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# Acoustic backscatter measurements with a 153 kHz ADCP in the northeastern Gulf of Mexico: determination of dominant zooplankton and micronekton scatterers

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## Abstract

A 153 kHz narrowband acoustic Doppler current profiler (ADCP) was used to measure volume backscattering strength ( $S_v$ ) during a deepwater oceanographic survey of cetacean and seabird habitat in the northeastern Gulf of Mexico.  $S_v$  was positively related to zooplankton and micronekton biomass (wet displacement volume) in 'sea-truth' net hauls made with a 1 m<sup>2</sup> Multiple Opening-Closing Net Environmental Sensing System (MOCNESS). A subset of these MOCNESS tows was used to explore the relationship between the numerical densities of various taxonomic categories of zooplankton and the ADCP backscatter signal. Crustaceans, small fish, and fragments of non-gas-bearing siphonophores in the net samples all showed significant, positive correlations with the acoustic signal, while other types of gelatinous zooplankton, pteropod and atlantid molluscs, and gas-filled siphonophore floats showed no significant correlation with  $S_v$ . Previously published acoustic scattering models for zooplankton were used to calculate expected scattering for several general zooplankton types and sizes for comparison with the field data. Even though gelatinous material often made up a large fraction of the total biomass, crustaceans, small fish, and pteropods were most likely the important scatterers. Since only crustacean and small fish densities were significantly correlated with  $S_v$ , it is suggested that  $S_v$  at 153 kHz can be used as a relative proxy for the abundance of these organisms in the Gulf of Mexico.

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**Keywords:** USA; Gulf of Mexico; Zooplankton; Acoustic models; Sound scattering; Correlation analysis; Randomization analysis; ADCP; 24–31°N × 84–90°W

## 1. Introduction

Along with traditional net measurements and optical techniques, measurements of acoustic

backscatter are currently recognized as an important way of studying zooplankton and micronekton (Greene and Wiebe, 1990; Wiebe et al., 1997; Greene et al., 1998; Foote and Stanton, 2000; Thomas and Kirsch, 2000). The subject remains an active area of both field and modeling research (e.g., Kirsch et al., 2000; Stanton and Chu, 2000; Warren, 2000; Wormuth et al., 2000; Griffiths et al., 2002). Acoustic Doppler current profilers (ADCPs) have been used to study patterns in

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acoustic backscattering from zooplankton (Flagg and Smith, 1989; Ashjian et al., 1994; Roe et al., 1998; Zimmerman and Biggs, 1999; Wade and Heywood, 2001), and it has been documented that volume backscattering strength ( $S_v$ ) measured with an ADCP has a positive relationship with the  $\log_{10}$  of bulk biomass of zooplankton and micronekton measured as wet displacement volume (WDV) in the northeastern Gulf of Mexico (Ressler et al., 1998; Zimmerman and Biggs, 1999; Wormuth et al., 2000). Yet a question remains: which organisms composing this bulk biomass are the targets that most influence the measured acoustic backscatter signal? This question is an important one, especially in light of (1) recent acoustical studies of zooplankton showing that taxonomic composition has a large influence on observed volume backscattering (Stanton et al., 1994a; Wiebe et al., 1996, 1997; Stanton and Chu, 2000), and (2) ecological field studies that employ acoustic estimates to identify 'hot-spots' in zooplankton biomass (these data were collected as part of the survey of cetacean and seabird habitat reported in Hess, 1999; Davis et al., 2002). This paper explores the interpretation of  $S_v$  data collected with a 153 kHz narrowband ADCP in the northeastern Gulf of Mexico using a limited analysis of 'sea-truth' net samples.

## 2. Methods

### 2.1. Zooplankton acoustics

Acoustic estimates of zooplankton concentration and biomass rely upon the assumption that  $S_v$  measured in the ocean at frequencies on the order of  $10^2$  kHz is due primarily to zooplankton and micronekton targets (Stanton et al., 1994b; Medwin and Clay, 1998). In the simplest case where all targets in the ensonified volume are the same size, have the same scattering characteristics, and are randomly oriented with respect to the acoustic beam,  $S_v$  in decibels (dB) can be expressed as

$$S_v = 10 \log_{10}(n\sigma_{bs}),$$

where  $S_v$  is the volume backscattering strength (dB re  $1 \text{ m}^{-1} 4\pi^{-1}$ ),  $n$  the number of targets per unit

volume ( $\text{number m}^{-3}$ ), and,  $\sigma_{bs}$  the acoustic backscattering cross-section of each target, averaged over orientation ( $\text{m}^2$ ).

If accurate acoustic backscatter measurements are made, one should in theory be able to invert acoustic measurements for the concentration or biomass of zooplankton and micronekton targets (the 'inverse problem'; see Holliday and Pieper, 1980, 1995). Yet in truth, zooplankton and micronekton assemblages are composed of many different types of animals, and  $\sigma_{bs}$  is a complex function of the acoustic frequency of the echosounder and the material properties, orientation, and size/shape/structure of the biological 'target' (Foote and Stanton, 2000). The goal of being able to unambiguously invert acoustic data for biological information (biomass, concentration, size, and taxa of target organisms) has not yet been fully realized in most field studies, even with advanced instrumentation, data collection, and modeling techniques (e.g., Wiebe et al., 1997; Benfield et al., 1998; Warren, 2000).

$S_v$  measurements with an ADCP do not represent the state of the art in zooplankton acoustics technology. Multi-frequency, special-purpose echosounders are preferred, because unlike an ADCP they usually can be calibrated with standard targets, they allow more flexibility in data collection, and the multiple frequencies provide additional information that can lead to more accurate measurements of zooplankton and micronekton (Stanton et al., 1994a; Foote and Stanton, 2000; Warren, 2000). Still, despite their limitations (e.g., Brierley et al., 1998), ADCPs are relatively inexpensive and widely available compared to special-purpose acoustic gear. Moored and vessel-mounted ADCPs can potentially be used to simultaneously collect current velocity data and study temporal and spatial patterns in zooplankton and micronekton biomass (Flagg and Smith, 1989; Ashjian et al., 1994; Roe et al., 1998; Zimmerman and Biggs, 1999; Wade and Heywood, 2001; Davis et al., 2002; Griffiths et al., 2002). When combined with net sampling of zooplankton and micronekton,  $S_v$  data from an ADCP may provide a way to estimate standing stocks (Zhou et al., 1994; Ressler et al., 1998; Wormuth et al., 2000).

Knowing the dominant biological scatterers is useful when interpreting  $S_v$  measurements and acoustic estimates of WDV. The working hypothesis in this paper was that in the field surveys discussed here,  $S_v$  would be positively correlated not only to the total amount of WDV biomass in Multiple Opening-Closing Net Environmental Sensing System (MOCNESS) samples, but more strongly to some components of the biomass than others. More specifically, it was hypothesized that (1) organisms larger than 2 mm in length could explain most of the scattering, and (2) non-gas-bearing gelatinous components of the zooplankton would scatter sound only weakly, while other targets (e.g. crustaceans, fish, hard-shelled zooplankton, and anything containing a gas bubble) presenting a relatively larger density or compressibility contrast with the surrounding water would be relatively stronger scatterers of sound (Medwin and Clay, 1998; Foote and Stanton, 2000) and would correlate strongly with measured  $S_v$ . These hypotheses are tested in this paper by non-parametric correlation analysis and simple order-of-magnitude scattering model calculations.

