ICES Journal of Marine Science Advance Access published June 30, 2014

ICES Journal of Marine Science

ICES International Council for the Exploration of the Sea
CIEM Conseil International pour l'Exploration de la Mer

ICES Journal of Marine Science; doi:10.1093/icesjms/fsu109

Material properties of Northeast Pacific zooplankton

Kaylyn N. Becker and Joseph D. Warren*

School of Marine and Atmospheric Sciences, Stony Brook University, 239 Montauk Highway, Southampton, NY 11968, USA

**Corresponding author: tel: +1 631 632 5045; fax: +1 631 632 5070; e-mail: joe.warren@stonybrook.edu*

Becker, K. N., and Warren, J. D. Material properties of Northeast Pacific zooplankton. – ICES Journal of Marine Science, doi: 10.1093/icesjms/fsu109.

Received 12 November 2013; revised 21 April 2014; accepted 28 May 2014.

We measured the density and sound speed contrasts relative to seawater of Northeast Pacific zooplankton. The density contrast (g) was measured for euphausiids, decapods (*Sergestes similis*), amphipods (*Primno macropa*, *Phronima* sp., and *Hyperiid* spp.), siphonophore bracts, chaetognaths, larval fish, crab megalopae, larval squid, and medusae. Morphometric data (length, width, and height) were collected for these taxa. Density contrasts varied within and between zooplankton taxa. The mean and standard deviation (s.d.) for euphausiid density contrast were 1.059 ± 0.009. Relationships between zooplankton density contrast and morphometric measurements, geographic location, and environmental conditions were investigated. Site had a significant effect on euphausiid density contrast. Density contrasts of euphausiids collected in the same geographic area ~4–10 d apart were significantly higher ($p < 0.001$). Sound speed contrast (h) was measured for euphausiids and pelagic decapods (*S. similis*) and it varied between taxa. The mean and s.d. for euphausiid sound speed were 1.019 ± 0.009. Euphausiid mass was calculated from measured density and volume, and a relationship between euphausiid mass and length was produced. We determined that euphausiid volume could be accurately estimated from two-dimensional measurements of animal body shape, and that biomass (or biovolume) could be accurately calculated from digital photographs of animals. Data from this study can improve the accuracy of theoretical acoustic scattering models for these taxa, resulting in more accurate estimates of zooplankton biomass in this region.

Keywords: density contrast, euphausiids, sound speed contrast, zooplankton.

Introduction

The California Current is a major eastern boundary current in the Northeast Pacific (NEP) ocean. The Northern California Current region in particular is characterized by high productivity and seasonal and decadal variability (Brodeur *et al.*, 2003). Ekman-driven coastal upwelling of cold nutrient-rich water supports fish production in the NEP through bottom-up trophic linkages (Ware and Thomson, 2005). Zooplankton in the NEP Ocean play the crucial ecological role of transferring energy from the primary producers to higher trophic levels. NEP euphausiids are an important food source for many species including several species of Pacific salmon (Brodeur and Pearcy, 1990), myctophids (Tyler and Pearcy, 1975), Pacific hake (Mackas *et al.*, 1997), and many seabirds and marine mammals (Croll *et al.*, 1998). *Euphausia pacifica* and *Thysanoessa spinifera* are the dominant euphausiid species in the NEP region (Gómez-Gutiérrez et al., 2005).

Active acoustic techniques allow researchers to study zooplankton abundances, distributions, and behaviour at finer temporal and spatial scales than could be achieved by traditional methods (Greenlaw, 1979; Foote and Stanton, 2000; Simmonds and MacLennan, 2005). Scientific echosounders transmit sound waves into the water and acoustic backscatter is created when those sound waves encounter a target with a different acoustic impedance than the surrounding seawater (Simmonds and MacLennan, 2005). To convert energy into biomass, accurate target strength values are needed for the scatterers in the water column (Simmonds and MacLennan, 2005).

Target strength is determined by the size, shape, orientation, and material properties of the target animal (Chu *et al.*, 2000; Stanton and Chu, 2000; Warren *et al.*, 2002; Smith *et al.*, 2010). Target strength can be measured directly in controlled experiments by using a calibrated scientific echosounder and measuring the backscatter of known targets (Foote, 1987; Simmonds and MacLennan, 2005). This can be logistically difficult for zooplankton due to their small size. Foote and Stanton (2000) recommended using an acoustic scattering model to estimate target strength for

zooplankton if there are no direct target strength estimates available. To accurately model acoustic scattering, the material properties of the target organism must be known.

Material properties such as the ratios of the density (g) and sound speed (h) for a target relative to the surrounding seawater, as well as animal length and shape, are important parameters in scattering models (Greenlaw, 1977; Warren and Smith, 2007; Forman and Warren, 2010; Smith *et al.*, 2010). These parameters vary between zooplankton taxa (Greenlaw and Johnson, 1982; Stanton *et al.*, 1996), within taxa (Forman and Warren, 2010), seasonally (Køgeler *et al.*, 1987), and geographically (Smith *et al.*, 2010). A small change (2–4%) in the material properties used in a scattering model can change the target strength prediction for zooplankton by up to 20 dB (Chu *et al.*, 2000). Demer and Conti (2005) showed that when the scattering model for *Euphausia superba* was improved with updated parameters, the resulting estimated biomass increased by a factor of 2.5. Smith *et al.* (2010) suggested it may be necessary to use length and material property measurements from live animals in the geographic area of the study for an accurate scattering model. Scattering models using measured material property values from the geographic area of study produce very different target strength estimates than models using material property values from literature (Smith *et al.*, 2013).

Acoustically targeted net tows are conducted in acoustic surveys to ground-truth the acoustic data and confirm the composition of zooplankton present in the sampled region. When acoustic scattering models are used to predict biomass, these predictions are often compared with the biomass of animals caught in net tows. To calculate biomass from organisms collected in the net, scientists often use published length and wet weight relationships because taking detailed morphometric measurements at sea is very time-consuming. Relationships for euphausiids are often based on measurements made on preserved or frozen animals, and preservation may affect the euphausiids weight (Davis and Wiebe, 1985; Harvey *et al.*, 2012). This study measured the length, width, and height of NEP euphausiids and used these data to calculate volume using two different methods. Euphausiid volume and density were used to calculate euphausiid mass, and a new length-to-weight relationship for unpreserved NEP euphausiids was produced.

We measured the density (g) and sound speed (h) contrasts for zooplankton in the NEP. Material properties for zooplankton in this region have been measured previously, but it was several decades ago (Greenlaw, 1977; Greenlaw and Johnson, 1982). This study is the first to report density contrast values for crab megalopae and larval squid. Environmental conditions (temperature, salinity, density, and fluorescence) and zooplankton morphometric measurements (length, width, and height) were also measured. The effects of environmental and morphometric variables on zooplankton density contrast were investigated. Information from this study could improve the acoustic scattering models for these taxa.

Methods

We sampled two areas offshore of the Oregon coast during the summer of 2012 (Figure 1). We sampled one region from 26 to 30 July (A1), then a different region (B) from 31 July to 3 August, and resurveyed the first site (A2) from 4 to 10 August (Figure 2). Density contrasts were measured for individual animals from the following taxa: euphausiids, amphipods (*Primno macropa, Phronima* sp., and *Hyperiid* spp.), decapods (*Sergestes similis*), chaetognaths, crab megalopae, larval fish, siphonophores, larval squid, and medusae (Figure 3). Sound speed contrasts were measured for euphausiids and decapods.

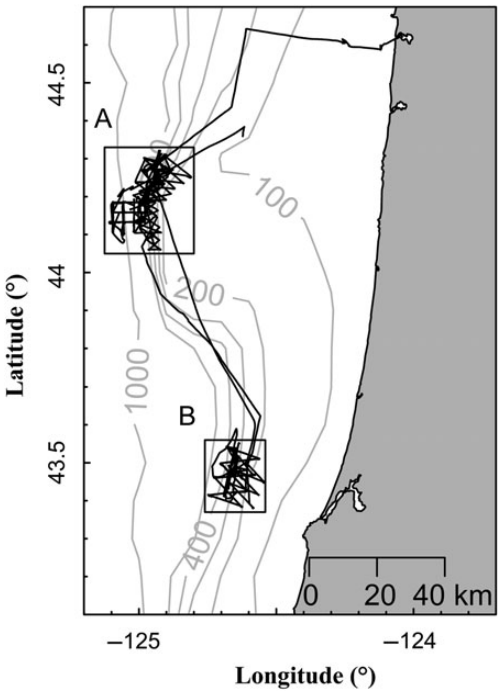

Figure 1. Cruise trackline of the RV "Oceanus" (solid black line) from 26 July 2012 to 10 August 2012. Region A and Region B are outlined. Bathymetry contours (grey lines) are shown at 100, 200, 300, 400, 500, and 1000 m. The latitude and longitude scale is in decimal degree notation.

Animal collection

Net tows were conducted at 37 stations from the RV *Oceanus* from 26 July 2012 to 10 August 2012. Zooplankton were collected using a 4 m^2 Isaacs–Kidd midwater trawl (IKMT; Isaacs and Kidd, 1953). The IKMT consisted of a 1 mm mesh net attached to a rigid v-shaped diving vane with a 1 mm mesh codend. The net tows targeted aggregations observed acoustically. The maximum depths of the net tows ranged from 29 to 550 m. Conductivity–temperature–depth (CTD) data were used to characterize the environmental conditions of regions where net tows were conducted.

When the net was retrieved, the contents were quickly transferred from the codend to a large tray (~15 l) filled with ambient surface seawater (from the ship's flow through seawater system). Individual zooplankton in the best condition (most viable) were hand-sorted by taxa into smaller containers (~1 l) filled with ambient surface seawater. Density and sound speed measurements were made immediately after sorting. Only live zooplankton were measured; most were measured within 5 h of collection, but no measurements were made more than 10 h after collection. In some cases with particularly large catches, containers with animals in ambient surface seawater were stored in a refrigerator until density and morphometric measurements could be performed.

