Regional differences in quality of krill and fish as prey along the Western Antarctic Peninsula

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ABSTRACT: The 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 the prey quality of krill and fish that are utilized by apex predators. We compared prey quality metrics, including elemental (C, N) content; total, neutral, and polar lipid content; and energy densities of known penguin prey items including krill (*Euphausia superba*, *Thysanoessa macrura*, and *E. crystallophias*) and fish (silverfish *Pleuragramma antarcticum* and the myctophid *Electrona antarctica*) along the WAP latitudinal gradient each January from 2009 to 2011. *E. antarctica* had the highest prey quality in terms of lipid content and energy density, followed by *T. macrura* and *P. antarcticum*, then *E. crystallophias* and *E. superba*. For all species, variations in C and N content were most strongly correlated with the animals' neutral lipid content, in that animals with the larger neutral lipid stores had significantly higher C and lower N content. Across all sexes and maturity stages, *E. superba* in the southern study region had ca. 20 % higher total lipid content than *E. superba* in the north, and a stepwise multiple linear regression analysis showed that latitude, sexual differences, and upper water column temperatures best explained this regional difference in lipid content. This regional variability in *E. superba* prey quality could affect the ability of apex predators that rely on *E. superba* to meet their energetic demands, and should be considered in future modeling efforts.

KEY WORDS: Krill · *Euphausia superba* · Silverfish · Myctophid · Lipid content · Prey quality · Antarctic Peninsula

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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 (Prézelin et al. 2000, Vernet et al. 2008, Steinberg et al. 2012). Krill are well recognized as an important trophic link in this region, serving as prey for higher predators such as penguins, seals, and whales (Costa & Crocker 1996, Fraser & Trivelpiece 1996). Predation on fish by 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 (Ainley et al. 1998, 2003, 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 among 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 Upper Circumpolar Deep Water (UCDW), delivered by the Antarctic Circumpolar Current, has also increased since regular sampling began in 1997, and intrusions of this relatively warm water onto the shelf are the

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main source of heat to the water column (Hofmann et al. 1996, Klinck et al. 2004, Martinson et al. 2008, Dinniman et al. 2012). 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 (Stammerjohn et al. 2008, 2012). As a result, a latitudinal 'climate migration' is occurring along the WAP, 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 (Prézelin et al. 2000, Ducklow et al. 2012). A comparison of 2 satellite-derived data sets, spanning nearly 30 yr (1978 to 1986 and 1998 to 2006) indicated that summertime surface chlorophyll *a* (chl *a*) along the far northern WAP declined by approximately 12% between these 2 time periods, with a stronger sub-regional decrease (~89%) in chl *a* north of 63° S and a substantial increase (~66%) farther south (Montes-Hugo et al. 2009). Another dramatic example of change in the WAP food web is the 83% decline in breeding pairs of the native, ice-obligate Adélie penguin *Pygoscelis adeliae* in the northern WAP, near Anvers Island, since the mid-1970s (Fraser et al. 2013). Suggested mechanisms contributing to this decline include the loss of overwinter pack-ice habitat, degradation of terrestrial summer breeding habitat, and decreases in prey quality and abundance (Chapman et al. 2010, 2011, Trivelpiece et al. 2011, Fraser et al. 2013).

Prey quality is mainly dictated by its energy density, which correlates directly with the animal's lipid content (Clarke 1980). Among seabirds, chick survival and recruitment are often correlated with chick 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). A recent analysis by Chapman et al. (2010, 2011) focused on Adélie penguin chick growth in the WAP, using an individual-based energetics model to highlight the importance of higher-quality prey items in chick diets, and showing that a small deficiency of 0.117 kg in fledgling 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 the ability of prey species 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, Flores et al. 2012). This would alter the length-specific literature values utilized in most modeling studies. Energetics models also rarely address parameters besides total lipid content that contribute to the nutritional value of prey. Jackson & Place (1990) showed that rockhopper penguins *Eudyptes chrysocome* have higher assimilation efficiencies for triglycerides relative to wax esters, demonstrating that different lipid classes can impact penguin metabolism. In addition, phytoplankton with high C to nutrient (N,P) ratios is of low nutritional value to zooplankton. Consumption of phytoplankton with high C:N,P ratios can shift zooplankton elemental composition, forcing zooplankton into a nutrient-limited state, as the C:N,P content of their food is not sufficient to meet their nutritional demands (Van de Waal et al. 2010). The caloric content of krill used in models is usually calculated from other measurements of the animals' biochemical composition, and to date, only 3 studies have directly measured *Euphausia superba* caloric content (Nagy & Obst 1992, Ainley et al. 2003, Färber-Lorda et al. 2009). Incorporating 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 from prey found farther south in terms of species composition or biochemical composition. 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 Adélie penguin prey items (krill and fish) collected along the WAP latitudinal gradient. Comparing prey quality metrics from different years and regions with different environmental characteristics allowed us to examine whether 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.

Fig. 1. Palmer Antarctica Long-Term Ecological Research study region and stations sampled. Collection sites for (A) *Euphausia superba* and (B) *E. crystallophias*, *Thysanoessa macrura*, *Pleuragramma antarcticum*, and *Electrona antarctica*. An: Anvers Island, Ad: Adelaide Island, MB: Marguerite Bay, Ch: Charcot Island. The North and South regions used for comparative analysis are indicated by brackets (note: 'North' is all stations north of, but not including, the '300' sampling line in Ducklow et al. 2012). Shades of blue are used to illustrate the bathymetry, with light blue representing the continental shelf and dark blue the continental slope and abyssal plain. The continental shelf is roughly 200 km wide and averages 430 m in depth (Ducklow et al. 2012)

MATERIALS AND METHODS

Study area and sample collection

Krill 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 ARSV 'Laurence M. Gould' each January from 2009 to 2012 (Ducklow et al. 2012). We divided the study grid into 'North' and 'South' sub-regions (Fig. 1) based on existing sea-ice dynamics described by Stammerjohn et al. (2008), and an apparent difference in Adélie penguin diet between these 2 regions (W. Fraser pers. comm.).

