Comparison of condition metrics and lipid content between *Euphausia pacifica* and *Thysanoessa spinifera* in the northern California Current, USA

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All authors have agreed to be listed and have approved of the author order and the final submitted manuscript.

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Abstract

Krill are a key component of pelagic food webs where they are vital to the transfer of energy from phytoplankton to higher trophic levels. Krill have a high lipid content compared to other zooplankton and form dense aggregations, making them an important prey source for higher trophic level fish, seabirds, and marine mammals. The two dominant euphausiid species in the northern California Current (NCC) are *Euphausia pacifica* and *Thysanoessa spinifera*. *E. pacifica* is the most abundant species of euphausiid in the NCC, but *T. spinifera* has a higher potential energetic content due to its larger body size and higher lipid density. Most studies have inferred differences in lipid content and body condition between the two species, but few studies have quantified these differences in the NCC. Here, we report on the body condition, carbon and nitrogen content, as well as lipid and fatty acid composition of these two krill species, and the extent to which these metrics vary across season, year, and reproductive status. Body condition, elemental composition and total lipids strongly differed between the species. *T. spinifera* had higher length-weight, Fulton's K, hepato-somatic index, carbon to nitrogen ratio, total lipid per wet weight, and storage lipid compared to *E. pacifica*, indicating that *T. spinifera* has a higher energetic value for predators. However, there were strong seasonal differences in the energetics of *T. spinifera*. Carbon and lipids were highest in non-reproductive *T. spinifera* from August through October. Although there were strong ontogenetic and inter-specific differences, the lipid and fatty acid compositions of both species followed a seasonal progression characterized by low lipids during the pre-upwelling period, an increase in lipids, triacylglycerols and diatom markers during upwelling, and increased proportions of dinoflagellate and bacterial diet markers during the fall post-upwelling period.

Keywords: krill; *Euphausia pacifica*; *Thysanoessa spinifera;* Northern California Current; upwelling; lipid; fatty acid; body condition; hepato-somatic index; carbon; nitrogen

Highlights:

- The lipid profiles of *E. pacifica* and *T. spinifera* followed the upwelling cycle
- *T. spinifera* had higher C:N, total lipids, and proportions of storage lipids
- The highest C:N and lipid occurred in *T. spinifera* from August to October
- Increased lipid storage in *T. spinifera* was associated with diatom markers
- *T. spinifera* are likely amassing neutral storage lipids in the fall for overwintering

1. Introduction

The northern California Current (NCC) is located in an eastern boundary upwelling region known for its enhanced productivity and high biomass of ecologically and commercially important species. Krill are a key component of this pelagic food web, where they transfer energy from phytoplankton to higher trophic levels. Krill have a relatively high biomass and elevated lipid content compared to other zooplankton, and they are known to form dense aggregations. These qualities make krill an important prey item for higher trophic level fish, seabirds, and marine mammals.

The two dominant euphausiid species in the NCC are *Euphausia pacifica* and *Thysanoessa spinifera*. *E. pacifica* are broadly distributed throughout the North Pacific, and they are the most abundant euphausiid in the NCC (Brinton, 1976), accounting for over 83% of all euphausiids collected over a 16 year time series off Newport, Oregon (Shaw et al., this issue). *T. spinifera* are concentrated in the eastern Pacific, but their distribution is patchier than *E. pacifica* and they are less abundant, accounting for 15% of all euphausiids collected over a 16-year time series off Newport, Oregon (Shaw et al., this issue). While *E. pacifica* are ubiquitous during both warm and cool ocean conditions, *T. spinifera* are more abundant during cool ocean conditions (Tanasichuk, 1998a, 1998b; Gomez-Gutierrez et al., 2005; Shaw et al., this issue).

Both species spawn during periods of high productivity and both species can reproduce multiple times within a year when environmental conditions are favorable (Feinberg and Peterson, 2003; Pinchuk and Hopcroft, 2006; Feinberg et al., 2010). In the NCC, *E. pacifica* spawn in response to phytoplankton blooms, which occur in association with summer upwelling (Du and Peterson, 2014b). *E. pacifica* have an intense period of spawning during the highest productivity months (May - September), though their eggs have been collected at lower numbers in February during winter phytoplankton bloom conditions. *T. spinifera* are intermittent spawners, even when ocean conditions seem suitable for spawning, and small peaks in egg density have been found from February–May in the NCC with higher sustained egg densities from July– August (Feinberg et al., 2010). Both species become non-reproductive in the fall, and *T. spinifera* may lose their sexual characteristics when they are not actively spawning. There is no evidence that *E. pacifica* or *T. spinifera* spawn during the fall and winter (October - January) (Ross et al., 1982; Feinberg and Peterson, 2003; Dorman et al., 2005; Feinberg et al., 2010). Although these species are omnivorous, the majority of their diet is composed of phytoplankton (Ohman, 1984).

These two species differ in their cross-shelf and alongshore distributions. *E. pacifica* are generally found offshore of or along the shelf break and at the heads of submarine canyons where they form dense aggregations (Gomez-Gutierrez et al 2005, Santora et at. 2011, Mackas et al., 1997; Ianson et al., 2011). *T. spinifera* are concentrated closer to shore, mostly inhabiting the continental shelf (Gomez-Gutierrez et al 2005, Tanasichuk, 1998). While krill are also known to aggregate in hotspots along the coast, most information on the alongshore distribution of krill comes from acoustic surveys that generally lack species-specific

distribution information. Acoustic surveys show that krill aggregate in regions with reduced offshore Ekman transport in the lee of upwelling centers where eddies form retentive recirculation features (Santora et al., 2011, 2012; Sydeman et al., this issue).

The spatial segregation of these two species, and the potential for species-specific aggregations in predictable locations, are factors important for higher trophic level predators that rely on krill as a key component of their diet. Krill are important prey for commercially important fish species such as Pacific whiting (Buckley and Livingston, 1997; Tanasichuk, 1999; Emmett and Krutzikowsky, 2008), juvenile salmon (Daly and Brodeur, 2015), and rockfish (Chess et al., 1988), as well as seabirds and marine mammals. Some studies have suggested species and size selective predation relative to spatial and temporal differences in prey availability. During colder ocean conditions, higher proportions of krill (primarily *T. spinifera*) were found in juvenile salmon diets (Daly and Brodeur, 2015). Blue whales are obligate krill feeders and will selectively feed on larger individuals of both species (Croll et al., 1998, 2005). A recent study in the southern California Current found that blue whales were primarily selecting *T. spinifera* even when other euphausiid species were present (Nickels et al., 2018). Together, *E. pacifica* and *T. spinifera* comprised 77% of the diet of Cassin's auklets, however, it is the abundance of *T. spinifera* in the spring that is correlated with the breeding phenology and breeding success of these birds (Ainley, 1990; Ainley et al., 1996; Abraham and Sydeman, 2004, 2006).

Although *E. pacifica* are the most abundant euphausiid in the NCC, *T. spinifera* have a larger body size and appears to store more lipids, leading to vastly different bioenergetics between the two species. Cross-shelf and alongshore differences in the biomass of these two species result in localized hotspots where predators might reliably encounter prey with species-specific differences in lipid content. Most studies have inferred species-specific differences in the lipid content and body condition of different krill species and life history stages, but few studies have quantified krill lipids in the NCC. The first comparison of lipid composition for these two species found that total lipids per dry mass were consistently lower in *E. pacifica* compared to *T. spinifera*, but limited sample sizes precluded strong conclusions among seasons or life history stage (Ju et al., 2009). Here, we report on the body condition, carbon and nitrogen content, and lipid and fatty acid composition of the two dominant krill species in the NCC, and we explore the extent to which these metrics vary with season, year, and reproductive status.

2. Materials and Methods

2.1. Sample collection and processing

Krill were collected using a bongo net with a mouth diameter of 0.6 m and 335-um mesh towed obliquely through the upper 100 m or 30 m of the water column. A closed cod end was used to limit disturbance to the live animals. Tows were sorted for live euphausiids

at sea. Actively swimming animals with no visible damage were gently transferred into coolers of ambient surface seawater for transport back to the laboratory. Individuals were processed as quickly as possible in the laboratory. Each individual was measured (body length; BL), identified to species and developmental stage (juvenile, adult, female, male) using a dissecting microscope, and individuals were frozen in cryovials at -80°C for later analysis. Body length was defined as the length from the curve of the carapace behind the eye to the distal end of the last abdominal segment. Individuals with defining sexual characteristics were classified as female or male regardless of length. Individuals of both species that did not have defining sexual characteristics were classified as adults if their body length was >10 mm, and as juveniles if their body length was ≤10 mm. Body length was converted to total length using published species and stage specific equations for the study region (*E. pacifica*: TL = 1.1954 * BL + 0.6548; *T. spinifera*: TL = 1.2031 * BL + 0.4720; (Shaw et al., 2013).

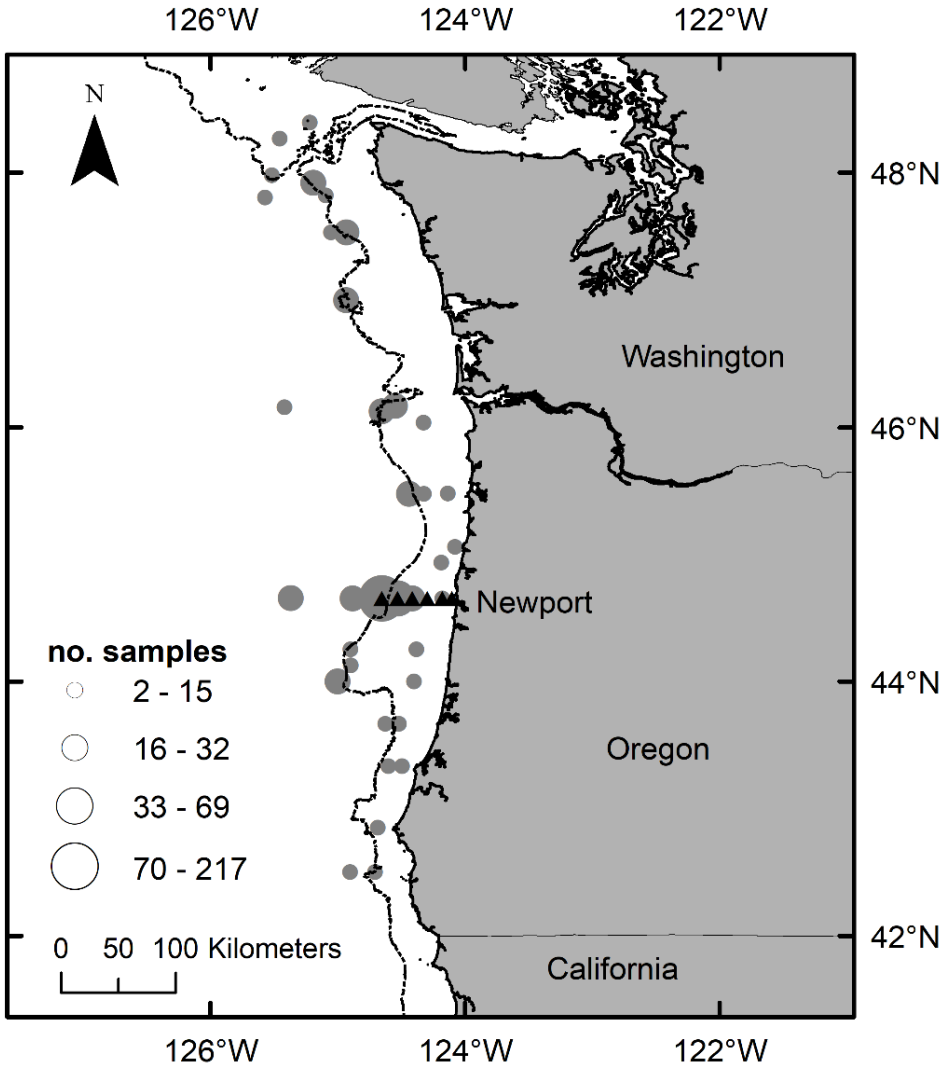

Figure 1. Map of the study area along the west coast of the USA showing the locations where krill were collected for body condition (circles) and lipid and fatty acid analysis (triangles). Individuals for body condition and lipid and fatty acid analysis were collected from 2007 to 2010 and 2010 to 2012, respectively. The size of the circle represents the number of individuals collected for analysis. Some krill were collected outside of the map domain: 29 individuals to the south at 38° 123° and 10 individuals offshore of Newport, OR at 44.6° 128°. Dashed line is the 200 m isobath representing the shelf break.

