Physical and biochemical properties of the euphausiids *Thysanoessa inermis*, *Thysanoessa raschii*, and *Thysanoessa longipes* in the eastern Bering Sea

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ABSTRACT

Euphausiids are an integral part of the Bering Sea ecosystem, linking primary production to upper level trophic levels as both consumers and prey. Species native to this region extend over a range of geographic provinces and serve as a critical component of the movement of energy through the food web. As one facet of the BEST-BSIERP Bering Sea program, we determined the proximate composition and essential allometric relationships of multiple species of euphausiids collected over three years in the eastern Bering Sea. Three euphausiid species were examined: *Thysanoessa inermis*, *Thysanoessa raschii*, and *Thysanoessa longipes*. While the three species were similar with respect to size, *T. inermis* had the highest average wet and dry weights per size class, as well as highest carbon and caloric concentrations. Among the three species, *T. inermis* and *T. longipes* had similar lipid concentrations, with *T. longipes* showing higher average lipid concentrations. Empirical equations were developed to describe fundamental relationships between length, weight, PC/PN, and calorie and lipid content for the three species over the full range of sizes encountered in the study area. Such relationships increase our understanding of how euphausiids contribute to the carbon budget and energy input in the eastern Bering Sea system and help to define realistic parameters for ongoing and future modeling efforts.

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1. Introduction

Euphausiids are an important component of the zooplankton community, particularly in high latitude ecosystems such as the Bering Sea. They are prey for many species, including commercially-important fish, seabirds, and whales (Byrd et al., 1997; Cianelli et al., 2004; Dwyer et al., 1987; Hewitt and Lipsky, 2008; Hunt et al., 1988; Moss et al., 2009; Shuntov et al., 2000; Smith, 1991). Three euphausiids – *Thysanoessa raschii*, *Thysanoessa inermis*, and *Thysanoessa longipes* – are the most abundant euphausiid species in the Bering Sea (Pinchuk and Coyle, 2008) and play an important role in energy transfer from lower to higher trophic levels. Among these species, *T. inermis* and *T. raschii* are more cosmopolitan and have been found at high latitudes throughout the northern hemisphere (Mauchline and Fisher, 1969). *T. longipes* has been documented primarily in the Japan, Okhotsk, and Bering Seas (Iguchi and Ikeda, 2005), but can be found as far north as the Arctic Ocean and as far south as 40°N, in the eastern Pacific (Boden et al., 1955; and references therein). This paper is a contribution to the BEST-BSIERP

Bering Sea Project where collaborative efforts across multiple trophic levels explored the linkages and interactions in the Eastern Bering shelf, the context of the current physical environment, and the potential for future climate impacts (Wiese et al., 2012).

Within the Bering Sea, these three species tend to segregate by oceanic habitat. *T. raschii* are generally found on the continental shelf in waters < 100 m, while *T. inermis* are typically found in the mid-range of water depths (∼150–200 m) and show a more polar distribution (Lindley, 1980). *T. longipes* are more common in deeper shelf, slope, and pelagic waters (> 200 m) (e.g. Pinchuk and Coyle, 2008; Smith, 1991) and have been found at depths up to 500 m in the Sea of Japan (Iguchi and Ikeda, 2004). There also appear to be interspecific differences in diet based on studies of these species in other regions which vary with location and season. In the boreal and Arctic regions of the North Atlantic, *T. raschii* is considered omnivorous and *T. inermis* believed to be mainly herbivorous, but with omnivorous tendencies (Båmstedt and Karlson, 1998; Falk-Petersen et al., 2000; Saether et al., 1986). Both species appear to be omnivorous during periods of food scarcity and while overwintering (Corkett and McLaren, 1979; Mauchline and Fisher, 1969; Nemoto, 1966). It is suspected that *T. inermis* and *T. raschii* also exploit detrital sources during sparse times (Falk-Petersen et al., 1981). The main dietary sources of *T. longipes* are not well known, but Iguchi and Ikeda

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(2005) observed that lab-reared animals from the Japan Sea would not feed on *Phaeodactylum tricornutum*, but did consume a diet of *Artemia nauplii* supplemented with *Isocrysis* sp. Variation in diets of these three species in the eastern Bering Sea during spring and summer and their trophic responses were also examined as part of the BEST-BSIERP Bering Sea project, but will be reported elsewhere.

There is a growing body of work on the physical attributes (length and weight) and proximate composition (carbon and nitrogen content; caloric content; lipid) of these three euphausiid species in different regions of the northern hemisphere. Hopkins et al. (1978) conducted extensive compositional measurements in the springtime and Falk-Petersen (1981) examined seasonal and interannual biochemical shifts for *T. inermis*, *T. raschii*, and *Meganyctiphanes norvegica* in Balsfjorden, Norway. Percy and Fife (1981), Iguchi and Ikeda (2005), Ikeda (1972), and Nomura and Davis (2005) have also contributed measures of fundamental properties for these three species. Specific studies have examined variations in lipid class with respect to winter (Sargent and Falk-Petersen, 1981), and seasonal change in total lipid and its constituents throughout the Trondheim, Bals, and Ulls Fjords (Saether et al., 1986). For *T. longipes*, in the Japan Sea, body allometry, weights, carbon, nitrogen, hydrogen, and ash measurements have been made (Iguchi and Ikeda, 2005).

Given the important role of euphausiids in high latitude ecosystems, proximate composition and length/weight relationships are needed. Several have been developed for *T. inermis* (Dalpadado and Skjoldal, 1991; Falk-Petersen, 1985; Kulka and Corey, 1982; Lindley, 1978; Matthews and Hestad, 1977; Sameoto, 1976) and for *T. raschii* (Sameoto, 1976; Falk-Petersen, 1985; Lindley, 1978; Vidal and Smith, 1986) in the Northern hemisphere (Siegel and Nicol, 2000). Kim et al. (2009) recently developed such relationships for *T. longipes* in the Oyashio region. Initial relationships describing lipid class concentration and total length were developed by Saether et al. (1986) for *M. norvegica*, *T. inermis*, and *T. raschii* collected in Norway. To our knowledge, no systematic study on the allometric relationships and chemical characteristics of eastern Bering Sea euphausiids has been reported.

Proximate composition studies can examine either individual euphausiids or composite samples. Typically, composite euphausiid samples are sorted by species, followed by other parameters such as sex, developmental stage, or location (e.g. Falk-Petersen et al., 1999; Mayzaud et al., 2003; Saether et al., 1986), but rarely by length. Yet size can be an influential factor in feeding habits (Hop et al., 2006), growth (Dalpadado and Ikeda, 1989; Falk-Petersen, 1985; Hopkins et al., 1984; Pinchuk and Coyle, 2008; Pinchuk and Hopcroft, 2007) and total lipid and lipid class (Mayzaud et al., 2003). Additionally, multiple measurements from a single composite sample are uncommon. If multiple measurements are taken from species-sorted composite samples, sex is not taken into account and individuals are very loosely sorted by size (Saether and Mohr, 1987; Saether et al., 1986). This study highlights the importance of allometry in proximate composition analyses in each of the three study species and focuses on creating a more complete analysis of each size class by taking multiple types of measurements from each different composite sample. Here, multiple chemical and physical characteristics of the three euphausiid species were measured throughout the spring/summer seasonal transition and among years. Fundamental relationships for euphausiid wet and dry weight, carbon, nitrogen, caloric and lipid composition using allometric measures were determined, and a series of equations to relate these characteristics across various size classes in the eastern Bering Sea developed. Understanding how these values differ among these three species provides a starting point for deciphering of how euphausiid proximate composition might respond to the dynamic Bering Sea environment.
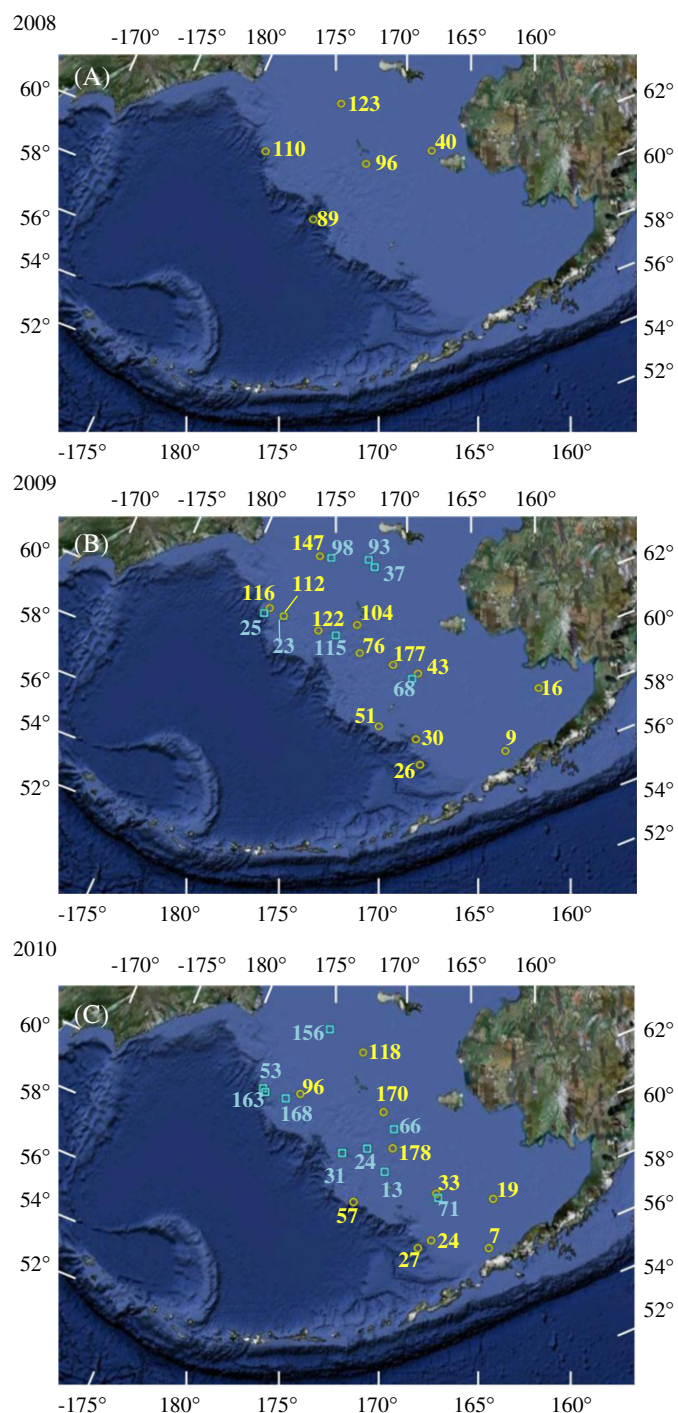