## 2.2. Data collection

Echo intensity data were collected during October 1996 and August 1997 with an RD Instruments narrowband 153 kHz ADCP mounted on the R.V. *Gyre*. Five-minute averages of echo intensity (200 pings) were collected while underway with the manufacturer's Transect 1.80 software (RD Instruments, 1994) and subsequently converted into  $S_v$  according to recommended procedures and instrument-specific calibration information supplied by RD Instruments (RD Instruments, 1998; Zimmerman and Biggs, 1999).  $S_v$  measurements were collected every 4 m over the depth interval 10–202 m: 10 m is the minimum distance allowed by the instrument (given its hull depth, transmit pulse, and blank after transmit to account for ringing of the transducer), and 202 m was used as the maximum because the signal-to-noise ratio of the data decreases appreciably below this depth.

'Sea-truth' net measurements were gathered in the study area with a 1 m<sup>2</sup> mouth area, 333 µm

mesh MOCNESS (for a full description, see Wiebe et al., 1985), which sampled in the upper 200 m of the water column. A MOCNESS can take up to nine discrete samples of zooplankton and micronekton. WDV was determined for each MOCNESS net and matched with an average value of  $S_v$  from the ADCP for the time of the tow and the depth range sampled by the net. For a 1–2 h MOCNESS tow, the horizontal distance covered by both acoustical and net sampling was approximately 7.4 km (4 nautical miles) or less at typical tow speeds of about 3.7 km/h (2 knots). The volume of water filtered by a single MOCNESS net in a tow varied depending on local conditions and the sampling objectives for a particular station, averaging 1481 m<sup>3</sup> (SD 716 m<sup>3</sup>) in 1996 and 436 m<sup>3</sup> (SD 279 m<sup>3</sup>) in 1997. In comparison to a MOCNESS net, an echosounder's acoustic beam spreads with range and covers a larger volume of water, potentially making the acoustic measurements more sensitive to rare, but acoustically very important, biological scatterers. Based on a simplified conceptual model of a single ADCP beam (a cone 4° wide, pointed at 30° from vertical), the ensonified volume of a 4 m depth bin at 10 m below the ship during each ping would be on the order of only 3 m<sup>3</sup>, but as this beam spreads with range the volume would grow to more than 900 m<sup>3</sup> in a 4 m bin 198 m below the ship. However, the narrowband ADCP samples echo intensity data only once in the last quarter of each depth bin during a ping rather than integrating echo intensity over the whole depth interval (RD Instruments, 1998, p. 15; Darryl Symonds, RDI, personal communication), making the effective sampling volume smaller than the preceding calculation suggests, and meaning that both the MOCNESS and the ADCP could undersample extremely rare zooplankton and micronekton targets.

A simple linear regression of the log<sub>10</sub> of WDV from the MOCNESS on  $S_v$  from the ADCP was performed, resulting in coefficient of determination ( $r^2$ ) values of 0.58 ( $n = 91$ , October 1996) and 0.37 ( $n = 134$ , August 1997). These results were reported in Wormuth et al. (2000), where the positive functional relationship developed by regression was used to estimate a predicted mean

biomass (PMB) at a given location for each cruise on the basis of  $S_v$  measurements.

To further explore the relationship between MOCNESS catch and  $S_v$ , a representative subsample of the tows was used for analysis of the zooplankton and micronekton taxa present. Unfortunately, given limited time and funds only nine tows were used (out of 37 total). At least one tow was selected from each of the three environmental regimes encountered in the study (cyclonic eddy, anticyclonic eddy, and confluence/other; see Biggs et al., 2000) and where possible from both diel periods (night and day). Four tows were counted from October 1996 and five tows were counted from August 1997, each with 3–9 nets each that sampled in the upper 200 m of the water column. Because of the low sample size, between-cruise differences were not examined, and the tows from both years were pooled for this analysis. The whole zooplankton sample from each net was filtered through a 2 mm mesh screen, and only the >2 mm size fraction retained on the screen was enumerated. Results were divided into the following categories: pteropod and atlantid molluscs, decapods, euphausiids, other crustaceans (including large copepods), gelatinous (non-siphonophore), gelatinous (siphonophore), gas-filled physonect siphonophore floats, small fish, and all other.

### 2.3. Correlation and randomization analyses

To test the hypothesis that certain components of the biomass had more influence on the measured backscatter signal than others, numerical density estimates of various categories of zooplankton from MOCNESS nets were compared with  $S_v$  collected at the same time in a correlation analysis. Since the numerical density data from this small subset of MOCNESS samples did not meet the assumption of normal distribution required for use of the standard Pearson  $r$  correlation coefficient, a non-parametric correlation analysis (Spearman rank correlation coefficient) tested for significance by randomization was used. Randomization methods are a valid test of the significance of the correlations despite the fact that the samples used were not randomly chosen,

although the assumption that the subsample is not biased with respect to the null hypothesis must still be made in order to generalize results from the subsample to the ‘population’ (Manly, 1997; Legendre and Legendre, 1998).

To test the obtained correlations for significance,  $S_v$  values were randomly assigned to the set of data from each zooplankton category, and then correlation between each category and  $S_v$  was calculated. This process was repeated many times, under the null hypothesis that if  $S_v$  and the zooplankton density in each of the categories were unrelated, all possible pairings would be equally likely to occur (Manly, 1997). A histogram of all the correlation values obtained during 100,000 randomizing iterations essentially forms a test distribution showing how often various Spearman  $r$  values might occur by chance, given the sample data.

### 2.4. Calculation of expected backscatter using scattering models

To determine whether the observed densities of categories of zooplankton and micronekton could have explained the observed volume scattering, zooplankton scattering models were used. Zooplanktonic organisms have been divided into three classes for the purpose of modeling: weakly scattering fluid-like bodies, elastic-shelled scatterers, and gas-bearing scatterers (e.g., Stanton et al., 1994a, 1998a). The  $\sigma_{bs}$  for each of these categories is modeled mathematically, and the expected  $S_v$  in dB is calculated from the expression  $S_v = 10 \log_{10}(n\sigma_{bs})$ .

Since size-frequency data were not gathered for these samples, rather than a rigorous ‘forward-problem’ analysis where expected scattering from every organism in a net sample is calculated and compared with field data (e.g., Wiebe et al., 1996; Warren, 2000), expected scattering was calculated instead for observed densities and likely sizes of suspected zooplankton targets. Sizes were based on qualitative observations of these samples as well as the literature on the subtropical zooplankton community in the Gulf of Mexico. Model calculations were made for (1) crustaceans and small fish, (2) non-gas-bearing siphonophores, (3)

siphonophores with gas floats, and (4) pteropods/atlantids. In these simple calculations, a uniform distribution of lengths in each proposed size class was assumed. Necessary model parameters for each category were drawn from the literature and adjusted if necessary to fit these samples, as described in more detail below. All calculations used the ADCP frequency  $f = 153 \text{ kHz}$  and assumed a speed of sound in seawater  $c = 1500 \text{ m s}^{-1}$ . Implementations of all scattering models were provided courtesy of J.D. Warren (Woods Hole Oceanographic Institution; see also Warren, 2000).