Measurements

Density

The titration method (Warren and Smith, 2007; Smith *et al.*, 2010) was used to measure the density of the animals. The titration method involves using two burets: one with ambient surface seawater and the

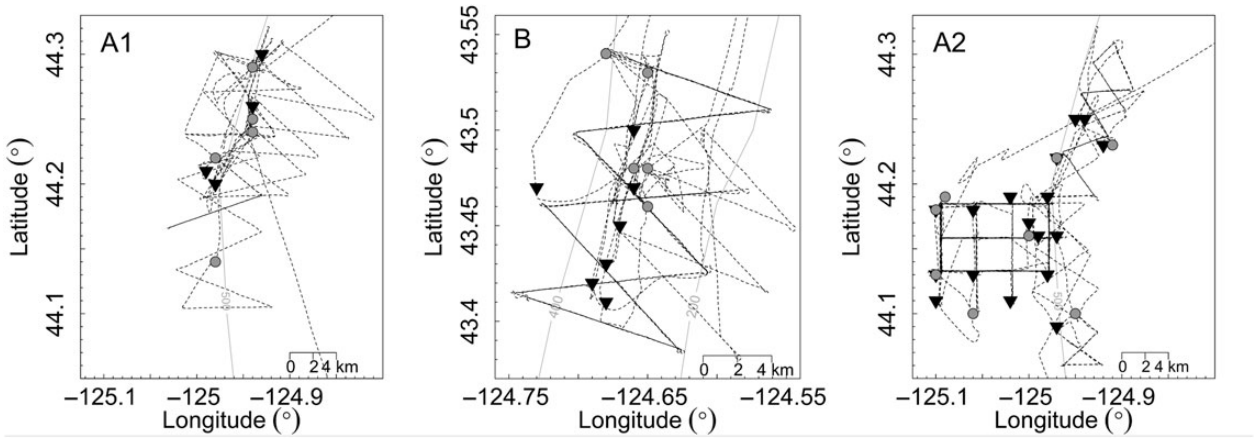

Figure 2. The ship's trackline is shown in black, net tows as black triangles, and CTD casts as grey circles. Bathymetry contours (grey lines) are shown for 200, 400, and 500 m. Sampling during the cruise took place within three surveys: Site A (27 July – 30 July 2012), site B (31 July – 3 August 2012), and second visit to site A (4 August – 10 August 2012) and are referred to as A1, B, and A2, respectively.

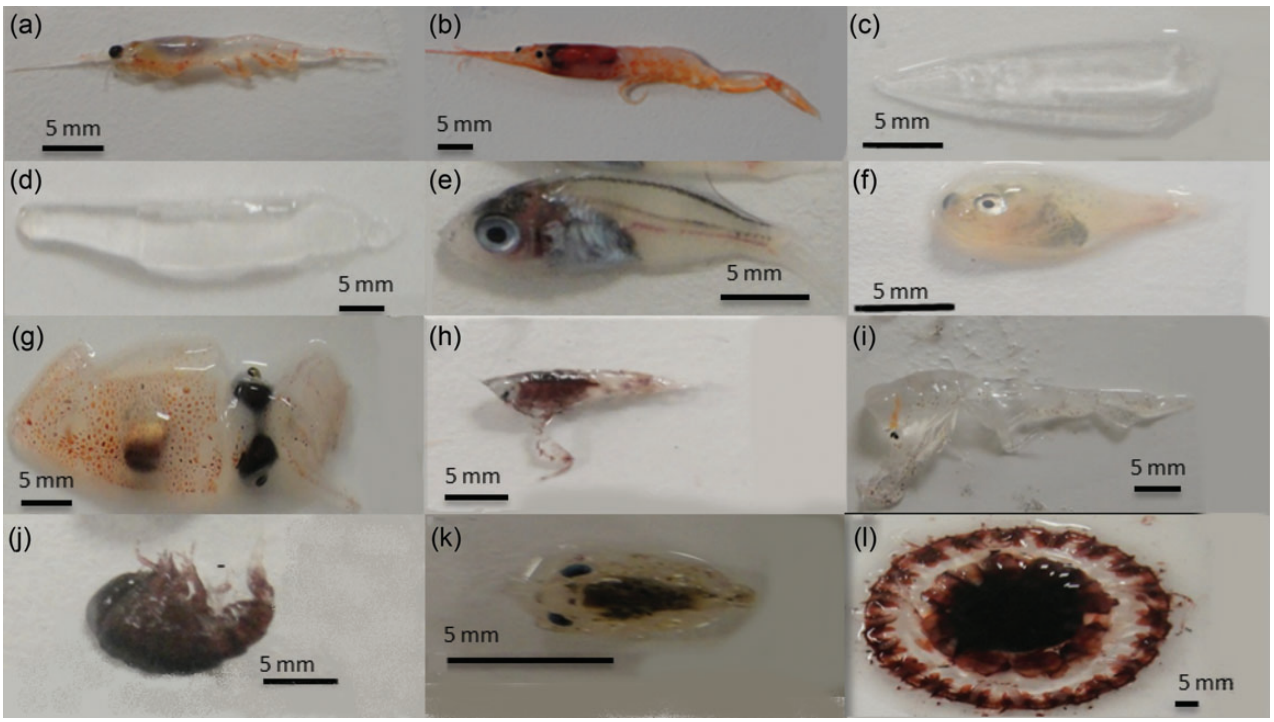

Figure 3. Photographs of zooplankton sampled. (a) Euphausiid, (b) *S. similis*, (c) siphonophore, (d) chaetognath, (e) larval rockfish (*Sebastes* sp.), (f) UID larval fish, (g) larval squid, (h) *P. macropa*, (i) *Phronima* sp., (j) *Hyperiid* spp. amphipod, (k) crab megalops, and (l) UID medusa.

other with a denser solution. Each solution was titrated into a beaker containing a single organism until the organism reached neutral buoyancy. The time of the density measurement depends on how much glycerin mix needs to be titrated into the solution for the animal to reach neutral buoyancy. In this study, measurements took between 2 and 10 min. Warren and Smith (2007) and Smith *et al.* (2010) used a hypersaline solution as the denser solution, but in this study, we used a glycerin mix solution. We used glycerin because it has a greater density (1.26 g ml^{-1}, ICSC, 2007), than hypersaline solutions we could make. Creating an equally dense hypersaline solution is challenging because salt would precipitate out of the hypersaline solution causing the density to fluctuate during titration. A 50/50 glycerin mix was created by diluting pure glycerin with an equal volume of ambient surface seawater, and this mix was used for all measurements.

Zooplankton were anaesthetized in a beaker containing ~200 ml of ambient surface seawater and an effervescent tablet which saturated the fluid with carbon dioxide. The temperature and salinity of the ambient surface seawater used in measurements were used to calculate seawater density using the CSIRO MATLAB Seawater Library. The density of the animal is calculated from V_{sw} the volume of seawater (ml), V_m the volume of glycerin mix (ml), ρ_{sw} the density of seawater (g ml^{-1}), and ρ_m the density of glycerin mix (g ml^{-1}) in the beaker [Equation (1)]. The density contrast is the ratio of animal density

to seawater density [Equation (2)].

$$\rho_a = \frac{(V_{\mathrm{sw}}\rho_{\mathrm{sw}}) + (V_{\mathrm{m}} \times \rho_{\mathrm{m}})}{V_{\mathrm{sw}} + V_{\mathrm{m}}}, \quad (1)$$

$$g_{\mathrm{animal}} = \frac{\rho_{\mathrm{animal}}}{\rho_{\mathrm{sw}}}. \quad (2)$$

This study was the first study to use glycerin instead of a hypersaline solution as the titrant. Preliminary results suggested that the titration using glycerin gave higher density values than when a hypersaline solution was used. We explored these results by conducting an experiment (6–13 August 2013) on grass shrimp (*Palaemonetes pugio*) collected from coastal Long Island. We measured the density of 41 shrimp using both methods. The glycerin titration resulted in consistently higher *g*-values than the hypersaline titration. To be able to compare data from this study with previous studies, we used the ratio of the mean shrimp *g*-values found using hypersaline solution to the mean shrimp *g*-values found using the glycerin to scale the glycerin-based data. The difference in the measured at sea *g*-value and unity was multiplied by the ratio of the hypersaline-derived *g*-value and glycerin-derived *g*-value for the lab experiments. These adjusted values are reported throughout this manuscript. We do not know the specific reason for the higher density contrast values from the glycerin method, but it may be due to a difference in osmotic pressure. The glycerin mix used in the titrations had a higher osmotic pressure (167.27 atm) than the hypersaline solution (105.30 atm). This may cause water to be expelled from the animal through osmosis at a faster rate than when the hypersaline solution is used. This would cause the animal to be more dense and result in a higher density contrast value which is what was observed in our data.

Sound speed

Sound speed measurements were made when net catches allowed for the collection of sufficient biovolumes (~10 ml or greater) of monospecific assemblages of organisms. Animals were sorted by hand to remove species other than the one of interest. In this study, we made sound speed measurements on euphausiids and the pelagic decapod *S. similis* due to their high abundances in net contents. A series of measurements of received signal level of the APOP (Acoustic Properties of zooPlankton) system were recorded using a digitizing storage oscilloscope (Chu *et al.*, 2000; Chu and Wiebe, 2005) with the chamber containing only seawater (from the ship's flow-through system) and with animals present. Temperature of the ambient seawater was recorded for each trial and salinity was recorded from the ship's flow-through system. Three sets of pings and echoes were typically recorded for both the seawater-only and animals-present trials. Data were analysed to determine the time-delay between the seawater-only and animals-present trials by an automated MATLAB program. The sound speed contrast (h) is a function of c_a, the sound speed through the zooplankton, c_{sw} the sound speed through seawater, Δ_t the travel time difference between two received waveforms (one with the chamber containing zooplankton and one without zooplankton), Φ the volume fraction (volume of the animals/volume of the acoustic chamber), and t_d the travel time of sound from the transducer to the receiver without zooplankton in the chamber [Equation (3)].

$$h = \frac{c_a}{c_{\mathrm{sw}}} = 1 + \frac{\Delta_t}{\Phi t_d}. \quad (3)$$

Morphometric measurements

After density contrasts were measured, the specimens were digitally photographed with a length scale for post-cruise measurement of their dimensions. Animals were photographed laterally and dorsally such that length, height, and width could be calculated from the image using a custom MATLAB program (Figure 4). The user clicks the endpoints for the body length measurement and the program generates ten equally spaced perpendicular guidelines in red which the user uses to measure the height (or width) along the body length. Euphausiid length was measured as the distance from the posterior of the eye to the end of the sixth abdominal segment [Standard Length (SL) 3 in Mauchline, 1980, as cited by Lawson *et al.* (2006)]. Total body length was measured for all other zooplankton taxa. The program recorded the body widths or heights at ten points along the body which provided an approximation of the body shape in both orientations.