Fig. 1. Coordinates for euphausiid sampling locations in years (A) 2008, (B) 2009, and (C) 2010. Station numbers associated with each tow are noted near each point. Refer to station names to identify which stations were revisited with season shown as ▫ spring or ⊙ summer (Google Earth, 2010).

2. Methods

2.1. Sampling locations

The study region spanned 55.28–62.25°N and 164.06–178.91°W (see Fig. 1 for station locations). Stations used for analysis were chosen based on the available length ranges and species of euphausiids obtained in night tows at those locations for each spring and summer season. Detailed information (station coordinates, tow type and depth, etc.) regarding collections associated with each

composite sample can be found in Appendix A. It should be noted that the study period comprised three of the coldest and highest ice extent years since 2001 (Stabeno et al., 2012).

2.2. Sampling procedures

Euphausiids were collected during six cruises in the spring and summer of 2008, 2009 and 2010 (see Fig. 1, and Wiese et al., 2012). Spring cruises took place between early April and mid-May in 2008 and 2009; in 2010, the spring cruise was delayed until mid-May and ended in mid-June. Summer cruises were conducted between June and late July. In 2008 and 2009, euphausiids were collected using a 70 cm bongo net, with 333 μm mesh. The net was towed obliquely, except in heavy ice conditions or rough weather when vertical deployments were used. Krill were collected using several nets in 2010: a 1 m ring net with 200 μm mesh, a 60 cm bongo net with 333 μm mesh, and a 1 m² MOCNESS equipped with black, 505 μm mesh nets (e.g. Wiese and Benfield, 2003). Immediately upon recovery, euphausiids were removed from cod ends, transferred into containers of ambient filtered sea water, and held in the dark until sorted. Net tows were conducted to catch krill in good condition for use in live experiments. These tows were neither quantitative nor designed to serve as a source of data on zooplankton distribution or abundance. Data on distribution and abundance of zooplankton were collected as a different component of the BEST project.

Total length determination followed that of Shaw et al. (2010) using species-specific body length (BL) to total length (TL) conversions based on measurements made during the BEST cruises. The species-specific equations for conversion of adult BL to TL as defined by Mauchline (1981) for the three species are as follows:

T. raschii TL $= 1.1887 \times$ BL $+ 0.6838$ ($n = 530$, $r^2 = 0.99$).
T. inermis TL $= 1.15325 \times$ BL $+ 0.9846$ ($n = 248$, $r^2 = 0.99$).
T. longipes TL $= 1.2408 \times$ BL $+ 0.3308$ ($n = 186$, $r^2 = 0.99$).

Euphausiids were measured with the aid of a dissecting microscope and then sorted by species and size. Additional details of the condition of each euphausiid were also recorded, including sex, reproductive state (gravid, blue ovary, presence of spermatophores etc.), and presence of parasites. Heavily parasitized animals were not used. All composite samples were binned in 2 mm TL increments to allow detailed comparisons and comprised animals at similar reproductive states whenever possible. Krill were frozen at $-80\,^{\circ}$C either individually or as composite samples (ranging from 2 to 50 animals depending on length) and stored at $-70\,^{\circ}$C until analysis.

2.3. Wet and dry weights, PC/PN, and caloric content

In the laboratory, individual euphausiids were thawed, rinsed briefly with deionized water to remove salts, blotted to remove excess moisture, and weighed. Samples were then immediately lyophilized overnight with a Virtis DBT 7.0 model freeze dryer and dry weights obtained. For *T. inermis* and *T. raschii*, measures of carbon and nitrogen content, calories, and total lipid were performed using composite samples at 2 mm size increments over the range of 8–28 mm (10 subsets). For *T. longipes*, all proximate measurements were obtained from 2010 collections when adequate numbers were present. Immediately prior to CHN or calorimetric analysis, euphausiids were homogenized by grinding with a Teflon-coated pestle. PC/PN determination utilized standard combustion methods employing a CE-440 Elemental Analyzer with atropine serving as the standard. Caloric content was determined with a Parr 1109 semi-micro oxygen bomb calibrated with benzoic acid pellets. Krill were prepared using the Parr 2812 Pellet Press; masses and non-combustible products were measured to calculate gross heat (cal/g) based on ash-free dry weight (AFDW). Ash was calculated as the percentage of remaining dry weight. Limited sample mass confined the number of caloric measurements to composite samples and thus values represent average composition of krill within each 2 mm size bin. Relative standard deviation of gross heat was 5–7% based on replicate measurements of unsorted euphausiid composites.

2.4. Lipid extraction and analyses

Total solvent-extractable lipid isolation employed microwave-assisted solvent extraction (MASE) using a MARS5 microwave digestion system. All glassware and Teflon parts were solvent-rinsed and/or combusted prior to use. Pre-weighed samples were transferred to glass test tubes and extracted with 30 mL of 2:1 dichloromethane: methanol solution at 80 °C for 30 min with an initial 4 min temperature ramp and a programmed cool down period of 5 min. Power was set at 1600 W. After cooling below 40 °C, lipid extracts were transferred to flasks and evaporated to dryness using rotary evaporation. Individual lipid samples were then re-dissolved in a small volume of the extraction solvent and filtered through combusted quartz wool to remove cellular debris. Both of these steps were repeated twice more to ensure complete transfer. Total lipids and major lipid classes were determined by thin-layer chromatography with flame ionization detection (TLC–FID) using an Iatroscan MK-V Analyzer (e.g., Harvey and Patton, 1981; Ju and Harvey, 2004). Aliquots of total extracts were spotted onto replicate S-III Chromar-ods, solvent focused, and total lipids determined. Integrated peak areas (HP ChemStation) were quantified using a calibration curve consisting of a standard mixture of lipid classes approximating euphausiid composition. Overall precision for total lipid and major classes was $\pm 10\%$ or better for replicates. For major lipid classes, extracted lipids were developed in hexane:diethyl ether:formic acid (85:15:0.2), which allowed individual neutral lipids to be separated in a single development; phospholipids remained at the origin and were not identified individually. Lipid classes were identified and calibrated using a mixture of commercial standards (phosphatidyl choline for phospholipids (PL), cholesterol for sterols (ST), nonadecanoic acid for free fatty acids (FFA), triolein for triacylglycerol (TAG), and palmityl stearate for wax esters (WE); Sigma Co.). Peak areas were quantified using individual class calibrations, developed in tandem, of the standard lipid mix as above.

2.5. Statistical analyses

Regression equations for paired parameters for each species in each season and year were determined using Sigma Plot (ver. 8.0, Systat Software). To determine differences between seasons and years both within and among species, tests for significant differences in slopes and elevations of the regressions were made using a Student t-test or ANCOVA as outlined in Zar (1999).