#### 2.4.1. Crustaceans and small fish

Stanton and Chu (2000) note that a fluid cylinder model is appropriate for a wide range of animals that have material properties close to those of water (e.g. euphausiids, copepods, salps, and the tissue portion of siphonophores). A randomly oriented, fluid, bent cylinder model described in Stanton et al. (1994a) was used here to model crustaceans (including decapods, euphausiids, and other crustaceans) and small fish (as done by Wiebe et al., 1996, 1997). The reflection coefficient  $r^1$  in the model was set to 0.058 and length-to-width ratio  $\beta_d$  to 8, matching the modeling of scattering from a decapod shrimp in Stanton et al. (1994a) as an approximation for weakly scattering crustaceans in these samples. These model parameters were assumed to be approximately correct for the small fish as well (assuming no gas-filled swimbladder is present and the observed scattering is primarily from the body of the fish), since most published material properties for fish fall within the range of those for euphausiids and decapods (see Table 1).

#### 2.4.2. Gelatinous organisms

Fragments of non-gas-bearing siphonophores made up a large proportion of the gelatinous material in the net samples (these relatively fragile

gelatinous organisms often break apart during collection). Although it is difficult to tell how many whole siphonophore targets are represented by the pieces, the concentration of identifiable 'individual' parts can sometimes provide an indication of abundance (Pugh, 2000). Stanton et al. (1994a) modeled both salps and decapods as weakly scattering fluid targets, but adjusted model parameters to account for the differing material properties of the two organisms. There are few published estimates of the material properties of gelatinous zooplankton in general or siphonophore tissue in particular (Table 1). Making the assumption that gelatinous salp tissue would approximate that of non-gas-bearing gelatinous siphonophores as well, in these calculations  $r$  was set at 0.0041 to match the reflection coefficient used for salp tissue in Stanton et al. (1994a). Use of a reflection coefficient much smaller than the one used for crustaceans and small fish makes sense intuitively, because the tissues of gelatinous zooplankton such as salps and siphonophores are likely to be >95% water (e.g., Vinogradov, 1953; Clarke et al., 1992). On the other hand, Gulf of Mexico planktonic crustaceans and fish have been reported to be only 75–88% water (Morris, 1982; Stickney and Torres, 1989) with the remainder composed of more dense protein and lipid material, therefore making the organisms stronger scatterers of incident sound (higher  $r$  value in the models).  $\beta_d$  was set to 3, the latter based on typical dimensions of whole calycophore siphonophores common in the Gulf of Mexico (Families Diphyidae and Abylidae in Pugh, 2000). Note that most of the siphonophores found in the samples described in this paper were not the long, linear-shaped, gas-bearing physonect siphonophores as discussed in Stanton et al. (1994a, 1998a,b), for which  $\beta_d \sim 18$ .

#### 2.4.3. Gas-bearing siphonophores

Values for the radius  $a$  of the siphonophore gas-filled float used in the calculations included 0.1, 0.5, and 1 mm (physonect siphonophore floats modeled by Stanton et al. (1998b) and Warren (2000) had a  $\sim 0.3$ – $0.5$  mm). Expected scattering was calculated by interpolating between values in a table of solutions to Anderson's (1950) spherical

<sup>1</sup>  $R$  is the reflection coefficient that depends on the material properties of the object.  $R$  [or here,  $r$ ] is related to those parameters by the equation  $R = (gh - 1)/(gh + 1)$ , where ' $g$ ' is the mass density of the body relative to that of the surrounding water and ' $h$ ' is the relative sound speed of the body' (Stanton et al., 1994a).

Table 1

Values for material properties of zooplankton found in the literature are listed

References	Organism	$g$	$h$	$r$
Chu et al. (2000)	Range of reported values <sup>a</sup>	0.9862–1.0622	0.9978–1.0353	(–)0.01–(+ )0.05
Kirsch et al. (2000)	<i>Neocalanus</i> copepods	—	—	0.0178
	Pteropods	—	—	0.1533
	Euphausiids	—	—	0.0341
Stanton and Chu (2000) <sup>b</sup>	Average values	1.04	1.04	0.039
Medwin and Clay (1998) <sup>c</sup>	Amphipods	1.055–1.088	1–1.009	0.027–0.047
	Cladocerans	1.011–1.017	—	—
	Copepods	1.023–1.049	1.006–1.012	0.014–0.030
	Decapods	—	0.997–1.006	—
	Euphausiids	1.010–1.050	1–1.046	0.0050–0.047
	Mysiids	1.075	—	—
	Fish flesh <sup>d</sup>	1.023	1.033	0.028
Monger et al. (1998) <sup>e</sup>	<i>Pleurobrachia</i> (ctenophore)	—	—	0.056
	<i>Aequorea</i> (hydromedusa)	—	—	0.03
Stanton et al. (1994a) <sup>f</sup>	Gas bubble	—	—	1
	Shrimp	—	—	0.058
	Salp	—	—	0.0041
	Gastropod	—	—	0.5
Foote (1990), Foote et al. (1990)	<i>Euphausia superba</i>	1.0357	1.0279	0.031
Clay and Medwin (1977) <sup>g,h</sup>	seawater	1	1	0
	<i>Euphausia pacifica</i>	1.03	—	—
	Preserved	1.016	1.033	0.024
	Fresh	1.038	—	—
	Fish flesh	1.03–1.06	1.03–1.08	0.030–0.068
	Fish bone	2.04	3.75	—
	Brine shrimp (unhatched)	1.19	—	—
	Hatched	1.12	—	—
	<i>Calanus marshallae</i> , fresh	1.02	1.007	0.013

<sup>a</sup>Non-shelled animals only;  $r$  is a calculated range using min/max of given range for  $g$  and  $h$ .<sup>b</sup>These  $g$  and  $h$  values are  $\pm 1$ –2%. The authors used a range of  $g$  and  $h$  of 1.01–1.06 in simulations, which led to 15–20 dB variations in target strength.<sup>c</sup>From a table summary on pp. 394–395 of Medwin and Clay. The range of values given is noted.<sup>d</sup>The  $g$  and  $h$  shown for fish flesh were calculated from  $c$  and density values given on p. 388 of Medwin and Clay.<sup>e</sup>Authors express the opinion that experimental error may have led to overestimates of  $r$  in their study, esp. for *Pleurobrachia*.<sup>f</sup> $r$ =unity for gas. Other coefficients were empirically determined from scattering data in the laboratory.<sup>g</sup>Experimentally determined; given values are  $\pm 0.0067$  and 0.0024, respectively.<sup>h</sup>Summarized from various sources in a table on p. 218 of Clay and Medwin.<sup>g</sup> $g$  is the density of the body relative to seawater,  $h$  is the sound speed relative to seawater, and  $r$  is the reflection coefficient defined as  $(gh - 1)/(gh + 1)$  by Stanton et al. (1994a). Italics denote calculation of  $r$  from minimum and maximum  $g$  and  $h$  values in listed source using this equation.

scattering model adapted for an air-filled sphere at one atmosphere of pressure (Stanton et al., 1998a; this implementation described further in Warren, 2000), based on the product of the acoustic wavenumber ( $k = 2\pi f/c$ ) and radius of the target. It was assumed that a gas-filled float would not change size at different depths in the

water column, since it is known that siphonophores can regulate the volume of their floats with changing ambient pressure to regulate buoyancy (Mackie et al., 1987). No value for  $r$  is specified by the user for this model, although  $r$  would be approximately unity for gas (Stanton et al., 1994a).