Table 1. Number of *Euphausia pacifica* and *Thysanoessa spinifera* analyzed for body condition: length-weight, C:N, Fulton's condition (K), hepato-somatic index (HSI) by life history stage. J: juvenile, A: adult, F: female, M: male.

		Euphausia pacifica				*Thysanoessa spinifera*			
Year	Month	J	A	F	M	J	A	F	M
2007	5			5					
	6			1	3				
	7		1	4	3				
	8	2		2					
	9			1	3				
	12								
2008	2		5						
	3							1	1
	4		1	22	15			5	3
	5		1	9	12			3	8
	6								
	7	13	10	42	13		1	14	8
	8			5	5			3	2
	9						1		
	10			4	2		4		
2009	1		5		2				
	2		3	3			2	1	
	3			6	4			6	5
	4			19	21			5	3
	5		1	17	6				
	6			6	5				
	8	3	1	86	62		24	9	15
	9			1	3		5		
	10	1	4	8	5				
2010	2		1	3	4		1	5	2
	6		2	8	8	1		3	
	8	6	5	18	13	1	7	1	5
	9	2	6	5	9	1	5	5	4
	10	4	8	10	5	4	7		
	11	2	4	5	6	1	2		
		33	58	290	209	8	59	61	56

2.2. Body Condition

Krill used to assess body condition were collected from stations located in the northern California Current from 38°N to 48°N during 2007 – 2010 (Figure 1). The total individuals analyzed comprised 590 *E. pacifica* and 184 *T. spinifera* of varying life history stages (Table 1). Although animals were collected over a wide latitudinal range, 64% of these individuals were collected from, or adjacent to, the Newport Hydrographic line (44.6°N) and 4% of the animals came from the most southern transect (38°N). To prepare krill for body condition metrics, krill were rinsed out of cryovials using nanopure water and blotted dry. Body length (BL), carapace length (CL), hepatopancreas length (HL), and hepatopancreas height (HH) were measured using a dissecting microscope; and wet weight (WW) was measured using a Mettler Toledo balance with 0.0001g accuracy.

2.2.1. Length-weight relationship

The condition of individuals is often used as a proxy for the relative health of the population of animals and how it varies ontogenetically or with changing environmental conditions. Length-weight relationships are a common metric to evaluate condition, as it is assumed that a heavier animal of a given length has more energy reserves and is thus in better condition. The most widely used length-weight relationships are from Ross (1982) for *E. pacifica* and Summers (1993) for *T. spinifera*. Here, we update the length-weight relationships for both species using data from the present study, which comprises individuals collected over multiple years and seasons.

2.2.2. C:N samples

Morphometric condition indices are widely used to assess the recent feeding conditions of animals collected in the field. However, animals with similar morphometrics can differ from each other in actual chemical composition due to factors that cannot be readily observed, such as differences in diet and reproductive condition. Carbon and nitrogen measurements are key to understanding individual fitness as a proxy for lipids. Animals to be processed for C:N were dried in a 40GC lab oven at 65°C for 48 hours, and briefly stored on desiccant until weighed. The individual samples were homogenized, and measured subsamples (1-2 g) were analyzed for total carbon and total nitrogen by a laboratory at Oregon State University using a Carlo-Erba NA-1500 Elemental Analyzer (Thermo Fisher Scientific).

2.2.3. Fulton's condition factor (K) and hepato-somatic index (HSI)

Another common morphometric condition index is the Fulton's condition factor (K), which is expressed as the ratio of body mass to the cube length (Nash et al., 2006). There are differences in appearance between *E. pacifica* and *T. spinifera*, where early life history stages of *T. spinifera* may be smaller than *E. pacifica*, but *T. spinifera* will have

visibly broader carapaces. This is similar for adult *T. spinifera* with some individuals having broader carapaces with clearly visible lipid droplets. We used Fulton's condition factor to quantify the condition of individuals as they relate to other condition metrics and to total lipid and fatty acid composition.

The hepato-somatic index (HSI) is a direct measure of body condition used to evaluate recent feeding conditions experienced by an individual (Shin, 2000; Ambriz-Arreola et al., 2012). The HSI differs from the Fulton's condition factor in that it accounts for the amount of food within the digestive gland. We assumed that a lower HSI indicates unfavorable feeding conditions and a higher HSI indicates relatively favorable feeding conditions (Shin, 2000; Nicol et al., 2004, O'Brien et al., 2011). This index is helpful for comparing recent feeding conditions of these two euphausiid species that have different cross-shelf distributions and thus likely encounter varying food resources. The HSI is defined as the ratio of the area of the hepatopancreas to the carapace length (Ambriz-Arreola et al., 2012).

$$Area = \pi \, x \frac{HL}{2} x \frac{HH}{2}$$

$$HSI = \frac{Area}{CL}$$

Where *HL* is the length of the hepatopancreas at its longest point, *HH* is the hepatopancreas height, and *CL* is the carapace length.

2.2.4. Body condition data analysis

Analysis of Covariance (ANCOVA) was used to determine whether length-weight differed by species, year, and life history stage and multiple comparison tests were conducted using Student's t-test. Juvenile *T. spinifera* were not included in this analysis due to low sample sizes. Length and weight were Log10 transformed prior to analysis. Analysis of variance (ANOVA) was used to test for differences in condition factors (C:N, Fulton's K, HSI) between species and among years and life history stages. Juveniles of both species were excluded from this analysis because of low sample sizes. Multiple comparison tests were conducted using Student's t-test. Not all life history stages were collected during each month, precluding statistical analysis of seasonal changes in body condition by life history stage, but patterns are discussed qualitatively.

Table 2. Number of *Euphausia pacifica* and *Thysanoessa spinifera* analyzed for lipids and fatty acids by life history stage. J: juvenile, A: adult, F: female, M: male.

		Euphausia pacifica				*Thysanoessa spinifera*			
Year	Month	J	A	F	M	J	A	F	M
2010	2			5	4		1	2	1
	4		4	5	3				
	9		4					6	6
	10		6	1	1		11		
	11		1	1	1		3		
2011	5		1	2	18				
	7							3	
2012	3			1	2				
	4	1	1	1					
	5	1	1	2	1		1	8	
	6		1	1	1	3	1	3	2
	8	2		2	2		17	2	4
	9	4	1	1	1				
	10	2	1	3	5		8		
	11	1	2	3	3				
2014	7							4	
		11	23	28	42	3	42	28	13

184

185 2.3. Lipids and fatty acids
186
187 Zooplankton have variable life history strategies that are often driven by seasonal
188 variability in food resources (Hagen and Auel, 2001). Previous studies have found that
189 neutral lipid storage in the form of wax esters and triacylglycerols (TAG) was a sensitive
190 indicator of seasonal energy storage in marine zooplankton (Hagen and Kattner 1998;
191 Kattner et al. 2007; Parrish 2013). Krill also contain high proportions of polar phospholipids
192 (PL) which are generally considered as membrane structural lipids but can also be used for
193 energy (Ju et al. 2006).
194 Fatty acid (FA) biomarkers have also been used as tracers of energetic flow from
195 phytoplankton to higher trophic levels based on the premise that different primary producers
196 form unique combinations of fatty acids that are somewhat conservatively transferred up the
197 food web (Dalsgaard et al. 2003; Kelly and Scheibling 2012). Here, we used six different
198 fatty acid indicators that have previously been identified as dietary indicators in
199 zooplankton: 1) bacterial contribution as the sum of odd and branched chain fatty acids
200 (Kaneda, 1991) 1991); 2) diatom contribution as the ratio of 16:1n-7/16:0 (Budge and
201 Parrish, 1998; Reuss and Poulsen, 2002; Viso and Marty, 1993); 3) a diatom to flagellate
202 indicator in PL as 20:5n-3/22:6n-3 (Budge and Parrish 1998; Dalsgaard et al. 2003); 4) a
203 diatom to flagellate indicator in TAG as 16:1n-7/18:4n-3 (Dalsgaard et al. 2003; Schmidt et
204 al. 2014); 5) a carnivory indicator as the ratio of 18:1n-9/18:1n-7 (El-Sabaawi et al., 2009;
205 Ko et al., 2016); and 6) a copepod indicator as the sum of C_{20+22} monounsaturated fatty acids
206 MUFA (Dalsgaard et al. 2003; Miller et al. 2017).
207 Krill collected from 2010 – 2012 and four additional female *T. spinifera* collected in
208 2014 (Table 2) were analyzed for lipid and fatty acid composition. Krill were mainly
209 collected from the Newport Hydrographic line (44.6°N), however 3 female *T. spinifera*, 2
210 female and 2 male *E. pacifica* were collected off northern California in 2011 (41°N; Figure
211 1). A total of 104 *E. pacifica* and 86 *T. spinifera* were processed for lipid and fatty acid
212 analysis (Table 2).
213 Krill were removed from the -80 ºC freezer, quickly measured for length and weight,
214 rinsed with distilled water, blotted dry, and then placed in 2 ml of chloroform under a layer
215 of nitrogen. Samples were stored at -20 ºC and were extracted and analyzed within 1 year of
216 collection.
217 Krill lipids were extracted in chloroform/methanol using a modified Folch procedure
218 (Folch et al., 1957; Parrish, 1987). Lipid classes (steryl/wax esters, TAG, free fatty acids,
219 sterols, alcohols, acetone mobile polar lipids, and PL) were analyzed using thin layer
220 chromatography with flame ionization detection (TLC/FID) with a MARK V Iatroscan
221 (Iatron Laboratories, Tokyo, Japan) as described by Parrish (1987). Briefly, krill extracts
222 were spotted on silica gel coated Chromarods and a three-stage development system was
223 used to separate lipid classes. The first separations consisted of 25- and 20-min developments
224 in 98.95:1:0.05 hexane:diethyl ether:formic acid. The second separation consisted of a 40-
225 min development in 79:20:1 hexane:diethyl ether:formic acid. The last separation consisted
226 of 15-min developments in 100% acetone followed by 10-min developments in 5:4:1
227 chloroform:methanol:water. Peak Simple software (ver. 3.67, SRI Inc) was used to integrate
228 lipid peaks and the signal detected in millivolts was quantified using lipid standards (Sigma,
229 St. Louis, MO, USA).

