estimation of digestion time. Digestion rate experiments were conducted during winter 2002. Single active and undamaged ctenophores were placed in 960 ml polypropylene jars containing 0.1 µm filtered seawater, and incubated in the dark in a large flow-through aquarium to maintain *in situ* sea surface temperature (–1.3 to –1.8°C). After an initial 24 h starvation, individual ctenophores were placed into 500 ml polypropylene jars containing prey in 0.1 µm filtered seawater and returned to the flow-through aquarium. Prey offered in experiments were the same species and sizes that were observed in ctenophore gut contents from *in situ* feeding, including larval and juvenile euphausiids *Euphausia superba* and *Thysanoessa macrura*, and the calanoid copepods *Calanoides acutus*, *Calanus propinquus*, and *Metridia gerlachii*. Experimental containers were checked hourly until the ctenophore ingested prey (t_o). After ingestion, the ctenophore was placed in a 500 or 960 ml container (depending on its size) with filtered seawater, and held in the flow-through aquarium. Digestion was observed hourly for the first 2 to 3 h of the experiment. Thereafter, the progress of digestion determined the frequency (every 1 to 2 h) of subsequent observations in order to minimize disturbance. During each inspection, ctenophores were submerged in a deep glass dish, briefly viewed under a dissecting microscope with dim light, and then placed into a fresh container of filtered seawater. The old container water was filtered through a 20 µm mesh sieve, back-washed into a small dish, and examined under a dissecting microscope. Experiments were continued until there were no recognizable remains of prey in the stomodeum and infundibulum, and no further material was egested. Of the 7 animals 6 were used in multiple experiments, each one preceded by 24 h of starvation. Animals that did not ingest prey within 48 h of the termination of the previous experiment were measured and frozen at –80°C.

Digestion time was defined as the time elapsed between ingestion of prey and clearing of the gastrovascular cavity, estimated to the nearest hour. In order to express digestion time in terms of ingested prey C, N, or DW, prey species of the same stage and/or size as those used in the digestion experiments were sorted, measured for length, rinsed briefly with cold distilled water to remove salts, blotted dry, and frozen at –80°C. In the laboratory, individual euphausiids or grouped copepods were placed onto preweighed, combusted filters, and wet weights (WW) were determined to the nearest 0.1 mg. Specimens were then dried at 60°C to a constant weight and analyzed for C and N.

Gut contents. Ctenophores collected during winter 2001 and autumn and winter 2002 were analyzed for gut contents within 30 min after retrieval, with the exception of a few high-density tows, where analysis took up to 2 h. Ctenophores collected by divers were visually inspected on site and analyzed as soon as the dive was completed (1 to 2 h). Individuals were measured for total length, and gut contents were examined either by dissection of the gastrovascular cavity or by suction-removal of gut contents using a pipette inserted into the gastrovascular cavity. Prey items were identified to the lowest possible taxonomic category. In order to reduce bias due to possible net-feeding, prey that were newly ingested and had not reached the proximate half of the stomach were eliminated from the final count.

Statistical analysis. Much of the data reported here were not normally distributed, and therefore, the median and range are used to describe the central trend of those data. For percentage and rate measurements, the geometric mean (Laws & Archie 1981, Zar 1990) is reported if the value was different from the calculated arithmetic mean. Correlation and regression analyses were calculated at the 5% significance level.

RESULTS

Chemical composition

A total of 32 *Callianira antarctica*, 8 from autumn and 24 from winter 2002, were measured for total length, WW, DW, and C and N content (Table 1). The relationship between length (L, mm) and dry weight (DW, mg) for autumn and winter was $DW = 0.58L^{1.59}$ ($r^2 = 0.92$) and $DW = 0.018L^{2.49}$ ($r^2 = 0.96$), respectively. None of the individuals had prey in their guts, although 44% did have lipids. There was no significant difference ($p > 0.5$) in C and N content between ctenophores with or without lipids in their guts. Although winter C and N (% DW) values were more variable than autumn values, there was no significant difference (Mann-Whitney U-test, % C: $p = 0.54$, % N: $p = 0.93$) between seasons. Therefore, averages of the combined data are shown as well (Table 1). The geometric mean C:N ratios were also similar between seasons (geometric mean [range] for autumn: 4.48 [4.0 to 5.17]; winter: 4.65 [3.64 to 9.67]). The relationship between ctenophore DW and body C and N for autumn and winter are shown in Fig. 2.

