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Distribution, Metabolism and Trophic Ecology of the Antarctic Cydippid Ctenophore, *Callianira antarctica*, West of the Antarctic Peninsula

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Distribution, Metabolism and Trophic Ecology of the Antarctic Cydippid Ctenophore, *Callianira antarctica*, West of the Antarctic Peninsula

by

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ABSTRACT

The distribution, abundance, chemical composition, metabolism, and feeding ecology of the tentaculate ctenophore, *Callianira antarctica* (Chun 1897), were investigated during austral winter 2001and autumn & winter 2002, in the vicinity of Marguerite Bay west of the Antarctic Peninsula. *Callianira antarctica* had a widespread distribution during autumn and winter, and variable abundance (0.02 to 2.6 ind. m^{-2}) during winter 2001 associated with specific circulation features. Size frequency distributions for autumn and winter suggest that more than half of the *C. antarctica* population may have experienced 'degrowth' during winter due to low food availability. *Callianira antarctica* is a fairly robust ctenophore with geometric mean (geomean) carbon (C) and nitrogen (N) values of 8.41 and 1.83% dry weight (DW), respectively. Winter oxygen consumption and ammonium excretion rates ranged from 0.059 to 0.410 µl O_2 [mg DW]$^{-1}$ h^{-1} and 0.60 to 31.1 µg-at N [g DW]$^{-1}$ h^{-1}, respectively, at 0^{o}C. Daily minimum maintenance rations based on respiration experiments were 2.7% to 3.6% of the total body carbon (TBC) for small ctenophores, and 1.4% to 1.9% TBC for larger ctenophores. Calanoid copepods and larval and juvenile Antarctic krill were offered to ctenophores in incubation experiments. Digestion times were variable, lasting 8 to 20 h, and were independent of ctenophore size and dependent on number and type of prey. Gut content analysis from

one autumn and two winter seasons indicated *C. antarctica* preyed on both copepods and krill *in situ*, with an increased dependence on larval krill during winter. Lipid biomarker analysis on *C. antarctica* and their potential prey confirmed these results. Divers observed aggregations of C. *antarctica* passively drifting with tentacles extended near dense concentrations of larval *Euphausia superba* during winter. These observations along with gut content and lipid biomarker analysis suggest that larval krill is an important prey item for *C. antarctica* during winter.

CHAPTER ONE

INTRODUCTION

The first scientific accounts of ctenophores in Antarctic waters were recorded in the late 1800's and early 1900's (Chun 1897, Moser 1909: as referenced in O'Sullivan 1986). More than a century later, our knowledge of Antarctic ctenophores and their role in the Southern Ocean ecosystem has only marginally improved. The lack of information on ctenophores is in part due to the fact that their delicate, gelatinous bodies are easily destroyed by most collection and preservation techniques (Harbison et al. 1978, Purcell 1988). The episodic nature of ctenophore populations, owing to their rapid growth rates and high fecundity (Reeve & Walter 1976, 1978, Harbison et al.1978, Swanberg & Båmstedt 1991a), has also made it difficult to quantify the abundance of these organisms.

More recent studies indicate that ctenophore densities in Antarctic seas display substantial seasonal and interannual variability (Lancraft et al. 1989, 1991), and at times may dominate total zooplankton biomass regionally (Williams et al. 1986, Pakhomov 1989, Pagès et al. 1996, 1997). For example, Voronina et al. (1994) reported that ctenophore biomass in the 0-200 m layer of oceanic stations in the Atlantic sector of the Antarctic increased from 1.7 to more than 40% of the total zooplankton biomass between summer and autumn. In addition, Kaufmann et al. (2003) reported that *Callianira* spp. was one of three dominant macrozooplankton species, making up 30 - 35% of the zooplankton biomass on a dry weight basis, during early winter and spring 2000 in a small embayment of Deception Island, just west of the Antarctic Peninsula.

Despite these recent developments, investigations concerning the role of ctenophores in the Antarctic ecosystem are lagging behind those done for most other geographic regions. The Black Sea has received considerable attention over the last decade due to the adverse ecological changes that have taken place as a result of a number of anthropogenic factors combined with invasions of non-endemic species of ctenophore into the region (see review in Kideys et al. 2000). Research related to the Black Sea has been published on everything from estimates of ctenophore abundance, distribution, growth and feeding rates, reproduction, and chemical composition to associations with physical features and prey abundances. Similar research has been done with ctenophores from the tropics (Kremer 1982, Kremer et al. 1986a&b, Reeve et al. 1989), temperate regions (Hirota 1974, Ikeda 1974, Kremer 1977, Larson 1987a, Larson 1987b, Larson 1987c, Youngbluth et al. 1988, Bailey et al. 1994, Purcell et al. 1994) and the arctic (Percy & Fife 1981, Hoeger 1983, Percy 1988, Percy 1989, Swanberg & Båmstedt 1991a, Swanberg & Båmstedt 1991b).

Because ctenophores are voracious predators and exhibit rapid population growth, their trophic impact on an ecosystem is of particular interest. Ctenophores in many regions of the ocean have been shown to have a marked predatory impact on copepods, euphausiids, and fish eggs and larvae (Reeve &Walter 1978, Greene et al.1986, Suthers & Frank 1990, Mills 1995, Purcell 1997, Shiganovoa & Bulgakova 2002, Shiganovoa et al. 2003). For instance, Larson (1987a) estimated that the tentaculate ctenophore *Pleurobrachia bachei*, and two species of medusae from the Saanich Inlet, BC, consumed 10 to 40% of *Euphausia pacifica* eggs and nauplii stock a day. The cydippid ctenophore *Mertensia ovum*, which is the dominant biomass macrozooplankter in regions

of the Canadian Arctic (Percy 1988, Swanberg & Båmstedt 1991a,1991b, Siferd & Conover 1992), is considered to be an important predator on crustacean zooplankton. Elsewhere, field and laboratory studies on the widely distributed cydippid ctenophore *Pleurobrachia pileus*, indicate that this species has the potential to seriously impact zooplankton populations where it exists (Reeve et al. 1978, Frank 1986, Chandy & Greene 1995, Båmstedt 1998).

In situ observations of Antarctic ctenophores under sea ice suggest that ctenophores may play a larger trophic role in the Antarctic ecosystem than previously believed. *Euphausia superba* is a keystone species in the Southern Ocean, thus a number of top predators, such as seals, penguins and whales, depend entirely or to a large extent on it as a food source (Fraser & Trivelpiece 1996, Costa & Crocker 1996). Numerous studies have been conducted on the impact of these top predators on adult krill, however little is known about predation on larval krill. Substantial numbers of larval and juvenile krill are associated with the under sea ice habitat during autumn and winter (Daly 1990). Daly and Macaulay (1991) suggested that ctenophores may be important predators on overwintering larval Antarctic krill, *E. superba*, based on diver observations of ctenophores feeding on larvae under sea ice during autumn and winter in the Scotia-Weddell seas. Hamner et al. (1989) and Hamner & Hamner (2000) also reported diver observations of the cydippid ctenophore, *Callianira antarctica*, under ice floes preying on larval krill during early autumn west of the Antarctic Peninsula. The presence of these predators in close proximity to the under-ice habitat and associated aggregations of larval krill could have a significant influence on the annual recruitment of larval krill.

Before the trophic impact of ctenophores on zooplankton populations in the Antarctic region can be reliably estimated, a better understanding of their ecology must first be achieved. The opportunity to do the latter arose during a series of Southern Ocean Global Ecosystem Dynamics Program (SO GLOBEC) research cruises in austral autumn and winter of 2001 and 2002 to the Marguerite Bay region, west of the Antarctic Peninsula, where divers once again observed large numbers of the ctenophore, *C. antarctica*, in the water column just below ice-associated aggregations of larval krill. SO GLOBEC is a collaborative research effort designed to examine the physical, chemical, and biological processes that contribute to the abundance and success of the Antarctic krill. Marguerite Bay, west of the Antarctic Peninsula (WAP), is a physically dynamic environment marked by unusually high Antarctic krill production and an important habitat for krill predators, making this an ideal study site for the program. For my Master's thesis, I investigated the distribution, abundance and trophic ecology of *C. antarctica* in vicinity of Marguerite Bay during autumn and winter. The seasonal size-frequency and broad-scale distribution of these ctenophores, as well as their vertical distribution and abundance in the water column during the winter 2002 season, are described. The elemental composition of ctenophores over autumn and winter are reported and applied to metabolic rates measured for one winter season to estimate daily maintenance rations. Lastly, the trophic relationship between *C. antarctia* and potential prey is investigated using winter digestion rates, seasonal measurements of ctenophore lipid composition and identification of biomarkers in their potential prey, and *in-situ* diet analyses in autumn and winter.

CHAPTER TWO

MATERIALS AND METHODS

Sampling platforms and study area. Data were collected during three cruises to the Antarctic during austral autumn and winter as part of the U.S. Southern Ocean GLOBEC Program in the vicinity of Marguerite Bay, west of the Antarctic Peninsula (Fig. 1). Two research vessels operated jointly in the study area during austral autumn and winter expeditions in 2001 and 2002. The RV *Lawrence M. Gould* concentrated on a small number of selected sites for extended durations (Fig. 2A), while the RVIB *Nathaniel B. Palmer* conducted a broad-scale grid survey of the study area (Fig. 2B). Data for this project were obtained aboard the RV *Lawrence M. Gould* during an autumn process cruise (7 April to 20 May 2002) and aboard the RVIB *Nathaniel B. Palmer* during two winter survey cruises (24 July to 31 August 2001 and 31 July to18 September 2002).

The study area, roughly located between 65° to 72° S and 72° to 64° W, is bound to the north by Adelaide Island and to the south by Alexander Island, with Marguerite Bay in the middle (Fig. 1). During winter, nearly the entire survey area was covered with pack-ice that was particularly thick in the southeastern portions of the survey grid. Sea ice cover was considerably less in the autumn, generally limited to waters deep within Marguerite Bay and along the coastline. Although most of the sampling was concentrated over shelf waters generally <500m in depth, certain bathymetric features, such as the cross-shelf Marguerite trench located in the center of the study area, and deep

water canyons in the northeast portions of the grid, as well as a number of stations at the shelf break (>3000m) provided sampling over deeper water.

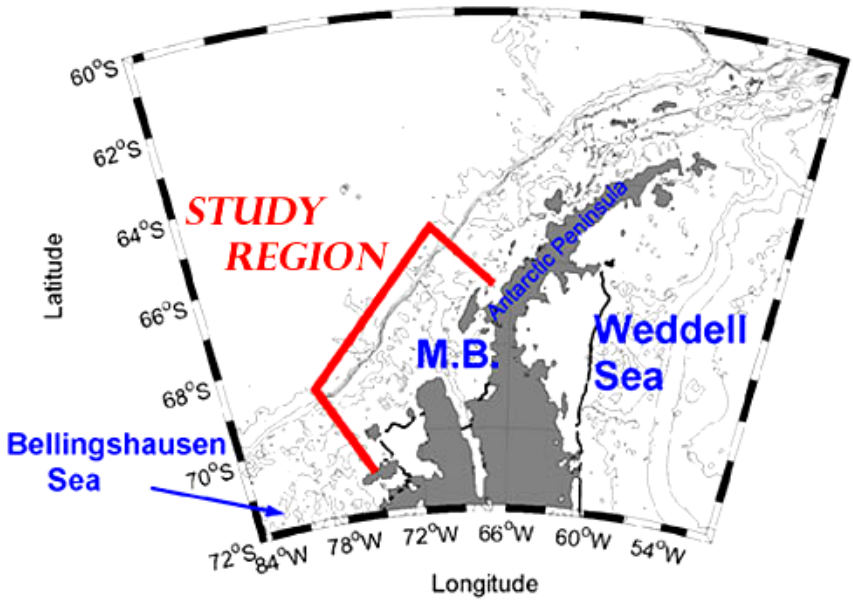

Figure 1. Location of study area near Marguerite Bay (MB), west of the Antarctic Peninsula. From: Howd et al. (2001).

A simplified description of the water mass structure over the study area during autumn and winter is as follows: During the autumn 2002 cruise, Antarctic Surface Water (AASW) was present in the upper 100 to 120 m with temperatures ranging from 0 to -0.5°C, and in some areas a subsurface minimum water mass (-0.5 to -1.8°C), known as Winter Water (WW), resided below it. Below the permanent pycnocline, typically from 120 to 150 m, a cooled form of Upper Circumpolar Deep Water (UCDW) occurred over the shelf (150 to 400m). This modified CDW results from intrusions of UCDW onto the shelf which subsequently mixes with the cooler surface waters. These water masses are characterized by warmer temperatures (1.0 – 2.0ºC), higher salinity (34.70 to 34.72), and

are thought to provide an upward diffusive flux of heat, salt, and nutrients (US SO GLOBEC 2002). The on-shelf intrusions of CDW occurred just west of Adelaide Island and in the central region of the study area, overlying the Marguerite Trough. Extreme surface cooling and ice freezing in winter 2001 & 2002 led to the erosion of the AASW and formation of the colder (-1.8ºC) and saltier (>34 ppt) WW at the surface.

A general clockwise circulation pattern persisted over the study area, starting with a strong northeastward flow associated with the Antarctic Circumpolar Current (ACC) along the shelf break, a strong southwestward flow along the coast of Adelaide Island and into Marguerite Bay, and a flow similar in magnitude out the southern portion of Marguerite Bay, around Alexander Island (Klinck et al. in press). Lastly, a mesoscale gyre, characterized by a weak clockwise flow, was located over the shelf in the northern portion of the study area during each cruise (Klinck et al. in press).

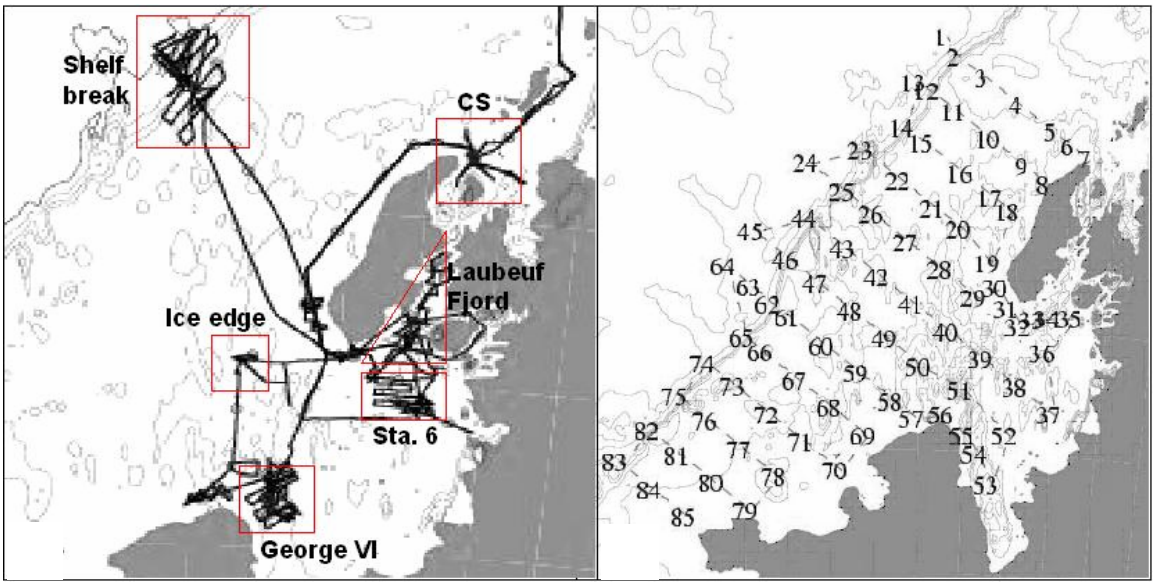

Figure 2. Station locations for the autumn 2002 process cruise (A) and approximate station locations for winter 2001 & 2002 survey cruises (B). The dark grey bathymetry lines running from northeast to southwest represent the shelf break.

Sampling. On board the *Gould* and *Palmer* the following equipment and methods were used to sample ctenophores and their prey: a 1.5-m^2 Tucker trawl having a 6.4 mm mesh graded down to a 707 µm mesh with a protected cod end, typically towed obliquely within the upper 200 m of the water column, and 1-m^2 and 10-m^2 MOCNESS (Multiple Opening/Closing Net and Environmental Sensing System) equipped with 335 µm and 3 mm mesh nets, respectively, towed obliquely from the surface to near bottom, sampling the entire water column with the first net on the down cast and on the up cast sampling discrete depth intervals with the remaining nets (Ashjian et al. in press). Nets were towed at a speed of 1.5 to 3 kts behind the ship, ice permitting. During winter 2002, ctenophores and their prey were also collected using a 1-m diameter Reeve Net (333 µm mesh net) with a 20 L protected cod end kept afloat with syntactic foam, and a 1-m diameter ring net (333 µm mesh). The Reeve Net and ring net were deployed in tandem to about 10 and 15 m depth, respectively, while the propellers were run at 15 - 25% to keep water circulating into the nets, but with little forward ship movement or ice sweep-down into nets. This method retrieved animals in exceptionally good condition. Ctenophores collected by net tows were immediately separated from the catch once on board, and gently placed in a bucket of 0.1 or 0.2 µm filtered seawater at or near sea surface temperature (-1.8 to 0^{o}C).

Ctenophores were also hand-collected by SCUBA divers under sea ice during winter 2001 and 2002. SCUBA dives were operated out of zodiacs and utilized a standard blue water diving rig, with a few modifications to accommodate the shallow nature of under-ice specimen collection. Divers collected ctenophores from the upper 10 m of the water column by gently rotating a pre-filled 20oz plastic Quarpac jar over the ctenophore and

slowly screwing on the lid, as described by Heine (1986). Once at the surface, the jars were placed in buckets of seawater to prevent the containers of water from freezing and injuring the ctenophores. SCUBA dives were generally conducted during mid-afternoon hours.

Ctenophores for live experiments were collected primarily with relatively short, near surface net tows or by divers. A list of analyses performed and tow/dive information is given in Table 1.

