Material properties of Pacific hake, Humboldt squid, and two species of myctophids in the California Current

Kaylyn N. Becker and Joseph D. Warren[a)]
School of Marine and Atmospheric Sciences, Stony Brook University, 239 Montauk Highway, Southampton, New York 11968, USA

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Material properties of the flesh from three fish species (*Merluccius productus*, *Symbolophorus californiensis*, and *Diaphus theta*), and several body parts of the Humboldt squid (*Dosidicus gigas*) collected from the California Current ecosystem were measured. The density contrast relative to seawater varied within and among taxa for fish flesh (0.9919−1.036), squid soft body parts (mantle, arms, tentacle, braincase, eyes; 1.009−1.057), and squid hard body parts (beak and pen; 1.085−1.459). Effects of animal length and environmental conditions on nekton density contrast were investigated. The sound speed contrast relative to seawater varied within and among taxa for fish flesh (0.986−1.027) and Humboldt squid mantle and braincase (0.937−1.028). Material properties in this study are similar to values from previous studies on species with similar life histories. In general, the sound speed and density of soft body parts of fish and squid were 1%−3% and 1%−6%, respectively, greater than the surrounding seawater. Hard parts of the squid were significantly more dense (6%−46%) than seawater. The material properties reported here can be used to improve target strength estimates from acoustic scattering models, which could increase the accuracy of biomass estimates from acoustic surveys for these nekton.
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I. INTRODUCTION

The California Current (CC) ranges from the coast of British Columbia, Canada (~50°N) to Baja California, Mexico (15°−25°N) and is one of the major eastern boundary currents in the Northeast Pacific ocean (Hickey, 1979). The seasonal upwelling of nutrients in the CC ecosystem supports many commercially important fish stocks such as anchovy, hake, mackerel, and sardine through bottom-up trophic linkages (Brodeur *et al.*, 2003; Ware and Thomson, 2005). The CC also supports a community of smaller, deep-dwelling fishes such as myctophids (lantern fish) which contribute significantly to the fish biomass in this region (Brodeur and Yamamura, 2005). The Humboldt squid (*Dosidicus gigas*) has recently expanded its northern range in the CC and has invaded the waters of central California (Zeidburg and Robison, 2007). It has been observed that *D. gigas* are active predators on myctophids and Pacific hake in this region (Field *et al.*, 2007).

Merluccius productus (Pacific hake) is an abundant fish species in the CC, and is both economically and commercially important (Methot and Dorn, 1995; Grover *et al.*, 2002). They are roughly 60% of the pelagic biomass in the CC ecosystem, and in 2012 the landings in the United States and Canada were 157 and 47×10^6 metric tons, respectively (Hicks *et al.*, 2012; Ware and McFarlane, 1995). In the CC ecosystem, Pacific hake act as a link in the food chain between other commercially important fish such as Pacific herring and marine mammals (Bailey *et al.*, 1982).

Myctophids are one of the most ecologically important and abundant taxonomic groups of mesopelagic fish in the ocean, yet they tend to be undersampled in most field studies because they are smaller than the mesh of large fish trawls (Gjøsaeter and Kawaguchi, 1980), and they can avoid plankton sampling gear (Brodeur and Yamamura, 2005). There are approximately 250 species in 33 genera and they inhabit all of the world's oceans except the Arctic (Catul *et al.*, 2011). Myctophids act as an important ecological link from zooplankton such as copepods and euphausiids to larger predators such as tuna and marine mammals (Brodeur and Yamamura, 2005). They can be found throughout the CC region, and they account for the majority of the biomass of fish in the Northeast Pacific region (Gjøsaeter and Kawaguchi, 1980).

Dosidicus gigas is one of the largest species of squid reaching lengths of 2.5 m, and its range in the Eastern Pacific is from 47°S to 40°N (Nigmatullin *et al.*, 2001). Field *et al.* (2007) examined gut contents of Humboldt squid found in the CC region, and they reported that Pacific hake and the myctophid, *Stenobrachius leucopsarus* were the most frequent species found. Humboldt squid are essential to the CC ecosystem because they are important prey for large fish and marine mammals which transfers energy to higher trophic levels (Gilly *et al.*, 2006). The Humboldt squid fishery is the largest squid fishery in the world, with landings of more than 800 000 tons in 2010 (FAO, 2010) making them an economically important species. Due to the lack of knowledge about the biology and life history of *D. gigas* the fishery started without accurate stock information and has not been managed with consistent methods (Nevdrez-Martinez *et al.*, 2010). *D. gigas* is susceptible to overfishing because their

[a)]Electronic mail: joe.warren@stonybrook.edu

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one year lifespan makes their population sensitive to recruitment variability (Nigmatullin *et al.*, 2001; Goss *et al.*, 2001).

Acoustic technology allows scientists to study nekton at finer temporal and spatial scales than can be achieved by traditional net sampling methods (Simmonds and MacLennan, 2005). Echosounders transmit acoustic energy into the water column which produces backscatter when the acoustic wave encounters a region or object with different acoustic impedance than the surrounding seawater (Shibata, 1970; Simmonds and MacLennan, 2005). This backscattered energy can be used to estimate animal biomass; however, to have an accurate estimate of biomass, a constrained estimate of target strength is needed for the scatterer (Simmonds and MacLennan, 2005; Yasuma *et al.*, 2009). Target strength is a logarithmic measure of the energy scattered by an object back toward the source and is a function of the size, shape, orientation, and material properties of the target (Shibata, 1970; Simmonds and MacLennan, 2005). It can be measured empirically; however, few studies have been conducted where TS and all the various parameters which may affect it are measured concurrently because it is logistically difficult (Foote *et al.*, 1987; Simmonds and MacLennan, 2005; Yasuma *et al.*, 2009). Physics-based mathematical target strength models can estimate target strength by using parameters such as length and material properties to calculate the target strength of an organism (Shibata, 1970; Yasuma *et al.*, 2009). Two material properties needed for the target strength models are the animal's density (g) and sound speed (h) contrasts relative to the density of the surrounding seawater (Shibata, 1970).

