INTERANNUAL AND REGIONAL DIFFERENCES IN KRILL AND FISH PREY QUALITY ALONG THE WESTERN ANTARCTIC PENINSULA

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Master of Science

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APPROVAL SHEET

This thesis is submitted in partial fulfillment of

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For Paul Littreal (1982-2012)

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ABSTRACT

Polar zooplankton and fish safeguard against the seasonality of food availability by using the summer months to build large reserves of lipids, which in turn are utilized to meet the metabolic demands of apex predators such as penguins, seals, and whales. A warming trend in the northern part of the western Antarctic Peninsula (WAP) has led to a decrease in perennial and summer sea ice, an increase in heat content over the shelf, and lower phytoplankton biomass, which could affect prey quality. We compared prey quality, including elemental (C, N) content and ratios, total, neutral, and polar lipid content, and energy densities, of known top-predator prey items (krill *Euphausia superba, Thysanoessa macrura,* and *Euphausia crystallorophias;* and fish *Pleuragramma antarcticum*, and *Electrona antarctica*) along the WAP latitudinal gradient in January of 2009-2011 as part of the Palmer Antarctica Long-Term Ecological Research study. *E. antarctica* had the highest prey quality in terms of total lipid content and energy density, followed by *T. macrura* and *P. antarcticum*, then *E. crystallorophias* and *E. superba*. For all species, variations in carbon and nitrogen content were best correlated with by the animals' neutral lipid content, in that animals with larger neutral lipid stores had significantly higher carbon and lower nitrogen content. Across all sexes and maturity stages, *E. superba* in the South had ca. 20% higher total lipid content than *E. superba* in the North. Total lipid content was also significantly higher in the South for *E. crystallorophias*, though this was largely due to the presence of larger individuals in the south combined with a significant positive relationship between length vs. weight-specific total lipid content for this species. For all prey species except *T. macrura*, there was a positive relationship between latitude or 0-120 m integrated Chl a vs. lipid content (neutral, polar, or total lipids), and a negative relationship between 0-120 m mean water temperature vs. lipid content. Trends opposite to those above found for *T. macrura*, suggest an optimal habitat for this species in the northern WAP which is characterized by warmer temperatures and lower Chl a. Patterns in Chl a were more important than upper water column temperature in explaining the observed latitudinal trends. If regional warming persists, the prey quality trends described for *E. superba,* combined with their regional abundance decline in the northern, coastal WAP could affect the ability of apex predators that rely on *E. superba* to meet their energetics demands.

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INTRODUCTION

The ecosystem dynamics of waters along the continental shelf of the western Antarctic Peninsula (WAP) are dominated by the seasonal advance and retreat of sea ice which in turn dictates the development of a strong summer phytoplankton bloom, forming the base of an energy-rich marine food web (Moline et al. 2008, Vernet et al. 2008, Ducklow et al. 2012a, Steinberg et al. in press). Krill are well recognized as an important trophic link in this region, serving as prey for higher predators such as whales, seals, penguins, and other sea birds (Costa & Crocker 1996, Fraser & Trivelpiece 1996). Antarctic krill (*Euphausia superba*) stocks in the WAP are large and persistent enough to support what some have postulated to be the most important assemblage of endothermic top predators in the world, in terms of energy flux (Croxall 1992, Atkinson et al. 2004, Ross et al. 2008).

Recent studies in the WAP also illustrate the importance of fish, especially the endemic, neritic Antarctic silverfish (*Pleuragramma antarcticum*) and oceanic myctophids, as a high-energy supplement to a krill-based diet (Chapman et al. 2011, Hückstädt et al. 2012). The hydrographic conditions of the WAP are unique in that Upper Circumpolar Deep Water (UCDW), delivered by the Antarctic Circumpolar Current (ACC), makes its way up onto the continental shelf and becomes modified UCDW as it mixes with shelf water (Dinniman et al. 2012, Martinson & McKee 2012). The modified UCDW forms a warmer layer in the mesopelagic, allowing oceanic and neritic species of pelagic fishes to mix, the intensity of which is dependent on the modified UCDW's temperature and salinity (Donnelly & Torres 2008). The incorporation of these fish species into the diets of animals classified as highly specialized krill predators can help sustain them through years of low krill abundance and can be energetically beneficial when provisioning young during key periods of growth (Chapman et al. 2011, Hückstädt et al. 2012).

Climate change is altering the WAP ecosystem and could potentially influence the availability and nutritional value of these prey items for apex predators. The WAP is one of the fastest warming regions on Earth, with an increase in mid-winter surface atmospheric temperatures of 6°C since 1950 (Vaughan et al. 2003). The average temperature of the UCDW has also increased since regular sampling began in 1997, with intrusions of this relatively warm, nutrient-rich water onto the shelf acting as the main source of heat to the water column (Martinson et al. 2008). This regional climate-ocean warming of the WAP has led to major changes in perennial sea-ice dynamics, characterized by a significant decrease in ice extent and duration (Smith & Stammerjohn 2001, Stammerjohn et al. 2008, Stammerjohn et al. 2012). As a result, a latitudinal 'climate migration' is occurring along the Peninsula, with a warmer, more humid, sub-polar climate moving south and progressively replacing a cold and dry, polar climate (Smith et al. 2003).

This warming of the WAP is affecting the function and structure of the marine pelagic food web at every level, from primary producers to penguins (Ducklow et al. 2012a). A comparison of two satellite-derived data sets, spanning nearly 30 years (1978-1986 and 1998-2006) indicated that summertime surface Chl a along the WAP declined by approximately 12% between these two time periods, with a stronger sub-regional decrease (~89%) in Chl a north of 63°S and a substantial increase (~66%) in Chl a occurring farther south (Montes-Hugo et al. 2009). These long-term Chl a trends have larger implications for krill densities and distribution, as *E. superba* aggregate in areas of high Chl a (Whitehouse et al. 2008). The abundance of *E. superba* has also declined in localized regions of the northern, coastal WAP (Ross et al. 2008, Steinberg et al., unpublished data), mirroring the larger-scale decline of Antarctic krill in the Southern Ocean (Atkinson et al. 2004). One of the most dramatic changes in the WAP food web is a roughly 80% decline in breeding pairs of the native, ice-obligate Adélie penguin in the northern WAP, near Anvers Island, since the mid-1970's (McClintock et al. 2008, Ducklow et al. 2012a). Sub-Antarctic, ice-intolerant Chinstrap and Gentoo

penguins have in turn established colonies nearby in 1976 and 1994, respectively (McClintock et al. 2008, Ducklow et al. 2012a).

It has been suggested that decreases in prey quality and abundance could also be contributing to the decline of Adélie penguins (Chapman et al. 2010, 2011). Prey quality is mainly dictated by its energy density, which correlates directly with the animal's lipid content (Clark 1980). Among searbirds, chick survival and recruitment is often correlated with their mass as they leave the nest site, and changes in prey quality can contribute to a reduction in fledgling mass and, potentially, a failure in recruitment (Golet et al. 2000, Chapman et al. 2010, 2011). This theory is partially confounded by recent increases of other krill specialists in the WAP, namely Gentoo and Chinstrap penguins along with humpback and blue whales (Branch et al. 2007, Ainley et al. 2009, Ducklow et al. 2012a). Prey quality and abundances must be high enough to meet energetic demands of these other krill specialists and suggests interspecific competition as another potential variable to explain the decrease in Adélie penguins and changes in other krill predators (Ainley et al. 2009, Friedlaender et al. 2011).

Energetics models are useful in quantifying bottom-up influences of a complex system by focusing on how external regulators, like the nutritional value of available prey, affect growth. Recently, an individual-based energetics model was created to simulate growth of Adélie penguin chicks in colonies along the WAP (Chapman et al. 2010, 2011). Their results highlighted the importance of gravid female *E. superba* and larger (>70mm) *P. antarcticum* to the diets of chicks, where a deficiency of 0.117 kg in fledging mass could result in a chick's failure to recruit. In these types of energetics studies, the biochemical composition of prey fed to chicks is usually estimated from length-specific literature values. These estimates do not consider the potential effects that increasing temperatures and a changing food base could have on energy storage functions for these mid-trophic level prey species.

The metabolic rates of ectotherms vary with ambient temperature and a temperature-driven increase in metabolic rates could inhibit prey species' ability to accumulate and store lipids in a region like the northern part of the peninsula, where phytoplankton is also decreasing (Peck et al. 2004, Montes-Hugo et al. 2009). These changes could also impact the metabolism of apex predators. Digestion efficiency in seabirds decreases as the lipid content of their prey decreases, meaning they are less effective at assimilating the maximum amount of energy available in lower quality foods (Brekke & Gabrielsen 1994). Energetics models rarely address parameters besides total lipid content that contribute to the nutritional value of prey. Jackson & Place (1990) showed that Rockhopper penguins have higher assimilation efficiencies for triglycerides when compared to wax esters, showing that different lipid classes can impact penguin metabolism. In addition, phytoplankton with high carbon to nutrient ratios is of low nutritional value to zooplankton. Consumption of high C:N phytoplankton can actually shift zooplankton elemental composition, forcing zooplankton into a nutrient-limited state, as the nutrient content of their food is not sufficient to meet their nutrient demands (Van de Waal et al. 2009). The caloric content of krill used in models is usually calculated from other measurements of the animals' biochemical composition. Only three studies to date have taken direct calorimetry measurements of *E. superba* (Nagy & Obst 1992, Ainley et al. 2003, Färber-Lorda et al. 2009), showing that spent females (eggs have been released) have a lower caloric content than mature males. Incorporating these relationships between prey quality and predator metabolism into energetics models will increase model accuracy by improving the quality of functions regulating modeled predator growth.

The climate gradient of the WAP makes it a unique region to address how differing environmental parameters can affect prey quality, such that prey in the northern WAP may differ in species composition or biochemical composition, than prey found farther south-where summer sea ice still persists. To assess whether regional warming and subsequent changes in phytoplankton are affecting prey quality along the WAP, we compared total, neutral, and polar lipid content, elemental

(C:N) ratios, and energy densities of known top predator prey items (krill *E. superba*, *Thysanoessa macrura*, and *Euphausia crystallorophias;* and fish *P. antarcticum* and *Electrona antarctica*) collected along the WAP latitudinal gradient. Comparing prey quality metrics from different years and regions with different environmental characteristics allowed us to examine if changes in prey physiology are related to parameters such as water temperature and Chl a. These relationships will be useful in future modeling efforts used to predict effects of regional warming on prey quality, enhancing our understanding of food web energy transfer in this dynamic ecosystem.

MATERIALS AND METHODS

Study area and sample collection

Zooplankton and fish used for prey quality analyses were collected on the annual, austral summer cruises of the Palmer Antarctica Long-Term Ecological Research (PAL LTER) program aboard the A.R.S.V *Laurence M. Gould* during January, 2009-2012. The PAL LTER study, encompasses 41,000 square nautical miles with regular sampling stations located in coastal, continental shelf, and oceanic slope zones, and in seasonal sea-ice zones (Ducklow et al. 2012a). Based on existing sea-ice dynamics described by Stammerjohn et al. (2008), we divided the study grid into North (all stations north of, but not including, the 300 sampling line) and South (all other stations) sub-regions (Figure 1).

Macrozooplankton were collected using a 2x2 m-square-frame net (700 μm mesh), towed obliquely from the surface to 120m, or occasionally shallower in coastal areas (Ross et al. 2008, Bernard et al. 2012). The net target depth was determined in real-time with a net-depth sensor housed in the termination of the tow conducting cable and confirmed with either a Vemco Minilog Temperature-Depth Recorder or a Star-oddi data storage tag (DAT). The volume of water filtered through the net was determined with a General Oceanics flow meter. Once on board, the contents of the cod end were gently transferred to a large tub filled with ambient surface seawater and

zooplankton or fish species of interest were removed. We focused on organisms that were previously identified as important prey items for penguins in colonies along the WAP, including: three krill species (*Euphausia superba*, *Euphausia crystallorophias*, *Thysanoessa macrura*) and two fish species (the myctophid *Electrona antarctica* and the Antarctic Silverfish *Pleuragramma antarcticum*) (W. Fraser, pers. comm.). Animal lengths were recorded for *E. superba* (Standard length 1, defined as the length between the eyes to the tip of the telson by Mauchline 1970), and fish (Standard Length, defined as the length between the most forward part of the head and the posterial end of the hypural bone; Total Length, defined as the length between the most forward part of the head and the end of the caudal fin rays, after Ricker & Westrheim1979), and sex/maturity stage was determined for *E. superba* (Makarov & Denys 1981). Total lengths for *T. macrura* and *E. crystallorophias* were calculated from wet weights based on literature values (Mayzaud et al. 2003, Ju & Harvey 2004). All animals for prey quality analyses were then frozen and stored at -80^{o}C.

Krill collected in 2009 and 2010 span the entire sampling grid and represent the majority of the data presented here. Fish were rarely collected, and thus cover a limited geographic and temporal (one sample from 2009 and the rest in 2010 and 2011) range. The grid was sampled from north to south over the course of 5 weeks, thus a seasonal comparison of *E. superba* was conducted in 2010 and 2012 in which krill were collected from one of the northern-most stations at the beginning and end of the cruise (6 January 2010 & 31 January 2010; 6 January 2012 & 30 January 2012) to determine if the seasonal progression of summer was potentially biasing observed longitudinal trends.

Prey quality analyses

In the laboratory, animals were thawed, rinsed three times with Milli-Q water, and placed in pre-combusted and pre-weighed glass tubes. Animals were either analyzed individually or combined with other animals of the same species and physical characteristic (e.g., size, sex) to form representative composite samples for individual sampling stations. *T. macrura* composite samples

consisted of 10 individuals, *E. crystallorophias* of 5 individuals, Juvenile *E. superba* of 2 individuals; all fish samples were analyzed individually. To test whether the composite samples were artificially altering variance, we analyzed half of the mature *E. superba* as individuals and half as 2-individual composites. An F-test was then used to compare the variances between these two groups and no significant differences were found for any of the prey metrics measured. This confirmed that the variances associated with the composite samples were still representative of individual adult *E. superba* in nature. Artificial composites were then created by averaging prey metric values of two morphometrically similar individual *E. superba* samples to use in data analysis along with the 2-individual *E. superba* composites.

Sample wet weights (WW) were determined with a Sartorius BP211D analytical balance, and then homogenized either using a Misonix ultrasonic liquid processor XL-2000 series or a Virtis "45" homogenizer. The samples were then freeze-dried using a LabconocoFreezone6 Plus freeze dryer and dry weights (DW) were determined. Sub-samples of the dry, homogenous powder were taken for the various prey quality analyses. When not in use, samples were stored in airtight containers with headspace that was flushed with N_2 gas to prevent sample degradation.

To determine total organic carbon and nitrogen content, a small sub-sample of freeze-dried, homogenized tissue was transferred to a pre-weighed, pre-combusted tube, placed in a desiccator with a small beaker of concentrated HCL for 16 h to remove organic carbonates, and then moved to a 60^{o}C drying oven for a minimum of 72 h. The acidified sample was then packed into tin capsules and the final sample weight was obtained using a Sartorius XP1000P microbalance. The sample was then processed using a Costech ECS 4010 CHNSO Analyzer for flash combustion with acetanilide as the standard. Roughly 100 representative krill samples and all fish samples were weighed pre- and post-acidification using a Sartorius BP211D analytical balance to estimate the mass of the organic carbonates lost to acidification; there was no discernible mass difference.

E. superba and *E. crystallorophias* accumulate both neutral (mainly triglycerides and wax esters, respectively) and polar (mainly phosphatidylcholine) lipids during the summer as a mechanism for energy storage for the winter, when food is scarce (Hagen et al. 1996, Ju et al. 2009). Separately analyzing neutral and polar lipid concentrations enables us to determine the relative influence of each in driving any observed total lipid trends. Neutral and polar lipid classes were extracted and separated utilizing a modified accelerated solvent extraction (ASE) method developed by Poerschmann and Carlson (2006). Briefly, the sample is placed in a cell with a silica-based sorbent at its outlet, the cell is pressurized and cycled through two *n*-hexane/acetone (9:1, v/v) extractions at 50^{o}C to collect the neutral lipids followed by two chloroform/methanol (1:4, v/v) extractions at 80^{o}C to collect the polar lipids. Each fraction was then dried completely under N_2 gas and resuspended in 500µL of hexane for the neutral fraction and 2000µL of chloroform for the polar fraction. A known volume of the resuspension was placed into a warm, pre-weighed aluminum cup. The solvent was allowed to evaporate and the tin cup was reweighed using a Sartorius XP1000P microbalance. Three aliquots of each sample were weighed, to calculate a mean and standard deviation. If the coefficient of variation (standard deviation/mean x 100) was less than 10%, the mean weight was used to calculate total lipid extracted from the sample. If the coefficient of variation was greater than 10%, a fourth aliquot was weighed.

