Density and sound speed of two gelatinous zooplankton: Ctenophore (*Mnemiopsis leidyi*) and lion's mane jellyfish (*Cyanea capillata*)

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The density and sound speed of two coastal, gelatinous zooplankton, *Mnemiopsis leidyi* (a ctenophore) and *Cyanea capillata* (lion's mane jellyfish), were measured. These parameters are important inputs to acoustic scattering models. Two different methods were used to measure the density of individual animals: one used a balance and graduated cylinder to determine the mass and displacement volume of the animal, the other varied the density of the solution the animal was immersed in. When the same animal was measured using both methods, density values were within 1% of each other. A travel-time difference method was used to measure the sound speed within the animals. The densities of both zooplankton slightly decreased as the animals increased in length, mass, and volume. The ratio of animal density and sound speed to the surrounding seawater (*g* and *h*, respectively) are reported for both animals. For *Mnemiopsis leidyi* ranging in length from 1 to 5 cm, the mean value (±standard deviation) of *g* and *h* were 1.009 (±0.004) and 1.007 (±0.001). For *Cyanea capillata* ranging in bell diameter from 2 to 11 cm, the mean value (±standard deviation) of *g* and single value of *h* were 1.009 (±0.004) and 1.0004. © *2007 Acoustical Society of America.* [DOI: 10.1121/1.2739433]

I. INTRODUCTION

Acoustic methods have been used for several decades to estimate the abundance and distribution of zooplankton and nekton in the marine environment (Foote and Stanton, 2000). These methods offer improved spatial coverage, vertical and horizontal resolution, and in some regions the ability to discriminate between different taxonomic groups. However, the acoustic methods provide indirect estimates of the biological scatterers in the water column, and the conversion of acoustic information to numerical abundance or biomass can be difficult. The process of transforming acoustic backscatter data into estimates of biologically relevant variables is known as the inverse problem and requires physics-based mathematical or empirical models that describe the acoustic scattering characteristics of a particular organism.

Ray-based models describing the scattering characteristics of several different types of zooplankton have undergone extensive development in the last few decades and are, in many cases, quite accurate when compared to empirical scattering data from individual animals (Stanton *et al.*, 1994; Stanton *et al.*, 1998). Although these models are not as accurate as full-diffraction solutions to the wave equation and require several initial assumptions, they can be expressed in relatively simple mathematical formulas. The inputs to these models include characteristics of the animals themselves

such as: animal shape and size, orientation relative to the acoustic wave fronts, and body composition. The model output is typically the amount of backscattered acoustic energy that would be reflected by a scatterer. The shape and size of the animal can be assessed through net tow samples taken during an acoustic survey and the orientation of the animal within the water column can be evaluated through the use of video methods. In addition to these factors, two of the most important inputs into these models are the ratios of density and sound speed of the animal and its surrounding medium, seawater (Anderson, 1950; Johnson, 1977; Greenlaw and Johnson, 1982; Stanton and Chu, 2000; Chu *et al.*, 2000). The density ratio is *g* ($g = \rho_a / \rho_{sw}$) and the sound speed ratio is *h* ($h = c_a / c_{sw}$) where ρ is the density and *c* is the speed of sound and the subscript indicates the property is of the organism (*a*) or surrounding seawater (sw).

There have been several studies that have measured the material properties of fluid-like scatterers such as copepods and euphausiids (Greenlaw and Johnson, 1982; Foote, 1990); but few, if any, measurements have been made of gelatinous zooplankton. Two very common estuarine and coastal gelatinous zooplankton are ctenophores (*Mnemiopsis leidyi*) and lion's mane jellyfish (*Cyanea capillata*). Ctenophores are found throughout the temperate and tropical coastal oceans (Mianzan, 1999) and have become an important invasive species in the Black and Caspian Seas (Mutlu, 1999; Ivanov *et al.*, 2000) where they were one of the severe impacts on the local ecosystem (Kideys, 1994; Shiganova and Bulgakova, 2000). The lion's mane jellyfish and other related scy-

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phozoans are seasonally abundant in northern waters (Houghton *et al.*, 2006) and may have an important impact on the marine ecosystem (Broduer *et al.*, 2002). Increases in the distribution and abundance of gelatinous zooplankton have been linked to shifts in ecosystems due to climatic variation (Purcell, 2005; Lynam *et al.*, 2005; Mills, 2001) as well as removal of apex predators from the ecosystem due to fishing pressures (Purcell and Arai, 2001).

