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Diel variation in the vertical distribution of deep-water scattering layers in the Gulf of Mexico



Marta D'Elia^a, Joseph D. Warren^b, Ivan Rodriguez-Pinto^a, Tracey T. Sutton^c, April Cook^c, Kevin M. Boswell^{a,*}

^a Marine Sciences Program, Department of Biological Sciences, Florida International University, United States

^b School of Marine and Atmospheric Sciences, Stony Brook University, United States

^c Oceanographic Center, Nova Southeastern University, United States

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ABSTRACT

Sound scattering layers (SSLs) are important components of oceanic ecosystems with ubiquitous distribution throughout the world's oceans. This vertical movement is an important mechanism for exchanging organic matter from the surface to the deep ocean, as many of the organisms comprising SSLs serve as prey resources for linking the lower trophic levels to larger predators. Variations in abundance and taxonomic composition of mesopelagic organisms were quantified using repeated discrete net sampling and acoustics over a 30-h survey, performed during 26–27 June 2011 at single site (27°28'51"N and 88°27'54"W) in the northern Gulf of Mexico. We acoustically classified the mesopelagic SSL into four broad taxonomic categories, crustacean and small non-swimbladdered fish (CSNSBF), large non-swimbladdered fish (LNSBF), swimbladdered fish (SBF) and unclassified and we quantified the abundance of mesopelagic organisms over three discrete depth intervals; epipelagic (0–200 m); upper mesopelagic (200–600 m) and lower mesopelagic (600–1000 m). Irrespective of the acoustic categories at dusk part of the acoustic energy redistributed from the mesopelagic into the upper epipelagic (shallower than 100 m) remaining however below the thermocline depth. At night higher variability in species composition was observed between 100 and 200 m suggested that a redistribution of organisms may also occur within the upper portion of the water column. Along the upper mesopelagic backscatter spectra from CSNSBF migrated between 400 and 460 m while spectra from the other categories moved to shallower depths (300 and 350 m), resulting in habitat separation from CSNSBF. Relatively small vertical changes in both acoustic backscatter and center of mass metrics of the deep mesopelagic were observed for CNSBF and LNSBF suggesting that these animals may be tightly connected to deeper (below 1000 m) mesopelagic habitats, and do not routinely migrate into the epipelagic.

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1. Introduction

Sound scattering layers (SSLs) are ubiquitous features throughout the world's oceans and the organisms comprising these layers are important components of these vast ecosystems (Gjøsaeter and Kawaguchi, 1980; Sutton and Hopkins, 1996a; Kaartvedt et al., 2009; Dypvik et al., 2012; Peña et al., 2014). The depths at which SSLs occur are dynamic and often dependent on the depth of the water column and time of day, which gives rise to well-recognized and remarkable diel vertical migration (DVM) patterns (Balls, 1948; Kampa and Boden, 1954; Hersey and Backus, 1962). The main organisms that comprise SSLs are euphausiids, crustaceans, cephalopods, siphonophores, myctophids, and other mesopelagic fish species (Torgensen

et al., 1997; Ressler, 2002; Båmstedt, 2003; Benoit-Bird and Au, 2006; Collins et al., 2008; Gødo et al., 2009) that serve as primary prey resources for larger nektonic predators (Markaida et al., 2008; Benoit-Bird, 2004; Kaltenberg et al., 2007). In the Gulf of Mexico, SSLs are primarily characterized by mesopelagic fishes with gonostomatids (bristlemouths) being numerically dominant, followed by myctophids (lanternfishes) (Hopkins and Lancraft, 1984). The dramatic vertical movement between biomes offers opportunities for intense ecological interactions between SSLs and surface-oriented communities facilitating predator-prey relationships and trophic transfer processes (Hopkins and Baird, 1985a; Sutton and Hopkins, 1996b; Williams et al., 2001; Cherel et al., 2008; Robinson et al., 2010). Understanding the spatial and temporal variation in the dynamics of SSLs will help to better characterize the important ecological role these organisms play as well as their potential to facilitate vertical integration of the oceanic food web (Sutton et al., 2008; Sutton, 2013).

* Corresponding author.

E-mail address: Kevin.boswell@fiu.edu (K.M. Boswell).

The distinct DVM of scattering layers is believed to be due to changing ambient light conditions (Ressler, 2002; Gødo et al., 2009), with descent away from the surface during daytime and the ascent to shallower waters in the night (Neilson and Perry, 1990; Ohman, 1990). The diel dynamics are believed to be a behavioral response to feeding opportunity and predation risk (Cohen and Forward, 2009) or metabolic advantages (Lampert, 1989). This pattern has been described for zooplankton (Enright and Hammer, 1967; Båmstedt, 2003), macrocrustaceans (Frank and Widder, 1996) and mesopelagic fish species (Gartner et al., 1987; Sutton, 2013). The vertical migration of pelagic species has been well documented both globally and within the Gulf of Mexico, the major groups constituting the scattering layers include the Myctophidae, Gonostomatidae, Sternoptychidae, Phosichthyidae, Stomiidae (Hopkins and Baird, 1985a, 1985b; Gartner et al., 1987; Lancraft et al., 1988; Sutton and Hopkins, 1996a; Ross et al., 2010), Crustaceans (Moore, 1950; Heffernan and Hopkins, 1981; Flock and Hopkins, 1992), and Cephalopoda (Passarella and Hopkins, 1991).