To determine caloric/energy content, a subsample of freeze-dried, homogenized tissue was formed into a pellet and ignited in a bomb calorimeter (Parr Instrument Co. Model 6300) using benzoic acid as a standard. The fish samples were comprised of one fish each and supplied enough dry mass to run a sample replicate. The percent difference was calculated for the replicates to analyze precision, and the two replicates were averaged to estimate the caloric density (kJ/g dry mass) of the sample. There was not enough dry mass to run replicates on krill samples, which consisted of a composite of two morphometrically similar individual krill from the same station. The fish sample

replicates were always within ± 3% of each other; the same precision for the individual krill samples was assumed.

Data analysis

Statistical differences between prey species, years, and North-South sub-regions sampled were calculated using a 2-way ANOVA when data met assumptions of normality and homogeneity. A Two-sample t-test was used to examine data sets that only spanned one year or one region. Data sets that did not conform to a normal distribution were ln-transformed. Data that did not meet the normality assumption after transformation were tested with the non-parametric Mann-Whitney test. Regression analyses were used to explore relationships between prey quality metrics and other environmental and temporal data which were obtained from the PAL LTER database (pal.lternet.edu/data/). Discrete Chl a values (taken every 15m, on average) were integrated and water temperature measurements (taken continuously via CTD) were averaged over the top 120m for each station where prey were collected. Significance for all statistical analyses was determined at $\alpha = 0.05$.

Data visualization

Maps were created with ArcGIS 10 Geostatistical Analyst to visualize 120 m integrated Chl a and mean water temperatures for the PAL LTER study region. Temperature interpolations were created with Ordinary Kriging and Chl a interpolations were created with the Inverse Distance Weighted (IDW) method. Oceanographic stations from the PAL LTER cruise with available water temperature and Chl a data were used in the analysis to increase the accuracy of the interpolations (stations depicted in Figure 2). Regression analyses only utilized data from stations where prey species were sampled concomitantly (stations depicted in Figure 1).

RESULTS

Hydrographic Setting

Upper water column (0-120 m) mean water temperatures at stations sampled for prey items were significantly warmer across the grid in January 2009 than 2010, averaging -0.01 °C and -0.58°C, respectively (Figure 2A,B; Table 1). For combined 2009 and 2010 data, mean upper water column temperatures were significantly warmer in the North, especially along the coast, than in the South, averaging 0.12 °C and -0.57 °C, respectively (Figure 2A,B; Table 2). Upper water column (0-120m) integrated Chl a was significantly lower in 2009 than 2010, averaging 52.2 mg m^{-2} and 119.4 mg m^{-2}, respectively (Figure 2C,D; Table 1). Integrated Chl a (2009 and 2010 combined data) was significantly lower in the North than in the South, averaging 60.8 mg m^{-2} and 103.8 mg m^{-2}, respectively with maximum values in the southern coastal regions and Marguerite Bay (Table 2). There was a wider range in both temperature and Chl a in 2010 compared to 2009, with a difference in maximum and minimum mean upper water temperature and integrated Chl a of 0.26 °C and 86.1 mg m^{-2} in 2009 compared to those of 1.32 °C and 598.1 mg m^{-2} in 2010. In 2011, integrated Chl a averaged 209.2 mg m^{-2} across the grid, significantly higher than in 2009 (Table 1).

Prey Quality

Species Comparison

Average nitrogen content for the three species of krill and *P. antarcticum* ranged from 0.083 – 0.092 mg N DW^{-1}, and *T. macrura* and *P. antarcticum* average nitrogen content was significantly lower ($p<0.05$) than *E. crystallorophias* and All *E. superba* (Table 3). Average carbon content for these species ranged from 0.42 – 0.49 mg C DW^{-1}, with *P. antarcticum* carbon content significantly higher than *T. macrura*, and both significantly higher than *E. crystallorophias* and *All E. superba* (Table 3). Average C:N ratios by mass of *T. macrura* and *P. antarcticum* (5.48 and 5.73, respectively) were significantly higher compared to *E. crystallorophias* and All *E. superba* (4.53 and

4.77, respectively) (Table 3). *E. superba* males had significantly higher nitrogen content and significantly lower carbon content and C:N values than juveniles and females (Table 3). The elemental composition of *E. antarctica* was significantly different from all other prey species, with a lower nitrogen content (0.059 mg N mg^{-1} DW^{-1}) and a higher carbon content (0.61 mg C mg^{-1} DW^{-1}), resulting in a the highest C:N ratio (10.3) of all species analyzed (Table 3).

The prey species with the highest overall lipid content was *E. antarctica* (55.0% DW), followed by *T. macrurca* (45.0 % DW), and *P. antarcticum* (38.6% DW) (although for the latter two species, lipid content was statistically indistinguishable). The total lipid content of the two fish species was mainly composed of neutral lipids, while *T. macrura* neutral and polar lipid contents were equal (Table 3). *E. crystallorophias* and All *E. superba* had the lowest overall total lipid contents (29.1% DW and 32.3% DW) (Table 3). For *E. superba*, males had significantly lower total lipid content (27.4% DW) than either juveniles or females (34.5% DW and 34.4% DW) (Table 3). *E. crystallorophias* and every sex/maturity stage of *E. superba* had higher polar lipid contents than neutral lipid contents (Table 3).

For all species analyzed, variations in carbon and nitrogen content were best explained by the animal's neutral lipid content, in that animals with a higher lipid composition were associated with higher carbon content and lower nitrogen content (Figure 3). The neutral lipid fractions of species in this study were mainly composed from triglycerides or wax esters. For *E. superba* and *P. antarcticum*, species whose neutral lipid content are mainly composed of triglycerides (as reviewed in Falk-Petersen et al. 2000, Lee et al. 2006), neutral lipid content vs. mg C mg^{-1} DW^{-1} or mg N mg^{-1} DW^{-1} were both best represented by linear regressions (Figure 3). For *T. macrura, E. crystallorophias,* and *E. antarctica*, species whose neutral lipid content was mainly composed of wax ester (as reviewed in Falk-Petersen et al. 2000, Lee et al. 2006), neutral lipid content vs. mg C mg^{-1} DW^{-1} was best represented by a linear regression, while lipid content vs. mg N mg^{-1} DW^{-1} was best represented by a quadratic polynomial (Figure 3). All regressions were significant ($p<0.05$)

Energy density values for All *E. superba*, *P. antarcticum* and *E. antarctica* were significantly different from each other. *E. antarctica* had the highest energy density (31.9 kJ g^{-1} DW^{-1}), followed by *P. antarcticum* (24.6 kJ g^{-1} DW^{-1}), and then by All *E. superba* (21.1 kJ g^{-1} DW^{-1}) (Table 3). Female *E. superba* energy density was significantly higher (22.0 kJ g^{-1} DW^{-1}) than male *E. superba* (19.5 kJ g^{-1} DW^{-1}) (Table 3).

Summer of 2009 vs. 2010

T. macrura and *E. crystallorophias* exhibited the most variability between years sampled of the five prey species investigated. *T. macrura* had a higher average total lipid content in 2009 (54.2% DW) than 2010 (31.2% DW), while *E. crystallorophias* showed the opposite trend, with lower total lipid content in 2009 (21.0% DW) than 2010 (34.5% DW) (Figure 4, Table 1). Prey carbon content between years followed that of total lipids – higher for *T. macrura* and lower for *E. crystallorophias* in 2009 vs. 2010. The trend was opposite for nitrogen (lower for *T. macrura* and higher for *E. crystallorophias* in 2009 vs. 2010), resulting in higher C:N values in 2009 than 2010 (5.88 and 4.79, respectively) for *T. macrura*, and lower C:N in 2009 than 2010 (3.92 and 4.94, respectively) for *E. crystallorophias* (Table 1). These interannual differences can be partially explained by differences in average individual total length of animals sampled in 2009 vs. 2010. There is a significant, positive relationship between average individual total length and total lipid content/carbon content/C:N for both species (Figure 5, Table 4) and a significant, negative relationship between nitrogen content and average individual total length for both species (Table 4). The average individual total lengths of *T. macrura* sampled in 2009 were significantly higher (14.2 mm) than those sampled in 2010 (12.3 mm) (Table 1). The reverse is true for *E. crystallorophias*, where the average individual total length was lower in 2009 (29.8 mm) than in 2010 (33.7 mm) (Table 1).

Differences between January of 2009 and 2010 were less prevalent in the other prey species of interest. Juvenile and All *E. superba* had slight but significantly higher carbon content in 2009

than in 2010. The C:N, total lipid, total length, and energy density of the fish *P. antarcticum* was higher in 2011 vs. 2010 (Table 1) (there was only one *P. antarcticum* fish collected in 2009, which was not included in the analysis). *P. antarcticum* sampled in 2011 were on average larger (111.5 mm) than those sampled in 2010 (91.0 mm), but there were no significant relationships between any of the prey quality metrics of interest and total length (Tables 1, 4). *P. antarcticum* had significantly lower average C:N ratios, lipid content and energy density in 2010 vs. 2011 (Figure 4, Table 1). (All of the *E. antarctica* collected were from 2011, Table 1).

Regional Comparison

Species/life stages for which there were significantly higher total lipid content in the South (all years combined) included *E. crystallorophias*, juvenile *E. superba*, female *E. superba,* and All *E. superba* (Figure 6, Table 2). While not significant, male *E. superba* and *E. antarctica* total lipid content were also generally higher in the South. *T. macrura* was the only species analyzed with higher lipid content in the North, though this difference was not significant (Table 2).

Nitrogen content was significantly higher for female *E. superba* and *Electrona sp.* in the North (Table 2). *T. macrura, E. crystallorophias,* male *E. superba*, and All *E. superba* also had higher average nitrogen content in the north, but not significantly so. Carbon content was significantly higher in the south for *T. macrura* and All *E. superba* (Table 2). All other prey species/life stages (*E. crystallorophias,* juvenile *E. superba*, male *E. superba,* female *E. superba, E. antarctica)* had higher average carbon content in the South, but this trend was not significant. These elemental trends resulted in higher C:N in the South for all prey species, with significant higher South C:N values for *T. macrura, E. crystallorophias,* female *E. superba* and All *E. superba* (Table 2).

The significant North-South difference in *E. crystallorophias* total lipid content and C:N values may again be partially explained by the significantly higher average individual length of

animals collected in the South (33.1 mm) vs. in the North (28.2 mm) (Table 2). As mentioned above, total lipid content scales positively with length of *E. crystallorophias* (Figure 5, Table 4). So, the significantly higher total lipid content and C:N values in the South (31.7% DW and 4.72, respectively) vs. the North (19.0% DW and 3.77, respectively) are more likely due to the different size distribution of animals in each region (i.e., larger in the south) rather than the impact of differing environmental parameters on animal physiology (Figure 6, Table 2). Juvenile *E. superba* total lipid content is also significantly, positively correlated with length (Figure 5, Table 4). However, juveniles of various lengths were sampled uniformly across the grid, so the significantly higher total lipid content in the South (37.6% DW) vs. the North (31.0% DW) is more likely due to regional influences on animal physiology (Figure 6, Table 2). There were no significant regional differences in energy densities for any prey species sampled (Table 2).

Relationship with length, latitude, hydrographic conditions, and time

Individual average total length was a good predictor for C:N and total lipid content in *T. macrura* (R^2 = 0.57 and 0.31, respectively), *E. crystallorophias* (R^2 = 0.64 and 0.48, respectively), and to a lesser extent juvenile *E. superba* (R^2 = 0.28 and 0.21, respectively) (Figure 4, Table 4). Nitrogen content was significantly, negatively related to length for all three species, and carbon content was significantly, positively related to length for only *T. macrura* and *E. crystallorophias* (Table 4). These individual elemental trends resulted in a significant, positive relationship in length vs. C:N for all three krill species (Table 4). The neutral lipid fraction is responsible for the majority of the variability for the significant, positive relationship in length vs. total lipid content for *T. macrura* and *E. crystallorophias*, while both the polar and neutral lipid fractions contribute equally to the significant positive relationship in length vs. total lipid content for juvenile *E. superba* (Table 4).

Latitude, mean upper water column temperature, Julian date sampled, and integrated Chl a are all highly correlated with each other due to the structure of the sampling cruise (starting in the

north at Adelaide Island and ending south at Charcot Island) (Figures 1, 2, and 7). All relationships between these properties were significant, with the exception of Julian Date Sampled vs. integrated Chl a (Appendix 1A). Latitude was the most important explanatory variable, resulting in the highest R^2 values for the relationships between mean upper water column temperature ($R^2 = 0.47$), Julian date ($R^2 = 0.46$), and integrated Chl a ($R^2 = 0.20$) (Figure 6). Mean upper water column temperature was negatively correlated with latitude, while Julian Date Sampled and integrated Chl a were both positively correlated with latitude (Figure 7).

T. macrura total lipid content was significantly, positively related to mean upper water column temperature ($R^2 = 0.39$) and significantly, negatively related to integrated Chl a ($R^2 = 0.79$) (Table 5). The polar lipid fraction accounts for most of the variability in the relationship between upper water column temperature vs. total lipid content, while both neutral and polar fractions contribute equally to the relationship between integrated Chl a vs. total lipids (Table 5). *E. crystallorophias* total lipid content was significantly, positively related to latitude ($R^2 = 0.35$) and integrated Chl a ($R^2 = 0.63$), and significantly, negatively related to upper water column temperature ($R^2 = 0.70$) (Table 5). The neutral lipid fraction accounts for most of the variability in relationships between environmental parameters and *E. crystallorophias* total lipid content (Table 5).

All *E. superba* total lipid content was positively, but weakly ($R^2 = 0.13$ for males and 0.05 for All), related to latitude and integrated Chl a (Figure 8, Table 5), with neutral and polar lipid fractions contributing equally to the relationship in latitude vs. total lipid content, and the polar lipid fraction to Chl a vs. total lipid content. Juvenile and male *E. superba* trends mirrored those found for All *E. superba*, with both life stages significantly, positively related to latitude, and both neutral and polar lipid fractions accounting equally for the variance (Figure 8, Table 5). Male total lipid content was also significantly, positively related to integrated Chl a, with the polar lipid fraction driving the relationship (Table 5). Juvenile and female *E. superba* total lipid content were both significantly,

positively related to Julian day and the polar lipid fraction explained the majority of the variance for juveniles, while the neutral lipid fraction explained more of the variability for females.

There were no significant relationships between any of the environmental parameters and *P. antarcticum* total lipid content, most likely due to the limited regional range of this fish (Figure 1, Table 5). *E. antarctica* neutral lipid content was significantly, positively related to latitude (R^2 = 0.44) and polar lipid content was significantly, negatively related to latitude (R^2 = 0.58) (Table 5). *E. antarctica* also had a significant, negative relationship between polar lipid content and Julian day (R^2 = 0.61).

E. superba seasonal comparison

The grid was sampled from north to south over the course of 5 weeks, thus a seasonal comparison of *E. superba* was conducted in 2010 and 2012 in which krill were collected from one of the northern-most stations at the beginning and end of the cruise to determine if the seasonal progression of summer was potentially biasing observed longitudinal trends. There was no significant difference between total lipid content for male *E. superba* sampled from the same northern station at the beginning (6 January 2010; 21.6% DW) and end (31 January 2010; 20.3% DW) of the cruise in 2010. Male and juvenile *E. superba* were higher in total lipid content at the end of the cruise (30 January 2012; 30.7% DW and 34.3% DW, respectively) than at the beginning (6 January 2012, 26.5% DW and 31.8% DW, respectively), but neither of these differences were significant.