There have been several studies that have used acoustics to measure the scattering from ctenophores (Alvarez Colombo *et al.*, 2003) and scyphozoan jellyfish (Båmstedt *et al.*, 2003; Brierley *et al.*, 2004, 2005). Gelatinous animals are thought to be weak scatterers given their fluid-like body composition and ability to remain neutrally buoyant in the water column, and on a per unit biomass basis they are weaker scatterers than crustacean or shelled gastropod zooplankton (Stanton *et al.*, 1996). However, since the gelatinous animals are often much larger (both in size and biomass) than the other zooplankton in the water column, they have relatively large target strength values on a per animal basis (e.g. Table II in Alvarez Colombo *et al.*, 2003).

While there has been some progress in the development of a scattering model for gelatinous zooplankton (Monger *et al.*, 1998; Mutlu, 1996), several studies of zooplankton scattering (Ressler, 2002; Stanton *et al.*, 1994) have calculated gelatinous zooplankton contributions using a model developed for fluid-like crustacean zooplankton. In both cases, several model inputs (particularly g and h) have been estimates based on fits of scattering model predictions to measurements of target strength rather than direct measurements. As a first step in improving the ability to accurately model the scattering from gelatinous zooplankton, accurate measurements of the density and sound speed of the animals are needed.

II. METHODS

Ctenophores and lion's mane jellyfish were collected from Shinnecock and Peconic Bay on Long Island, New York during June–August 2006. Animals were collected using a small dip net and buckets. While some gelatinous animals cannot be handled without causing extensive damage to their bodies, the ctenophores and lion's mane jellyfish are relatively hardy animals and were not noticeably harmed by the collection process. In order to minimize the possibility of measuring damaged animals, the animals were placed in buckets or tanks containing water similar in temperature (24–28 °C) and salinity (25–26) to the water they were collected in. A temperature and salinity sensor (YSI 85, YSI Incorporated) was used to measure the properties of the water used in the experiment from which seawater density (ρ_{sw}) and sound speed (c_{sw}) were calculated. Seawater density and sound speed were calculated using the CSIRO MatLAB Seawater Library for each experiment and varied little between experiments (1.016–1.0185 g ml^{-1} and 1521–1532 m s^{-1}). The animals were monitored for several hours or days and only animals that appeared to be healthy and mobile were used in the experiments. The animals were alive throughout the experiments.

A. Pipette method for density measurements

Measurements of an individual animal's density were made using two different methods. Individual animals were measured in order to ascertain the range of density values for each type of animal. The pipette method is a slight modification of the method used by Lowndes (1942). It consists of taring a graduated cylinder (either 50, 100, or 1000 ml depending on the size of the animal) containing a known volume of seawater (V_o) on an electronic balance. The animal was removed from the bucket and placed on paper towels where the excess water from the animal was removed. The animal was then placed into the graduated cylinder and the mass of the animal (m_a) was recorded. With the animal remaining in the graduated cylinder, a pipette was used to remove water from the cylinder until the total volume (animal and remaining water) was equal to the original volume in the cylinder. The water that was removed from the cylinder was then weighed on the balance (m_{rw}) and its volume calculated. The volume of extracted water is equal to the animal's volume (V_a). Weighing the extracted water in order to calculate the volume was a more accurate method for finding the volume of the animal than visually recording the water displaced on the graduated cylinder after the animal had been added. The resolution of the graduated cylinder was poor because a large cylinder was needed to hold the gelatinous animals. With these measurements, the density of the animal was calculated (Eq. (1))

$$\rho_a = \frac{m_a}{V_a} = \frac{m_a}{\left(\dfrac{m_{rw}}{\rho_{sw}}\right)}. \tag{1}$$