3. Results

Individual and composite samples of each species were collected during all cruises whenever available and both seasonal and annual collections were compared where possible. In 2009 and 2010, adequate numbers of *T. inermis* and *T. raschii* allowed evaluation of both the spring and summer seasons, with animals collected during the summer of 2008 included for comparison. The collection of *T. longipes* in 2010 provided enough data to compare both seasons. While the summer of 2009 provided a sufficient number of samples, the spring of 2009 did not. Similarly, these samples were still included for

comparison. Significant relationships were found among all eight sets of paired parameters, which describe important physical and biochemical properties. The empirical relationships determined for the three species are shown in Table 1. Detailed descriptions of the trends observed and intra- and inter-species statistical comparisons are presented in the sections below. Average values for composite

Table 1
Equations describing the relationships between euphausiid physical and chemical properties observed in the Bering Sea. Abbreviations include: wet weight (WW); dry weight (DW); carbon (C); nitrogen (N); and energy (E). Energy is measured in cal $\times$ individual^{-1} and average total length is measured in mm. All other variables are measured in units of mg $\times$ individual^{-1}.

Relationship	Field years	Species	Equation	R^2	P	Regression comparison	Graph reference
Wet weight and total length	2008–2010	*T. inermis*	$WW = 0.012 \times TL^{(2.98)}$	0.97	< 0.0001	1	*6a*
	2008–2010	*T. raschii*	$WW = 0.009 \times TL^{(3.02)}$	0.95	< 0.0001		
	2009–2010	*T. longipes*	$WW = 0.009 \times TL^{(3.06)}$	0.99	< 0.0001		
Dry weight and wet weight	2008–2010	*T. inermis*	$DW = 0.239 \times WW^{(1.048)}$	0.93	< 0.0001	2	*6b*
	2008–2010	*T. raschii*	$DW = 0.270 \times WW^{(0.965)}$	0.96	< 0.0001		
	2009–2010	*T. longipes*	$DW = 0.109 \times WW^{(1.189)}$	0.96	< 0.0001		
Carbon and dry weight	2008–2009	*T. inermis*	$C = 0.448 \times DW^{(1.079)}$	0.99	< 0.0001	3	*6c*
	2008–2009	*T. raschii*	$C = 0.448 \times DW^{(1.024)}$	0.99	< 0.0001		
	2010	*T. longipes*	$C = 0.341 \times DW^{(1.130)}$	1.00	< 0.0001		
Nitrogen and dry weight	2008–2009	*T. inermis*	$N = 0.1212 \times DW^{(0.823)}$	0.86	< 0.0001	4	*6d*
	2008–2009	*T. raschii*	$N = 0.0997 \times DW^{(0.988)}$	0.95	< 0.0001		
	2010	*T. longipes*	$N = 0.1596 \times DW^{(0.774)}$	0.96	< 0.0001		
Carbon and total length	2008–2009	*T. inermis*	$C = 0.0029 \times TL^{(2.87)}$	0.71	< 0.0001	5	*6e*
	2008–2009	*T. raschii*	$C = 0.0014 \times TL^{(2.93)}$	0.69	< 0.0001		
	2010	*T. longipes*	$C = 0.000012 \times TL^{(4.64)}$	0.90	< 0.0001		
Lipid and dry weight	2009	*T. inermis*	$L = 0.409 \times DW^{(0.964)}$	0.91	< 0.0001	6	*6f*
	2009	*T. raschii*	$L = 0.453 \times DW^{(0.758)}$	0.78	0.001		
	2010	*T. longipes*	$L = 0.292 \times DW^{(1.11)}$	0.95	< 0.0001		
Energy and dry weight	2009	*T. inermis*	$E = 4.44 \times DW^{(1.10)}$	0.98	< 0.0001	7	*6g*
	2009	*T. raschii*	$E = 4.81 \times DW^{(1.02)}$	0.97	< 0.0001		
Energy and carbon	2009	*T. inermis*	$E = 12.90 \times C^{(0.963)}$	1.00	< 0.0001	8	*6h*
	2009	*T. raschii*	$E = 10.08 \times C^{(1.03)}$	1.00	< 0.0001		

1, 3, 5–8 = slopes not statistically different when all data pooled.
2, 4 = slopes statistically different when all data pooled.
1, 3, 6–8 = slopes statistically similar among all species.
2 = slopes statistically different among all species.
4, 5 = slopes statistically different between *T. raschii* and *T. longipes*.
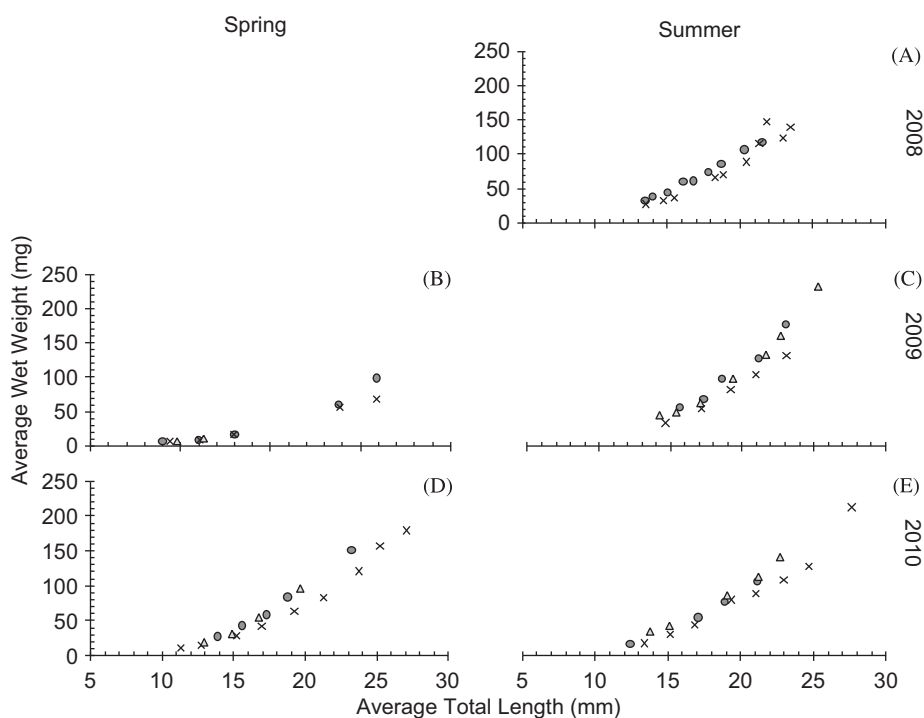

Fig. 2. Average total length and wet weight regression for Bering Sea euphausiids. Graphs are divided by season and sampling year: (A) July, 2008 (B) April–May, 2009 (C) June–July, 2009 (D) May–June, 2010 (E) June–July, 2010. Symbols represent ● *T. inermis*, △ *T. raschii*, and ✕ *T. longipes*.

samples were normalized to a single animal, e.g. mg C individual^{-1} or average carbon content (mg C mg dry weight^{-1}) for each parameter among each 2 mm size bin. The relationships for each set of paired parameters are referenced (Figs. 2–6); error bars were not shown as most are smaller than the symbol area. All errors associated with each measure are included in Appendix B. Cruise-specific data, listed in the appendices, will be made public domain and can be accessed via the Bering Sea Project Data Archive (http://beringsea.eol.ucar.edu/data/).
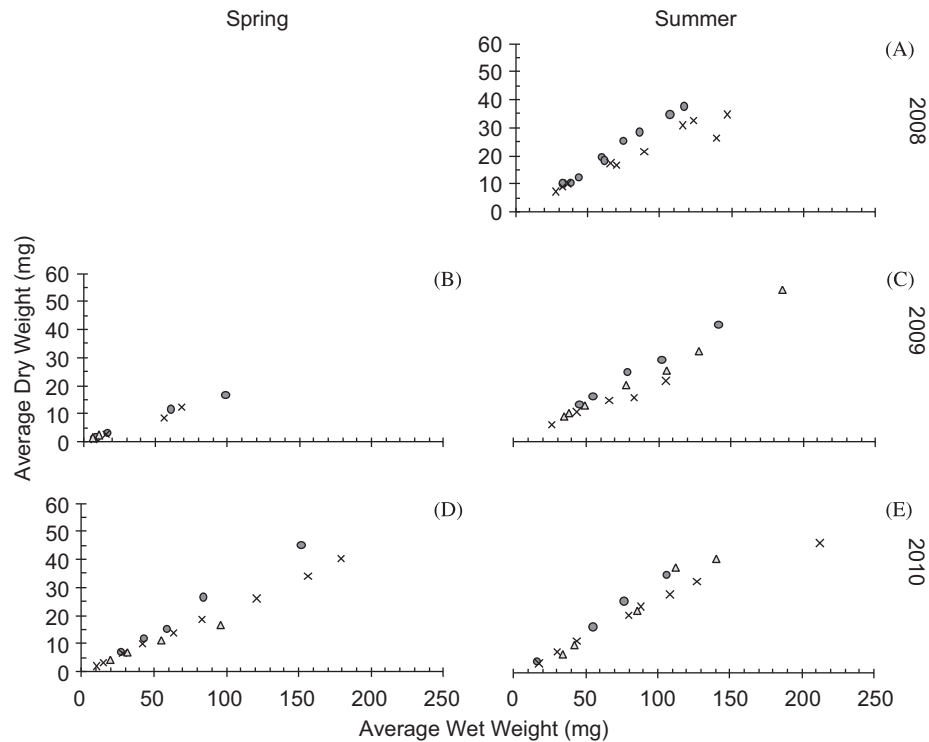