Table 1. Collection information and analysis performed on *Callianira antarctica* for each field season. CS=Crystal Sound, RI=Renault Island, LF=Laubeuf Fjord, Sb=Shelf break, TT=Tucker Trawl, MOC=MOCNESS

Analysis	Season	Collection Method	Stations
Gut Content Analysis	Winter 2001	TT, SCUBA	15, 19, 22, 71
	Fall 2002	TT	George VI, LF
	Winter 2002	TT, 1-m and 10-m MOC Drift Net, SCUBA	4, To 4, 5, 11, 13, 14, 16, 17, 23, 26, 40 to 28, 44, 45, 62 to 48, 65, 66/67, 72, 75, To 81, RI2
Chemical Composition	Fall 2002	TT	Sb, George VI, LF
	Winter 2002	TT, 1-m MOC, Drift Net, SCUBA	4, To 4, 5, 9, 13, 16, 17, 23, 26, 28, 34, 49, RI 2
Lipids	Fall 2002	TT	LF
	Winter 2002	TT, 1-m MOC, Drift Net	4, 16, 26, 40 to 28, 49, 65
Respiration	Winter 2002	TT, 1-m MOC, Drift Net, SCUBA	4, To 4, 14, 16, 17, 23, 26, 28, 34, RI 2
Digestion Time	Winter 2002	TT, 1-m MOC; Drift Net, SCUBA	4, 17, 62 to 48, 65, 66/67
Vertical Distribution	Winter 2002	1-m and 10-m MOC	CS, 9, 11, 13, 16, 22, 26, 42, 44, 65, 72, 75

Distribution and abundance. To determine the distribution of *C. antarctica* throughout the study area, presence/absence data was recorded from net collections conducted during the three field seasons. In addition, *in situ* distribution observations of ctenophores and larval krill under-ice were made from WHOI SeaRover ROV deployments on both winter cruises. ROV deployments most often occurred during late evening/early morning hours, however a few deployments were done during afternoon or early evening hours.

Vertical distribution and depth integrated abundance of ctenophores during winter 2002 was determined using discrete tow data from both the 1-m^2 and 10-m^2 MOCNESS nets. Both net systems were equipped with flow meters so that total volume water filtered could be recorded and ctenophore abundance calculated for each depth interval. The poor condition of ctenophores in preserved samples from the first two cruises precluded obtaining accurate counts of ctenophores caught in the nets, therefore on the last cruise a concerted effort was made to record ctenophore counts on board.

Under-ice vertical distribution and densities of *C. antarctica* were obtained during SCUBA dives at two stations during the 2002 winter cruise. This was accomplished with a primary diver swimming 10 meter horizontal transects at 0, 2, 4, 6, 8 and 10 meters below the ice. Depth was measured using a depth gauge attached to a square meter sampler. A safety diver attached a visible chain 10 meters in length to the undersurface of the ice for the primary diver with the square-meter sampler to swim beneath. A second diver swam beside the primary diver recording the number of ctenophores that passed through the square meter on a dive slate. One horizontal swim was done for each depth interval.

Chemical composition. Only ctenophores in good condition were analyzed for chemical analysis. Total length (distance from the mouth to the tip of the aboral keels), oral-aboral length (distance from the mouth to the anal pore), and width were measured to the nearest mm while the ctenophore was suspended in a large petri-dish filled with filtered sea water. After draining the seawater from the petri-dish, the ctenophore was gently blotted with a kimwipe to remove excess water and frozen at –80°C. After returning to the laboratory, individual ctenophores were placed in pre-weighed aluminum boats and weighed to the nearest 0.1 mg. Specimens were then dried at 60°C until a constant dry weight (DW) was achieved. Dried ctenophores were homogenized, sub-sampled, and then analyzed for Carbon (C) and Nitrogen (N) content by the University of California Santa Barbara (UCSB), Marine Science Institute Analytical Laboratory.

Metabolic rates. Active and undamaged ctenophores collected during winter 2002 were used for respiration and excretion experiments. Animals were primarily collected from the upper 10 m of the water column either by divers or drift nets. *In situ* temperatures in the northern half of the study area, where collection for respiration experiments was concentrated, ranged vertically from -1.8°C just below the ice to ca 2°C in deeper water (typically >200 m).

Oxygen (O_2) consumption rates were measured on individual ctenophores using sealed vessel respirometry (Ikeda et al. 2000). O_2 concentrations were monitored continuously for about 24 h using a 30-channel oxygen electrode system as the animals reduced the oxygen in sealed, water-jacketed chambers to intermediate (~ 30 mm Hg) partial pressures. Electrodes were calibrated using air and nitrogen saturated seawater at experimental temperature. Ctenophores were kept in the dark and water temperature was

maintained at 0.5°C (± 0.1°C) using a refrigerated water-bath. Once respiration experiments were completed, all but two of the ctenophores, which were subsequently used for digestion time experiments, were frozen at –80°C. O_2 consumption rates were calculated over thirty minute intervals following the initial excitatory period, which was usually one to two hours, and above the critical oxygen partial pressure (30mm Hg) for the animal. The values for each interval were then summed and averaged over the entire time period to give a mean respiration rate for each individual. Water from the respiration chambers was subsampled and analyzed immediately for ammonium excretion, or frozen at -20ºC and analyzed within a week of collection. Ammonium samples were analyzed following methods described in Gordon et al. (1993). Individual ctenophores were placed in preweighed aluminum boats, weighed to the nearest 0.1 mg, and then dried at 60°C. The dried remains of the individuals were homogenized and analyzed for C/N and ash content as described above.

Estimation of digestion time. Active and undamaged ctenophores were placed in individual polypropylene jars containing 0.1 µm filtered seawater and incubated in the dark in a large flow-through aquarium at *in situ* sea surface temperature (-0.59 to -1.82º C). Small ctenophores were kept in 500 ml containers and medium to large ctenophores in 960 ml containers. After a 24-hour starvation period, individual ctenophores were placed into a 500 ml polypropylene jar containing prey in 0.1µm filtered seawater and returned to the flow-through aquarium. Juvenile and larval euphausiids (*E. superba* or *Thysanoessa macrura*) and small calanoid copepods were used as prey. 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) of filtered

seawater, and once again incubated in the flow-through aquarium. The digestion process was observed hourly for the first two to three hours of the experiment. Progress of digestion determined the frequency of subsequent observations in order to minimize disturbance. During each inspection, the ctenophore was gently scooped out of the jar using a medium-sized petri-dish and viewed under a dissecting microscope under dim light. The condition of the prey was noted. The ctenophore was placed into a fresh container of filtered seawater after each inspection. The old water from the container was filtered through a 20 µm mesh sieve and any remaining material was back-washed into a small petri-dish and examined under a dissecting microscope for egested matter. The experiment continued until there were no recognizable prey remains in the stomodeum and infundibulum, and no further material was egested. Six out of seven of the animals were used in multiple experiments, with each one preceded by a 24 h starvation period. Animals that refused to feed and had not ingested anything within 48 hours of the termination of the previous experiment were measured and frozen at –80^{o}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, and frozen at -80^{o}C. In the laboratory, individual euphausiids and grouped copepods (3 small or 2 large), were placed onto preweighed, combusted filters, and wet weights (WW) determined to the nearest 0.001 mg. Specimens were then placed in combusted glass vials and dried at 60^{o}C to a constant weight. Two of the *Thysanoessa macrura* samples were ground and sub-sampled, while the remainder of the euphausiid samples

were cut in half and analyzed separately. For these samples, the %C and %N values for each individual were estimated as an average of the two halved values. The copepods and their filters were analyzed whole. Prey samples were analyzed for C/N at UCSB.

Lipid composition. Ctenophores collected in nets were measured for total length to the nearest mm and their guts removed to reduce bias. Potential prey specimens were also collected, measured and/or staged. Ctenophore and prey samples were immediately frozen and stored at –80°C until analysis could be performed at shore based facilities. Before lipid analysis, wet weights of ctenophore and prey samples were measured by thawing and briefly rinsing with Nano-pure water. A subset of ctenophore and prey samples were then dried at 60°C for 48 hrs for measurements of water content, which were then used to convert wet weight of the animals to dry weight values. Lipids were extracted and analyzed by the Chesapeake Biological Laboratory, University of Maryland Center for Environmental Science. A detailed description of lipid extraction methods and analysis is given in Ju et al. (submitted)

Gut contents. Ctenophores in good condition were analyzed for gut contents within two hours after collection. Individual ctenophores were measured for total length to the nearest mm, and gut contents examined either by dissection of the gastrovascular cavity or by suction-removal of the gut contents by a pipette inserted into the gastrovascular cavity. Prey items were identified to the lowest possible taxonomic category. In order to reduce biased results 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, therefore the median and range were used to describe the central trend of those data. For

percentage and rate measurements, the geometric mean (Laws & Archie 1981, Zar 1990), labeled as geomean throughout the text and tables, was reported if the value was different from the calculated arithmetic mean. Correlation and regression analyses were calculated at the 5% significance level.

CHAPTER THREE

LENGTH FREQUENCY AND VERTICAL DISTRIBUTION

RESULTS

Length frequency. The oral-aboral lengths of 45 and 86 ctenophores from autumn and winter 2002, respectively, were measured to determine size distribution. There was a similar wide range in lengths of *C. antarctica* collected in both autumn (11 mm to 90 mm) and winter (7 to 92 mm), and no apparent relationship between length and geographic location (i.e. north, central or southern portions; Fig. 3).

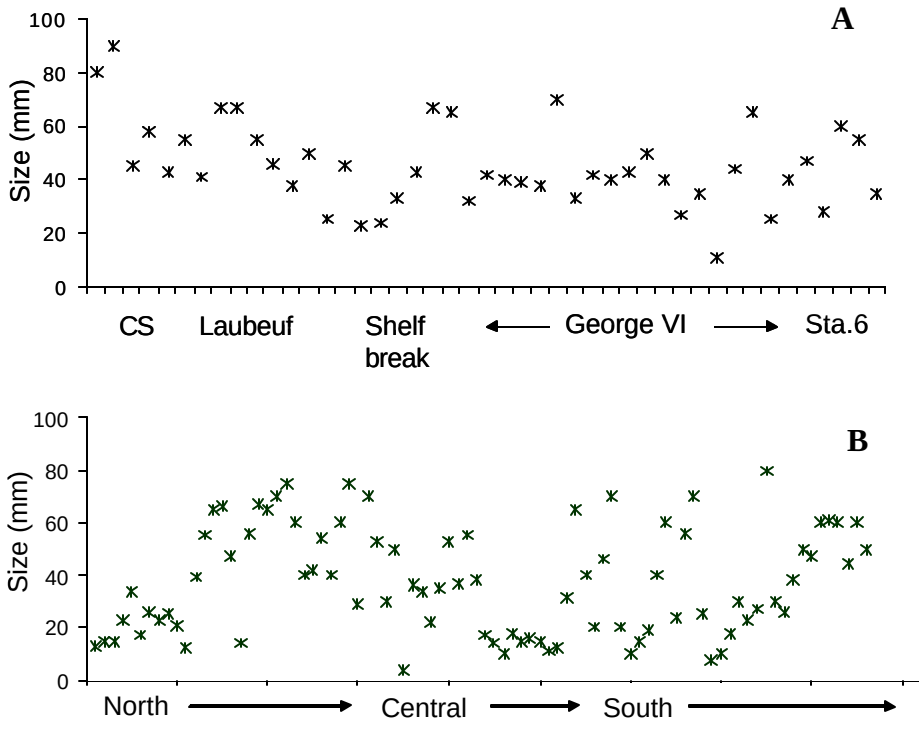

Figure 3. *Callianira antarctica.* Aboral lengths of ctenophores measured for each station in (A) autumn and (B) winter. CS=Crystal Sound.

Although the size ranges were similar between seasons, the dominant length classes were distinctively different (Fig. 4). A majority of the animals collected during autumn were medium-sized adults, with 48.9% of the individuals in the 40-50 mm length range and < 2% smaller than 20 mm. The mean length for autumn ctenophores was 45.4 mm. A greater number of small animals were collected during winter (> 20% smaller than 20 mm in length); however, the frequency distribution for this season indicates that there were two length classes, with modes centralized around 20 mm and 60 mm (Fig. 4).

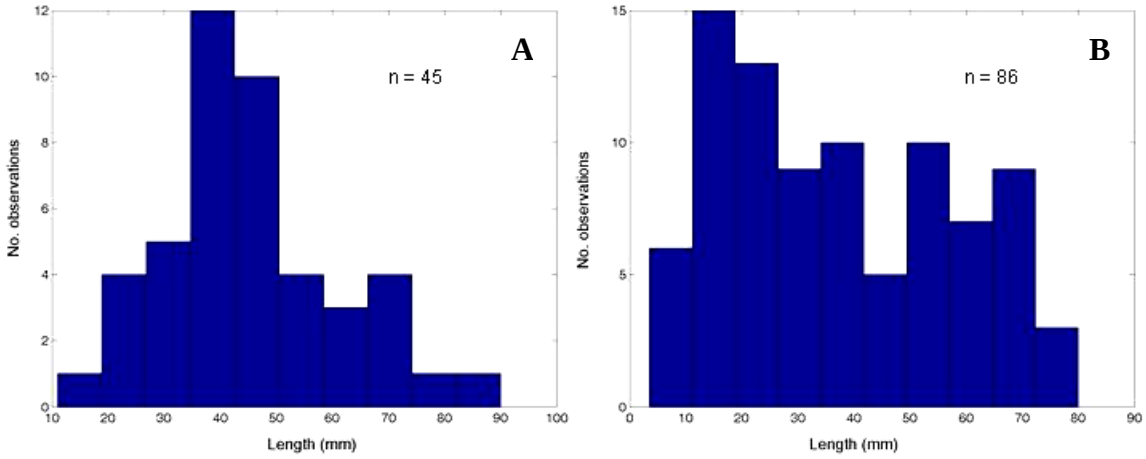

Figure 4. *Callianira antarctica*. Length frequency for (A) autumn and (B) winter 2002.

Horizontal distribution. The presence/absence of ctenophores over the study area during the three sampling periods is shown in Fig. 5. For both winter seasons, there was a broad distribution of *C. antarctica*, extending over large portions of the study area. Ctenophores were found in the north, south and central regions of the study area, on the shelf and at the shelf break, and near the coasts of Adelaide and Alexander Islands. The lack of observations inside Marguerite Bay in Fig. 5C is due to thick pack ice prohibiting the ship from reaching stations in this area, and therefore does not indicate an absence of

ctenophores in this region. This wide-ranging distribution of ctenophores suggested ctenophore occurrence was not governed by physical features of the study area, such as bathymetry, hydrography, or ice-edge. During winter 2002, 31 of the 94 net tows/ROV deployments did not catch/observe a single ctenophore, however none of the 41 stations sampled were absent of ctenophores. In other words, ctenophores were present at all of the stations sampled, but were not sampled by all of the net tows/ROV deployments done at that station; indicating small scale spatial and temporal variability (Fig. 5C). The same assessment cannot be made for winter 2001 because only those stations where ctenophores were collected/observed were recorded. The autumn cruise occupied a much smaller number of stations for longer periods of time (Fig. 2B), thus, the area covered was greatly reduced compared to the winter surveys. However, the decreased extent of the pack ice allowed for sampling deeper within Marguerite Bay, as well as in the smaller fjords and sounds located behind and in the vicinity of Adelaide Island. Similar to winter 2002, ctenophores were found at all stations sampled in autumn: on and off the shelf, in Marguerite Bay, and along the coasts of Adelaide and Alexander Islands (Fig. 2B). Once again, ctenophores had a heterogeneous temporal distribution, as 21 of the 54 net tows recorded did not collect ctenophores, although ctenophores were present at every station sampled.

Vertical distribution and abundance. Discrete depth tows during winter 2002 indicated a broad range in vertical distribution (0-500 m) for *C. antarctica*, though most of the ctenophores occurred within and around the pycnocline (120-150 m; Fig. 6). Nearly the entire water column was sampled, with all but two of the tows over relatively shallow shelf waters (ca 500-800 m). The two net tows conducted in waters depths

greater than 1000 m did not catch any ctenophores deeper than the deepest depth interval sampled on the shelf. There were a similar number of net tows conducted during the day (n=5) and night (n=6), allowing for discernment of the diurnal distribution of *C. antarctica*. During the day, ctenophores were concentrated within the upper 200 m of the water column, with peak abundance at 150-200 m (3.8 ind m^{-3} $x10^3$). Ctenophore distribution reached deeper depths at night, though most of the ctenophores were still concentrated in the upper 250 m of the water column, with two depth maxima at 0-50 m (1.7 ind m^{-3} $x10^3$) and 100-200 m (2.7 ind m^{-3} $x10^3$).