Foote (1980) showed that at a 120 kHz frequency, the gas-filled swimbladder in 25–45 cm fish can account for 90% or more of the backscatter from the animal. Since the swimbladder is such a strong scatterer, target strength models have been developed using properties of the swimbladder (reviewed in Simmonds and MacLennan, 2005). These models assume that all the backscatter from the fish is a result of the swimbladder, and do not account for the added backscatter or dampening effect the surrounding fish flesh may have on the target strength of the fish. Fish use swimbladders for buoyancy control, so the size and shape of a swimbladder are not constant. This variability may change how much the swim bladder contributes to the total backscatter, making fish flesh scattering more important (Gorska *et al.*, 2007). Additionally, not all fish have gas-filled swimbladders. Some fish including certain species of myctophids have a lipid-filled swimbladder (Butler and Pearcy, 1972), and other fish, including commercially important species such as the Atlantic mackerel (*Scomber scumbus*) have no swimbladder at all (Sigfusson *et al.*, 2001).

Knowledge of the acoustic properties of fish flesh may allow for the development of more accurate target strength models for fish. However, it should be noted that model predictions of TS can have inaccuracies due to limitations of the model itself or inaccuracies in the parameters input to the model. Gorska *et al.* (2007) modeled the acoustic scattering of groups of Atlantic mackerel and found that the backscatter was dominated by fish flesh at low frequencies (18 and 38 kHz). The material properties for fish flesh used in the scattering model in Gorska *et al.* (2007) were from calculations and were not measured directly, so empirical material property values may improve the accuracy of these models. Several studies have measured various acoustic properties of fish: Brawn (1969) measured the density of different body parts of Pacific herring (*Clupea pallasii);* Shibata (1970) measured the material properties of fish flesh from the several species including Pacific herring and common mackerel (*Pneumatophorus j. japonicas*); Butler and Pearcy (1972) report the specific gravity of previously frozen Oregon myctophids including California headlight fish (*Diaphus theta*)*;* Iida *et al.* (2006) reports estimates of material properties for fish flesh from an acoustic camera (Sand lance and *Stichaeidae*); Yasuma *et al.* (2009) measured the material properties of whole Japanese sand eel (*Ammodytes personatus*); Forman and Warren (2010) reported material property values for whole striped mummichug (*Fundulus majalis*) and common mummichug (*Fundulus heteroclitus*); and Davison (2011) measured the specific gravity (relative to freshwater) of 71 species of mesopelagic fish species including California headlight fish and California lantern fish (*Symbolophorus californiensis*) after air was removed from the swimbladder. In addition Neighbors and Nafpaktitis (1982) report the buoyancy of many species of mesopelagic fish including the California headlight fish and California lantern fish. This study is the first to report material property data for Pacific hake. These data are particularly important because acoustic surveys are the stock assessment method used for this fishery. The target strength value currently used in these assessments is based on only a few *in situ* observations (Williamson and Traynor, 1984; Hesler *et al.*, 2004).

Similarly, additional data on the material properties of Northeast Pacific myctophids are needed to better understand how they scatter sound. Myctophids, euphausiids, and other micronekton create the deep scattering layer (DSL) in the Pacific (Catul *et al.*, 2011; Dietz, 1948; Hazen and Johnston, 2010). Although empirical target strength measurements have been made for a few species of myctophids (Benoit-Bird and Au, 2001; Yasuma *et al.*, 2006; Yasuma *et al.*, 2010), none have been made for myctophids in the Northeast Pacific.

Sampling squid utilizing traditional net methods presents challenges because of their varying abundance, quick movement, and ability to avoid nets (Starr and Thorne, 1998). Goss *et al.* (2001) suggested that acoustic tools could be used for squid stock assessments even though they are weaker scatterers than fish. Several studies have reported on various acoustic properties of different species of squid: *Todarodes pacificus* (Arnaya *et al.*, 1989; Kang *et al.*, 2005; Kang *et al.*, 2006; Kawabata, 2005), *Ommastrephes bartrami* (Arnaya *et al.*, 1989), *Loligo bleekeri* (Arnaya *et al.*, 1989), *Loligo reynaudii* (Soule *et al.*, 2010), and *Dosidicus gigas* (Benoit-Bird *et al.*, 2008). Many of these studies have focused on target strength, or investigating how the target strength is affected by tilt angle; but only two have focused on material properties of these animals. Kang *et al.* (2006) measured material properties (for the Japanese common squid *Todarodes pacificus*) and Iida *et al.* (2006) estimated material properties of Japanese common squid mantle using an acoustic camera. No previous studies (that we are aware of) have reported material property values for Humboldt squid.

Benoit-Bird *et al.* (2008) was the first study to empirically measure target strength of *D. gigas*. They proposed that scattering may be caused by different body parts of the Humboldt squid (the beak, arms, eyes, and braincase) because the target strength changed with the removal of these body parts. Since material property measurements for these body parts did not exist, there was no way to compare the empirical measurements with theoretical target strength predictions from scattering models.

This study measured density (*g*) and sound speed (*h*) contrast of nekton collected from two locations in the California Current system: the Oregon coast and Monterey Bay. We measured the material properties of Humboldt Squid body parts (mantle, braincase, arm, tentacle, eye, beak, and pen [gladius]); Pacific hake (*Merluccius productus*) flesh; and the flesh of two species of myctophids: the California Lantern fish (*Symbolophorus californiensis*) and the California Headlight fish (*Diaphus theta*). Density and sound speed contrasts were calculated for body parts of fish and squid specimens. Relationships between the material properties of specimens with geographic location, animal size, and environmental parameters (e.g., fluorescence, temperature, salinity, and density) were investigated. Understanding how material property measurements are affected by these parameters could refine target strength estimates from acoustic scattering models. Improving estimates of target strength will make biomass estimates from acoustic surveys more accurate.

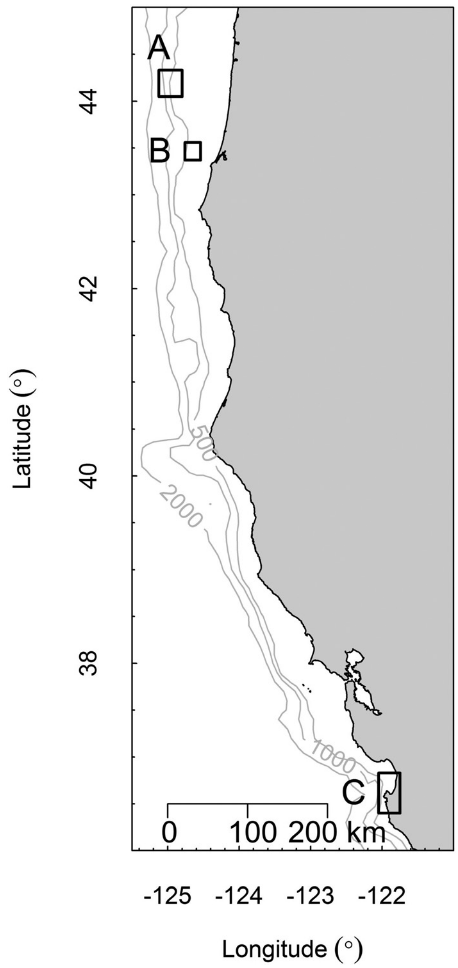

FIG. 1. Nekton were sampled in two regions in the California Current. These regions include: coastal Oregon from 26 July to 10 August 2012 (A, B); Monterey Bay from 9–11 November 2012 (C). Bathymetry lines are gray with the depth labeled in meters.