We collected macrozooplankton using a 2×2 m square-frame net (700 μ m mesh), towed obliquely

from the surface to 120 m (Ross et al. 2008, Bernard et al. 2012). When the bottom depth of a station was less than 120 m, the net was fished to ~20 m above the sea floor. 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 krill 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 (W. Fraser pers. comm.), including 3 krill species (*Euphausia superba*, *E. crystallophias*, *Thysanoessa macrura*) and 2 fish species (the myctophid *Electrona antarctica* and the Antarctic silverfish *Pleuragramma antarcticum*). Animal lengths were recorded with a set of digital calipers for *E. su-*

perba (standard length 1, the length from the eyes to the tip of a uropod; Mauchline 1970), and fish (standard length, the length between the most forward part of the head and the posterial end of the hypural bone; total length, the length between the most forward part of the head and the end of the caudal fin rays; Ricker & Westrheim 1979), and sex/maturity stage was determined for *E. superba* (Makarov et al. 1981). Total lengths for *T. macrura* and *E. crystallorophias* were calculated from wet weights based on literature values (Färber-Lorda 1994, Mayzaud et al. 2003, Ju & Harvey 2004). All animals for prey quality analyses were then frozen and stored at -80°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 range (1 sample in 2009, 5 in 2010, and 17 in 2011). As the grid was sampled from north to south over the course of 5 wk, a comparison was conducted in 2010 and 2012 in which *E. superba* were collected from one of the northern-most stations at the beginning and end of the cruise (6 and 31 January 2010; 6 and 30 January 2012) to determine whether the seasonal progression of summer was potentially biasing observed longitudinal trends.

Prey quality analyses

In the laboratory, animals were either analyzed individually or combined with other animals of the same species and physical characteristics (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, and juvenile *E. superba* of 2 individuals; all fish 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 2 groups, and no significant differences were found for any of the prey metrics. This confirmed that the variances associated with the composite samples were representative of individual adult *E. superba* in nature. Artificial composites were then created by averaging prey metric values of 2 morphometrically similar individual *E. superba* samples of the same sex to use in data analysis along with the 2-individual *E. superba* composites.

Sample wet weights were determined with a Sartorius BP211D analytical balance, and samples were

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 Labconco Freezone 6 Liter Plus freeze dryer and dry weights (DW) were determined. Sub-samples of the dry, homogenous powder were taken for the various prey quality analyses.

To determine total organic C and N content, ~50 mg sub-samples of freeze-dried, homogenized tissues were placed in a desiccator with a small beaker of concentrated HCl for 16 h to remove inorganic C, and then moved to a 60°C drying oven for a minimum of 72 h. The acidified samples were then weighed, packed into tin capsules, and analyzed using a Costech ECS 4010 CHNSO Analyzer with flash combustion using acetanilide as the standard.

We concentrated the majority of our analysis efforts on animal lipid content in order to provide detailed prey quality data (e.g. stage, sex, length) that can be used in energetics models, but also calculated caloric values to provide additional energetics information. Analyzing neutral and polar lipid concentrations separately enabled us to determine the relative influence of each in driving any observed trends in total lipids, as some krill use both lipid classes as storage lipids (Hagen et al. 1996, Ju et al. 2009). Neutral and polar lipid classes were extracted and separated utilizing a modified accelerated solvent extraction method developed by Poerschmann & Carlson (2006). Briefly, each sample was placed in a cell with a silica-based sorbent at its outlet, and the cell was pressurized and cycled through 2 *n*-hexane/acetone (9:1, v/v) extractions at 50°C to collect the neutral lipids followed by 2 chloroform/methanol (1:4, v/v) extractions at 80°C to collect the polar lipids. Each fraction was then dried completely under N_2 gas and resuspended in 500 μl of hexane for the neutral fraction and 2000 μl of chloroform for the polar fraction. The final lipid concentration of each fraction was determined gravimetrically using a Sartorius XP1000P microbalance.

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, Model 6300) using benzoic acid as a standard. We only directly measured caloric/energy content for adult *E. superba* and our fish samples because there was not enough dry mass in an individual *T. macrura*, *E. crystallorophias*, or juvenile *E. superba* sample to run on a standard bomb calorimeter. Instead, caloric values for these groups were calculated using published equations from Färber-Lorda et al. (2009).

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 2-sample *t*-test was used to examine data sets that only spanned 1 yr or 1 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. These data analyses were performed in the R statistical programming language (www.r-project.org).

Stepwise multiple linear regression models were used to assess the relative importance of several environmental and temporal forcing factors in affecting latitudinal trends in *E. superba* prey quality metrics (N and C content; neutral, polar, and total lipid content). Potential variables used in the model included: year, sex (analyzed as a categorical variable: juvenile, male, female), latitude (analyzed as a continuous variable), 0–120 m integrated chl *a*, 0–120 m integrated primary production, 0–120 m average water temperature, and day of the year of sample collection. Measurements of discrete chl *a* (taken every 15 m of depth, on average), primary production (taken every 20 m of depth, on average), and water temperature (taken continuously via CTD) at every station where prey were collected were obtained from the PAL LTER database (www.pal.lternet.edu/data/). Discrete chl *a* and primary production values were integrated over the top 120 m to use in the regression analyses. All regression analyses were performed using SAS statistical software. 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 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 Fig. 2). Regression analyses only utilized data from stations where prey species were sampled concomitantly (stations depicted in Fig. 1).