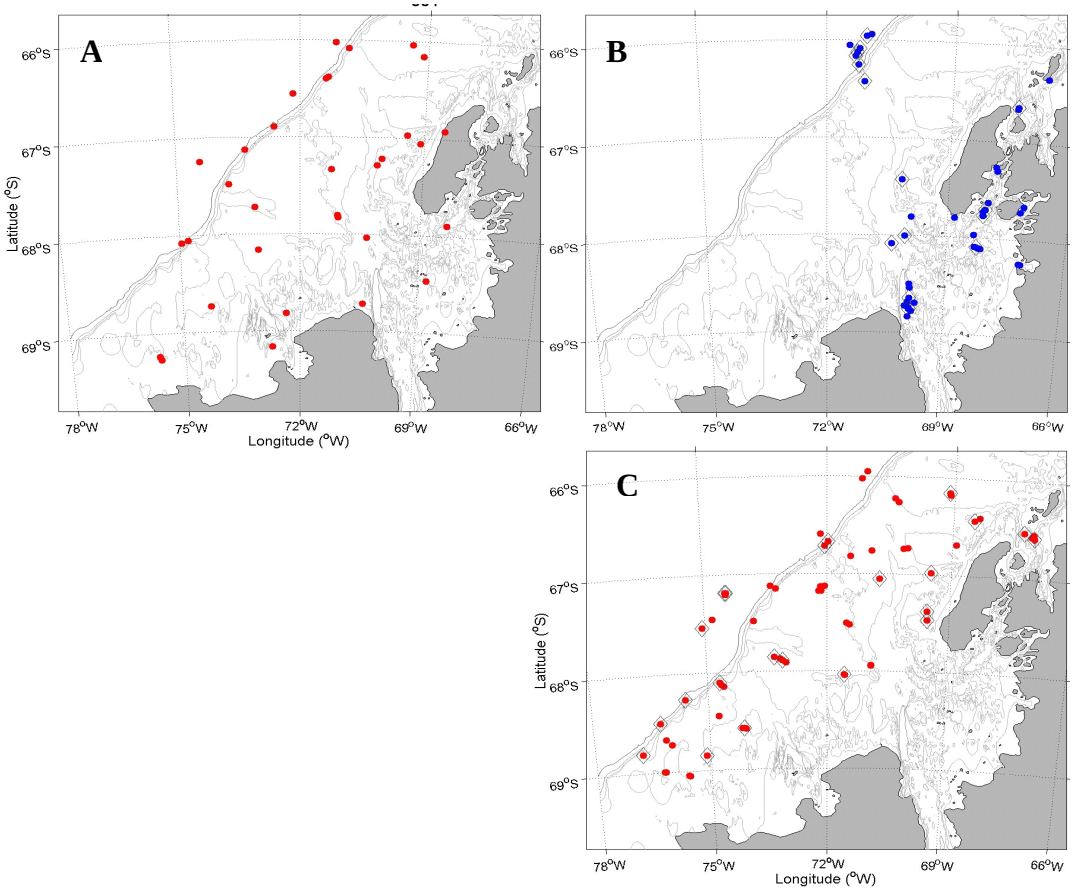

Figure 5. *Callianira antartica.* Presence/absence of ctenophores over the study area during (A) winter 2001, (B) autumn 2002, and (C) winter 2002. The filled circles indicate locations where ctenophores were observed/collected and hollow triangles indicate absence.

Integrated abundances were generally low, < 3.0 m^2 but variable between stations (Fig. 7). The lowest abundances (< 0.10 ind m^{-2}) were found in deeper water at the shelf break, and the highest (> 1.0 ind m^{-2}) were located at two stations further on-shelf, at the north and south ends of the study area. Circulation patterns over the shelf, as illustrated by the dynamic topography calculated at the surface relative to 400 m, reveals a large closed gyre located over northern section of the study area (Fig. 7). The station with greatest abundance (2.6 ind m^{-2}) of ctenophores, Station 16, was located within this large clockwise-flowing gyre located off of Adelaide Island. The other station of notable abundance was located offshore from Alexander Island, in the southern area of the study region. High numbers of ctenophores may have been entrained in the southwestward flow that was evident over the shelf during autumn and winter of 2001 & 2002 (Klinck et al. in press) and advected to this region from the north; hence leading to the elevated abundance relative to those stations located closer to the shelf-break.

Under-ice vertical distribution and abundance was only sampled at two dive locations in winter 2002. I had anticipated sampling at a number of dive stations in both autumn and winter, but due to the high number of tasks needing to be carried out in a limited amount of dive time, combined with the number of complicating issues involved with diving in the Antarctic, there were limited opportunities to complete the under-ice sampling. Also, ctenophores were absent from the upper 10 meters of the water column at dive stations during autumn. Of the two stations completed, a ctenophore was counted in one 10 m transect at 5-10 m depth. General observations were noted for each dive during both winter and autumn seasons. Based on these observations, higher abundance of ctenophores (ca. 0.5-2 m^{-3}) and aggregations of larval krill under the ice were present

over most of the study area during winter 2001. There was a complete absence of ctenophores and a paucity of larval krill under the sea ice during autumn 2002. During winter 2002, relatively high numbers of ctenophores and krill were once again seen, although much reduced in comparison with the first winter. In addition, juvenile krill seemed to be as abundant under the sea-ice as larval krill during winter 2002, which was not the case in winter 2001. These observations are similar to ones made from ROV deployments during both winter seasons.

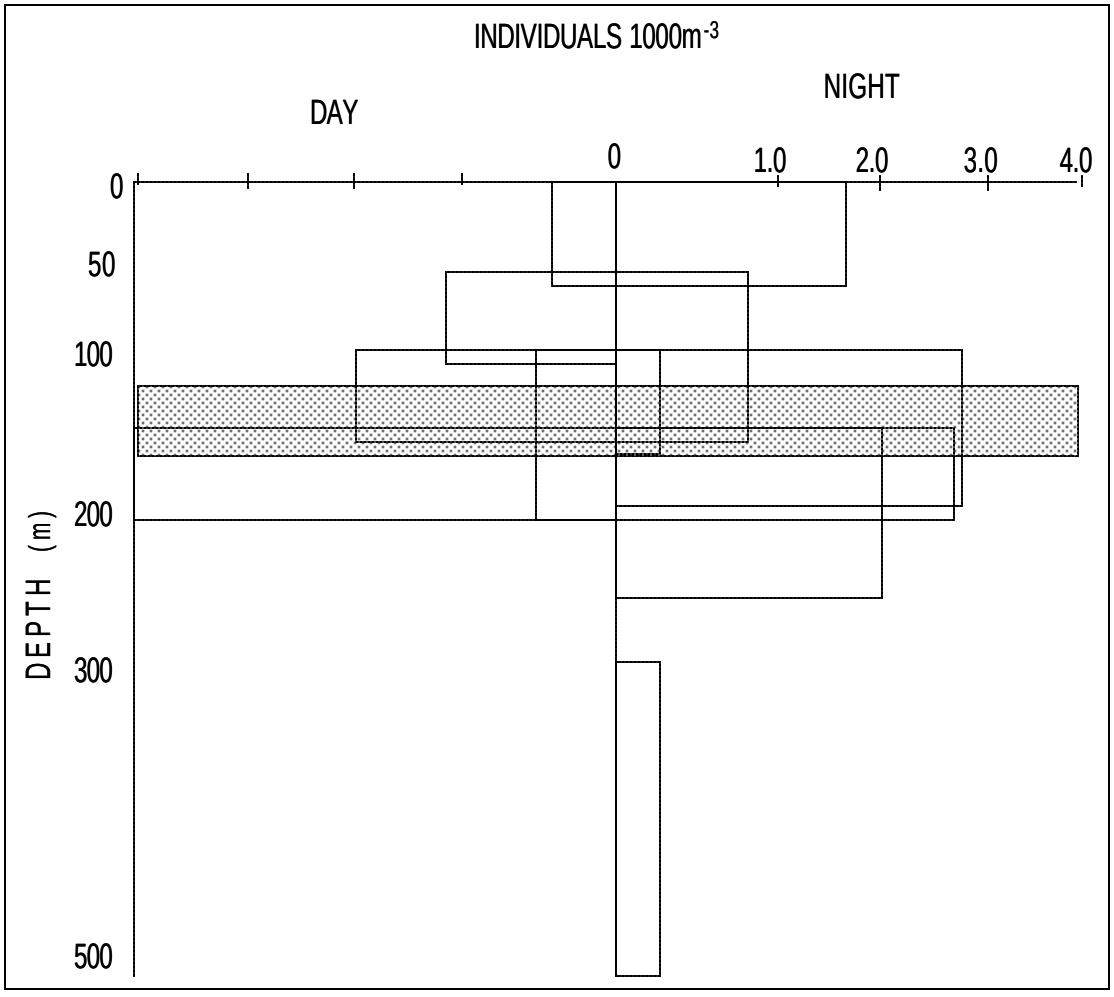

Figure 6. *Callianira antarctica.* Diel vertical distribution during winter 2002 measured for 13 stations total (5 day and 6 night). The pycnocline is indicated by the shaded area located between 150-200m.

DISCUSSION

Length frequency. The wide range in ctenophore lengths found over autumn and winter for *C. antarctica* is not uncommon for polar species of ctenophore, and may represent the presence of multi-year classes. Oral-aboral lengths of less than 10 to greater than 50 mm have been reported for *M. ovum* from the Arctic (Percy 1989, Swanberg & Båmstedt 1991b, Siferd & Conover 1992) for summer, autumn and winter. Their persistent presence and length distribution over many seasons suggests that *M. ovum* is a long lived species, possibly two or more years (Percy 1989). The same could be true for *C. antarctica*, however sampling during spring and summer months would be needed to confirm this. Ctenophore lengths did not appear to be related spatially with the different regions or physical features (i.e. ice edge) of the study area. In the Arctic, Swanberg and Båmstedt (1991b) found larger *M. ovum* at the ice edge and smaller animals in open water. The less turbulent waters within the pack-ice would provide a more favorable environment for larger gelatinous organisms, therefore we would expect to see a difference in the sizes of organisms inhabiting ice-covered versus open water. In this study, the abundance of ctenophores off-shore was reduced and fewer animals were measured; consequently the small sample sizes for each station did not permit estimation of mean lengths for these different regions, which could have indicated such a relationship.

Ctenophore lengths changed seasonally from a unimodal distribution in autumn to a bimodal distribution in winter. The mean ctenophore length during autumn, 45.4 mm, fell directly between the smaller (10-40 mm) and larger (50-70 mm) size cohorts for winter. This type of bimodal size distribution, usually suggestive of a recent reproductive

event, is uncommon for winter populations of ctenophores, although *Pleurobrachei pileus* from the Black Sea was shown to have two reproductive events a year, including one in winter (Mutlu & Bingel 1999). Spawning in ctenophores can be prolonged, as in the case of *M. ovum*, where ctenophore eggs in Resolute Passage can be found over most of the year; however, large numbers of these eggs are only found between spring and summer (Siferd & Conover 1992). Egg production in ctenophores is highly dependant on food supply (Reeve et. al 1989) and temperature (Kremer 1994, Sullivan et al. 2001, Weisse et al. 2002), both of which are reduced in the upper water column in the Antarctic during autumn and winter (Siegel 1988, Lancraft et al. 1991, Ashjiaan et al. in press). Therefore it is unlikely, although not impossible, that the two size cohorts are due to a reproductive event occurring in late autumn/early winter. The bimodal length frequency for winter may have also been the result of a portion of the ctenophore population experiencing 'degrowth'. During times of low food availability ctenophores are known to metabolize their own body tissue, causing them to shrink in size (Reeve & Walter 1978). Ashjian et al. (in press) reported a significant reduction in zooplankton biomass in the Marguerite Bay region from autumn to winter 2001; thus it is possible that *C. antarctica* were suffering from decreased prey availability and utilizing internal reserves. However, a portion of the population may have experienced growth, as indicated by the larger size cohort. The circumstances causing the success of some of ctenophores and the starvation of others is not clear, however the patchy food environment may be one such variable. One last and very possible explanation for the bimodal length frequency is that the population sampled during autumn may not have been the same one sampled during winter. Although this is always a possibility when sampling marine populations, the

different sampling strategies used between autumn and winter further complicates matters. Autumn collections were intensified at stations closer to the coastline of Adelaide and Alexander Islands, with not as much coverage provided mid-shelf and in southern portions of the study area, whereas winter sampling close to shore and in the fjord regions was hindered by heavy pack ice. Despite the fact ctenophore lengths did not appear to be related to region in either season, it is possible that different length frequency distributions for autumn and winter 2002 resulted from sampling different populations.

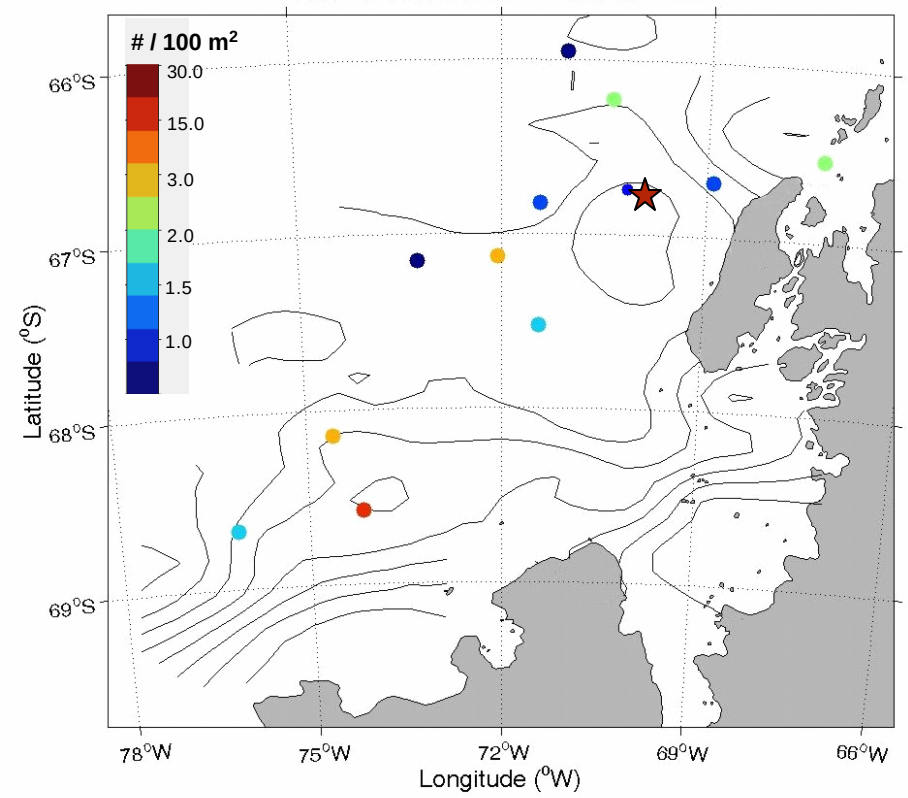

Figure 7. *Callianira antarctica.* Depth integrated abundance (m^{-2}) over the study area during winter 2002. The circles specify stations where abundance was measured with net tows, and are colored according to their relative abundance. The station of highest abundance, designated by the red star, is associated with the large clockwise gyre, as illustrated by the dynamic topography calculated at the surface relative to 400 m. The dominant circulation features shown with the dynamic topography in this figure for autumn 2002 were similar to those occurring in winter (Klink pers comm.).

Distribution and abundance. *Callianira antarctica* occurred mostly within the upper 200 meters of the water column during both day and night hours, though diurnal differences in depth maxima were observed. During the day, ctenophore abundance gradually increased down to about 150 to 200 m, where the maximum abundance occurred. In contrast, ctenophore abundance at night decreased from a sub-maximum concentration at 0-50 m down to about 100 to 200 m, where the largest abundances were found. Lancraft et al. (submitted) observed a similar depth distribution pattern during autumn for *C. antarctica* in Croker Passage: a shallow and deep depth maxima during the night, and during the day a single depth maxima near that of the deeper night-time depth maxima.

Both day and night depth maxima for *C. antarctica* in this study were located within and just below the pycnocline, where greater concentrations of prey may accumulate. Vertical distributions described for *Callianira* spp. in the Antarctic have shown increased ctenophore concentrations at depths where zooplankton prey are found in abundance. In Port Foster, Deception Island, *Callianira* spp. remained in the 100-150 m depth range coincident with *Euphausia crystallorphias* and *E. superba* during early winter, and with *Metridia gerlachei* during early summer (Kaufmann et al. 2003). In Croker Passage, *C. antarctica, Thermisto gaudichaudi* and *E. superba* were the only zooplankton species, in addition to salps, to occur in surface waters at night during autumn. *Callianira antarctica* in the Marguerite Bay region during winter may concentrate at shallower depths during the night to increase their predation effort on larval krill associated with the under-ice surface, as was observed during nighttime ROV deployments. However, this behavior was also observed during SCUBA dives conducted during daytime hours. Larval krill

and copepods in the Antarctic are not known to under-go diel vertical migration (DVM), thus it is unlikely that ctenophores were following a DVM pattern of their prey. Hence, the increased concentration of ctenophores in the surface waters may have been due to other unknown factors. The volume of water sampled for all six night tows was twice the volume sampled during daytime tows. Therefore, diurnal differences in ctenophore distribution may have been an artifact of sampling.

The depth-integrated abundances of *C. antarctica* were variable but low, with the largest abundance (2.6 ind m^{-2}) two orders of magnitude greater than the smallest (0.02 ind. m^{-2}). The horizontal distribution of these abundances over the study area indicated that higher numbers of ctenophores were associated with the large clockwise gyre occupying the northern portion of the shelf, and lower numbers occurring over the shelf break, where the strong northeast flow associated with the ACC may disperse ctenophores in this region. Local hydrology and topography interact to produce retentive features, such as gyres, that support entrapment of gelatinous zooplankton into large aggregations (Graham et al. 2001). For example, in the summer of 1979, Pagès et al. (1994) found high abundances of gelatinous zooplankton in the eastern part of the Weddell Gyre. The spatio-temporal horizontal distribution of *P. pileus* over a number of seasons was found to be related to the general circulation of the Black Sea, where high concentrations of ctenophores were found at the northern peripheries of anti-cyclonic eddies (Mutlu & Bingel 1999). Higher densities of *C. antarctica* were also found in the southern shelf region of the shelf, where the southwestward flow from Marguerite Bay may advect large numbers of *C. antarctica* to this region. Ashjian et al. (in press) reported elevated abundances of zooplankton over the southern shelf region located in the

southwestward current during autumn and winter of 2001. Large aggregations of *C. antarctica* coinciding with elevated abundances of krill and copepods occurring in the southern shelf region, or within the northern shelf meso-scale gyre, may have a distinct predatory impact on these populations.