Three classical vertical migration patterns have been reported in the literature: strong migrants, which undertake extensive vertical movement transferring biomass between the mesopelagic and the epipelagic; weak- migrants, which undertake little diel vertical migration; and non-migrants, which do not undergo any vertical migration (Andersen and Sardou, 1992; Collins et al., 2008; Olivar et al., 2012; Sutton, 2013). Variations in patterns notwithstanding, DVMs involve an enormous number of organisms and comprise the largest synchronized movement of biomass on the planet (Hays, 2003). There are several patterns commonly observed in the DVM of micronekton and macrozooplankton, including that the timing of the DVM is often associated with crepuscular periods (Lü et al., 2007; O'Driscoll et al., 2009). Some organisms are preferentially located shallower at night than during the day (Gjøsaeter and Kawaguchi 1980; Nishikawa et al., 2001; Harvey et al., 2009); while some organisms (e.g., some myctophid species) may not migrate and remain deep throughout the diel cycle (Watanabe et al., 1999; Harvey et al., 2009; Gødo et al., 2009; Olivar et al., 2012). Further complicating the study of these migrations is the fact that these organisms are patchily distributed and exhibit large variation in biomass within the epipelagic zone (Nishikawa et al., 2001).

The vertical distribution of biomass and species is commonly described via depth-discrete net sampling, occasionally in conjunction with acoustic backscatter data. Each of these methodologies has strengths and limitations. Net sampling can provide information on species composition, abundance, biomass and vertical distribution, while hydroacoustic sampling provides continuous, quantifiable, high-resolution (both temporally and spatially), non-invasive data on the spatial distribution of scatterers. Additionally, acoustic backscatter data collected at multiple frequencies has the potential to classify scattering layers into taxonomic groups (Jech and Michaels, 2007; Anderson et al., 2007; De Robertis et al., 2010; Trenkel and Berger, 2013). The acoustic backscattering spectral characteristics are a function of an organism's physical properties, orientation, morphology, size, and behavior (Stanton et al., 1996; Martin et al., 1996; Stanton and Chu, 2000). Therefore, organisms with different biophysical characteristics will often produce distinctive frequency-dependent responses, facilitating acoustically-based taxonomic differentiation (McQuinn et al., 2013).

Studies of the vertical migration of macrozooplankton and mesopelagic fishes in the slope waters of the Gulf of Mexico have primarily focused on net sampling (e.g., Hopkins and Baird, 1985a, 1985b; Gartner et al., 1987; Ross et al., 2010), with occasional complementary use of single frequency acoustic Doppler current profilers (Ressler, 2002; Kaltenberg et al., 2007). However, advances in multifrequency approaches have facilitated improved

interpretation of acoustic backscatter permitting scattering attributes to be assigned to relevant taxonomic groups (Korneliusson and Ona, 2003; Jech and Michaels, 2007; Lavery et al., 2007; Warren and Wiebe, 2008; Benoit-Bird, 2009; Fernandes, 2009; De Robertis et al., 2010; Gauthier et al., 2014).

In areas dominated by a single taxonomic group the acoustic response across different frequencies can be interpreted using acoustic measurements on "monospecific" ground-truthed echograms. However, epipelagic and mesopelagic ecosystems are often comprised of multi-species complexes with significant temporal and spatial overlap among species (Sutton, 2013), complicating ground-truthing efforts. In these cases, acoustic backscattering models can be used to predict acoustic responses of broad taxonomic categories and permit the investigation of larger-scale temporal and spatial variation acoustic scattering patterns.

In this work frequency responses derived from acoustic scattering models of dominant net-collected organisms were used to classify the species assemblages of sound scattering layers into four broad taxonomic categories. Observations were collected during a full diel period (30 h) acoustic backscatter sampling effort in the Gulf of Mexico. Vertical distributions of the four derived acoustic categories were quantitatively described through the use of acoustic metrics, focusing on differences between day and night periods and the different organism assemblages.

2. Methods

Net samples and acoustic backscatter data for this study were collected as part of a Natural Resource Damage Assessment conducted by the National Oceanic and Atmospheric Administration (NOAA) (see <http://www.darrp.noaa.gov>), pursuant to the *Deep-water Horizon* oil spill (DWHOS). To quantitatively characterize the pelagic fauna in the area and depths of the DWHOS, direct biological sampling and acoustic surveys were conducted aboard the NOAA ship FSV *Pisces* (hereafter *Pisces*; acoustics) and M/V *Meg Skansi* (hereafter *Meg Skansi*; MOCNESS collections) (Fig. 1). Sampling sites were an offshore extension of the standard SEAMAP plankton sampling grid, extending from the Texas shelf to the Florida west coast shelf. Grid cells are 30 × 30 NM, with sampling stations located at the center of each cell. The position of the additional stations was determined by extending the standard 30 NM Fall SEAMAP sampling grid into the offshore vicinity of the spill site.