Total lipids extracts were transesterified with anhydrous 14% boron trifluoride (BF_3) in methanol and heated to 85°C for 90 min to form fatty acid methyl esters (FAME) (Budge and Parrish, 1998; Morrison and Smith, 1964) FAMEs were analyzed on an HP 6890 gas chromatograph (GC) with flame ionization detection (FID) equipped with a 7683 autosampler and a ZB wax+ GC column (Phenomenex, USA). The column was 30 mm long, with an internal diameter of 0.32 mm and a 0.25 µm film. The oven temperature began at 65°C for 0.5 min and then the temperature was increased to 195°C (40°C min^{-1}), held for 15 more min, then increased again (2°C min^{-1}) to a final temperature of 220°C. Final temperature was held for 3.25 min. The carrier gas was hydrogen flowing at 2 ml min^{-1}. Injector temperature started at 150°C and increased (200°C min^{-1}) to a final temperature of 250°C. The detector temperature was constant at 260°C. Peaks were identified using retention times based upon standards purchased from Supelco (37 component FAME, BAME, PUFA 1, PUFA 3). Chromatograms were integrated using Galaxie Chromatography Data System (Ver. 1.9.3.2, Varian).

2.4. Statistical analyses of krill lipid and fatty acid data

Individual fatty acids >1 % in all samples as well as the percentage of bacterial fatty acids (∑odd and branched chains), copepod indicators ($\sum C_{20} + C_{22}$ MUFA), % TAG, % PL and total lipid density per wet weight (WW, µg mg^{-1}) were included in multivariate analyses using PRIMER *v7* (Primer-E Ltd). TAG and PL accounted for the major acyl lipid classes in krill (Table 3). Individual krill were too small to yield a large enough sample for analysis of fatty acid lipid classes, but inclusion of percentage TAG (neutral lipid storage) and PL (membrane structures) allowed us to determine the fatty acids that were associated with trophic accumulation and neutral lipid energy storage, versus those that were associated with membranes (Copeman and Parrish, 2003; Copeman et al., 2018).

Differences in lipid-based condition metrics (total lipid, TAG) and summary fatty acid parameters (diatom indicator, carnivory indicator, copepod indicator) were tested between species and among developmental stages using a 2-way ANOVA followed by Student's t multiple comparison tests. Juveniles were excluded from the analysis due to low sample sizes.

Non-metric multidimensional scaling (nMDS) explored differences in the fatty acid/lipid class composition of krill by species, ontogenetic stage, and oceanographic condition. Data were square-root transformed prior to analyses and nMDS was performed on a Bray-Curtis dissimilarity matrix between individual krill. nMDS plots were labeled by species, life history stage, and oceanographic condition to visually assess separation among parameters. Oceanographic condition was classified as pre-upwelling (January - April), upwelling (May - September), post-upwelling (October - December) (Huyer, 1977). Differences in lipid and fatty acid composition between species, ontogenetic stage, and upwelling condition were tested using a permutational multivariate ANOVA (perMANOVA) in PRIMER v7. The perMANOVA test uses distance matrices to partition distances among sources of variation and fits linear models. Significance tests were conducted using F-tests based on sequential

sums of squares from permutations of the data.

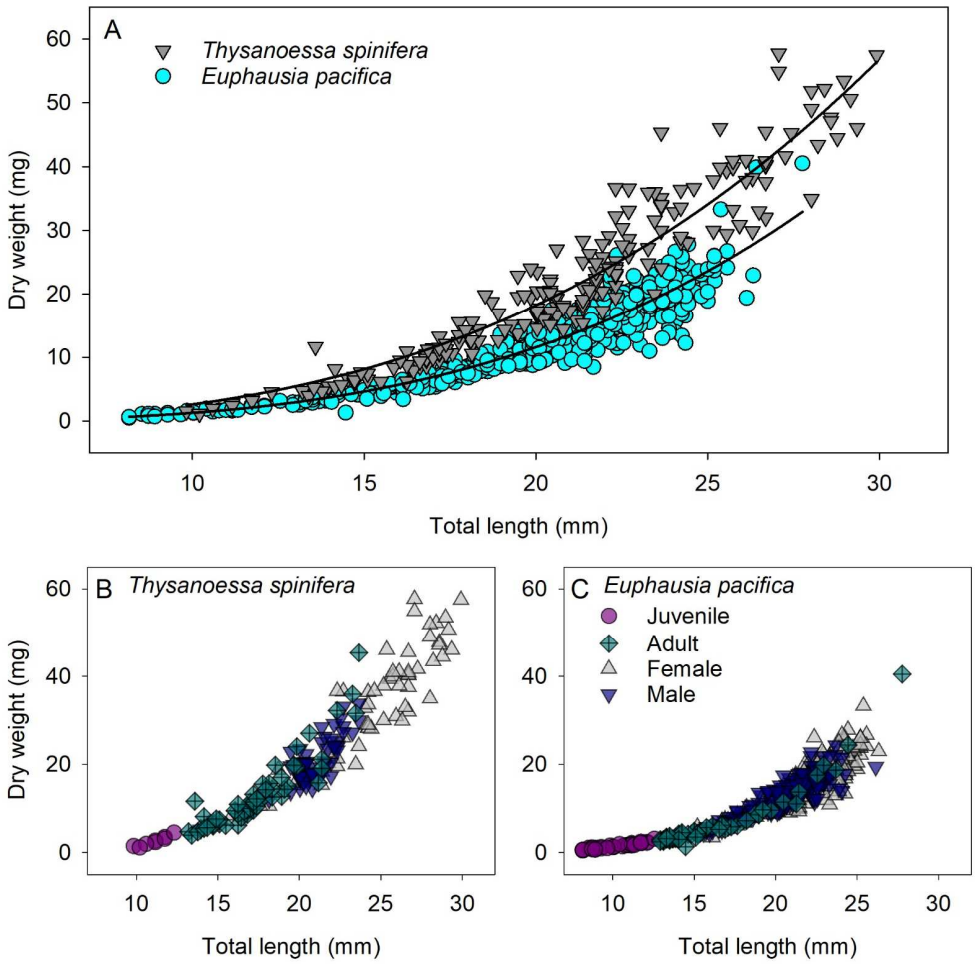

Figure 2. Total length (TL) to dry weight relationship for (A) all *E. pacifica* and *T. spinifera* and separated by species and life history stage (B,C).

3. Results

3.1. Body Condition

3.1.1. Length-weight relationship

The relationships between dry weight (DW) and total length (TL) were determined using log-transformed linear regressions. Results from the present study found that both species followed allometric growth curves similar to previously published relationships in Ross (1982) for *E. pacifica* and Summers (1993) for *T. spinifera* (Figure 2A). Equations are based on a TL range of 8.2–27.8 mm for *E. pacifica* and 9.8–29.9 mm for *T. spinifera*:

285
286 $DW = 0.0008 * TL^{3.19}$ (n = 633; $R^2 = 0.88$) for *E. pacifica*,
287 $DW = 0.004 * TL^{2.81}$ (n = 201; $R^2 = 90$) for *T. spinifera*.
288
289 There were no significant differences in the slopes of the length-weight relationship
290 between *E. pacifica* and *T. spinifera* ($p = 0.20$) however the Y intercepts were
291 significantly different ($p < 0.001$) suggesting that, at a given length, *T. spinifera* have a
292 significantly larger mass than *E. pacifica* (Figure 2A). There were also no differences in
293 the slope or Y intercept for either species among years. The slopes of the length-weight
294 regression did not differ with life history stage for *E. pacifica* ($p = 0.73$), however there
295 were significant differences in the Y intercept among life history stages ($p < 0.001$) with
296 juvenile and male *E. pacifica* having significantly higher mass per given length compared
297 to adult and female *E. pacifica* (Figure 2C). Similarly, the slopes of the length-weight
298 regression did not differ with life history stage for *T. spinifera* ($p = 0.09$), however there
299 were significant differences in the Y intercept among the life history stages ($p = 0.02$)
300 with adult and male *T. spinifera* having significantly higher mass per given length
301 compared to female *T. spinifera* (Figure 2B). The wet weight to dry weight relationship
302 was strongly significant for both species (*E. pacifica*; $R^2 = 0.91$; *T. spinifera* $R^2 = 0.93$)
303 indicating that rinse water was effectively removed from the animals prior to analysis.
304

3.1.2. C:N samples

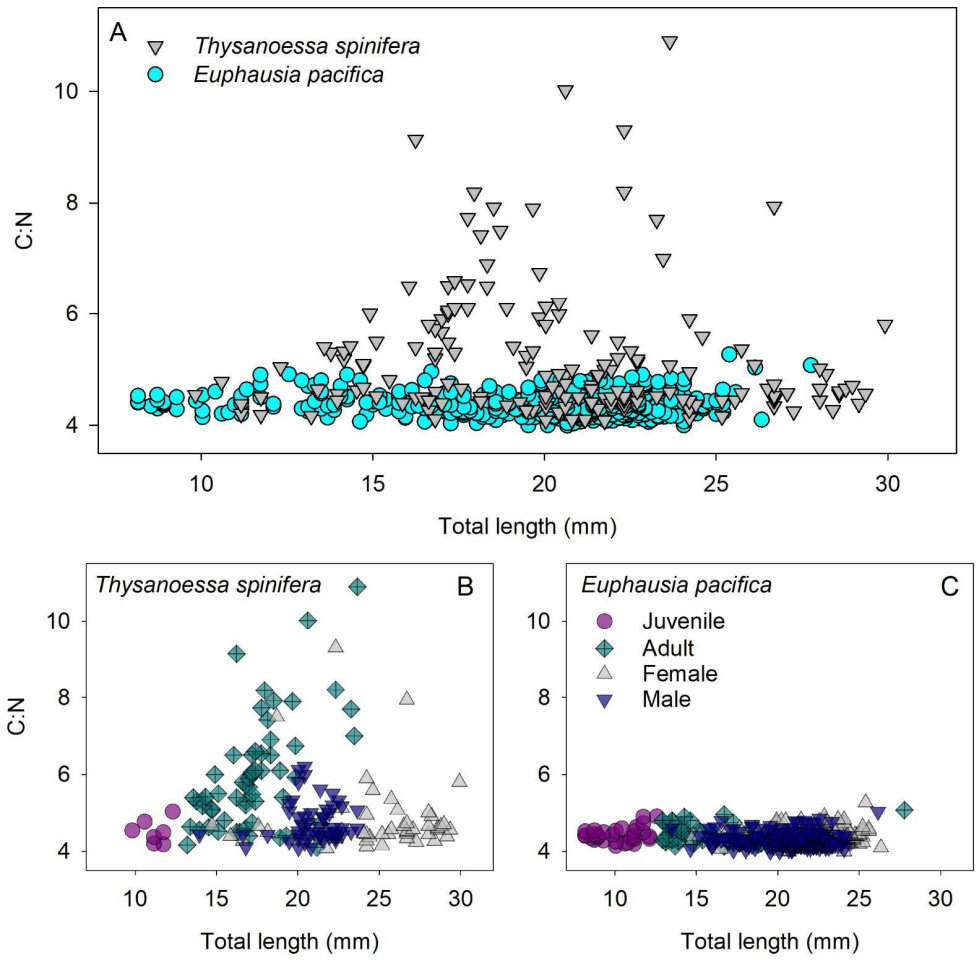

Figure 3. Carbon to nitrogen (C:N) to total length for (A) all *E. pacifica* and *T. spinifera* and separated by species and life history stage (B, C).