The mean abundance for *C. antarctica* (0.45 ind m^{-2}) during winter was much lower than values reported for other ctenophores from temperate and tropical regions during different seasons. For instance, abundance of *P. pileus* in the Black Sea during winter was as high as 696 ind m^{-2} (Mutlu & Bingel 1999). In the Norwegian Sea, *P. pileus* sampled during summer had a mean abundance of 12.4 ind m^{-2}, and a maximum abundance of 111 ind m^{-2} (Båmstedt 1998). *Pleurobrachia pileus* off Southwestern Nova Scotia was found in similar abundance, although there were extreme inter-annual variations (Frank 1986). *Callianira antarctica's* mean abundance was also an order of magnitude lower than that of the Arctic ctenophore *M. ovum*. Percy (1989) found that the Arctic ctenophore *M. ovum* from Frobisher Bay had a stable population structure, with similar mean abundances in summer and winter, 4.2 and 3.4 ind m^{-2}, respectively. *Mertensia ovum* in Resolute Passage was also shown to have a low winter and summer abundance, although maximum abundance during spring was as high as 911 ind m^{-2} (Siferd & Conover 1992). However, the mean abundance for this species in the Barents Sea during spring was low, 0.95 ind m^{-2} (Swanberg & Bamstedt 1991b). These observations demonstrate the large variability in *M. ovum* abundance over the Arctic. The same may be true for *Callianira* sp., as Lancraft et al. (1991, submitted) reported a much lower mean winter (0.016 ind m^{-2}) and autumn abundance (0.034 ind m^{-2}) for the Scotia Sea and Crocker Passage than was seen in the WAP region during this study.

In this study, *C. antarctica* was the dominant ctenophore found in autumn and winter for both years. Their predators, *Beroe* sp., were uncommon during these sampling periods. The lack of abundance data from other seasons prohibits making an accurate evaluation of the population structure of *C. antarctica* in the Marguerite Bay region. Nevertheless, *C. antarctica's* widespread distribution during both autumn and winter, combined with fact that this species, along with *Beroe sp.,* is the predominant ctenophore mentioned in reports concerning zooplankton ecology in this and nearby regions, indicate that this species, like *M. ovum* in the Arctic, is a persistent member of the zooplankton community in waters west of the Antarctic Peninsula.

CHAPTER FOUR

CHEMICAL COMPOSITION, METABOLISM AND FEEDING ECOLOGY

RESULTS

Chemical composition. A total of 32 *C. antarctica*, 8 from autumn and 24 from winter 2002, were measured for total length, WW, DW, and C/N content. The seasonal relationship between length and dry weight for *C. antarctica* is shown in Fig. 8A. Autumn ctenophores ranged in length from 35.0 to 83.6 mm, with a median length of 46.5 mm (Table 2). Dry weights ranged from 149.9 to 757.6 mg and averaged 3.9% (± 0.8 SD) WW. Water accounted for 96 to 98% WW during autumn. Winter ctenophores ranged from 8.5 to 98.0 mm in length, and had a median length of 25.5 mm (Table 2). Dry weights ranged from 2.8 mg to 1.4 g, and averaged 4.4% (± 0.5 SD) WW. Water comprised 94 to 97% WW for winter ctenophores. The average ash content of ctenophores (n = 9) during winter was 78.9% (± 0.03 SD) DW.

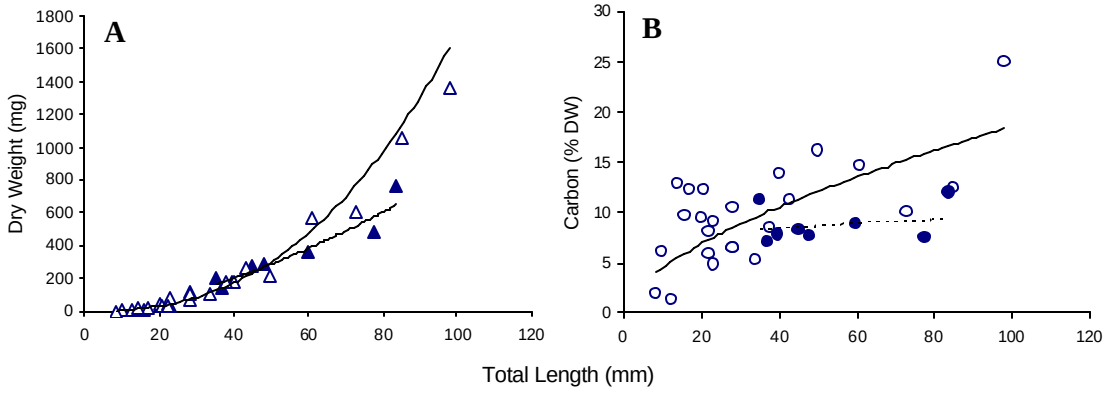

Figure 8. *Callianira antarctica*. The seasonal relationship between total length and (A) dry weight and (B) carbon concentration for autumn (filled symbols) and winter (open symbols) 2002. Autumn: $DW=(0.58)TL^{1.5855}$, $\%C=(4.8983)TL^{0.1435}$; Winter: $DW=(0.0179)TL^{2.4861}$, $\%C=(1.0683)TL^{0.6194}$

Table 2. *Callianira antarctica*. Total length, dry weight (DW), and water content as percent of the DW for autumn and winter 2002

	Total Length (mm)		Dry Weight (mg)		Water (%WW)		Carbon (% DW)		Nitrogen (% DW)		
Season	Median	Range	Median	Range	Mean	Range	Mean	Range	Mean	Range	*n*
Autumn	46.5	35.0 - 83.6	276	150 - 758	96.1	95.7 - 97.9	8.60	7.00 - 12.0	1.92	1.55 - 2.38	8
Winter	25.5	8.5 - 98.0	76.6	2.8 - 1366	95.5	94.2 -97.0	8.35	1.41 - 24.9	1.80	0.30 - 4.43	24
Combined	34.5	8.5 - 98.0	132.6	2.8 - 1366	95.7	94.2 - 97.9	8.41	1.41 - 24.9	1.83	0.30 - 4.43	32

There was a weak positive correlation ($r = 0.31$, $p = 0.05$) between total length and carbon concentration (%DW) during autumn, which may be attributed to the small sample size, and a higher positive correlation ($r = 0.69$, $p = 0.05$) during winter (Fig. 8B). Body carbon and nitrogen content for autumn animals ranged from 7.0 to 12.0% DW and 1.6 to 2.4% DW, respectively. The range for winter carbon (1.4 to 24.9% DW) and nitrogen (0.3 to 4.4% DW) values was much broader, possibly due to the larger sample size. Geomean carbon and nitrogen (%DW) values of *C. antarctica* are given in Table 2. The total body carbon and nitrogen content increased with ctenophore size for both seasons (Fig. 9A-B). The similarity between the autumn and winter slopes of these data suggests that there was little seasonal change in body carbon and nitrogen content.

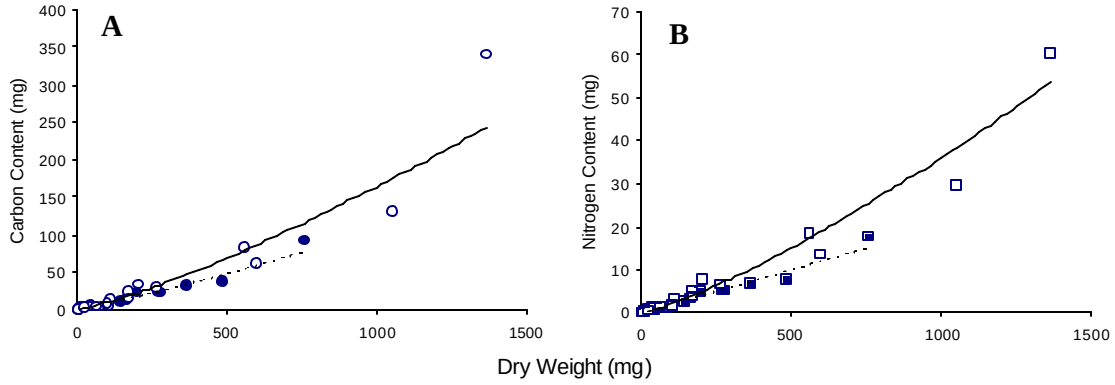

Figure 9. *Callianira antarctica*. The seasonal relationship between dry weight and (A) total carbon and (B) total nitrogen for autumn (filled symbols) and winter (open symbols) 2002. Autumn: $C=(0.034)DW^{1.17}$, $N=(0.016)DW^{1.03}$; Winter: $C=(0.029)DW^{1.25}$, $N=(0.006)DW^{1.26}$

Metabolic Rates. During winter 2002 ammonium excretion rates were measured for 15 ctenophores ranging in total length from 8.5 to 85.0 mm, with a median length of 28.0 mm. Oxygen consumption is reported for a subset of these ctenophores (n = 10), having the same range in total length but a median length of 31.0 mm (Table 3). Both oxygen consumption and nitrogen excretion rate per individuals increased with increasing ctenophore body size (Fig. 10). The regression of oxygen consumption versus DW for *C. antarctica* yielded a value of b = 0.92 for the allometric equation:

$$Y = aW^b,$$

where *Y* is metabolic rate, *a* is the intercept, *W* is dry weight (mg), and *b* is the exponent reflecting the effect of size (Fig. 10). This *b* value is near unity, indicating that the oxygen consumption per unit mass decreased only slightly with increasing ctenophore size. The geometric (GM) regression model (linear regression of log-log transformed data) for oxygen consumption as a function of DW indicated a larger decrease in respiration per unit mass with increasing ctenophore size (*b* = 0.80). Both the geometric and conventional regressions for oxygen consumption as a function of body carbon showed a weight-dependent relationship (*b* = 0.85 and 0.71, respectively) between respiration and carbon content. The weight-specific oxygen consumption and ammonium excretion rates decreased with increasing size, indicating greater relative metabolic requirements for smaller ctenophores. Dry weight-specific and carbon-specific oxygen consumption rates calculated for individual *C. antarctica* ranged from 0.059 to 0.411 µl O_2 $[mg\,DW]^{-1}$ h^{-1} and 0.471 to 7.15 µl O_2 $[mg\,C]^{-1}$ h^{-1}, respectively. Dry weight-specific nitrogen excretion rates ranged from 0.60 to 31.1 µg-at N $[g\,DW]^{-1}$ h^{-1}. Geomean oxygen consumption and nitrogen excretion rates are provided in Table 3.

Table 3. Oxygen consumption and ammonium excretion rates for *Callianira antarctica* and 7 other species of ctenophore

Species	Oxygen consumption			Ammonia excretion	Temperature	n
	µl O2 ind^{-1} hr^{-1}	µl O2 $[mg\ DW]^{-1}$ h^{-1}	µl O2 $[mg\ C]^{-1}$ h^{-1}	µg-at N $[g\ DW]^{-1}$ h^{-1}	°C	
Callianira antarctica	14.9	0.163	2.11	9.39	0	10,16
[a]*Mertensia ovum*	nd	0.074 (+ 0.028)	nd	0.24	0	59
[b]Mertensiidae sp.	12.1 (± 6.30)	0.129	nd	8.11	-1.6	8*
[b]*Beroe* sp.	15.6 (+ 3.40)	0.025	nd	2.64	-1.5	7*
[c]*Pleurobrachia pileus*	1.08 - 1.17	0.140 - 0.280	nd	nd	7 - 7.5	4
[d]*Bolinopsis infundibulum*	nd	0.054	3.05	nd	5 - 6	10
[e]*Bathocyroe fosteri*	nd	0.042 (+ 0.021)	nd	0.01 - 0.14	9 - 12	49
[f]*Mnemiopsis leidyi*	30.4	0.070 - 0.231	4.12 - 13.6	0.483 - 1.53	10 - 24	40

[a]Percy (1988), [b]Ikeda & Bruce (1986), [c]Ikeda (1974), [d]Baily et al. (1994), [e]Youngbluth et al. (1988), [f]Kremer (1977)
*Number of experiments performed; 2 to 5 animals each.

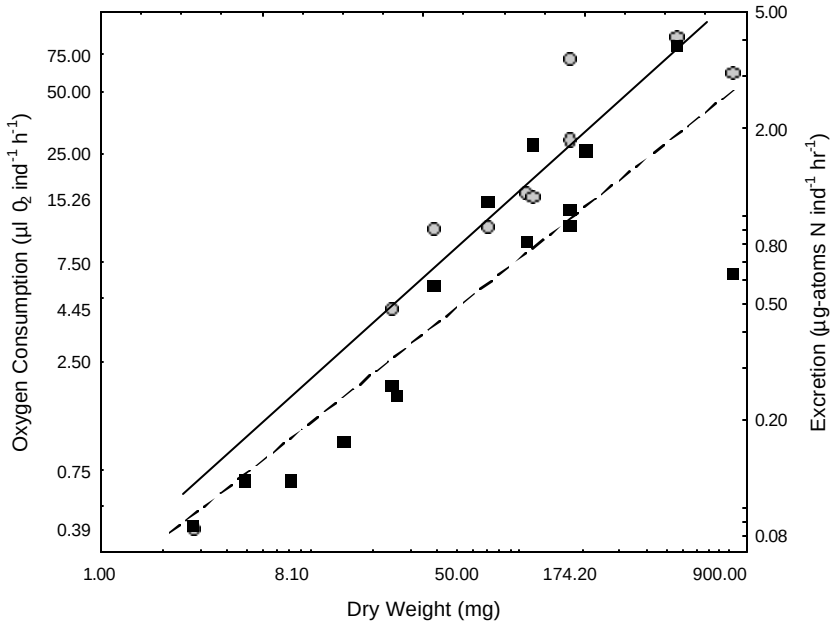

Figure 10. *Callianira antarctica*. The relationship between oxygen consumption (circles), ammonium excretion (squares) and dry weight. T = 0.5° C. The equations for respiration and excretion are, respectively: Oxygen consumption = $0.237\ DW^{0.92}$ ($r^2 = 0.91$), and ammonium excretion = $0.051\ DW^{0.58}$ ($r^2 = 0.76$).

The ratio of oxygen uptake to nitrogen-excretion rate (atomic O:N ratio) varied from 6.37 to 138, with no relationship to ctenophore size. The geomean O:N ratio was 28.8, indicating protein-oriented metabolism (Mayzaud & Conover 1988). Other studies on ctenophore respiration and excretion have determined that ctenophores metabolize both protein and lipids (Kremer 1977), therefore many authors assume an intermediate RQ

value of 0.8 when determining carbon respiration. The proportion of each component metabolized, however, may vary significantly with season and food availability (Hoeger 1983, Kremer 1982, Percy 1988) and is further complicated by different biochemical pathways for nitrogen metabolism (Mayzaud & Conover 1988). For this reason, both lipid and protein RQ values were used to determine the amount of carbon that *C. antarctica* potentially needed to consume each day to support metabolism. The range in minimum daily carbon requirements was estimated by converting the mean oxygen consumption rate per individual to carbon respired using Gnaiger's (1983) respiratory quotient (RQ) values of 0.97 for protein and 0.72 for lipid catabolism. According to Gnaiger (1983), the excretory end-product determines the RQ value in protein catabolism: 0.97 for ammonia and 0.84 for urea. Since gelatinous zooplankton are ammonotelic, 0.97 is the appropriate RQ value for protein for this study. Based on the oxygen consumption rates for *C. antarctica*, daily carbon requirements for small ctenophores (= 30 mm TL) ranged from 3.6 to 190.3 µg, and for larger ctenophores (> 30 mm TL) 150.5 µg to 1.13 mg. The daily carbon requirement varied between 2.7% and 3.6% of the body total carbon for small ctenophores, and between 1.4% and 1.9% of the total body carbon for larger ctenophores.

Feeding behavior. During winter 2001 and 2002, SCUBA divers observed high numbers of *Callianira* sp. (> 1 ctenophore m^3) just under the pack ice where larval krill aggregated. The ctenophores were passively drifting, mouth oriented upwards, with their tentacles extended outward approximately ten times their body length or greater, characteristic of an ambush entangling predator (Greene 1985). Ctenophores imaged under ice during late night hours by an ROV showed similar behavior. Our combined

observations of ctenophore predatory behavior under sea ice, and the presence of prey in the guts of ctenophores collected during late afternoon and evening tows, suggest that these ctenophores search for food continuously over a 24 h period.

Callianira antarctica feeding behavior also was observed during experiments in winter 2002. After ctenophores were placed in 500 ml polypropylene jars containing prey, they typically proceeded to set out their tentacles by swimming in a circular pattern around the jar. Due to jar volume constraints, ctenophores were not able to release their tentacles to the extensive lengths observed *in situ* by divers and the ROV. ROV images also indicated that once ctenophores had extended their tentacles, they drifted passively with currents. In jars, after one or more prey were caught in a tentacle, the ctenophores typically stopped swimming and began retracting their tentacles, drawing the prey close to their body. The actual ingestion of prey into the mouth was observed on only two occasions. In both instances, once the ctenophore had drawn the prey closer to its body, it 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 fairly quickly from the mouth down into the stomodeum (pharynx).

Digestion time. During winter 2002, 21 digestion time experiments were performed with ctenophores ranging in size from 20 to 55 mm total length. Temperature was nearly constant (-1.0 to -1.8^{o}C), however type and number of prey varied with each experiment. 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*. Nearly half of the experiments

(48%) involved digestion of one prey item and 14% involved 2 prey items. The largest meal digested was 6 prey (n=1). In order to compare digestion rates among experiments involving different prey types, digestion times were normalized by prey DW, body carbon or body nitrogen. The DW, carbon and nitrogen values for the prey are listed in Table 4.

Table 4. Average dry weight (DW), body carbon (C) and body nitrogen (N) values for each stage of prey used in digestion time experiments

Prey	Stage/Sex	DW (µg)	C (µg)	N (µg)	*n*
Euphausia superba	F4	514 + 27.4	160[†]	43.6[†]	8
Euphausia superba	F5	809 + 41.6	221[†]	60.1[†]	10
Euphausia superba	F6	1,080 ± 51.0	277[†]	75.2[†]	26
Euphausia superba	Juv/20 mm	10,309[‡]	4,264[‡]	879[‡]	33
Thysanoessa macrura	Juv/11–15mm	6,478	3,279	565	5
Thysanoessa macrura	Juv/15-20 mm	14,530	7,369	1039	4
Metridia gerlachi	Fe	313	103	20.1	6
Calanus propinquus	Fe & Ma	1,173	571	88.6	19

[†] C = 406*DW-37.2, N =83.3*DW-1.10 (Daly submitted)
[‡] C = $0.06*L^{3.73}$, N = $0.02*L^{3.57}$, DW = $0.7*L^{3.20}$ (Daly unpublished)

The digestion process may be described in terms of five stages based on observations from 18 of the winter experiments (Table 4, Fig. 11). The time intervals for each digestion stage are shown for each experiment in Fig. 12. Three digestion time experiments were omitted from the assessment of average stage duration, because small, lingering portions of prey tissue or an excessive amount of food ingested resulted in exceptionally long digestion times. The digestion process began with the ingestion of prey (Stage I), and ended when most (<0.5 mm digested matter remaining) or all of the digested matter was cleared from the gut (Stage V). *Callianira antarctica* typically

digested the soft tissue first, and egested the exoskeletal remains through its mouth last. There were a few occasions, however, when soft tissue remained after all of the exoskeletal parts were egested. For all eighteen experiments analysed, Stage II occurred within 5 h after ingestion of prey, and Stage III took place within 9 h. The duration of Stages IV and V were much more variable, ranging from 3 to 18 h and 5 to 21 h, respectively, and appeared to be highly influenced by prey type and/or carbon content (Fig. 12).