This method was performed a minimum of three times on each individual to determine the precision of the method. The mean value of the measurements that were within 15% of the mean value of all measurements was then used for the rest of the data analysis. In approximately 10% of the measurements, one of the three measurements was substantially (more than 15% different from the mean) different than the other two. The presence of these outliers decreased as more measurements were made suggesting that familiarity and experience with the measurement technique is essential for accurate measurements of the mass and volume of the animal. This method requires the use of an electronic balance but could be modified to work at sea if a linked dual-balance method was used (Childress and Mickel, 1980; Chu and Wiebe, 2005).

There are several potential sources of errors with this method including: inadequate removal of excess water from the gelatinous animals and damaging the animal in the process. Since animal density measurements were the goal of this experiment, most of the water trapped internally by the ctenophores was removed by squeezing the animal throughout the drying process. As a consequence, pieces of the ctenophore were occasionally removed by the paper towel causing the mass and volume to slightly decrease (by approximately 5%) between each trial and possibly affecting the density measurements. An additional concern was that air bubbles might be introduced on or in the animal during the

removal of excess water and placement of the animal in the graduated cylinder. However, air bubbles were not observed on or in the animal when it was put into the cylinder. While air bubbles are a great concern for target strength measurements of individual animals (as bubbles are quite strong scatterers), the presence of bubbles on the animals for these measurements would result in only small errors in density or sound speed.

B. Titration method for density measurements

Another method for measuring the animal's density was used that could be easily applied to measurements made at sea where ship motion often causes difficulty when using an electronic balance. This method is a modification of that used by others (Greenlaw, 1977; Greenlaw and Johnson, 1982) where the density of animals was measured by placing them in a series of solutions of varying density and noting the solutions where the animal became buoyant and nonbuoyant. While this method can be done at sea without the use of a balance, the resolution of this method is a function of the number of solutions available. In order to improve the resolution of the density measurements in this study, an animal was placed into a beaker containing a known volume of seawater (V_o) of the same density as the zooplankton were collected in. Two burets were mounted on a ring stand above the beaker. One contained a solution of saltwater with a higher density (ρ_{ss}) than the animal's normal environment and the other contained normal seawater (ρ_{sw}). The saltier water was added to the beaker until the animal began to rise and float at the surface (indicating that the solution's density was greater than that of the animal), then the normal seawater was added until the animal began to sink (at which point the solution's density was just slightly less than that of the animal). While the solutions were being added to the beaker, it was necessary to stir or mix the solution. By measuring the volumes of saltier water (V_{ss}) and normal seawater (V_{sw}) added to the beaker, the animal's density can be found (Eq. (2)).

$$\rho_a = \frac{(V_o + V_{sw})\rho_{sw} + V_{ss}\rho_{ss}}{V_o + V_{sw} + V_{ss}}. \tag{2}$$

The process of adding saltier and normal water can proceed for several iterations if an increased precision of animal density is desired, however only one addition of saltier and normal seawater was used for this study. Potential inaccuracies in this method would result from errors in measuring the volume of water added, poor mixing of the solution in the beaker leading to stratification and, most importantly, the possibility that the addition of saltier water will cause the animal to adjust to the new osmotic pressure. If these measurements are made rapidly, it is thought that this error will be minimized, however it is not known at what time scales these changes may occur. This method is more time consuming than the pipette method, so only one measurement using this method was made for each animal.