There were strong differences in C:N by length and life history stage between the two species. The C:N ratio of *E. pacifica* showed little variation with total length or life history stage (Figure 3A,C). However, C:N increased dramatically for some *T. spinifera* individuals in the 15-25 mm TL size range, mainly adults and a few females (Figure 3A,B). There were no significant differences in *E. pacifica* C:N among years by life history stage (life history * year interaction; $p = 0.97$) and there were no significant differences among years (year effect; $p = 0.69$). C:N in adult *T. spinifera* was significantly higher in 2008 compared to other years (life history * year interaction; $p < 0.001$) yet the overall year effect was not significant ($p = 0.08$).

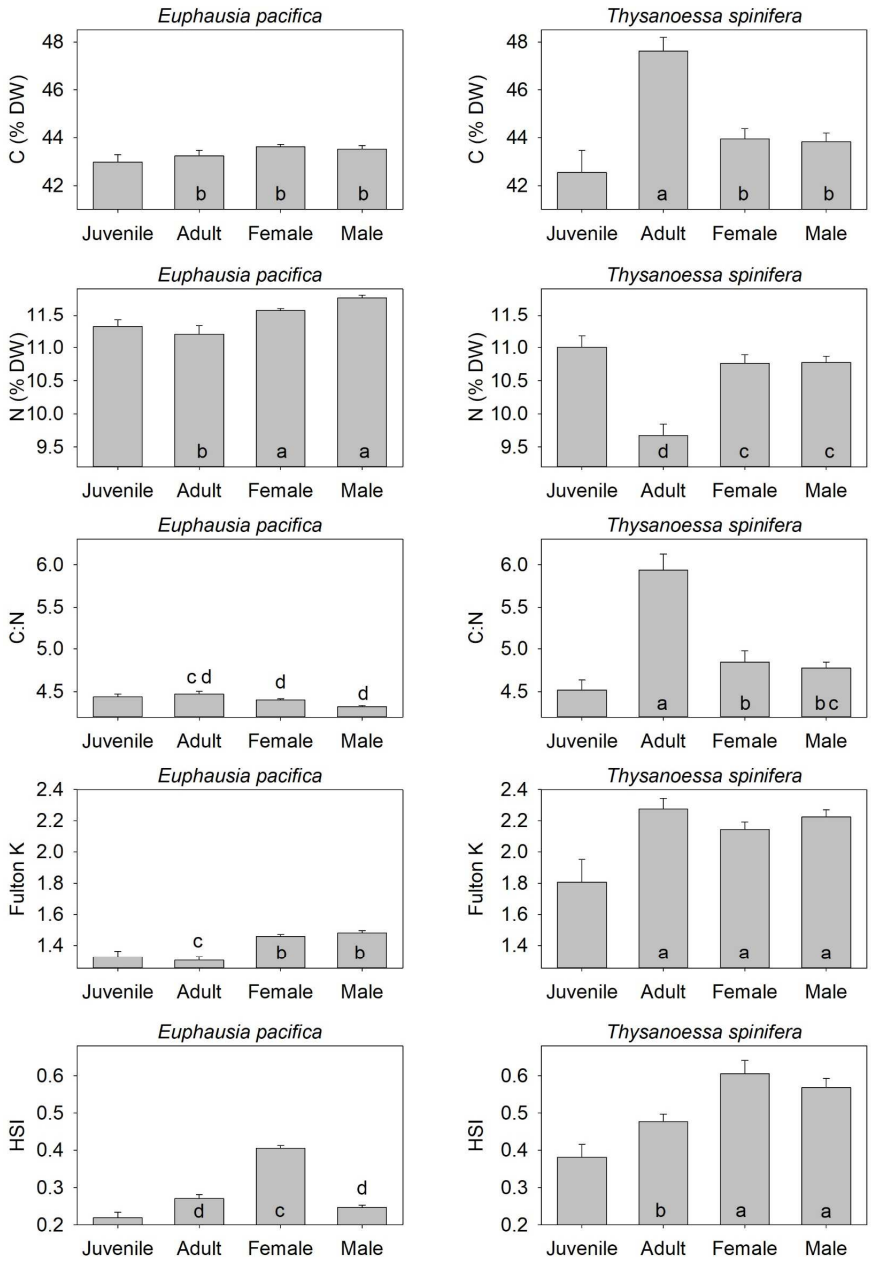

Figure 4. Average condition metrics (±1 SE) for *E. pacifica* and *T. spinifera* by life history. Percent carbon, percent nitrogen, carbon to nitrogen ratio (C:N), Fulton's condition factor (K), hepato-somatic index (HSI). Letters denote statistical significance (alpha <0.05): life history stages with different letters are statistically different and life history stages with the same letter(s) are not statistically different. Low sample sizes precluded statistical analysis of juveniles.

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There were strong differences in C:N between species and among life history stages (Figure 4). The C:N ratio was higher in *T. spinifera* compared to *E. pacifica* with the highest C:N in adult *T. spinifera* followed by females and males. These high C:N ratios were largely driven by the high proportion of carbon in *T. spinifera* adults compared to the other life history stages. There were no significant differences in C:N among *E. pacifica* life history stages.

Confounding effects of all life history stages not being collected during each month precluded statistical analysis of seasonal changes, yet there are evident patterns. C:N ratios and total lipid remained fairly stable throughout the year for *E. pacifica* while *T. spinifera* showed a strong seasonal signal in C:N ratios and total lipid, with C:N remaining quite stable from February - July and then increasing substantially in August, peaking in October, then dropping in November back to levels similar to July (Figure 5). This increase in C:N and total lipid coincided with the time period when most *T. spinifera* adults were collected for analysis. During these months (August - November), C:N was highest in the non-reproductive adult life history stage (6.01 ±0.20; n = 55) compared to females (5.45 ±0.34; n = 18), males (5.04 ±0.12; n = 26), and juveniles (4.52 ±0.12; n = 7) during those same months. This suggests that the adult life history stage is concentrating carbon and lipids during this time period, however we cannot disentangle seasonality from life history stage as adults were mainly collected in the fall.

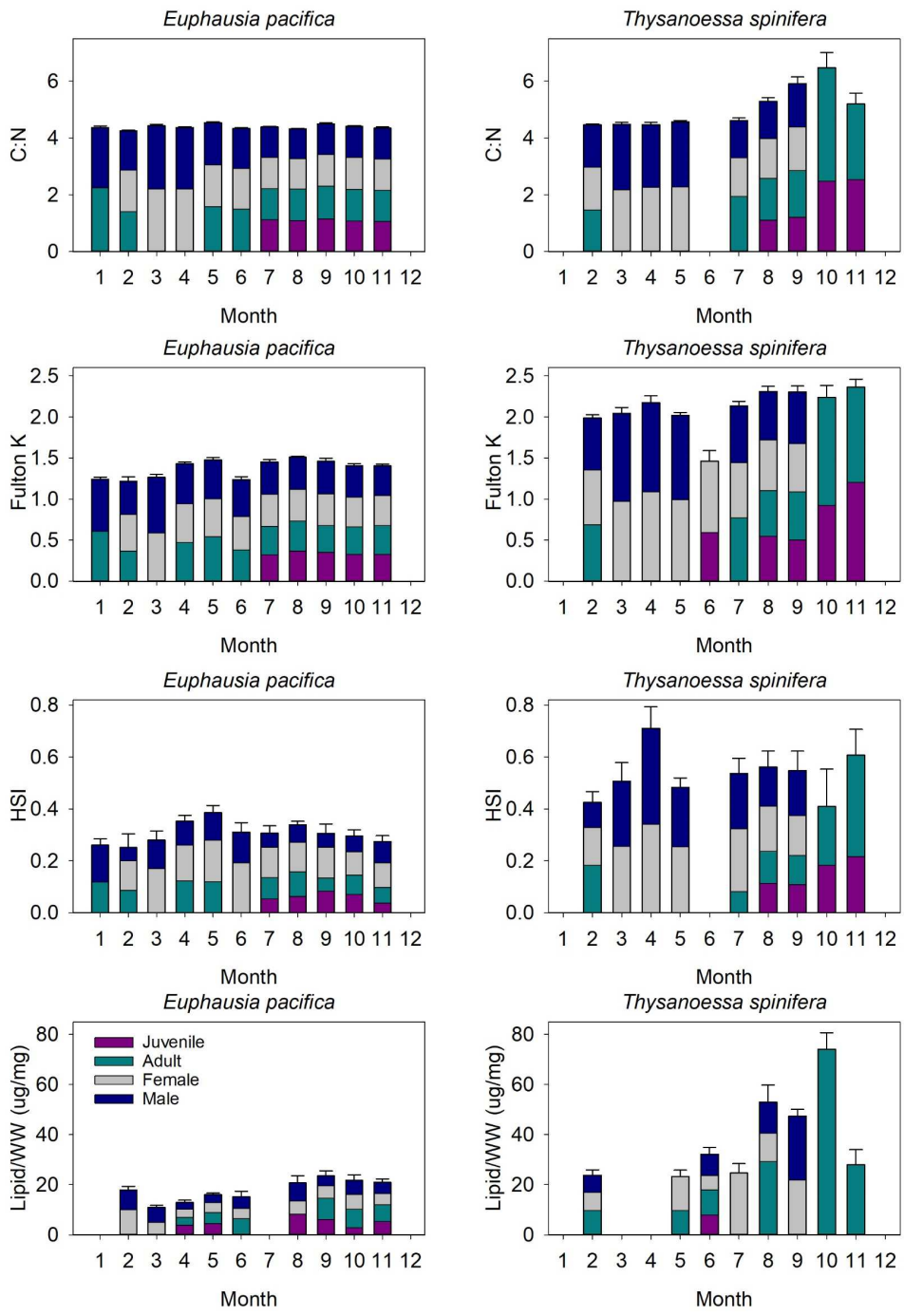

Figure 5. Average condition metrics and total lipid (±1 SE) for *E. pacifica* and *T. spinifera* by month: carbon to nitrogen ratio, Fulton's condition factor (K), hepato-somatic index (HSI), and total lipid per wet weight (µg/mg). Shading represents the proportion of the mean represented by each life history stage.

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3.1.3. Fulton's condition factor (K) and hepato-somatic index (HSI)

Fulton's condition factor (K) and HSI are species-specific condition factors based on morphometrics. As expected, these condition metrics differed significantly between species, with some differences among life history stages (Figure 4). Fulton's K and HSI were both significantly higher across all stages of *T. spinifera* compared to *E. pacifica.* Fulton's K was similar across all stages of *T. spinifera* but female and male *E. pacifica* had higher Fulton's K compared to adults ($p<0.001$). The HSI in the adult life history stage of *T. spinifera* was lower than the HSI in females and males while female *E. pacifica* had a significantly higher HSI compared to adults and males (Figure 4).

There were no significant differences in *E. pacifica* Fulton's K or HSI as a function of year or life history stage (year effect; $p = 0.50$ and 0.69 respectively) or as an interactive effect of years by life history stage (life history * year interaction; $p = 0.44$ and 0.98 respectively). There were also no significant differences in *T. spinifera* HSI among years by life history stage (life history * year interaction; $p = 0.21$) and there were no significant differences among years (year effect; $p = 0.63$), however Fulton's K in adults was significantly higher in 2008 compared to other years (life history * year interaction; $p = 0.01$), yet the overall year effect was not significant ($p = 0.56$).

Similar seasonal patterns in Fulton's K occurred for both species with a distinct decrease in Fulton's K in June (Figure 5). Very few *T. spinifera* were collected for analysis in June (1 juvenile and 3 females) during this study, so this decrease should be interpreted with caution for this species.

The hepato-somatic index (HSI) followed a clear seasonal trend for *E. pacifica* with HSI steadily increasing at the beginning of the year, peaking in May and then steadily declining through November (Figure 5). The HSI was more variable for *T. spinifera* with the lowest values in February and October and the highest values in April.