II. METHODS

Nekton specimens were collected off the coast of Oregon on the *RV Oceanus* from 26 July to 10 August 2012 (Fig. 1). One Humboldt squid and one Pacific hake were collected by jigging with a rod and reel over water depths of 365 and 354 m, respectively. An additional Pacific hake and all myctophids were collected using a 4 m^2 Isaacs-Kidd midwater trawl (IKMT) in targeted net tows (Devereux and Winsett, 1953) with maximum depths ranging from 210 to 350 m. The IKMT had a 1 mm mesh net attached to a rigid v-shaped diving vane with a 1 mm mesh cod-end. Eight additional Humboldt squid specimens were also caught by jigging with a rod and reel (maximum depths ranging from 300 to 500 m) in Monterey Bay on the *RV Fulmar* from 9–11 November 2012 [Fig. 1(C)]. Animals caught with jigging were brought on board, and their lengths were recorded (mantle length for squid and standard length for hake). Animals caught in the IKMT were immediately transferred from the cod end into a large (∼15 L) tray and hand-sorted by species into smaller containers (1 L) until they could be measured. Due to the small size of our experimental apparatus, the squid and fish were dissected immediately after collection for the density and sound speed experiments. In Monterey Bay, when an abundance of squid specimens were caught at once, the squid were kept alive in a covered holding tank equipped with a flow through surface seawater system until measurements could be performed. A digital photograph of each animal (with a length scale) was taken before all squid and Pacific hake specimens were dissected. The capture, euthanization, and disposal of all vertebrate specimens were conducted under an approved institutional care permit.

A. Density measurements

The density contrast (*g*) was measured utilizing the titration and pipette methods (Warren and Smith, 2007; Smith *et al.,* 2010; Forman and Warren, 2010). The titration method was used to obtain the specimen's density aboard the research vessels, while the pipette method was used to measure the squid beak and pen pieces density in the laboratory after the cruise. The pipette method was conducted after the cruise because it involved using a microbalance which is difficult to use at sea.

The titration method uses two burets, one with surface seawater and the other with a solution with a greater density than seawater and titrating each liquid into a beaker containing an individual specimen until the specimen reaches neutral buoyancy. Previously, Warren and Smith (2007) and Smith *et al.* (2010) used a hypersaline solution as the denser solution, but this study used a glycerin mix solution. We used glycerin because it had a high density (1.26 g ml^{-1}, ICSC, 2007) and creating a hypersaline solution dense enough for measuring nekton body parts is difficult as salt would precipitate out of solution causing the hypersaline solution density to fluctuate during the titration. We needed to dilute the glycerin (create a glycerin mix) in order for the viscosity to be low enough to flow through the burets. The glycerin mix was created by diluting pure glycerin with surface seawater, a 50% glycerin and 50% ambient seawater mix was used for all measurements. If the specimen was buoyant in seawater before the density measurements, we titrated freshwater until the specimen achieved neutral buoyancy.

For hake, pieces of muscle were cut into roughly $2 \times 2 \times 1$ cm (length, width, thickness) pieces for measurements. For myctophids, the gut contents, head, and tail were removed and then the body was cut into multiple pieces for measurement. The size of the myctophid body pieces varied depending on the body size of the animal. Humboldt squid were dissected with a knife and several body parts including the mantle, arm, tentacle, braincase, eye, pen, and beak were removed for measurements. Squid mantle was cut into $\sim 3 \times 3 \times 1$ cm pieces for measurement. Arms and tentacles were cut into pieces with dimensions of $\sim 3 \times 2 \times 1$ cm with slight variations of width and thickness depending on the position of the cut along the tapered arm or tentacle as well as variations due to squid size. On the *RV Oceanus*, the braincase was cut into several small pieces roughly $3 \times 2 \times 1$ cm with width and thickness varying among pieces due to the shape of the braincase, however on the *RV Fulmar*, the braincase was cut in half and measured with rough dimensions of $3 \times 3 \times 2$. The eyes of the squid were measured whole and were approximately 4 cm in diameter.

The squid beak and pen pieces had a density that was very close to or larger than the density of glycerin as they did not float in pure glycerin. They were measured using the pipette method in the lab after the cruise. The squid pen extends almost the entire mantle length of the animal and is not uniformly shaped, so it was cut into pieces with lengths of 3–5 cm and stored in seawater until they could be measured. All surrounding tissue was removed from the beaks by soaking them in seawater and the top and bottom jaws were separated and stored in seawater for measurement back at the lab. All other measurements were taken immediately after animals were collected, and body parts were stored in surface seawater after dissection until they could be measured. All measurements were made within 5 h of the squid being collected:

$$\rho_{\text{part}} = \frac{(V_0 + V_{\text{sw}})\rho_{\text{sw}} + V_g \rho_g}{V_0 + V_{\text{sw}} + V_g}. \quad (1)$$

The density of the body part ρ_{part} was calculated using Eq. (1), where V_0 is the volume of seawater initially in the beaker, V_{sw} is the volume of seawater added to the beaker, ρ_{sw} is the density of seawater, V_g is the volume of glycerin mix added, and ρ_g is the density of glycerin mix. The density contrast (g) is the ratio of body part density to seawater density [Eq. (2)],

$$g = \frac{\rho_{\text{part}}}{\rho_{\text{sw}}}. \quad (2)$$

This study used glycerin as titrant, and preliminary results suggested that using glycerin gave larger density values than using a hypersaline solution. Given that previous studies have used a hypersaline solution as a titrant, we conducted an experiment on grass shrimp (*Palaemonetes pugio*) collected from coastal Long Island. Forty-one grass shrimp were measured once with both the hypersaline solution, and the 50% glycerin solution. We found that using glycerin as the titrant resulted in consistently higher density values than the hypersaline solution. Due to these findings, we used the ratio of the mean shrimp g values found with hypersaline to the mean shrimp g values found with glycerin to scale the glycerin-based data to comparable values. To scale the data in this study, 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. The adjusted values are reported in this manuscript. The exact cause of the higher density values when using glycerin as a titrant is not known, however, we speculate that it may be due to osmotic pressure. We calculated the osmotic pressure for our glycerin solution and hypersaline solution and found that the glycerin solution was higher (167 atm) than the hypersaline solution (105 atm). The higher osmotic pressure of glycerin may cause water to diffuse from the specimen at a faster rate than when a hypersaline solution is used. This would result in the specimen becoming more dense which supports our observations.