DISCUSSION

Species comparison

T. macrura are the smallest, relatively most abundant euphausiids found throughout the WAP region, concentrated around the northern continental shelf/slope intersection (Nordhausen 1992, Ward et al. 2004, Ross et al. 2008). While *T. macrura* are found in stomach contents of Adélie

penguins along the WAP, they are usually overlooked as a potentially valuable prey item (Ross et al. 2008). Only three studies to date have discussed *T*. *macrura*-penguin dynamics, all in association with Rockhopper and Macaroni penguins on the sub-Antarctic Heard Island (Brown & Klages 1987, Klages et al. 1989, Deagle et al. 2007). In one of these, Deagle et al. (2007) found that, euphausiids constituted 43% of the diet by mass in the late-summer diet of Macaroni penguins, the majority of which were *T*. *macrura*. *T*. *macrura* have higher total lipid content than the other krill species analyzed in this study, and similar to the fish *P*. *antarcticum* (although our *T*. *macrura* total lipid values were generally higher than previously reported for this species; Table 3, Falk-Petersen 2000, Farber-Lorda & Mayzaud 2010). This could make *T*. *macrura* a high quality food item for penguins. However, *T*. *macrura* may not be optimal prey for other reasons. The small size and diffuse swarming behavior of *T*. *macrura* relative to other krill species (Daly & Macaulay 1988) may make for inefficient foraging by krill predators. In addition, we found that neutral and polar lipid fractions in *T*. *macrura* were distributed evenly, and previous studies have shown that the neutral lipid fraction is mainly composed of wax esters *T*. *macrura* (Hagen & Kattner 1998, Falk-Petersen et al. 2000). Some penguin species have roughly 20% lower assimilation efficiency for wax esters relative to triglycerides – the main component of the neutral lipid class for *E*. *superba* and *P*. *antarcticum* (Jackson & Place 1990) also potentially detracting from the benefits of a high total lipid content.

E. *superba* and *E*. *crystallorophias* are well-recognized and well-studied prey items for whales, penguins, and seals (Ross et al. 2008, Chapman et al. 2010, Friedlaender et al. 2011). Total lipid contents for these two species were similar statistically, and they were the only two species sampled with higher polar than neutral lipid content. Our results are consistent with previous studies showing that *E*. *superba* males have lower total lipid contents and energy densities than females (Clarke et al. 1980, Färber-Lorda et al. 2009). Unlike previous studies (Färber-Lorda et al. 2009), we found no significant difference in total lipid between mature female and juvenile *E*. *superba*, although total lipid content is somewhat dependent upon juvenile length (Figure 5, Table 4).

P. antarcticum had higher total lipid content than *E. crystallorophias* and *E. superba*, and higher relative neutral lipid content than any of the three krill species sampled (Table 3), emphasizing their value as a high energy prey item. Previous studies report that the neutral lipid fraction in *P. antarcticum* is predominantly composed of triglycerides, which are assimilated at higher efficiencies than the wax esters found in *T. macrura*, *E. crystallorophias*, and *E. antarctica* (Jackson & Place 1990, Whörmann et al. 1997, Hagen et al. 2000). *P. antarcticum* are slow-growing, notothenioid fish that were historically a consistent prey item for Adélie penguins along the WAP, but range contractions coincident with regional warming have now restricted their abundances to waters south of Adelaide Island (Figure 1) (Emslie & Patterson 2007, Fraser pers. comm.). The mechanisms associated with this range contraction are unknown, but are likely related to sea-ice dynamics as *P. antarcticum* spawning and embryo development takes place below the seasonal pack-ice (Bottaro et al. 2009). When available, Adélie penguins most frequently take fish 95-120 mm in standard length, corresponding to year-3 and year-4 age classes (McDaniel & Emslie 2002, Ainley et al. 2003, Chapman et al. 2011). The standard length of fish sampled in the present study ranged from 57.6 - 116.8 mm, with an average of 89.9 mm, representing fish from age classes 2, 3, and 4+ (Hubold & Tomo 1989, Chapman et al. 2011). There are few biochemical data available for these older age classes (Chapman et al. 2011). We thus added our lipid data to the model of Chapman et al. (2011), who found that a sigmoidal curve best represented the relationship between *P. antarcticum* standard length and total lipid content; our samples fit well within their model (Figure 9), extending their estimations for the year-3 and year-4 age classes.

E. antarctica is a numerically dominant, oceanic species of myctophid mainly found near the continental shelf/slope interface of the WAP (Donnely & Torres 2008). They also access shelf and coastal regions through intrusions of warm, UCDW water and are present in both the northern and southern WAP (Donnely & Torres 2008, Steinberg et al., unpublished data). Their exceptionally high lipid content, dominated by the neutral lipid fraction, resulted in the highest overall energy densities

for all species tested. They are important in the diets of higher predators (Lancraft et al. 2004, Casaux et al. 2011, Hückstädt et al. 2011), and their occurrence in northern, coastal regions of the WAP makes *E. antarctica* an energy-rich option for predators residing near Anvers Island, where *P. antarcticum* no longer persists (McDaniel & Emslie 2002). However, the neutral lipid fraction of *E. antarctica* has been documented as being mainly composed of wax esters which, as noted above, may be assimilated at lower efficiency in some species of penguins (Jackson & Place 1990, Phleger et al., 1997, Connan et al. 2010).

For all species analyzed, variations in carbon and nitrogen content were best explained by the animal's neutral lipid content, in that animals with higher neutral lipid stores had higher carbon and lower nitrogen content. The neutral lipid fractions of species in this study were likely composed of triglycerides or wax esters. Triglycerides (found in *E. superba* and *P. antarcticum*) are made from the attachment of three fatty acids to glycerine through ester bonds and are composed of 77% C and 0% N (Ventura 2006). Wax esters (found in *T. macrura, E. crystallorophias,* and *E. antarctica*) are fatty acids esterified with fatty alcohols and are composed of 81% C and 0% N (Ventura 2006). Proteins, free amino acids, RNA, DNA, chitin (in krill) and phospholipids contribute to the overall nitrogen content of an organism (Ventura 2006). As animals retained higher concentrations of neutral lipids, the overall contribution of the lipids to the dry weight increased, increasing the overall carbon content relative to nitrogen (Figure 3). The trend is consistent among zooplankton and fish, which highlights the strong influence of the neutral lipid class on prey elemental composition.

Differences in prey quality between the summer of 2009 and 2010

The majority of our samples were collected in January of 2009 and 2010, years that represented two archetypal progressions of sea ice for the WAP region. The austral spring of 2008 was marked by early ice retreat over the shelf and inshore, allowing high spring winds to maintain deeper mixed layers which contributed to the lower Chl a and primary productivity in the summer of

2009 (Figure 2c,10; Table 1) (Ducklow et al. 2012b). Conversely, there was anomalously late sea-ice retreat in spring 2009. The lingering sea ice protects the waters from high spring winds, while ice melt enhances stratification contributing to shallower mixed layers, likely increasing Chl a and primary productivity in the summer of 2010 (Figure 2d; Table 1) (Vernet et al. 2008, Ducklow et al. 2012b). Total sea-ice extent (defined as total area enclosed by the outer ice edge) in the PAL LTER sampling grid was 11,111 km^2 in January of 2009 and 12,408 km^2 in January of 2010 (S. Stammerjohn, pers. comm.). The majority of our fish samples were taken in 2011, which was also a year of late sea-ice retreat and high Chl a (Table 1) (S. Stammerjohn, pers. comm.).

There were significant interannual differences in 2009 vs. 2010 for total length and all prey quality metrics for *T. macrura* (both higher in 2009) and *E. crystallorophias* (both higher in 2010). The prey quality differences are not solely explained by differences in environmental parameters in 2009 vs. 2010, as length is a confounding factor for the analysis. *T. macrura* lipid content was higher in 2009 vs. 2010, though this was largely due to the presence of larger individuals in 2009 combined with a significant positive relationship between length and weight-specific total lipid content for this species. The same is true for *E. crystallorophias*, but with the opposite trend. *E. crystallorophias* lipid content was higher in 2010 vs. 2009, but this is mainly attributed to the presence of larger individuals in 2010.

Surprisingly, there were no significant interannual differences in total lipid content of *E. superba* in these two opposing sea-ice years. The growth and reproductive cycles of krill are influenced by environmental parameters such as sea ice, temperature, and food availability (Quetin & Ross 2001, Kawaguchi et al. 2007). Along the WAP, years with early ice retreat (e.g., 2009) are usually associated with late *E. superba* spawning, while years with late sea-ice retreat (e.g., 2010) are associated with early spawning (Quetin & Ross 2001). The timing of krill spawning is associated with the phenology of lipid accumulation during the summer in preparation for winter, so years of delayed spawning would likely exhibit a delay in lipid accumulation, with the reverse being true in

years of early spawning (Chapman et al. 2010). Chapman et al. (2010) postulated that delayed spawning and lipid accumulation in years of early ice retreat are due to an associated late seasonal phytoplankton bloom. Following the Bering Sea model, water column stratification from an early ice melt is eroded by spring winds and the bloom is delayed until surface warming from summer sunlight can restore stratification (Hunt et al. 2002, Chapman et al. 2010). Chl a peaks later in the summer, and krill reach maximum lipid accumulation later in the season, with the reverse being true for years of late sea-ice retreat. Our data did not support this hypothesized flexibility in lipid accumulation phenology. There were no significant interannual differences in total lipid content or energy densities for *E. superba*, but juvenile, female, and All *E. superba* had higher total lipid contents in 2009 than 2010, and lipid was lower in males during 2009 (Table 1). If lipid accumulation phenology had shifted in response to an early sea-ice retreat and a corresponding delay in the summer bloom, total lipid contents and energy densities should have been lower for all the different groups of *E. superba* sampled in 2009. This suggests that the phenology of *E. superba* lipid accumulation in the WAP was not affected by the timing of sea-ice retreat during this study.

P. antarcticum samples had higher total lipid content and energy densities in 2011 than 2010, which can be attributed to standard length differences in fish collected from each sampling year (Figure 9).

Regional comparison of prey quality

Demarcation of the North and South sub-regions was based on a 12-year study (1992-2004) of sea-ice dynamics conducted by Stammerjohn et al. (2008). Waters in the North are characterized by a highly variable, but lengthy, season of low sea-ice concentration, while the South's sea-ice season is longer with greater sea-ice persistence (Dierssen et al. 2002, Stammerjohn et al. 2008). Indeed, summer sea ice was present in the far southern portion of the WAP during every sampling year of this study. Another feature of the South is a persistent, cyclonic gyre located on the shelf off

of Marguerite Bay that has been hypothesized to retain Chl a and larval krill populations (Klinck et al. 2004, Wiebe et al. 2011). Marguerite Bay has also been recognized as a biological hot spot of enhanced productivity with high Chl a (Vernet et al. 2008), macro- and microzooplankton biomass (Marrari et al. 2011, Price et al., in prep), and apex predators (Friedlaender et al. 2011).

Significant regional differences in prey quality for the combined 2009 and 2010 juvenile, female, and All *E. superba* suggest that colder water temperatures and elevated Chl a increase the prey quality of krill. The physiological response of organisms to climate change is usually thought of as secondary in importance to broad, ecosystem-based trends, but polar invertebrates and ectotherms, whose metabolic rates vary with the ambient environment, have narrow temperature tolerances, which may prove important as the WAP region continues to warm (Peck et al 2004, Ducklow et al. 2012). The changing food base in the WAP could also affect *E. superba* physiology. Along with the previously discussed reduction in summertime, surface Chl a, there has been a restructuring of the phytoplankton, where cells >20μm are more prevalent in the South, and smaller-celled organisms such as flagellates are becoming more prevalent in the North (Montes-Hugo et al. 2009). *E. superba* preferentially feed on diatoms and have significantly lower grazing efficiencies when particles are <20μm (McClatchie & Boyd 1983, Haberman et al. 2003). Declines in this preferred food source could also affect the ability of krill to accumulate lipid stores in preparation for winter. This hypothesis is supported by the significantly higher total lipid content in the South for juvenile, female, and All *E. superba* groups (with male *E. superba* and the fish *E. antarctica* exhibiting the same general trend). The overall decline in diatom abundance in the North also has implications for *E. superba* winter survival and feeding ecology. Diatoms from the summer phytoplankton bloom aggregate and sink out of surface waters, providing a strong seasonal pulse of labile organic carbon to the benthos (Smith et al. 2008). *E. superba* can access benthic habitats year-round (including abyssal plains as deep as 3500m) and utilize phytodetritus as an alternate food source (Clarke & Tyler 2008, Schmidt et al. 2011). The importance, frequency, and seasonality of

krill benthic feeding is still not well understood, but decreasing diatom biomass in the north would equate to a lower POC flux to the benthos, potentially resulting in lower overall food availability for krill during the winter months. The magnitude of environmental variability between North and South is likely an important forcing factor affecting regional differences in prey quality. The differences in upper water column temperature and Chl a between the North and South were more extreme in 2010 than in 2009. This was reflected in North-South prey quality comparisons for each year; there were no significant North-South differences in 2009 in *E. superba* prey quality, while juvenile, male, and All *E. superba* had significantly higher total lipid content in the South in 2010.

For female *E. superba*, the increased statistical power associated with the higher number of samples enabled detection of significant regional differences in the combined 2009 and 2010 data that were not apparent when each year was analyzed separately. This is most likely related to the high variability associated with total lipid content for the females as a group. Reproduction in *E. superba* peaks during January and February, months coinciding with the seasonal phytoplankton bloom (Quetin et al. 1994, Fälk-Peterson et al. 2000). Female krill will produce multiple egg batches over the spawning season, severely altering their body size and energy stores to accommodate the brood of developing embryos beneath their carapace (Quetin & Ross 2001). This reproductive cycle has a direct effect on an individual krill's biochemical constituents, as mature gravid females have higher lipid stored than spent females (Farber-Lorda et al. 2009).

Regional comparisons of prey quality for both *T. macrura* and *E. crystallorophias* (2009 and 2010 combined) were confounded by interannual variability in length of animals sampled – when broken down by year, there were no significant differences between North and South for any prey metric. Thus, comparisons presented in Table 2 cannot be entirely attributed to regional influences. Additional samples, separated by sex/maturity stage, would be required to detect regional differences in these species.

Relationship of prey quality with length, latitude, hydrographic conditions, and time

We found significant relationships between length vs. C, N, and lipid content for *T. macrura*, *E. crystallorophias*, and juvenile *E. superba* (Table 4, Figure 5), supporting previous studies (Ju & Harvey 2004, Färber-Lorda & Mayzaud 2010). The neutral lipid fraction accounted for the majority of the variability in length vs. total lipid content for both *T. macrura* and *E. crystallorophias*. This positive, significant relationship between length and the neutral lipid class has been explained as a buoyancy regulating mechanism for krill; as their body grows and becomes heavier, relative neutral lipid content increases so that the animal remains neutrally buoyant (Falk-Petersen 1985). The polar lipid content was positively, but not significantly, related to length, which is surprising as the polar fraction is mainly composed of phospholipids which function as structural and storage lipids for euphausiids (Hagen et al. 1996, Ju et al. 2009). The role of phospholipids as major components of cell membranes would presumably result in increasing polar lipid concentrations with somatic growth, but this was not supported by our data.

The environmental and temporal properties included in our analyses (latitude, 0-120m mean water temperature, Julian day sampled, and 0-120m integrated Chl a) are all highly correlated with one another, due to the structure of our cruise track (starting in the north at Anvers Island and ending far south at Charcot Island) and the North-South difference in climate regime. Thus, although below we discuss prey quality in relation to these specific environmental and temporal parameters, we note it is likely that significant relationships between these properties are the result of a mixture of influences, instead of just one.

All lipid classes for juvenile, male, and All *E. superba* were positively related to latitude, supporting results from our regional analysis (Figure 8). Males and All *E. superba* were also significantly, positively related to Chl a, and juveniles and females were significantly, positively related to Julian date sampled, suggesting that growth trends in juveniles and the reproductive cycle of females are contributing to the observed latitudinal trend. Although there were significant regional

differences in average female *E. superba* total lipid content, these did not result in a significant relationship with latitude (although the trend was positive, with a slope of 1.2) or any other environmental parameters. This is most likely due to the high variability in *E. superba* females as a group, associated with the cyclical nature of the spawning season and corresponding changes in biochemical composition. Chl a explained a larger proportion of the variability in trends in total lipid content than mean upper water column temperature, and is the environmental parameter contributing most to observed latitudinal and regional lipid trends.

There was a significant, negative relationship between latitude and Chl a and polar lipid content, and a significant, positive relationship between mean upper water temperature and polar lipid content for *T. macrura* (Table 5). This trend was opposite of that expressed in other species, for which polar lipid content was generally positively related to latitude and Chl a and negatively related to mean upper water temperature. (Note – there was no significant relationship between length and polar lipid content in *T. macrura,* thus no confounding influence of length differences with latitude). We suggest that the polar lipid class is more susceptible to environmental variability than the neutral lipid class for *T. macrura*. Like most polar zooplankton, it is essential that *T. macrura* obtain large deposits of wax esters, the main component of their neutral lipid fraction, during the summer season to survive through the winter months (Nordhausen 1994, Falk-Petersen et al. 2000). *T. macrura* is unusual in that it stores enough lipids to start reproducing in September, before the summer phytoplankton bloom, (Falk-Petersen et al. 2000, Lee et al. 2006). Unlike triacylglycerols, wax esters are used for long-term energy storage, and rates of catabolism are highly regulated by lipases (Lee et al. 2006). *T. macrura* may thus rely on the polar lipid fraction for energy during the summer, making this fraction more susceptible to environmental influences (Sargent et al. 1977, Håkanson 1984, Lee et al. 2006). Trends in the relationship between environmental parameters and *T. macrura* prey quality were opposite to those of other species of krill. Lipid content in *T. macrura* was generally higher in the North, where temperatures were warmer and there was lower Chl a. This is also where

maximum abundance of this species is known to occur at the slope/shelf interface (Ross et al. 2008) thus these conditions must be optimal for *T*. *macrura*.