2.1. Acoustic data collection

Acoustic data presented here were collected at site 27°28'51"N and 88°27'54"W in the northern Gulf of Mexico for a 30-h continuous period from June 26th–27th, 2011 aboard the *Pisces*. Data were recorded using a multi-frequency scientific echosounder system (Simrad EK60) with four transducers mounted to the ship's retractable centerboard, extending 9 m below the water surface, operating at 18, 38, 120 and 200 kHz. Only the lower frequencies (18 and 38 kHz) were used to measure acoustic backscatter through the water column (~1000 m) given range dependent losses in attenuation and signal strength at higher frequencies.

Each transducer was calibrated according the standard sphere method (Foote et al., 1987). Pulse duration was set at 4 ms and the power at 2000 W for both 18 and 38 kHz frequencies, and ping repetition rate was set at 0.2 pings s⁻¹. During each survey, water temperature and conductivity were collected with a CTD (SBE 911+; Sea-Bird Electronics, Inc.) to characterize water chemistry and vertical water column structure, and derive sound speed profiles.

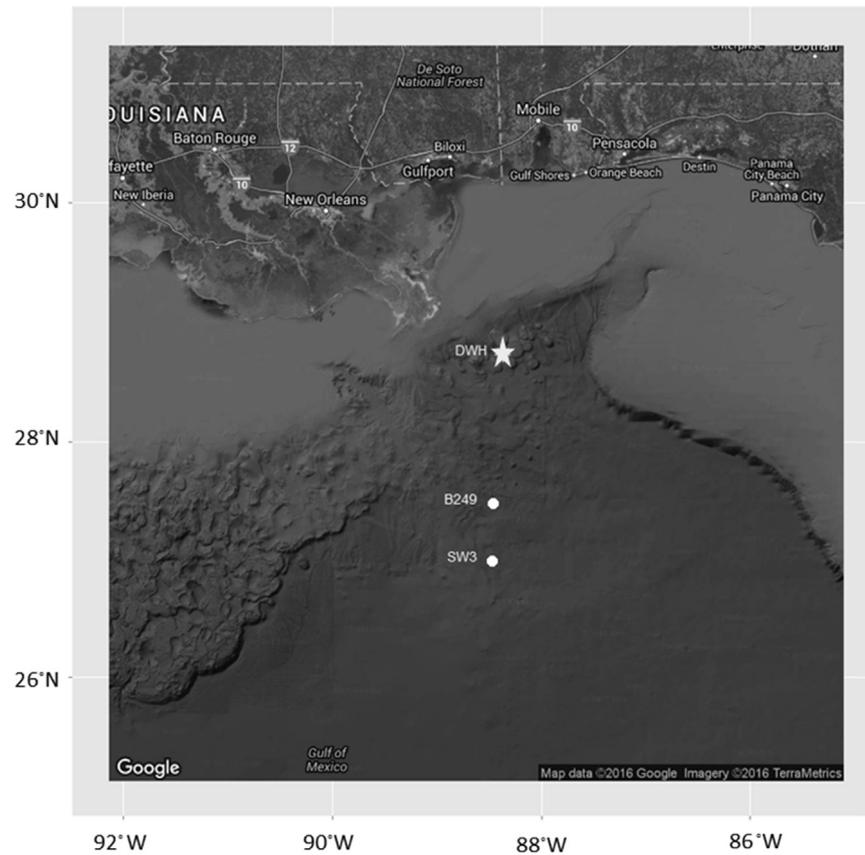


Fig. 1. Sampling stations occupied by FSV *Pisces* and M/V *Meg Skansi* during 24–27 June 2011 within the northern Gulf of Mexico. The 30-h study period is located at the station labeled B249. The star denotes the Deepwater Horizon (DWH).

2.2. Acoustic data processing

Recorded backscatter data (mean volume backscattering strength; S_V , dB re 1 m^{-1}) were imported and manually scrutinized in Echoview (v 5.4, Myriax software Pty Ltd). Data from the surface to a depth of 14 m were excluded from analysis due to bubble interference and the acoustic near-field. Analyses were limited to 1000 m in depth. Sources of acoustic noise (i.e., false bottom, intermittent spikes and background noise) were excluded from the analysis. False bottoms were visually detected and manually excluded. To remove spike noise, each sample was compared in turn to the equivalent sample in the range domain of the preceding and successive sample. If the single ping-to-ping difference in S_V was greater than 10 dB, the sample was replaced with the mean S_V of four neighboring samples (two samples located before and two samples following) the spike.

Background noise was identified and removed following a modified process described by De Robertis and Higginbottom (2007). A minimum signal to noise ratio of 10 dB was applied as threshold for the 18 kHz data and 15 dB for the 38 kHz data. The effect of noise is frequency-dependent, therefore a greater signal-to-noise-ratio (SNR) threshold was applied for the higher frequency. Samples that did not satisfy this threshold were considered indistinguishable from the background noise and excluded from analysis. The cleaned echograms at 18 and 38 kHz were thresholded at $-80 \text{ dB re } 1 \text{ m}^{-1}$ and averaged into $5 \text{ m} \times 5 \text{ m}$ cells to match ping geometries ensuring that the position and extent of each sample at one frequency could be matched with the equivalent sample on the other frequency.