The pipette method (Warren and Smith, 2007; Forman and Warren, 2010) was used to measure the Humboldt beak and pen pieces. For this method, the body part was placed in a graduated cylinder filled with a known volume of seawater and the mass of the body part was recorded (m_{part}). Seawater was then removed from the graduated cylinder with a pipette until the volume of seawater was equal to the original volume in the graduated cylinder. The removed water was weighed on a microbalance, and the mass was recorded (m_{rw}). Temperature and salinity of the seawater was recorded, and the density of the seawater (ρ_{sw}) was calculated using the CSIRO MATLAB Seawater Library. This method was performed three times on each body part and the mean was used for data analysis. These measurements were then used to calculate the density of the body part according to Eq. (3),

$$\rho_{\text{part}} = \frac{m_{\text{part}}}{V_{\text{part}}} = \frac{m_{\text{part}}}{\left(\frac{m_{\text{rw}}}{\rho_{\text{sw}}}\right)}. \quad (3)$$

B. Sound speed measurements

Sound speed contrast (h) was measured using the APOP (Acoustic Properties of zooPlankton) system (Chu *et al.*, 2000). The body parts were put in an acoustic chamber and two broadband transducers (350–650 kHz, Materials Systems, Inc.) were attached at each end of the chamber. The sound speed was recorded for the chamber containing only seawater, and again with the animal parts added to the chamber. For this method, the acoustic chamber needed to be mostly filled with animal parts, so it required several of the same type of part. Due to this requirement, the sound speed was only measured for Pacific hake muscle tissue, Humboldt squid mantle, and Humboldt squid braincase. Three consecutive sets of one hundred pings were collected for each group of specimens measured. We report the mean value of the three hundred consecutive pings as the sound speed contrast for the specimen group. The sound speed contrast (h) was calculated using Eq. (4) where c_a is the sound speed through the animal parts, c_{sw} is the sound speed through seawater, Δ_t is the travel time difference between two received waveforms (one with the empty chamber and one with the chamber containing the animal parts), Φ is the volume fraction (volume of the animals parts/volume of the acoustic chamber), and t_d is the travel time of sound from the transducer to the receiver without animal parts in the chamber

$$h = \frac{c_a}{c_{sw}} = 1 + \frac{\Delta_t}{\Phi t_d}. \qquad (4)$$

C. Morphometric measurements

A digital photograph of the specimens with a length scale was taken before the sound speed measurements and after the density measurements; these photographs were used for post-cruise dimension measurements. Body parts or tissue pieces were photographed laterally and dorsally such that length, width, and height (or thickness) could be calculated from the photographs using a custom MATLAB program. Similar images were also taken for Humboldt squid and Pacific hake prior to their dissection, and these pictures were also analyzed to obtain length and height measurements of the whole animal after the cruise.

D. Environmental variables

On the *RV Oceanus* and *RV Fulmar*, environmental variables were recorded using a Seabird Conductivity-Temperature-Depth (CTD) sensor model SBE 43 and SBE 19 plus, respectively. The CTD was deployed at 22 location on the *RV Oceanus*, and four locations on the *RV Fulmar*. The CTD measures temperature, salinity, dissolved oxygen, and fluorescence of the water column. Relationships between the material properties of specimens and animal length, temperature, salinity, dissolved oxygen, fluorescence, and geographic location were investigated. Linear regressions were used to investigate the effect of environmental parameters collected as well as animal length on nekton density contrasts. Data from CTD casts that are representative of the environment in which the specimen were caught were used for this analysis. Two sample t-tests were used to determine significant differences of density contrasts resulting from parameters such as specimen (hake), species (fish), body parts (squid), and location captured (squid). The details and results of these tests are discussed within the results below. Unless otherwise noted, values are reported as mean and standard deviations throughout this manuscript.

III. RESULTS

A. Nekton density contrast

1. Pacific hake

The density of the seawater used to calculate the density and sound speed contrasts was $1.022 \pm 0.001\ \text{g ml}^{-1}$, and ranged from 1.021 to $1.022\ \text{g ml}^{-1}$. Two Pacific hake were collected off the coast of Oregon on the R/V Oceanus. The first hake was collected in a net trawl and had a standard length of 28.9 cm. The second hake was collected by jigging and had a standard length of 40 cm. Twenty hake flesh pieces were measured and their density contrast varied with a mean value of 1.029 ± 0.004 and a range of 1.023–1.036 (Table I, Fig. 2). Since only two hake specimens were collected, we did not investigate the relationship between hake length and density contrast, although we note that there was no significant

TABLE I. A summary of the mean and standard deviation (s.d.) of animal length, density contrast (g), and sound speed contrast (h) for all nekton taxa and body parts measured. The number of individual animals (i) and number of measurements (n) (from i individual animals) are provided. Mantle length and standard length are reported for squid and fish, respectively. Sound speed measurements were on myctophids that were not identified to species, but are likely to be a mix of the two species present.

		Body length (cm)				Density contrast (g)		Sound speed contrast (h)	
Species	i	Mean ± s.d.	Range	Body part	n	Mean ± s.d.	Range	n	h
Humboldt squid (*Dosidicus gigas*)	9	43.9 ± 6.9	28-53	Mantle	48	1.027 ± 0.003	1.020–1.032	3	1.027, 1.018, 1.023
				Braincase	29	1.025 ± 0.133	1.012–1.057	2	0.937,[a] 1.028[b]
				Arm	38	1.029 ± 0.004	1.024–1.048	NA	NA
				Tentacle	25	1.037 ± 0.007	1.027–1.049	NA	NA
				Eye	9	1.014 ± 0.005	1.009–1.024	NA	NA
				Pen	7	1.151 ± 0.057	1.085–1.235	NA	NA
				Beak	2	1.360 ± 0.14	1.260–1.459	NA	NA
Pacific hake (*Merluccius productus*)	2	28.9, 40.0	NA	Flesh pieces	20	1.029 ± 0.004	1.023–1.036	4	0.988,[a] 0.988,[b] 0.986,[a] 1.027[b]
California lantern fish (*Symbolophorus californiensis*)	13	NA	NA	Flesh pieces	26	0.9992 ± 0.005	0.9919–1.014	1	1.015
California headlight fish (*Diaphus theta*)	10	NA	NA	Flesh pieces	20	1.013 ± 0.005	1.002-1.021		

[a]Pliable tissue.
[b]Firm tissue.