C. Sound speed measurements

Similar to previous measurements of sound speed in zooplankton, the travel-time difference method was used (Greenlaw and Johnson, 1982; Foote, 1990). This method uses the difference in travel time for an acoustic wave traveling from a transmitter to a receiver through a pathway that either contains a known volume of zooplankton or is empty. This ray-based method is applicable when the acoustic wavelength used is much smaller than the characteristic size of the scatterers, which is close to the length scales of this study where the acoustic wavelength (8 mm) is less than the typical animal dimensions (~ 3–10 cm). A t tube (PVC plumbing T joint of various sizes) was used with a 192 kHz transducer clamped to each end and the entire apparatus submerged in seawater. Measurements of the travel time for an acoustic wave from the transmitter to the receiver were made with the chamber empty and with animals inside the chamber. To maximize the accuracy of this method, the animals should fill the t tube as much as possible so that the acoustic pathway is most likely to contain animal tissue rather than seawater. Because of the size and number of animals placed in the tube, we are confident that animal tissue was distributed throughout the volume of the t tube.

The t-tube volume was measured (V_{tube}) as well as the volume of animals that were put inside the t tube (V_a). The transmitted wave form was a 5 μs long, 192 kHz sinusoid signal. A data acquisition program was used to transmit the wave form to the signal generator, then to a power amplifier, and finally to the transmitting transducer. The receiving transducer was connected to a digital oscilloscope which digitized the received wave form and the signal was recorded. The difference in travel time between the signals recorded when the chamber was empty and contained animals was measured (Δt) as well as the travel time from transmitter to receiver when the chamber was empty (t_d). Both measurements were used to calculate h, the speed of sound of the animal (c_a) relative to that of seawater (c_{sw}) (Eq. (3)).

$$h = \frac{c_a}{c_{sw}} = 1 + \frac{\Delta t}{\frac{V_{tube}}{V_a} t_d}. \tag{3}$$

This method and equation have been used in previous studies (Chu and Wiebe, 2005) and provides an accurate measure of the sound speed of fluid-like zooplankton; however, it is very difficult to get measurements for an individual animal since ideally the t-tube chamber should be completely filled with animals. Because of this constraint, measurements of sound speed were made for several ctenophores at a time and therefore only average measurements of sound speed for a group of ctenophores are reported.

It should be noted that the techniques used in this study produce values of density or sound speed based on the assumption that the animal has uniform material properties throughout its body. This is not the case for either animal and particularly for the lion's mane jellyfish simply holding the animal makes these differences readily apparent. Without separating the different organelles or structures from each other, these methods cannot provide information about how the material properties vary within a specific animal. Specific parts of other gelatinous zooplankton have been shown to

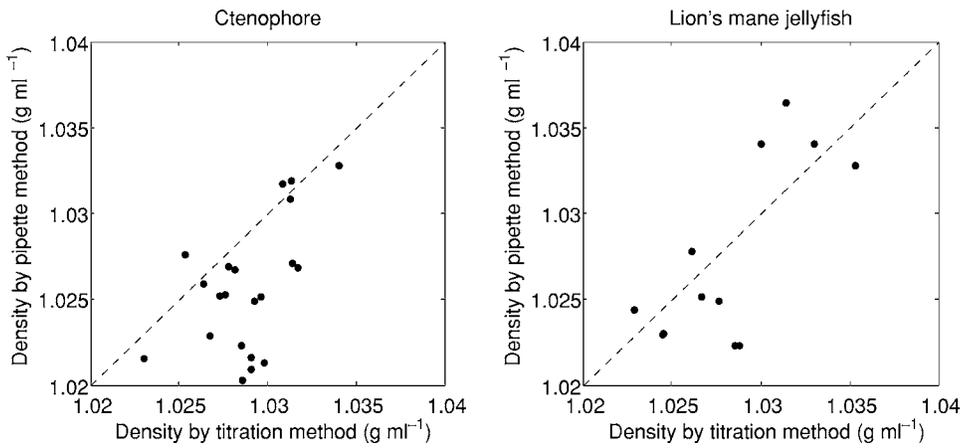J. D. Warren and J. N. Smith: Material properties of gelatinous zooplankton

FIG. 1. Comparison of the pipette and titration method measures of animal density for individual ctenophores (left) and lion's mane jellyfish (right). While there is good agreement between the two methods, the titration method tends to produce a higher measure of ctenophore density than the pipette method which may be due to the animal adjusting to the increased density of the surrounding seawater.

have different scattering efficiencies (Stanton *et al.*, 1998; Warren *et al.*, 2001) and that is likely true for these animals as well.