We used the morphometric measurements from the MATLAB program to calculate the volume of euphausiids using two different approximations of the animal's shape: cylinder and a truncated cone. The cylinder volume equation used the euphausiids' maximum height (or width) and length measurements to calculate volume. The truncated cone method used all ten height (or width) measurements collected along the euphausiid body. In this method, the volume of each segment was calculated using the equation for the volume of a truncated cone. For the total euphausiid volume, the volumes for all ten segments were added together. The truncated cone method incorporates the changing shape of the euphausiid along the length of the body. We compared the results of the two methods, and investigated if they had a relationship with density contrast with a linear regression. We used the euphausiid volume and density to calculate mass, and investigated the relationship of euphausiid weight and length with a linear regression. We log (base 10) transformed both variables (euphausiid weight and length) to be able to compare our data with previous published values.

Environmental variables

Vertical profiles of environmental parameters were recorded at 22 different locations using a Seabird CTD rosette model SBE 43.

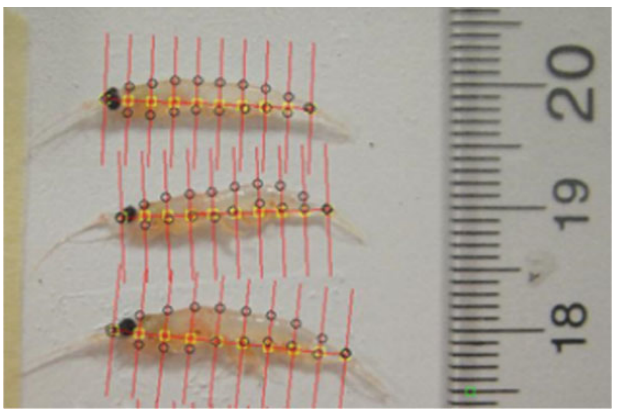

Figure 4. An example digital image showing how the morphology (body shape and size) of animals were measured with a custom MATLAB program. The open circles show where the user clicked the perimeter of the animal's body. The scale in the image is in centimetres.

The CTD measured temperature, salinity, dissolved oxygen, and fluorescence of the water column with a vertical resolution of 0.05 m. The closest CTD cast (in time and space) to each net tow was used to represent the environmental variables present during that tow. For each environmental variable, a mean water column, mean surface, and *in situ* values were calculated for data analysis. The mean water column value was calculated by taking the mean of the values measured from the minimum depth to maximum depth of the CTD cast. The surface mean was calculated by taking the mean of each variable from the surface to 3 m depth. The depth of 3 m was chosen because the mixed layer depth was 3 m or greater for all CTD casts. The *in situ* value was calculated by taking the mean of the variables measured within 10 m around the maximum depth of the associated targeted net tow. For each variable (temperature, salinity, density, fluorescence, and dissolved oxygen), the mean water column, mean surface, and *in situ* values were used to investigate whether environmental conditions affect zooplankton density contrast.

Statistical analysis

Linear regressions were used to investigate the effect of environmental parameters collected on zooplankton density contrast. In addition, linear regressions were used to identify relationships between zooplankton morphometric measurements, and relationships between density contrast zooplankton morphometrics. A type III analysis of variance (ANOVA) was used to determine if site has a significant effect on euphausiid density contrast and sound speed. We used a type III, or unbalanced ANOVA because of the imbalance of measurements between each site; however, the resulting F-statistic and p-value were identical regardless of whether a balanced or unbalanced was performed. A Tukey's honestly significant difference (HSD) test was used to look at the significant difference of euphausiid density contrasts between sites. Unless otherwise noted, values are reported as mean and standard deviation (s.d.) throughout this manuscript.

Results

Animal shape

Morphometric measurements of length, height, and width (when possible) were taken on every zooplankter after measuring its density (Table 1). Lengths were recorded for both lateral and dorsal images, however did not differ significantly ($p = 0.76$, two-sample t-test). All length values reported in this manuscript are from the lateral images. All length distributions were unimodal except for *S. similis* which was bimodal (Figure 5). Euphausiid lengths were 18.1 ± 1.9 mm, and ranged 11.2–27.5 mm. The mean and s.d. of the two length classes of *S. similis* (<37 and >37 mm) were 29.6 ± 3.09 and 41.4 ± 2.58 mm, respectively. The lengths for siphonophore bracts, chaetognaths, larval fish, amphipods, and medusae were variable (Table 1). This may be a result of measuring multiple species or age classes within each taxon.

Ten measurements of height and width at locations along the body were recorded for each zooplankter. Overall, the maximum height and width measurements were variable with length, and all maximum height values were higher than the maximum width values for all zooplankton except for the crab megalopae (Table 1). The mean of the maximum height measurement (3.03 ± 0.46 mm) for euphausiids was significantly higher ($p < 0.001$) than the mean maximum width measurement (2.56 ± 0.38 mm). The heights (and widths) of krill varied greatly with length (Figure 6). Linear regressions of euphausiid height and length as well as euphausiid width and length were not strongly correlated with R^2 of 0.26 and 0.32, respectively (Figure 7).

Euphausiid volume and wet weight

Morphometric measurements were used to calculate euphausiid volume. The truncated cone method resulted in a krill volume (70.10 ± 24.8 mm^3) that was almost half the volume calculated with the cylinder method (135.11 ± 50.9 mm^3). This was expected, however, because the truncated equation incorporates the taper of the euphausiid body. A linear regression of the truncated and cylinder volumes calculated from the two methods showed that they are

Table 1. The mean and s.d. of length, maximum height, maximum width, density contrast (g), and sound speed contrast (h) for all zooplankton taxa and species sampled.

		Length (mm)	Max height (mm)	Max width (mm)	Density contrast	Sound speed contrast	
Zooplankton taxon	***n***	**Mean ± s.d.**	**Mean ± s.d.**	**Mean ± s.d.**	**Mean ± s.d.**	***n***	**Mean ± s.d.**
Euphausiids	740	18.1 ± 1.86	3.03 ± 0.456	2.56 ± 0.383	1.058 ± 0.009	17	1.019 ± 0.009
Sergestes similis: all	204	30.9 ± 7.76	4.72 ± 0.850	3.73 ± 0.645	1.037 ± 0.005	2	1.028 ± 0.001
Large (>37 mm)	22	41.4 ± 2.58	6.45 ± 0.508	4.89 ± 0.339	1.031 ± 0.005	N/A	N/A
Small (<37 mm)	182	29.6 ± 3.09	4.51 ± 0.611	3.59 ± 0.530	1.038 ± 0.004	N/A	N/A
Siphonophores: all	108	22.4 ± 2.70	9.53 ± 3.71	4.34 ± 1.22	1.011 ± 0.009	N/A	N/A
Lensia sp.	91	21.8 ± 1.41	8.18 ± 1.37	4.12 ± 0.943	1.012 ± 0.009	N/A	N/A
Unidentified	16	24.6 ± 2.97	16.3 ± 3.65	N/A	1.002 ± 0.004	N/A	N/A
Chaetognaths	94	47.5 ± 5.16	4.97 ± 1.25	N/A	1.006 ± 0.012	N/A	N/A
Larval fish: all	91	22.5 ± 7.62	6.55 ± 2.03	N/A	1.021 ± 0.015	N/A	N/A
Sebastes sp.	65	20.5 ± 4.27	6.33 ± 1.00	2.316 ± 0.392	1.019 ± 0.015	N/A	N/A
Unidentified	26	27.7 ± 11.1	7.103 ± 3.45	N/A	1.028 ± 0.013	N/A	N/A
Larval squid	44	24.2 ± 7.51	12.1 ± 3.25	N/A	1.029 ± 0.019	N/A	N/A
Amphipods: all	38	15.0 ± 7.70	4.24 ± 1.32	3.42 ± 1.31	1.037 ± 0.011	N/A	N/A
Primno macropa	24	12.5 ± 1.93	3.59 ± 0.77	2.66 ± 0.500	1.041 ± 0.011	N/A	N/A
Phronima sp.	8	28.7 ± 2.97	6.16 ± 1.15	5.22 ± 0.836	1.027 ± 0.006	N/A	N/A
Hyperiid spp.	6	6.87 ± 0.648	4.27 ± 0.572	N/A	1.032 ± 0.006	N/A	N/A
Crab megalopae	25	9.20 ± 4.82	3.51 ± 0.540	4.57 ± 0.490	1.066 ± 0.006	N/A	N/A
Unidentified medusae	5	33.3 ± 4.17	33.0 ± 5.07	N/A	1.002 ± 0.006	N/A	N/A

The number taxa sampled is n. The ϕ value for the sound speed contrasts was 0.30 ± 0.21 with a range of 0.10 – 1.00.