Metabolic rates

During winter 2002, oxygen consumption and ammonium excretion rates (Table 2) were measured for 10 ctenophores ranging in total length from 8.5 to 85.0 mm, with a median length of 31.0 mm. Oxygen

consumption (µl O_2 ind.$^{-1}$ h^{-1}) increased with increasing ctenophore DW (mg) according to the equation: $y = 0.237\ DW^{0.919}$ ($r^2 = 0.91$; Fig. 3). Carbon-specific oxygen consumption showed a slightly lower slope, $y = 3.762\ x^{0.707}$ (x, mg C; $r^2 = 0.95$), due to the higher carbon content in larger individuals. Nitrogen excretion rate (µmol N ind.$^{-1}$ h^{-1}) scaled less steeply with ctenophore DW (mg): $y = 0.006\ DW^{0.487}$ ($r^2 = 0.62$; Fig. 3). Since the slopes of all curves were less than 1, weight-specific oxygen consumption and excretion rate both declined with increasing weight (Table 2, Fig. 3), as is typical of virtually all species studied to date (Withers 1992). The lower slope of the excretion vs. weight curve resulted from a more profound drop in weight-specific excretion rate with increasing weight than was observed in the oxygen consumption data. Thus, DW-specific oxygen consumption rates calculated for individual *Callianira antarctica* ranged from 0.059 to 0.411 µl O_2 mg^{-1} DW h^{-1} for individuals weighing 1049 and 174.2 mg DW, respectively (Table 2); DW-specific nitrogen excretion rates ranged from 0.043 to 2.221 nmol N mg^{-1} DW h^{-1} for individuals weighing 1049 and 2.8 mg DW, respectively.

The ratio of oxygen uptake to nitrogen-excretion rate (atomic O:N ratio) varied from 5.6 to 122.4, with no relationship to ctenophore size (Table 2). Plotting µmol O ind.$^{-1}$ h^{-1} vs. µmol N ind.$^{-1}$ h^{-1}, with the y-intercept constrained to pass through 0, yields a slope of 30.3, which is a good global approximation for the winter O:N ratio (geometric mean 25.5, arithmetic mean 38.3). These results suggest a metabolism based primarily on lipid, with a few low values suggesting recent prey capture and protein digestion.

Since ctenophores were apparently metabolizing both protein and lipids (cf. Kremer 1977), the range of minimum daily carbon requirements was estimated by converting the mean oxygen consumption rate per individual to carbon utilization using Gnaiger's (1983) respiratory quotient (RQ) values of 0.97 for protein and 0.72 for lipid catabolism. *Callianira antarctica*'s daily carbon requirement during winter ranged from 3.60 to 190 µg C (1.2 to 8.9% of total body carbon) for smaller ctenophores (8.5 to 28 mm total length [TL]), and from 151 µg to 1.13 mg C (0.44 to 3.6% of total body carbon) for larger ctenophores (34 to 85 mm TL).

Feeding behavior

During winter 2001 and 2002, SCUBA divers observed high numbers of *Callianira*

passively drifting with their mouth oriented upward and tentacles extended outward to approximately 10 times their body length or more, characteristic of an ambush entangling predator (Greene 1985). Ctenophores imaged under ice during late night hours by a remotely operated vehicle (ROV) showed similar behavior.

Callianira antarctica feeding behavior was also observed during digestion experiments. Individuals set out their tentacles while swimming in a circular pattern. After prey became entangled in a tentacle, the ctenophore retracted the tentacle, drawing the prey close to its body, and then rotated several times in the tentacular plane, effectively landing the prey held by the tentacle into its mouth. The prey, along with the portion of tentacle surrounding it, was moved quickly (typically <30 min) from the mouth down into the stomodeum (pharynx). *C. antarctica* was able to successfully capture and ingest *Euphausia superba* furcilia and juveniles up to 24 mm in length, the size range observed swarming near the undersurface of sea ice in winter.