RESULTS

Hydrographic setting

For combined 2009 and 2010 data, water temperature and chl *a* followed the predicted latitudinal trends. 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 (Fig. 2A,B, Table 1). Integrated chl *a* (2009 and 2010 combined data) was significantly lower in the North than in the South, averaging 61 mg m^{−2} and 104 mg m^{−2}, respectively, with maximum values in the southern coastal regions and Marguerite Bay (Table 1).

Prey quality

Species comparison

The elemental compositions for the 3 species of krill and *Pleuragramma antarcticum* were similar, with average N content ranging from 83.1 to 92.3 µg mg^{−1} DW and average C content ranging from 415 to 485 µg mg^{−1} DW. Average C:N ratios by mass of *Thysanoessa macrura* and *P. antarcticum* (5.5 and 5.7, respectively) were significantly higher compared to *Euphausia crystallorophias* and total *E. superba* (4.5 and 4.8, respectively; Table 2). The elemental composition of *Electrona antarctica* was significantly different from all other prey species, with a lower N content (59.1 µg mg^{−1} DW) and a higher C content (608 µg mg^{−1} DW), resulting in the highest C:N weight ratio (10.3) of all species analyzed (Table 2).

The prey species with the highest overall lipid content was *E. antarctica* (55% DW), followed by *T. macrura* (45% DW) and *P. antarcticum* (39% DW), although for the latter 2 species, lipid content was statistically indistinguishable. *E. crystallorophias* and total *E. superba* had the lowest overall total lipid contents (29% and 32% DW, respectively; Table 2). For *E. superba*, males had significantly lower total lipid (27% DW) content than either juveniles (35% DW) or females (34% DW; Table 2).

For the measured energy density values, total *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), followed by *P. antarcticum* (24.6 kJ g^{−1} DW) and total *E. superba* (21.1 kJ g^{−1} DW; Table 2). Female *E. superba* energy density was significantly higher (22.0 kJ g^{−1}

Fig. 2. Regional maps of mean upper water column temperature and integrated chl *a*. (A, B) mean water temperature 0–120 m ($^{\circ}\text{C}$) and (C, D) 0–120 m integrated chl *a* (mg m^{-2}) for the study region from CTD and discrete bottle data collected during the 2009 (A and C) and 2010 (B and D) austral summer cruises in January. Stations occupied are solid, black circles

DW) than male *E. superba* ($19.5 \text{ kJ g}^{-1} \text{ DW}$; Table 2). Using published equations, *T. macrura* had significantly higher energy densities ($28.5 \text{ kJ g}^{-1} \text{ DW}$) than

the other krill species, and *E. crystallorophias* ($21.8 \text{ kJ g}^{-1} \text{ DW}$) was statistically similar to *E. superba* (Table 2).

Table 1. Regional comparison of environmental parameters and prey quality. Regional averages (ranges in parentheses) for properties measured in the North and South regions (as defined in Fig. 1), for prey species (euphausiids: *Thysanoessa macrura*, *Euphausia crystallorophias*, *E. superba*; fish: *Pleuragramma antarcticum*, *Electrona antarctica*). All regional comparisons are combined 2009 and 2010 data, except for 2011 chl *a*, *P. antarcticum*, and *E. antarctica* comparisons, which include 2011 data. **Bold** type is used to designate significant differences, and p-values are given for all significant results ($p \leq 0.05$); ns: not significant; DW: dry weight. Dash (–) indicates data from only 1 region and no comparisons were made