#### 2.4.4. Pteropods/atlantids

For elastic-shelled scatterers, body lengths of 1, 2, 10, and 20 mm at concentrations of 0.001, 0.01, and 0.1 animal per  $\text{m}^3$  were used (this is a reasonable range of concentrations and sizes, and includes the concentrations found in these samples). Other model parameters included  $r = 0.5$  based on modeling of a gastropod by Stanton et al. (1994a). Warren (2000) used this same value of  $r$  for modeling the scattering by pteropods of the genus *Limacina*.

### 3. Results

#### 3.1. Summary of sample composition

For the 55 individual net samples from nine tows in the upper 200 m of the water column, the average catch was numerically dominated by euphausiids and non-physonect siphonophore fragments (Fig. 1, top panel). Decapods, other crustaceans, other gelatinous material, and small (mostly larval) fish were also fairly common. When broken down into gross taxonomic categories used to model sound scattering by zooplankton, fluid-like scatterers (crustaceans and small fish, gelatinous plankton) were most common numerically while elastic-shelled zooplankton (pteropods, atlantid molluscs) were uncommon and gas-filled physonect siphonophore floats were numerically quite rare. When shown as reflectance-weighted density, with the mean in each category multiplied by the  $r$  factor used in scattering models for each category (note that this does not account for the size of the targets), a somewhat different conclusion may be drawn (Fig. 1, bottom panel): fluid-like crustaceans and small fish and elastic-shelled molluscs appear equally important given the combination of their scattering characteristics and observed densities, while fluid-like gelatinous plankton and gas-bearing plankton appear much less so.

When concentrations of zooplankton categories are plotted individually versus  $S_v$  (Fig. 2), it is clear that when  $S_v$  increases, so does total WDV and the densities of euphausiids, decapods, other crustaceans, small fish, and gelatinous siphono-

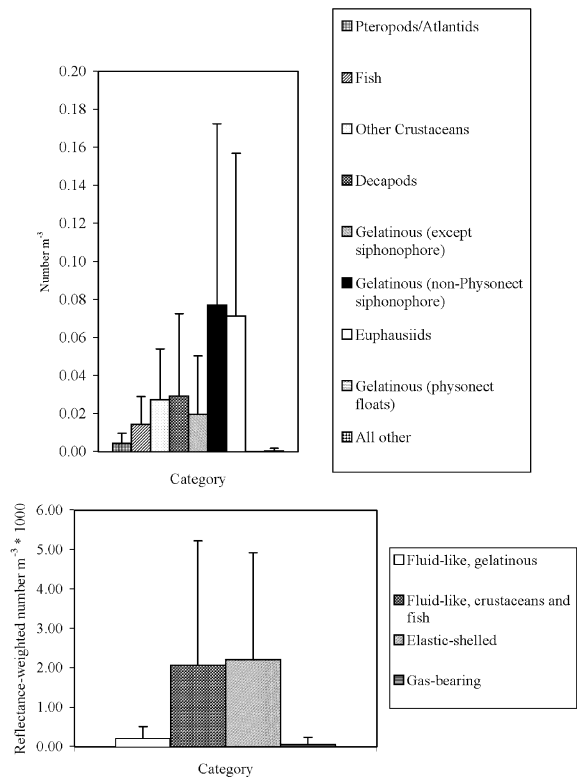


Fig. 1. Mean numerical density of various taxa (top panel) in the samples and the reflectance-weighted mean number of organisms in the samples (bottom panel) that fall into four gross anatomical scattering model classes (organisms  $> 2$  mm in length only). The 'All Other' and 'Gelatinous (physonect floats)' categories are the extremely small eighth and ninth bars from left on the top panel, and the 'Gas-bearing' category is the small last bar on the bottom panel. Error bars represent one standard deviation of the mean.

phore fragments (asterisks in Fig. 2). This autocorrelation between potential predictors makes it difficult to determine whether particular components of the total biomass may be driving the established relationship between WDV and  $S_v$ . Yet these categories do not always covary with one another. A MOCNESS deployment in which the nets were tripped sequentially at one depth (150 m) during a dawn vertical migration provides an interesting anecdotal example (Fig. 3). In this tow, the nets represent different times instead of different depths in the water column. The goal of this tow strategy was to catch vertically migrating organisms as they passed through 150 m. Fig. 3 is