Clearance rates, ingestion rates, and daily rations

Clearance rates of prey assemblages ranged from 3.2 to 17.9 l ind.$^{-1}$ d^{fecti}

Both simple and multiple linear regression analyses indicated that ctenophore length was not a significant source of variation in digestion time, even allowing for the maximum digestion time as an outlier (Fig. 5a). In contrast, prey carbon ($r^2 = 0.91$; Fig. 5b), nitrogen ($r^2 = 0.85$) and dry weight ($r^2 = 0.88$) were all important determinants of digestion time. The maximum digestion time was included in these analyses as it was the result of a highly carbon-rich meal from the ingestion of 2 juvenile *Thysanoessa macrura* (see below), and is likely representative of prey ingested *in situ*. Given that elemental content varies among prey species, prey type was a secondary factor influencing digestion times, i.e. species rich in carbon (lipids) and nitrogen, such as the euphausiid *T. macrura* and the copepod *Calanus propinquus*, usually took longer to digest

bison 1989). The presence/absence and net change in volume of lipid reserves in *C. antarctica* was observed before, during, and after winter digestion experiments (Fig. 8). Lipid was not present in stomodea at the beginning of 29% of the experiments (50% using larval *Euphausia superba* as prey and 50% using *Metridia gerlachii* or *Calanus propinquus*). None of the ctenophores that ingested larval *E. superba* accumulated lipid after digestion, whereas lipids always accumulated from copepod digestion.

For ctenophores with lipid initially present (53%), the lipid droplet always increased in volume, even when digesting krill larvae, although the amount varied with prey number and type. Digestion of *Calanus propinquus* resulted in the largest increase (>100%) in lipid volume (Fig. 8). The percent increase in lipid volume from digesting *Metridia ger-*

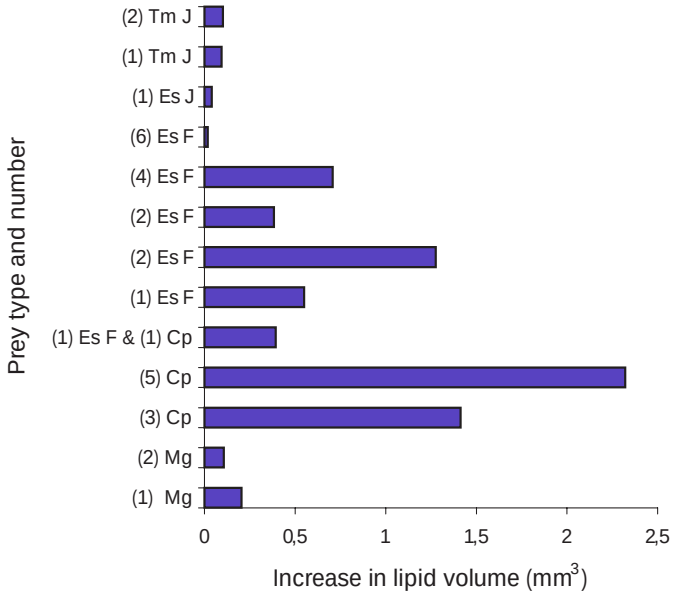

Fig. 8. *Callianira antarctica*. Measured increases in gut lipid volume after digestion of prey. The number (in parentheses) and type of prey digested are shown for each experiment. Es: *Euphausia superba*; Tm: *Thysanoessa macrura*; Cp: *Calanus propinquus*; Mg: *Metridia gerlachii*; J: juvenile; F: furcilia

being the dominant prey in autumn, and euphausiid larvae prevailing in winter. Copepod species that could be identified included *Calanoides acutus*, *Metridia gerlachii*, and *Calanus propinquus*. A single amphipod, *Primno macropa*, was also observed in the winter 2001 gut contents. Because a significant proportion of the gut material in all individuals was too digested to be identified, we could not determine reliable counts of total prey consumed per ctenophore nor could we estimate *in situ* feeding rates from gut contents.

DISCUSSION

Chemical composition

The elemental composition of *Callianira antarctica* was more variable in winter than in autumn, but not significantly different. Ctenophore body carbon is unevenly distributed among tentacles, the gut wall, and comb rows (Reeve et al. 1989); therefore, some of the variability in carbon may be attributed to loss of tentacles during net collections. Because geometric mean carbon and nitrogen values (Table 1) for both seasons were similar, averages of the pooled data are used in the discussion below.