Two additional parameters [nautical area scattering coefficient (NASC; $\text{m}^2 \text{ n mi}^{-2}$) and area backscattering strength (S_a , dB)]

derived from S_V were used for statistical analyses. These parameters are generated by integrating S_V data into variables that are proportional to animal biomass. The vertical and temporal differences in the areal acoustic scattering patterns were examined between the 18 and 38 kHz, in addition to the difference in S_V estimates between these two frequencies (i.e. $\Delta S_V = S_{V18} - S_{V38}$). The ΔdB windows were applied to measured ΔS_V for the 30-h study on a voxel by voxel basis. The acoustic backscatter for each scattering category was then integrated into 5 min (horizontal) by 10 m (vertical) windows, which were exported from Echoview for further analysis.

Data were analyzed in three discrete depth domains: the epipelagic (0–200 m), upper mesopelagic (200–600 m), and lower mesopelagic (600–1000 m); that were chosen to circumscribe reported depths of vertical biomass/faunistic discontinuities (reviewed in Sutton (2013)) and align with concurrent discrete-depth net sampling. For each depth range, several metrics were calculated using Python (v. 2.7) with the SciPy module (Jones et al., 2001–2011) as reported in Urmy et al. (2012). These included mean area acoustic backscatter strength S_a , center of mass, occupied area, inertia, evenness and aggregation index. Center of mass (CM) was used to define the mean vertical position of the acoustic backscatter while inertia (I) was used to describe the dispersion of the acoustic backscatter around its mean location (Bez and Rivoirard 2001; Urmy et al., 2012). Occupied area (P_{occ}), defined as the proportion of water occupied by the acoustic backscatter, was calculated as the proportion of the water column with values above the echogram's threshold (-80 dB). The aggregation index (AI), was used to describe the presence of patches in the water column (Woillez et al., 2007; Urmy et al., 2012). AI indicates whether small areas of acoustic backscatter are much denser than

the rest of the distribution. A description of the mathematical expression of each metric is reported in [Urmy et al. \(2012\)](#).

Given that acoustic scattering is often proportional to biomass in the water column ([Simmonds and MacLennan, 2005](#)), we use the term biomass to refer to the total magnitude of acoustic backscatter (defined as NASC or s_a) that is attributed to the taxonomic categories based on total net catch, where NASC represents the Nautical Area Scattering Coefficient that defines the area backscattering coefficient (s_a) in terms of nautical area.

2.3. Net/Trawl analysis

Net samples for acoustic ground-truthing were collected with a 10-m² MOCNESS midwater trawl, a multiple-net system (3-mm mesh) with real-time depth sensing and opening/closing capability ([Wiebe et al., 1985](#)) allowing the collection of discrete-depth samples. The sampling time and location that most closely aligned with the 30-h acoustic record was station SW3 taken during the summer *Meg Skansi* survey ([Fig. 1](#)). Sampling was conducted at this site (27°00'N and 88°30'W) during night (June 24–25, 2011; 2121–0326 h local time) and day (June 25, 2011; 0859–1430 h local) cycles. Five depth strata were sampled during each deployment: 0–200, 200–600, 600–1000, 1000–1200, and 1200–1500 m. Samples were preserved at sea (10% formalin: seawater) and quantitatively processed on shore. All individuals were identified to species, the first 25 individuals of each species were measured, and total bulk wet-weight (post-fixation) of each species was determined. Both number and biomass per species were standardized by sampling effort (volume of water sampled) and vertical distributions of organisms were examined.

2.4. Development of scattering categories

Biological data were aggregated into acoustic groups based on the dominant scattering mechanism for that organism. For example, all fishes with gas-filled swimbladders were grouped into one category. Length-frequency histograms were created for all animals with length data from the net tow analysis and used to sub-divide the acoustic scatterers into length-based sub-categories (e.g., small, and large non-swimbladder fishes). Theoretical target strength (TS, in dB re 1 m²) models ([Table 1](#)) were used to calculate TS values at 18 and 38 kHz for each of these groups with the size classifications based on the length-frequency information. The TS values at these two frequencies were then used to create dB-difference ($\Delta TS = TS_{18} - TS_{38}$) windows ([Watkins and Brierley, 2002](#); [Warren and Demer 2010](#)) that were used to categorize the acoustic scattering layers observed to their most-likely biological organism ([Fig. 2](#)). In doing this, we are assuming that the ΔTS windows are equivalent to ΔS_V windows. This assumption is categorically true for monospecific (type and size) aggregations of scatterers, however many studies ([Lavery et al., 2007](#); [Warren and](#)

[Wiebe, 2008](#)) have successfully used this approach for more diverse and complex assemblages of organisms. The different groups and size classes for each type of organism were selected based on variations in the length-frequency data from the net tows as well as to avoid overlapping dB- difference windows. Based on this approach the defined acoustic scattering categories were: crustacean and small non-swimbladder fishes (CSNSBF), large non-swimbladder fishes (LNSBF), swimbladder fishes (SBF), and unclassified organisms. Depth strata with low variability in dB-differences represent either empty regions of the water column or scattering layers where the species composition remains static; whereas depth strata with a large variability are assumed to represent regions where scatterers are moving rapidly or where the faunal composition of the scatterers changes along the survey.