Fig. 3. Wet versus dry weights relationship for Bering Sea euphausiids in spring and summer over the study period. Graphs are divided by season and sampling year: (A) July, 2008 (B) April–May, 2009 (C) June–July, 2009 (D) May–June, 2010 (E) June–July, 2010. Symbols represent ● T. inermis, △ T. raschii, and ✕ T. longipes.
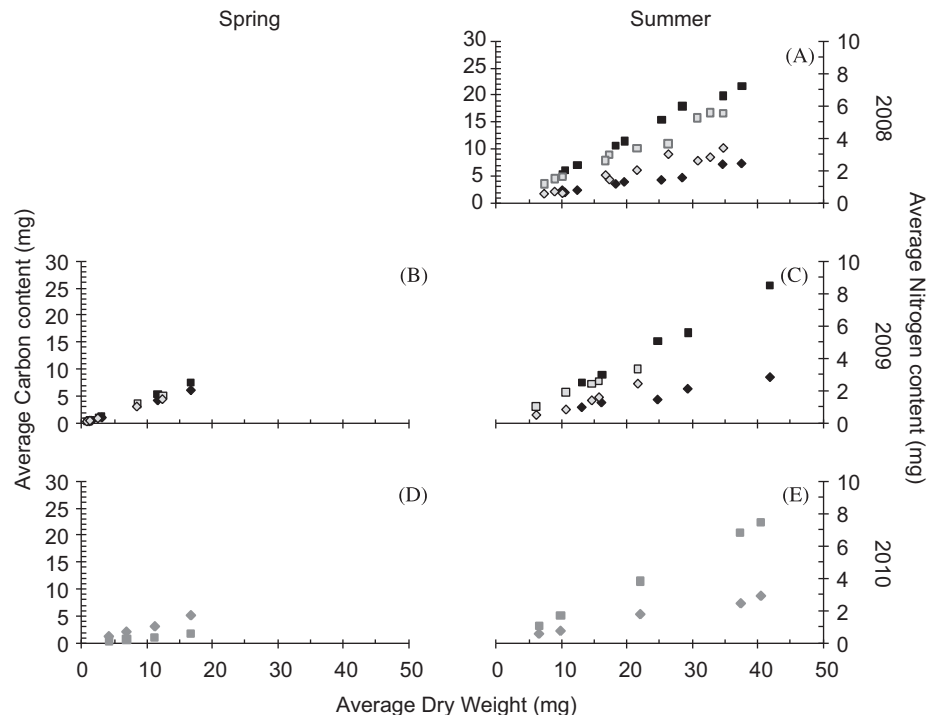

Fig. 4. Average carbon and nitrogen content for Bering Sea euphausiids. Spring collections are featured on the left panel with summer on the right. Graphs are organized by season and sampling year; (A) July, 2008 (B) April–May, 2009 (C) June–July, 2009 (D) May–June, 2010 (E) June–July, 2010. Symbols for carbon and nitrogen are shown as ■ Carbon—T. inermis, ▨ Carbon—T. raschii, ▨ Carbon—T. longipes, ◆ Nitrogen—T. inermis, ◇ Nitrogen—T. raschii, and ◆ Nitrogen—T. longipes.
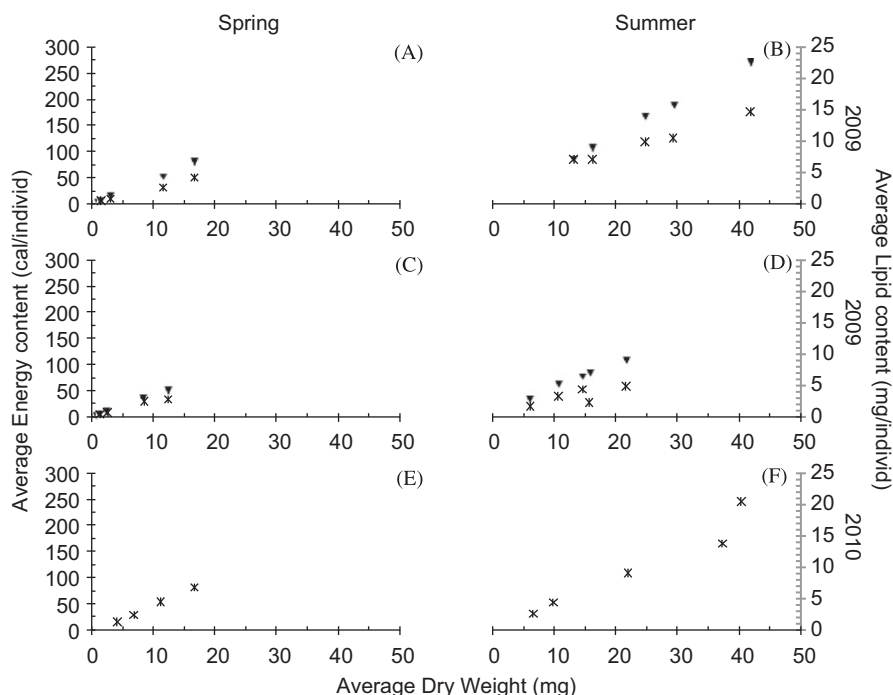
Fig. 5. Average calorie (▼) and lipid (✳) measurements for Bering Sea euphausiids during 2009 and 2010. Spring collections are shown on the left and summer on the right for *T. inermis* (A, B), *T. raschii* (C, D), and *T. longipes* (E, F).

3.1. Wet weight versus total length

Wet weight increased exponentially with average total length for all three species in spring and summer (Fig. 2). Average total lengths for *T. inermis* ranged 9–23 mm during the spring and 12–23 mm in the summer, with corresponding wet weights per individual of 7–152 mg and 16–142 mg. Average total lengths ranged 9–27 mm during spring and 13–28 mm during summer, with average wet weights of 7–179 mg and 18–213 mg, respectively, for *T. raschii*. For *T. longipes*, average lengths of 10–20 mm were seen in spring with wet weights of 6–96 mg per individual and summer lengths of 14–25 mm with wet weights of 34–185 mg. *T. inermis* had a higher wet weight per unit length compared to *T. raschii*, except for spring 2009, and showed similar or larger wet weight per unit length compared to *T. longipes* throughout the studied months. When all cruises were combined, however, the WW:TL relationship for both *T. raschii* and *T. inermis* show no significant differences across summed seasons or years for each species. The few individual *T. longipes* collected from the spring of 2009 precluded detailed seasonal comparisons, but annual comparisons showed no differences. Additionally, no significant differences were noted between any of the three species when all data were compared. Only *T. longipes* showed differences within its data sets, most likely due to the sample size in spring, 2009.

3.2. Dry weight versus wet weight relationships

When comparing *T. inermis* data, there were significant changes seen among summed years, but not between the pooled seasons; analysis of *T. raschii* data revealed similar results. *T. longipes* exhibited opposite trend where seasons differed, but years did not. All three species yielded significant differences when data sets were compared within each species, as well. *T. inermis* generally had the highest DW:WW, regardless of season or year (Fig. 3; Appendix B). On average, *T. raschii* had the lowest wet weight for each size class, except in the summer of 2010 when *T. longipes* had equal or greater water content. *T. longipes* were more variable, but generally were

within the same range as the other two euphausiid species. Dry weight with respect to size class for *T. inermis* was generally highest of the three *Thysanoessa* species, followed by *T. longipes* and then *T. raschii*. Comparisons among species for all data sets revealed that each species was statistically different from the other.

3.3. Carbon and nitrogen content

The C/DW relationships within each species did not statistically differ when all data were pooled, or when comparing between seasons or summers, with the exception of *T. raschii* in the summer seasons (2008 and 2009). Although differences were not significant among species, *T. inermis* had the higher average carbon content than *T. raschii* over a range of dry weights for spring and summer. *T. raschii* carbon to dry weight ratios were the lowest per individual, and those of *T. longipes* were intermediate (Fig. 4).