Digestion times for all experiments (n = 21) ranged from 5 to 46 h, although in 86% of the experiments digestion was completed within 8 to 20 h, with a median time of 11.5 h. Neither total digestion time nor the hourly digestion rate as a function of ingested prey dry weight (digestion [mg prey DW]$^{-1}$ h^{-1}) were correlated ($p = 0.5$) with ctenophore size (Fig. 13). Total digestion time was positively correlated with ingested prey dry weight, carbon content, and nitrogen content (Fig. 14); the strongest correlation being with ingested carbon ($r = 0.95$, $P < 0.05$). The influence of prey type on digestion time was directly related to the elemental composition of the prey, i.e. species rich in carbon and nitrogen usually took longer to digest than species lower in elemental composition. Based on two trials, *T. macrura* typically took 1.4 times longer to digest than a *E. superba* of similar or larger size, probably because *T. macrura* had on average 1.7 times higher carbon content (*E. superba*: 4.26 mg C; *T. macrura*: 7.37 mg C). However, when multiple *E. superba* furcilia 6 were ingested, the meal, totalling less than 2.0 mg of carbon content, took almost a half hour longer to digest than the *E. superba* juvenile mentioned previously. In this case, the size of the food bolus or refractory body components may have retarded the digestion process. Even though digestion time

increased with the ingestion of more than one individual of the same prey type, a doubling or tripling of prey ingested did not usually correspond with a doubling or tripling in digestion time (Fig. 15).

Table 5. *Callianira antarctica*. Digestion stage categories defined from winter 2002 digestion time experiments

Stage	Hours	Description
I	--	Newly ingested prey, perfectly intact. Can usually see small amount of tentacle mass in bottom of pharynx.
II	1 to 5	Losing distinguishable shape due to soft tissue digestion.
III	2 to 9	Soft tissue completely separated from carapace, and usually sequestered at the bottom of the pharynx as one mass.
IV	3 to 18	Only small amount (equal to or less than 1.0 mm^2) of digestive tissue remaining in stomodeum. Pieces of exoskeleton may or may not be completely egested.
V	5 to 21	Most or all soft tissue and/or exoskeletal pieces digested or egested.

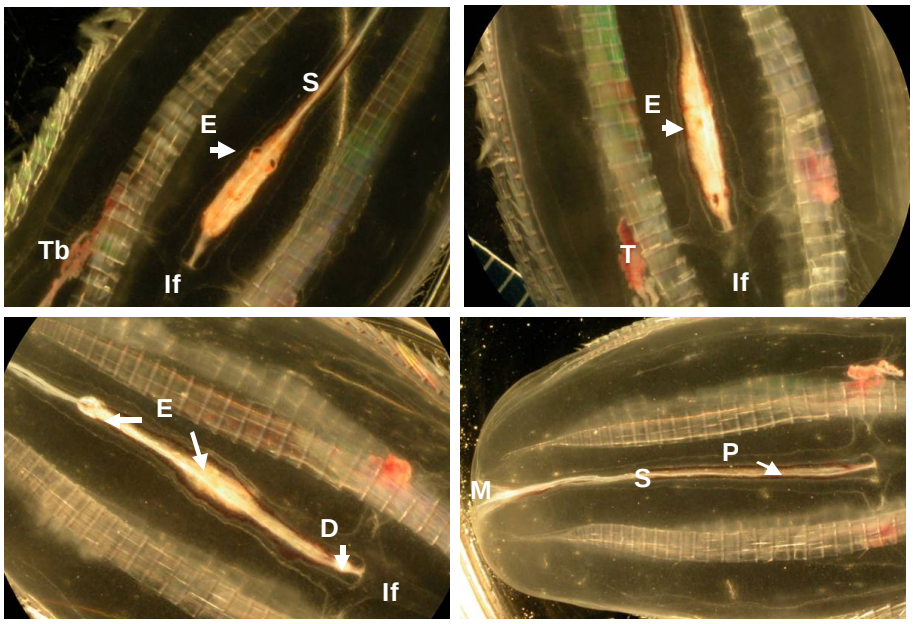

Figure 11. *Callianira antarctica*. Images of *Euphausia superba* in the ctenophore stomodeum during digestion Stage (from top left to bottom right) I, II,III/IV and V of digestion. Es=*Euphausia superba*, S=stomodeum, T=tentacle, If= infundibulum, Ex=exoskeleton, Dm=digested matter, M=mouth, Pc= pharyngeal canal.

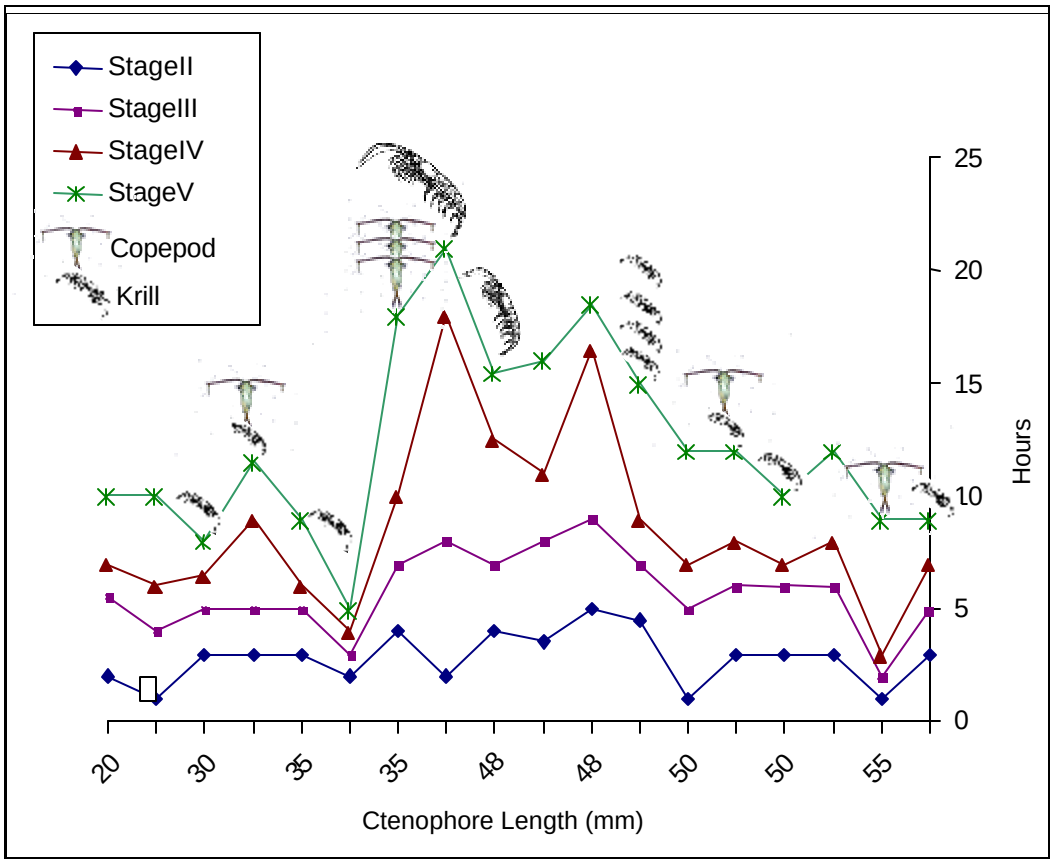

Figure 12. *Callianira antarctica*. Digestion stage intervals (h) for each experiment in relation to ctenophore length. The type, as identified in the legend, and number of prey digested are displayed for selected experiments.

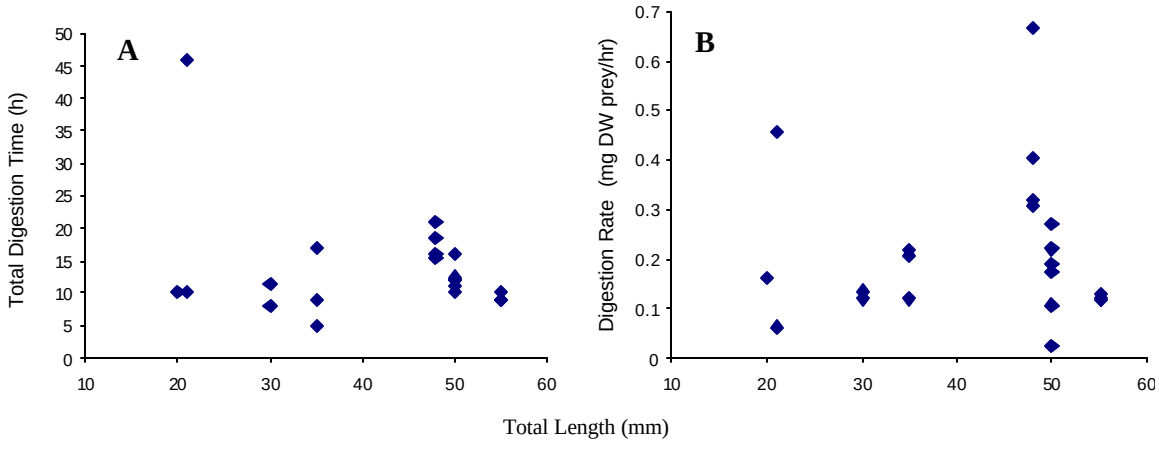

Figure 13. *Callianira antarctica*. Ctenophore length versus (A) digestion time and (B) weight-specific digestion rate.

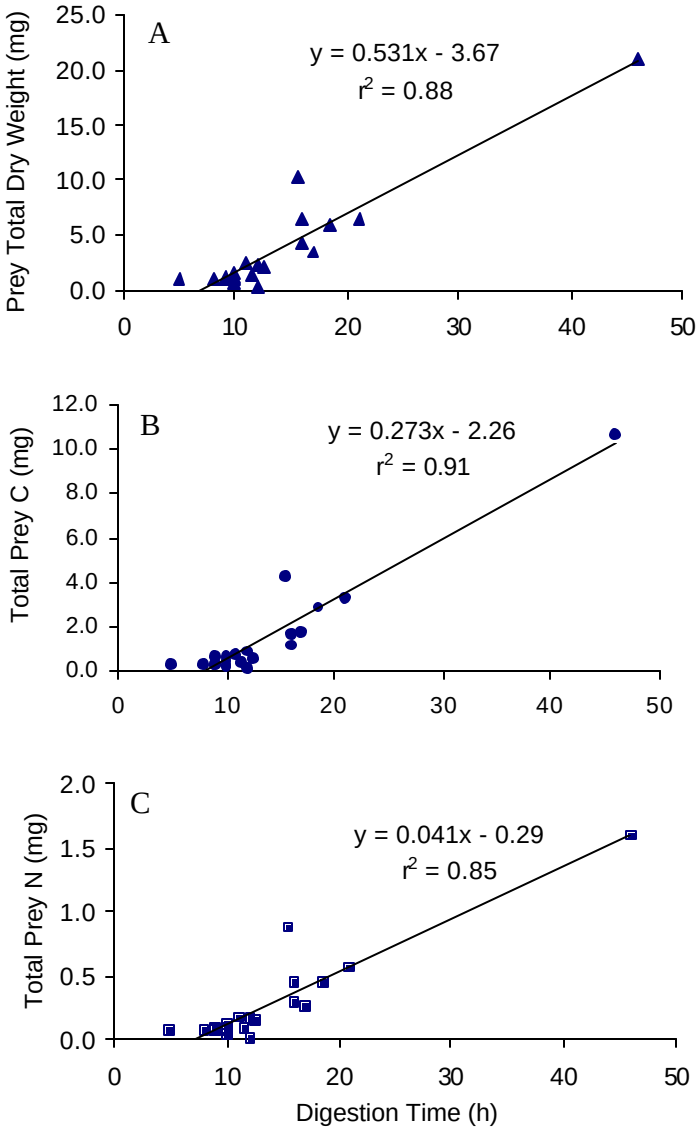

Figure 14. *Callianira antarctica*. The relationship between total digestion time and (A) ingested prey dry weight, (B) total carbon, and (C) total nitrogen content.

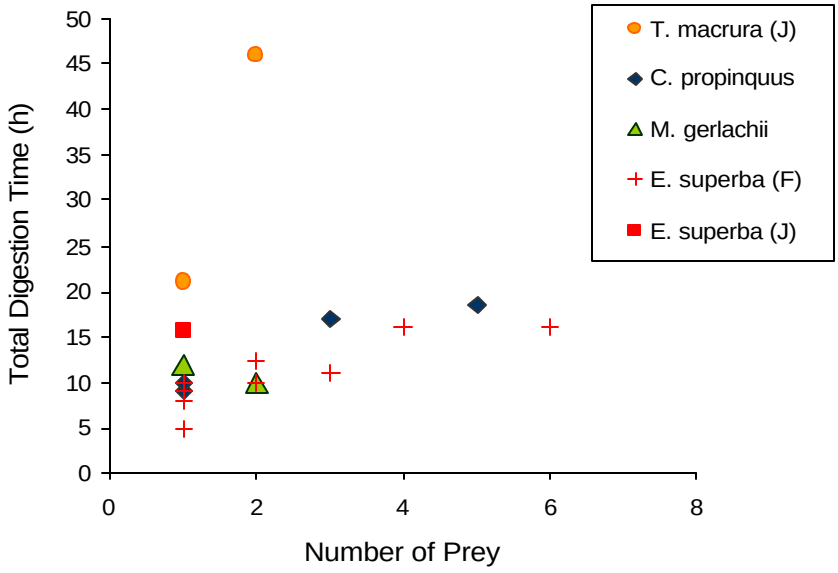

Figure 15. *Callianira antarctica*. Number of prey ingested versus total digestion time. Prey types are represented by different symb ols as indicated by the figure legend.

Lipid storage. *Callianira antarctica* does not have oil sacs like those found in *M. ovum*, instead lipids from prey accumulate in the stomodeum (Larson & Harbison 1989). The presence or absence, and accumulation of lipid reserves found in the stomodeum of *C. antarctica* collected during this study was recorded before, during and after winter digestion experiments (Fig. 16). Lipid was not present in the ctenophore stomodeum at the beginning of 29% of the experiments, half of which involved digestion of larval *E. superba*, and the other half involved digestion of *M. gerlachii* and *C. propinquus*. None of the experiments with larval *E. superba* as prey resulted in the presence of lipid after digestion, but all of the experiments with copepods did result in the presence of lipid. Of the experiments that began with lipid present in the ctenophore stomodeum (53%), in all cases, including those with krill larvae, the lipid "droplet" increased in volume with each meal, the amount of increase varying with prey number and type. Digestion of *C.*

propinquus resulted in the largest percent increases (>100%) in lipid volume (Fig. 16). The percent increase from *M. gerlachii* and euphausiid juveniles was consistently low, whereas larval *E. superba* was highly variable, but lower than that of *C. propinquus*.

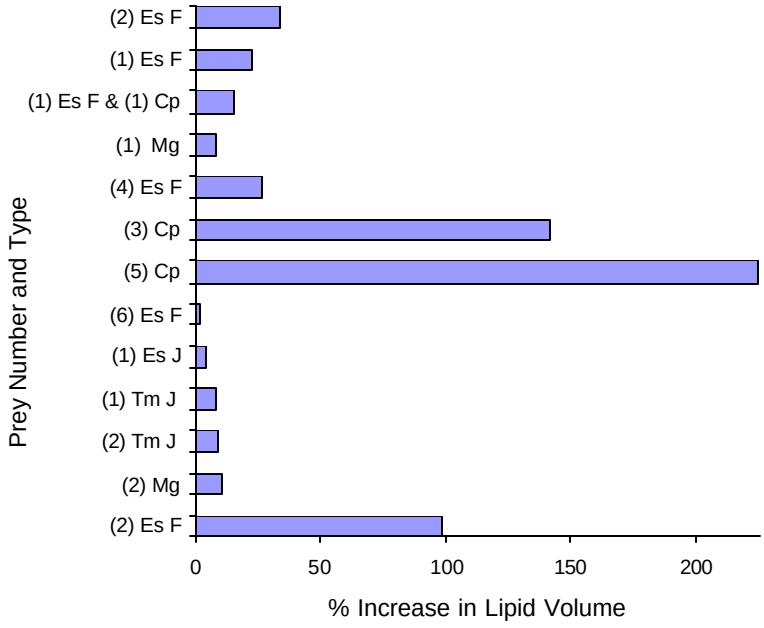

Figure 16. *Callianira antarctica*. Percent increase in lipid volume measured in guts of *C. antarctica* after digestion of prey. Length of the ctenophore, and the number (in parentheses) and type of prey digested are shown for each experiment. Es F=*Euphausia superba*, Tm=*Thysanoessa macrura*, Cp=*Calanus propinquus*, Mg=*Metridia gerlachii*, J=juvenile.