2.5. Statistics

A descriptive statistic (mean and standard deviation) was used to summarize the vertical distribution of the four acoustic categories across three depth domains (epipelagic, upper mesopelagic and lower mesopelagic/bathypelagic) and four temporal intervals. Acoustic scattering profiles were averaged hourly, then aggregated over four local time periods: dawn (0400–1000), day (1000–1600), dusk (1600–2200), and night (2200–0400); the difference in the amount of scattering as a function of depth was examined. Dawn and dusk periods were determined by local sunrise and sunset. Five of the derived spatial indices, aggregation index (*AI*), total integrated backscatter (S_a), occupied area (P_{occ}), center of mass (*CM*) and inertia (*I*) were chosen to describe the vertical patterns observed in scattering layers.

3. Results

3.1. Water column structure

The water column structure did not vary greatly between night and day periods with a thermocline located at approximately 45 m depth during both periods ([Fig. 3](#)). The surface waters were relatively warm with mean surface temperatures of 28.9 °C. Maximum salinity (approximately 36.7 PSU) varied with depth between night and day, with the halocline depth shifting between 97 m and 125 m, between day and night, respectively. Similarly, the depth of the dissolved oxygen (DO) minima in the upper mixed layer varied temporally, and was detected at 95 m (5.3 mg L⁻¹) during the day and shifted downward to 124 m (5.1 mg L⁻¹) at night.

3.2. Net data

The bristlemouth fishes of the genus *Cyclothone* (Stomiiformes, Gonostomatidae) numerically dominated the deep-pelagic

Table 1. Categories of the acoustic scatterers along with the information and scattering model used to generate the dB difference classification windows. The abbreviations are provided for each scattering category.

Organism	Length (mm)	$\Delta dB = TS_{18} - TS_{38}$	Scattering model used	Taxonomic composition from net collections
Crustaceans/small NSBF (CSNSBF)	15–70 mm	–14 dB to –9dB	SDWBA (Calise and Skaret, 2011 ; Conti and Demer, 2006)	Euphasiacea, Decapoda, Mysidacea, <i>Cyclothone</i> , small Melamphaidae, Aulopiformes, Anguilliformes
	50 mm – 150 mm	–9 dB to –3 dB	Yasuma, 2004 as cited by Yasuma et al. (2010)	
Large NSBF (LNSBF)	150–600 mm	–3 dB to 0 dB	Yasuma, 2004 as cited by Yasuma et al. (2010)	Stomiidae, <i>Gonostoma elongatum</i> (invested with fat), <i>Nannobranchium</i> spp., Bathylagidae, Large Melamphaidae, Nemichthyidae, Chiasmodontidae, Ceratioidei
SB fish (SBF)	25–300 mm	3 dB to 12 dB	Ye, 1997 ; Stanton, 1988	Myctophidae, Sternoptychidae, Phosichthyidae
Unclassified	N/A	0 dB to 3 dB	No model used	Gelatinous zooplankton, Cephalopoda, Pteropoda