Property		North	South	p
0–120 m water temperature (°C)		0.12 (–0.60–0.72)	–0.57 (–1.69–0.21)	<0.001
2009 & 2010, 0–120 m integrated chl <i>a</i> (mg m ^{–2})		60.78 (20.45–169.91)	103.82 (17.47–623.43)	0.05
2011, 0–120 m integrated chl <i>a</i> (mg m ^{–2})		39.92 (10.78–73.70)	255.84 (24.41–621.70)	<0.001
<i>Thysanoessa macrura</i>	Nitrogen (µg N mg ^{–1} DW)	87 (75–118)	79 (67–93)	ns
	Carbon (µg C mg ^{–1} DW)	432 (392–507)	462 (419–522)	0.03
	C:N ratio	5.07 (3.78–6.25)	5.97 (4.56–7.58)	0.04
	Total lipids (%DW)	46.22 (20.59–71.31)	43.81 (22.89–70.40)	ns
	Total length (mm)	12.56 (10.14–14.87)	14.68 (11.62–17.39)	0.01
<i>Euphausia crystallorophias</i>	Nitrogen (µg N mg ^{–1} DW)	100 (96–104)	90 (81–100)	ns
	Carbon (µg C mg ^{–1} DW)	378 (372–382)	424 (380–458)	ns
	C:N ratio	3.77 (3.67–3.94)	4.72 (3.91–5.16)	0.009
	Total lipids (%DW)	19.01 (16.96–22.41)	31.66 (20.54–42.10)	<0.001
	Total length (mm)	28.17 (26.83–29.47)	33.09 (30.20–36.38)	0.003
Juvenile <i>Euphausia superba</i>	Nitrogen (µg N mg ^{–1} DW)	83 (74–94)	86 (72–106)	ns
	Carbon (µg C mg ^{–1} DW)	413 (362–451)	424 (390–474)	ns
	C:N ratio	4.91 (3.94–5.72)	4.99 (3.92–6.02)	ns
	Total lipids (%DW)	30.96 (14.57–48.89)	37.57 (21.64–64.51)	0.007
	Total length (mm)	32.66 (27.01–38.87)	32.32 (28.08–37.17)	ns
Male <i>Euphausia superba</i>	Nitrogen (µg N mg ^{–1} DW)	93 (71–110)	91 (71–100)	ns
	Carbon (µg C mg ^{–1} DW)	388 (316–464)	415 (359–503)	ns
	C:N ratio	4.20 (3.37–5.59)	4.63 (3.50–6.39)	ns
	Total lipids (%DW)	24.55 (14.06–45.06)	30.54 (15.03–54.27)	ns
	Total length (mm)	48.63 (40.84–52.62)	48.17 (43.23–52.53)	ns
	Energy density (kJ g ^{–1} DW)	19.23 (16.02–23.27)	19.84 (16.38–24.36)	ns
Female <i>Euphausia superba</i>	Nitrogen (µg N mg ^{–1} DW)	92 (83–104)	86 (76–97)	0.005
	Carbon (µg C mg ^{–1} DW)	420 (365–454)	433 (376–474)	ns
	C:N ratio	4.60 (3.68–5.09)	5.06 (4.05–6.21)	0.01
	Total lipids (%DW)	30.77 (12.46–39.50)	36.26 (25.47–54.72)	0.03
	Total length (mm)	48.18 (40.34–51.88)	48.31 (43.41–52.60)	ns
	Energy density (kJ g ^{–1} DW)	21.83 (19.00–23.75)	22.13 (19.68–25.33)	ns
Total <i>Euphausia superba</i>	Nitrogen (µg N mg ^{–1} DW)	91 (71–110)	87 (71–106)	ns
	Carbon (µg C mg ^{–1} DW)	405 (316–464)	425 (359–503)	0.001
	C:N ratio	4.55 (3.37–5.72)	4.92 (3.50–6.37)	0.004
	Total lipids (%DW)	28.51 (12.36–48.89)	35.21 (15.03–64.51)	<0.001
	Total length (mm)	42.61 (27.01–52.62)	42.51 (28.08–52.60)	ns
	Energy density (kJ g ^{–1} DW)	20.46 (16.02–23.75)	21.45 (16.38–25.33)	ns
<i>Pleuragramma antarcticum</i>	Nitrogen (µg N mg ^{–1} DW)		85 (68–98)	–
	Carbon (µg C mg ^{–1} DW)		485 (442–539)	–
	C:N ratio		5.73 (4.72–6.97)	–
	Total lipids (%DW)		38.60 (27.41–46.82)	–
	Standard length (mm)		89.93 (57.62–116.82)	–
	Energy density (kJ g ^{–1} DW)		24.63 (22.36–26.93)	–
<i>Electrona antarctica</i>	Nitrogen (µg N mg ^{–1} DW)	62 (61–64)	58 (56–62)	0.05
	Carbon (µg C mg ^{–1} DW)	592 (587–597)	612 (555–646)	ns
	C:N ratio	9.52 (9.24–9.80)	10.50 (9.49–11.47)	ns
	Total lipids (%DW)	50.60 (44.41–56.79)	56.05 (50.74–59.82)	ns
	Standard length (mm)	78.87 (77.64–80.10)	75.88 (54.49–90.09)	ns
	Energy density (kJ g ^{–1} DW)	31.94 (31.82–32.07)	31.92 (29.96–32.68)	ns

Table 2. Prey quality measurements by species. Means (SE in parentheses) for all sampling years combined (2009 to 2011) for prey species (euphausiids: *Thysanoessa macrura*, *Euphausia crystallorophias*, *E. superba*; fish: *Pleuragramma antarcticum*, *Electrona antarctica*). All euphausiid length data are given as total length, while fish data are given as standard length. DW: dry weight

Property	<i>T. macrura</i>	<i>E. crystallorophias</i>	Juvenile <i>E. superba</i>	Male <i>E. superba</i>	Female <i>E. superba</i>	Total <i>E. superba</i>	<i>P. antarcticum</i>	<i>E. antarctica</i>
Nitrogen ($\mu\text{g N mg}^{-1}\text{DW}$)	83.1 (2.38×10^{-3})	92.3 (1.69×10^{-3})	85.4 (1.38×10^{-3})	92.2 (1.83×10^{-3})	87.8 (0.94×10^{-3})	88.4 (0.84×10^{-3})	85.4 (2.29×10^{-3})	59.1 (0.82×10^{-3})
Carbon ($\mu\text{g C mg}^{-1}\text{DW}$)	445.4 (8.12×10^{-3})	415.2 (7.00×10^{-3})	418.6 (4.40×10^{-3})	401.3 (6.80×10^{-3})	429.4 (4.27×10^{-3})	416.8 (3.17×10^{-3})	484.3 (8.13×10^{-3})	607.6 (9.08×10^{-3})
C:N ratio	5.5 (0.22)	4.5 (0.14)	5.0 (0.10)	4.4 (0.13)	4.9 (0.08)	4.8 (0.06)	5.7 (0.20)	10.3 (0.27)
Neutral lipids (%DW)	22.5 (1.69)	11.5 (1.25)	14.6 (0.89)	10.0 (1.09)	13.7 (0.59)	12.9 (0.53)	25.7 (1.77)	48.4 (1.77)
Polar lipids (%DW)	22.4 (1.70)	17.7 (1.30)	19.7 (1.16)	17.3 (0.96)	20.8 (0.82)	19.3 (0.59)	12.9 (1.01)	6.54 (0.62)
Total lipids (%DW)	45.0 (3.17)	29.1 (2.09)	34.5 (1.17)	27.4 (1.77)	34.4 (1.15)	32.3 (0.95)	38.6 (1.34)	55.0 (1.42)
Length (mm)	13.5 (0.43)	32.1 (0.74)	32.5 (0.53)	48.4 (0.47)	48.3 (0.45)	42.6 (0.79)	89.9 (4.26)	76.5 (3.79)
Energy density ($\text{kJ g}^{-1}\text{DW}$)	28.5 (2.79) ^a	21.8 (0.76) ^a	20.8 (1.73) ^a	19.5 (0.54)	22.0 (0.30)	21.1 (0.33)	24.6 (0.42)	31.9 (0.29)