3.2. Lipids and fatty acids

3.2.1. Species and ontogenetic stage

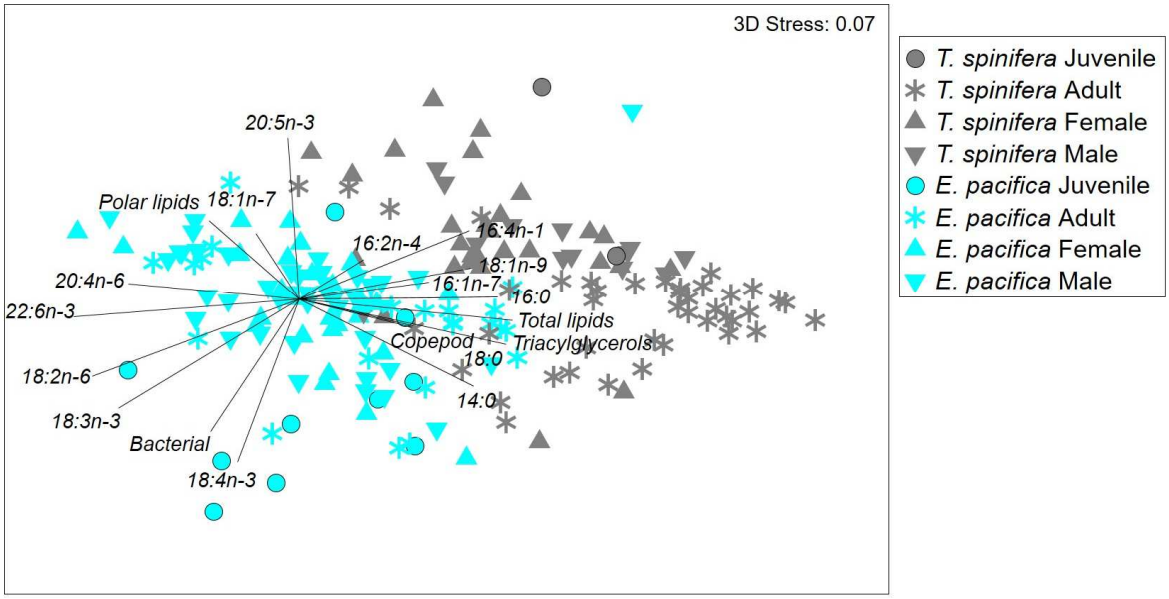

Figure 6. Non-metric multidimensional (nMDS) scaling of the fatty acids and lipid classes by species and life history stage. Vectors represent the relative loading strength (length) and direction for each fatty acid and lipid class.

The spatial segregation of the proportions of fatty acid and neutral and polar acyl lipid classes between *E. pacifica* and *T. spinifera* were visualized as a function of ontogenetic stage (Figure 6) and oceanographic upwelling condition (next section, Figure 8) using nMDS. There was clear separation between the species, with *T. spinifera* having higher total lipids per WW and higher proportions of neutral storage lipids (TAG) than were generally found in all life history stages of *E. pacifica*. Higher total lipids and TAG in *T. spinifera* were associated with diatom trophic indicator fatty acids (20:5n-3, 16:1n-7 and 16:4n-1) and elevated proportions of copepod indicator fatty acids. *E. pacifica* had lower total lipids per WW, a higher proportion of polar PL, and were associated with dinoflagellate trophic indicator fatty acids such as 18:4n-3 and 22:6n-3 at all developmental stages.

A two-way perMANOVA investigating differences in the fatty acid and lipid composition between krill species and among ontogenetic stage showed both significant main and interactive effects (Pseudo-$F_{3,180} = 3.63$, $p = 0.0013$). Significant interactive effects were detected because the fatty acid and lipid profile of *T. spinifera* was more variable across life history stages compared to *E. pacifica.* This was confirmed using separate species-specific one-way perMANOVAs with pairwise comparisons between life history stages. The lipid and fatty acid composition was significantly different ($p<0.05$) across all life history stages of *T. spinifera* except for the juvenile stage where sample sizes were too low for

390 statistical analysis (Figure 6). For *E. pacifica,* only the juvenile stage was different from
391 other developmental stages. However, since all juvenile *E. pacifica* were collected in the late
392 summer and fall we cannot rule out oceanographic upwelling condition as the main factor
393 driving this difference.
394 Strong univariate patterns emerged between the species and life history stages for some
395 lipid and fatty acid classes (Figure 7, Table 3). *T. spinifera* had significantly higher total lipid
396 density ($p<0.001$; 40.65 ± 2.89 µg/mg), TAG ($p<0.001$; 13.69 ± 1.11%), carnivory indicator
397 ($p<0.001$; 1.87 ± 0.04), diatom indicator ($p<0.001$; 0.24 ± 0.009), and copepod indicator
398 ($p<0.001$; 2.17 ± 0.19) compared to *E. pacifica* (total lipids: 18.97 ± 1.85 µg/mg; TAG: 3.47
399 ± 0.96%; carnivory indicator: 1.42 ± 0.04; diatom indicator: 0.20 ± 0.008; copepod indicator:
400 1.24 ± 0.12). There were also significant differences among life history stages with *T.*
401 *spinifera* adults having higher concentrations of total lipids (63.0 µg mg^{-1}) compared to
402 males (38.95 µg mg^{-1}) and females (26.84 µg mg^{-1}). *T. spinifera* adults also had significantly
403 higher proportions of TAG (24.4%) and carnivory marker ratios (ratio 2.32) compared to
404 other stages. Male *T. spinifera* had the highest ratio of the diatom indicator (0.29%)
405 compared to other life history stages. Although juvenile *T. spinifera* were excluded from the
406 analysis due to small sample size (n = 3), diatom indicator ratios of juveniles were similar to
407 those of males. There were no significant differences in total lipids, percent TAG, carnivory
408 marker or diatom marker ratios among life history stages of *E. pacifica* (Figure 7, Table 3).
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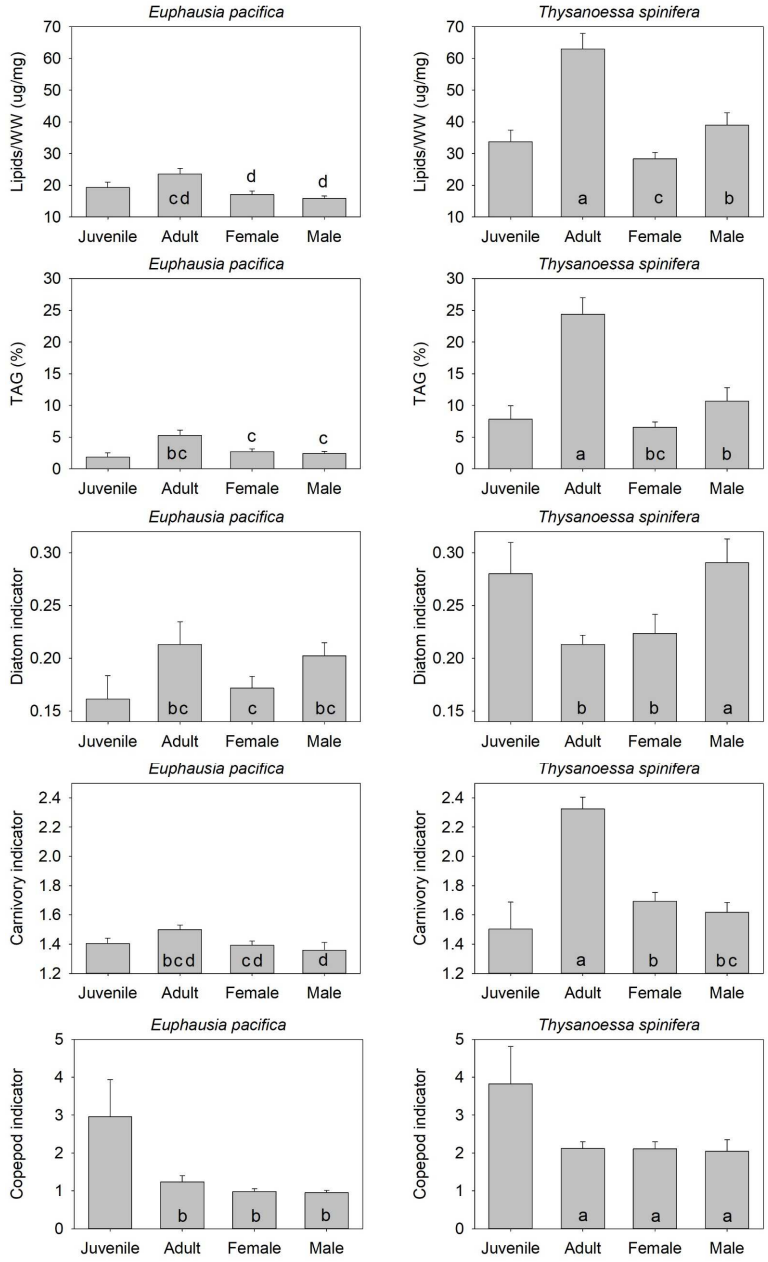

Figure 7. Lipid and fatty acid classes by species and life history stage. Total lipids per wet weight (ug/mg), triacylglycerols (TAG), ratio of 16:1n-7 to 16:0 (diatom indicator), ratio of 18:1n-9 to 18:1n-7 (carnivory indicator), and $\sum C_{20} + C_{22}$ MUFA (copepod indicator). Letters denote statistical significance (alpha <0.05): life history stages with different letters are statistically different and life history stages with the same letter(s) are not statistically different. Low sample sizes precluded statistical analysis of juveniles.

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Table 3. Lipid and fatty acid composition (±1 SE) of *Euphausia pacifica* and *Thysanoessa spinifera* by life history stage.