Callianira antarctica has a high water content and low organic mass, which is characteristic of all gelatinous zooplankton and of ctenophores in particular (Percy & Fife 1981, Hoeger 1983, Clarke et al. 1992). The mean DW (4.2% WW) is within the range (1 to 7%) reported for other ctenophores (Kremer 1977, Hoeger 1983, Martinussen & Båmstedt 1999), and closely resembles values given for other polar cydippids, such as *Pleurobrachia* sp. (4.4%) from the Antarctic (Clarke et al. 1992), and *P. pileus* (4.0%) and *Mertensia ovum* (4.5 to 4.9%) from the Arctic (Hoeger 1983, Percy 1988). Because ctenophores are considered to be in isotonic equilibrium with their surrounding water, regional differences in salinity may impact comparisons of dry weight (Shiganova et al. 2001).

Carbon (8.41% DW) and nitrogen (1.83% DW) levels in *Callianira antarctica* were also similar to or higher than values for other ctenophores from polar regions, and higher than temperate and tropical species. For example, *C. antarctica* elemental values were similar to those for an Antarctic *Beroe* sp. (9.51 and 2.22% DW; Clarke et al. 1992) and Mertensiidae species (11.2 and 2.4%; Ikeda & Bruce 1986), but 2-fold higher than values for an Antarctic *Pleurobrachia* sp. (4.11 and 0.74% DW; Clarke et al. 1992) and for *P. pileus* (C:3.4%) from the Arctic (Hoeger 1983). *C. antarctica* elemental levels were also more than 4 times higher than those in epipelagic ctenophores from temperate and tropical regions (reviewed in Youngbluth et al. 1988). Thus, polar ctenophores tend to have elevated organic carbon levels relative to levels in species from lower latitudes, as previously noted by Ikeda (1974).

Metabolic rates

Metabolism, excretion, and carbon content for 12 other species of ctenophores inhabiting polar, temperate, and tropical regions are presented in Table 5 for comparison with *Callianira antarctica*. As noted in the previous section, the high water content of ctenophores (>95%, Bailey et al. 1994) results in low, yet highly variable amounts of organic matter or metabolizing tissue, making interspecific comparisons a perilous road to follow. For the 13 species in Table 5, organic carbon content varies between 0.6 and 11.2% of DW, which has a profound effect on the DW-specific metabolism. Expressed in terms of dry weight, and with all species at normal ambient environmental temperature (0 to 25°C), *C. antarctica*'s metabolism at 0.5°C ranks second out of 13, falling just under a temperate species (*Beroe cucumis*, 15°C) and comparable with a tropical species (*Beroe ovata*, 25°C). Expressed as carbon and at ambient temperature, *C. antarctica*'s metabolism ranks ninth, clustering with the rest of the polar species. If the inter-regional comparisons are taken one step further, by correcting all measurements of oxygen consumption to a common

(Table 5). Moreover, when excretion rates are extrapolated to 0°C there is no evidence of a cold adapted response, i.e. polar and tropical species having similar excretion rates; instead, the tropical species are actually higher (Table 5). These interesting differences in metabolism between high and low latitude ctenophores warrant further investigation.

Interestingly, the O:N ratios observed in *Callianira antarctica* and the other polar species (mean 24) were about twice as high as those from the tropical regions (mean 13), suggesting a greater dependence on lipid in the polar species. Within *C. antarctica*, individual O:N was highly variable (Table 2), suggesting a protein-based metabolism immediately after prey capture and a lipid-based metabolism post-digestion, depending on the type of prey ingested.