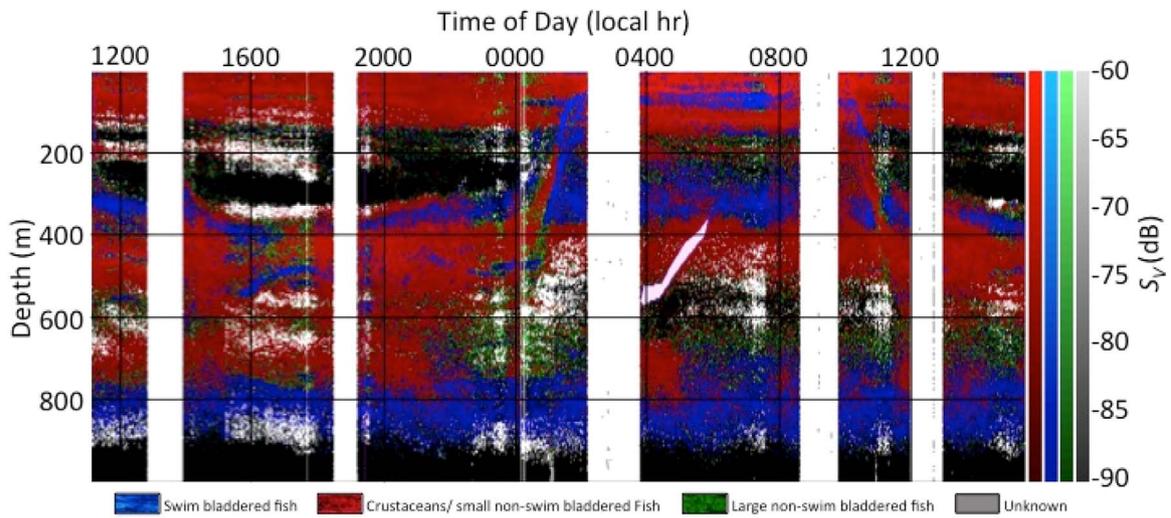


Fig. 2. Echogram illustrating the acoustically derived taxonomic categories used in the analysis. Each category is represented by a unique color: blue=SBF; red=CSNSBF; green=LNSBF; grey='unclassified' category; black = no data. The classifications are based on the compute $\Delta S_V = S_{V18} - S_{V38}$ windows. The blank area in the middle of the echogram corresponds to echoes attributed to false bottom and subsequently removed from the analysis. The vertical white bands represent time periods with no acoustic acquisition. (For interpretation of the references to color in this figure legend, the reader is referred to the web version of this article.)

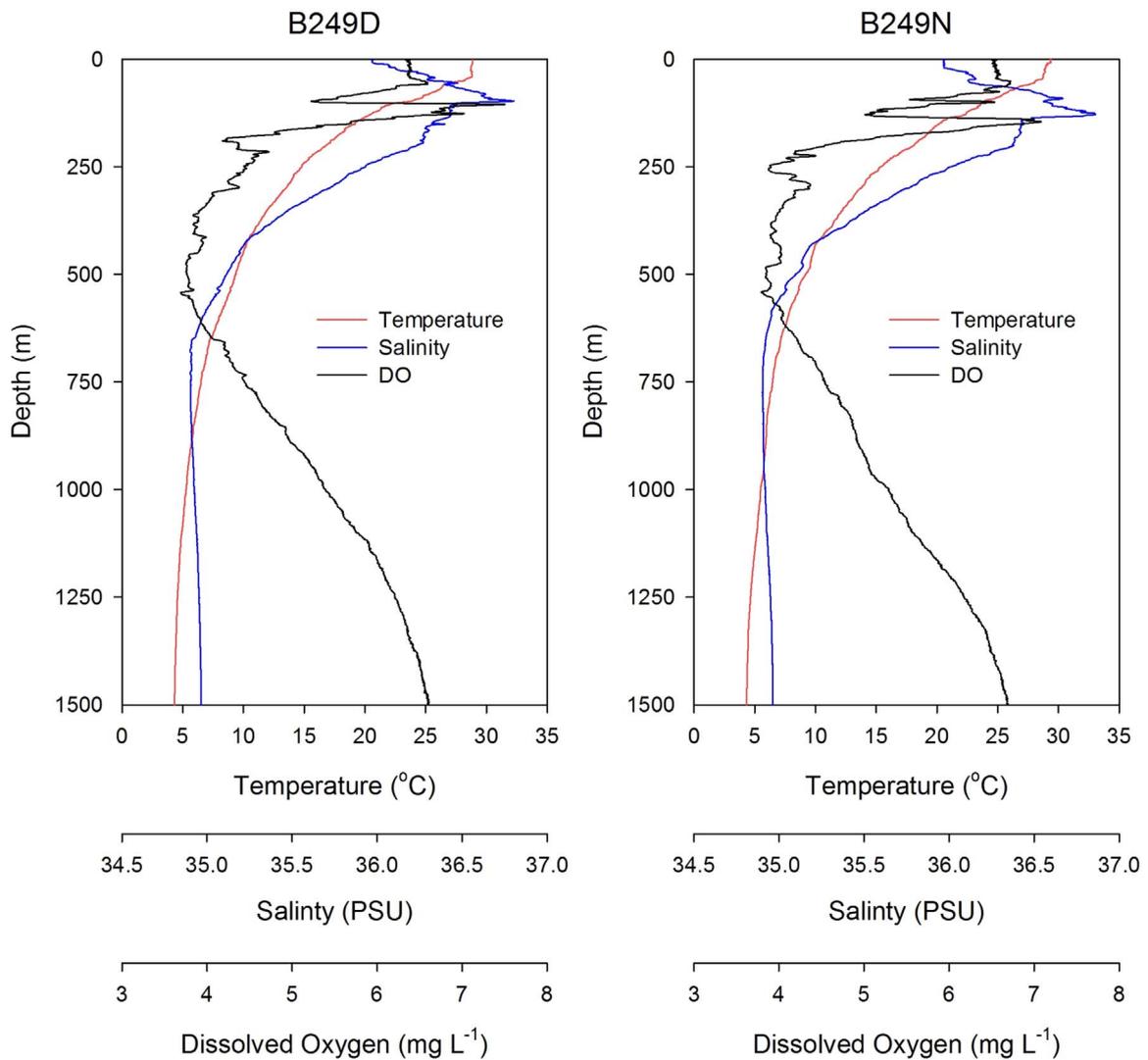


Fig. 3. CTD casts for day (left panel) and night (right panel) during study period. The epipelagic domain occupies 0–200 m, upper mesopelagic from 200 to 600 m and the lower mesopelagic 600–1000 m.