	Euphausia pacifica				*Thysanoessa spinifera*			
	Juvenile	Adult	Female	Male	Juvenile	Adult	Female	Male
No. of samples	11	23	28	42	3	42	28	13
Total Lipids (ug/mg)	19.3 ± 1.7	23.6 ± 1.8	17.1 ± 1.1	15.9 ± 0.7	33.8 ± 3.6	63.0 ± 4.9	28.3 ± 2.1	39.0 ± 4.0
Lipid class (%)								
Hydrocarbon	5.4 ± 0.6	2.4 ± 0.6	1.8 ± 0.2	2.4 ± 0.3	1.3 ± 0.2	1.0 ± 0.1	2.1 ± 0.3	1.4 ± 0.4
Steryl/Wax esters	0.1 ± 0.1	0.6 ± 0.2	1.2 ± 1	0.2 ± 0.1	6.2 ± 1.9	4.8 ± 0.3	3.9 ± 0.6	4.4 ± 0.7
Triacylglycerols (TAG)	8.6 ± 2.9	18.9 ± 2.4	14.6 ± 1.6	13.2 ± 1.4	22.5 ± 4.2	34.4 ± 1.7	21.8 ± 1.4	24.2 ± 3.2
Free fatty acids (FFA)	15.2 ± 1.9	10.5 ± 0.8	11.6 ± 1.3	12.2 ± 0.7	5.4 ± 1.9	5.3 ± 0.6	6.1 ± 0.7	7.2 ± 1.5
Sterols (ST)	14.3 ± 2.1	13.7 ± 1.0	14 ± 0.8	15.2 ± 0.7	12.1 ± 2.2	6.8 ± 0.6	9.4 ± 0.7	7.5 ± 0.7
Acetone mobile polar lipids (AMPL)	17.6 ± 2.6	9.5 ± 1.2	8.6 ± 0.6	8.3 ± 0.7	12.7 ± 2.9	5.3 ± 0.7	6.5 ± 0.9	10.2 ± 3
Phospholipids (PL)	38.7 ± 1.8	43.7 ± 1.1	48.1 ± 1.1	48.1 ± 1.2	38.7 ± 0.9	41.9 ± 1.1	51.5 ± 1.4	44.3 ± 1.2
Fatty acid composition (%)								
14:00	4.4 ± 0.4	4.2 ± 0.3	3.4 ± 0.2	3.3 ± 0.3	4.7 ± 1.3	5.3 ± 0.2	3.7 ± 0.2	4.7 ± 0.2
16:00	22 ± 1.3	19.3 ± 0.2	18.4 ± 0.2	18.4 ± 0.3	29.8 ± 7.3	26.2 ± 0.4	23.5 ± 0.5	21.5 ± 0.8
18:00	4.0 ± 0.5	1.8 ± 0.1	1.5 ± 0	1.4 ± 0.0	3.7 ± 0.5	2.7 ± 0.1	2.0 ± 0.1	2.4 ± 0.1
∑SFA[1]	33.2 ± 1.8	26.9 ± 0.5	24.9 ± 0.5	24.7 ± 0.6	38.8 ± 9.3	35.1 ± 0.5	29.9 ± 0.7	29.5 ± 1.0
16:1n-7	3.4 ± 0.4	4.2 ± 0.4	3.2 ± 0.2	3.8 ± 0.3	8.3 ± 1.9	5.6 ± 0.2	5.1 ± 0.4	6.1 ± 0.4
18:1n-9	7.2 ± 0.3	7.7 ± 0.2	7.9 ± 0.1	8.2 ± 0.3	9.5 ± 2.1	11 ± 0.3	9.3 ± 0.2	8.3 ± 0.3
18:1n-7	5.1 ± 0.2	5.2 ± 0.1	5.7 ± 0.1	6.1 ± 0.1	6.2 ± 0.6	4.8 ± 0.1	5.7 ± 0.2	5.2 ± 0.2
∑MUFA[2]	20.2 ± 1.3	20.0 ± 0.5	19.3 ± 0.3	20.6 ± 0.5	29.4 ± 4.2	25.3 ± 0.4	24.9 ± 0.7	23.3 ± 0.7
16:2n-4	0.9 ± 0.2	1.8 ± 0.2	1.3 ± 0.1	1.2 ± 0.1	1.6 ± 0.2	1.2 ± 0.1	1.9 ± 0.4	1.7 ± 0.1
16:4n-1	0.3 ± 0.1	0.7 ± 0.1	0.3 ± 0.1	0.3 ± 0.0	1.5 ± 0.6	1.7 ± 0.2	1.1 ± 0.1	2.9 ± 0.3
18:2n-6	2.4 ± 0.1	2.1 ± 0.1	2.4 ± 0.1	2.4 ± 0.1	0.5 ± 0.2	0.9 ± 0.1	0.9 ± 0.1	0.8 ± 0.1
18:3n-3	2.0 ± 0.1	1.6 ± 0.1	1.8 ± 0.1	1.6 ± 0.1	0.2 ± 0.1	0.6 ± 0.1	0.6 ± 0.1	0.4 ± 0.1
18:4n-3	4.4 ± 0.5	3.6 ± 0.5	3.1 ± 0.4	3.0 ± 0.3	0.4 ± 0.2	1.7 ± 0.1	0.8 ± 0.1	1.0 ± 0.2
20:4n-6	1.0 ± 0.1	1.3 ± 0.1	1.7 ± 0.1	1.6 ± 0.1	0.2 ± 0.2	0.7 ± 0.1	1.1 ± 0.0	1.0 ± 0.1
[illegible]	15.9 ±	20.1 ±	21.2 ±	20.7 ±	19.3 ±	19.9 ±	24.3 ±	24.7 ±

3.2.2. Species and seasonal trends

The lipid and fatty acid composition differed significantly as a function of upwelling conditions (Pseudo-$F_{2,182}$= 4.19, p=0.002) with a similar response pattern for both species (Figure 8), though the pattern was more pronounced for *T. spinifera.* Both species had lower lipid density, lower storage lipids (TAG) and high proportion of polar membrane lipids (PL) and associated polyunsaturated fatty acids (PUFAs), 22:6n-3 and 20:4n-6 early in the season prior to the onset of upwelling (January - April). During the upwelling months (May - September), the lipid and fatty acid composition of both species shifted as a result of increases in lipids per WW and TAG as well as trophic indicators of diatom lipid storage (16:1n-7, 16:4n-3). The fatty acid and lipid compositions of both species were characterized by increased proportions of the dinoflagellate marker (18:4n-3) and increased bacterial contribution post-upwelling (October - December).

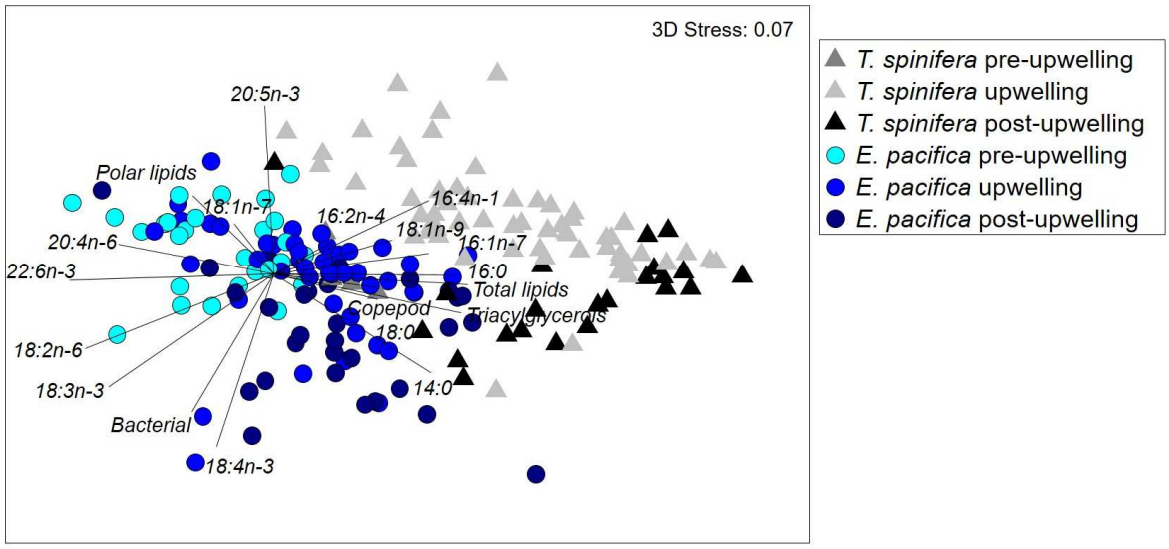

Figure 8. Non-metric multidimensional (nMDS) scaling of the fatty acids and lipid classes by species and oceanographic condition. Pre-upwelling is January - April, upwelling is May - September, and post-upwelling is October - December. Vectors represent the relative loading strength (length) and direction for each fatty acid and lipid class.

Although the lipid and fatty acid composition in both species followed a similar seasonal pattern (Figure 8), univariate analyses suggest that *T. spinifera* had higher diatom biomarkers compared to *E. pacifica* across all oceanographic conditions. To explore whether these differences are species-specific, or whether they were confounded by unequal sampling across seasons, we compared diatom-flagellate indicators (both PL and TAG) for both species during upwelling (May – September) and downwelling (October – April) conditions (Figure 9). Phospholipids, a membrane lipid class, have fatty acids that are generally considered to be more species-specific, and less influenced by short-term dietary input. Phospholipids have higher concentrations of long chain essential fatty acids such as 22:6n-3, 20:5n-3 and 20:4n-6 while TAGs are less fatty acid specific and are thus more reflective of diet (Bell and Dick, 1991; Budge et al., 2006; Copeman et al., 2018). Diatom-flagellate indicators typical of PL (20:5n-3/22:6n-3) and typical of TAGs (16:1n-7/18:4n-3) showed the same trend of elevated diatom contribution in *T. spinifera* compared to *E. pacifica* across both upwelling and downwelling periods (Figure 9). This indicates that there is stronger diatom dominance in *T. spinifera* diets that is not just a function of differential TAG lipid storage or differential seasonal sampling.

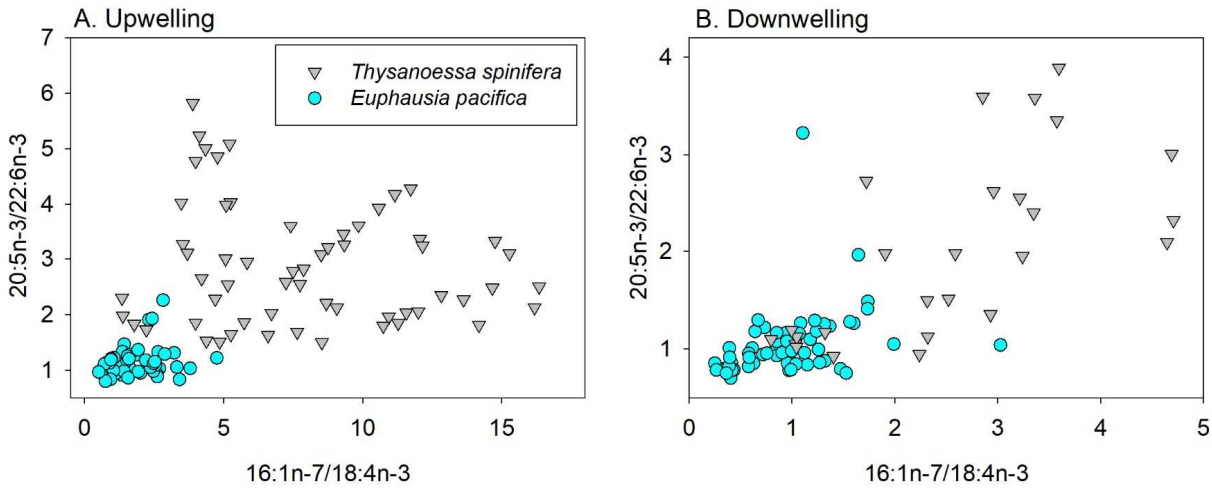

Figure 9. Diatom-flagellate indicator typical of phospholipids (20:5n-3/22:6n-3) in relation to diatom-flagellate indicator typical of triacylglycerols (16:1n-7/18:4n-3) from *Thysanoessa spinifera* and *Euphausia pacifica* during (A) upwelling (May – September) and (B) downwelling (October – April) months. Note different scales on both axes indicating increased storage of both diatom-derived indicators typical of phospholipids and triacylglycerols during upwelling periods.

4. Discussion

4.1. Ontogeny

The adult stage in our study was defined as individuals >10 mm with no distinguishing sexual characteristics. Fewer *E. pacifica* in our study were classified as adults based on these criteria (24% in the lipid analysis and 10% in the body condition) compared to *T. spinifera* (51% in the lipid analysis and 34% in the body condition). This pattern was also apparent from a 16-year time series of euphausiids from the same region where Shaw et al. (this issue) found that only 2% of all adult *E. pacifica* had no secondary sexual characteristics while 45% of adult *T. spinifera* could not be sexed. In that study, the authors also found that unsexable *E. pacifica* adults were rare from January - July and more common from August – December, when they also observed smaller adults. They also found that *T. spinifera* had the highest biomass in August and many of these individuals did not have defining sexual characteristics despite being in the size range of large adults (≥20mm), suggesting that adult *T. spinifera* may lose secondary sexual characteristics when they are not actively spawning. The majority of adult *T. spinifera* in the present study were collected in August and September, and many of these individuals were also in the larger size range (mean 17.1). The absence of sexual characteristics in larger animals suggests that they are finished reproducing for the season and can allocate energy to amassing lipid stores.