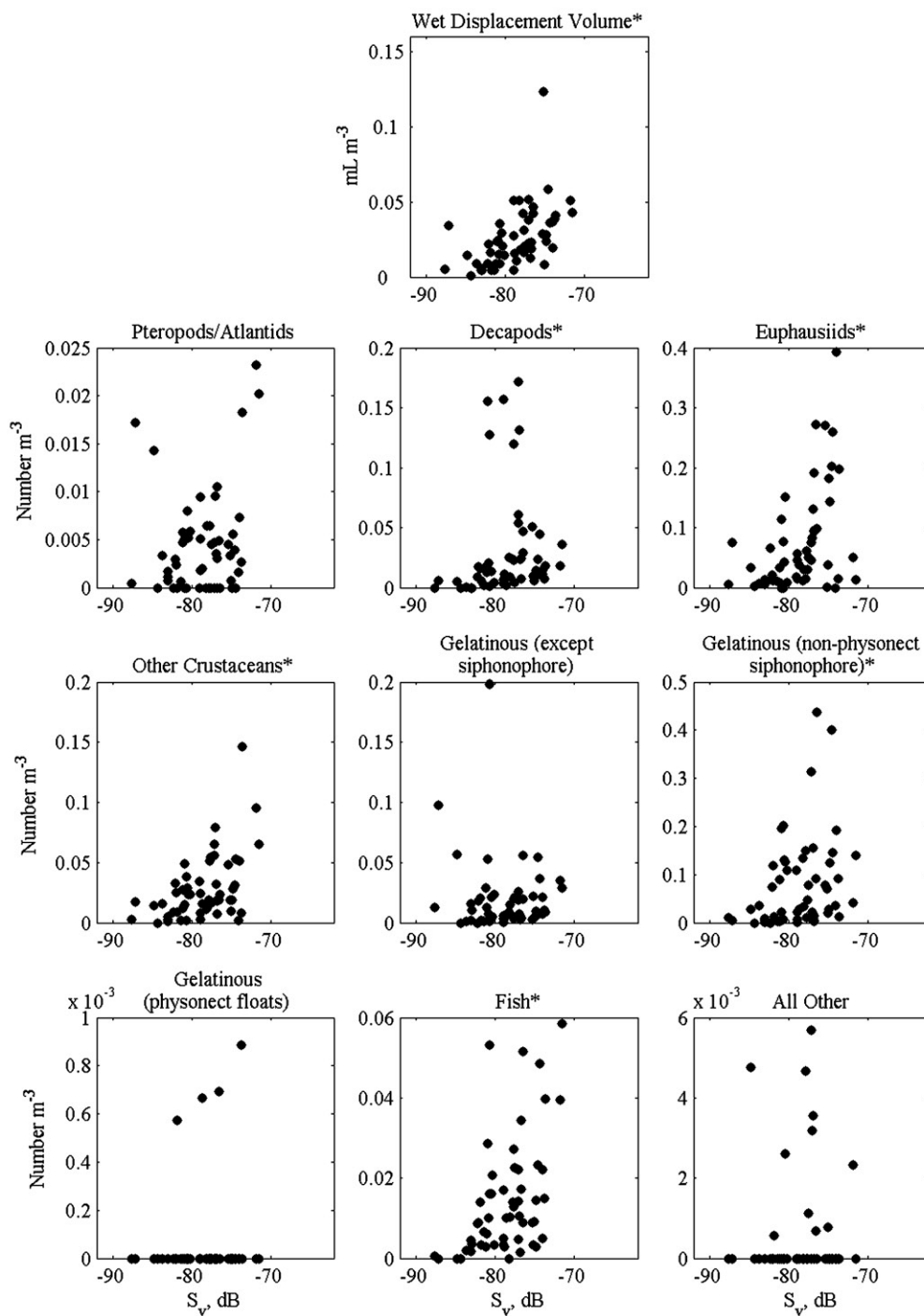


Fig. 2. Scatterplots of WDV and numerical densities of various zooplankton categories as a function of  $S_v$  (organisms > 2 mm in length only). Those plots marked by an asterisk (\*) show a statistically significant positive relationship with  $S_v$ .



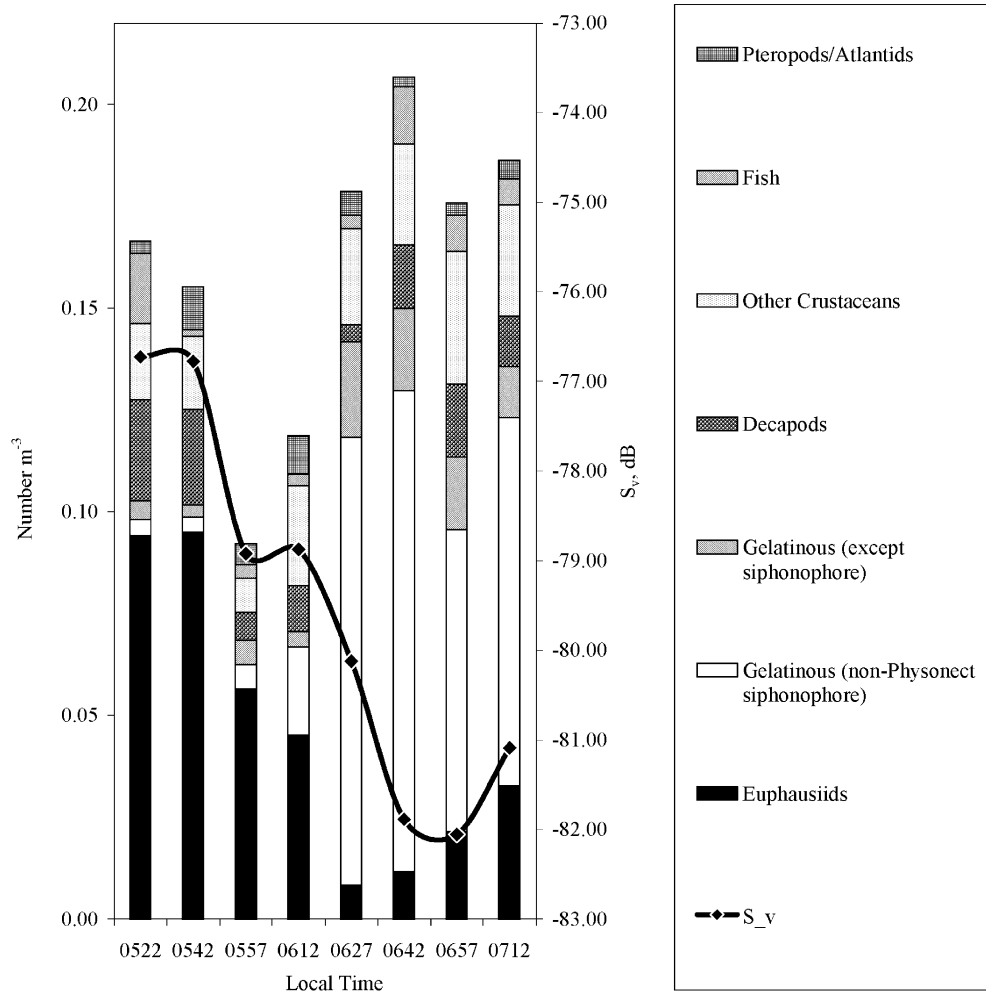


Fig. 3. Numerical density data from MOCNESS nets fished sequentially at one depth (bars; organisms > 2 mm in length only) and average  $S_v$  collected during the same tow (line). No physonect floats were found in these samples.

striking, because the concentration of euphausiids is tracked very closely by  $S_v$ . The number of gelatinous siphonophore fragments also changes, but in an almost completely opposite fashion. Note that variation in pteropod/atlantid densities appeared unrelated to  $S_v$ , and that there were no gas-filled siphonophore floats counted in the samples from this tow.

### 3.2. Correlation and randomization results

Spearman rank correlations between each zooplankton category and  $S_v$  are shown in Table 2.

These results quantify the general patterns seen in Fig. 2, suggesting that only small fish, decapods, euphausiids, other crustaceans, and gelatinous siphonophore fragments were positively associated with  $S_v$ . Randomization analysis suggested that these associations were statistically significant, since absolute values of Spearman  $r > 0.3$  occurred rarely (<5% of the time ( $P < 0.05$ )) and were not likely to have occurred by chance. In general, 'significant' correlations were rarely obtained by chance in the randomization runs. Note that neither pteropods/atlantids nor gas-filled siphonophore floats were significantly associated with  $S_v$ .

### 3.3. Scattering model results

The results of scattering model calculations are shown in Fig. 4. Symbols indicate predicted  $S_v$  for observed zooplankton densities in each of 55 MOCNESS nets at several assumed size classes for each taxonomic group modeled. A 1:1 reference line for perfect agreement between predicted and observed scattering is shown. Fig. 5 shows predicted scattering for the same assumed size

classes plotted as a function of a range of densities for each group. The mean  $S_v$  and mean density observed in this study for each group are indicated.