In contrast, all significant relationships between *E*. *crystallorophias* and environmental or temporal parameters were associated with the neutral lipid class (but for which length is likely a confounding variable). The neutral and total lipid fractions for *E*. *crystallorophias* were significantly, positively related to latitude and Chl a, and are significantly, negatively related to mean upper water temperature.

For *E*. *antarctica* there was a significant, positive trend in latitude vs. neutral lipid content and a significant, negative trend in latitude vs. polar lipid content (Table 5). However, there was no overall significant trend for latitude vs. total lipid content (neutral and polar fractions summed). This highlights the value of examining lipid classes separately, which can reveal dynamics that are lost when examining total lipid pools only. The significant, positive relationship between latitude and neutral lipid content supports the hypothesis that warmer water temperatures and lower Chl a in the North is associated with lower lipid content. *E*. *antarctica* are planktivorous, subsisting mainly on copepods, amphipods and small euphausiids (Hoddel 1996). Marguerite Bay, where all of the South *E*. *antarctica* samples were collected, is considered a biological hotspot characterized by high Chl a and zooplankton biomass (Ashijan et al. 2004, Vernet et al. 2008). The positive relationship between latitude and neutral lipid content suggests that Marguerite Bay is a better habitat for fish with ready access to food, which aids in accumulating wax ester stores. The mechanism behind the negative relationship between latitude (and Julian date sampled) vs. *E*. *antarctica* polar lipid content is unknown, as the function of the polar lipid fraction in *E*. *antarctica*, beyond structural purposes, is poorly understood. Further analysis of individual fatty acids or conducting a compound class distribution (i.e., measuring gross concentrations of saturated and unsaturated fatty acids, fatty alcohols, alkanes, etc.) would provide additional insights into these opposing lipid class dynamics.

SUMMARY AND CONCLUSIONS

Our characterization of prey quality for five mid-trophic species important to penguin diets along the WAP further reinforced the importance of fish as a high-energy supplement to a krill-based diet, due to the relatively higher total lipid content and energy density of fish. The krill *T. macrura* is also high in total lipid content, making it a potentially important prey item for apex predators along the WAP. However, *T. macrura*'s small body size and aggregation behavior may counteract this benefit, from a predator's perspective.

This study was also the first to relate sea ice dynamics and environmental variability caused by rapid regional warming with prey quality along the WAP. We found significant regional differences in *E. superba* total lipid content and significant relationships between latitude and *E. superba* prey quality, as higher total lipid contents were found at higher latitudes. Neutral and polar lipids equally contributed to total lipid trends, indicating that both are important to krill as they create energy stores in preparation for winter. Relating *E. superba* total lipid content to environmental and temporal variability showed that 0-120 m integrated Chl a and the Julian date that samples were taken were important drivers in observed latitudinal trends. There was no significant difference in prey quality for *E. superba* between January 2009 vs. 2010, two sampling years with different sea ice dynamics, contradicting the lipid phenology hypothesis presented by Chapman et al. (2010). For *T. macrura* and *E. crystallorophias*, animal length confounded January 2009 vs. 2010 and North vs. South comparisons, and more samples separated by length, sex, and maturity stages are required to accurately characterize any potential trends in prey quality along the sampling grid for these species.

Putting some of our conclusions in the larger context of the WAP ecosystem, rapid regional warming has fundamentally altered ecosystem structure and, if trends continue, the northern WAP will soon be characterized by a lack of perennial or summer sea ice, warmer water temperatures, and phytoplankton dominated by smaller cells as opposed to diatoms (Martinson et al. 2008,

Stammerjohn et al. 2008, Montes-Hugo et al. 2009). We found that these types of conditions are associated with lower prey quality for *E. superba*, which could have significant ramifications for the rich assemblage of endothermic top predators that make their summer home in the WAP and utilize krill as their main food source (Croxall et al. 1992, Chapman et al. 2010). Across all sexes and maturity stages, *E. superba* in the South had roughly 20% higher total lipid content than in the North, meaning northern apex predators will have to consume more prey to meet their energetic demands or increase their reliance on other prey sources. *E. superba* are also experiencing localized regional declines in the northern, coastal WAP and there is currently no functional replacement for this dominant trophic link (Ross et al. 2008, Steinberg et al., unpublished data). The krill *T. macrura* are high in abundance and prey quality, but their small body size, diffuse aggregation behavior, and high wax ester content compared to *E. superba* might make them an inefficient target prey species (Daly & Macauluy 1988, Jackson & Place 1990, Ross et al. 2008). The krill *E. crystallorophias* and fish *P. antarcticum* are also high quality prey, but their ranges are restricted to the South, where summer sea ice still persists (McDaniel & Emslie 2002, Ducklow et al. 2012a). The myctophid *E. antarctica* represents a potential, energy rich option for coastal marine predators residing in the North, although this fish species' neutral lipid content increased with increasing latitude, also making it a relatively better quality prey in the South. Incorporating these species-specific prey quality dynamics into future energetics modeling efforts will increase model accuracy by improving the quality of functions regulating predator growth.

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Table 1. January 2009 vs. 2010 comparison of environmental parameters and prey quality. Averages and ranges (in parentheses) for properties measured in January 2009, 2010, and 2011 for prey species: Euphausiids – *T.macrura*, *Thysanoessa macrura; E. crystallorophias*, *Euphausia crystallorophias;* Juvenile *E. superba*, Juvenile *Euphausia superba;* Male *E. superba*, Male *Euphausia superba*; Female *E. superba*, Female *Euphausia superba;*All *E. superba*, All *Euphausia superba;* Fish – *P. antarcticum, Pleuragramma antarcticum; E. antarctica, Electrona antarctica*. P-values are given for all significant results (where $p \leq 0.05$); ns, not significant; dash (-) indicates data only spanned one sampling year and no interannual comparisons were made. All prey metric data are presented as dry weight (DW), and energy density as kilojoules (kJ).

Property	2009	2010	2011	Significance
0-120m Average Water Temp (°C)	**-0.01 (-0.98-0.72)**	**-0.58 (-1.69-0.36)**		**p < 0.001**
0-120m Integrated Chl a (mg m^{-2})	**52.19 (17.47-103.59)**	**119.42 (25.38-623.43)**	**209.16 (10.78-621.70)**	**p < 0.001 ('09 vs '10)** **p < 0.001 ('09 vs '11)** ns ('10 vs '11)
T. macrura Nitrogen (mg N mg^{-1} DW^{-1})	**0.080 (0.067-0.118)**	**0.089 (0.082-0.097)**		**p = 0.003**
T. macrura Carbon (mg C mg^{-1} DW^{-1})	**0.46 (0.39-0.52)**	**0.42 (0.40-0.47)**		**p = 0.03**
T. macrura (mg C:mg N)	**5.88 (3.78-7.58)**	**4.79 (4.28 -5.13)**		**p = 0.003**
T. macrura Total Lipids (%DW)	**54.20 (42.78-71.31)**	**31.23 (20.59-41.43)**		**p < 0.001**
T. macrura Total Length (mm)	**14.22 (10.14-17.39)**	**12.30 (10.62-13.68)**		**p = 0.03**
E. crystallorophias Nitrogen (mg N mg^{-1} DW^{-1})	**0.099 (0.094-0.10)**	**0.088 (0.081-0.093)**		**p < 0.001**
E. crystallorophias Carbon (mg C mg^{-1} DW^{-1})	**0.39 (0.37-0.41)**	**0.43 (0.42-0.46)**		**p < 0.001**
E. crystallorophias (mg C:mg N)	**3.92 (3.67-4.29)**	**4.94 (4.66-5.16)**		**p < 0.001**
E. crystallorophias Total Lipids (%DW)	**21.02 (16.95-27.01)**	**34.54 (28.18-42.10)**		**p = 0.009**
E. crystallorophias Total Length (mm)	**29.78 (26.83-32.19)**	**33.66 (30.20-36.38)**		**p = 0.005**
Juvenile *E. superba* Nitrogen (mg N mg^{-1} DW^{-1})	0.084 (0.077-0.10)	0.086 (0.072-0.105)		ns
Juvenile *E. superba* Carbon (mg C mg^{-1} DW^{-1})	**0.43 (0.40-0.47)**	**0.42 (0.36-0.45)**		**p = 0.03**
Juvenile *E. superba* (mg C:mg N)	5.14 (4.36-6.02)	4.82 (3.92-5.70)		ns
Juvenile *E. superba* Total Lipids (%DW)	36.88 (19.61-64.51)	32.27 (14.57-46.68)		ns
Juvenile *E. superba* Total Length (mm)	**33.66 (27.01-38.87)**	**31.34 (28.08-38.05)**		**p = 0.03**
Male *E. superba* Nitrogen (mg N mg^{-1} DW^{-1})	0.096 (0.076-0.106)	0.090 (0.071-0.106)		ns
Male *E. superba* Carbon (mg C mg^{-1} DW^{-1})	0.41 (0.36-0.46)	0.40 (0.32-0.50)		ns
Male *E. superba* (mg C:mg N)	4.34 (3.50-5.59)	4.45 (3.37-6.39)		ns
Male *E. superba* Total Lipids (%DW)	25.79 (14.06-45.06)	28.23 (17.36-54.27)		ns
Male *E. superba* Total Length (mm)	**46.96 (40.84-50.18)**	**49.28 (43.23-52.62)**		**p = 0.02**
Male *E. superba* Energy Density (kJ g^{-1} DW^{-1})	18.92 (16.02-23.27)	19.77 (16.75-24.36)		ns
Female *E. superba* Nitrogen (mg N mg^{-1} DW^{-1})	0.088 (0.076-0.097)	0.088 (0.078-0.104)		ns
Female *E. superba* Carbon (mg C mg^{-1} DW^{-1})	0.43 (0.39-0.47)	0.42 (0.37-0.46)		ns
Female *E. superba* (mg C:mg N)	4.96 (4.27-6.21)	4.86 (3.68-5.70)		ns
Female *E. superba* Total Lipids (%DW)	36.42 (29.20-54.72)	32.20 (12.36-42.10)		ns
Female *E. superba* Total Length (mm)	47.68 (40.34-51.88)	48.86 (43.41-52.60)		ns
Female *E. superba* Energy Density (kJ g^{-1} DW^{-1})	22.43 (19.68-25.33)	21.48 (19.00-23.74)		ns
All *E. superba* Nitrogen (mg N mg^{-1} DW^{-1})	0.089 (0.076-0.106)	0.088 (0.071-0.106)		ns
All *E. superba* Carbon (mg C mg^{-1} DW^{-1})	**0.43 (0.36-0.47)**	**0.41 (0.32-0.50)**		**p = 0.003**
All *E. superba* (mg C:mg N)	4.88 (3.50-6.21)	4.69 (3.37-6.39)		ns
All *E. superba* Total Lipids (%DW)	34.04 (14.06-64.51)	30.74 (12.36-54.27)		ns
All *E. superba* Total Length (mm)	42.07 (27.01-51.88)	43.96 (28.08-52.62)		ns
All *E. superba* Energy Density (kJ g DW^{-1})	21.6 (16.02-25.33)	20.58 (16.75-24.36)		ns
P. antarcticum Nitrogen (mg N mg^{-1} DW^{-1})	0.09	0.090 (0.084-0.097)	0.082 (0.068-0.098)	ns ('10 vs '11)
P. antarcticum Carbon (mg C mg^{-1} DW^{-1})	0.46	0.47 (0.46-0.50)	0.50 (0.44-0.54)	ns ('10 vs '11)
P. antarcticum (mg C:mg N)	**5.16**	**5.29 (4.72-5.90)**	**6.14 (4.97-6.97)**	**p = 0.05 ('10 vs '11)**
P. antarcticum Total Lipids (%DW)	**42.56**	**34.52 (27.41-38.08)**	**41.96 (37.98-46.82)**	**p = 0.02 ('10 vs '11)**
P. antarcticum Standard Length (mm)	**57.62**	**83.13 (70.35-88.83)**	**99.40 (85.40-116.82)**	**p = 0.01 ('10 vs '11)**
P. antarcticum Energy Density (kJ g^{-1} DW^{-1})	**-**	**23.35 (22.36-24.77)**	**25.18 (23.74-26.93)**	**p = 0.04 ('10 vs '11)**
E. antactica Nitrogen (mg N mg^{-1} DW^{-1})			0.059 (0.056-0.064)	-
E. antactica Carbon (mg C mg^{-1} DW^{-1})			0.61 (0.56-0.64)	-
E. antactica (mg C:mg N)			10.30 (9.24-11.47)	-
E. antactica Total Lipids (%DW)			54.96 (44.41-59.82)	-
E. antactica Standard Length (mm)			76.48 (54.49-90.09)	-
E. antactica Energy Density (kJ g^{-1} DW^{-1})			31.92 (29.96-32.68)	-

Table 2. Regional comparison of environmental parameters and prey quality. Regional averages and ranges (in parentheses) for properties measured in the North and South - as defined in Figure 1, for prey species: Euphausiids – *T.macrura, Thysanoessa macrura; E. crystallorophias, Euphausia crystallorophias;* Juvenile *E. superba,* Juvenile *Euphausia superba;* Male *E. superba,* Male *Euphausia superba*; Female *E. superba*, Female *Euphausia superba;* All *E. superba*, All *Euphausia superba*; Fish – *P. antarcticum, Pleuragramma antarcticum; E. antarctica, Electrona antarctica*. All regional comparisons are combined 2009 and 2010 data, except for 2011 Chl a, *P. antarcticum,* and *E. antarctica* comparisons, which included 2011 data. P-values are given for all significant results (where $p \leq 0.05$); ns, not significant; dash (-) indicates data only spanned one region and no comparisons were made. All prey metric data are presented as dry weight (DW), and energy density as kilojoules (kJ).