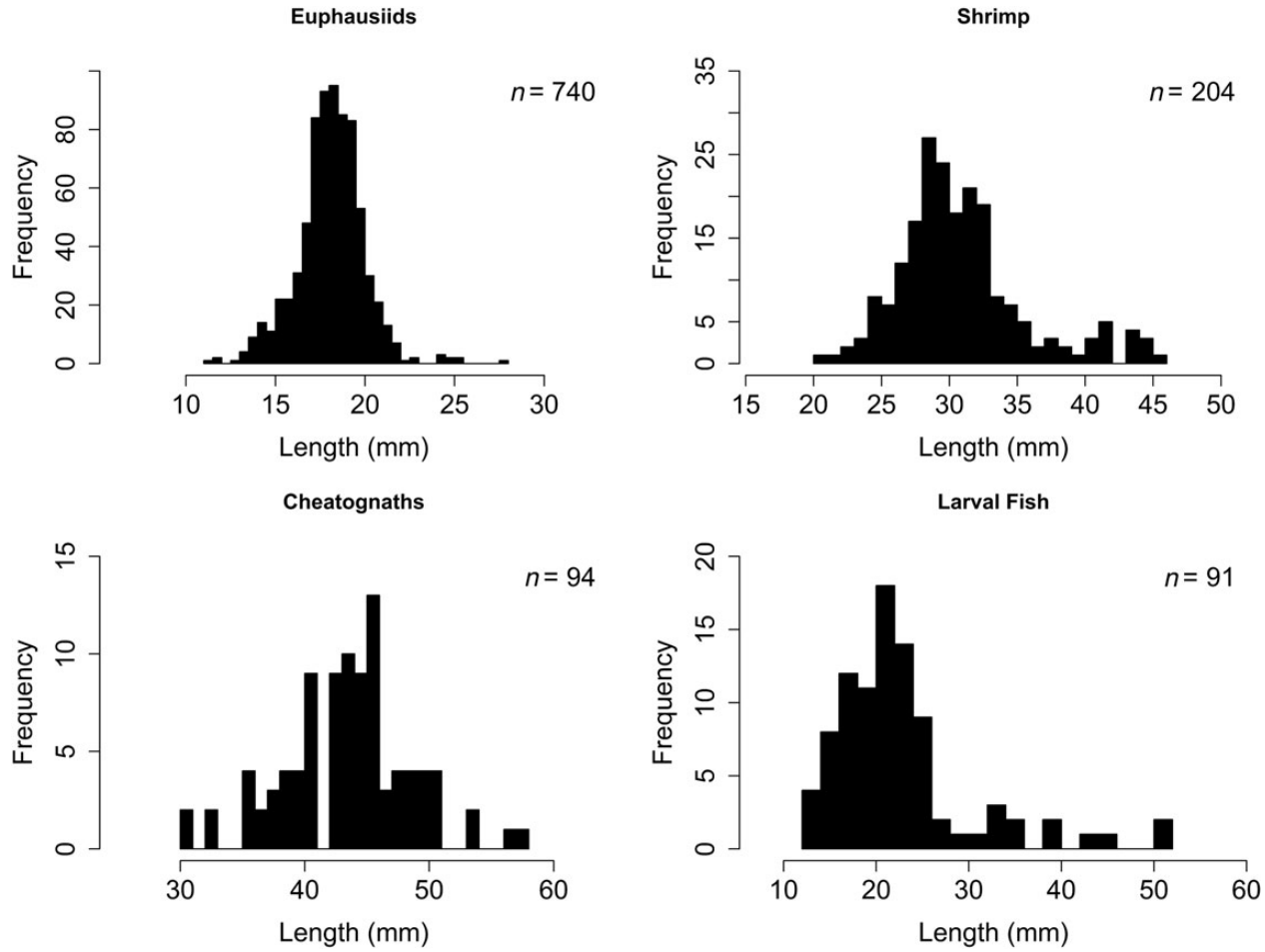

Figure 5. Length distributions for four different zooplankton taxa sampled.

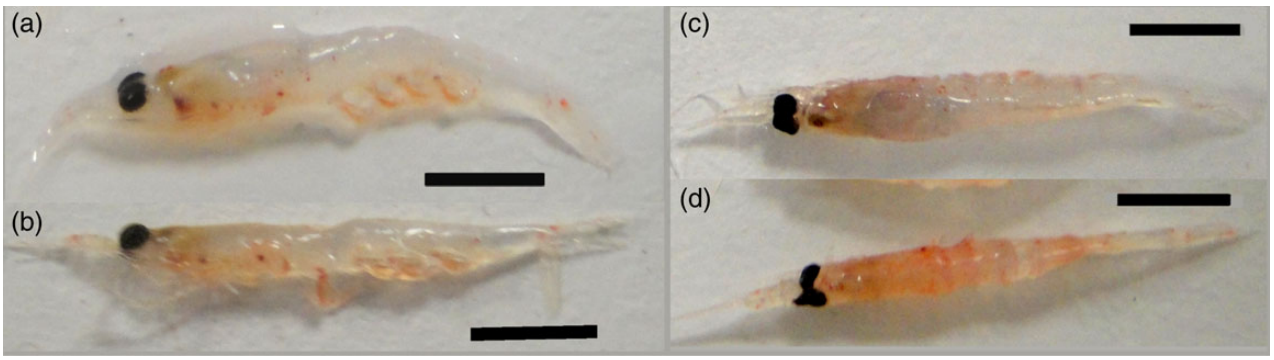

Figure 6. Photographs of four euphausiids measured in this study with the same length (18 mm) and varying heights (a and b) and widths (c and d). (a) Maximum height of 4.5 mm and a volume of 0.130 cm^3. (b) Maximum height of 2.2 mm and a volume of 0.040 cm^3. (c) Maximum width of 3.6 mm and the volume 0.089 cm^3. (d) Maximum width of 1.9 mm and the volume was 0.061 cm^3. The scale bar in the photos shows a length of 5 mm.

correlated ($R^2 = 0.86$, $p < 0.001$; Figure 8a). There was no significant difference ($p = 0.73$, two-sample t-test) between the truncated volume calculated using height or width values. Since the resulting volumes were not significantly different regardless of whether height or width values were used, we calculated the volumes using height values for the remainder of analysis. These results support the common assumption in modelling zooplankton body shape that euphausiid cross sections are circular in shape (Stanton and Chu, 2000)

Euphausiid density (measured) and truncated volume (calculated from morphometric data) were used to calculate the mass of each euphausiid measured in this study. Euphausiid mass was highly variable (76.9 $\pm$ 27.3 mg). The resulting equation from the linear regression of the log-transformed mass or weight (W) and

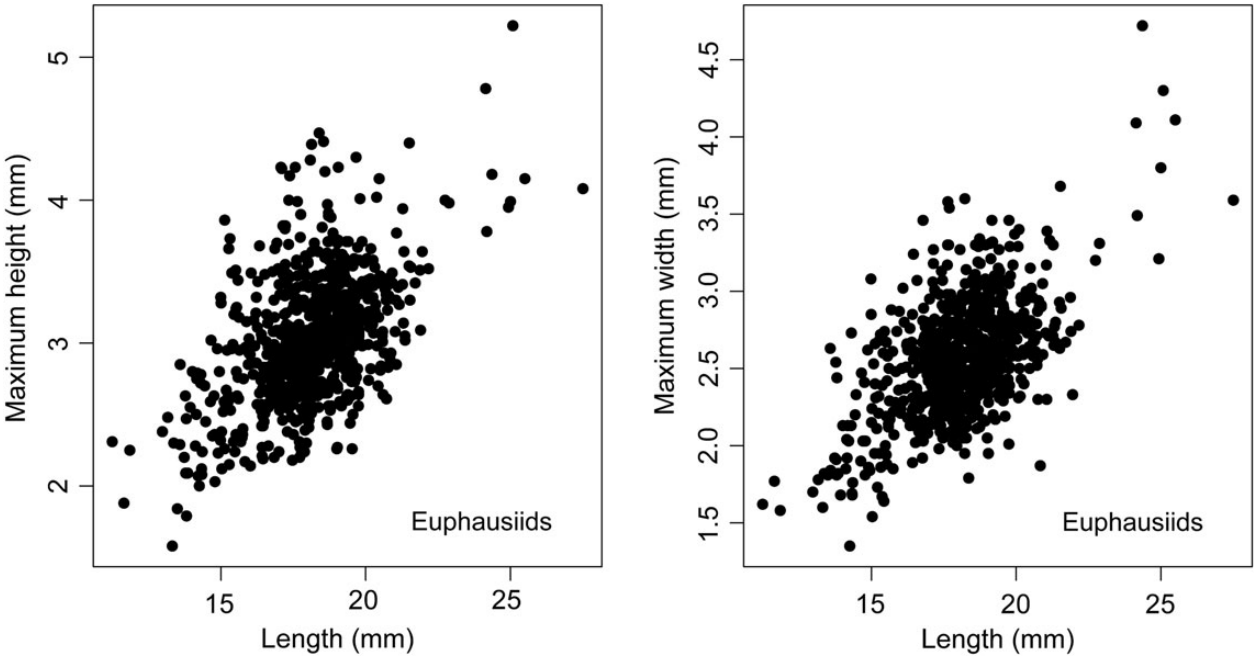

Figure 7. Relations between euphausiid maximum height (mm) and length (mm) (left panel), and between maximum width (mm) and length (mm) (right panel).

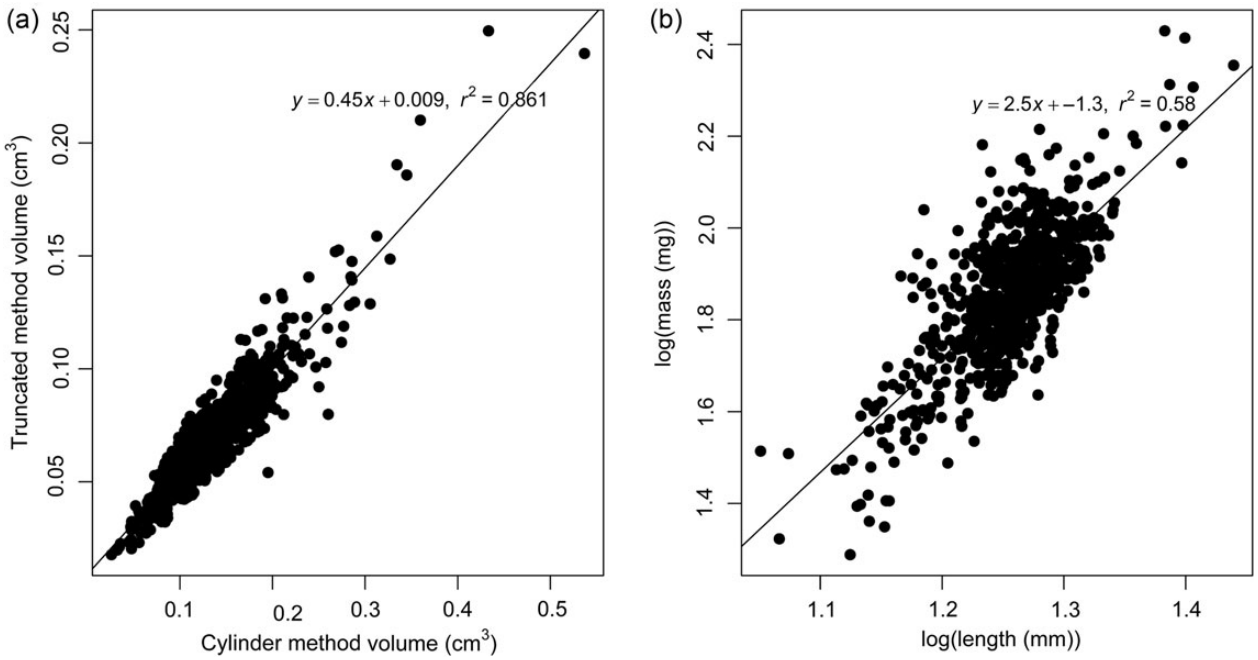

Figure 8. (a) Linear regression of euphausiid volume calculated with the truncated and cylinder method. (b) Linear regression of euphausiid log mass and log length. Mass was calculated from measured density and volume. The regression equations and correlation coefficients are shown.

length (L) was $W = 0.0527 \times L^{2.496}$ with an $R^2 = 0.58$ (Figure 8b). We used equations from the literature and the equation we developed to calculate the weight of each euphausiid measured in this study from their measured lengths. We summed the individual krill weights (calculated from the regression equations) and individual krill masses (calculated from density and volume) to create a total biomass value (Table 2). The per cent difference of the total biomass from density and volume and the total biomass from regression equations from this study and previous studies was calculated (Table 2).