^aValues were calculated and not directly measured

Fig. 3. 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: *Thysanoessa macrura*, *Euphausia crystallorophias*, *E. superba*; fish: *Pleuragramma antarcticum*, *Electrona antarctica*). Error bars are 1 SE. Asterisks (*) indicate significant differences in total lipid content between regions. See Table 1 for test statistics

Interannual comparison

T. macrura and *E. crystallorophias* exhibited the most interannual variability of the 5 prey species investigated, although these interannual differences can be partially explained by differences in total length of animals sampled in 2009 vs. 2010. There was no significant difference in prey quality of *E. superba* in January 2009 vs. 2010. Thus for all further analyses, years were combined.

Regional comparison

Species/life stages for which there were significantly higher total lipid contents in the South (all years combined) included *E. crystallorophias*, juvenile *E. superba*, female *E. superba*, and total *E. superba* (Fig. 3, Table 1). While not statistically different, *E. antarctica* and male *E. superba* were generally higher in the South than North. *T. macrura* was the only species analyzed with higher lipid content in the North, although this difference was not significant (Table 1).

North–South differences in total lipid content and C:N values for *E. crystallorophias* may be partially explained by the higher average individual length of animals collected in the South (33.1 mm) vs. the North (28.2 mm; Fig. 3, Table 1). We found a significant, positive relationship between average individual total length vs. total

Fig. 4. Average individual total length (mm) vs. total lipid content (% dry weight, DW) for the euphausiids (A) *Thysanoessa macrura*, (B) *Euphausia crystallorophias*, and (C) juvenile *E. superba*. Regressions are for combined 2009 and 2010 data. See Table 3 for regression equations and statistics

Table 3. Relationships between length vs. elemental composition and lipid fraction by species. Average individual length (mm) vs. elemental composition ($\mu\text{g N mg}^{-1}$ dry weight, DW, or $\mu\text{g C mg}^{-1}$ DW) and lipid fractions (%DW) for euphausiid prey species: *Thysanoessa macrura*, *Euphausia crystallorophias*, juvenile *E. superba*. No significant length vs. composition relationships were found for other species (not shown). Regression equations are: Elemental Composition ($\mu\text{g N mg}^{-1}$ DW or $\mu\text{g C mg}^{-1}$ DW) or Lipid Fraction (%DW) = $m(\text{Average Individual Length, mm}) + b$. R^2 values are presented with p-values for all significant relationships (where $p \leq 0.05$); ns, not significant. See also Fig. 4

Elemental composition	Slope (m)	Intercept (b)	R^2	p	n	Lipid fraction	Slope (m)	Intercept (b)	R^2	p	n
<i>Thysanoessa macrura</i>											
Nitrogen ($\mu\text{g N mg}^{-1}$ DW)	-0.003	0.12	0.49	<0.001	22	Neutral	2.87	-17.18	0.52	0.0003	21
Carbon ($\mu\text{g C mg}^{-1}$ DW)	0.01	0.28	0.35	0.006	22	Polar				0.15, ns	22
C:N ratio	0.37	0.48	0.57	<0.001	22	Total	4.14	-12.12	0.31	0.01	21
<i>Euphausia crystallorophias</i>											
Nitrogen ($\mu\text{g N mg}^{-1}$ DW)	-0.002	0.15	0.65	<0.001	14	Neutral	1.13	-24.74	0.45	0.006	15
Carbon ($\mu\text{g C mg}^{-1}$ DW)	0.006	0.21	0.44	0.007	14	Polar				0.081, ns	15
C:N ratio	0.15	-0.4	0.64	<0.001	14	Total	1.94	-33.09	0.48	0.004	15
Juvenile <i>Euphausia superba</i>											
Nitrogen ($\mu\text{g N mg}^{-1}$ DW)	-0.001	0.12	0.21	0.02	28	Neutral	0.75	-9.91	0.20	0.005	39
Carbon ($\mu\text{g C mg}^{-1}$ DW)				0.08, ns	28	Polar	0.8	-6.26	0.13	0.03	39
C:N ratio	0.09	2.02	0.28	0.004	28	Total	1.46	-12.97	0.21	0.004	39

Fig. 5. Relationship between latitude and environmental or temporal parameters. Latitude (decimal degrees, DD) vs. 0–120 m mean water temperature, day of the year, and 0–120 m integrated chl *a*. The x- and y-axes in plots have been reversed to better depict the North to South trend. Regressions are for 2009 and 2010 combined data. Regression equations are (Property) = $m(\text{Latitude}) + b$, and are all significant ($p < 0.05$); see Appendix 1 for regression equations and statistics

lipid content, C content, and C:N for *T. macrura* and *E. crystallorophias* (Fig. 4, Table 3) as well as a significant, negative relationship between N content and average individual total length (Table 3). Thus, the significantly higher total lipid content and C:N values in the South vs. the North for these 2 species are likely due to the larger size of animals in the South (Fig. 3, Table 1). This was confirmed by a re-analysis using both the *E. crystallorophias* and *T. macrura* data standardized for length, for which we found no significant North–South differences in total lipid content and C:N for either species. Juvenile *E. superba* total lipid content was also significantly positively correlated with length (Fig. 4, Table 3). However, juveniles of various lengths were sampled uniformly across the grid, so the significantly higher total lipid content in the South (37% DW) vs. the North (31% DW) is more likely due to regional influences on animal physiology (Fig. 3, Table 1).