Property	North	South	Significance
0-120m Average Water Temp (^{o}C)	**0.12 (-0.60-0.72)**	**-0.57 (-1.69-0.21)**	**p < 0.001**
2009 & 2010, 0-120m Integrated Chl a (mg m^{-2})	**60.78 (20.45-169.91)**	**103.82 (17.47-623.43)**	**p = 0.05**
2011, 0-120m-Integrated Chl a (mg m^{-2})	**39.92 (10.78-73.70)**	**255.84 (24.41-621.70)**	**p < 0.001**
T. macrura Nitrogen (mg N mg^{-1} DW^{-1})	0.087 (0.075-0.118)	0.079 (0.067-0.093)	ns
T. macrura Carbon (mg C mg^{-1} DW^{-1})	**0.43 (0.39-0.51)**	**0.46 (0.42-0.52)**	**p = 0.03**
T. macrura (mg C:mg N)	**5.07 (3.78-6.25)**	**5.97 (4.56-7.58)**	**p = 0.04**
T. macrura Total Lipids (%DW)	46.22 (20.59-71.31)	43.81 (22.89-70.40)	ns
T. macrura Total Length (mm)	**12.56 (10.14-14.87)**	**14.68 (11.62-17.39)**	**p = 0.01**
E. crystallorophias Nitrogen (mg N mg^{-1} DW^{-1}	0.100 (0.096-0.104)	0.090 (0.081-0.100)	ns
E. crystallorophias Carbon (mg C mg^{-1} DW^{-1})	0.38 (0.37-0.39)	0.42 (0.38-0.46)	ns
E. crystallorophias (mg C:mg N)	**3.77 (3.67-3.94)**	**4.72 (3.91-5.16)**	**p = 0.009**
E. crystallorophias Total Lipids (%DW)	**19.01 (16.96-22.41)**	**31.66 (20.54-42.10)**	**p < 0.001**
E. crystallorophias Total Length (mm)	**28.17 (26.83-29.47)**	**33.09 (30.20-36.38)**	**p = 0.003**
Juvenile *E. superba* Nitrogen (mg N mg^{-1} DW^{-1})	0.083 (0.074-0.094)	0.086 (0.072-0.106)	ns
Juvenile *E. superba* Carbon (mg C mg^{-1} DW^{-1})	0.41 (0.36-0.45)	0.42 (0.39-0.47)	ns
Juvenile *E. superba* (mg C:mg N)	4.91 (3.94-5.72)	4.99 (3.92-6.02)	ns
Juvenile *E. superba* Total Lipids (%DW)	**30.96 (14.57-48.89)**	**37.57 (21.64-64.51)**	**p = 0.007**
Juvenile *E. superba* Total Length (mm)	32.66 (27.01-38.87)	32.32 (28.08-37.17)	ns
Male *E. superba* Nitrogen (mg N mg^{-1} DW^{-1})	0.093 (0.071-0.11)	0.091 (0.071-0.10)	ns
Male *E. superba* Carbon (mg C mg^{-1} DW^{-1})	0.39 (0.32-0.46)	0.42 (0.36-0.50)	ns
Male *E. superba* (mg C:mg N)	4.20 (3.37-5.59)	4.63 (3.50-6.39)	ns
Male *E. superba* Total Lipids (%DW)	24.55 (14.06-45.06)	30.54 (15.03-54.27)	ns
Male *E. superba* Total Length (mm)	48.63 (40.84-52.62)	48.17 (43.23-52.53)	ns
Male *E. superba* Energy Density (kJ g^{-1} DW^{-1})	19.23 (16.02-23.27)	19.84 (16.38-24.36)	ns
Female *E. superba* Nitrogen (mg N mg^{-1} DW^{-1})	**0.092 (0.083-0.104)**	**0.086 (0.076-0.097)**	**p = 0.005**
Female *E. superba* Carbon (mg C mg^{-1} DW^{-1})	0.42 (0.37-0.45)	0.43 (0.38-0.47)	ns
Female *E. superba* (mg C:mg N)	**4.60 (3.68-5.09)**	**5.06 (4.05-6.21)**	**p = 0.01**
Female *E. superba* Total Lipids (%DW)	**30.77 (12.46-39.50)**	**36.26 (25.47-54.72)**	**p = 0.03**
Female *E. superba* Total Length (mm)	48.18 (40.34-51.88)	48.31 (43.41-52.60)	ns
Female *E. superba* Energy Density (kJ g^{-1} DW^{-1})	21.83 (19.00-23.75)	22.13 (19.68-25.33)	ns
All *E. superba* Nitrogen (mg N mg^{-1} DW^{-1})	0.091 (0.071-0.11)	0.087 (0.071-0.106)	ns
All *E. superba* Carbon (mg C mg^{-1} DW^{-1})	**0.41 (0.32-0.46)**	**0.43 (0.37-0.50)**	**p = 0.001**
All *E. superba* (mg C:mg N)	**4.55 (3.37-5.72)**	**4.92 (3.50-6.37)**	**p = 0.004**
All *E. superba* Total Lipids (%DW)	**28.51 (12.36-48.89)**	**35.21 (15.03-64.51)**	**p < 0.001**
All *E. superba* Total Length (mm)	42.61 (27.01-52.62)	42.51 (28.08-52.60)	ns
All *E. superba* Energy Density (kJ g^{-1} DW^{-1})	20.46 (16.02-23.75)	21.45 (16.38-25.33)	ns
P. antarcticum Nitrogen (mg N mg^{-1} DW^{-1})		0.085 (0.068-0.098)	-
P. antarcticum Carbon (mg C mg^{-1} DW^{-1})		0.49 (0.44-0.54)	-
P. antarcticum (mg C:mg N)		5.73 (4.72-6.97)	-
P. antarcticum Total Lipids (%DW)		38.60 (27.41-46.82)	-
P. antarcticum Standard Length (mm)		89.93 (57.62-116.82)	-
P. antarcticum Energy Density (kJ g^{-1} DW^{-1})		24.63 (22.36-26.93)	-
E. antactica Nitrogen (mg N mg^{-1} DW^{-1})	**0.062 (0.061-0.064)**	**0.058 (0.056-0.062)**	**p = 0.05**
E. antactica Carbon (mg C mg^{-1} DW^{-1})	0.59 (0.59-0.60)	0.61 (0.56-0.65)	ns
E. antactica (mg C:mg N)	9.52 (9.24-9.80)	10.50 (9.49-11.47)	ns
E. antactica Total Lipids (%DW)	50.60 (44.41-56.79)	56.05 (50.74-59.82)	ns
E. antactica Standard Length (mm)	78.87 (77.64-80.10)	75.88 (54.49-90.09)	ns
E. antactica Energy Density (kJ g^{-1} DW^{-1})	31.94 (31.82-32.07)	31.92 (29.96-32.68)	ns

Table 3. Prey quality measurements by species. Averages and ranges (in parentheses) for all sampling years combined (2009-2011) for prey species: Euphausiids – *T.macrura*, *Thysanoessa macrura; E. crystallorophias*, *Euphausia crystallorophias;* Juvenile *E. superba*, Juvenile *Euphausia superba;* Male *E. superba*, Male *Euphausia superba*; Female *E. superba*, Female *Euphausia superba;* All *E. superba*, All *Euphausia superba*; Fish – *P. antarcticum, Pleuragramma antarcticum; E. antarctica*, *Electrona antarctica*. All euphausiid length data are given as total length, while fish data are given as standard length. All prey metric data are presented as dry weight (DW), and energy density as kilojoules (kJ).

Property	*T. macrura*	*E. crystallorophias*	Juvenile *E. superba*	Male *E. superba*	Female *E. superba*	All *E. superba*	*P. antarcticum*	*E. antarctica*
Nitrogen (mg N mg^{-1} DW^{-1})	0.083 (0.067-0.118)	0.092 (0.081-0.104)	0.085 (0.072-0.106)	0.092 (0.071-0.106)	0.088 (0.076-0.104)	0.088 (0.071-0.106)	0.085 (0.068-0.098)	0.059 (0.056-0.064)
Carbon (mg C mg^{-1} DW^{-1})	0.45 (0.39-0.52)	0.42 (0.37-0.46)	0.42 (0.36-0.47)	0.40 (0.32-0.50)	0.43 (0.37-0.47)	0.42 (0.32-0.50)	0.49 (0.44-0.54)	0.61 (0.56-0.64)
Mg C:mg N	5.48 (3.78-7.58)	4.53 (3.67-5.16)	4.96 (3.92-6.02)	4.42 (3.37-6.39)	4.91 (3.68-6.22)	4.77 (3.37-6.39)	5.73 (4.72-6.97)	10.30 (9.24-11.47)
Neutral Lipids (%DW)	22.47 (11.25-36.35)	11.47 (4.62-19.30)	14.60 (5.75-29.54)	10.03 (1.85-25.72)	13.65 (2.54-20.44)	12.85 (1.85-29.54)	25.71 (15.03-35.53)	48.42 (33.74-53.97)
Polar Lipids (%DW)	22.35 (9.19-35.29)	17.67 (11.93-28.46)	19.74 (7.00-46.42)	17.34 (9.30-30.09)	20.78 (9.81-34.28)	19.34 (7.00-46.42)	12.90 (7.10-20.03)	6.54 (4.54-10.68)
Total Lipids (%DW)	45.02 (20.59-71.31)	29.13 (16.95-42.10)	34.52 (14.57-64.51)	27.37 (14.06-54.27)	34.43 (12.36-54.72)	32.26 (12.36-64.51)	38.60 (27.41-46.82)	54.96 (44.41-59.82)
Total/Standard Length (mm)	13.52 (10.14-17.39)	32.10 (26.83-36.38)	32.47 (27.01-38.87)	48.41 (40.84-52.62)	48.27 (40.3-52.60)	42.55 (27.01-52.62)	89.92 (57.62-116.82)	76.48 (54.49-90.09)
Energy Density (kJ g^{-1} DW^{-1})				19.52 (16.02-24.36)	22.04 (19.00-25.33)	21.07 (16.02-25.33)	24.63 (22.36-26.93)	31.92 (29.96-32.68)

Table 4. Relationship between length vs. elemental composition and lipid fraction by species. Average individual length (mm) vs. elemental composition (mg N mg^{-1} DW^{-1} or mg C mg^{-1} DW^{-1}) and lipid fractions (% dry weight, DW) for euphausiid prey species: *T.macrura*, *Thysanoessa macrura; E. crystallorophias*, *Euphausia crystallorophias;* Juvenile *E. superba*, Juvenile *Euphausia superba*. There were no significant length – composition relationships for other species (not shown). Regression equations are: Elemental Composition (mg N mg^{-1} DW^{-1} or mg C mg^{-1} DW^{-1}) or Lipid Fraction (%DW) = m (Average Individual Length, mm) + b. R^2 values are given in front of p-values for all significant relationships (where $p \leq 0.05$); ns, not significant. See also Figure 4.

Species	Elemental Composition	Slope (m)	Intercept (b)	R^2	Lipid Fraction	Slope (m)	Intercept (b)	R^2	n
T. macrura	Nitrogen (mg N mg^{-1} DW^{-1})	-0.003	0.12	0.49 ($p < 0.001$)	Neutral	2.87	-17.18	0.52 ($p = 0.0003$)	21
	Carbon (mg C mg^{-1} DW^{-1})	0.01	0.28	0.35 ($p = 0.006$)	Polar			$p = 0.15$, ns	22
	C:N	0.37	0.48	0.57 ($p < 0.001$)	Total	4.14	-12.12	0.31 ($p = 0.01$)	21
E. crystallorophias	Nitrogen (mg N mg^{-1} DW^{-1})	-0.002	0.15	0.65 ($p < 0.001$)	Neutral	1.13	-24.74	0.45 ($p = 0.006$)	15
	Carbon (mg C mg^{-1} DW^{-1})	0.006	0.21	0.44 ($p = 0.007$)	Polar			$p = 0.081$, ns	15
	C:N	0.15	-0.4	0.64 ($p < 0.001$)	Total	1.94	-33.09	0.48 ($p = 0.004$)	15
Juvenile *E. superba*	Nitrogen (mg N mg^{-1} DW^{-1})	-0.001	0.12	0.21 ($p = 0.02$)	Neutral	0.75	-9.91	0.20 ($p = 0.005$)	39
	Carbon (mg C mg^{-1} DW^{-1})			$p = 0.08$, ns	Polar	0.8	-6.26	0.13 ($p = 0.03$)	39
	C:N	0.09	2.02	0.28 ($p = 0.004$)	Total	1.46	-12.97	0.21 ($p = 0.004$)	39

Table 5. Relationship between environmental parameters and lipid composition by species. Various regional or environmental parameters vs. lipid fractions (% dry weight, DW) for prey species: Euphausiids – *T.macrura, Thysanoessa macrura; E. crystallorophias, Euphausia crystallorophias;* Juvenile *E. superba,* Juvenile *Euphausia superba;* Male *E. superba,* Male *Euphausia superba*; Female *E. superba*, Female *Euphausia superba;* All *E. superba,* All *Euphausia superba*; Fish – *P. antarcticum, Pleuragramma antarcticum; E. antarctica, Electrona antarctica*. Regression equations are: Lipid Fraction (%DW) = m (Environmental Parameter) + b. Regressions for data from all sampling years combined (2009-2011), unless otherwise noted. R^2 are given in front of p-values for all significant relationships (where $p \leq 0.05$); ns, not significant. See also Figure 7.

		Latitude (DD)			0-120m Mean Water Temp (°C)			0-120m Integrated Chl a (mg m^{-2})			
Species	**Lipid Fraction**	**Slope (m)**	**Intercept (b)**	**R^2**	**Slope (m)**	**Intercept (b)**	**R^2**	**Slope (m)**	**Intercept (b)**	**R^2**	**n**
T. macrura	Neutral			p = 0.75, ns			p = 0.14, ns	**-0.26**	**36.32**	**0.72 (p =0.0003)**	21
	Polar	**-3.15**	**230.35**	**0.24 (p = 0.03)**	**10.43**	**21.97**	**0.51 (p = 0.0003)**	**-0.27**	**36.66**	**0.71 (p = 0.0003)**	22
	Total			p = 0.17, ns	**16.96**	**44.97**	**0.39 (p = 0.003)**	**-0.53**	**73.32**	**0.79 (p = <0.0001)**	21
E. crystallorophias	Neutral	**2.04**	**-128.78**	**0.39 (p = 0.01)**	**-5.12**	**8.22**	**0.67 (p = 0.0002)**	**0.03**	**6.67**	**0.67 (p = 0.006)**	15
	Polar			p = 0.19, ns			p = 0.07, ns			p = 0.08, ns	15
	Total	**3.25**	**-194.19**	**0.35 (p = 0.02)**	**-8.29**	**23.87**	**0.63 (p = 0.0004)**	**0.05**	**20.83**	**0.70 (p =0.004)**	15
Juvenile,	Neutral	**1.32**	**-73.43**	**0.24 (p = 0.02)**			p = 0.77, ns			p = 0.16, ns	39
E. superba	Polar	**2.31**	**-134.45**	**0.24 (p = 0.002)**			p = 0.55, ns			p = 0.09, ns	39
	Total	**3.50**	**-198.69**	**0.26 (p = 0.001)**			p = 0.87, ns			p = 0.07, ns	39
Male, *E. superba*	Neutral	**1.60**	**-95.61**	**0.17 (p = 0.02)**			p = 0.23, ns			p = 0.25, ns	34
	Polar	**1.41**	**-76.07**	**0.17 (p = 0.02)**			p = 0.17, ns	**0.06**	**12.79**	**0.19 (p = 0.01)**	34
	Total	**3.01**	**-171.69**	**0.23 (p = 0.004)**			p = 0.14, ns	**0.10**	**20.39**	**0.13 (p = 0.04)**	34
Female,	Neutral			p = 0.08, ns			p = 0.42, ns			p = 0.16, ns	36
E. superba	Polar			p = 0.35, ns			p = 0.66, ns			p = 0.66, ns	36
	Total			p = 0.12, ns			p = 0.47, ns			p = 0.68, ns	36
All *E. superba*	Neutral	**1.35**	**-77.18**	**0.14 (p = <0.0001)**			p = 0.73, ns			p =0.12, ns	109
	Polar	**1.52**	**-81.70**	**0.15 (p = <0.0001)**			p = 0.27, ns	**0.40**	**16.68**	**0.06 (p = 0.01)**	109
	Total	**2.83**	**-156.06**	**0.20 (p = <0.0001)**			p = 0.42, ns	**0.05**	**28.22**	**0.05 (p = 0.02)**	109
P. antarcticum	Neutral			p = 0.35, ns	*2009&2010 data only		p = 0.98, ns			p = 0.63, ns	13
	Polar			p = 0.42, ns			p = 0.50, ns			p = 0.29, ns	13
	Total			p = 0.53, ns			p = 0.64, ns			p = 0.90, ns	13
E. antarctica	Neutral	**3.32**	**-174.41**	**0.44 (p = 0.04)**	*2011 data not available					p = 0.07, ns	10
	Polar	**- 1.34**	**96.19**	**0.58 (p = 0.01)**						p = 0.31, ns	10
	Total			p = 0.14, ns						p = 0.07, ns	10