Density measurements

Density contrast varied within and between zooplankton taxa (Figure 9). The number of measurements made on each taxon was

Table 2. A summary of wet weight (mg) and length (mm) regression equations from the literature and their correlation coefficients.

Publication	*n*	Type of euphausiids	Method	Equation	R^2	Total biomass (g)	Difference (%)
Davis and Wiebe (1985)	93	Atlantic euphausiids	Preserved specimens	$WW = 0.0138 \times l^{3.071}$	0.99	76.71	36.9
Wiebe *et al.* (2004)	100	Antarctic euphausiids	Preserved specimens	$WW = 0.0055 \times l^{3.206}$	0.98	45.40	19.0
Kim *et al.* (2009)	67	*E. pacifica*	Preserved	$WW = 0.0082 \times l^{3.130}$	0.99	54.16	3.3
Harvey *et al.* (2012)	530	*T. inermis*	Frozen/thawed	$WW = 0.012 \times l^{2.98}$	0.97	51.13	8.7
	248	*T. raschii*	Frozen/thawed	$WW = 0.009 \times l^{3.02}$	0.95	43.10	23.0
	186	*T. longipes*	Frozen/thawed	$WW = 0.009 \times l^{3.06}$	0.99	48.45	13.5
This study	740	Pacific euphausiids	Calculated from density and volume	$WW = 0.0527 \times l^{2.496}$	0.58	54.69	2.4

The total biomass presented here is the summation of the weights calculated using the regression equation and the lengths of euphausiids measured in this study. The total biomass in this study from measured density and volume was 56.0 g. The difference column is the per cent difference of the total biomass from the regression equation and the total biomass from density and volume in this study.

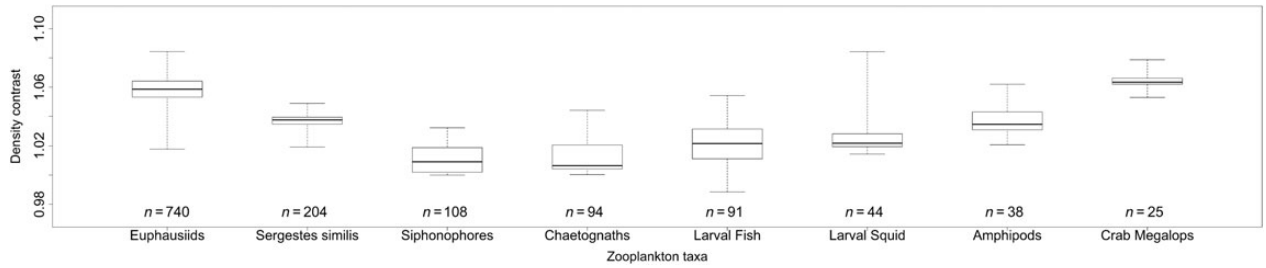

Figure 9. Density contrast for eight different zooplankton taxa. The lower line of each box represents the 1st quartile, the middle bolded line represents the median, and the top line of the box represents the 3rd quartile. The whiskers of the plot represent the minimum and maximum values.

a result of the net tow composition and animal condition. Euphausiids dominated the composition of most of the net tows and therefore resulted in the greatest number of measurements. The density of the ambient seawater used in our measurements was 1.0217 ± 0.0005 g ml^{-1}. The relationship between density contrast and the following variables was investigated for most zooplankton taxa: geographic location, depth collected, morphometrics, fluorescence, and seawater density. Only relationships between *g* and morphometric variables were investigated for crab megalopae, larval squid, amphipods, and medusae because there were not enough measurements for these taxa to investigate the effect of environmental conditions. Since this study investigated many variables relationship with density contrast, we will only report relationships with an R^2 value of >0.60.

Euphausiids

A total of 740 euphausiids were measured. The species of euphausiid was not identified as they were measured. Their *g*-values ranged from 1.018 to 1.084 with a mean and s.d. of 1.058 ± 0.009. No effect of environmental variables, depth collected, length, or volume was found on euphausiid density contrast. However, euphausiid density contrast did vary by geographic regions with different environmental conditions (Figure 10). The mean euphausiid *g* was higher at sites A2 and B than at A1. An ANOVA revealed a significant effect of site on density contrast ($p < 0.001$). However, a Tukey HSD test showed that density contrast of A2 and B did not differ significantly ($p = 0.15$). Environmental conditions at the three sites were similar and fluorescence values were low (Table 3). Smith *et al.* (2010) found a weak negative relationship between Bering Sea (BS) euphausiids and mean fluorescence. The fluorescence values in this study were much lower, and density contrasts higher than Smith

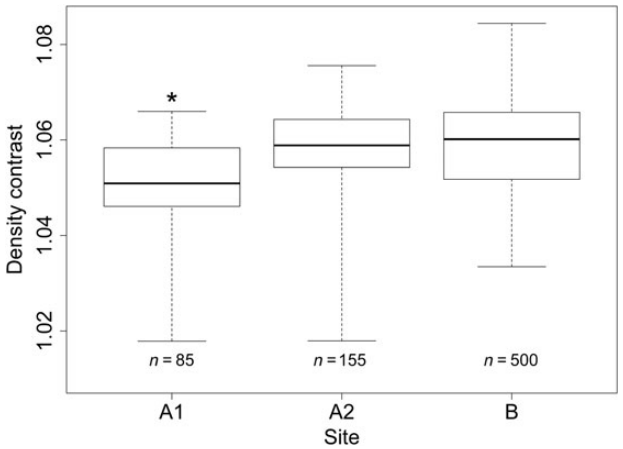

Figure 10. Euphausiid density contrast at the three different sample sites, A1, B, and A2. The lower line of each box represents the 1st quartile, the middle bolded line represents the median, and the top line of the box represents the 3rd quartile. The whiskers of the plot represent the minimum and maximum values. *Site A1 was significantly lower than the other sites. Euphausiid density contrasts at A2 and B were not significantly different.

et al. (2010). To investigate if their proposed relationship held true, we performed a linear regression on the mean euphausiid density contrasts and mean fluorescence values from each site in both studies (our sites: A1, A2, B; Smith *et al.*, 2010, sites: West and East) and found a significant negative relationship between density contrast and fluorescence ($R^2 = 0.92$, $p < 0.001$; Figure 11).

Shrimp (S. similis)

We measured the density contrast of 204 shrimp whose g-values ranged from were 1.037 ± 0.005 and ranged from 1.013 to 1.049. *Sergestes similis*' length distribution was bimodal, and the two length classes of the shrimp (<37 and >37 mm) had significantly different g-values ($p < 0.001$, two-sample t-test; Figure 12).

Table 3. The range of mean water column temperature, salinity, density, and fluorescence values for the three sampling sites A1, B, and A2.

Site	Temperature (°C)	Salinity	Density (g ml^{-1})	Fluorescence (mg m^{-3})
A1	7.62 – 8.16	33.46 – 33.58	1.027 – 1.027	0.032 – 0.058
B	7.76 – 8.34	33.47 – 33.65	1.027 – 1.027	0.032 – 0.038
A2	5.46 – 8.82	33.07 – 34.09	1.026 – 1.030	0.031 – 0.132

The mean water column environmental variables were calculated by taking the average of the values measured from the minimum to maximum depth of the CTD cast.

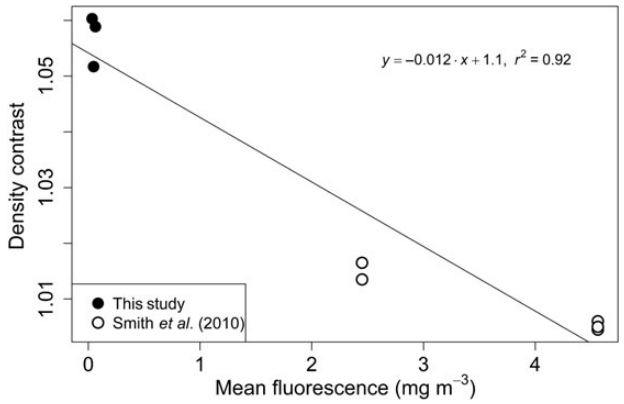

Figure 11. Euphausiid density contrast values (g) vs. mean water column fluorescence at sites from our study (A1, A2, and B) and from Smith *et al.* (2010). The regression equation and correlation coefficient are shown.

Siphonophore bracts

We measured 108 siphonophore bracts; 91 of these were identified as *Lensia* sp. The density contrast of *Lensia* sp. was 1.012 ± 0.009. The unidentified siphonophores had a density contrast of 1.002 ± 0.004. No effects of environmental or morphometric measurements on siphonophores density contrast were found.

Chaetognaths

The density contrast of 94 chaetognaths was 1.013 ± 0.012. No strong correlations between chaetognath g and environmental variables were found.

Larval fish

Ninety-one larval fish were measured; 65 of these larval fish were identified as larval rockfish (*Sebastes* sp.). The density contrast of larval rockfish was 1.019 ± 0.015, and the density contrast of unidentified larval fish was 1.028 ± 0.013.

Larval squid

Forty-four larval squid were measured. Their density contrast was 1.029 ± 0.02. No relationship between larval squid density contrast and morphometric variables was found.

Amphipods

We measured 38 amphipods; 24 were identified as *P. macropa* with a density contrast of 1.041 ± 0.012; 8 were identified as *Phronima* sp. with a density contrast of 1.027 ± 0.006; and 6 were identified as Hyperiid spp. amphipods with a density contrast of 1.032 ± 0.006. Density contrast varied among amphipod species (Figure 12). *Primno macropa* density contrast is significantly different from the density contrasts of *Phronima* sp. and *Hyperiid* spp. amphipods ($p < 0.001$, $= 0.015$, two-sample t-test). *Phronima* sp. and *Hyperiid* spp. density contrasts were not significantly different ($p = 0.14$, two-sample t-test).

Crab megalopae

Twenty-five crab megalopae were measured in this study, and their density contrast was 1.066 ± 0.006. There was no correlation between crab megalopae density contrast and length.