Carbon was strongly correlated with total length for all three species (Fig. 6, Table 1), and did not statistically differ for each species when data were pooled. No differences were seen between seasons in the same year for *T. inermis* (2009) or *T. longipes* (2010), unlike *T. raschii*. Additionally, no C:TL differences were observed between summer data sets for *T. inermis* or *T. raschii*; *T. longipes* did not have additional summer data for a comparison. Among species, only *T. raschii* and *T. longipes* differed, statistically.

During the summer, *T. raschii* was generally more nitrogen-rich than either *T. inermis* or *T. longipes*. On the statistical side, as with C:DW and C:TL, pooled data within each species did not differ. Differences between combinations of years and seasons within each species mirrored those of the C:TL correlations. Similarly, only differences between *T. raschii* and *T. longipes* were noted among species.

3.4. Calories and lipids

Individual caloric and lipid content of krill showed an increase in energy stores as the season progressed (Fig. 5). Nevertheless,
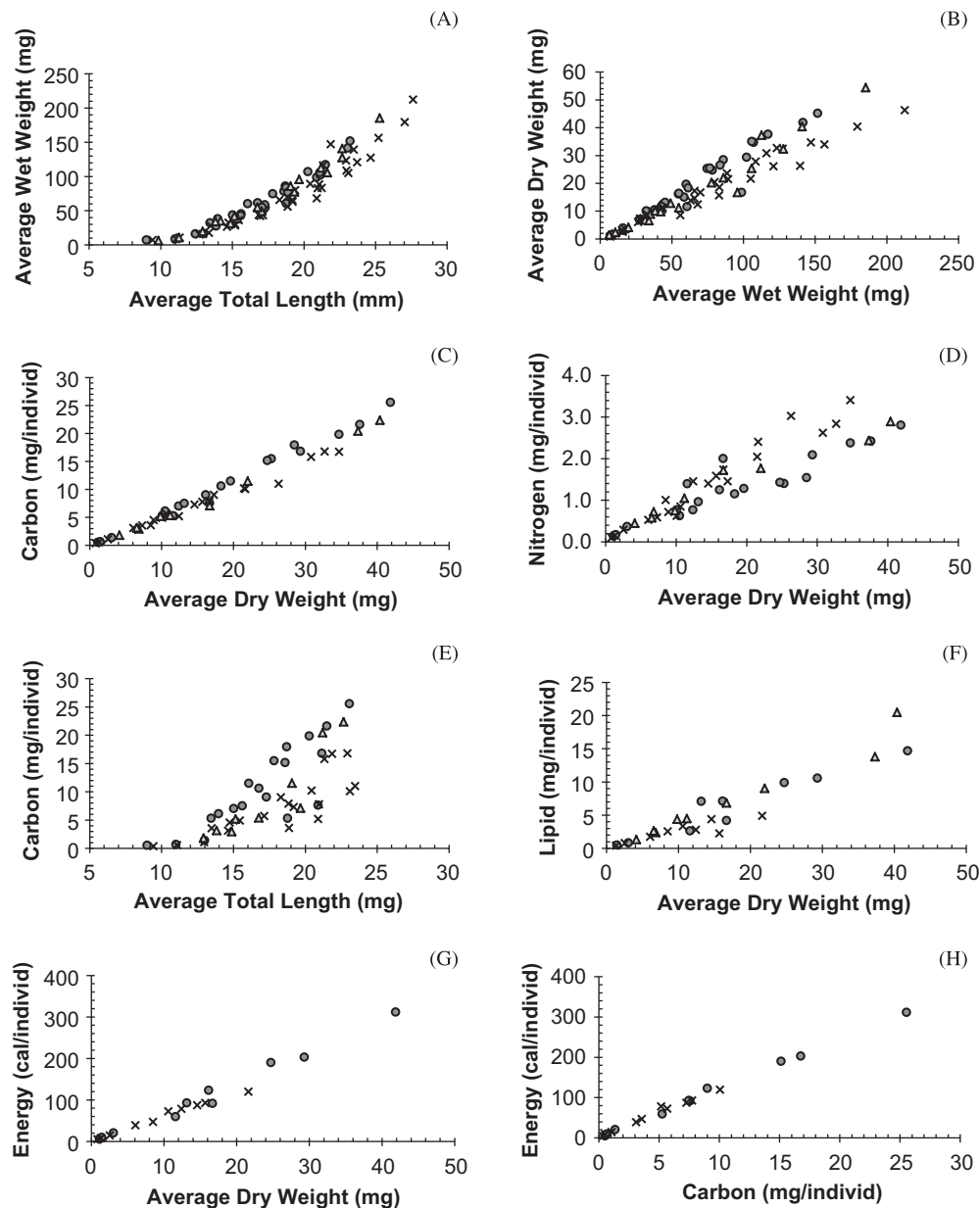
Fig. 6. Regression relationships for each species with combined data from all seasons and years for length, weight, carbon, nitrogen, calories, and lipid content. Regressions are derived from empirical equations described in Table 1. Available data for each euphausiid are listed in each panel. Symbols are shown as ● *T. inermis*, △ *T. raschii*, and ✕ *T. longipes*.

neither caloric concentration (as calories per gram AFDW) nor lipid (as a percent of dry weight) had showed a consistent relationship to size class within a species. As a general observation, *T. longipes* had the highest lipid content of the three species. *T. raschii* were consistently within the lower range of values measured for all three species. The high *T. longipes* lipid content seen in spring may be a consequence of these krill being collected nearly a full month later in the season as compared to the other two species of euphausiids. Seasonal differences were not significant between DW and lipid; DW and energy; or C and energy between *T. inermis* (2009) or *T. longipes* (2010). Among those three paired sets of variables, *T. raschii* only exhibited seasonal differences between DW and energy.

3.5. Lipid class analysis

Lipid class analysis was performed for the largest size class of euphausiids collected in summer 2009 (*T. raschii* and *T. inermis*) or

2010 (*T. longipes*) with results shown in Table 3. Phospholipids were the dominant lipid class for all three species, with differences in types and amounts of storage lipids among species. Wax esters, a storage class found in significant amounts within *T. inermis*, were either absent or present in minor quantities in *T. raschii* and *T. longipes*.

3.6. Empirical relationships among the three euphausiid species

The relationships observed between average total lengths and average wet weights for each species were similar in spring and summer seasons for all years. Interestingly, all three *Thysanoessa* species had similar patterns of biomass among years (Fig. 6), but annual changes were subtle and did not show a consistent trend. The uniformity seen for each species across the project period allowed each species to be represented by a single regression, reflecting the tight correlations between length and wet weight over multiple seasons and years (Fig. 6A). The same approach was

applied to a number of other paired characteristics, including an additional comparison of total length with carbon content remained constant over time. The equations that describe these important relationships, and their corresponding correlation parameters, are described in Table 1 with their accompanying statistical evaluation. The comparisons focus on individual species aggregated over the project period to allow the broadest range of sizes to be evaluated; however, small subsets also show significant differences. For example, some summer seasons were significantly different from each other, but spring seasons were not. Significant differences were found between species for all WW and DW sets.

4. Discussion

4.1. Krill as a food source

Within the Bering Sea, euphausiids are prey to a variety of predators, including fish like walleye pollock (*Theragra chalcogramma*), various species of salmon (Brodeur et al., 2000; Coyle et al., 2011; Tadokoro et al., 1996); seabirds (Jahncke et al., 2005), marine mammals including whales and seals (Smith, 1991; Springer et al., 1996); and potentially squid (Ormseth and Spital, 2010). Foraging regions of these predators differ within the Bering Sea, and may vary for migrating species such as whales (Smith, 1991). While the proximate composition for krill show remarkable consistency over a range of sizes, distribution patterns of krill species have the potential to confer an advantage on predators whose ranges overlap with the more lipid-rich species, such as *T. longipes*. Pinchuk and Coyle (2008) showed that within the Pribilof region of the Bering Sea, *T. inermis* and *T. longipes* remained in deeper waters whereas *T. raschii* stayed closer to the shelf. During recent colder years (1999–2002), Pinchuk et al. (2008) observed that *T. inermis* in the Gulf of Alaska were more abundant than subsequent years with warmer temperatures and lower chlorophyll. Spatial separation of krill species and differences in proximate conditions might have implications for success of predators. The higher lipid content of *T. inermis* suggests it may provide a higher quality diet than *T. raschii* despite the fact that overall caloric content was not substantially different (Fig. 5). *T. longipes* could also provide a lipid-rich diet for regional predators.