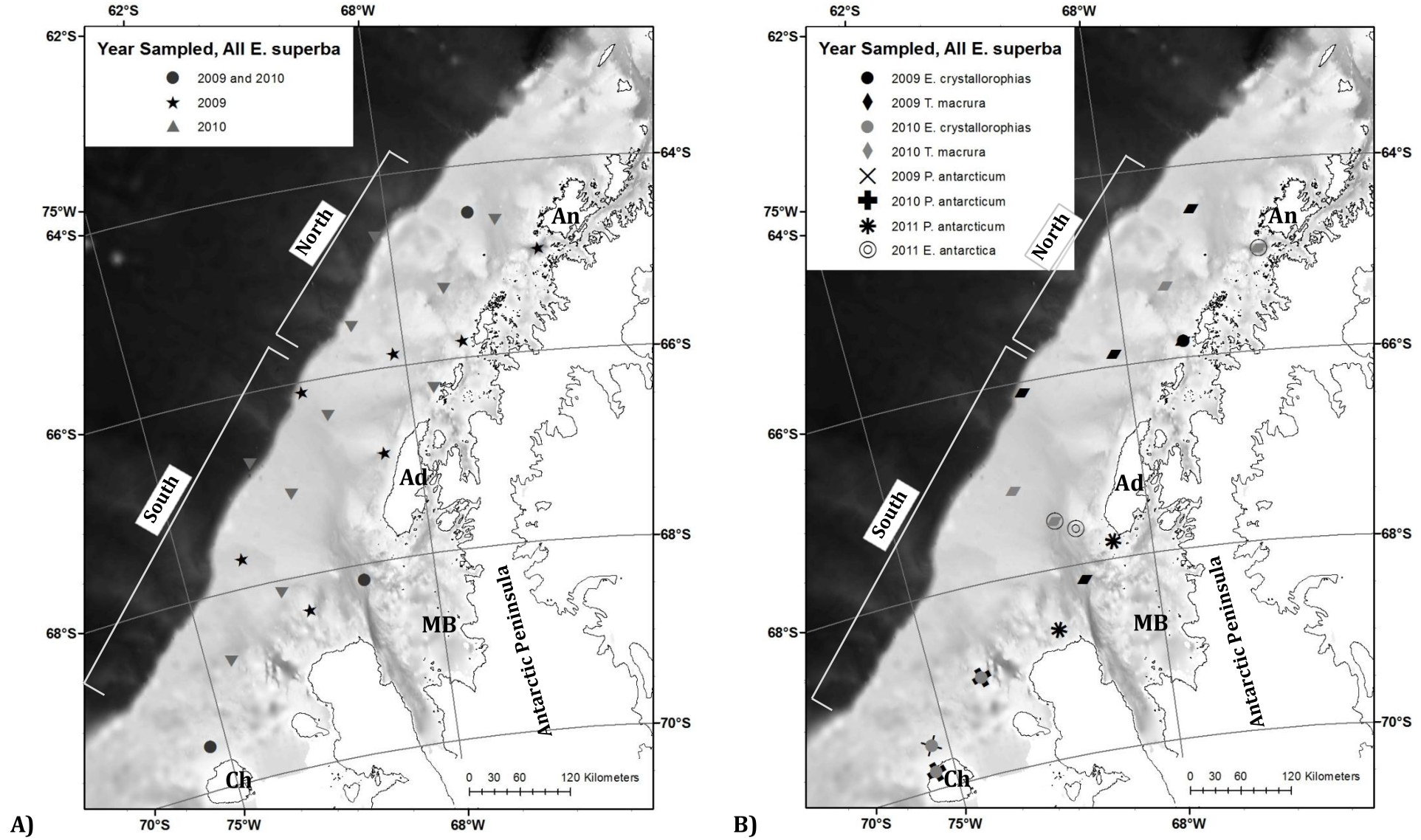
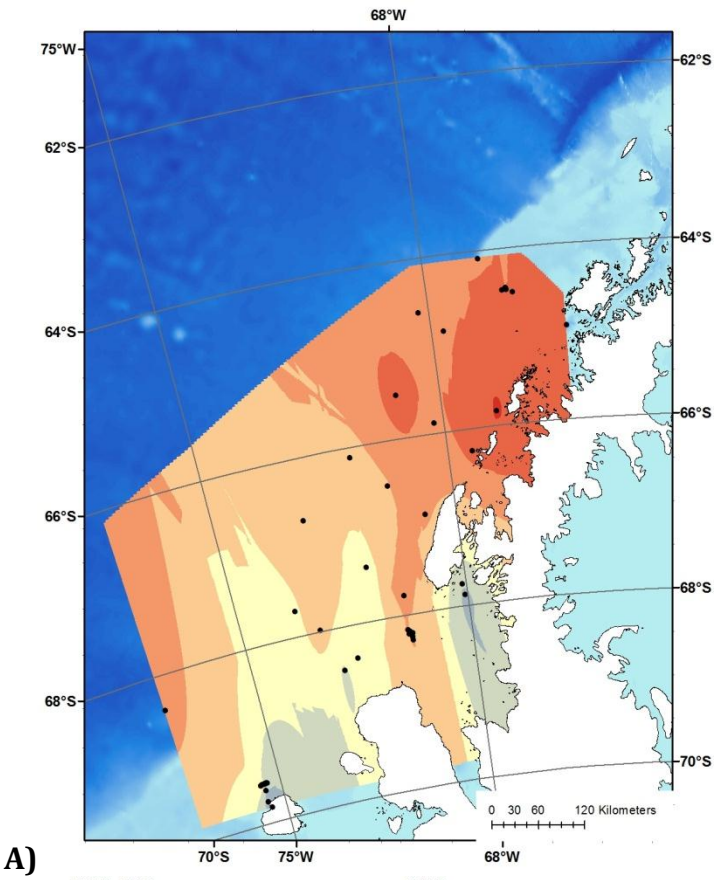


Figure 1. PAL LTER study region and stations sampled. Map of study region where A) *E. superba*, *Euphausia superba* and B) *E. crystallorophias, Euphausia crystallorophias; T. macrura*, *Thysanoessa macrura*; *P. antarcticum, Plueragramma antarcticum; E. antarctica, Electrona antarctica*. were collected. An: Anvers Island, Ad: Adelaide Island, MB: Marguerite Bay, Ch: Charcot Island. The North and South regions used for comparative analysis are indicated in brackets, and based on contrasting sea-ice characteristics described by Stammerjohn et al. (2008). Shades of grey are bathymetry, with light grey representing the continental shelf and dark grey the continental slope and abyssal plain. The continental shelf is roughly 200 km wide and averages 430 m in depth (Ducklow et al. 2012a).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75°W
62°S
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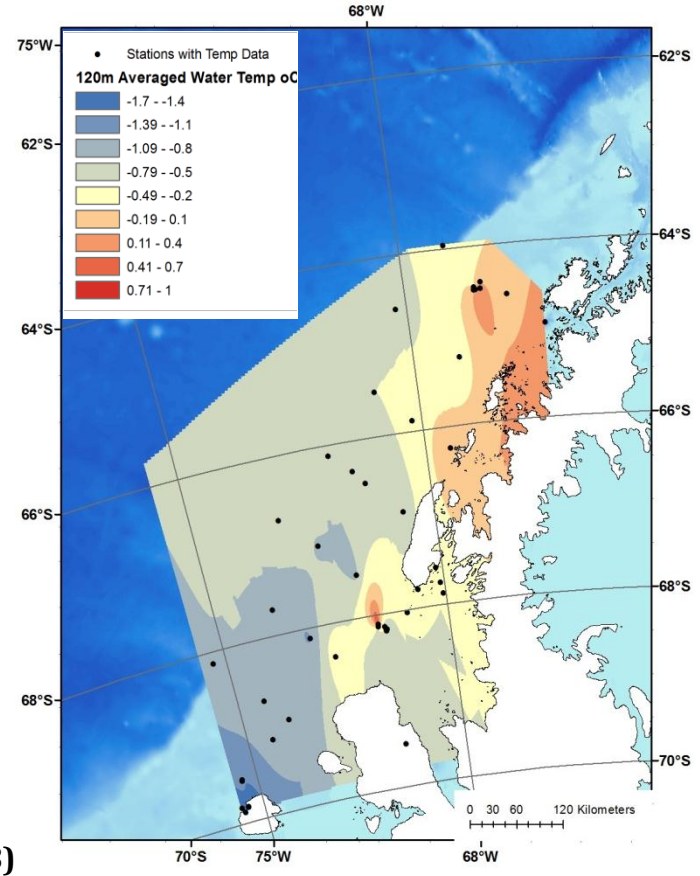
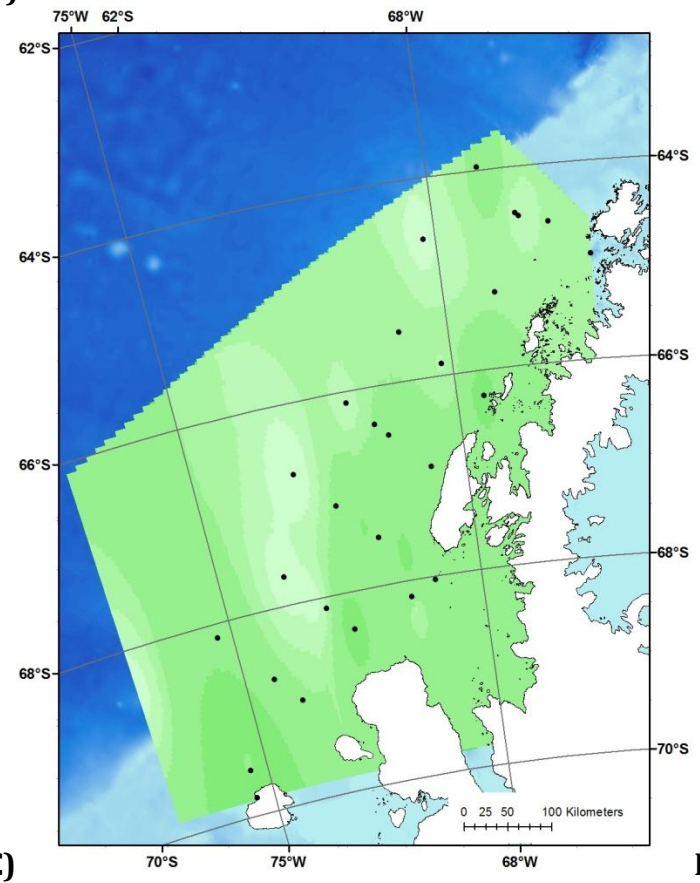
66°S
68°S
70°S
0 30 60 120 Kilometers

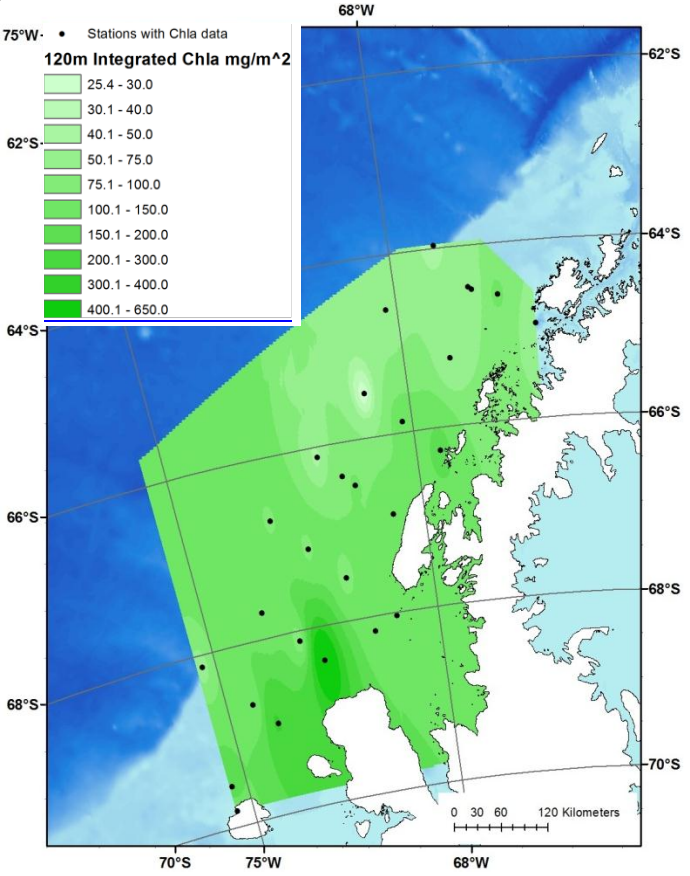
A)


Stations with Temp Data
120m Averaged Water Temp oC
-1.7 - -1.4
-1.39 - -1.1
-1.09 - -0.8
-0.79 - -0.5
-0.49 - -0.2
-0.19 - 0.1
0.11 - 0.4
0.41 - 0.7
0.71 - 1
68°W
75°W
62°S
64°S
66°S
68°S
70°S
0 30 60 120 Kilometers

B)

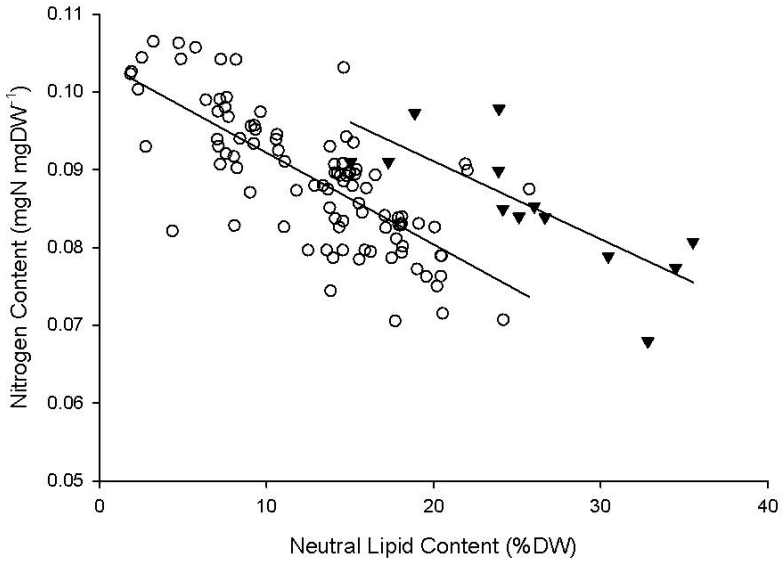

75°W
62°S
68°W
64°S
66°S
68°S
70°S
0 25 50 100 Kilometers

C)

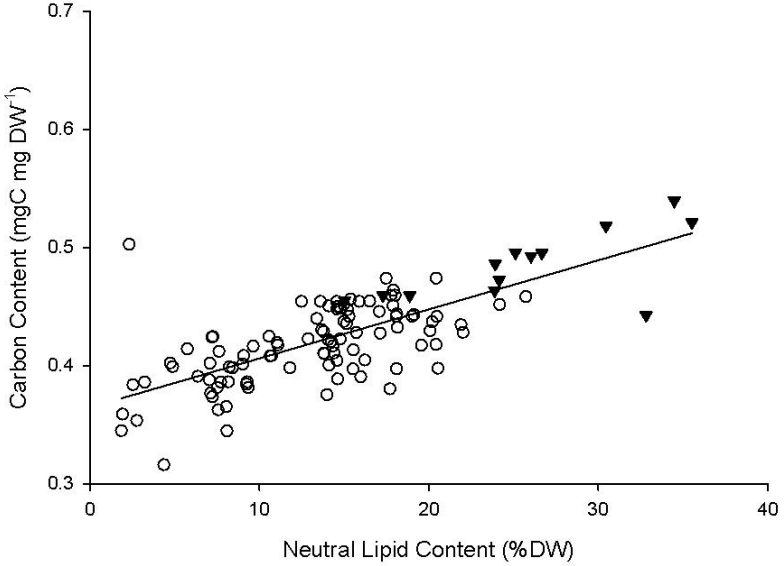

Stations with Chla data
120m Integrated Chla mg/m^2
25.4 - 30.0
30.1 - 40.0
40.1 - 50.0
50.1 - 75.0
75.1 - 100.0
100.1 - 150.0
150.1 - 200.0
200.1 - 300.0
300.1 - 400.0
400.1 - 650.0
75°W
62°S
68°W
64°S
66°S
68°S
70°S
0 30 60 120 Kilometers

D)

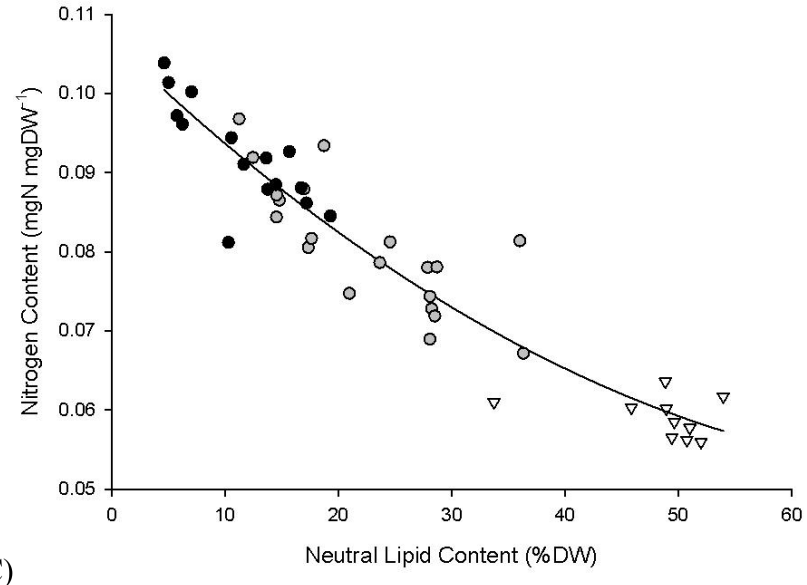
Figure 2. Regional maps of mean upper water column temperature and integrated Chl a. Mean water temperature 0-120, (°C, A and B) and 0-120m integrated Chl a (mg m^{-2}, C and D) for the study region from CTD and discrete bottle data collected during the 2009 (A and C) and 2010 (B and D) summer cruises in January. Stations occupied are solid, black circles.