Relationship with latitude, hydrography, and time

Latitude, mean upper water column temperature, day of the year sampled, and integrated chl *a* were all highly correlated with each other due to the structure of the sampling cruise (starting in the north at Anvers Island and ending south at Charcot Island; Figs. 1, 2, & 5). All relationships between these properties were significant, with the exception of day of the year sampled vs. integrated chl *a* (see Appendix 1). Latitude was the most important explanatory

variable, resulting in the highest R^2 values for the relationships between mean upper water column temperature ($R^2 = 0.47$), day of the year ($R^2 = 0.46$), and integrated chl *a* ($R^2 = 0.20$; Appendix 1).

Total lipid content for total *E. superba* (Fig. 6) and for both juvenile and male *E. superba* (data not shown) increased with increasing latitude south, similar to results for other variables along the North–South gradient as described above. To analyze whether temporal or environmental parameters explained any of these observed trends in variability in *E. superba* prey quality, we conducted a stepwise multiple linear regression analysis for each prey metric (see ‘Materials and methods’). Since some of the variables were highly correlated with each other, we also analyzed interactions between the variables. If variables in the selected model had a correlation coefficient >0.8 , the variable explaining the least amount of variability was dropped in favor of a simpler model. Combinations of the selected independent variables explained 17 to 34% of the variability in prey quality metrics (Table 4). For the majority of prey metrics analyzed, sex and latitude were consistently important variables. Primary production, sex, and sample year were important explanatory variables in the C content model, and mean water temperature was important in all lipid models. Lower N and higher C and all lipid classes were associated with males, and lower N and higher lipid content for all lipid classes were associated with higher latitudes. Lipid values were also positively correlated to water temperature after accounting for the influence of latitude.

Fig. 6. Latitude (decimal degrees, DD) vs. *Euphausia superba* total lipid content (% dry weight, DW). The x- and y-axes in plots have been reversed to better depict the North to South trend. Regressions are for 2009 and 2010 combined data. Regression equations are (Total Lipid Content) = $m(\text{Latitude}) + b$; $y = 2.83x - 156.06$, $r^2 = 0.20$. Regression is significant ($p < 0.05$)

E. superba lipid content over seasonal progression of summer

Total lipid content was similar for *E. superba* sampled from the same northern station at the beginning and end of the cruise in 2010 (males, 6 and 31 January, 21.6% and 20.3%, respectively, $p > 0.05$) and in 2012 (males, 6 and 30 January, 26.5% and 30.7%; juveniles, 31.8% and 34.3%, respectively, $p > 0.05$).

DISCUSSION

Species comparison

Thysanoessa macrura are the smallest, most abundant euphausiids found throughout the WAP, concentrated around the northern continental shelf /slope intersection (Nordhausen 1992, 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). *T. macrura* had higher total lipid content by % dry weight than the other krill species analyzed in our study, and were statistically similar to the fish *Pleuragramma antarcticum* (although our *T. macrura* total lipid values were generally higher than previously reported for this species; our Table 2, Falk-Petersen et al. 2000, Färber-Lorda & Mayzaud 2010), thus *T. macrura* has potential to be a high-quality food item for penguins. The 2 other species of krill, *Euphausia 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 2 species were statistically similar, and they were the only species sampled with higher polar than neutral lipid content.

E. superba total lipid content as %DW in our study was roughly 50% higher than that reported by Färber-Lorda et al. (2009) in summer in the southern sector of the Indian Ocean, and by Clarke (1980) and Torres et al. (1994) in summer and fall, respectively, in the Scotia Sea. Hagen et al. (1996) reported very similar values to ours in summer in the Weddell Sea, and Atkinson et al. (2002) measured values 30% higher than ours from autumn in the Lazarev Sea. This variability amongst studies highlights the importance of considering season and region when estimating krill lipid content.

P. antarcticum had higher total lipid content than *E. crystallorophias* and *E. superba*, and higher relative neutral lipid content than any of the 3 krill species sampled (Table 2). *P. antarcticum* 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 (Fig. 1) (Emslie & Patterson 2007, W. Fraser pers. comm.). When available, Adélie penguins most frequently take fish 95 to 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 to 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). Few biochemical data are available for these older age classes (Chapman et al. 2011). We thus added our lipid data to the model of Chapman et al. (2011); our samples, which include year-3 and year-4 age classes not previously incorporated, fit well within their model with the exception of our 2010 data (Fig. 7). This deviation in 2010 may have been due to a fish diet deficiency, as Pinkerton et al. (2013) showed that

Table 4. Explanatory variables and statistical scores obtained from the best model among stepwise multiple regression analyses of various biochemical properties of *Euphausia superba*. Variables included in the best model for elemental composition ($\mu\text{g N mg}^{-1}$ dry weight, DW, or $\mu\text{g C mg}^{-1}$ DW) and lipid fractions (%DW) for all combined *E. superba* data. Latitude is the absolute value of the decimal degree (DD). 'n' defines the number of data points used to create the model. Test statistics include R^2 and p-values for the overall model (in parentheses) and the coefficient for the regression equation, the standard error (SE) associated with the model coefficient, the *t*-value, and the 2 tailed p-value used in testing the null hypothesis for each significant model variable