The relation of metabolism to weight in *Callianira antarctica* was typical of that reported for ctenophores in that *b*, the exponent in the equation $y = ax^b$, was close to 1.0 (0.92; Fig. 3) where y is metabolic rate, x is weight, and a is a constant for the species. A b value of 0.92 indicates that weight-specific metabolism declines only slightly with increasing weight. b values for metabolism vs. weight are reported for 8 of the species in Table 5. The only species to have an exponent less than 0.9 is *Bolinopsis vitrea*, a tropical cydippid (Kremer et al. 1986a). Ctenophores as a group thus seem to have a consistently higher exponent than most taxa, whose b values fall at approximately 0.75 (Prosser 1973). In contrast to oxygen consumption vs. mass, weight-specific excretion in *C. antarctica* showed a strong decline with increasing weight (b = 0.49), indicating either a lower hunting success in large individuals or a greater dependence on stored lipid, or both.

temperature of 0°C using a Q_{10} of 2.0 (Hochachka & Somero 2002), *C. antarctica*'s carbon-specific metabolism (2.641 µl O_2 mg^{-1} C h^{-1}) is the highest rate followed by the temperate predator *Mnemiopsis leidyi* (2.059 µl O_2 mg^{-1} C h^{-1}). Like the other Antarctic mertensiid ctenophore shown in Table 5, *C. antarctica*'s high carbon content and oxygen consumption rate suggest a very active predatory species with a cold adapted metabolism. The sluggish and very delicate mesopelagic species, *Bathocyroe fosteri*, provides a counterpoint to the more active species presented in Table 5, ranking at the bottom of the list for all rates.

Carbon-specific nitrogen excretion also shows a trend with temperature, in that polar and mesopelagic species have rates that are an order of magnitude lower than those in temperate and tropical species

Maintenance carbon rations and body turnover

Smaller (≤30 mm) *Callianira antarctica* required a higher daily carbon intake (1.17 to 8.91% body C) to support metabolic processes than larger ctenophores (>30 mm; 0.44 to 3.62% body C) during winter, owing to higher weight-specific respiration rates combined with a lower carbon content per unit weight. Our winter maintenance rations are much lower than the daily rations estimated from autumn ingestion experiments, suggesting that autumn feeding could have supported ctenophore growth, assuming that metabolic demand0.092oScap.or (P6.1243 0 TD 0 Tc2 1 Tf -0.49eee47753[.3(ge i TD4Jnoveeight-6a[5 cal ei .gnhtered

was similar. Even though winter feeding rates could not be estimated from gut contents, it is instructive to examine whether *C. antarctica* could have obtained sufficient food to support their metabolic requirements. If we assume a conservative assimilation efficiency of 70% (Reeve et al. 1978), the daily carbon requirement for smaller *C. antarctica* during winter would be satisfied with the ingestion of 1 larval (F6) *Euphausia superba*, 1 adult *Calanus propinquus*, or 2 *Metridia gerlachii*. Larger ctenophores would need to ingest up to 6 larval (F6) *E. superba*, 16 *M. gerlachii*, 3 *C. propinquus* or 1 juvenile *E. superba* or *Thysanoessa macrura* each day. If we consider average digestion times (e.g. 10.0 and 16.5 h for prey items under 1.0 and 2.0 mg C, respectively) and allow for multiple meals, gut contents from this study suggest that *C. antarctica* could meet, and often exceed, the maintenance daily carbon requirement, even during winter.

Feeding ecology: experimental

Callianira antarctica clearance rates are comparable to the lower end of rates reported for tropical and temperate ctenophores (range: 0.3 to 53 l ind.$^{-1}$ d^{-1}, water temperature range: 16 to 30°C; Larson 1987b, Stoecker et al. 1987, Monteleone & Duguay 1988, Kremer & Reeve 1989, Buecher & Gasser 1998, Purcell et al. 2001). The temperature difference between our experiments and those reported in the literature from warmer climates is a major factor contributing to the lower clearance rates. A 4 to 8-fold increase in feeding rates would be conservatively orfercontributing to t5uaturet3i0d

order of magnitude drop in prey concentrations. Given these results, our rates may be underestimated as well.