Nitrogen Content (mgN mgDW-1)
0.11
0.10
0.09
0.08
0.07
0.06
0.05
0
10
20
30
40
Neutral Lipid Content (%DW)

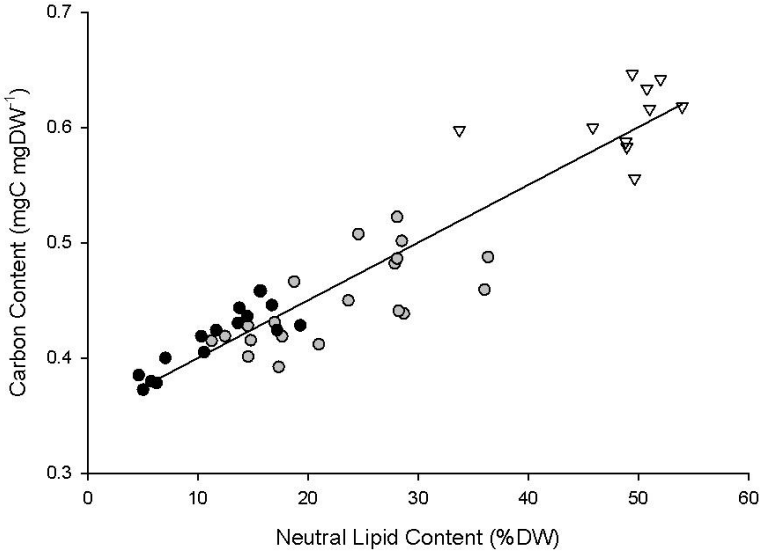
A)


Carbon Content (mgC mg DW-1)
0.7
0.6
0.5
0.4
0.3
0
10
20
30
40
Neutral Lipid Content (%DW)

B)


Nitrogen Content (mgN mgDW-1)
0.11
0.10
0.09
0.08
0.07
0.06
0.05
0
10
20
30
40
50
60
Neutral Lipid Content (%DW)

C)


Carbon Content (mgC mgDW-1)
0.7
0.6
0.5
0.4
0.3
0
10
20
30
40
50
60
Neutral Lipid Content (%DW)

D)

Figure 3. Relationship between neutral lipid content and elemental composition by species. Neutral lipid content (% dry weight, DW) vs. elemental composition (mg N mg^{-1} DW^{-1} or mg C mg^{-1} DW^{-1}) for prey species. A and B represent species whose neutral lipids were mainly composed of triglycerides – (○) All *Euphausia superba;* (▼) *Pleuragramma antarcticum*. C and D represent species whose neutral lipids were mainly composed of wax ester – (◎) *Thysanoessa macrura;* (●) *Euphausia crystallorophias;* (▽) *Electrona antarctica*. A linear regression was the best fit for data in graphs: A, B and D. Regression equations are (Elemental Composition, mg N mg^{-1} DW^{-1} or mg C mg^{-1} DW^{-1}) = m(Neutral Lipid Content, %DW) + b. A quadratic polynomial was the best fit for data in graph C. Regression equation was: (Nitrogen Content, mgN mg^{-1} DW^{-1}) = a(Neutral Lipid Content, %DW)^2 + m(Neutral Lipid Content, %DW) + b. Regressions are for combined 2009 & 2010 data and all are significant ($p \leq 0.05$).

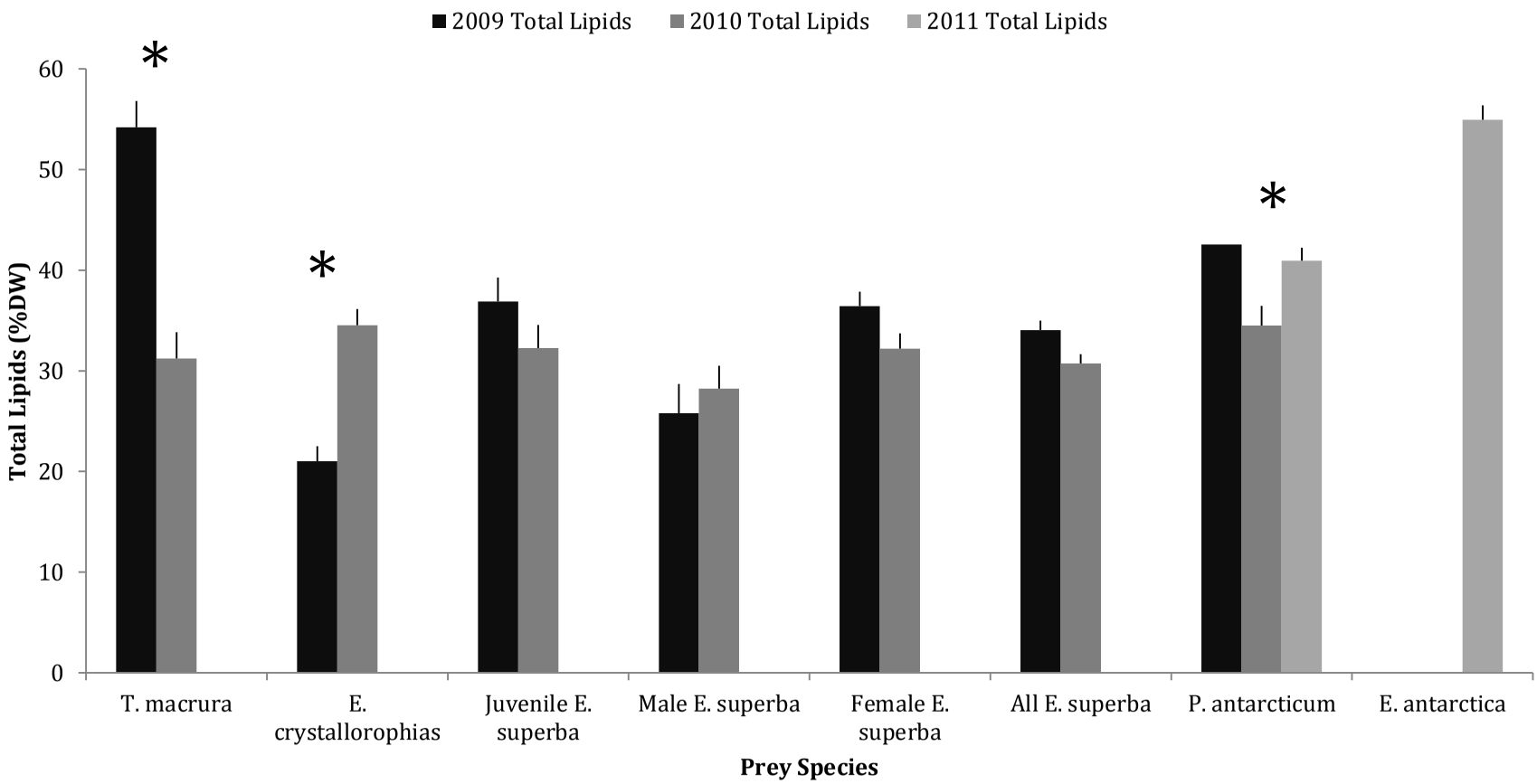
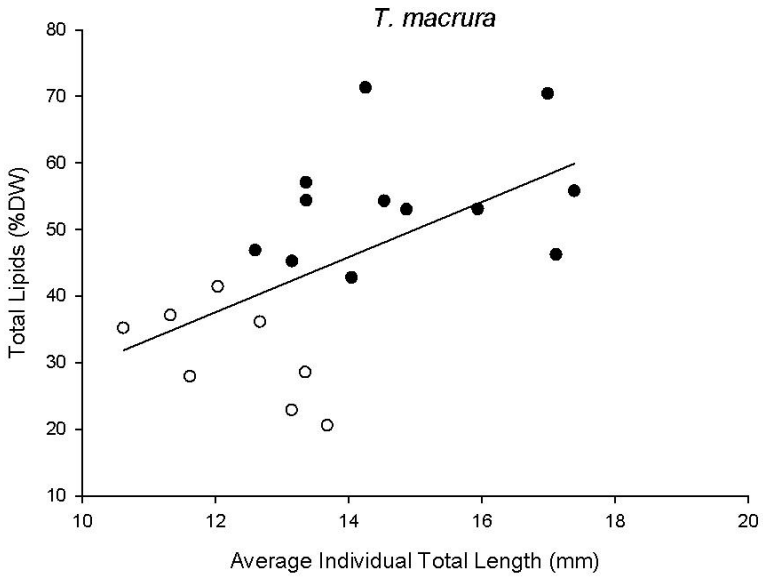
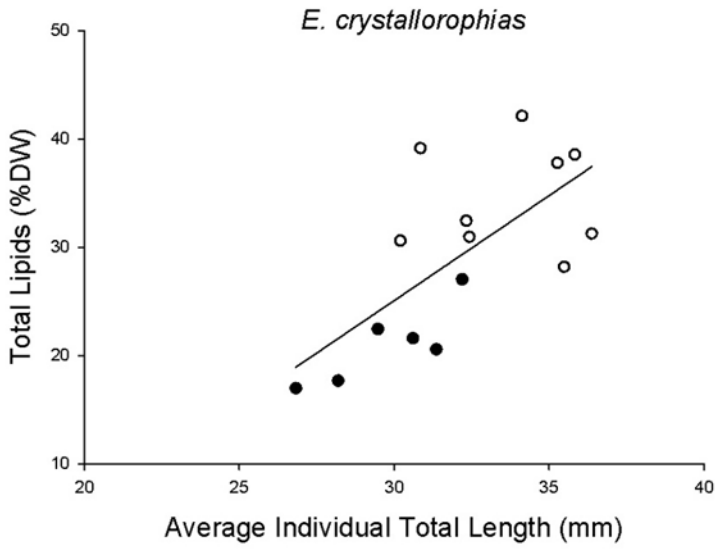


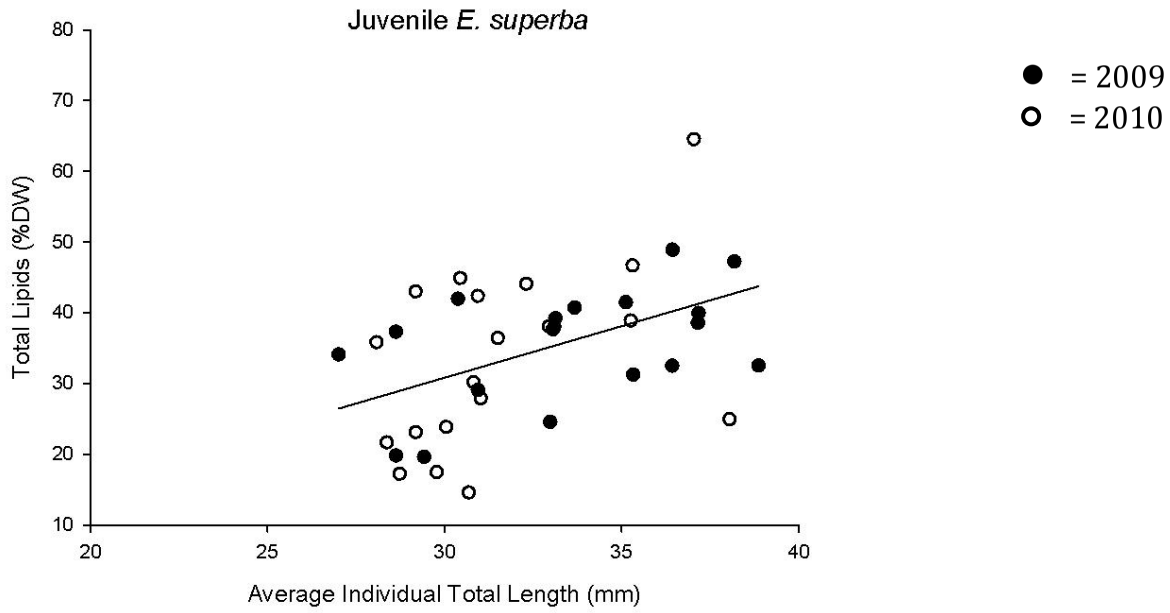
Figure 4. January 2009 vs. 2010 comparison of total lipid content by species. Average total lipid content (%dry weight, DW) in 2009, 2010, and 2011, across the entire sampling grid, for prey species: Euphausiids – *T.macrura, Thysanoessa macrura; E. crystallorophias, Euphausia crystallorophias;* Juvenile *E. superba*, Juvenile *Euphausia superba;* Male *E. superba*, Male *Euphausia superba*; Female *E. superba*, Female *Euphausia superba;* All *E. superba*, All *Euphausia superba*. Fish – *P. antarcticum, Pleuragramma antarcticum; E. antarctica, Electrona antarctica*. Error bars are 1 standard error. Asterisks (*) indicate significant differences in total lipid content between years. See Table 1 for test statistics.


T. macrura
Total Lipids (%DW)
Average Individual Total Length (mm)
10
20
30
40
50
60
70
80
10
12
14
16
18
20

A)


E. crystallorophias
Total Lipids (%DW)
Average Individual Total Length (mm)
10
20
30
40
50
20
25
30
35
40

B)


Juvenile E. superba
= 2009
= 2010
Total Lipids (%DW)
Average Individual Total Length (mm)
10
20
30
40
50
60
70
80
20
25
30
35
40

C)

Figure 5. Relationships between length and total lipid content by species. Average individual total length (mm) vs. total lipid content (% dry weight, DW) for the euphausiids: *T. macrura*, *Thysanoessa macrura; E. crystallorophias*, *Euphausia crystallorophias;* Juvenile *E. superba*, Juvenile *Euphausia superba*. Regressions are for combined 2009 & 2010 data. See Table 4 for regression equations and statistics.

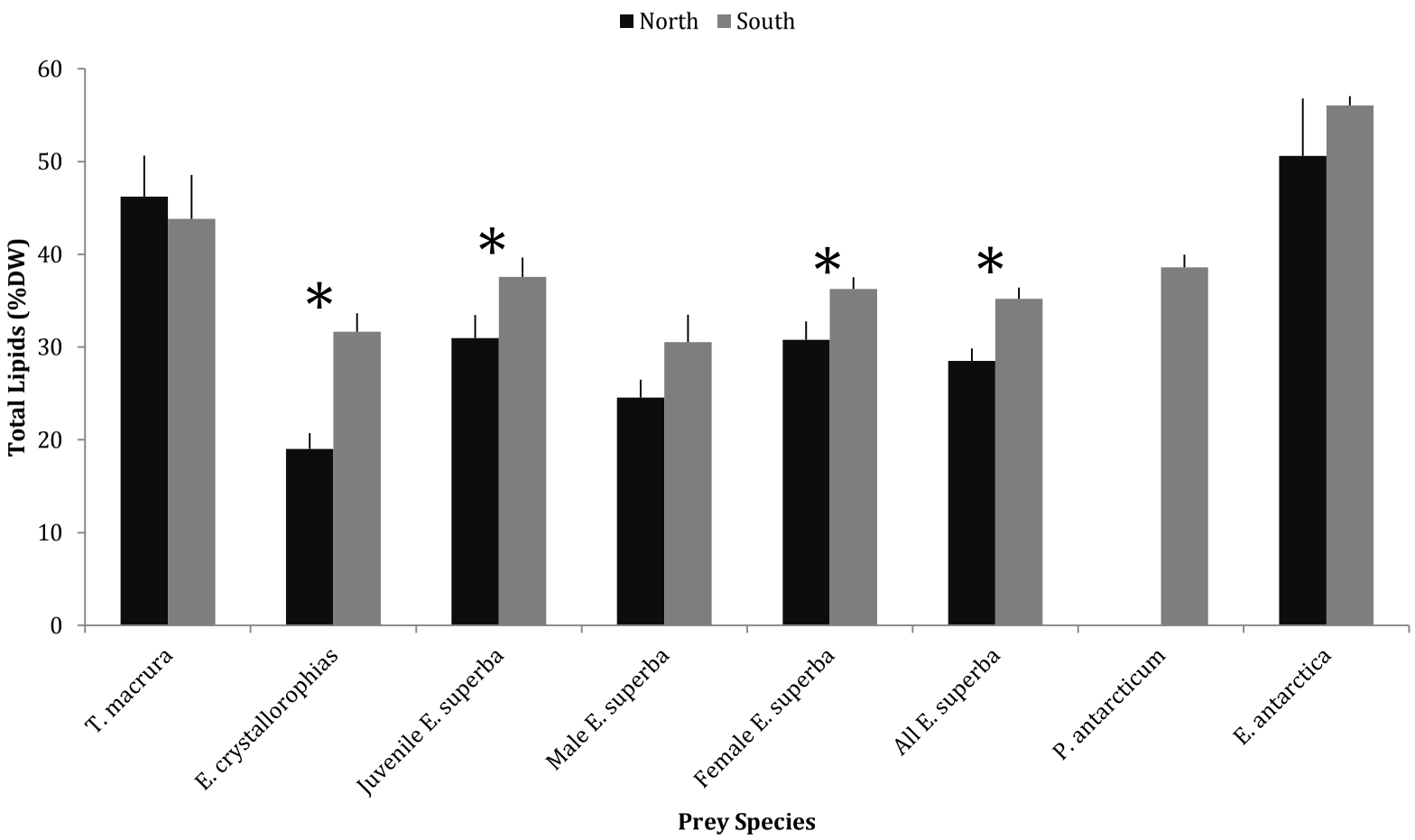


Figure 6. Regional comparison of total lipid contents by species. Average total lipid content (as % dry weight, DW) in the North and the South regions, for all sampling years (2009-2011), for prey species: Euphausiids – *T.macrura, Thysanoessa macrura; E. crystallorophias, Euphausia crystallorophias;* Juvenile *E. superba*, Juvenile *Euphausia superba;* Male *E. superba,* Male *Euphausia superba*; Female *E. superba*, Female *Euphausia superba;* All *E. superba*, All *Euphausia superba*. Fish – *P. antarcticum, Pleuragramma antarcticum; E. antarctica, Electrona antarctica*. Error bars are 1 standard error. Asterisks (*) indicate significant differences in total lipid content between regions. See Table 2 for test statistics.