III. RESULTS

The pipette method was used to measure the density of 21 individual ctenophores after becoming proficient with the procedure such that replicate measurements of the same animal were similar. These same animals also had their density measured using the titration method. One measurement per animal was made using the titration method. Density values ranged from 1.0203 to 1.0328 g ml^{-1} with the pipette method and from 1.0230 to 1.0340 g ml^{-1} for the titration method, although the mean values for each method were similar: 1.0257 (pipette) and 1.0289 (titration) g ml^{-1} (Fig. 1). A paired *t* test showed that the two measurement methods were statistically different ($n=21$, $t=4.5831$, $p<0.001$), however the means of the two distributions differ by only 0.003 g ml^{-1} which is small relative to the range of densities measured. The mean (and range) of *g* for the ctenophores was found to be: 1.0071 (1.0018–1.0140) for the pipette method and 1.0102 (1.0045–1.0153) for the titration method. Using the small sample size method, we calculated the 90% confidence interval for the mean value of *g* for both the pipette (1.0057–1.0085) and titration (1.0093–1.0111) methods using the critical value of a Student's t distribution ($n=21$).

Twelve lion's mane jellyfish were measured using both the pipette and titration methods. As with the ctenophores, replicate measurements using the pipette method were similar and only one titration measurement was made per animal. Jellyfish density ranged from 1.0223 to 1.0364 g ml^{-1} with the pipette method and from 1.0229 to 1.0353 g ml^{-1} for the titration method, although the mean values for each method were similar: 1.0275 (pipette) and 1.0283 (titration) g ml^{-1} (Fig. 1). A paired *t* test showed that the two measurement methods were statistically similar ($n=12$, $t=-0.7678$, $p=0.46$). The mean (and range) of *g* for the lion's mane jellyfish was found to be: 1.0088 (1.0037–1.0176) for the pipette method and 1.0096 (1.0043–1.0165) for the titration method. Using the small sample size method, we calculated the 90% confidence interval for the mean value of *g* for both the

pipette (1.0062–1.0115) and titration (1.0077–1.0115) methods using the critical value of a Student's *t* distribution ($n=12$).

A comparison of the two density measurements for each animal shows that there is overall good agreement between the two techniques (Fig. 1) although the titration method generally results in densities that are larger than the densities from the pipette method. Two potential explanations for this discrepancy are that the pipette method will tend to underestimate the true density of the animal or that the titration method will tend to overestimate the true density of the animal. If there is excess water remaining on the animal before the mass and volume (of the animal and excess water) are measured, then the measurement will be less than the density of the animal since some fraction of the mass and volume being measured will have the density of seawater rather than of the animal. Conversely, the titration method which increases the density of the solution that the animal is in may result in a bias towards higher density measurements if the animal is able to adjust (via osmotic processes) to the new solution by increasing its own density.