Variable	Coefficient	SE	<i>t</i>	p
Nitrogen ($\mu\text{g N mg}^{-1}$ DW) ($R^2 = 0.17$, $p < 0.001$, $n = 99$)				
Intercept	0.192	0.035	5.57	<0.001
Male	0.005	0.002	2.82	0.006
Latitude (DD)	-0.002	0.001	3.06	0.003
Carbon ($\mu\text{g C mg}^{-1}$ DW) ($R^2 = 0.27$, $p < 0.001$, $n = 95$)				
Intercept	0.466	0.105	44.27	<0.001
Male	-0.016	0.006	-2.57	0.012
0–120 m integrated primary production ($\text{mg m}^{-2} \text{d}^{-1}$)	3.85×10^{-6}	1.07×10^{-6}	3.58	0.001
Year	0.038	0.008	4.62	<0.001
Neutral lipids (%DW) ($R^2 = 0.29$, $p < 0.001$, $n = 109$)				
Intercept	-114.507	25.141	4.55	<0.001
Male	-3.485	0.991	3.52	0.001
Latitude (DD)	1.941	0.379	5.12	<0.001
0–120 m mean water temperature ($^{\circ}\text{C}$)	3.267	1.073	3.04	0.003
Polar lipids (%DW) ($R^2 = 0.21$, $p < 0.001$, $n = 109$)				
Intercept	-110.235	29.411	3.75	<0.001
Male	-2.214	1.159	1.91	0.059
Latitude (DD)	1.966	0.444	4.43	<0.001
0–120 m mean water temperature ($^{\circ}\text{C}$)	2.410	1.255	1.92	0.058
Total lipids (%DW) ($R^2 = 0.34$, $p < 0.001$, $n = 109$)				
Intercept	-222.776	43.056	5.17	<0.001
Male	-5.808	1.697	3.42	0.002
Latitude (DD)	3.878	0.650	5.97	<0.001
0–120 m mean water temperature ($^{\circ}\text{C}$)	5.757	1.838	3.13	0.002

postlarval *P. antarcticum* (50–89 mm standard length) exclusively consumed copepods, and 2010 was a year of anomalously low copepod abundances in the WAP (M. Gleiber et al. unpublished data).

Electrona antarctica is a numerically dominant, oceanic species of myctophid mainly found near the continental shelf/slope interface of the WAP (Donnelly & Torres 2008). These myctophids also access shelf and coastal regions through intrusions of warm, UCDW water and are present in both the northern and southern WAP (Donnelly & Torres 2008). Their exceptionally high lipid content, dominated by the neutral lipid fraction, resulted in the highest overall energy density. They are important in the diets of higher predators such as Weddell, crabeater, and Antarctic fur seals and various marine birds (Hopkins et al. 1993, Casaux et al. 2011, Hückstädt et al. 2012), 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).

The high lipid content of *T. macrura* and *E. antarctica* may suggest high prey quality, but this conclusion is somewhat tempered by the high percentage of neutral lipids in these species, components of which may be less easily assimilated. Previous studies have shown that the neutral lipids in both of these species are mainly composed of wax esters (Hagen & Kattner 1998, Connan et al. 2010), rather than the triglycerides that dominate the neutral lipid classes of *E. superba* and *P. antarcticum* (Wöhrmann et al. 1997, Ju et al. 2009). Some penguin species have roughly 20% lower assimilation efficiency for wax esters relative to triglycerides, detracting from the overall prey quality for species that store wax esters in high concentrations (Jackson & Place 1990).

Regional comparisons of prey quality

The North is characterized by a variable, but lengthy, season of low sea-ice concentration, while the South's sea-ice season is longer (Dierssen et al.

Fig. 7. Individual standard length (mm) vs. total lipid content (% dry weight, DW) for the fish *Pleuragramma antarcticum* (adapted from Chapman et al. 2011). The formula for the energy density function is: $Lip(L) = [(Lip_{max} - Lip_{min}) \times 1/(1 + e^{-k_{lip}(L - k_{lip50})})] + Lip_{min}$, 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 0.1 mm^{-1}); and $k_{lip50} = L$ at which the lipid content is 50 % of its maximum value (set to 50 mm)

2002, Stammerjohn et al. 2008). In our study, summer sea ice was present in the far southern portion of the WAP during each sampling year. Another feature of the South is a persistent, cyclonic gyre located on the shelf off Marguerite Bay that has been hypothesized to retain phytoplankton and larval krill (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, Garzio & Steinberg 2013), and apex predators (Friedlaender et al. 2011).

Regional differences in prey quality for the combined 2009 and 2010 juvenile, female, and total *E. superba* suggest that some confluence of environmental factors improve habitat in the South and 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, Flores 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 community, where cells $>20 \mu\text{m}$ are more prevalent in the South, and smaller-celled organisms such as flagellates are becoming more prevalent in the far North (Montes-Hugo et al. 2009). *E. superba* preferentially feed on diatoms and have significantly lower grazing efficiencies when particles are $<20 \mu\text{m}$ (McClatchie & Boyd 1983, Haberman et al. 2003). Declines in diatoms, a preferred food source, could affect the ability of krill to accumulate lipid stores in preparation for winter. This hypothesis is consistent with the significantly higher total lipid content in the South for juvenile, female, and total *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* access benthic habitats year-round (including abyssal plains as deep as 3500 m) and utilize phytodetritus as an alternate food source (Clarke & Tyler 2008, Schmidt et al. 2011, 2013, Flores et al. 2012). The importance, frequency, and seasonality of krill benthic feeding is still not well understood, but decreasing diatom biomass in the northern WAP would equate to a lower particulate organic carbon flux to the benthos, potentially resulting in lower overall food availability for krill during winter months.