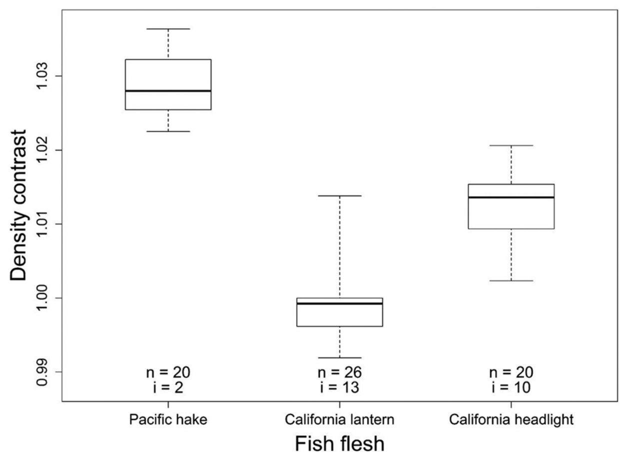

FIG. 2. Density contrast for all fish species sampled. Pacific hake and myctophid density contrast differed significantly ($p < 0.001$). Density contrast also varied significantly between the two species of myctophids measured ($p < 0.001$). The lower line of each box represents the 1st quartile, the middle bolded line represents the median, the top line of the box represents the 3rd quartile, and the whiskers of the plot represent the minimum and maximum values. The number of measurements is noted by *n* and the number of individuals measured is noted by *i*.

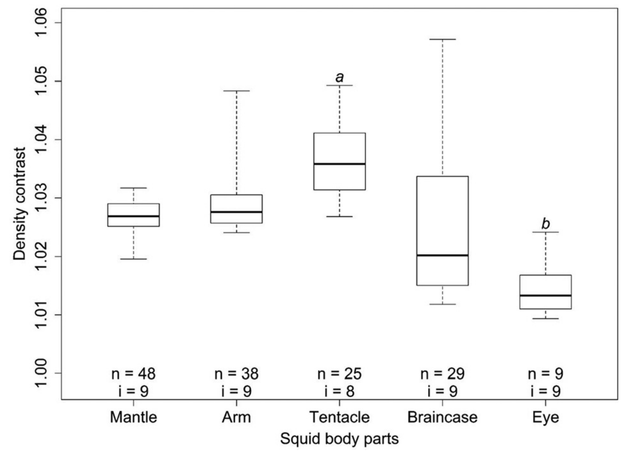

FIG. 3. Density contrast of the sampled body parts of Humboldt squid. The mean density contrasts of the tentacle and eye were significantly different ($p < 0.001$, two-sample *t*-test) (significance indicated by *a*,*b*) than the other squid body parts. The lower line of each box represents the 1st quartile, the middle bolded line represents the median, the top line of the box represents the 3rd quartile, and the whiskers of the plot represent the minimum and maximum values. The number of measurements is noted by *n* and the number of individuals measured is noted by *i*.

difference ($p = 0.647$, two-sample *t*-test) between the density contrasts of the two hake specimens collected.

2. Myctophids

Digital photographs were not taken of all myctophids used for measurements before dissection, but a small sample of measured myctophids ($n = 11$) were measured and their lengths ranged from 5.4 to 7.9 cm. A total of 46 myctophid flesh pieces were measured: 26 California Lantern fish and 20 California Headlight fish (Table I, Fig. 2). The two species of myctophids had significantly different density contrasts ($p < 0.001$, two-sample *t*-test) and the density contrast of Pacific hake flesh was significantly greater than myctophid fish flesh ($p < 0.001$, two-sample *t*-test).

3. Humboldt squid

Nine Humboldt squid were collected; one off the coast of Oregon (mantle length of 28 cm) on the *R/V Oceanus* and eight in Monterey Bay (mantle lengths ranging from 41 to 53 cm) on the *R/V Fulmar*. The density contrast (g) varied among the squid body parts with the beak and pen being the densest parts of the squid (Table I; Figs. 3 and 4). The density contrasts of two body parts (tentacles, eyes) were significantly different [higher ($p < 0.001$, two sample *t*-test) and lower ($p < 0.001$, two sample *t*-test), respectively] than the mantle, arms, braincase and eye (Fig. 3).

Six beaks were measured, but in order to displace enough water for the method they were measured in two groups. The two groups had density contrasts 1.46 ± 0.046 and 1.26 ± 0.021. Since the beak pieces had to be combined to measure their density, and the squid within the two groups had varying mantle lengths and were caught in different locations, we could not investigate the effect of squid size (mantle length) and environmental parameters on beak density contrast. Density was measured for 7 pens, and they had a density contrast with a range of $1.085-1.235$ with a mean and standard deviation of 1.151 ± 0.057. No relationship between pen density contrast and mantle length was found.

The squid collected in Oregon was smaller [28 cm in mantle length (ML)] than the squid collected in Monterey Bay (41–56 cm ML).We found that the density contrast for the mantle of the squid collected in Oregon was significantly lower ($p = 0.001$, two-sample *t*-test) and the braincase density contrast was significantly higher ($p < 0.001$, two-sample *t*-test) than the squid collected in Monterey Bay (Fig. 5). No

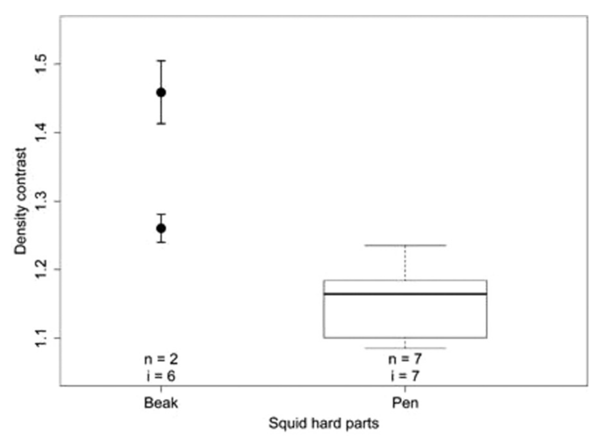

FIG. 4. Density contrast of the Humboldt squid beak and pen (gladius). The number of individual squid measured is denoted by *i* and the number of measurements made is denoted by *n*. Only six Humboldt squid beaks were collected. In the pipette method, each measurement was repeated three times, and the mean and standard deviation of those measurements for the two groups of beaks are shown. The measurements plotted for the pen are the mean of the measurements of seven pens collected from seven individual squid. There are only two beaks measurements because they did not displace enough water in the graduated cylinder to be measured alone via the pipette method and had to be measured in groups of three. The lower line of each box represents the 1st quartile, the middle bolded line represents the median, the top line of the box represents the 3rd quartile, and the whiskers of the plot represent the minimum and maximum values.