It is clear from Figs. 4 and 5 that calycephore siphonophores cannot explain much of the observed backscatter at any of the sizes modeled and densities observed in this study, though fragments of these organisms were positively correlated with  $S_v$ . It is also apparent that although the largest

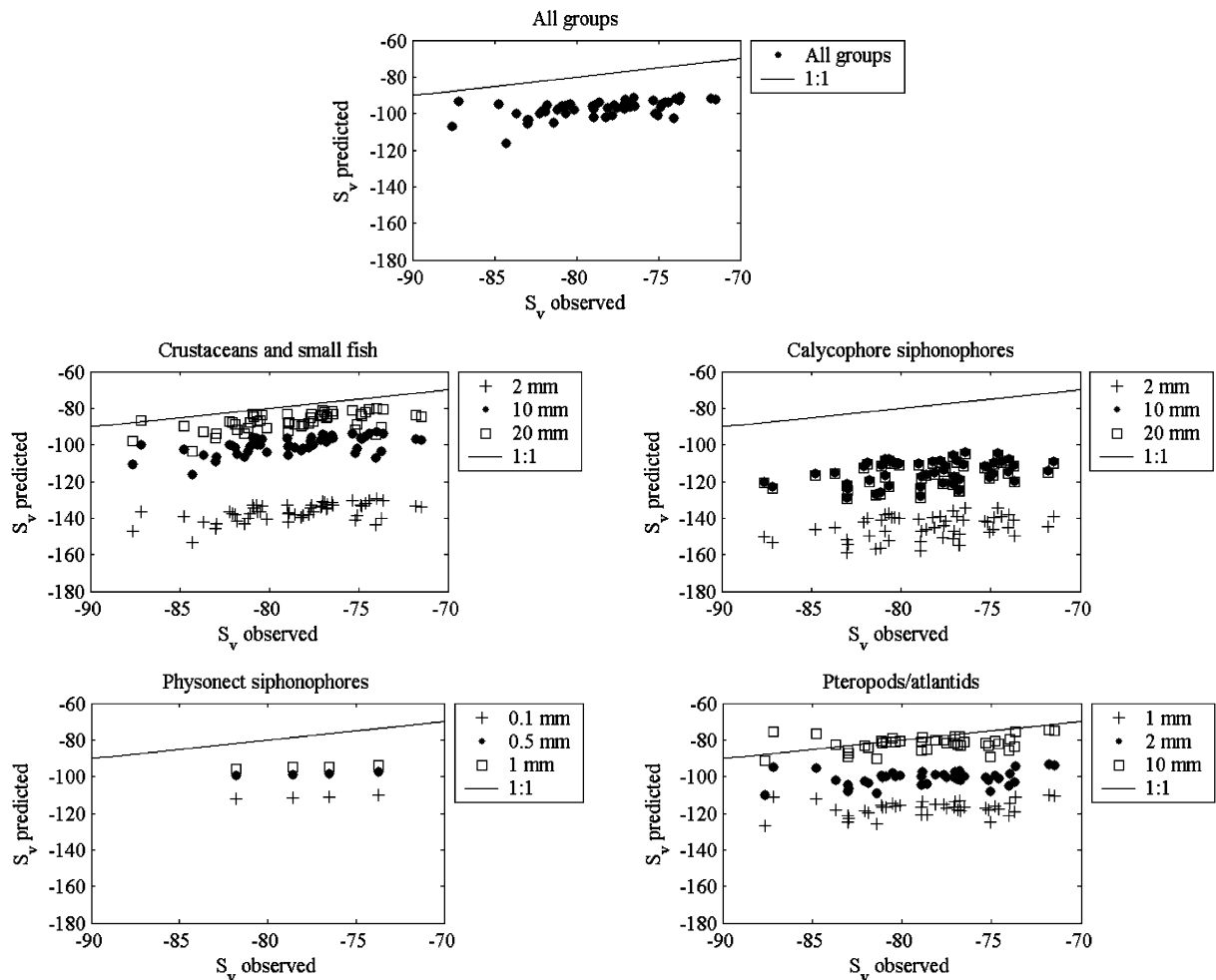


Fig. 4. Observed  $S_v$  and predicted scattering for several zooplankton groups. A 1:1 predicted:observed reference line is shown in each panel. The legend indicates symbols for scattering model predictions for organisms occurring at observed densities from each of 55 MOCNESS nets and at several different possible sizes. For crustaceans, small fish, and calycephore siphonophores, the 'sizes' are lengths; for physonect floats, they are spherical radii; and for pteropods/atlantid molluscs, they are equivalent spherical diameters. The top panel shows combined predicted scattering for 10 mm crustaceans and fish, 20 mm calycephore siphonophores, 1 mm physonect siphonophores, and 2 mm pteropods/atlantids at observed densities.

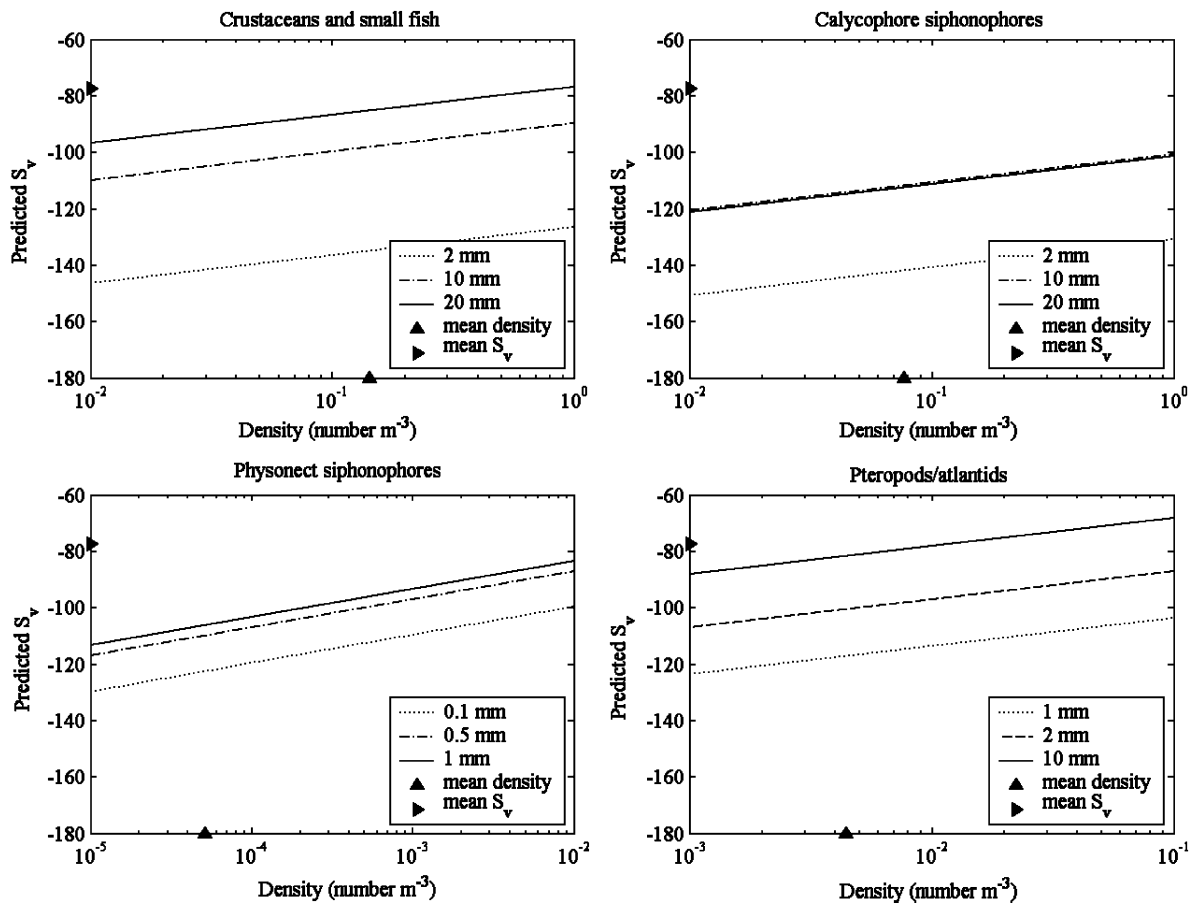


Fig. 5. Predicted scattering for several zooplankton groups at a range of possible densities and sizes. Parameters in the models are the same as those used in Fig. 4. The mean density and mean  $S_v$  observed in this study are indicated by the triangles on the axes.