4.2. Life strategies of polar euphausiids

The life cycles of high latitude zooplankton are strongly influenced by the highly seasonal nature of their food supply (Hagen and Auel, 2001, and references therein). Euphausiids that live at high latitudes in both hemispheres commonly employ one of several general reproductive strategies that exploit the seasonal food abundance in different ways (Falk-Petersen et al., 2000). *T. inermis* builds up an abundant store of energy during the summer phytoplankton bloom and uses it to fuel gonad maturation and reproduction starting in late winter or early spring. This timing enables offspring to exploit the summer phytoplankton bloom in order to build up sufficient energy reserves for over-wintering. A second strategy, employed by *T. raschii*, is to use the energy from the spring phytoplankton bloom to fuel reproduction directly. Since *T. raschii* inhabit shallower waters, they may switch to detrital feeding during the winter as an alternate food supply (Mauchline and Fisher, 1969; Falk-Petersen et al., 1981). Little is known about the reproductive cycle of *T. longipes*, and the information available is confined to the west Pacific subarctic regions. The reproductive season for *T. longipes* – March or April through May – overlaps with reported spring bloom periods in

Table 2
Major biochemical properties for euphausiids determined from this study and comparisons from other regions in the Northern Hemisphere. Spring months range from April–June and summer months from June through September.

Species	% C (from DW)	% N (from DW)	% Water	Cal/g AFDW	Ash (% DW)	Lipid (% DW)	Region	Field Years	Ref.
Spring									
T. inermis	43.8–45.5	11.5–12.0	68.3–83.9	4353–6552	10–31	22.4–30.4	Bering Sea	2008–2010	1
T. raschii	40.1–42.0	11.1–11.8	76.7–87.8	5488–6301	22–33	22.3–29.7	Bering Sea	2008–2010	1
T. longipes	42.3–47.8	9.4–10.8	76.6–82.5	N/A	N/A	31.4–40.7	Bering Sea	2010[a]	1[a]
T. inermis	43.92 ± 2.81	9.59 ± 1.75		5241 ± 349	17.94 ± 0.62	22.66 ± 0.72	Balsfjorden	1977	2
T. raschii	40.64 ± 4.38	10.20 ± 2.11		5094 ± 468	18.56 ± 7.11	13.70 ± 0.71	Balsfjorden	1977	2
T. longipes	43.7	10.2			12.4		Japan Sea	1997–1998	3
Summer									
T. inermis	50.2–62.8	5.4–7.7	66.8–75.8	6920–7678	7–13	35.0–53.6	Bering Sea	2008–2010	1
T. raschii	41.7–53.5	6.2–11.5	72.1–81.1	5537–6835	9–13	14.2–31.3	Bering Sea	2008–2010	1
T. longipes	47.7–55.3	6.5–8.8	66.8–80.8	N/A	N/A	36.9–50.6	Bering Sea	2009–2010	1
T. inermis			68.2–79.6	6260–6600	5.9–7.4	52.4	Frobisher Bay	1971	4
T. inermis						40–50	Balsfjorden	1976–1977	5[b]
T. raschii			82.2		10.9	7.2	Bering Sea	1969	6
T. raschii						35	Balsfjorden	1976–1977	5[b]
T. longipes	45.1–55.9	6.6–10.3	62.6–77.3		7.1–13.4		Japan Sea	1997–1998	3
T. longipes						2.2–10.7	Bering Sea	2001–2004	7

(1) This study; (2) Hopkins et al., 1978; (3) Iguchi and Ikeda, 2005; (4) Percy and Fife, 1981; (5) Falk-Petersen et al., 1981; (6) Ikeda, 1972; (7) Nomura and Davis, 2005.
[a] Data from Spring 2010 only.
[b] Year class group-1 data.

both the Oyashio Sea and the Japan Sea (Kim, 2009 and references therein); however, it is unknown what role the bloom plays in the accumulation of lipid by *T. longipes*.

These different feeding and reproductive strategies in behavior of Bering Sea euphausiids have implications for energy transfer to higher trophic levels. Given that euphausiids are an important food source for a variety of species in the Bering Sea, including nesting seabirds and commercially important fish populations, the differences in energy content among species have potential impacts on their predators. The observation that average caloric and lipid content increased with season for both *T. inermis* and *T. raschii*, suggests that both species are adequate food sources, although *T. inermis* have higher carbon and calorie concentrations per individual.

4.3. Potential impact of climate change

The similarity seen among many of the physical and biochemical properties in the three species of euphausiids over all three years should also be viewed in light of the prevailing oceanic conditions. After a decade of measured increases in mean annual temperature for the eastern Bering Sea, the three field years of this study were near or below the long term temperature mean (Stabeno et al., 2012). As such, this study cannot directly address potential consequences for euphausiids in a warming ocean. Indeed, results from this study, carried out as it was under climate conditions similar to historic conditions in the Bering Sea, may be more applicable as baseline data for how the Bering Sea used to be before it started warming. *T. inermis* is a more polar species than *T. raschii* (e.g. Lindley, 1980) and an increase in ocean temperature in the Bering Sea could shift the distribution of *T. inermis* further north as they seek out their preferred water temperature. Assuming there are predators that rely on *T. inermis*, a shift in the distribution of this euphausiid in relation to changing water temperatures could impact the distribution or survival of predators that feed at specific locations. If such a shift in *T. inermis* distribution were to occur, *T. raschii* is likely to be the more locally available prey. With its more shallow water distribution and lower lipid content, it may be a lower-quality prey item with subsequent consequences throughout the food web.

4.4. Composition comparisons of high latitude euphausiids

Results of detailed proximate analysis among the three species of euphausiids examined here are similar to those for the same species in other regions of the northern hemisphere (Table 2). The majority of springtime measurements obtained from other sources and regions fall within the range of our size-based measurements. While %N is slightly higher for Bering Sea *T. inermis* and *T. raschii* than seen by Hopkins et al. (1978), caloric and lipid content are within the lower range of values measured

during our study. Our lipid content values are much higher, even at the lower end of our range, than those of Nomura and Davis (2005). Caloric content, % water and % ash measurements for *T. inermis* and *T. raschii* from Balsfjorden, Norway fall mostly within range observed here. For *T. raschii*, the lipid content found here is much higher than that measured by Ikeda (1972) in the Bering Sea.

The compositional similarity among euphausiids in various regions is intriguing. Indeed, it appears that high-latitude euphausiids in both the northern and southern hemispheres have adopted similar life history strategies (Hagen and Auel, 2001 and references therein). *T. inermis* shows similarities in lipid composition and life history strategies to *E. crystallorophias* in Antarctica, while *T. raschii* shows similarities to *E. superba*. *T. longipes* does not have an established Antarctic congener, but *T. macrura* may be a suitable alternate as both species are omnivorous, maintain lipid stores, and contain notable quantities of wax esters (Phleger et al., 1998; Hagen and Kattner, 1998). *T. macrura* is said to exhibit some degree of carnivory; morphological characteristics, i.e. predatory arms, and observations by Iguchi and Ikeda (2005) suggest that *T. longipes* could be classified similarly (Phleger et al., 1998). *T. macrura* has been observed in waters deeper than 1800 m (Falk-Petersen et al., 1999) as well as between 120 and 220 m (Nordhausen, 1994); likewise, *T. longipes* has been documented at both pelagic and epipelagic depths (Pinchuk and Coyle, 2008).

Lipid classes for the three *Thysanoessa* species and their Antarctic congeners are summarized in Table 3. For these comparisons, relationships derived from these results are contingent on the allometric sorting of euphausiids. Färber-Lorda et al. (2008) assembled a suite of equations for *E. superba* by sorting according to sex and developmental stage; although, they also noted that size was also statistically significant. Mayzaud et al. (2003) observed that for *T. macrura* and *E. crystallorophias* size was a significant factor in relation to lipid content. Phospholipids represent an important component of lipid storage as well as structural constituents in sub-arctic euphausiids, which can obscure the role of lipids as important energy reservoirs. Among the three euphausiids examined here, *T. inermis* show substantial stores of wax esters, not unlike other high latitude euphausiids such as the Antarctic species *E. crystallorophias* (Nicol et al., 2004). Composite samples separated by size and sex were not feasible in the present study due to frequent small catches of krill, yet the three euphausiid species show predictable relationships over the entire range of sizes in this study. There appear to be predictable patterns among multiple euphausiids species across the high latitude oceans.

4.5. Summary

The incorporation of euphausiids into process models in the Bering Sea and other regions is a complicated process. Different

Table 3
Lipid class comparisons, expressed as % of total lipid, of polar and sub-arctic euphausiids in Arctic and Antarctic regions.