4.2. Fulton's K, hepato-somatic index (HSI), carbon to nitrogen (C:N)

Many studies have investigated euphausiid body condition in south polar regions, but there are fewer studies from temperate seas. There have been some studies on the body composition of *E. pacifica* from the eastern Pacific (Iguchi and Ikeda, 1994; Ikeda and Hirakawa, 1998; Kusumoto et al., 2004; Kim et al., 2010) and only one study that specifically investigated the body condition of *T. spinifera* (Ju et al., 2009), though some other *Thysanoessa* species have been studied extensively, especially in northern polar regions (Falk-Petersen et al., 1981; Hopkins et al., 1984; Ikeda and Skjoldal, 1989; Kim et al., 2010; Harvey et al., 2012). Our emphasis here is on the ontogenetic and seasonal differences in body condition of the two dominant species in the NCC. Condition indices, such as length-weight, Fulton's K condition factor, and hepato-somatic index (HSI) are tools for quick evaluation of the condition of an animal based on factors that can be easily observed or measured. Such conditions are likely to be strongly influenced by both species and ontogeny and are most useful for comparisons within a given species and developmental stage to evaluate the effects of environmental or spatial patterns on condition factors. In the present study, morphometric indices reflect patterns found with other indices, such as C:N and lipid classes, lending credibility to using morphometrics to assess individual condition.

The Fulton's K condition factor, HSI, and C:N were all higher in *T. spinifera* compared to *E. pacifica* but some varied among life history stages. No changes in Fulton's K occurred across life history stages of *T. spinifera* indicating that Fulton's K was not very sensitive to ontogenetic changes in this species, a pattern that has also been documented for some fish

493 (Mozsár et al., 2015; Copeman et al. 2008). However, the C:N ratio was highest in adult *T.*
494 *spinifera* followed by females and males. Carbon is the major source for lipid production,
495 and indeed the percent carbon per dry weight, total lipid, TAG, and the carnivory marker all
496 followed similar patterns for *T. spinifera;* all were highest for the adult life history stage
497 (discussed below). These patterns cannot be attributed solely to differences in life history
498 stage as they likely vary with seasonal shifts in lipids related to growth, reproduction, storing
499 lipids for overwintering, or a combination of these. While the highest *T. spinifera* carbon and
500 lipid values occurred in the adult life history stage, the majority of those individuals were
501 collected from August – October, when non-sexually mature *T. spinifera* are also most
502 abundant (Shaw et al., this issue). Therefore, disentangling the effect of life history stage
503 versus seasonal shifts might not be possible if most adult stage *T. spinifera* occur August –
504 October. However, this distinction might only be important for predators that target particular
505 life history stages.
506 HSI provides a relatively quick assessment of recent feeding conditions, as the size of the
507 hepatopancreas changes based on feeding and thus it provides a more rapid assessment than
508 instantaneous growth rate measurements, which integrate feeding over the past molt cycle
509 (Shin 2000). The hepato-somatic index (HSI) followed a clear seasonal trend for *E. pacifica*
510 with HSI steadily increasing at the beginning of the year, peaking in May and then steadily
511 declining through November. This species follows a similar seasonal pattern in growth and
512 reproduction. *E. pacifica* growth and spawning are fueled by phytoplankton blooms that
513 occur in association with upwelling. *E. pacifica* lengths increase from January – July and
514 then decrease again into the fall (Shaw et al., this issue). Energy from feeding in spring is
515 more likely allocated to growth while energy from summer phytoplankton blooms is devoted
516 to reproduction, hence the decrease in length in summer even though food resources are still
517 plentiful.
518 Food sources and energy allocation can be contributing factors in varying C:N ratios.
519 While the HSI was lowest in adult *T. spinifera* compared to other stages, the carnivory
520 marker was higher in this life history stage, indicating a possible shift in food source during
521 this stage. Laboratory experiments rearing *E. pacifica* and *T. spinifera* from eggs showed that
522 *E. pacifica* can grow, mature, and spawn on a diet of phytoplankton (Feinberg et al., 2010).
523 *T. spinifera* raised on the same diet grew until early furcilia stages but then development
524 stalled and few matured to the juvenile stage, suggesting that they are eating a more
525 omnivorous diet starting early in their life history. Indeed, all life history stages of *T.*
526 *spinifera* analyzed in this study had significantly higher concentrations of the carnivory and
527 copepod marker (discussed below) compared to the same life history stages of *E. pacifica*.
528 Further, stable isotope analysis has suggested that *T. spinifera* occupy a higher trophic
529 position than *E. pacifica* (Miller et al., 2010).
530 While several studies have found a strong positive relationship between Fulton's K and
531 the amount of total lipids in fish (Herbinger and Friars, 1991; Chellappa et al., 1995; Mozsár
532 et al., 2015), we did not see a strong relationship with Fulton's K and total lipid for either
533 species of krill. Further, the Fulton's condition factor decreased for both species in June.
534 Adult krill biomass also decreases in June (Shaw et al. this issue), as do biomass and egg
535 production of *Calanus* spp. (Zeman et al. this issue) in our region. These patterns across

zooplankton taxa suggest that larger processes in the NCC are affecting growth and reproduction during this time and warrant further study.

4.3. Lipids and fatty acids

Lipids are important to cold water marine organisms as a source of energy, as important structural components for cell membranes, and as precursors for biologically active compounds (Falk-Petersen et al., 2009; Parrish, 2013). Previous studies in temperate upwelling and polar systems have found that krill lipids cycle with reproductive stage and that increased lipid levels were positively correlated with the seasonal rise in phytoplankton production (Falk-Petersen et al. 2000; Ju et al. 2009). In agreement with previous studies, we found inter-specific and seasonal differences in all lipid metrics (total lipids, lipid classes and fatty acids) for both *E.pacifica* and *T. spinifera*, although these metrics were more variable in the latter species.

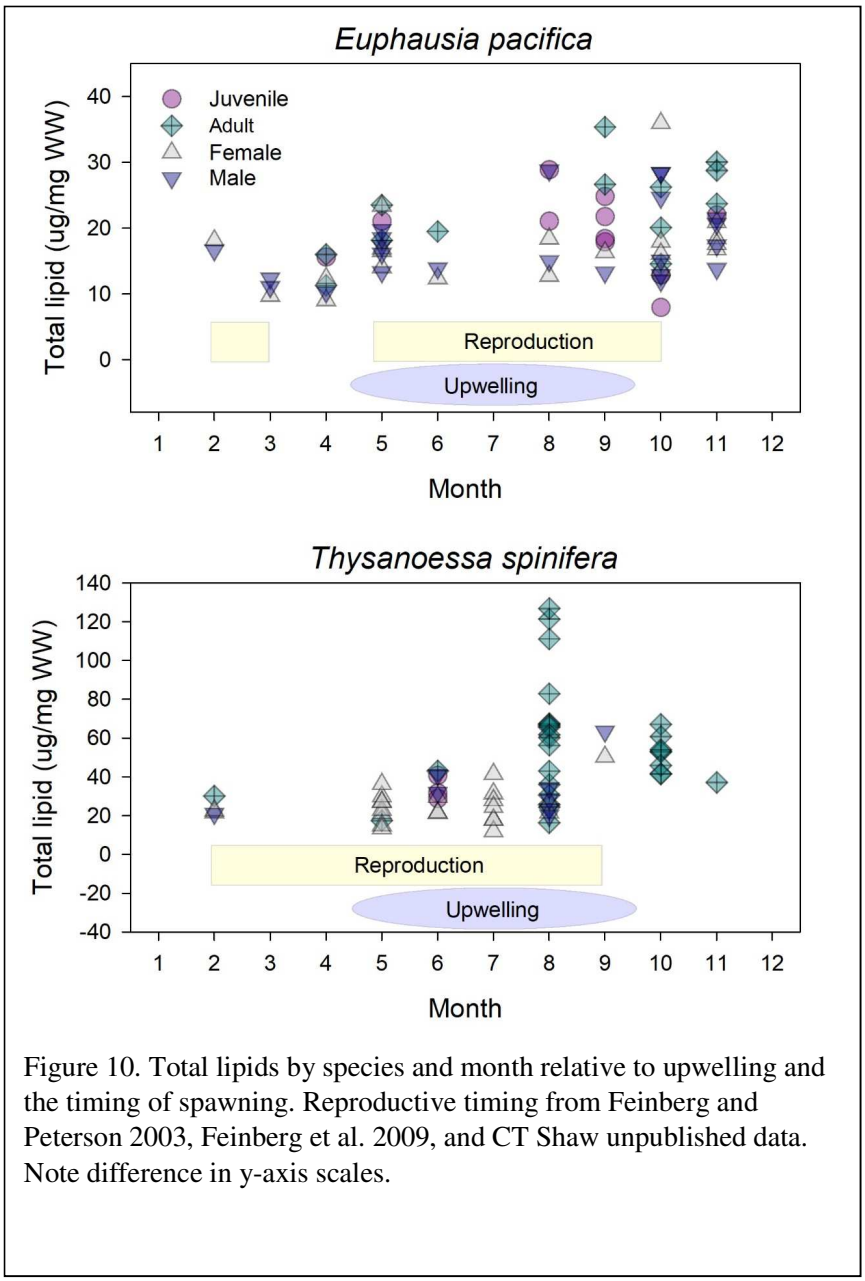

Figure 10. Total lipids by species and month relative to upwelling and the timing of spawning. Reproductive timing from Feinberg and Peterson 2003, Feinberg et al. 2009, and CT Shaw unpublished data. Note difference in y-axis scales.

There are very few studies on lipid dynamics in euphausiids from the NCC, but the values for total lipids (µg/mg) that we report are in strong agreement with other studies (Ju et al. 2009). Using the WW:DW conversion equations from Ju et al. (2009), we converted our average lipids per WW for *E. pacifica* (~19 µg mg^{-1}, across all stages and months) and *T. spinifera* (~41 µg mg^{-1}) to lipids per DW. The converted DW values for *E.pacifica* (77 µg mg^{-1}) and *T.spinifera* (168 µg mg^{-1}) were within the range reported by Ju et al. (2009) (*E. pacifica* ~90µg mg^{-1} and *T.spinifera* ~140 µg mg^{-1}). Generally, these values also fall within the range of other North Pacific and North Atlantic species (Cabrol et al., 2019; Ju et al., 2009; Pleuthner et al., 2016) but are much lower than values reported for many Antarctic and

polar species (Falk-Petersen et al., 2000; Hellessey et al., 2018; Huenerlage et al., 2016). Total lipid for both species spanned a wide range of values, but most *E. pacifica* were in the 10 - 30 µg mg^{-1} range, while most *T. spinifera* ranged from 20 - 70 µg mg^{-1} regardless of time of year (Figure 10). The fact the highest lipid content in *E. pacifica* (~35 µg mg^{-1}) is in the lower range of values for *T. spinifera* underscores the desirability of *T. spinifera* as a prey item.