Table 2

Spearman rank correlation  $r$  of various categories of zooplankton and acoustic volume backscattering strength from a 153 kHz ADCP ( $n = 55$ )

	$r$
Pteropods/atlantids	0.1948
Decapods	<u>0.5096</u>
Euphausiids	<u>0.4946</u>
Other crustaceans	<u>0.47597</u>
Gelatinous (not siphonophore)	0.19066
Gelatinous (siphonophore)	<u>0.4153</u>
Physonect siphonophore floats	<u>0.0736</u>
Small fish	<u>0.5291</u>
All other	0.0854

Significant correlates at the  $\alpha = 0.05$  level based on randomization are underlined.

physonect siphonophores are important sound scatterers even at low concentrations, since they are quite rare (they occurred in only 4 of 55 cases in this data set) these organisms are not likely to have explained a large portion of the variability in  $S_v$ . The results are more ambiguous for weakly scattering crustaceans and fish and pteropods/atlantids. If animals in either category were of sufficient size (10–20 mm for crustaceans and small fish, 2–10 mm for pteropods/atlantids), predicted  $S_v$  values suggest that the concentrations of both groups could have contributed substantially to the observed backscatter.

The combined predicted scattering for 10 mm crustaceans and fish, 20 mm calycophore

siphonophores, 1 mm physonect siphonophores, and 2 mm pteropods/atlantids at observed densities is shown in the top panel of Fig. 5. The mean difference between predicted and observed scattering is  $\sim 19$  dB.

## 4. Discussion

### 4.1. Dominant zooplankton sound scattering organisms

Non-parametric correlation analysis indicated that densities of small (mostly larval) fish, decapods, euphausiids, other crustaceans, and gelatinous calycophore siphonophore material were significantly associated with average  $S_v$  (listed in order from greatest correlation to least, all positive Spearman  $r$  values between 0.42 and 0.52; see Table 2). Randomization testing indicated that these correlations were not likely to have occurred by chance. On average, both the amount of gelatinous material and the densities of crustaceans and small fish in the samples increased with  $S_v$  (Fig. 2). Yet, in a case where the densities of gelatinous material and densities of euphausiids varied inversely during a tow, it is telling that euphausiids indeed appeared to closely track  $S_v$  while the concentration of weakly scattering gelatinous material (non-gas-bearing siphonophore fragments) did not (Fig. 3). Other zooplankton categories included in the analysis, including pteropods and gas-bearing siphonophores, did not show any significant association with acoustic backscattering strength.

Non-gas-bearing calycophore siphonophores are relatively common in the Gulf of Mexico: siphonophore densities ranging from 0.001 to 4.2 per  $m^3$  (daytime mean  $0.680 m^{-3}$ , nighttime mean  $0.516 m^{-3}$ ) have recently been reported for the oceanic Gulf of Mexico, with calycophore siphonophores constituting greater than 89% of the total numbers of identifiable fragments (Gasca, 1999). Yet scattering model results support the contention that non-gas-bearing gelatinous zooplankton in this size range are unimportant acoustic targets (Figs. 4 and 5). Model predictions for calycophore siphonophore fragments were

several orders of magnitude below observed levels, even assuming that they were all as large as 20 mm in length at densities much higher than those observed here.

In some acoustic field studies at temperate latitudes, gas-bearing physonect siphonophores (concentrations of  $1\text{--}20 m^{-3}$ ; Warren, 2000) have been shown to strongly influence  $S_v$  patterns, though in these studies the organisms were several orders of magnitude more common than in the samples analyzed here. Modeling of expected scattering in this study showed that gas-bearing physonect siphonophores, while very strong acoustic targets, occurred in these samples at extremely low densities (mean 0.5 in  $10,000 m^{-3}$ , range 0–8 in  $10,000 m^{-3}$ ) and therefore could not have explained most of the observed variability in  $S_v$ . They may contribute to measured scattering when they do appear (four cases out of 55, in Figs. 2 and 4), although the  $S_v$  corresponding to those MOCNESS nets where they were found was not unusually high (Range  $-82$  to  $-74$  dB for those cases). Even assuming that the MOCNESS undersampled these organisms, Smith (1982) reported that Gulf of Mexico physonect siphonophore concentrations derived from open-water SCUBA surveys averaged only 5 organisms in  $10,000 m^3$  of water (range of  $<1\text{--}12$  in  $10,000 m^{-3}$ ). Particularly given that sampling of echo intensity by the ADCP could bias against extremely rare but strong targets (noted in the Methods section), these organisms most probably never occur at high enough concentrations to correlate with  $S_v$  measurements in this sub-tropical system.

As with gas-bearing animals, hard-shelled zooplankton scatter sound much more strongly per unit biomass than do crustaceans or gelatinous organisms (Stanton et al., 1994a), and pteropods in particular have been shown to be well correlated with and even dominate  $S_v$  under some conditions (a temperate system with concentrations of order  $1\text{--}100$ 's of pteropods  $m^{-3}$ ; Wiebe et al., 1996). The mean concentration of  $>2$  mm pteropods/atlantids was only  $0.004 m^{-3}$  (SD 0.005, range  $0\text{--}0.023 m^{-3}$ ) in this study. The concentration of  $<2$  mm pteropods/atlantids was probably greater, perhaps by a factor of 10 (J.H. Wormuth, Texas

A&M University, personal communication), but these smaller organisms are much weaker scatterers (see 1 mm pteropods in Fig. 4). Other data collected in the northeastern Gulf of Mexico with a high-resolution towed zooplankton sampler (HRS; see Sutton et al., 2001 for description) suggest that on average most pteropods in the upper 100 m are <2 mm in equivalent spherical diameter (ESD), and 98% of the >2 mm pteropods have an ESD of <4 mm (A. Remsen, University of South Florida, unpublished data). Thus, a pteropod with ESD 10 mm would be quite unusual. Since densities of pteropods >2 mm were not significantly correlated with  $S_v$ , it is suggested that they contribute to volume scattering but do not dominate the variability of  $S_v$  in the Gulf of Mexico.