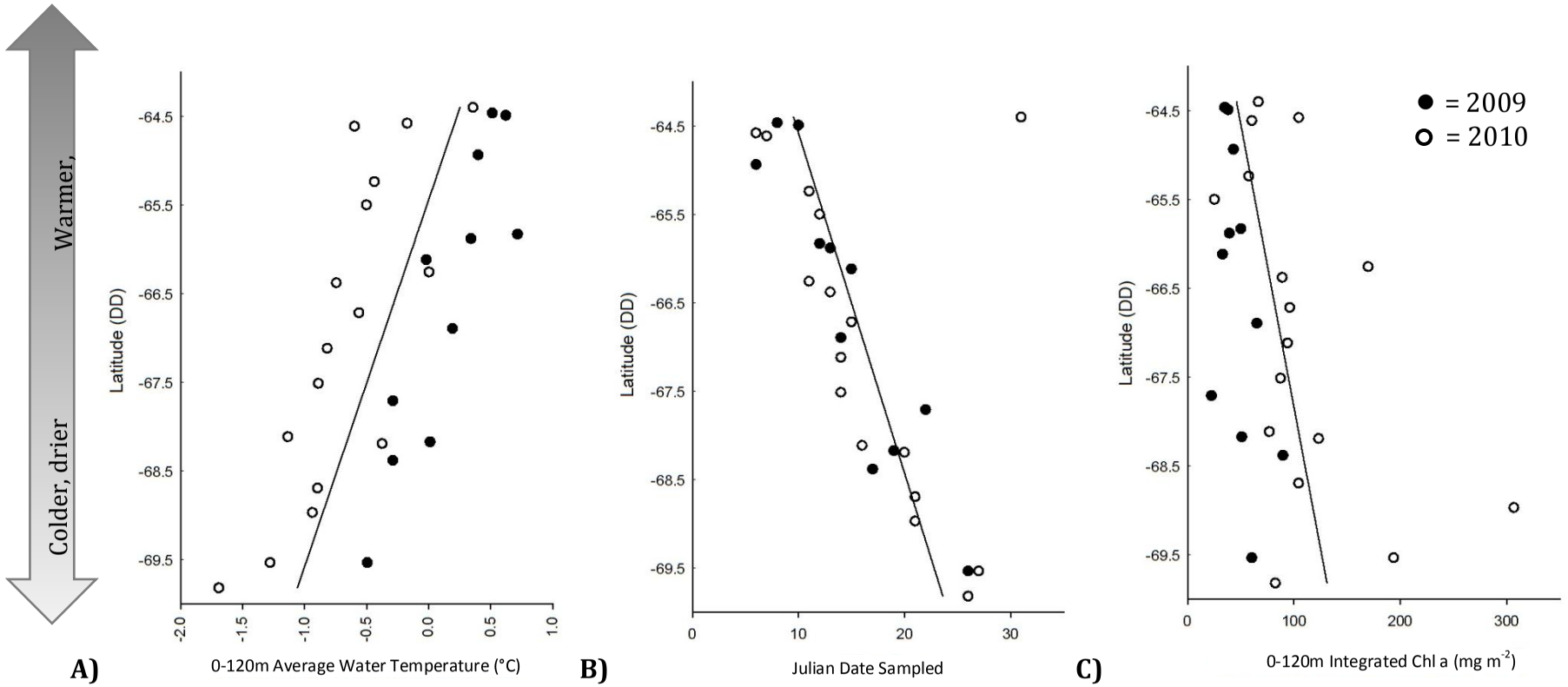


Figure 7. Relationship between latitude and environmental or temporal parameters. Latitude (decimal degrees, DD) vs.0-120m mean water temperature, Julian day, and 0-120m integrated Chl a. X- and Y-axes in plots have been reversed to better depict North to South trend. Regressions are for 2009 and 2010 combined data. Regression equations are (Property) = m(Latitude) + b and are significant ($p < 0.05$); see Table 5 for regression equations and statistics.

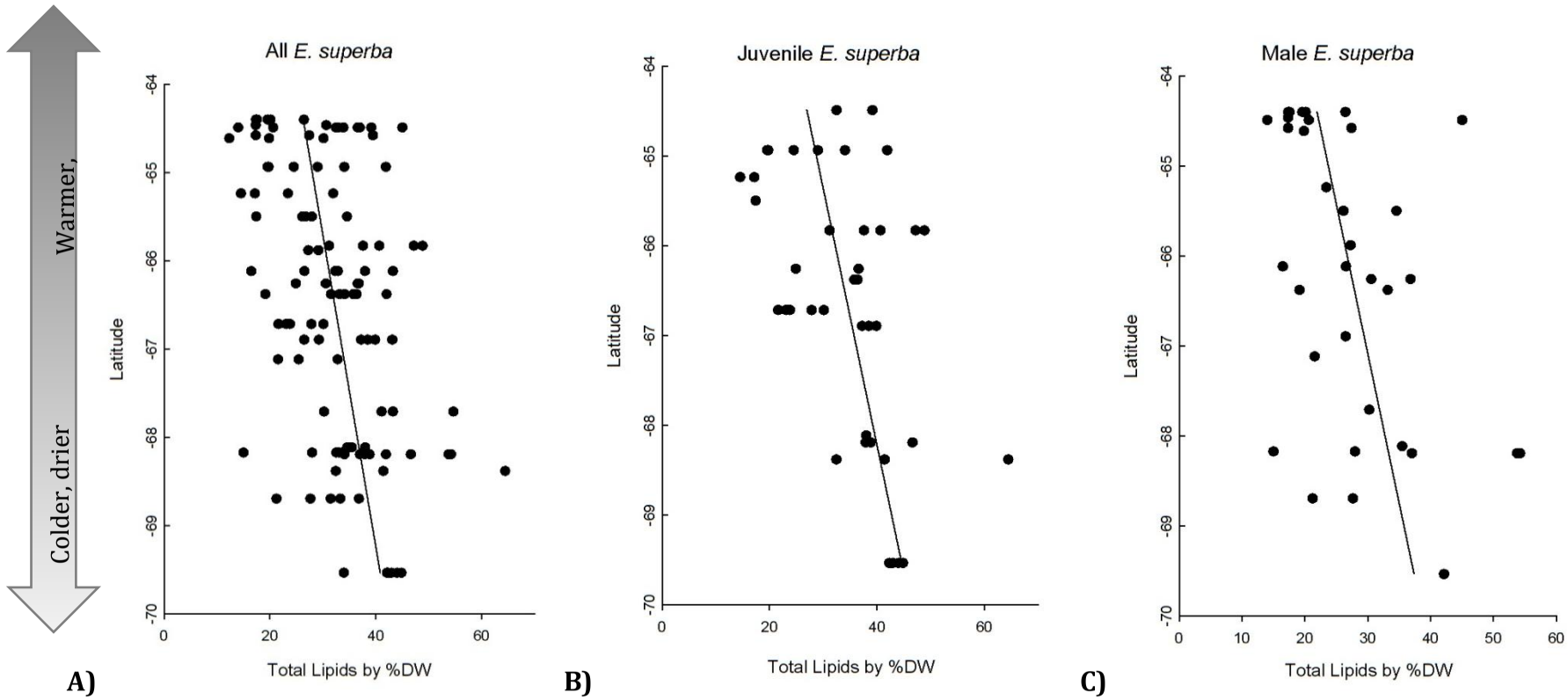


Figure 8. Relationship between latitude and total lipid content for *Euphausia superba*. Latitude (decimal degrees, DD) vs. All, juvenile, and male *E. superba*, *Euphausia superba*, total lipid content (% dry weight, DW). X- and Y-axes in plots have been reversed to better depict North to South trend. Regressions are for 2009 and 2010 combined data. Regression equations are (Total Lipid Content) = m(Latitude) + b. Regressions are significant ($p < 0.05$); see Table 5 for regression formulas and statistics.

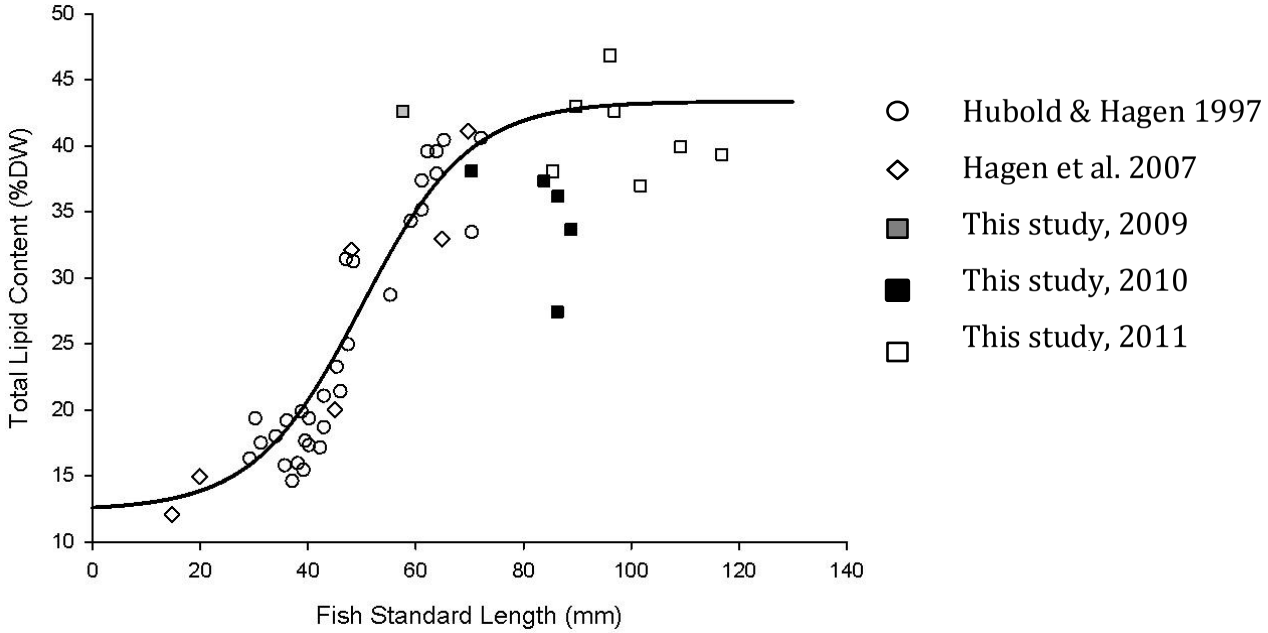


Figure 9. Relationship between length and total lipid content relationship for *Pleuragramma antarcticum*. Individual standard length (mm) vs. total lipid content (% dry weight, DW) for the fish *Pleuragramma antarcticum*. Figure adapted from Chapman et al. (2011). The formula for the *Pleuragramma antarcticum* energy density function is: $Lip(L) = [(Lip_{max}-Lip_{min})*1/(1+e^{-klip(L-klip50)})]+Lip_{min}$. Where $Lip(L)$ = lipid content of fish with total length L (mm); Lip_{max} = maximum lipid content (as proportion dry mass); Lip_{min} = minimum lipid content (proportion dry mass); k_{lip} = controls the rate of increase in lipid content with increasing L (set to $0.1mm^{-1}$); and k_{lip50} = L at which the lipid content is 50% of its maximum value (set to 50mm).

APPENDIX

Table A1. Relationship between environmental and temporal parameters. Regression statistics for the relationship between latitude (decimal degrees, DD), Julian date, 0-120m mean water temperature (^{o}C) and 0-120m integrated Chl a (mg m^{-2}). Regression equations are in linear form: $y = m(x) + b$. R^2 values are given in front p-values for all significant relationships (where $p \leq 0.05$); ns, not significant. Regressions are for combined 2009 and 2010 data. See also Figure 6.

2009 & 2010			
	Water Temp	**Date**	**0-120m Integrated Chl a (mg m^{-2})**
Latitude (DD)	$R^2 = 0.47$, $p < 0.0001$ m = (-0.24), b = (15.82)	$R^2 = 0.46$, $p = 0.0001$ m = (2.60), b = (-157.81)	$R^2 = 0.20$, $p = 0.018$ m = (15.69), b = (-964.54)
0-120m Mean Water Temp (^{o}C)		$R^2 = 0.17$, $p = 0.034$ m = (-4.43), b = (14.35)	$R^2 = 0.20$, $p = 0.019$ m = (-0.005), b = (0.05)
Julian Date Sampled			p = 0.16, ns m = (0.03), b = (13.21)

Table A2. Julian date vs. lipid composition by species. Relationship between Julian date vs. lipid fractions (% dry weight, DW) for prey species: Euphausiids – *T.macrura*, *Thysanoessa macrura; E. crystallorophias*, *Euphausia crystallorophias;* Juvenile *E. superba*, Juvenile *Euphausia superba;* Male *E. superba*, Male *Euphausia superba*; Female *E. superba*, Female *Euphausia superba;* All *E. superba*, All *Euphausia superba*. Fish – *P. antarcticum*, *Pleuragramma antarcticum; E. antarctica*, *Electrona antarctica*. Regression equations are: Lipid Fraction (%DW) = m (Julian Date) + b. R^2 given in front of p-values for all significant relationships (where $p \leq 0.05$); ns, not significant.

Species	Lipid Fraction (%DW)	Slope (m)	Intercept (b)	R^2	n
T. macrura	Neutral			p = 0.18, ns	21
	Polar			p = 0.36, ns	22
	Total			p = 0.84, ns	21
E. crystallorophias	Neutral	**0.46**	**1.46**	**0.28 (p = 0.04)**	15
	Polar			p = 0.43, ns	15
	Total			p = 0.09, ns	15
Juvenile *E. superba*	Neutral			p = 0.06, ns	39
	Polar	**0.52**	**12.3**	**0.18 (p = 0.007)**	39
	Total	**0.77**	**23.63**	**0.19 (p = 0.006)**	39
Male *E. superba*	Neutral			p = 0.58, ns	34
	Polar			p = 0.64, ns	34
	Total			p = 0.93, ns	34
Female *E. superba*	Neutral	**0.33**	**8.76**	**0.21 (p = 0.005)**	36
	Polar			p = 0.16, ns	36
	Total	**0.56**	**26.07**	**0.17 (p = 0.01)**	36
All *E. superba*	Neutral			p = 0.10, ns	109
	Polar			p = 0.11, ns	109
	Total			p = 0.07, ns	109
P. antarcticum	Neutral			p = 0.07, ns	13
	Polar			p = 0.37, ns	13
	Total			p = 0.09, ns	13
E. antarctica	Neutral			p = 0.22, ns	10
	Polar	**-0.43**	**13.85**	**0.61 (p = 0.008)**	10
	Total			p = 0.60, ns	10

VITA

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Born in Annapolis, Maryland on August 13, 1985. Graduated from Hickory High School in 2003. Earned a B.S. in Biology with a minor in Mathematics from James Madison University in 2007. Worked as a research intern with Dr. William Peterson at Hatfield Marine Science Center of Oregon State University examining growth rates of the krill *Euphausia pacifica* through cohort analysis. Worked as a lab technician for Dr. Fu-Lin Chu at the Virginia Institute of Marine Science, College of William & Mary, investigating the modification of fatty acids and sterols by planktonic heterotrophic protists in the marine food web. Worked as a field technician under Dr. George Kling, from University of Michigan, for the Arctic Long-Term Ecological Research project (ARC-LTER). Entered the Masters program at the Virginia Institute of Marine Science, College of William & Mary, under graduate advisor Dr. Deborah K. Steinberg in 2009.