Lipid biomarker analysis. A composite sample of 7 ctenophores collected in autumn (2002) and 2 ctenophores collected in winter (2002) were analyzed for total lipid content and lipid class composition. Total lipid content in *C. antarctica* was slightly higher in winter (4.76 ± 0.57 % DW) than in autumn (3.51%DW), with phospholipids (PL) accounting for more than 50 % of the total lipid content (Fig. 17). Free fatty alcohols (FALC), which are products of hydrolysis of dietary wax esters, were also detected at levels > 10% of total lipid content. The lipid class composition differed

seasonally in that significant amounts of wax esters (WE) and triacylglycerols (TG) were only detected in animals from autumn. Both euphausiids and copepods contained relatively large quantities of lipid, =10% of dry weight, with the exception of larval krill from winter, which had comparatively smaller quantities (Fig. 17). WE were by far the dominant lipid class for copepods during both seasons, while TG and PL were observed in equal amounts in the adult *E. superba*. Larval *E. superba* from winter contained mostly PL, and smaller amounts of cholesterol and TG.

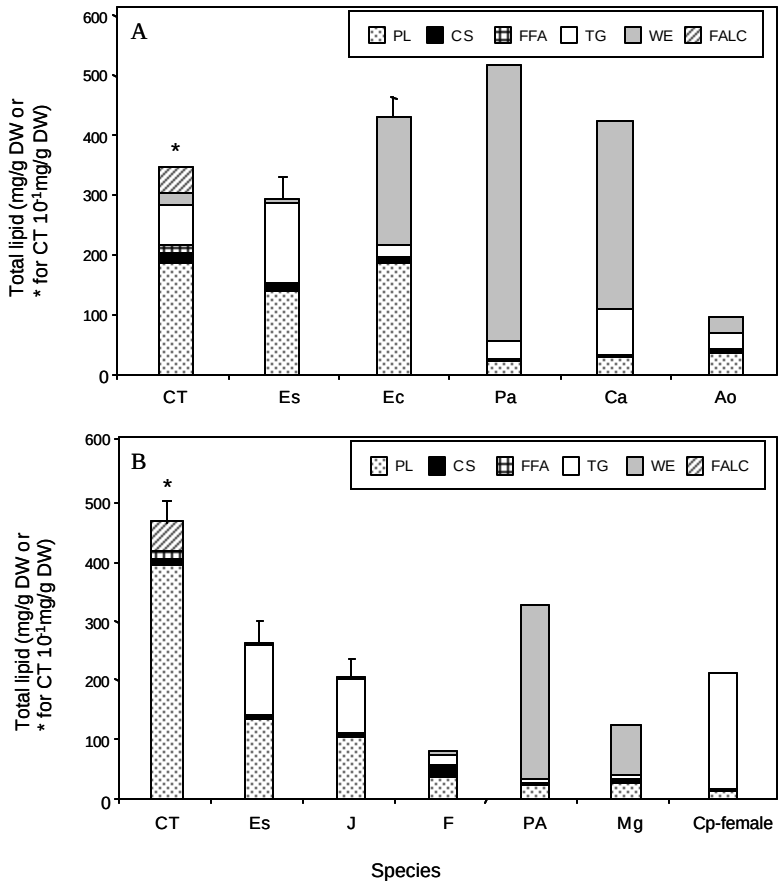

Figure 17. Total lipid content and lipid class compositions (PL=Polar lipids, CS=Cholesterol, FFA=Free fatty acids, TG =Triacylglycerols, WE=Wax esters, FALC=Free fatty alcohols) of ctenophores and their potential prey sampled during autumn (A) and winter (B). CT= *Callianira antarctica*, ES=*Euphausia superba*, EC=*Euphausia crystallorophias*, PA=*Paraeuchaeta antarctica*, CA=*Calanoides acutus*, AO=*Antarctomysis ohlini*, MG=*Metridia gerlachei*, CP=*Calanus propinquus*. Data without error bars represent the composite samples. From: Ju et al. submitted.

Table 6. *Callianira antarctica*. Fatty acid and alcohol composition (% of total fatty acid and alcohol) of ctenophores sampled during autumn and winter, 2002. From: Ju et al. submitted

	Fall* (n=5)		Winter (n=2)	
	Acid	**Alcohol**	**Acid**	**Alcohol**
n-Saturates				
12:0	Tr	-	1.3±0.6	-
14:0	6.6	2.8	5.6±0.8	-
16:0	15.5	2.2	16.3±1.0	-
18:0	1.5	0.1	1.4±0.1	-
20:0	0.1	Tr	0.1±0.1	0.1±0.1
22:0	-	-	-	0.2±0.0
Monounsaturates				
14:1(n-3)	Tr	-	Tr	-
16:1(n-9)	Tr	-	Tr	-
16:1(n-7)	7.6	0.4	6.4±0.6	-
16:1(n-5)	0.2	-	0.2±0.0	-
16:1(n-3)	Tr	-	Tr	-
18:1(n-9)	14.4	0.9	10.2±0.9	-
18:1(n-7)	5.1	-	5.9±1.2	-
18:1(n-5)	0.4	-	0.5±0.1	-
20:1+	11.6	24.7	3.5±0.6	38.6±0.2
22:1+	1.2	68.1	0.7±0.1	59.1±0.6
24:1(n-9)	-	-	-	0.5±0.1
Polyunsaturates				
16:2(n-6)	0.6	-	0.9±0.0	-
16:3(n-4)	0.2	-	Tr	-
16:4(n-1)	0.4	-	Tr	-
18:3(n-3)	0.1	-	0.2±0.1	-
18:4(n-3)	1.0	-	1.8±0.8	-
18:2+	1.1	-	2.4±0.4	-
20:2(n-6)	0.2	-	0.7±0.1	-
20:4(n-3)	0.3	-	0.6±0.2	-
20:4(n-6)	0.5	-	0.7±0.1	-
20:5(n-3)	21.4	-	26.0±1.3	-
22:4(n-3)	Tr	-	-	-
22:5(n-6)	Tr	-	0.5±0.2	-
22:6(n-3)	9.3	-	12.1±0.9	-
Branched & odd chain	0.5	Tr	1.6±0.3	1.5±0.5
Total concentration (mg g-1 dry wt.)	19.3	3.8	34.3±2.5	6.9±0.5

*Composite samples were used for analysis
+Indicate all isomers combined
-Not detected, Tr = trace amount (<0.1% of total concentration)

Table 7. Fatty acid (FA) and alcohol (ALC) compositions (% of total fatty acid and alcohol) of *Callianira antarctica* and there potential prey. ES=*Euphausia superba*, EC=*Euphausia crystallorophias*, PA=*Pareuchaeta antarctica*, CA=*Calanoides acutus*, AO=*Anarctomysis ohlini*, MG = *Metridia gerlachei*, CP=*Calanus propinquus*. From: Ju et al. (submitted)

a) Fall 2002

	ES -adult (n=4)		EC-adult (n=3)		PA* (n=20)		CA* (n=50)		AO* (n=2)	
Species	**Acid**	**ALC**	**Acid**	**ALC**	**Acid**	**ALC**	**Acid**	**ALC**	**Acid**	**ALC**
n-Saturates										
12:0	-	-	1.3±0.1	-	-	-	-	-	1.3	-
14:0	11.6±0.7	11.0±9.7	1.7±0.3	66.5±1.8	1.1	39.0	4.5	14.8	5.1	18.5
16:0	24.4±1.1	5.9±8.1	17.9±0.7	5.9±8.1	2.9	25.1	10.1	20.0	17.0	24.3
18:0	1.4±0.2	-	1.1±0.1	-	0.1	0.7	0.6	0.9	1.1	0.9
20:0	Tr	-	-	-	Tr	0.2	0.2	0.4	0.1	0.6
22:0	-	-	-	-	-	Tr	-	-	-	0.2
Monounsaturates										
14:1(n-3)	0.1±0.0	-	Tr	-	0.4	0.4	Tr	0.1	0.1	0.1
16:1(n-9)	0.1±0.0	-	0.1±0.0	-	Tr	-	Tr	-	0.1	-
16:1(n-7)	7.2±0.7	-	6.0±0.7	1.7±0.2	27.0	4.9	9.3	3.7	9.1	3.1
16:1(n-5)	0.2±0.0	-	0.1±0.0	-	0.2	-	0.3	-	0.2	-
16:1(n-3)	0.1±0.0	-	0.1±0.0	-	-	-	Tr	-	Tr	-
18:1(n-9)	13.2±1.4	76.5±20.5	38.6±2.0	Tr	27.0	7.3	6.2	5.3	16.9	10.5
18:1(n-7)	7.6±0.4	-	13.4±1.5	-	2.5	Tr	4.6	Tr	6.4	Tr
18:1(n-5)	0.1±0.0	-	0.1±0.0	-	0.7	-	1.1	-	0.7	-
20:1^{+}	1.5±0.1	-	-	-	8.4	12.9	10.3	44.3	6.7	24.3
22:1^{+}	0.8±0.1	2.5±4.9	-	-	1.2	6.1	9.2	9.7	-	13.7
24:1(n-9)	-	-	-	-	-	0.6	-	-	-	2.3
Polyunsaturates										
16:2(n-6)	0.9±0.1	-	1.0±0.1	-	0.5	-	0.9	-	0.6	-
16:3(n-4)	0.2±0.0	-	0.1±0.0	-	0.6	-	1.1	-	0.1	-
16:4(n-1)	0.7±0.0	-	0.1±0.0	-	1.7	-	4.5	-	0.3	-
18:3(n-3)	0.1±0.0	-	0.1±0.0	-	0.1	-	0.1	-	0.1	-
18:4(n-3)	1.2±0.3	-	0.9±0.1	-	1.9	-	2.7	-	0.6	-
18:2^{+}	0.7±0.0	-	1.6±0.2	-	1.0	-	1.3	-	0.9	-
20:2(n-6)	-	-	-	-	Tr	-	Tr	-	0.2	-
20:4(n-3)	0.2±0.1	-	0.1±0.0	-	0.2	-	0.7	-	1.3	-
20:4(n-6)	-	-	-	-	1.1	-	0.2	-	0.2	-
20:5(n-3)	21.3±1.2	-	13.2±1.2	-	13.6	-	20.0	-	15.1	-
22:4(n-3)	-	-	-	-	0.5	-	1.4	-	0.4	-
22:5(n-6)	-	-	-	-	Tr	-	-	-	0.3	-
22:6(n-3)	3.9±0.5	-	0.9±0.2	-	6.2	-	7.3	-	11.4	-
Branched & odd chain	2.4±0.1	-	1.7±1.1	1.5±0.3	1.9	3.0	2.6	1.0	1.7	1.5
Total concentration (mg g^{-1} dry wt.)	236.2±32.8	0.2±0.1	217.7±12.5	79.5±8.6	222.9	118.4	190.7	148.0	56.9	8.0

Continued on the next page

Table 7. (continued)

b) Winter 2002

Species	ES -adult (n=6) Acid	ES -juvenile (n=4) Acid	ES -furciliae* (n=4) Acid	ES -furciliae* (n=4) ALC	PA* (n=10) Acid	PA* (n=10) ALC	MG* (n=20) Acid	MG* (n=20) ALC	CP-female* (n=10) Acid
n-Saturates									
12:0	-	1.9±1.3	3.2	-	2.2	1.3	0.9	-	0.9
14:0	13.4±1.9	11.6±1.8	3.2	37.6	1.4	32.3	0.5	37.5	2.6
16:0	24.5±1.9	25.1±1.4	19.3	35.4	2.8	33.2	5.6	34.1	13.1
18:0	1.3±0.2	1.7±0.3	1.0	2.5	0.3	1.6	0.4	2.8	1.0
20:0	Tr	Tr	Tr	0.3	Tr	Tr	Tr	Tr	0.5
22:0	-	-	0.1	-	-	Tr	-	Tr	0.2
Monounsaturates									
14:1(n-3)	0.2±0.0	Tr	Tr	-	-	0.4	Tr	0.2	Tr
16:1(n-9)	Tr	Tr	Tr	-	0.1	-	Tr	-	Tr
16:1(n-7)	9.5±1.2	9.4±1.2	4.3	0.7	26.4	3.1	9.4	3.7	4.5
16:1(n-5)	0.3±0.2	0.3±0.1	0.1	0.5	0.2	1.0	0.1	0.9	0.2
16:1(n-3)	Tr	0.1±0.0	0.1	0.4	Tr	1.0	Tr	0.9	Tr
18:1(n-9)	13.2±0.8	12.1±0.7	10.5	1.4	33.9	6.4	25.4	8.9	1.6
18:1(n-7)	7.7±1.2	6.8±0.6	8.5	-	2.7	1.9	3.1	1.2	1.4
18:1(n-5)	0.1±0.1	0.2±0.0	0.3	-	0.7	-	0.4	0.2	2.0
$20:1^{+}$	1.3±0.5	0.9±0.0	1.2	3.8	3.3	5.7	12.0	0.8	4.6
$22:1^{+}$	0.6±0.4	-	-	11.8	0.2	4.2	-	0.3	45.6
24:1(n-9)	-	-	-	-	-	1.6	-	1.7	2.3
Polyunsaturates									
16:2(n-6)	1.0±0.2	1.4±0.1	0.8	-	0.6	-	0.8	-	0.5
16:3(n-4)	0.2±0.0	0.3±0.1	0.2	-	0.2	-	0.3	-	0.1
16:4(n-1)	0.7±0.1	1.3±0.3	0.5	-	0.4	-	0.7	-	Tr
18:3(n-3)	0.3±0.0	0.3±0.1	0.2	-	0.2	-	0.2	-	Tr
18:4(n-3)	1.7±0.4	2.7±0.6	1.6	-	3.0	-	2.7	-	0.4
$18:2^{+}$	1.8±0.7	1.7±0.6	1.9	0.7	2.0	0.4	3.2	0.4	0.7
20:2(n-6)	Tr	-	0.1	-	Tr	0.2	Tr	-	Tr
20:4(n-3)	0.3±0.2	Tr	0.2	-	0.3	-	0.6	-	0.9
20:4(n-6)	0.3±0.3	0.2±0.1	1.0	-	0.2	-	0.3	-	Tr
20:5(n-3)	13.6±1.1	14.5±2.3	24.4	-	9.4	-	18.4	-	5.7
22:4(n-3)	-	-	-	-	-	-	-	-	0.2
22:5(n-6)	0.2±0.1	-	Tr	-	0.7	-	1.2	-	4.9
22:6(n-3)	4.0±1.2	2.6±0.6	12.6	-	7.6	-	12.6	-	0.6
Branched & odd chain	3.8±0.8	8±0.1	4.7	5.1	1.3	5.8	1.1	6.4	2.3
Total concentration (mg g^{-1} dry wt.)	223.4±61.0	210.0±17.0	59.5	2.5	188.4	93.7	108.1	55.6	194.5

None or only trace amounts (<0.1 mg g^{-1} dry wt.) of fatty alcohols ($20:1^{+}$) were found in ES-adult, ES-juvenile, and CP.
*Composite samples were used for analysis.
+Indicate all isomers combined.
-Not detected.
Tr = trace amount (<0.1% of total concentration).

Table 8. Sterol composition (% total concentration) of Callianira antarctica and their potential prey. CT= Callianira antarctica, ES=Euphausia superba, EC=Euphausia crystallorophias, PA=Pareuchaeta antarctica, CA=Calanoides acutus, AO=Anarctomysis ohlini, MG= Metridia gerachei, CP=Calanus propinquus. From: Ju et al. (submitted)

a) Fall 2002

Sterols	CT* (n=5)	ES-adult (n=4)	EC-adult (n=3)	PA* (n=20)	CA* (n=50)	AO* (n=2)
24-norcholesta-5,22-dien-3β-ol ($C_{26}\Delta^{5,22}$)	0.4	-	-	13.1	9.6	0.2
cholesta-5,22-dien-3β-ol ($C_{27}\Delta^{5,22}$)	2.7	0.5±0.1	-	7.7	14.3	1.0
5α-cholest-22-en-3β-ol	0.4	-	-	1.9	-	1.8
Cholest-5-en-3β-ol (Cholesterol)	73.0	71.3±3.9	55.7±9.0	46.8	36.3	88.2
5α-cholestan-3β-ol (Cholestanol)	0.8	3.6±4.2	-	-	-	1.5
Cholesta-5,24-dien-3β-ol ($C_{27}\Delta^{5,24}$)	22.0	24.6±2.9	28.4±9.2	30.5	25.6	5.7
Cholest-7-en-3β-ol ($C_{27}\Delta^{7}$)	0.1	-	15.9±1.3	-	14.1	1.7
24-methylcholesta-5,24(28)-dien-3β-ol ($C_{28}\Delta^{24(28)}$)	0.6	-	-	-	-	-
24-methylcholest-5-en-3β-ol ($C_{28}\Delta^{5}$)	0.1	-	-	-	-	-
Total sterols (mg g^{-1} dry wt.)	0.3	1.8±0.7	2.5±1.0	2.1	1.6	4.6

b) Winter 2002

Sterols	CT (n=2)	ES-adult (n=6)	ES-juvenile (n=4)	ES-furciliae* (n=4)	PA* (n=10)	MG* (n=20)	CP-female* (n=10)
24-norcholesta-5,22-dien-3β-ol ($C_{26}\Delta^{5,22}$)	0.3±0.2	0.6±0.6	1.6±1.4	0.4	-	6.2	2.1
cholesta-5,22-dien-3β-ol ($C_{27}\Delta^{5,22}$)	1.7±0.4	0.8±0.2	0.8±0.1	4.9	12.8	12.7	17.9
5α-cholest-22-en-3β-ol	0.1±0.1	Tr	Tr	-	-	-	-
Cholest-5-en-3β-ol (Cholesterol)	80.7±1.3	82.3±4.8	85.4±2.1	78.6	71.8	61.8	37.4
5α-cholestan-3β-ol (Cholestanol)	1.0±0.6	0.6±0.8	Tr	2.4	9.5	3.7	-
Cholesta-5,24-dien-3β-ol ($C_{27}\Delta^{5,24}$)	15.9±0.4	15.7±4.8	12.1±1.8	13.7	5.3	15.7	32.8
Cholest-7-en-3β-ol ($C_{27}\Delta^{7}$)	-	-	-	-	-	-	9.1
24-methylcholesta-5,24(28)-dien-3β-ol ($C_{28}\Delta^{24(28)}$)	0.2±0.0	-	-	Tr	0.7	-	0.7
24-methylcholest-5-en-3β-ol ($C_{28}\Delta^{5}$)	Tr	-	-	-	-	-	-
Total sterols (mg g^{-1} dry wt.)	1.2±0.2	2.8±1.2	1.9±0.4	4.6	4.8	0.4	0.7

*Composite samples were used for analysis.
-Not detected.
Tr = trace amount (<0.1% of total concentration).