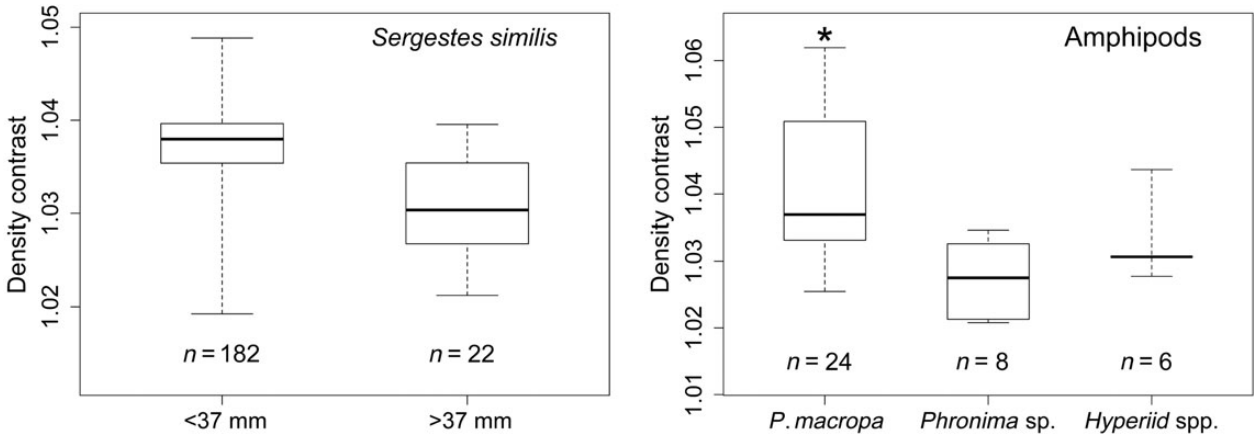

Figure 12. Density contrast varied within and among zooplankton taxa. The density contrasts were significantly different between the two length classes of Sergestid shrimp. Density contrast varied significantly between the species of amphipods sampled in this study. **P. macropa* density contrast was significantly higher than the density contrasts of *Phronima* sp. and *Hyperiid* spp. amphipods. *Phronima* sp. and *Hyperiid* spp. density contrasts were not significantly different.

Medusae

We measured five unidentified medusae, and their density contrast was 1.002 ± 0.0006.

Sound speed measurements

We measured the sound speed of 17 groups of euphausiids and two groups of shrimp. Each group was measured three times, and the mean of these three measurements was used for analysis. The mean and s.d. of the ambient seawater density in the sound speed measurements were 1.0230 ± 0.0003 g ml^{-1}. Euphausiid sound speed contrast ranged from 0.992 to 1.029 and had a mean and s.d. of 1.019 ± 0.009. The sound speed contrast for *S. similis* was 1.028 ± 0.001. Site had a significant effect on euphausiid density contrast, but it did not show a significant effect on sound speed contrast ($p = 0.89$). This may be the result of the low sample size.

Discussion

We used glycerin as the titrant for our density measurements. We chose glycerin because of its high density (1.26 g ml^{-1}), but we found that using glycerin gave consistently higher animal density values than hypersaline. This may be due to the high osmotic pressure of glycerin. Mukai *et al.* (2004) used glycerin to measure the density of *E. pacifica* using the bottle method and report similar minimum density values as our study; however, our maximum values were larger. These differences could be the result of methodological differences, such as how long the euphausiids were immersed in the glycerin. The density of the euphausiid will be more affected by osmotic pressure the longer the euphausiid is exposed to glycerin. Our measurements took between 2 and 10 min; however, Mukai *et al.* (2004) do not report the length of the time of their measurements. The effects of the high osmotic pressure of glycerin on euphausiid density should be investigated further if glycerin is used for density measurements in the future.

Only a handful of studies (Greenlaw, 1977; Greenlaw and Johnson, 1982; Køgeler *et al.*, 1987; Foote *et al.*, 1990; Chu and Wiebe, 2005; Smith *et al.*, 2010) have published *g*- and *h*-values for euphausiids, and even fewer have published values for other zooplankton taxa. The only material property data published for NEP zooplankton are over 30 years old (Greenlaw, 1977; Greenlaw and Johnson, 1982). This study provides more recent information on NEP zooplankton material properties, and the first density contrast values for the amphipods *P. macropa*, and *Phronima* sp., larval rockfish (*Sebastes* sp.), larval squid, and crab megalopae. This study also provides information on the morphometrics of zooplankton and calculates volumes for euphausiids.

Zooplankton morphometric measurements

Detailed morphometric measurements of zooplankton are rarely taken at sea because it can be difficult and time-consuming. By taking digital photographs (with a scale bar) during the cruise and using a relatively simple post-cruise analysis programme, high-resolution data of zooplankton morphometrics could be collected. Taking digital photographs of zooplankton at sea and analysing the picture post-cruise is a more efficient use of valuable cruise time than making the same measurements by hand on a moving vessel. We were able to use these data to study the effects of length, width, and height on the density contrasts of zooplankton, and to calculate euphausiid volume. We calculated euphausiid volume using two different equations: for a cylinder and a truncated cone. We found that euphausiid volume calculated using the cylinder method was nearly twice that using the truncated cone method, and they were highly correlated ($R^2 = 0.86$; Figure 8a). It is interesting that the two methods are not 100% correlated considering they are using height and length values from the same animal. The truncated method incorporates the taper of the body by using all ten height measurements to calculate volume, and is most likely the source of the observed discrepancy.

It is essential to accurately measure or estimate zooplankton volume because it (or the related biomass) is an ecologically important parameter. Euphausiid length was not strongly related to either maximum height or maximum width ($R^2 = 0.26, 0.32$, respectively) of the animal (Figure 7). The maximum height and width vary for krill of the same length (Figure 6); therefore, using only animal length to estimate euphausiid volume will not be accurate. Calculating volume using the cylinder method requires only two measurements (length and maximum height or width), but this produces an overestimation of animal volume and does not incorporate the taper of the euphausiid body. Volumes from the cylinder method and truncated method are highly correlated ($R^2 = 0.86$; Figure 8a), so one could use the regression equation to convert the measured cylinder volume to the truncated volume. It is relatively simple to take digital photographs of euphausiids collected in a net tow at sea before preservation, then use these high-resolution measurements on a subset of the animals caught to calculate the volume using both methods and produce a regression equation. Then, it would only be necessary to make two measurements (length and maximum height or width) on the rest of the euphausiids caught and calculate animal volumes directly. The benefits of this method include capturing realistic (i.e. non-preserved) values of animal size, shape, and volume information at sea while post-cruise analysis of the images can be used to examine differences in these parameters. Biovolume regressions produced in this manner would be site- and species-specific which will likely be more accurate than using published values from different geographic regions or species.

The weight–length regression from this study was compared with published equations for euphausiids (Table 2). Our correlation coefficient is lower than the other studies, but this was expected because our mass values were calculated using density values which varied widely among individual euphausiids. Euphausiid height and width varied greatly with length, so it is not surprising that our R^2-value is lower when we compare weight with length alone. However, unlike previous studies, our measurements were from animals that were not preserved or frozen. Greenlaw (1977) found that there was a significant difference ($p = 0.01$) between the density values of fresh and preserved euphausiids. Preservation or freezing may affect the wet weight–length relationship for euphausiids, so our findings may be more representative of the true relationship. Total biomass of the euphausiids measured in this study was calculated using the measured density and calculated volumes (truncated cylinder method) and compared with biomasses from weight–length regression equations from this study and the literature (Table 2). Not surprisingly, the closest biomass estimate was from the regression equation in this study, but interestingly, the next closest biomass estimate was from a study (Kim *et al.*, 2009) of *E. pacifica* which is a prevalent species of euphausiid in the NEP region. The different weight–length regressions produced biomass estimates that varied by more than 35%, so the length to weight conversion process is likely to increase the uncertainty in acoustic estimates of biomass. The photographic measurement method detailed in this study may be a relatively simple and quick way to generate length to weight relationships from live organisms

during a cruise which will result in a more accurate estimate of biomass.

Density measurements

Euphausiids

NEP Euphausiid density contrast values measured in this study span a wider range (1.018–1.084) and have a higher mean (1.058) than other published values. However, all other published euphausiid density contrast values fall within the range of values reported in this study. Greenlaw (1977) only reported density values for fresh and preserved *E. pacifica* (1.063 and 1.043 g ml^{-1}, respectively). However, Greenlaw and Johnson (1982) showed a density contrast value of 1.037 for fresh *E. pacifica* and cited Greenlaw (1977) in a table. They also reported a *g*-value for preserved euphausiids from Greenlaw (1977), but it is the same number (1.043) as the density which does not make sense. Overall, Greenlaw and Johnson (1982) reported a range of density contrast values for *E. pacifica* (1.035–1.040) and *T. raschii* (1.013–1.050). Køgeler *et al.* (1987) reported values for *Thysanoessa inermis, Thysanoessa raschii*, and *Meganyctiphanes norvegica* (1.025–1.049); Foote *et al.* (1990) reported a mean and s.d. for *E. superba* (1.036 ± 0.0067); and Chu and Wiebe (2005) also reported values for *E. superba* (1.007–1.036); and Smith *et al.* (2010) reported values for BS euphausiids (1.001–1.041).

Smith *et al.* (2010) found a significant weak negative relationship between BS euphausiid g and fluorescence ($R^2 = 0.17$, $p < 0.001$). They suggested that material properties may change with food availability; well-fed animals may have different material properties than starved animals. The average water column fluorescence values they reported ranged from 1.7 to 3.6 mg m^{-3}. However, the values of average water column fluorescence seen in this study were more than an order of magnitude lower and ranged from 0.031 to 0.132 mg m^{-3}. These values were consistent with fluorescence values reported in this region for the months of July and August (Anderson, 1964). If the relationship of fluorescence and euphausiid *g* holds true, then perhaps the higher *g*-values may be a result of a lack of available food in the environment. Although other studies that have reported euphausiid *g*-values do not report fluorescence values, Chu and Wiebe (2005) and Foote *et al.* (1990) were conducted in the Western Antarctica Peninsula region of the Southern Ocean which is a region of high productivity (Falkowski *et al.*, 1998). Køgeler *et al.* (1987) sampled from the Barents Sea which is also a productive region (Sakshaug and Slagstad, 1992). Greenlaw and Johnson (1982) made their density measurements on *E. pacifica* offshore of Oregon in summer; however, they only report measurements on 64 organisms (this study measured 740 euphausiids) which could be why our values have a wider range. Perhaps the euphausiids measured by previous studies came from areas of higher productivity, and in turn have lower density contrast values than this study. To investigate this further, we combined data from this study and Smith *et al.* (2010) and found that there was a significant negative relationship between the mean euphausiid density contrast and mean fluorescence (Figure 11). This further supports the relationship proposed in Smith *et al.* (2010), although more data need to be collected to confirm it.