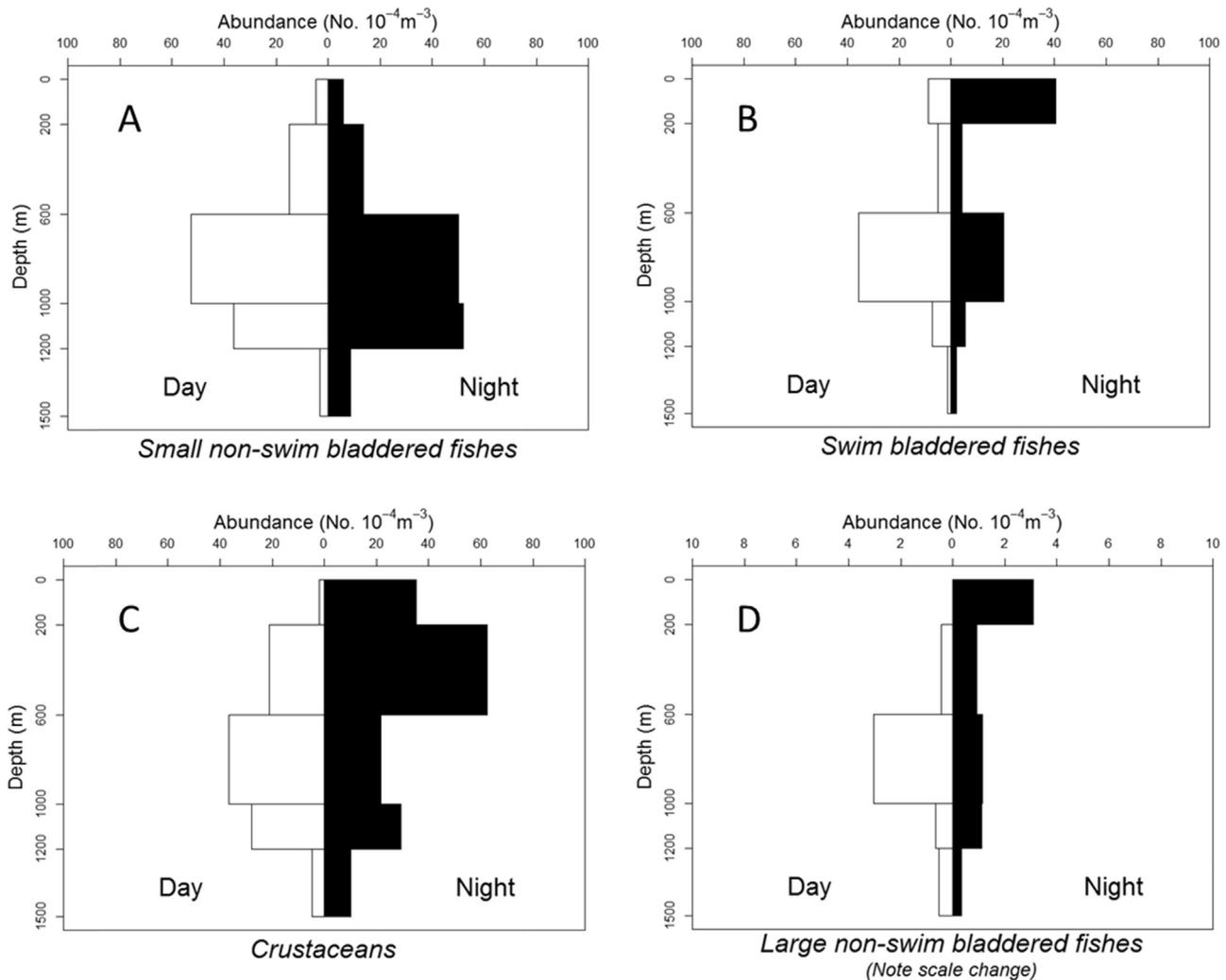


Fig. 4. Diel vertical distribution of micronekton at station SW3, cruise MS7, 24–25 Jun 2011, in the northern Gulf of Mexico: (A) Small non-swimbladderred fishes (especially *Cyclothone* spp.); (B) swimbladderred fishes (esp. lanternfishes and hatchetfishes); (C) crustaceans (esp. euphausiids and decapod).

micronekton assemblage collected ($\sim 27\%$ of all individuals, all taxa, and more than 95% of the small non-swimbladderred fishes (small Melamphaidae, Aulopiformes, Anguilliformes). There was very limited or no diel vertical migration by the species of this genus, with similar day/night abundance maxima between 200–600 m and 600–1000 m, though the deeper region had slightly higher values than the shallower region (Fig. 4a). Among other common taxa, diel vertical migration was readily apparent, particularly among the swimbladderred fishes (Fig. 4b; especially lanternfishes [Myctophidae] and hatchetfishes [Sternoptychidae]), crustaceans (Fig. 4c; esp. Euphausiacea and decapod shrimps [Sergestidae]), and large non-swimbladderred fishes (Fig. 4d; esp. dragonfishes [Stomiidae]).