	T. raschii	T. inermis	T. longipes	T. macrura (F)	E. superba	E. crystallorophias
	June–July	June–July	June–July	Austral summer	Austral fall	Austral fall
PL	98.3	82.6	85.2	45.4	48.5	43.3
TAG	1.3	1.0	11.9	ND	46.1	4.7
WE	0.2	16.2	2.4	53	1.6	49.8
ST	0.2	0.2	0.3	ND	3.3	1.5
FFA	TR	TR	0.2	1.6	0.5	0.7
DAG				ND		
Total (%)	100	100	100	100	100	100
	Bering Sea this study	Bering Sea this study	Bering Sea this study	S. Indian Ocean Mayzaud et al. (2003)	Marguerite Bay, Antarctica Ju et al. (2009)	Marguerite Bay, Antarctica Ju et al. (2009)

species in the same ecosystem cannot all be treated identically since there may be considerable differences in habitat preferences, diet preferences, timing of reproductive activity, vertical migration, etc. (Falk-Petersen et al., 2000; Mayzaud et al., 2000; Feinberg and Peterson, 2003; Mayzaud et al., 2003; Gómez-Gutiérrez et al., 2005; Ju et al., 2009; Taki, 2011). The results described here allow for both consistent and calibrated measures of major biochemical and physical metrics for the three major Bering Sea euphausiid species, and consequently enhance the growing body of knowledge on their distribution and preferred habitats. Coupling this improved information on fundamental properties with specifics of chemical composition will contribute to increasingly accurate carbon budgets for the Bering Sea.

5. Conclusions

Thysanoessa raschii, *T. inermis* and *T. longipes* showed remarkable consistency in proximate composition among all years of this study. Allometric characteristics of Bering Sea euphausiids, regardless of species, proved to be significantly correlated for a number of physical and chemical characteristics. Lipid composition data suggest that *T. raschii* are dependent on the bloom to fuel reproduction in the spring and summer, while *T. inermis* appear to store energy and use it for reproduction in the late winter or early spring. *T. longipes* may also exploit the bloom when available, but lipid content suggests that their diet remains omnivorous even during bloom conditions. Lipid composition data also suggest that the higher WE levels in *T. inermis* make it a more desirable prey item for species that are growing and reproducing during the short productive season in the Bering Sea. The Bering Sea Project comprised three of the coldest years in the Bering Sea since 1998. Results presented here may be more typical of the Bering Sea ecosystem as it was prior to extremes in reduction of sea ice, and should be useful as a standard for comparison with similar studies conducted during warmer years.

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Appendix A. Supplementary material

Supplementary data associated with this article can be found in the online version at doi:10.1016/j.dsr2.2012.02.007.

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Appendix 1: Information for each station from which collected samples were analyzed. B=Bongo net; RN=Ring net; MOC=MOCNESS; WC=water column.

Season	Cruise	Station no.	Station name	Lat °N (decimal)	Long °W (decimal)	Net cast date (UTC)	Tow time (UTC)	Net type	Tow type	WC depth (m)	Calculated depth of tow (m)[a]	Species and length ranges[b]
Summer, 2008	HLY-0803	40	W-2	60.4936	168.0000	2008-07-11	8:05	B, 70 cm	Oblique	30	21	R22
	HLY-0803	89	P14-4.5	57.8024	175.0218	2008-07-21	11:15	B, 70 cm	Oblique	2665	92	I14, I16, I20
	HLY-0803	96	MN-8	59.8965	172.1976	2008-07-23	10:49	B, 70 cm	Oblique	73	57	R12, R14
	HLY-0803	110	MN-19	59.8975	178.8003	2008-07-25	12:57	B, 70 cm	Oblique	157	85	I12, I14, I16, I18, I20, R14, R18
	HLY-0803	123	70M-56	61.9402	174.3643	2008-07-27	11:40	B, 70 cm	Oblique	74	60	R18, R20, R22
Spring, 2009	HLY-0902	23	MN-17	59.8969	177.6009	2009-04-11	12:48	B, 70 cm	Vertical	142	139	I8, I10, I2
	HLY-0902	25	MN-19	59.8995	178.9100	2009-04-12	8:47	B, 70 cm	Oblique	650	106	I18, I20
	HLY-0902	37	SL7.5	62.0051	172.0449	2009-04-17	10:10	B, 70 cm	Vertical	53	48	L10
	HLY-0902	68	AS1	58.1781	169.0879	2009-04-25	10:21	B, 70 cm	Vertical	73	65	R18, R20
	HLY-0902	93	BN1	62.2510	172.5169	2009-05-02	9:48	B, 70 cm	Vertical	58	53	L8, L10
	HLY-0902	98	SL-12	62.1854	175.1517	2009-05-04	9:47	B, 70 cm	Vertical	81	75	R8, R10, R12
	HLY-0902	115	BL-21	59.4661	174.0546	2009-05-06	10:19	B, 70 cm	Oblique	116	106	R10, R12
Summer, 2009	KN195-10	9	UAP-4	55.7592	163.5510	2009-06-16	11:30	B, 70 cm	Oblique	96	57	I16, I18, I20, R16, R18, R20
	KN195-10	16	CN-0	57.8438	161.3190	2009-06-17	11:00	B, 70 cm	Oblique	50	39	R22
	KN195-10	26	CN-18	55.2812	168.4038	2009-06-19	9:40	B, 70 cm	Oblique	1700	106	I16, I18, I20, I22, L20
	KN195-10	30	CNN-8	56.1430	168.6980	2009-06-20	11:10	B, 70 cm	Oblique	458	106	I16, I20, L18
	KN195-10	43	NP-5	58.3628	168.7385	2009-06-22	10:15	B, 70 cm	Oblique	70	53	R18, R20
	KN195-10	51	NP-13	56.5098	170.8777	2009-06-23	11:30	B, 70 cm	Oblique	128	89	L12, L14, L16, L22
	KN195-10	76	SQ-1	58.9313	172.4170	2009-06-28	10:50	B, 70 cm	Oblique	104	50	R14, R16
	KN195-10	104	MN-9	59.8997	172.7818	2009-07-02	11:30	B, 70 cm	Oblique	78	53	R14, R16, R18, R20, R22
	KN195-10	112	MN-17	59.9012	177.5877	2009-07-03	11:45	B, 70 cm	Oblique	143	53	I14, I22
	KN195-10	116	SB-12	60.1023	178.6063	2009-07-04	11:08	B, 70 cm	Oblique	154	50	L22, L24
	KN195-10	122	XB2-12	59.5603	175.1998	2009-07-05	12:00	B, 70 cm	Oblique	173	53	I14
	KN195-10	147	SL-16	62.1922	175.9577	2009-07-08	10:25	B, 70 cm	Oblique	95	60	R14
	KN195-10	177	70M-29	58.6162	170.2908	2009-07-10	10:55	B, 70 cm	Oblique	76	50	R14, R16
Spring, 2010	TN249	13	Z4	57.6767	170.5844	2010-05-14	10:40	RN, 1m	Oblique	77	32	R26
	TN249	24	Z15	58.3792	171.7526	2010-05-15	9:15	RN, 1m	Oblique	99	32	R18
	TN249	31	ZC4	58.1597	173.2525	2010-05-16	10:27	RN, 1 m	Oblique	114	43	I12, R24
	TN249	53	EV2	59.7818	178.6930	2010-05-20	10:45	RN, 1 m	Oblique	286	71	I14, I16, I22, L12, L14, L18
	TN249	66	NZ4.5	59.0725	170.1838	2010-05-23	10:20	RN, 1 m	Oblique	68	46	R10, R12
	TN249	71	HBR1	56.9218	167.3255	2010-05-25	10:40	RN, 1 m	Oblique	78	50	R14, R16
	TN249	156	SL12	62.1880	175.1469	2010-06-05	10:05	B, 60 cm	Oblique	79	64	R18, R20, R22, R26
	TN249	163	MN19	59.8933	178.8984	2010-06-07	10:45	B, 60 cm	Oblique	659	60	L16
	TN249	168	EV7	59.6867	177.2954	2010-06-08	11:38	B, 60 cm	Oblique	185	85	I18, I22
Summer, 2010	TN250	7	UAP6	55.3120	164.3856	2010-06-18	11:29	B, 60 cm	Oblique	100	57	R20, R26
	TN250	19	CN6	56.8921	164.0591	2010-06-20	10:46	B, 60 cm	Oblique	72	48	R18
	TN250	24	CN16	55.5540	167.6811	2010-06-21	9:30	B, 60 cm	Vertical	140	60	L12, L14, L18, L20, L22
	TN250	27	CN18	55.2962	168.4106	2010-06-22	10:44	B, 60 cm	Vertical	1652	80	I16, I18
	TN250	33	CNN5	57.0502	167.4498	2010-06-23	11:21	B, 60 cm	Oblique	70	50	R14, R16, R20, R22,R24
	TN250	57	SB4	56.6294	172.2696	2010-06-27	11:23	B, 60 cm	Oblique	148	46	I18
	TN250	96	MN15	59.9014	176.4050	2010-07-03	11:34	MOC	Oblique	138	100	I16,I18, I20
	TN250	118	ML7	61.5243	172.6189	2010-07-06	6:48	MOC	Oblique	66	50	I12
	TN250	170	70m36	59.6014	170.9157	2010-07-10	20:55	MOC	Oblique	71	55	I16
	TN250	178	70m28	58.4460	170.1837	2010-07-11	10:13	B, 60 cm	Oblique	74	57	R12

[a] Wire out was listed as depth for any vertical drop.