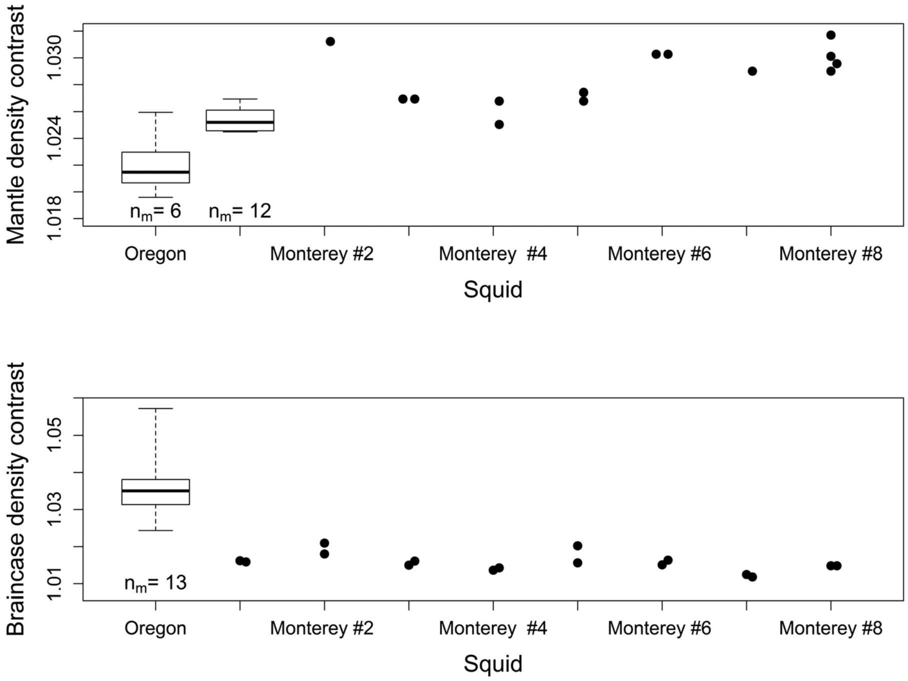

FIG. 5. Density contrast of the Humboldt squid mantle and braincase for each individual squid measured. The mantle density contrast of the squid caught in Oregon was significantly lower (two-sample *t*-test, $p = 0.001$) and density contrast for the braincase was significantly higher (two-sample *t*-test, $p < 0.001$ than the squid collected in Monterey bay. The lower line of each box represents the 1st quartile, the middle bolded line represents the median, the top line of the box represents the 3rd quartile, and the whiskers of the plot represent the minimum and maximum values.

other body parts of the squid showed a significant difference between the two study regions.

B. Nekton sound speed contrast

The sound speed contrast (h) was measured for Pacific hake flesh pieces, myctophid flesh pieces, Humboldt squid mantle, and Humboldt squid braincase (Table I). The pieces of flesh from the first hake we caught were split randomly into two groups and each group was measured twice. Flesh pieces from the second hake and the Humboldt braincase pieces were separated by the firmness of the flesh (pliable and firm), and each of these groups were measured.

C. Environmental variables

The low number of specimens measured was the result of poor catches from net tows and jigging. The small number of hake collected limited investigations on the effect of environmental conditions on hake flesh density contrast. The environmental conditions differed between Oregon and Monterey Bay (Fig. 6) with the Oregon water column having a wider range of densities than Monterey. Fluorescence had the most striking difference, with the surface fluorescence being much higher in Monterey Bay than in Oregon (Fig. 6). The effect of environmental conditions on the density contrast of myctophid flesh and Humboldt squid body parts was investigated and no significant relationships were found.

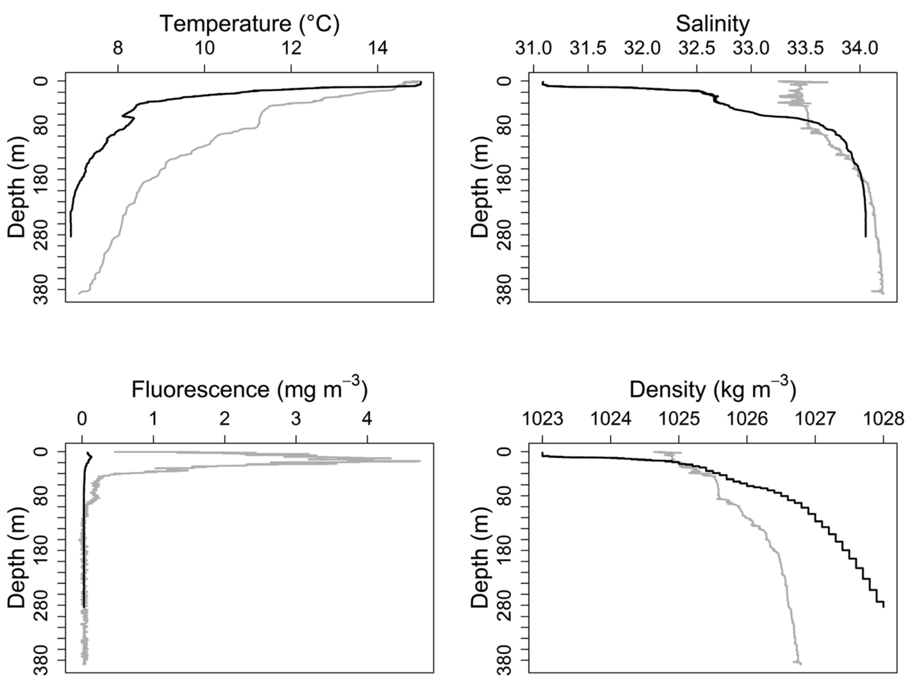

FIG. 6. Vertical profiles of environmental data from CTD casts in Oregon (black line) and Monterey Bay (gray line).The selected CTD casts shown are representative of the environment where each squid was caught in each location.