Our experimental prey concentrations were 2 orders of magnitude higher than mean *in situ* zooplankton densities (range: <5 to 20 µg C l^{-1}, maximum 40 µg C l^{-1}) obtained using Bongo nets in the top 300 m during April/May 2001 (E. A. Pakhomov unpubl.). ROV observations, however, indicated that larval krill densities reached as high as 500 ind. l^{-1} (~303 mg C l^{-1}) under sea ice (S. Gallager pers. comm.); thus, experimental prey concentrations were within the range of concentrations *Callianira antarctica* may have encountered *in situ*. Based on *in vitro* ingestion rates, daily rations for *C. antarctica* ranged from 6 to 136% of total body carbon. At the highest mean *in situ* zooplankton biomass (~40 µg C l^{-1}) a minimum daily ration for the larger ctenophore, using the equation in Fig. 4, would be 17% of body carbon. By comparison, Reeve (1980) estimated daily rations for temperate ctenophores to be >200% of body C d^{-1} for food concentrations exceeding 1000 µg C l^{-1}. Since we know little about either ctenophore or prey densities in the Southern Ocean, predation impact assessments are beyond the scope of this study. Nevertheless, our preliminary *in vitro* ingestion rates point out that *C. antarctica* could have a high predation impact over a wide range of natural prey concentrations. Depending on ctenophore density, their predation impact could be particularly noticeable during winter, when secondary productivity is low.

Digestion time

Slow digestion may be the limiting factor in the amount of carbon *Callianira antarctica* can process. Autumn (9 h) and average winter (11.5 h) digestion times were substantially longer than values reported for temperate and tropical ctenophores (Fig. 11; range 0.2 to 5.8 h, temperature = 5 to 26°C). Copepods in tropical waters (25 to 27°C) are typically digested in less than 3 h (Reeve 1980, Kremer et al. 1986b, Larson 1987a), whereas *C. antarctica* took 9 to 12 h to digest a single copepod. To our knowledge, there are no other digestion times for polar ctenophores available for

lipid volumes occurred after digesting copepods, particularly *Calanus propinquus*. The lack of lipid accumulation after ingesting lipid-rich *Thysanoessa macrura* may have resulted from the long digestion times or the types of fatty acids associated with this prey.

Ju et al. (2004) analyzed lipids in *Callianira antarctica* body tissues (gut contents and lipids removed) as well as lipid biomarkers from potential prey from our study area. Their findings suggest that lipid content in ctenophores is higher in winter than in autumn, and that fatty acids specific to larval *Euphausia superba* and fatty alcohols from wax esters found in calanoid copepods are elevated in ctenophores in winter. Therefore, lipid reserves may be important to *C. antarctica*'s overwintering survival.

Feeding ecology: *i i*

Diver and ROV observations of ctenophore predatory behavior during day and night, and the presence of prey in the guts of ctenophores collected during late afternoon and evening net tows, suggest that *Callianira antarctica* forages for food continuously over a 24 h period. Feeding success was moderate, regardless of season, as 40 to 50% of ctenophore guts during autumn and both winters did not contain any digested material. The large percentage of guts lacking prey could be an artifact of net collection (ctenophore regurgitation) or our efforts to reduce net feeding bias by not including freshly ingested prey in our estimates. Some of the excluded ctenophores had up to 11 larval krill in their guts. The similarity in feeding incidence between autumn and winter, despite a large seasonal variability in prey abundance, suggests that other factors, such as prey patchiness, may significantly influence feeding. High frequencies of empty guts were also reported for *Mertensia ovum* (52 to 70%) during early spring and summer from the Arctic (Siferd & Conover 1992), where prey densities are also highly seasonal.

Recognizable prey in gut contents indicated that *Callianira antarctica* were primarily feeding on larval euphausiids during winter 2001, on copepods during autumn 2002, and on both larval euphausiids and copepods during winter 2002. Tentaculate ctenophores are opportunistic feeders and, as a result, their gut contents should reflect encountered *in situ* prey concentrations and composition (Frank 1986, Siferd & Conover 1992). Diver and ROV observations under sea ice and results from net tows (Daly 2004, Ashjian et al. 2004) over 3 seasons correspond well with ctenophore gut contents: larval *Euphausia superba* concentrations in the study area were highest during winter 2001, lowest during autumn 2002, and variable in winter 2002. Ctenophores may compensate for the seasonal decrease in prey abundance and increase in food patchiness during winter by exploiting larval krill aggregations under sea ice. Hence, high densities of larval krill under sea ice may provide a significant food source for overwintering *C. antarctica* and, conversely, *C. antarctica* may significantly affect krill mortality.

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