Some species have been shown to have a relationship between the size of the animal and their material properties (e.g., Antarctic krill, Chu and Wiebe (2005)), so regressions between animal size, mass, and volume and animal density were calculated (Fig. 2, Table I). Because density, mass, and volume are all three-dimensional quantities, linear regressions between these variables were calculated. However, animal size (length) is a one-dimensional quantity and in order to compare quantities that are of different dimension, the data were fit to a power law relationship. The density values used in the analysis were from the pipette method. Density of individual ctenophores decreased as length of the animal increased. The range of lengths of animals measured is quite small, 1–5 cm, so this relation may not extrapolate to larger animals. A similar relationship between animal size and animal density was found for the lion's mane jellyfish. The range of bell diameters in this data set was from 2 to 11 cm. Similar relationships were found between density and either the mass or volume of the animal for both types of gelatinous zooplankton. This is not surprising considering that animal size, mass, and volume were strongly correlated with each other ($R^2>0.95$ for all combinations).
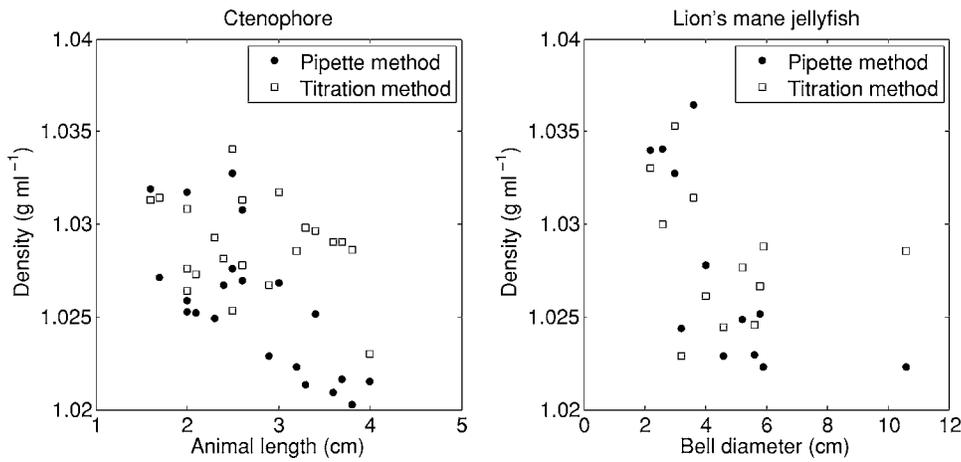
FIG. 2. Density of individual ctenophores (left) and lion's mane jellyfish (right) measured by the pipette (circles) and titration (squares) methods compared to animal size. Both methods show that as animal size increases animal density decreases. A similar negative relationship was found between animal mass or volume and animal density.

Measurements of h were made on three different groups of ctenophores containing 5, 7, and 10 animals, respectively. The volume of the empty t tube was 86 ml and the volume of the animals placed in the tube was 79, 70, and 60 ml, respectively. The value of h for each the three groups was 1.0066, 1.0079, and 1.0077 with an average value of h for all groups of 1.0074. Replicate measurements (with the chamber empty and full) were made for each trial. The mean value of the second set of measurements (1.0073) was nearly the same as the first trial, although the range of h values was larger (h =1.0106, 1.0056, and 1.0058). It is not known if the increased range of h values measured is due to the additional handling of the animals, although it is reassuring that the mean values between trials were very similar.

The h value for a single lion's mane jellyfish was also measured with this method, with h being 1.0004. The lion's mane jellyfish were larger than the ctenophores such that a larger t tube (with a volume of 241 ml) was used. Even with the larger sampling chamber, the lion's mane jellyfish were of such volume and shape that only one animal was able to fit in the t tube and occupied approximately one quarter of the t-tube volume. This animal was significantly damaged after removal from the sampling apparatus so only one h measurement was able to be made. No other lion's mane jellyfish that were collected were able to be placed in the sample chamber with the current experimental setup. The h

value reported here should be viewed with appropriate skepticism as it is a single measurement from one animal and the volume of the animal was small compared to the t-tube volume.

IV. DISCUSSION

While it is not surprising that gelatinous zooplankton have g and h values that are much closer to unity than other fluid-like zooplankton (e.g., crustaceans), the variability in these values is surprising. There were relationships between g and the size of the animal, but relationships between h and animal size were unable to be tested in this experiment. It is unknown whether there are also seasonal or daily changes in these parameters, nor the effect that food availability, predation rate, or energetic expenditures by the animal may have on these parameters.