We did not find a correlation between our euphausiid *g*-values and length. These findings are consistent with Smith *et al.* (2010) who also did not find a relationship between BS euphausiid density contrasts and lengths. Our findings do contrast with Chu and Wiebe (2005), who reported a positive linear relationship between Antarctic euphausiids (*E. superba* and *Euphausia crystallorophias*) length, and *g*-values. This may be a result of sampling different species. Euphausiids sampled in Chu and Wiebe (2005) were much larger with a mean length of 36.7 mm, while our euphausiids had a mean length 18.1 mm. Perhaps, density contrast is more variable in smaller euphausiids.

We found that euphausiid density contrast significantly varied by site. Sites A1 and B are different geographically and temporally (Figure 2), but A1 and A2 only differed temporally (sampled ~5–10 d after A1; Figure 10). This finding is important because it suggests that density contrast of zooplankton can vary over time as well as geographically. We do not know if the differences in density contrast of euphausiids at A1 and A2 were a result of environmental conditions changing, different groups of zooplankton present, animal composition changing, or a combination of these things. The fact that there was a significant difference in the density contrast of euphausiids from the same area within the period of a typical acoustic survey is important. This result should be investigated further in future studies to understand if it is necessary to measure material properties at the same time and geographic location of an acoustic survey to develop an accurate acoustic scattering model.

Other zooplankton

There are few studies that report material properties for zooplankton other than euphausiids: Greenlaw (1977), Greenlaw and Johnson (1982), Chu *et al.* (2003), Chu and Wiebe (2005), Lawson *et al.* (2004), and Smith *et al.* (2010). Warren and Smith (2007) and Forman and Warren (2010) report material properties of coastal species that may be comparable with the taxa in this study. We studied the effect of morphometric and environmental variables on zooplankton *g*-values. Smith *et al.* (2010) is the only other study that has looked at these relationships with zooplankton other than euphausiids. We found some relationships between zooplankton density contrast and these variables, but only relationships with a correlation coefficient lower than 0.6 were found. More detailed discussion of these findings by taxon is found below.

The range of density contrast values we measured for NEP *S. similis* was 1.019–1.049. Greenlaw (1977) is the only study that contains material property estimates for *S. similis* and they report a density of 1.051 for preserved specimens. They do not report a density contrast (*g*) value, but the range, mean, and s.d. of density values of our samples were 1.041–1.070, and 1.059 ± 0.005 g cm^{-3}. The value reported in Greenlaw (1977) is close to this study's density values for NEP *S. similis*. They also report finding a significant difference between density values of fresh euphausiids and preserved euphausiids ($p = 0.01$), so their *g*-value may be different, since the NEP shrimp were measured immediately after collection. Forman and Warren (2010) reported *g*-values for decapods from coastal Long Island (*P. pugio and Crangon septemspinosa*), and their values ranged from 0.870 to 1.085. Chu and Wiebe (2005) reported two mean and s.d. *g*-values for the decapod *Mysid arctomysis*: 1.041 ± 0.008 and 1.024 ± 0.008. Smith *et al.* (2010) reported that density contrast varies within and between species. The range of NEP decapod *g*-values measured here overlaps with both of these studies. The *g*-values from Forman and Warren (2010) have a much lower range than ours, but this might be a result of density contrast varying by species. Smith *et al.* (2010) found that BS euphausiid *g* had a negative relationship with fluorescence, and proposed this could be due to well-fed euphausiids containing more lipids which would result in

a lower density. Our results show a similar pattern; larger shrimp could be correlated with better fed shrimp which would decrease their density contrast (Figure 12).

The range of the density contrast for siphonophore bracts measured was 1.00–1.032. The density contrast for Antarctic siphonophores is 1.02 which falls within our range of values, and is the only other published density contrast for siphonophores (D. Chu, pers. comm. as cited by Lawson *et al.*, 2004). Our wider range of values may be a result of a larger sample size, or different species and location. Since relationships between siphonophore *g* and both morphometric and environmental variables have not been previously studied, it is not clear whether the non-existence of these relationships is significant to this study.

The density contrast of NEP chaetognaths was 1.013 ± 0.012. Smith *et al.* (2010) is the only other study that published *g*-values for chaetognaths, and the density contrast of BS chaetognaths was 1.014 ± 0.007 which is very similar to our measurement. The density contrast found for all larval fish was 1.021 ± 0.015, and larval rockfish was 1.019 ± 0.015. No other studies have reported *g*-values for larval fish in the NEP. Smith *et al.* (2010) reported *g*-values for larval fish in the BS with a mean of 1.023, which is close to the NEP *g*-values. Chu *et al.* (2003) reported *g*-values for cod larvae that had a range of 0.969–1.014. Our values are higher; however, this may be because the larvae sampled in this study were a different species than the larvae in Chu *et al.* (2003). The larvae sampled by Chu *et al.* (2003) were also smaller than the larval fish sampled in this study [Chu *et al.* (2003) lengths ranged from 4.48 to 10.94 mm; our NEP length ranged from 12.26 to 51.07 mm].

The range of amphipod *g*-values measured in this study was 1.021–1.062. This study is the first to report density values for *P. macropa*, and *Phronima* sp. There have been other studies which have published values for other species of amphipods. Greenlaw and Johnson (1982) reported *g*-values for four amphipods (*Cyphocaris* sp., *Gammarus pulex, Parathemisto pacifica*, and *Sciva* sp.) which ranged from 1.055 to 1.088. Chu and Wiebe (2005) published mean *g*-values for *Themisto* sp. amphipods of 1.024 and 1.051, and Smith *et al.* (2010) published *g*-values for BS amphipods (*Themisto libellula*) that ranged from 1.001 to 1.029. Our values overlap with some of these published values, but the range of values presented by Smith *et al.* (2010) is on the lower end of our range. Again, this could be a result of *g*-values changing with species, location, or food availability. We found that density contrast varied significantly with amphipod species in this study (Figure 12). This finding shows that it may be important to have species-specific material property values for amphipods, to have an accurate scattering model for amphipods.

The range of *g*-values for the five unidentified NEP medusae we measured was 1.002–1.003. Two studies have published density contrasts for medusae: Warren and Smith (2007) and Smith *et al.* (2010), with ranges of 1.004–1.02 and 1.001–1.006, respectively. The NEP medusa density contrasts overlap with the findings of both these studies. This study had a very small sample size ($n = 5$), so these results may not be a good representation of the medusae in this region.

Currently, no published *g*-values exist for larval squid or crab megalopae. The crab megalopae had the highest mean *g*-value (1.066) of the zooplankton sampled in this study. The density contrast of larval squid was 1.029 ± 0.019. No effect of length was seen on density contrast of these taxa.

Sound speed measurements

The sound speed was only measured for groups of euphausiids and sergestid shrimp because not all zooplankton taxa were caught in high enough biovolumes for the method. The sound speed contrast for NEP euphausiids in this study had a mean and s.d. of 1.019 ± 0.009 and ranged from 0.992 to 1.029. This is higher than the values reported for BS euphausiids by Smith *et al.* (2010) who reported a mean and s.d. of 1.006 ± 0.008. However, the range for NEP euphausiids sound speed contrast in this study agreed with the range Smith *et al.* (2010) reported for the BS euphausiids (NEP: 0.992–1.029, BS: 0.990–1.017). This study's range of sound speed contrasts for NEP euphausiids also agrees with the range Greenlaw and Johnson (1982) reported for *E. pacifica* (1.00–1.022). This is important since it is likely that *E. pacifica* was one of the species in the NEP euphausiids we measured. The NEP euphausiid sound speed contrasts in this study are lower than those reported by Køgeler *et al.* (1987) for *M. norvegica* and a mixture of *T. inermis* and *T. raschii* (1.030 ± 0.01 and 1.026 ± 0.005), Foote (1990) for *E. superba* (1.028 ± 0.002), and Chu and Wiebe (2005) for *E. superba* (1.030 ± 0.004). There was no effect of site on the sound speed contrasts of the NEP euphausiids. This may be a result of a small number of measurements, and may not be representative of the true effect.

The sound speed values we measured for *S. similis* (1.028 and 1.027) are much higher than the two values in Greenlaw and Johnson (1982), the only other study to publish *h*-values for this species (1.006 and 0.997). Forman and Warren (2010) reported sound speed contrasts for two species of decapods (*P. pugio* and *Crangon septemspinosa*) from coastal Long Island, and the mean and s.d. of their values were 0.995 ± 0.008 and 0.973 ± 0.046, respectively. These values are lower than the values found in this study for *S. similis*, but this could be because *P. pugio* and *Crangon septemspinosa* are different species and live in coastal rather than a pelagic environments. More sound speed measurements on decapods need to be taken to be able to understand how sound speed contrasts change within species, between species, and between environments.

Material property parameters are important in acoustic scattering models, and changes in these parameters can have large effects on the model-estimated target strength. Chu *et al.* (2000) showed that a 2–4% change in material property values could change the target strength estimate of a scattering model up to 20 dB. Many scientists use material property values from Foote *et al.* (1990) in their scattering models for euphausiids as well as many other zooplankton. Changes in target strength can significantly alter biomass estimates. Demer and Conti (2005) updated a scattering model for Antarctic krill (*E. superba*) and showed that the target strength estimate from the new model was ~3–7 dB different from the old model depending on krill lengths. This small change in target strength increased the biomass by a factor of 2.5. The density contrast values found in this study differ from the values in Foote *et al.* (1990) by more than 2%, so using values from this study to model NEP euphausiids could significantly affect the target strength estimate. Updated target strength estimates for NEP euphausiids may have significant changes in biomass estimates. Obtaining an accurate euphausiid biomass estimate for the NEP is essential because euphausiids are a crucial link in this ecosystem because they transfer energy from primary producers to higher trophic levels. Using the material property values presented in this study may result in a more constrained estimate of target strength and biomass estimates for NEP zooplankton.