The individual lipid compositions (i.e., FA, alcohols and sterols) of *C. antarctica* were relatively constant between seasons. Fatty acid (FA) and alcohol composition of ctenophores sampled in autumn and winter are shown in Table 6, and results for their prey shown in Table 7. The total FA concentration in winter (34.3 mg $[g\ DW]^{-1}$) was substantially higher than the autumn concentration (19.3 mg $[g\ DW]^{-1}$). *Callianira antarctica* contained a wide range of FA, ranging from C_{12} to C_{24}, however the 20:5(n-3), 16:0, and 18:1(n-9) species were the primary FA observed in ctenophores. These fatty acids were also dominant in both copepods and krill for both sampling seasons. Small amounts of monounsaturated fatty alcohols, particularly 20:1 and 22:1, were also found in both autumn and winter ctenophores. *Euphausia superba* furcilia and the copepod, *Paraeuchaeta antarctica*, were the only prey items to contain these alcohols at noticeable levels. The sterol concentration in ctenophores also increased between autumn and winter, from 0.3 to 1.2 $\pm$ 0.2% DW, respectively, though low sterol levels were observed overall (Table 8). The sterol distributions of ctenophores were similar to those for krill, particularly *E. superba* furcilia. The two dominant sterols found in ctenophores, cholesterol and choleta-5, 24-dienol ($C_{27}\Delta^{5,24}$), were found in similar concentrations in all prey species.

Gut contents. The gut contents of *C. antarctica* during winter 2001 (*n = 20*), autumn 2002 (*n = 43*) and winter 2002 (*n = 82*) were examined to determine *in situ* feeding. For all seasons, 40% or more of ctenophore guts did contain prey remains (excluding lipids), and of those with digested matter, very few contained recognizable prey in Stages I or II of digestion. A majority of the digested matter found in gut contents from all three sampling periods consisted of small portions of small "clumps" of

light-colored gummy material typical of Stage IV digestion. Diet items in varying stages of digestion indicated that ctenophores ingested multiple overlapping meals.

During winter 2001, 20% of the guts were completely empty, 30% had lipid only, and 50% of the ctenophores had digested matter in their guts (Fig. 18). Thirty-five percent of the digested matter was recognizable prey. Euphausiid furcilia made up the majority of recognizable prey (82.6%), and copepods and amphipods (e.g., *Primno macropa*) both contributed 8.7%. *Calanus propinquus*, which was the only identified species of copepod, made up 4% of the copepods (Fig. 19). During autumn 2002, 20.5% of the guts were completely empty, 20.5% of the ctenophores had lipid only, and 59.1% had digested matter of some form in their guts (Fig. 18). Only 16% of the digested matter was recognizable prey, consisting mostly of copepods (39% *C. acutus*, 28% *C. propinquus*, and 22% unidentified remains of copepods), and few euphausiid furcilia (11% of recognizable prey; Fig. 19). Although a larger number of ctenophores were examined for gut content analysis during winter 2002, the results were similar to those from the two previous seasons. Of the 82 ctenophores examined, 28.1% of the guts were completely empty, 26.8% had lipid only, and 45.1% had some form of digested matter (Fig. 18). Only 11% of the digested matter found in the guts was recognizable prey remains, the rest typically consisted of material in Stages III and IV of digestion. The recognizable prey consisted of euphausiids and copepods at 38.5% and 61.5%, respectively. *M. gerlachii* and *C. acutus* were the only species of copepod that could be identified (8% of recognized prey each; Fig. 19). Copepods that were too far into the digestion process to be identified to genera made up 31% of recognizable prey.

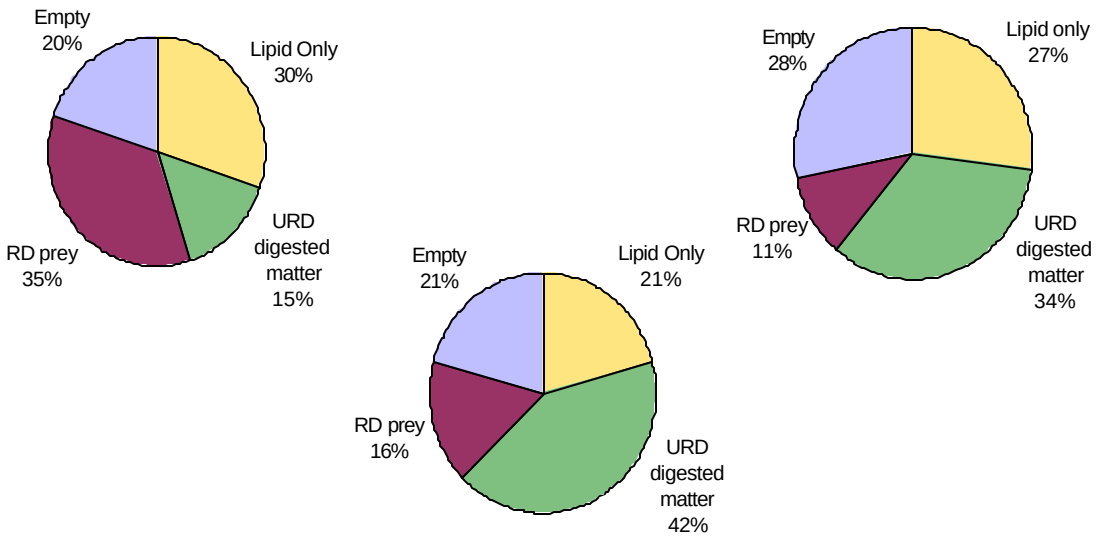

Figure 18. *Callianira antarctica*. Gut contents of ctenophores collected during three seasons; from left to right: winter 2001 (n = 20), autumn 2002 (n = 43), winter 2002 (n = 82). RD=Recognized, URD=Unrecognized.

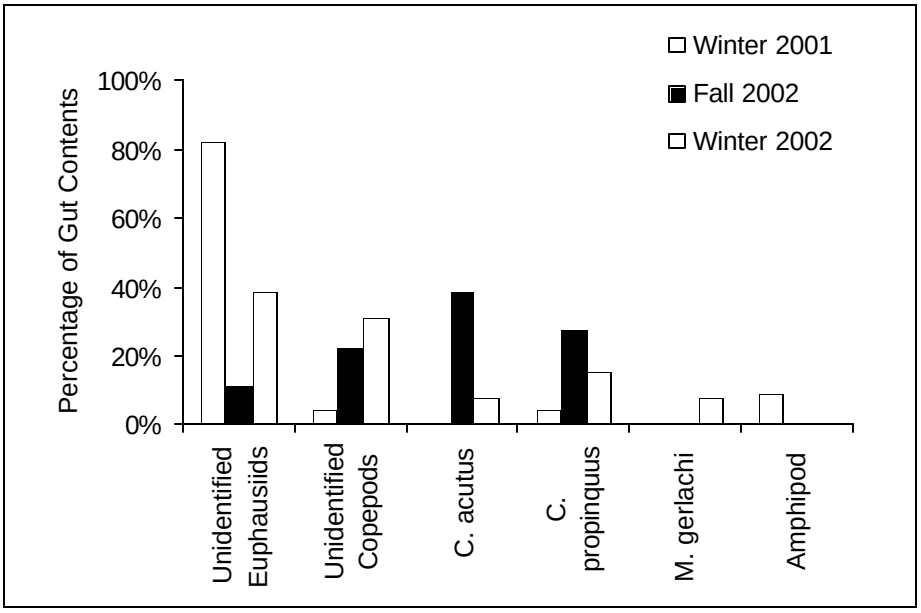

Figure 19. *Callianira antarctica*. Prey type making up the "recognizable prey" portion of gut contents from ctenophores collected during three seasons: winter 2001 (n=23), autumn 2002 (n=18), winter 2002 (n=13).

DISCUSSION

Chemical composition. *Callianira antarctica* did not undergo a large seasonal change in elemental composition between autumn and winter, but there was greater variability in the carbon and nitrogen content of winter ctenophores than in autumn animals, particularly for larger individuals. These findings may have been an artifact of the small sample sizes, especially for autumn. Variability in ctenophore body carbon has been related to prey availability (Kremer 1982, Reeve et al. 1989), which was shown to largely decrease between autumn and winter in our study area (Ashjian et al., in press). Therefore patchy distribution of prey during winter may account for the variability in the winter samples. Another source of variability in the elemental composition could be due to the collection method. Given that the body carbon in ctenophores is unevenly distributed among the tentacles, gut wall and comb rows (Reeve et al. 1989), loss of portions of the tentacles on some individuals during net collection would contribute to differences in carbon content. However during winter, gentler collection with SCUBA and drift nets, in addition to net tows, allowed for retrieval of ctenophores in excellent condition. In addition, regardless of the collection method, great effort was made to ensure that only complete animals in excellent condition were saved for chemical analysis, which would greatly reduce this source of error. Because the geomean carbon and nitrogen values for both seasons were similar to each other (autumn: 8.6 and 1.80% DW, respectively; winter: 8.35 and 1.92% DW, respectively) 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 ctenophores and other gelatinous zooplankton (Percy & Fife 1981,

Hoeger 1983, Clarke et al. 1992). Because of the high water content and the fact that conventional drying methods do not completely free gelatinous tissue of its bound moisture (Larson 1986, Clarke et al. 1992), the measured dry weights may be overestimated. The methodology used in this study, however, is similar to that used by other gelatinous zooplankton investigators; therefore, the data may be compared to other published values. The mean DW for *C. antarctica* (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 *M. ovum* (4.5 to 4.9%) from the Arctic (Hoeger 1983, Percy 1988). The 78.9% ash content for *C. antarctica* is slightly higher than the ash content reported for *Pleurobrachia* sp. (68.3%) from the Southern Ocean (Clarke et al. 1992), and is consistent with the high ash content values typical of gelatinous zooplankton due to the considerable inorganic salt content of the dry mass (Ikeda 1971, Hoeger 1983, Kremer et al. 1986a, Larson 1986).

Body carbon and nitrogen contents of *C. antarctica* are low in comparison with non-gelatinous marine zooplankton, but are similar to other ctenophores from polar regions, and higher than temperate and tropical species. The geomean carbon and nitrogen values, 8.41 and 1.83% DW respectively, for *C. antarctica* are four to five times lower than most non-gelatinous species of zooplankton from the Southern Ocean (Donnelly et al. 1994), but are only slightly lower than values for *Beroe* sp. (9.51 and 2.22% DW; Clarke et al. 1992) and Mertensiidae sp. (11.2 and 2.4%; Ikeda & Bruce 1986), and two-fold higher than those for *Pleurobrachia* sp. (4.11 and 0.74% DW; Clarke et al. 1992)

from the Southern Ocean. The mean carbon value for *C. antarctica* is also more than double the value for *P. pileus* (3.4%) from the Arctic, but similar to that for *Beroe gracilis* (7.2%; Hoeger 1983). Carbon and nitrogen concentrations in *C. antarctica* are also more than four times higher than those in epipelagic ctenophores from temperate and tropical regions (reviewed in Youngbluth et al. 1988). The elevated carbon levels in *C. antarctica* in comparison to temperate and tropical ctenophores are expected, as high latitude species typically have higher carbon content than similar species in lower latitudes (Ikeda 1977). The more than two-fold difference in carbon and nitrogen concentrations between *C. antarctica* and *Pleurobrachia sp.* from both the Arctic and Antarctic is not as easily explained. Both groups are moderately robust species of cydippids that, for the most part, are able to withstand net collection techniques that severely damage more delicate ctenophores. *Callianira antarctica* is a larger species of ctenophore (Hoeger 1983, O'Sullivan 1986), however, that may structurally require a higher carbon and nitrogen concentration. Without further morphometric analysis of the two species we cannot account for the difference in elemental composition.

Metabolic rates. *Callianira antarctica* metabolic rates were very similar to those of Mertensiid ctenophores from the Antarctic, but were higher than those measured for *M. ovum* from the Arctic (Table 2). The geomean weight-specific oxygen consumption rate for *C. antarctica* (0.163 µl O_2 [mg DW]$^{-1}$ h^{-1}) is only slightly higher than the mean value for Mertensiidae sp. (0.129 µl O_2 [mg DW]$^{-1}$ h^{-1}) measured at –1.6^{o}C during austral spring in the Prydz Bay region of the Antarctic (Ikeda and Bruce 1986). The geomean nitrogen excretion rates from these same studies are very close as well: 9.39 µg-at N [mg DW]$^{-1}$ h^{-1} for *C. antarctica* vs. 8.11 µg-at N [mg DW]$^{-1}$ h^{-1} for Mertensiidea sp. The wet

and dry weights of *C. antarctica* and Mertensiidae in the experiments were nearly identical, and the temperatures were similar despite the difference in season. In contrast, the geomean weight-specific oxygen consumption rate for *C. antarctica* was more than twice the mean rate measured for the Arctic cydippid *M. ovum* (0.074 ± 0.028 µl O_2 [mg DW]$^{-1}$ h-1), and *C. antarctica*'s geomean nitrogen excretion rate was almost two orders of magnitude greater than the mean value for *M. ovum* (0.24 µg-at N [mg DW]$^{-1}$ h^{-1}) during winter (Percy 1988). The season of sampling, temperature, size range, and mean DW (%WW) for *C. antarctica* were all similar to that of *M. ovum*, however, the median total wet and dry weight (mg) for *C. antarctica* was only a quarter of mean wet and dry weight (mg) for *M. ovum*. The larger mass of *M. ovum* may account for the lower specific metabolic rate in comparison to *C. antarctica*, as larger animals tend to have lower weight-specific respiration and nitrogen excretion rates (Ikeda 1970, 1974 & 1985).

The metabolic rates of ctenophores are also significantly affected by feeding history (Kremer 1982). Percy (1988) attributed a 30% decline in *M. ovum* respiration rates between summer and winter to a substantial decrease in seasonal abundance of prey. Adult *M. ovum* occurs in the upper 30 m of the water column in Frobisher Bay in the Canadian eastern Arctic throughout the year, but were not collected in nets set just below the sea ice during winter, and therefore may not take advantage of the zooplankton community below the undersurface of the ice (Percy 1989). In contrast, during our study, diver observations and gut content analysis proved *C. antarctica* to be an effective predator on larval and juvenile krill associated with the undersurface of sea ice. Exploitation of this winter food source may provide a predatory advantage and contribute

to *C. antarctica's* higher winter metabolic rate compared with that of *M. ovum*. The disparity in metabolic rates between *C. antarctica* and *M. ovum* also can be considered in a evolutionary context by application to the hypothesis that the Arctic is a "younger" ecosystem and its species may not be fully adapted to the colder waters; therefore, the metabolic rates of Arctic species will be lower than those species from the Antarctic (Holeton 1974, Clarke 1984; as referenced in Ikeda et al. 2000). While this application may be interesting, and possibly valid, the hypothesis has yet to be substantiated (Ikeda 1989).

The geomean weight-specific oxygen consumption rate of *C. antarctica* is at the lower end of the range given for *P. pileus* (0.140–0.280 µl O_2 [mg DW]$^{-1}$ h^{-1}; Ikeda 1974) and other ctenophores from temperate and tropical regions (0.129-0.848 µl O_2 [mg DW]$^{-1}$ h^{-1}; as referenced in Percy 1988). These findings are consistent with the general rule that oxygen consumption for polar species of zooplankton is low in comparison to temperate and tropical species (Ikeda 1970 & 1974, Clarke & Peck 1991), due in large part to the differences in habitat temperature (Ikeda 1985). If a Q_{10} of 2 is assumed (Prosser 1961, Percy 1988), at 10°C *C. antarctica* would respire at a rate (0.326 µl O_2 [mg DW]$^{-1}$ h^{-1}) slightly greater than rates measured for *Pleurobrachia* spp. at similar temperatures (0.26-0.28 O_2 [mg DW]$^{-1}$ h^{-1} at 7.5-13°C; Hirota 1972, Ikeda 1974), indicating cold adaptation in *C. antarctica*.

The linear regression of log-log transformed data (GM) for oxygen consumption in terms of dry weight and carbon content indicated a weight-dependent respiration for *C. antarctica*. Values of '*b*' indicating weight-dependent respiration in the range of 0.6 to 0.9 are characteristic of ctenophores and marine zooplankton in general (Ikeda 1974,

Ikeda & Mitchell 1982, Kremer et al. 1986b, Bailey et al. 1994, Percy 1988, Ikeda et al. 2000). However values ranging from 0.9 to 1.28, indicative of weight-independent respiration, have been reported for ctenophore species such as *Mnemiopsis leidyi* (Kremer 1977), *Mnemiopsis mccradyi* (Kremer 1982) and *Bathyocyroe fosteri* (Youngbluth et al.1988). Bailey et al. (1994) attributed the variability in '*b*' values among species of ctenophores to methodological treatments as well as low sample sizes in the studies. Further experiments with larger samples sizes are necessary in order to confirm *C. antarctica*'s metabolic relationship to size.

Maintenance carbon rations and body turnover. Smaller *C. antarctica* required a higher carbon-specific maintenance ration to support metabolic processes than larger ctenophores during winter. The minimum amount of carbon that *C. antarctica* needed to ingest daily during winter was calculated to be 3.61 µg to 0.190 mg for small ctenophores (average 2.7% to 3.6% total body carbon), and 0.151 to 1.13 mg for larger ctenophores (average 1.4% to 1.9% total body carbon). The higher maintenance ration for smaller *C. antarctica* was due to having higher weight-specific respiration rates combined with a lower carbon content on a per unit weight basis. The mean daily maintenance ration (1.5% body C d^{-1}; Ikeda & Bruce 1986) for large Mertensiidae from the Antarctic in early summer is within the range of average values for large *C. antarctica*. The range in maintenance rations reported here are greater than that estimated for *M. ovum* of a similar size range from the Arctic during winter (ca. 0.2 to 1.5% body C d^{-1}, RQ: 0.8; Siferd & Conover 1992), but smaller than that reported for mesopelagic and epipelagic ctenophores (5 to 11% body C d^{-1}) from tropical waters between spring and autumn (Kremer et al. 1986b, Youngbluth et al. 1988).