The highest total lipid values for *T. spinifera* were in August, near the end of their spawning season when the majority of the *T. spinifera* were non-reproductive adults (Figure 10). Adults are likely not devoting energy to spawning this late in the season and may be amassing stored lipids for overwinter survival. Although the highest total lipids for *E. pacifica* were in September and October, values for *E. pacifica* were in a similar range in most months. Similar to our study, Ju et al (2009) also found that total lipids in *E. pacifica* showed little seasonal variation, however lipid concentrations were elevated in *T. spinifera* during early summer (June). Their study did not find a clear trend of varying lipid concentration with life history stage for either species. This could be due in part to low sample sizes and lumping all adult life history stages together instead of distinguishing between adult, female, and male.

As reported previously for NCC krill, phospholipids proportionally comprised the major lipid class (Ju et al., 2009, 2006) and we report values ranging from 38% to 52% in both species across all reproductive and seasonal variables. Phospholipids, along with sterols, act as vital structural lipid components of cell membranes where they modulate cell transport and membrane fluidity (Ackman, 1989; Parrish, 2013). However, phospholipids also serve as metabolic fuel in zooplankton and fish, particularly in lipid-limiting situations such as during egg or early larval development (Ju et al., 2006; Laurel et al., 2008; Tocher et al., 1985).

Lipid-rich zooplankton, such as copepods and euphausiids from polar and temperate regions, accumulate large amounts of storage lipid during periods of high phytoplankton/food availability that are subsequently followed by periods of starvation (Hagen et al., 1996; Lee et al., 2006). Generally, triacylglycerols are used for shorter-term lipid storage while wax esters are used for longer periods of food deprivation (Kattner et al., 2007; Lee et al., 2006). For this reason, higher levels of wax ester storage are often found in krill from polar regions compared to species from temperate and upwelling systems (Cabrol et al., 2019; Falk-Petersen et al., 2000; Hagen and Kattner, 1998; Ju et al., 2009). The use of triacylglycerols instead of wax esters for energy storage in polar regions is an indicator of year-round feeding in species such as *E. superba* (Atkinson and Snÿder, 1997). Low levels of wax esters in *E. pacifica* and *T. spinifera* during this study indicates reduced seasonality in food availability compared to polar regions. High triacylglycerol storage in adult *T. spinifera* from late summer/fall drives the increased trends in total lipids described previously and may be an adaptation to the onset of reduced food availability during winter (Du and Peterson, 2014b). In contrast, levels of triacylglycerols were much lower and seasonally stable across all stages of *E. pacifica,* indicating an alternative food sources or different energetic allocation strategy compared to *T. spinifera*.

Euphausiids store lipids for a variety of reasons, including reproduction and overwintering, depending on their habitat and life history strategies (Falk-Petersen et al.,

1981; Hagen et al., 1996; Torres et al., 1994; Hagen and Kattner, 1998; Falk-Petersen et al., 2000; Hagen and Auel, 2001; Huenerlage et al., 2015). For example, *Thysanoessa inermis* amass stored lipids during the primary production season and use these reserves for gonad development and spawning early in the season prior to the establishment of large phytoplankton blooms (Hopkins et al., 1984). *T. spinifera* eggs were regularly found in our study area both prior to and after the onset of upwelling, so this species may employ a similar strategy and use stored lipids to fuel early season spawning. Although *E. pacifica* spawning activity occasionally occurred prior to the onset of upwelling, it was always in association with early season phytoplankton blooms, so it was most likely not fueled by stored energy reserves (Figure 10). Ju et al. (2009) concluded based on growth rates, spawning duration, and lipid allocation strategies that *T. spinifera* does not allocate energy to reproduction at the expense of growth, while *E. pacifica* allocates more energy to reproduction, shows negative growth, and has consistently low lipid levels.

Both species showed a similar seasonal progression in fatty acids, with lower lipid density and lower storage lipids prior to the onset of upwelling (January - April). During the upwelling months (May - September) the lipid and fatty acid composition shifted in both species, with increases in total lipids, storage lipids, and trophic indicators of diatom lipid storage (16:1n-7, 16:4n-1). Post-upwelling, lipids in both species were characterized by increased proportions of the dinoflagellate marker (18:4n-3) and increased bacterial markers. These patterns have also been documented in the copepod community in the NCC (Miller et al., 2017), and a laboratory study showed that *E. pacifica* feed preferentially on ciliates and dinoflagellates during the non-upwelling periods, but feed almost exclusively on diatoms during the upwelling season (Du and Peterson, 2014a). While this suggests changes in food availability and diet throughout the year, the increase in lipids in *T. spinifera* in the fall, when they have increased dinoflagellate biomarkers, indicates that they are storing lipids for overwintering, a strategy previously documented for other krill species (Hagen et al., 1996; Torres et al., 1994; Falk-Petersen et al., 2000; Hagen and Auel, 2001; Huenerlage et al., 2015).

Fatty acid biomarkers have been used for over 45 years (Lee et al., 1971) to determine trophic relationships in zooplankton and extensive reviews of this approach are available for both pelagic and benthic marine systems (Budge et al., 2006; Dalsgaard et al., 2003; Kelly and Scheibling, 2012). The use of the carnivory index (18:1n-9/18:1n-7) is based on the knowledge that zooplankton which feed on metazoans and protists have higher relative concentrations of 18:1n-9 while those that feed more exclusively on phytoplankton have a higher proportion of 18:1n-7 (Dalsgaard et al. 2003; Falk-Petersen et al. 2000). However, both of these fatty acids are ubiquitous in marine systems and can be modified to a large degree within the consumer. Nonetheless, multiple studies have now confirmed the utility of this index by finding a positive correlation between two independent indices of carnivory: Δ^{15}N trophic level indicator and 18:1n-9/18:1n-7 (El-Sabaawi et al., 2010; Schmidt et al., 2006). Here we found constant ratios of the carnivory index in *E. pacifica* but significantly higher ratios of the carnivory index in the adult stage of *T. spinifera* at the end of the summer/fall. For these same *T. spinifera*, we see high proportions of total lipids per WW and triacylglycerols. This indicates that switching diets to include metazoans or protists during

periods of low phytoplankton production may be a successful strategy to store energy prior to winter. Elevated carnivory in *T. spinifera* did not co-vary with elevated copepod markers. The dietary copepod marker $\sum C_{20+22}$ MUFA is used to indicate the incorporation of lipids from herbivorous copepods that store wax esters. Species such as the genus *Calanus* biosynthesize large amounts of 20:ln-9 and 22:1n-11, which are produced by elongation of 18:1n-9 and 20:1n-11, respectively (Kattner and Hagen, 1995). The absence of a relationship between the carnivory index and the copepod index indicates that *T. spinifera* are not eating large wax-ester storing copepods.

4.4. Krill as a prey source

Body condition, elemental composition, and total lipids strongly differed between the two species. *T. spinifera* had higher length-weight, Fulton's K, HSI, C:N, total lipid, and neutral storage lipids (TAG) compared to *E. pacifica*, indicating that *T. spinifera* have a higher energetic value for predators. However, there were strong seasonal differences in *T. spinifera* energetics. Carbon and lipids were highest in the adult stages, which were mainly collected from August through October. Higher trophic levels foraging on krill during these months would obtain more lipid rich food from fewer individuals compared to feeding during the spring.

The breeding success of seabirds has been linked to krill distributions. A lipid-rich food source that is located close to shore increases breeding success by decreasing the distance adults need to travel on foraging trips. A substantial proportion of the diet of Cassin's auklets in the central California Current consists of euphausiids (77% *E. pacifica* and *T. spinifera* combined) (Abraham and Sydeman, 2004). Cassin's auklet breeding is initiated earlier in the year with increased consumption of *E. pacifica,* while fledging rate is positively correlated with consumption of *T. spinifera* (Abraham and Sydeman, 2004). Further, an 11-year time series found that auklets decrease the amount of *E. pacifica* in their diet and increase the amount of *T. spinifera* during the progression of chick rearing (Abraham and Sydeman, 2006). The timing of this prey switching varied annually, occurring sometime between the beginning of June and the end of July. During this time period, both *E. pacifica* and *T. spinifera* have higher lipids per wet weight and higher TAG, as well as higher trophic indicators of diatom lipid storage compared to non-upwelling periods. Abrahams and Sydeman (2006) attribute the seasonal switch in prey to increased availability of *T. spinifera* compared to *E. pacifica* during summer in the central California Current. However, the timing of prey switching also coincides with the time period when *T. spinifera* had the highest carbon, lipids and elevated PUFA densities ($\mu g\ mg^{-1}$) in our region, making them an energetically superior food source.

Distributions of shearwaters, auklets, hake, and blue whales have been found to overlap with the acoustic signal of euphausiids (Mackas et al., 1997; Croll et al., 2005; Santora et al., 2012, 2011). However, associating predator distributions with particular species of krill is more difficult. In the central California Current, acoustic krill signal was correlated with the abundance of *E. pacifica* from net samples, but this relationship broke down for *T. spinifera* (Santora et al., 2011). During the same study, shearwaters were positively correlated with the acoustic krill signal but not with the abundance of *E. pacifica* or *T. spinifera*, and auklets

were not correlated with krill abundance from either nets or acoustics. This underscores the difficulty in assessing the spatial overlap of predators and the species-specific distribution and abundance of krill from acoustics. Advances in the ability to distinguish different species of euphausiids from multi-frequency acoustic returns (McQuinn et al., 2013), or from habitat distribution models, would greatly enhance our ability to understand foraging energetics and trophic interactions across large spatial scales.

Future climate scenarios predict increased warming and more frequent anomalous events in the NCC (Di Lorenzo and Mantua, 2016; Oliver et al., 2018). This could have negative impacts on predators seeking lipid rich prey. *T. spinifera* shifted their cross-shelf distribution from the inner shelf to outer shelf during positive (warm) phases of the Pacific Decadal Oscillation (Shaw et al., this issue). During the recent prolonged anomalous warm event in the NCC from 2014-2016, *T. spinifera* were absent and the biomass of *E. pacifica* was greatly reduced (Peterson et al., 2017; Shaw et al., this issue). These distributional shifts or reduced biomass can result in a mismatch in prey availability to planktivorous fish or central-place foragers that rely on prey closer to their colony as opposed to foraging farther away (Cushing, 1990; Bertram et al., 2001; Elliott et al., 2009). An increase in the frequency or duration of warm events could impact the bioenergetics of the food web for higher trophic levels that rely on krill as their predominant prey.

5. Conclusions

There were species-specific and seasonal differences in the lipid and fatty acid composition of krill, with *T. spinifera* having a higher length-weight, Fulton's K, hepato-somatic index, carbon to nitrogen ratio, total lipid and storage lipids compared to *E. pacifica*, indicating that *T. spinifera* have a higher energetic value for predators. However, there were strong seasonal differences in the energetics of *T. spinifera*. Carbon and lipids were highest in non-reproductive life history stages of *T. spinifera* from August through October, possibly in preparation for overwintering. Higher trophic levels foraging on krill during this time period would obtain more lipid rich food from fewer individuals, compared to feeding during the spring. Future warming events might disrupt the availability of *T. spinifera* as they are more associated with cool ocean conditions. While *E. pacifica* is the most abundant euphausiid in the NCC, *T. spinifera* have a larger body size and a higher concentration of lipids compared to *E. pacifica* throughout the year. Cross-shelf and alongshore differences in the biomass of these two species result in localized hotspots where predators might encounter prey with species-specific differences in lipid content. The ability to distinguish different species of euphausiids from acoustic returns would greatly enhance our ability to understand foraging energetics and trophic interactions across large spatial scales.

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