Conclusion

This paper reports the first material properties values on NEP zooplankton in over three decades. We measured the density contrasts of euphausiids, decapods (*S. similis*), siphonophores, chaetognaths, larval fish, larval squid, amphipods (*P. macropa, Phronima* sp.), crab megalopae, and medusae. Values of *g* varied within and between taxa as well as among different geographic regions. Density contrast of euphausiids varied with site with the euphausiids sampled at site A1 were significantly lower than euphausiids sampled at sites A2 and B. Euphausiid g-values were significantly different for animals from the same geographic region (A) which were sampled ~10 d later. We also observed weak relationships between zooplankton *g*-value and several morphometric and environmental parameters. Sound speed contrast was measured for groups of two zooplankton taxa, euphausiids, and pelagic decapods (*S. similis*). Sound speed contrasts varied within and between taxa; however, no effect of location was found for euphausiid sound speed contrast. The material property values in this study may improve estimates of target strength from scattering models for NEP zooplankton. More material property data are needed to help us further understand how they are affected by morphometric, geographic, and environmental variables. This study provides material property data for NEP zooplankton which can improve acoustic scattering models, which may lead to more accurate estimates of zooplankton biomass in this region.

Acknowledgements

This project was funded by the Office of Naval Research (Grant N00014-11-1-0146) to Kelly Benoit-Bird, Dezhang Chu, and JDW. This work would not have been possible without the help of the Captain and crew of the RV Oceanus. Due to all of our equipment for this cruise being destroyed in a freight train derailment (which we were notified ~2 d before the cruise began), we are forever grateful to the generosity of our fellow cruise scientists (Kelly Benoit-Bird and Dezhang Chu) who shared equipment. Additionally, Angel White, Fred Prahl, and Mary Hitch at Oregon State University generously loaned us equipment and supplies when we (essentially) showed up on their doorstep unannounced and in need of assistance. Neal McIntosh, David Cade, Aaron Gann, and Chad Waluk conducted all net and CTD casts aboard the RV Oceanus. Stephanie Mincieli and Emily Markowitz assisted with shipment preparation and data collection aboard the ship. Alyssa Stevens collected zooplankton morphometric data after the cruise. Sam Urmy provided helpful comments and suggestions on this manuscript.

References

Anderson, G. C. 1964. The seasonal and geographic distribution of primary productivity off the Washington and Oregon coasts. Limnology and Oceanography, 9: 284–302.

Brodeur, R., and Pearcy, W. 1990. Trophic relations of juvenile Pacific salmon off the Oregon and Washington coast. Fishery Bulletin, 88: 617–636.

Brodeur, R. D., Pearcy, W. G., and Ralston, S. 2003. Abundance and distribution patterns of nekton and micronekton in the Northern California Current Transition Zone. Journal of Oceanography, 59: 515–535.

Chu, D., Wiebe, P., and Copley, N. 2000. Inference of material properties of zooplankton from acoustic and resistivity measurements. ICES Journal of Marine Science, 57: 1128–1142.

Chu, D., and Wiebe, P. H. 2005. Measurements of sound-speed and density contrasts of zooplankton in Antarctic waters. ICES Journal of Marine Science, 62: 818–831.

Chu, D., Wiebe, P. H., Copley, N. J., Lawson, G. L., and Puvanendran, V. 2003. Material properties of North Atlantic cod eggs and early-stage larvae and their influence on acoustic scattering. ICES Journal of Marine Science, 60: 508–515.

Croll, D. A., Tershy, B. R., Hewitt, R. P., Demer, D. A., Fiedler, P. C., Smith, S. E., Armstrong, W., *et al.* 1998. An integrated approach to the foraging ecology of marine birds and mammals. Deep Sea Research II: Topical Studies in Oceanography, 45: 1353–1371.

Davis, C. S., and Wiebe, P. H. 1985. Macrozooplankton biomass in a warm-core Gulf Stream ring: time series changes in size structure, taxonomic composition, and vertical distribution. Journal of Geophysical Research: Oceans (1978–2012), 90: 8871–8884.

Demer, D. A., and Conti, S. G. 2005. New target-strength model indicates more krill in the Southern Ocean. ICES Journal of Marine Science, 62: 25–32.

Falkowski, P. G., Barber, R. T., and Smetacek, V. 1998. Biogeochemical controls and feedbacks on ocean primary production. Science, 281: 200–206.

Foote, K. G. 1987. Fish target strengths for use in echo integrator surveys. Journal of the Acoustical Society of America, 82: 983–987.

Foote, K. G. 1990. Speed of sound in *Euphausia superba*. Journal of the Acoustical Society of America, 87:1405–1408.

Foote, K. G., Everson, I., Watkins, J. L., and Bone, D. G. 1990. Target strengths of Antarctic krill (*Euphausia superba*) at 38 and 120 kHz. Journal of the Acoustical Society of America, 87:16–24.

Foote, K. G., and Stanton, T. K. 2000. Acoustical methods. *In* ICES Zooplankton Methodology Manual (Chapter 6), pp. 223–258. Ed. by R. Harris, P. H. Wiebe, J. Lenz, H. R. Skjoldal, and M. Huntley. Academic Press, London.

Forman, K. A., and Warren, J. D. 2010. Variability in the density and sound-speed of coastal zooplankton and nekton. ICES Journal of Marine Science, 67: 10–18.

Glycerin; ICSC No. 0624 (U.S. National Version) [Online]. National Institute for Occupational Safety and Health, Centers for Disease Control and Prevention, Atlanta, GA, 2007. http://www.cdc.gov/niosh/ipcsneng/neng0624.html (last accessed 10 December 2012)

Gómez-Gutiérrez, J., Peterson, W. T., and Miller, C. 2005. Cross-shelf life-stage segregation and community structure of the euphausiids off central Oregon (1970–1972). Deep Sea Research II: Topical Studies in Oceanography, 52: 289–315.

Greenlaw, C. F. 1977. Backscattering spectra of preserved zooplankton. Journal of the Acoustical Society of America, 62: 44–52.

Greenlaw, C. F. 1979. Acoustical estimation of zooplankton populations. Limnology and Oceanography, 24: 226–242.

Greenlaw, C. F., and Johnson, R. K. 1982. Physical and acoustical properties of zooplankton. Journal of the Acoustical Society of America, 72: 1706–1710.

Harvey, H. R., Pleuthner, R. L., Lessard, E. J., Bernhardt, M. J., and Tracy Shaw, C. 2012. Physical and biochemical properties of the euphausiids *Thysanoessa inermis*, *Thysanoessa raschii*, and *Thysanoessa longipes* in the eastern Bering Sea. Deep Sea Research II: Topical Studies in Oceanography, 65: 173–183.

Isaacs, J.D., and Kidd, L.W. 1953. Isaacs–Kidd midwater trawl. Scripps Institute Oceanography Ref, 53–53.

Kim, H. S., Yamaguchi, A., and Ikeda, T. 2009. Abundance, biomass and life cycle patterns of euphausiids (*Euphausia pacifica*, *Thysanoessa inspinata* and *T. longipes*) in the Oyashio region, western subarctic Pacific. Plankton and Benthos Research, 4: 43–52.

Køgeler, J., Falk-Petersen, S., Kristensen, Å., Pettersen, F., and Dalen, J. 1987. Density- and sound speed contrasts in sub-Arctic zooplankton. Polar Biology, 7: 231–235.

Lawson, G. L., Wiebe, P. H., Ashjian, C. J., Gallager, S. M., Davis, C. S., and Warren, J. D. 2004. Acoustically-inferred zooplankton distribution in relation to hydrography west of the Antarctic Peninsula. Deep Sea Research II: Topical Studies in Oceanography, 51: 2041–2072.

Lawson, G. L., Wiebe, P. H., Ashjian, C. J., Dezchang, C., and Stanton, T. K. 2006. Improved parameterization of Antarctic krill target

strength models. Journal of the Acoustical Society of America, 119: 232–242.

Mackas, D. L., Kieser, R., Saunders, M., Yelland, D. R., Brown, R. M., and Moore, D. F. 1997. Aggregation of euphausiids and Pacific hake (*Merluccius productus*) along the outer continental shelf off Vancouver Island. Canadian Journal of Fisheries and Aquatic Sciences, 54: 2080–2096.

Mauchline, J. 1980. Measurement of body length of *Euphausia superba* Dana. BIOMASS Handbook, 4: 4–9.

Mukai, T., Iida, K., Ando, Y., Mikami, H., Maki, Y., and Matsukura, R. 2004. Measurements of swimming angles, density, and sound speed of the krill *Euphausia pacifica* for target strength estimation. OCEANS'04 MTS/IEEE TECNO OCEAN '04 Conference Proceedings, pp. 383–388.

Sakshaug, E., and Slagstad, D. 1992. Sea ice and wind: effects on primary productivity in the Barents Sea. Atmosphere-Ocean (Canadian Meteorological and Oceanographic Society), 30: 579–591.

Simmonds, J., and MacLennan, D. 2005. Fisheries Acoustics: Theory and Practice, 2nd ed. Blackwell Science., Oxford, UK.

Smith, J. N., Ressler, P. H., and Warren, J. D. 2010. Material properties of euphausiids and other zooplankton from the Bering Sea. Journal of the Acoustical Society of America, 128: 2664–2680.

Smith, J. N., Ressler, P. H., and Warren, J. D. 2013. A distorted wave Born approximation target strength model for Bering Sea euphausiids. ICES Journal of Marine Science, 70: 204–214.

Stanton, T. K., and Chu, D. Z. 2000. Review and recommendations for the modelling of acoustic scattering by fluid-like elongated zooplankton: euphausiids and copepods. ICES Journal of Marine Science, 57: 793–807.

Stanton, T. K., Chu, D. Z., and Wiebe, P. H. 1996. Acoustic scattering characteristics of several zooplankton groups. ICES Journal of Marine Science, 53: 289–295.

Tyler, H., and Pearcy, W. 1975. The feeding habits of three species of lanternfishes (family Myctophidae) off Oregon, USA. Marine Biology, 32: 7–11.

Ware, D. M., and Thomson, R. E. 2005. Bottom-up ecosystem trophic dynamics determine fish production in the Northeast Pacific. Science, 308: 1280–1284.

Warren, J. D., and Smith, J. N. 2007. Density and sound speed of two gelatinous zooplankton: ctenophore (*Mnemiopsis leidyi*) and lion's mane jellyfish (*Cyanea capillata*). Journal of the Acoustical Society of America, 122: 574–580.

Warren, J. D., Stanton, T. K., McGehee, D. E., and Chu, D. 2002. Effect of animal orientation on acoustic estimates of zooplankton properties. IEEE Journal of Oceanic Engineering, 27: 130–138.

Wiebe, P., Ashjian, C., Gallager, S., Davis, C., Lawson, G., and Copley, N. 2004. Using a high-powered strobe light to increase the catch of Antarctic krill. Marine Biology, 144: 493–502.

Handling editor: David Demer