Relationship of prey quality with latitude and hydrography

Results from our stepwise multiple regression analyses for *E. superba* showed that sexual differences and latitude were most important in explaining the variability in modeled prey metrics (Table 4). Sexual differences in *E. superba* lipid and C,N content similar to those observed in our study (Table 2) have been described previously (Clarke 1980, Färber-Lorda et al. 2009) and explained more of the variability in *E. superba* prey metrics than any of the temporal or environmental variables tested. Males expend much of their energy on high growth rates (presumably to increase reproductive success), resulting in a much lower lipid content and a higher mortality, which in turn makes their biochemical composition markedly

different from juveniles and mature females (Clarke 1980, Kawaguchi et al. 2007, Färber-Lorda et al. 2009). Thus geographic differences in sex ratios could have an effect on predator nutrition, highlighting the importance of including sexual differentiation in any energetics or food web study of *E. superba*.

Integrated primary production was also an important explanatory variable for *E. superba* carbon content, with carbon content increasing as primary production increased (Table 4). It is interesting then that primary production was not also an important explanatory variable for *E. superba* lipid content, because carbon is the main element from which lipid molecules are constructed (Ventura 2006). Perhaps instead of using the surplus food to produce lipid stores, that energy is shunted towards other compounds such as proteins, amino acids, carbohydrates, chitin, or RNA, which could explain the results of our carbon model.

Latitude was the next most important explanatory variable across the majority of the prey metrics analyzed, with N content decreasing with increasing latitude, and neutral, polar, and total lipid content increasing with increasing latitude (Table 4). The N relationship with latitude is driven by lipid variability because variations in N content were best explained by the animal's neutral lipid content (Fig. 8). Based on previous studies, the neutral lipid fractions of *E. superba* are mainly composed of triglycerides (Hagen et al. 1996, Ju et al. 2009). Triglycerides are comprised of 3 fatty acids bonded to a glycerol backbone through ester bonds and are composed of 77% C and 0% N (Ventura 2006). Proteins, free amino acids, RNA, DNA, chitin, and phospholipids contribute to the overall N content of krill (Ventura 2006). Thus, as *E. superba* retained higher concentrations of neutral lipids, the overall contribution of the lipids to the dry weight increased, decreasing the overall N content of the animal (Fig. 8).

While less important than sex and latitude, temperature was also an explanatory variable included in all lipid class models for *E. superba* (Table 4), with warmer water temperatures resulting in higher lipid content. This appears contrary to results discussed above showing that lipid content was higher in the (colder) South. However, we posit that this relationship may be explained by presence of more highly productive inshore stations in the South. A number of the inshore stations were warmer and more productive than their offshore counterparts on the same or more northerly sampling lines (Fig. 2). For example, in 2010, the 0–120 m mean temperature for an offshore station in the far northern section of the sam-

Fig. 8. Relationship between neutral lipid content and nitrogen content for *Euphausia superba*. Regression equations: y (Elemental Composition, $\mu\text{g N mg}^{-1}$ dry weight, DW) = $m \times x$ (Neutral Lipid Content, %DW) + b ; $y = -0.012x + 0.104$, $r^2 = 0.54$. Regressions are for combined 2009 and 2010 data and all are significant ($p \leq 0.05$)

pling region was 0.2°C cooler than an inshore station located only 200 km to the south. The inshore stations are in general more productive as well, and perhaps better habitat for krill. A recent study by Garzio & Steinberg (2013) in the WAP showed that microzooplankton biomass was also higher inshore vs. offshore. Thus, higher phytoplankton and microzooplankton prey availability for *E. superba* in more productive, and sometimes warmer, inshore waters in the south may lead to higher lipid content of *E. superba*.

CONCLUSION

Rapid regional warming in the WAP ecosystem is fundamentally altering ecosystem structure, and if the trends continue, the northern WAP will soon be characterized by a lack of perennial or summer sea ice, lower phytoplankton biomass, 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 a confluence of environmental factors that affect prey quality in the WAP, leading to significantly higher *Euphausia superba* total lipid content across all sexes and maturity stages in the South than in the North. Our model also indicated latitude as a significant variable in predicting *E. superba* nitrogen and lipid content, and that southern, inshore, more productive stations are likely favorable for krill lipid accumulation. These regional differences could have ramifications for the

rich assemblage of apex predators that summer in the WAP, and suggests that northern apex predators may have to consume more prey to meet their energetic demands or increase their reliance on other prey sources. The krill *E. crystallophias* and fish *Pleurogramma antarcticum* are also high-quality prey, but their ranges are largely restricted to the South, where summer sea ice still persists. The myctophid *Electrona antarctica* represents a potential, energy-rich option for coastal marine predators residing in the North, but its reliance on intrusions of UCDW for transport across the shelf raises questions on how often this prey item is reliably available. Incorporating these species-specific prey quality dynamics into future energetics modeling efforts focused on the WAP will increase model accuracy by improving the quality of functions regulating predator growth.

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Appendix 1. Relationships between environmental and temporal parameters. Regression statistics for the relationship between latitude (decimal degrees, DD), day of the year, 0–120 m mean water temperature (°C), and 0–120 m integrated chl *a* (mg m⁻²). Regression equations are in linear form: $y = m(x) + b$. R² values are presented with corresponding p-values for all significant relationships (where $p \leq 0.05$); ns, not significant. Regressions are for combined 2009 and 2010 data. See also Fig. 5

	Water temperature				Day of the year				0–120 m integrated chl <i>a</i> (mg m ⁻²)			
	R ²	p	m	b	R ²	p	m	b	R ²	p	m	b
Latitude (DD)	0.47	<0.0001	-0.24	15.82	0.46	0.0001	2.60	-157.81	0.20	0.018	15.69	-964.54
0–120 m mean water temp (°C)					0.17	0.034	-4.43	14.35	0.20	0.019	-0.005	0.05
Day of the year sampled										0.16, ns	0.03	13.21

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