[b] Krill of the same species and size class from the same season and year were occasionally composited from different catches to provide enough sample for multiple types of analysis. Species are abbreviated using the first letter of the species name, i.e. I=*T. inermis*. Size ranges are represented using the first number in the particular increment, i.e. 8=8–10 mm; 18=18–20 mm, etc.

Appendix 2: Individual results for all euphausiids used to determine major physical and biochemical properties of collected animals. TL=total length; WW=wet weight; DW=dry weight; AFDW=ash free dry weight

Season Errors	Species	TL range (mm)	Avg TL (mm)	No. krill	Average WW (mg) (± 0.02 mg)	Average DW (mg) (± 0.02 mg)	% Water	g C/g DW (± 1.3E − 3 g/g)	g N/g DW (± 8.E − 5 g/g)	%C:%N	(± 5–7%) (Cal/g AFDW)	Cal/ind	% Ash	Lipid (mg/g DW)
Summer, 2008	T. inermis	12–14	13.4	1	32.3	10.1	69	0.521	0.076	6.9				
		14–16	14.0	1	38.1	10.5	72	0.580	0.060	9.7				
		14–16	15.0	1	43.8	12.4	72	0.564	0.062	9.1				
		16–18	16.1	1	60.1	19.6	67	0.585	0.065	9.0				
		16–18	16.8	1	61.5	18.3	70	0.578	0.063	9.2				
		16–18	17.8	1	74.7	25.3	66	0.611	0.055	11.0				
		18–20	18.7	1	86.0	28.5	67	0.628	0.054	11.6				
		20–22	20.3	1	107.0	34.7	68	0.571	0.068	8.3				
		20–22	21.5	1	117.2	37.6	68	0.574	0.064	8.9				
	T. raschii	12–14	13.5	1	27.8	7.3	74	0.483	0.081	6.0				
		14–16	14.7	1	32.6	8.9	73	0.506	0.081	6.3				
		14–16	15.5	1	36.2	10.1	72	0.483	0.062	7.8				
		18–20	18.3	1	65.9	17.3	74	0.520	0.084	6.2				
		18–20	18.8	1	69.9	16.7	76	0.471	0.104	4.5				
		20–22	20.4	1	89.3	21.5	76	0.473	0.095	5.0				
		20–22	21.3	1	116.1	30.8	73	0.512	0.085	6.0				
		20–22	21.9	1	147.1	34.7	76	0.481	0.098	4.9				
		22–24	22.9	1	123.3	32.7	73	0.512	0.087	5.9				
		22–24	23.5	1	139.4	26.3	81	0.417	0.115	3.6				
Spring, 2009	T. inermis	08–10	9.0	26	7.1	1.1	84	0.441	0.117	3.8	4353	4.4	11	N/A
		10–12	11.0	43	8.6	1.5	83	0.438	0.115	3.8	6558	6.6	31	304 ± 47
		12–14	13.0	20	16.5	3.1	81	0.444	0.119	3.7	6652	14.9	27	260 ± 37
		18–20	18.8	9	60.6	11.6	81	0.455	0.120	3.8	5102	53.0	10	224 ± 29
		20–22	20.9	5	98.8	16.7	83	0.454	0.120	3.8	5493	84.1	11	250 ± 32
	T. raschii	08–10	9.4	23	7.1	0.9	88	0.408	0.112	3.6	5561	3.4	28	N/A
		10–12	11.1	42	8.4	1.3	84	0.401	0.111	3.6	5955	5.6	30	285 ± 38
		12–14	13.0	37	15.9	2.5	84	0.416	0.114	3.6	5613	10.9	24	294 ± 53
		18–20	18.9	20	55.9	8.5	85	0.420	0.118	3.6	5488	36.5	22	297 ± 36
		20–22	20.9	8	68.1	12.4	82	0.416	0.117	3.6	6301	52.4	33	223 ± 14
	T. longipes	08–10	9.8	1	6.4	1.5	77							
		10–12	11.3	9	10.6	2.4	78							
Summer, 2009	T. inermis	14–16	15.6	11	45.4	13.2	71	0.568	0.073	7.8	7028	85.8	7	536 ± 83
		16–18	17.3	12	54.7	16.2	70	0.558	0.077	7.2	7594	106.7	13	437 ± 52
		18–20	18.6	19	78.3	24.7	68	0.612	0.058	10.6	7678	166.1	13	399 ± 27
		20–22	21.2	12	102.1	29.3	71	0.572	0.071	8.0	6920	188.0	7	359 ± 53
		22–24	23.1	12	141.5	41.9	70	0.610	0.067	9.1	7433	269.6	13	350 ± 22
	T. raschii	14–16	14.6	37	26.5	6.1	77	0.511	0.087	5.9	6409	34.3	12	280 ± 22
		16–18	17.1	21	43.4	10.6	76	0.535	0.080	6.7	6835	63.0	13	313 ± 38
		18–20	19.2	8	65.8	14.6	78	0.499	0.096	5.2	5990	78.6	10	300 ± 27
		20–22	21.0	14	83.1	15.7	81	0.494	0.101	4.9	5909	84.7	9	142 ± 13
		22–24	23.1	16	105.0	21.6	79	0.465	0.111	4.2	5537	108.9	9	225 ± 45
	T. longipes	12–14	14.2	1	35.0	8.9	75							
		14–16	15.4	21	38.3	10.1	74							
		16–18	17.1	6	49.2	12.9	74							
		18–20	19.3	7	77.7	20.2	74							
		20–22	21.6	4	105.6	25.4	76							
		22–24	22.7	5	127.8	32.4	75							
		24–26	25.3	3	185.3	54.4	71							

Season Errors	Species	TL range (mm)	Avg TL (mm)	No. krill	Average WW (mg) (± 0.02 mg)	Average DW (mg) (± 0.02 mg)	% Water (± 1.3E−3 g/g)	g C/g DW	g N/g DW (± 8.E−5 g/g)	%C:%N	(± 5–7%) (Cal/g AFDW)	Cal/ind	% Ash	Lipid (mg/g DW)
Spring, 2010	*T. raschii*	10–12	11.3	50	10.7	2.0	81							
		12–14	12.7	50	15.3	3.1	80							
		14–16	15.2	20	28.7	6.5	77							
		16–18	17.0	20	42.3	9.8	77							
		18–20	19.2	11	63.2	13.8	78							
		20–22	21.2	12	83.1	18.6	78							
		22–24	23.7	5	120.9	26.1	78							
		24–26	25.2	4	156.5	34.0	78							
		26–28	27.0	2	179.4	40.4	77							
	T. inermis	12–14	13.9	2	27.5	7.0	74							
		14–16	15.6	4	42.8	11.7	73							
		16–18	17.3	4	58.6	15.1	74							
		18–20	18.7	10	83.8	26.5	68							
		22–24	23.2	3	151.7	45.2	70							
	T. longipes	12–14	12.9	7	19.8	4.1	79	0.430	0.108	4.0				314 ± 69
		14–16	14.9	6	31.5	6.8	78	0.429	0.106	4.0				347 ± 27
		16–18	16.8	7	54.9	11.2	80	0.478	0.094	5.1				398 ± 37
		18–20	19.7	2	95.7	16.7	83	0.423	0.103	4.1				407 ± 38
Summer, 2010	*T. raschii*	12–14	13.4	7	17.6	3.4	81							
		14–16	15.2	20	30.3	7.5	75							
		16–18	16.8	20	43.7	11.3	74							
		18–20	19.4	15	79.8	20.4	74							
		20–22	21.1	24	88.5	23.6	73							
		22–24	23.0	2	108.6	27.9	74							
		24–26	24.7	2	127.3	32.4	75							
		26–28	27.6	2	212.5	46.3	78							
	T. inermis	12–14	12.4	1	16.1	3.9	76							
		16–18	17.1	9	55.0	16.4	70							
		18–20	18.9	17	76.6	25.5	67							
		20–22	21.1	4	105.8	35.0	67							
	T. longipes	12–14	13.8	4	34.1	6.6	81	0.477	0.088	5.4				395 ± 49
		14–16	15.1	11	42.2	9.8	77	0.526	0.076	6.9				445 ± 69
		18–20	19.1	8	85.9	22.0	74	0.522	0.081	6.5				410 ± 48
		20–22	21.2	10	112.6	37.3	67	0.547	0.065	8.4				369 ± 26
		22–24	22.7	3	140.9	40.4	71	0.553	0.072	7.7				506 ± 11