Since the sound speed contrast data are limited, the effects of environmental conditions on sound speed were not investigated.

IV. DISCUSSION

Density (g) and sound speed (h) contrasts are crucial parameters for acoustic scattering models which are often used to convert acoustic data to biomass estimates. Knowledge of how these values vary with species, animal length, and environmental conditions could improve the accuracy of acoustic scattering models for nekton. This was the first study to examine how material properties of Pacific hake, myctophids, and Humboldt squid were affected by animal length and environmental conditions. Effect of environmental parameters on density contrast has been documented for zooplankton taxa (Smith *et al.*, 2010), but no effect on myctophid density contrast was found in this study. This may be because fish have a more complex body structure than zooplankton, and their flesh is not as susceptible to fluctuations in the environment.

It is important for studies of material properties of marine organisms to include information about the environmental conditions (e.g., seawater density) in the study so that data reported in terms of relative material properties (contrasted with ambient seawater) can be converted and compared to absolute values of these material properties or vice versa. When applicable, published absolute material property values were converted to relative material properties values in order to compare the data from this study to previously published work. Combining the data from this study with previously published work, shows that material property values can vary widely between and within species (Fig. 7). Pacific hake density contrast overlaps with the density contrast reported by Shibata (1970) and Brawn (1969) for Pacific herring, and the value reported for Japanese sand eel by Yasuma *et al.* (2009). These species are all pelagic, and the similarities in their density contrasts may be due to these species having a similar life history. The range of density

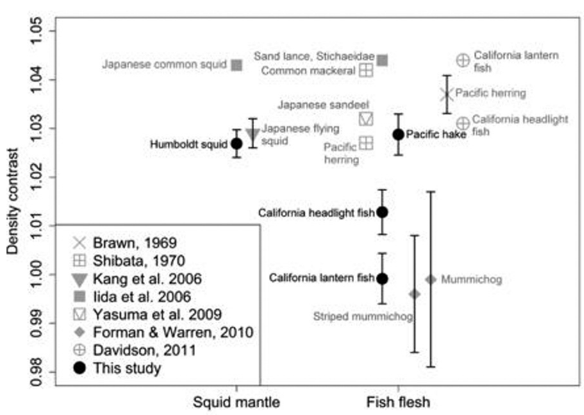

FIG. 7. Comparison of published values of density contrast for squid mantle and fish flesh to values measured in this study. For fish flesh, the black and gray circles are Pacific hake and myctophid values, respectively. Iida *et al.* (2006) reported a fish density contrast value from acoustic images of Sand lance and *Stichaeidae*. If absolute density was reported, density contrast was calculated utilizing the animal and seawater densities reported in the publication.

contrasts for the myctophids measured in this study agrees with the range of values Forman and Warren (2010) reported for coastal fish, but is also lower than the estimate by Iida *et al.* (2006). The differences seen between the fish density contrast values in this study and previous studies could be due to a number of factors including species differences, differences in methods (i.e., measuring whole fish, or previously frozen fish flesh), fish age or size, or variances in the environmental conditions in which the fish were captured. For example, most of the fish measured in Forman and Warren (2010) were smaller (<5 cm) than the fish measured in this study, and they were collected from a coastal rather than pelagic ecosystem. In addition, Sigfusson *et al.* (2001) showed that the ultrasonic velocity of Atlantic mackerel fish flesh varied with fat content.

The mean density contrasts of flesh from California Lantern fish (*Symbolophorus californiensis*) and California headlight fish (*Diaphus theta*) were significantly different from each other ($p < 0.001$). Even though these two fish are different species, they are very similar in that they both are triglyceride-storing lantern fish (Neighbors and Nafpaktitis, 1982). Neighbors and Nafpaktitis (1982) review the lipid compositions, water contents, swimbladder morphologies, and buoyancies of 19 midwater fishes including both *Symbolophorus californiensis* and *Diaphus theta*. Neighbors and Nafpaktitis (1982) reported that *Diaphus theta* was less dense than *Symbolophorus californiensis,* but they measured whole fish, not just fish flesh. Davison *et al.* (2011) also reports that *Diaphus theta* was less dense that *Symbolophorus californiensis*, and their values are higher than the range of values measured in this study (Fig. 7). The results of this study contradict the findings of Neighbors and Nafpaktitis (1982) and Davison *et al.* (2011) who measured the whole animal, and the other components of the fish body such as skull, spine, and swimbladder would have important effect on the overall buoyancy of the fish. In addition, Butler and Pearcy (1972) measured the specific gravity of *Diaphus theta* capture off the Oregon coast. They do not specifically explain what the specific gravity measurement is in relation to (i.e., freshwater or seawater). It is likely that it is in relation to freshwater, therefore their mean specific gravity value (1.038) can be compared to the absolute density of *D. theta* in this study (mean: $1.035\,\mathrm{g\,ml^{-1}}$, range: $1.024-1.043\,\mathrm{g\,ml^{-1}}$). Butler and Pearcy (1972) value is within the range of the density values in this study for *D. theta* which could be due to both studies specimens coming from the same geographic region. The difference in the mean of both studies could be due to measuring fish flesh vs the whole fish.

Acoustic surveys are used throughout the world for fisheries stock assessments (Simmonds and MacLennan, 2005). We found that Pacific hake density contrast was significantly different than the density contrasts from both myctophid species, and both myctophid species were significantly different from each other. Our data suggest it may be important to use species specific material property values in scattering models to achieve the most accurate estimate of target strength. To investigate this further, more fish flesh material property data are needed to understand how the density values change with species. Chu *et al.* (2000) reported that a small change

(2%–4%) in material property values could have a very large effect on target strength estimates from scattering models. In order to understand how the values reported in this study would affect target strength, we used a similar approach as Smith *et al.* (2013) and investigated how target strengths would change with different material property values. Pacific hake flesh was nearly twice as dense as California headlight fish flesh. The swimbladder (when present and filled with air) dominates the acoustic scattering of an animal, making the difference in fish flesh density of secondary importance. However, if the differences measured in this study occurred in species without an air-filled swimbladder, they could result in large differences in target strength (up to 15 dB). Gathering species-specific material property data is important because variation in density contrast estimates could result in differences in biomass estimates of several orders of magnitude.