Previous studies of scattering by gelatinous animals (Mutlu, 2005; Ressler, 2002) have used an acoustic reflection coefficient ($R=0.056$) that was determined empirically by fitting backscatter target strength data to a theoretical scattering model (Monger et al., 1998). The reflection coefficient can be related to g and h by $R=(gh-1)/(gh+1)$. Applying the mean values of g and h found in this study ($g=1.009$, $h=1.007$) results in a reflection coefficient that is seven times smaller ($R=0.008$). If the smaller reflection coefficient from this study is used instead of the Monger et al. (1998) value,

TABLE I. Regression coefficients, residuals, and sample size for comparisons of animal density (ρ) with animal size, mass, and volume. Three-dimensional quantities (density, mass, and volume) were linearly related, but because animal size is a one-dimensional quantity a power law relationship was used to compare size and density. For the linear regression equation $y=bx+a$, the dependent variable (y) corresponds to density and the independent variable (x) corresponds to either mass or volume. For the power law equation $y=cx^d$ the dependent variable (y) corresponds to density and the independent variable (x) corresponds to animal size. Density values are from the pipette method. NA means not applicable.

	Ctenophores ($n=21$)			Lion's mane jellyfish ($n=12$)		
	ρ, length	ρ, mass	ρ, volume	ρ, bell diameter	ρ, mass	ρ, volume
b	NA	−0.002	−0.002	NA	−0.0003	−0.0003
a	NA	1.031	1.031	NA	1.031	0.031
d	−0.0096	NA	NA	−0.0091	NA	NA
c	1.0351	NA	NA	1.0411	NA	NA
R^2	0.49	0.58	0.59	0.58	0.49	0.49
Standard error	2.50E-4	5.33E-4	5.31E-4	4.20E-4	1.10E-3	1.10E-3

then numerical densities of gelatinous animal would increase by at least an order of magnitude as the animal's backscattering cross-section (σ_{bs}) is a function of the reflection coefficient squared (Monger *et al.*, 1998).

Using the minimum measured values of g and h (1.0018 and 1.005) for a ctenophore produces a reflection coefficient of 0.0034 and if the maximum values of g and h (1.014, 1.0079) are used the reflection coefficient is 0.011. While these values are still much smaller than those found by Monger *et al.* (1998), the variability in these values would also affect numerical abundance estimates of gelatinous animals. These data also raise the possibility that modelers of acoustic scattering from zooplankton will need to use a distribution of values for g and h in their models rather than a single value as is commonly done. Distribution functions of zooplankton length and orientation are being used more frequently in acoustic modeling efforts (e.g., Demer and Conti, 2005; Lawson *et al.*, 2006) and distribution functions describing the range of measured g and h values should be used as well.

The values of g and h found in this study are much smaller (roughly half) of those found empirically by Monger *et al.* (1998). The animals used in this study are different species than those in the Monger *et al.* (1998) study although the size of the animals are similar. The ctenophores and lion's mane jellyfish were also found in water that was probably less dense (i.e., warmer and fresher) than Puget Sound (site of the Monger *et al.* (1998) study). It is unknown whether gelatinous animals adjust their material properties relative to their environment, although it is likely that they have this ability since the species in this study are found in a wide range of environments from shallow estuarine bays (seawater density $\sim$1.008 g ml^{-1}) to off-shore oceanic conditions (seawater density $\sim$1.024 g ml^{-1}). The values of g and h found in this study may only apply to animals that are in a similar estuarine environment and investigation of whether g and h are dependent on the density of the surrounding seawater is needed.

Acoustic techniques offer one assessment method for measuring the distribution and abundance of gelatinous zooplankton, however accurate scattering model inputs are important for accurate predictions of animal numerical abundance. Given that many studies have attributed relatively high target strengths to gelatinous scatterers (Table II in Alvarez Colombo *et al.*, 2003), it is important to have accurate scattering models and model inputs that support these empirical observations.

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