In contrast to pteropods and atlantids, the densities of crustaceans and small fish showed a significant, positive association with  $S_v$  (Table 2). Crustaceans and small fish >2 mm in length occurred at an average density of  $0.142 \text{ m}^{-3}$  (SD 0.120, range 0.002–0.482) in these samples. Although the exact size distribution in these samples is not known, Scott (2001) summarized size-frequency data for >2 mm zooplankton from oblique meter net collections in upper 100 m of the shelf and slope of the northeastern Gulf of Mexico, and found that 18–55% of various crustacean categories in this size fraction were >10 mm in length, depending on the taxonomic group (amphipods, shrimp-like decapods, euphausiids, and larval stomatopods). Many of these were <15 mm in length, yet both meter nets and the  $1 \text{ m}^2$  MOCNESS probably underestimate the true abundance of larger (>15 mm) micronektonic crustaceans and fish, which are likely to be stronger swimmers and are able to avoid capture, particularly during daytime. The precise magnitude of the net avoidance problem is not known, so no simple correction for this can be applied (Hopkins et al., 1996). Hopkins and Lancraft (1984) sampled the northeastern Gulf of Mexico with Tucker trawls that have a much larger mouth area ( $6.5 \text{ m}^2$ ), and found that large crustaceans (>15 mm greatest linear dimension) may not be common, averaging perhaps  $0.003 \text{ m}^{-3}$  in the upper 400 m at night. However, the total nighttime

concentration of dominant species of myctophid fish with lengths ranging between 8 and 70 mm averaged  $0.007 \text{ m}^{-3}$  in Tucker trawls (Gartner, 1993), but could be as great as  $0.01\text{--}0.03 \text{ m}^{-3}$  (Hopkins, 1982; Gartner et al., 1987).

Of the four groups for which scattering model predictions were made, only (1) crustaceans and small fish and (2) pteropods/atlantids occurred frequently enough and were potentially strong enough targets to have accounted for a substantial portion of the observed acoustic backscatter. If predicted scattering for 10 mm crustaceans, 2 mm pteropods, 20 mm calycophore siphonophores, and physonect floats with 1 mm radius are combined (top panel in Fig. 5), the difference between predicted and observed  $S_v$  averages  $\sim 19 \text{ dB}$ . These predictions on average are dominated by scattering from crustaceans, small fish, and pteropods, yet only crustacean and small fish densities were significantly associated with  $S_v$ . Observed and predicted backscattering values often disagree by as much as 10 dB in ‘forward problem’ studies using data collected in the field (Wiebe et al., 1996; Warren, 2000; Griffiths et al., 2002), but the  $\sim 19 \text{ dB}$  difference suggests something is being missed. If net avoidance is indeed a significant factor, it would likely bias density estimates not for small pteropods, but for larger crustaceans and fish that the MOCNESS may not have sampled quantitatively. For instance, Gulf of Mexico myctophids feed preferentially upon large copepods and euphausiids >5 mm (Hopkins and Gartner, 1992); if their distribution is correlated with that of the larger crustacean zooplankton in these samples, their presence may also contribute to  $S_v$ . This may explain why crustaceans and fish densities from the MOCNESS correlated with volume backscattering, but scattering model calculations based upon observed densities of zooplankton from the MOCNESS net do not fully account for observed  $S_v$ .

#### 4.2. Caveats

There are multiple caveats for comparing zooplankton scattering model predictions and acoustic field data. There is some uncertainty in the acoustic measurements themselves. When

scattering model predictions are compared to observed ADCP  $S_v$  values, it should be noted that although the precision of these  $S_v$  estimates is on the order of 1 dB for these averages (RD Instruments, 1998), accuracy (when considering the manufacturer's calibration procedure and instrument performance) is only  $\sim 5$  dB (Darryl Symonds, RDI, personal communication). Applicability of the scattering models to different taxa is also an issue. For instance, the only models for pteropods available in the literature are for helical *Limacina*. Other types of pteropods (e.g., the pteropod *Cuvierina* has a roughly cylindrical shape) were also present in these samples.

There are also uncertainties in the parameters needed as input to the scattering models. Stanton and Chu (2000) recently reviewed modeling of acoustic scattering by zooplankton. Orientation of the target with respect to the transducers influences measured scattering. For example, Griffiths et al. (2002) found that the inclined ADCP beams ( $30^\circ$  from the vertical) could introduce an offset into  $S_v$  observations ( $\sim 5$  dB overestimate of scattering). However, if  $S_v$  is measured from multiple animals over many echoes and the range of orientations includes broadside, errors due to orientation would likely be small (Stanton et al., 1998a; Stanton and Chu, 2000). Scattering model parameters include the material properties of the zooplankton targets (Table 1), which are not well known and can vary with depth; particularly for weakly scattering targets such as fluid-like zooplankton, small differences can have large effects on predictions (from a few dB to 15–20 dB; Chu et al., 2000; Stanton and Chu, 2000). For example, Kirsch et al. (2000) found a much lower value of  $r$  for pteropods ( $r = 0.1533$ ) than was used here. The use of the Kirsch et al. value would reduce predicted scattering for pteropods in Figs. 4 and 5 by approximately 10 dB, making a substantial contribution to  $S_v$  by pteropods less likely. For gas-bearing scatterers, modeling of scattering by gas bubbles suggests an increase in resonance frequency with increasing depth and ambient pressure (Medwin and Clay, 1998), even if the animal regulates the size of the gas enclosure so that it remains constant with increasing depth (Mackie et al., 1987). This could potentially

increase target strength as the resonance frequency approached the survey frequency. However, except for the smallest enclosures modeled here (0.1 mm radius), simple models for predicting the resonance frequency of an air bubble given by Medwin and Clay (1998, Eq. 8.2.15) show that 153 kHz is well above the resonance frequency given changes in ambient pressure for all depths sampled.

Finally, size-frequency data should ideally be used to make rigorous calculations of expected scattering for each animal in 'sea-truth' net samples. Since those size-frequency data were not available in this study, the calculations presented here are intended only (1) to demonstrate that ADCPs can measure  $S_v$  comparable to scattering model predictions and (2) to give a first approximation of the relative contribution to  $S_v$  at 153 kHz of the zooplankton groups sampled.

#### 4.3. Conclusions

Correlation and randomization analyses showed that the numerical density of crustaceans, small fish, and siphonophore fragments  $> 2$  mm in length all had significant, positive associations with  $S_v$ . Zooplankton biomass in these samples contained a great deal of gelatinous material, yet subsequent calculations using zooplankton scattering models showed that gelatinous components of the zooplankton should scatter sound only weakly. Although they are relatively strong acoustic targets, gas-bearing siphonophores were quite rare and uncorrelated with  $S_v$  in this study. Likewise, strongly scattering pteropod and atlantid molluscs were uncorrelated with backscatter. They are more common than gas-bearing siphonophores and may contribute to  $S_v$  at 153 kHz in this system, though they probably do not on average dominate variability in acoustic backscatter. Crustacean and fish densities were correlated with  $S_v$ , although these densities combined with those of the other zooplankton in the MOCNESS catches did not fully account for observed  $S_v$  in scattering model calculations for a set of reasonable size classes. This may be because the MOCNESS (although it captures some zooplankton quantitatively) underestimates the abundance of  $> 15$  mm crustaceans and fish,

which are probably important sound-scattering organisms. On average, variability in  $S_v$  appeared to be most sensitive to the crustacean and fish component of the zooplankton and micronekton community sampled. Since midwater fish (Hopkins et al., 1996) and paralarval cephalopods (Cady, 2001) sought by apex predators as food depend in turn upon lower-trophic-level crustaceans and fish, these findings support the contention that ADCP-derived biomass estimates may be useful to identify areas of increased prey potential for cetaceans and seabirds in the northern Gulf of Mexico (Wormuth et al., 2000; Ressler, 2001; Davis et al., 2002).

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