Even if we assume a very conservative assimilation efficiency of 70% (Reeve et al. 1978), the maximum daily carbon requirement to support metabolism for small *C. antarctica* during winter would be satisfied with the ingestion of one larval (F6) *E. superba*, one adult *C. propinquus*, or two *M. gerlachii.* Larger ctenophores (>20 mm) would need to ingest up to 6 larval (F6) *E. superba*, 16 *M. gerlachii*, 3 *C. propinquus* or 1 juvenile *E. superba* or *T. macrura* each day. Average winter digestion times (e.g., 10.0 and 16.5 hours for prey items under 1.0 and 2.0 mg C, respectively) would allow for multiple meals each day, suggesting that *C. antarctica* may have been able to meet, and possibly exceed, the maintenance daily carbon requirement. Ingestion rate experiments with *C. antarctica* in austral autumn indicated that at prey concentrations of *ca* 40 µg C^{-1} l^{-1}, the minimum daily ration was equivalent to 17% of body carbon (Scolardi et. al submitted). Ingestion rates for winter are not likely to be as high as the autumn rates due to reduced temperatures and prey concentrations, yet a reduction in ingestion rates as large as one half the original would still bring in sufficient food to meet minimum maintenance rations, although very little to none will be left for allocation to growth and reproduction.

Feeding ecology: *experimental.* Sluggish digestion rates may be the limiting factor in the amount of carbon *C. antarctica* can process in excess to the minimum maintenance ration on a daily basis. The mean winter digestion time for *C. antarctica* (11.5 h) was substantially longer than values reported for temperate and tropical ctenophores (Fig. 20; range 0.2 - 5.8 h, T = 5 - 26°C). Copepods in tropical waters (25 – 27°C) are typically digested in less than 3 hours (Reeve 1980, Kremer et al. 1986a, Larson 1987b), whereas *C. antarctica* took 9 to 12 h to digest a single copepod in our study. Unfortunately there

are few investigations on digestion processes of polar ctenophores for comparison. *Mertensia ovum* from the Canadian High Arctic digested <1 mm to 6 mm copepods significantly faster (1.5 to 4 h; Siferd & Conover 1992) than *C. antarctica*. The *M. ovum* rate is shown in Fig. 20 as a comparison with the other published rates, but was not included in the functional relation between digestion rate and temperature because temperatures in the experimental aquaria (=1.5°C) were higher than *in situ* winter temperatures, which would have resulted in more rapid digestion of prey. Also, the authors did not include egestion of the indigestible exoskeleton in the gut evacuation time, which may have shortened the actual digestion time. For all other published digestion rates, temperature explained almost 50% of variability in the digestion time of different prey types ranging from fish eggs to euphausiid larvae (Fig. 20).

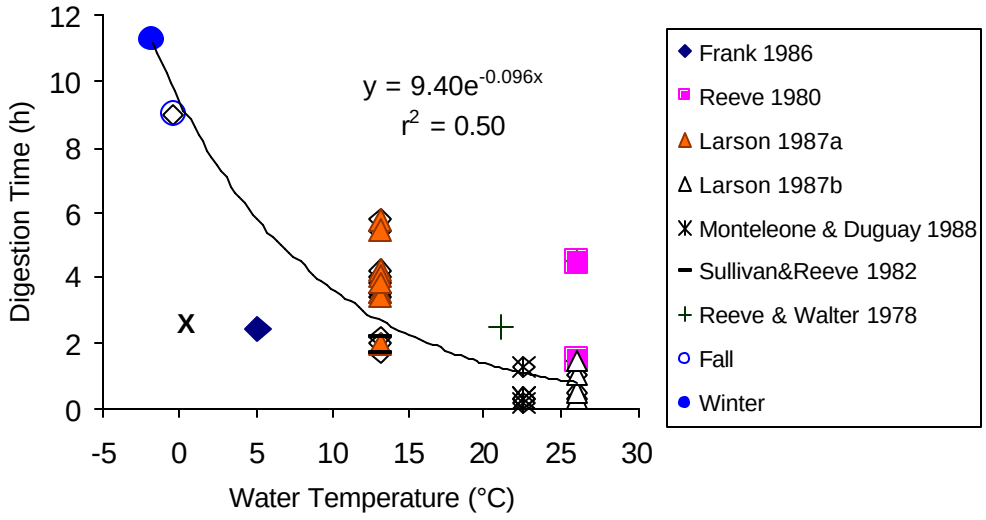

Figure 20. Relationship between digestion time and incubation temperature for ctenophores. Data from: Reeve and Walter (1978), Reeve (1980), Sullivan & Reeve (1982), Frank (1986), Larson (1987a,b), Monteleone and Duguay (1988) and this study. *Callianira antarctica* rates designated by triangle; the data designated by the **X**, (Siferd & Conover 1992), was not included in the functional relationship; see explanation in text.

Winter digestion times for *C. antarctica* were independent of ctenophore size, but highly correlated with prey number. The influence of prey number was two-fold: digestion time lengthened with the increasing amount of prey carbon consumed, and was further retarded by the size of the food bolus and/or accumulating chitineous exoskeletons in the gastrovascular cavity. Other studies have shown a lack of correlation between digestion time and ctenophore size, but a positive correlation with prey number (Martinussen & Båmstedt 1999, Larson 1987b). However, Martinussen & Båmstedt (1999) also found that that digestion time in two species of scyphomedusa decreased with increased medusa diameter, but increased with prey number. In addition, Reeve (1980) reported that the mean digestion time of *Mnemiopsis mccradyi* decreased from two to one h after it reached > 4 mm in length. However, this decrease was attributed to a change in the selection of food at this size; after this adjustment, the digestion time remained consistent through 13 mm. Reeve (1980) observed an increase in digestion time in *M. mccradyi* with increasing prey number as well.

Prey type also was a significant factor in influencing winter digestion time. The influence of prey type is a function of the prey tissue structure, which governs the digestion process (Hirota 1974, Larson 1987a, Martinussen & Båmstedt 1999). For *C. antarctica*, prey with greater lipid or carbon content, such as *C. propinquus* and *T. macrura*, took longer to digest than other prey of similar size. That the digestion rate did not increase linearly with increasing ingested prey carbon indicates some level of enzymatic mediation is involved. The remaining variability in digestion times that cannot be explained by prey number or prey type may, therefore, reflect differences in enzyme function (Hirota 1974).

Callianira antarctica assimilation efficiencies appeared to be very high since they egested little other than clear pieces of disarticulated exoskeleton during digestion experiments. The major organic component of exoskeletons is chitin, which on average is 4.6% DW in copepods (Båmstedt 1986), and 4.0% DW in *E. superba* (Raymont 1983); hence, carbon assimilation efficiencies could be >90%. The accumulation of lipid droplets in the stomodeum of *C. antarctica* suggests, however, that some portion of prey carbon is not immediately assimilated. In his review of lipid composition of Antarctic zooplankton, Clarke (1984) found accumulation of wax ester (storage lipid) droplets in every ctenophore, tentatively identified as *Pleurobrachia* sp., that he examined. Arctic gelatinous zooplankton are known to store lipid after feeding on copepods, which has been suggested as a survival strategy during times of low food availability (Percy 1988). Percy (1988) found that the ratio of oxygen consumed to nitrogen excreted (O:N) in *M. ovum* increased in winter, suggesting a shift towards lipid based metabolism fuelled by increased lipid reserves accumulated from their lipid-rich prey (copepods). The results obtained from this study, however, indicate that *C. antarctica* lipid stores are not used as an over-wintering strategy. Ctenophores in autumn had small concentrations of wax esters (storage lipid) and triacylglycerols (short term energy reserves), but zero levels of this lipid during winter. The total lipid concentration actually increased in *C. antarctica* from autumn to winter, but was mostly due to an enrichment in structural lipids (PO). In addition, excretion measurements for *C. antarctia* resulted in a geomean O:N ratio that was more indicative of protein than lipid-oriented metabolism. Furthermore, the possible 'degrowth' of some portion of the ctenophore population during winter, as suggested by

the length frequency distributions from autumn and winter, does not support the theory of lipid accumulations being used as an over-wintering strategy by *C. antarctica*.

Accumulations of lipids in the gut of ctenophores may be used to infer ctenophore diets. Lipid class analyses of these accumulations were not performed for this study, however, literature on lipid deposits in the stomodeum of Antarctic ctenophores (Clarke 1984, Larson & Harbison 1989), indicates that these accumulations consisted mostly of WE or TG. Due to the fact that lipid in Antarctic copepods are largely comprised of WE or TG (Clarke 1984, Hagen et al. 1993), whereas the lipid content of Antarctic euphausiids is more variable, implies that these sequestered lipids are mostly from the digestion of copepods. For example, copepodite stage V *C. propinquus* has a reported lipid content of 25 – 47% DW stored largely as WE (Conover & Huntley 1991), whereas immature *E. superba* in the WAP region had generally low levels of lipids (12 – 20% DW) stored primarily as TG (Stübing et al. 2003, Ju & Harvey in press). Lipid content analysis of larval *E. superba* from this study had low lipid concentration, with no indication of WE. However, *T. macrura* typically has a total lipid content of >50% DW, also predominantly stored as WE (Clarke 1984, Falk-Petersen et al. 1999), and therefore may also be a source of these lipid stores.

Copepods as the primary source for the lipid accumulations is further supported by the digestion rate experiments, where differences in the quantity and type of lipids found in prey used in winter experiments resulted in varying accumulations of lipid in the stomodeum of *C. antarctica*, with the largest amount occurring after the digestion of copepods, particularly *C. propinquus*, rather than the digestion of larval euphausiids. Therefore, of the 20 to 30% of the ctenophores examined for gut contents that contained

only lipid droplets, with no other evidence of prey in their gut, it is likely that they had previously ingested copepods. These results, however, do not exclude krill as a possible prey source. Observations of lipid in the guts of ctenophores also do not necessarily indicate recent feeding either, as Larson & Harbison (1989) noted that accumulated lipids in the gut of *C. antarctia* from the Ross Sea during summer remained there for more than two weeks.

The results of the lipid biomarker analyses allow us to make more definitive connections between ctenophore and their prey. The observed low lipid concentrations (2-7% of dry weight) dominated by PO in *C. antarctica* is consistent with results reported for other Antarctic ctenophores (Clarke 1984, Nelson et al. 2000). Wax esters and TG were detected in *C. antarctica* in autumn, but not in winter. The presence of these two neutral lipid classes may reflect active feeding on lipid-rich copepods in autumn, and their absence in winter may suggests reduced feeding activity (Ju et al. submitted). Major fatty acids (16:0, 16:1(n-7), 18:1(n-9), and 20:5(n-3)) observed in ctenophores were also found in larval and adult krill. Significant amounts of the MUFA 20:1 and 22:1 were found in ctenophores, which are known to be important components of wax esters in calanoid copepods, although *E. superba* furcilia in this study also contained these alcohols at noticeable levels. Cholest-5,22-dien-3β-ol ($C_{27}\Delta^{5,22}$), the major sterol in the Antarctic ice diatom *Nitzschia cylindrus* (Nichols et al. 1986; as referenced in Ju et al. submitted) accounted for a significant fraction of the total sterols in copepods and larval krill. The appearance of this sterol in ctenophores indicates that copepods and larval krill may be a significant food source for *C. antarctica* during winter.

Lipid compositions in *C. antarctica* showed similarities with both copepods and adult krill for both seasons and larval krill in winter. While adult krill were considered in the analysis, it is questionable that *C. antarctica* could successfully capture and ingest adult krill, although the breaking strength of ctenophore tentacles suggests that the tentacles of large C. antarctica could successfully handle prey as long as 4 cm (Matsumoto pers. comm.) The absence of copepod associated WE in winter animals does suggest a possible shift towards larval krill as a major source of food, which was strongly supported by gut contents analysis from the first winter, but to a lesser degree in winter 2002.

Feeding ecology: *in situ*. Recognizable prey items from gut contents indicated that *C. antarctica* were preying predominantly on larval euphausiids during winter 2001, predominantly on copepods during autumn 2002, and on larval euphausiids and copepods during winter 2002. Although there is some level of selectivity in prey capture with ambush predators, as they tend to catch relatively large, fast-moving prey (Greene et al. 1986, Larson 1987c, Madin 1988, Purcell 1997), tentaculate ctenophores are opportunistic feeders, and as a result their gut contents reflect *in situ* prey concentrations and compositions (Frank 1986, Siferd & Conover 1992). Diver and ROV observations under sea ice and results from net tows (Daly in press; Ashijian et al. in press) over three sampling periods support what was seen in the gut contents: larval *E. superba* concentrations were highest during winter 2001, lowest during autumn 2002, and variable in winter 2002.

Although overall prey abundance varied between season and years, 40 – 55% of the gut contents for all three seasons did not contain any digested material, neither

recognized nor unrecognized. This seasonal consistency contradicts the findings of Frank (1986), who concluded that the feeding incidence of *P. pileus* off southwestern Nova Scotia in the spring, which varied from an average of 46% to 84%, paralleled the total zooplankton biomass available to ctenophores. Contrary to this, frequencies of empty guts reported for *M. ovum* (52% to 70%) from the Arctic (Siferd & Conover 1992), where prey densities are highly seasonal, compared to those for *Bolinopsis vitrea* (40 – 80%) from Bimini Harbor (Kremer et al. 1986a), which has low, but steady prey densities year round, show a similar range in feeding incidence despite differences in seasonal variability of total prey biomass. This comparison indicates that factors other than total zooplankton biomass, such as prey patchiness, may significantly influence feeding in ctenophores. The results of this study suggest that *C. antarctica* overcome decreased prey concentrations and increased prey patchiness by exploiting larval krill aggregations under the sea ice. The important role of larval krill aggregations under sea ice in the feeding ecology of *C. antarctica* implies that the success of larval krill could be directly tied to the success of ctenophores during winter.

While experimental digestion rates and information on ingestion rates indicate that *C. antarctica* are capable of meeting their metabolic requirements, the question still remains: do in-situ observations indicate that *C. antarctica* is successfully feeding? This is not immediately obvious, as feeding incidences of ca 50% could mean half of the ctenophores are fed or half are starved. We must give success a quantitative value, such as minimum daily ration. Assuming that a large ctenophore ingests its minimum daily carbon requirement (1.13 mg C) in one sitting, then the equation in Fig. 14B can be used to calculate the time of digestion. If it takes a total of 12.4 hours for the ctenophore to

digest its minimum carbon requirement for that day, then it can be said that there is a 52% chance that this ctenophore will be caught with food in its gut. This is a noticeably good match with the actual feeding incidence observed from the gut content analysis. Therefore, feeding incidences near 50% indicate that it is possible for ctenophores to successfully obtaining enough food to sustain metabolic needs during autumn and winter.

CHAPTER FIVE

SUMMARY

Callianira antarctica, was the dominant ctenophore in the Marguerite Bay region with a widespread distribution during autumn and winter consisting mostly of adult ctenophores. The annual occurrence of this species, based on both literature accounts and this study, suggests that there is a stable, persistent population of *C. antarctica* in the WAP region. The mean abundance of *C. antarctica* during winter (0.45 ind. m^{-2}) is significantly lower than ctenophore populations in temperate regions, but similar to the abundance of *M. ovum* found in the artic. Specific circulation features, such as the large clock-wise gyre located over the north shelf where dense aggregations of ctenophores (>1 ind. m^{-2}) were found, may concentrate prey and predators within these areas, increasing chances of predation on zooplankton in an otherwise patchy environment. Ctenophores were mostly distributed in the upper 200 meters of the water column; however the depth of maximum abundance occurred within and just below the pycnocline, where higher concentrations of prey may be found. Day/Night tows indicating a sub-maximum occurrence of *C. antarctica* in the upper 50 m at night, and ROV observations of large numbers *C. antarctica* directly under the sea-ice with tentacles extended, suggests an increased predation impact on larval krill at night.

Callianira antarctica is a physically robust tentaculate ctenophore containing relatively high concentrations of carbon and nitrogen. *Callianira antarctica*'s winter metabolic rates were within the range of rates reported for other ctenophore species from

the Antarctic and the Arctic, and lower than that for most ctenophores from temperate waters. Winter digestion rates of *C. antarctica* were slow compared with that of ctenophores from temperate and tropical habitats, and were highly dependent on prey type and number. The extended digestion times during winter may ultimately limit the amount of carbon ctenophores can process on a daily basis and, therefore, the amount of carbon available for growth or reproduction after metabolic requirements are satisfied.

Despite the decrease in potential prey abundances between autumn and winter (Ashjian et al. in press), the fact that (1) average digestion times (e.g., 10.0 and 16.5 hours for prey items under 1.0 and 2.0 mg C, respectively) would allow multiple meals each day, and (2) about 50% of the collected ctenophores had food in their gastrovascular cavity, suggest that *C. antarctica* may have been able to meet, and possibly exceed, the maintenance daily carbon requirement, even during winter. However, length frequencies distributions from fall and winter suggest ctenophores may be experiencing degrowth in winter. Whether this decrease actually resulted from degrowth in ctenophores, or was the result of sampling two different populations is unclear. Diver observations, net collections, and gut content analysis indicate that this species is an opportunistic predator that feeds on both copepods and krill during the day and night. Lipid biomarker analysis and prey composition in the gut contents of ctenophores collected over autumn and winter suggest ctenophores do not utilize lipid reserves in times of low food availability, but instead may compensate for the seasonal decrease in prey abundance and increase in food patchiness by relying on under-ice aggregations of larval and juvenile krill to sustain metabolic needs. Hence, dense aggregations of *C. antarctica* under the ice could have significant affects on the recruitment of larval euphausiids.

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