Fish sound speed contrasts (h) varied within and among taxa (Table I). The Pacific hake values herein overlap with the values reported by Shibata (1970), Iida *et al.* (2006), Yasuma *et al.* (2009), and Forman and Warren (2010) (Fig. 8). Rigid and pliable flesh differed in sound speed contrast which suggests that hake flesh sound speed may vary within the animal. The sound speed contrast of unidentified myctophids was within the range of h values found in Forman and Warren (2010), but is lower than the estimate by Iida *et al.* (2006) (Table I). The difference in this study's sound speed contrast for fish flesh could be because we measured different species than both Forman and Warren (2010) and Iida *et al.* (2006).

The density contrast values were variable among the different body parts of Humboldt squid (Figs. 3 and 4). The Humboldt squid mantle density is the most similar to the value found in Kang *et al.* (2006), but is lower than the estimate by Iida *et al.* (2006) (Fig. 7). Since the mantle covers the majority of the body of the squid, it is not surprising that we found similar density contrast values between the mantle pieces in this study and the whole Japanese flying squid in

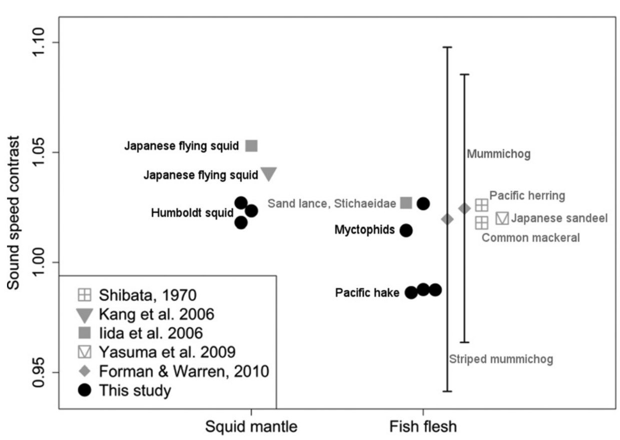

FIG. 8. Comparison of published values of sound speed contrast for squid mantle and fish flesh to values measured in this study for fish flesh, the black and gray circles are Pacific hake and myctophid values respectively. Iida *et al.* (2006) reported a fish sound speed contrast value from acoustic images of Sand lance and *Stichaeidae*. If absolute sound speed was reported, sound speed contrast was calculated utilizing the animal and seawater densities reported in the publication.

Kang *et al.* (2006). However, our density contrast values are much lower than the estimate by Iida *et al.* (2006), but this could be due to the fact that the data in Iida *et al.* (2006) were estimated from an acoustic camera, and not a direct measurement. In order to understand the significance of the difference between our estimates and previous studies, we calculated how much the target strength estimate would change if only material properties were changed. We found an 11% difference in numerical abundance when the density contrast for Japanese flying squid instead of Humboldt squid was used in a scattering model which may be important if acoustic surveys were to be used for stock assessment purposes. More data need to be collected on different species of squid in order to develop species-specific acoustic scattering models for squid.

Benoit-Bird *et al.* (2008) proposed that the braincase of the squid is a significant source of acoustic scattering for Humboldt squid because it is composed of dense cartilage and contains statoliths which contain aragonite crystals. The range of density contrast of Humboldt squid braincase pieces was 1.012–1.057 with a mean of 1.025. We found that the mantle and braincase density contrasts from our Oregon squid were significantly different than the density contrasts from the Monterey squid (Fig. 5). One possible explanation for this finding could be that squid body composition changes with maturation. While a relationship between age and mantle length for Humboldt squid has not been defined, it is generally accepted that length is positively correlated with age. Markaida *et al.* (2004) investigated the age, growth, and maturation of Humboldt squid and found that age of maturation was affected by size and sex, so mantle length was not an absolute way to determine if the squid was mature. Differences in environmental conditions could also be the cause of the difference in the Oregon and Monterey squid. Further investigation of whether size (or age or maturation) or environmental conditions affects Humboldt squid density contrast is needed to confirm what caused the difference of mantle and braincase density contrasts between our two study sites.

Density contrast varied within and among different body parts of squid. The beak and pen were the densest body parts with values of 1.360 ± 0.14 and 1.151 ± 0.057, respectively. The density contrast of the tentacle pieces of the squid was higher than the arms (Table I). The arms and tentacles of the Humboldt squid both contain sucker rings which are more rigid than most squid tissue. The difference in the density contrast between these two body parts could be due to the tentacle pieces containing a higher number of sucker rings than the arms. Although the number of rings on tentacles and arms was not investigated in this study, the tentacles are used for prey capture and it is likely they contain more sucker rings.

Kang *et al.* (2006) and Iida *et al.* (2006) both report sound speed values for Japanese flying squid. The range of sound speed contrasts for measured mantle and braincase pieces were lower than both previous studies (Fig. 8). These differences could be due to sound speed changing between species, or that a whole squid was measured in Kang *et al.* (2006) and the value in Iida *et al.* (2006) was an estimate from an acoustic camera. The difference in sound speed of the two types of braincase pieces suggests that sound speed may vary within the braincase itself. More sound speed data are needed to investigate further how sound speed contrast varies within and between species of squid.

Species-specific material property data for nekton are limited, and scientists often use material property values from the closest species available. We found that the difference in material properties for the hake and myctophids had a large effect on the numerical abundance if these values were to be used to convert acoustic data to biomass. Additionally, small differences between the density contrast for Japanese flying squid reported by Kang *et al.* (2006) and the value we report for Humboldt squid mantle led to substantial differences when used to calculate numerical abundances. Overall, in order to have an accurate target strength estimate, accurate species-specific material property values are required for modeling.

V. CONCLUSION

This study reports the first measured material property values for Pacific hake flesh, myctophid fish flesh, and Humboldt squid body parts. Our results show that density and sound speed contrasts for fish flesh vary within and among taxa. We found that there was a significant difference in the density contrasts of two species of myctophids, *Symbolophorus californiensis* and *Diaphus theta*. The density contrasts vary between the different body parts of the Humboldt squid, and the density contrasts of the mantle and braincase were significantly different between the squid collected in Oregon and Monterey Bay. It is unclear if this difference is due to a difference of squid size or environment. Future studies are needed to investigate the effect of environmental conditions and animal length on the material properties of these nekton. The material property data in this study may help improve the target strength estimates of Pacific hake, myctophids, and Humboldt squid. This study could also help improve the scattering models for fish species without swim bladders where their backscatter will be dominated by their flesh and other body components. Improving target strength estimates could constrain biomass estimates from acoustic surveys for these nekton.

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