3.3. Variation in 18 and 38 kHz scattering profiles

Profiles of NASC at 18 and 38 kHz (Fig. 5) indicated changes in the vertical distribution of scatterers in the water column among distinct periods of the day (i.e., dawn, day, dusk and night). Both frequencies showed that strong backscattering layers occurred during the day at 100 m and 500 m in the epipelagic and upper mesopelagic. In the lower mesopelagic, scattering layers were strongest at 800 m (18 kHz) and 700 m (38 kHz), respectively, albeit much lower than in the upper water column.

At dusk a redistribution of the acoustic backscatter occurred, with NASC shifting from the upper and lower mesopelagic toward

the epipelagic domain. As expected the bulk of acoustic scattering was concentrated above 200 m during the night and then moved deeper at dawn (Fig. 5). Differences in backscatter intensity between 18 and 38 kHz (ΔS_V) showed that most of the epipelagic during the day had low variability and indicated that either no vertical movement or change in species composition during the survey occurred in this domain during this time period (Fig. 5). At dusk a redistribution of scattering was detected in the epipelagic region between 50 and 200 m, ostensibly due to diel vertical migration. Over the course of the night a more variable species composition was observed between 100 and 200 m compared to the day.

3.4. Response in scattering categories by depth domain

As expected, diel patterns were found for most metrics describing the scattering categories across the three depth domains (Table 2). Results are discussed for each scattering category in the context of the comparisons between night and day.

3.4.1. Crustacean and small Non-swimbladderred Fishes (CSNSBF)

During the daytime, crustaceans and small NSBF (CSNSBF) comprised approximately 65% of the total water column backscatter (30% in the epipelagic, 25% in the upper mesopelagic and less than 10% in the lower mesopelagic) (Fig. 6). Within the

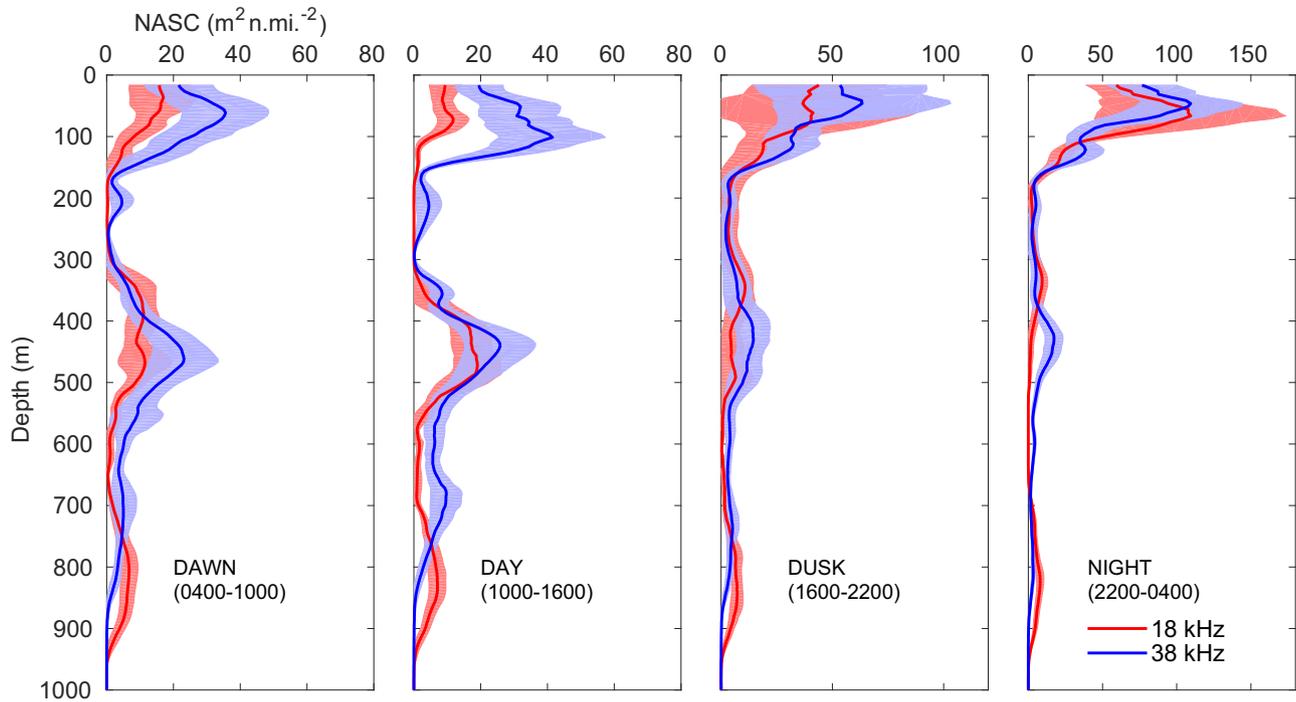


Fig. 5. NASC at 18 kHz (red) and 38 kHz (blue) for dawn, day, dusk, and night periods showing changes in the distribution of scatterers in the water column over a continuous 30-h period. Note the x-axis scales vary for each subplot. Solid lines represent the mean value while the shaded regions represent \pm a standard deviation. Note that the x axis scale is variable among panels. (For interpretation of the references to color in this figure legend, the reader is referred to the web version of this article.)

epipelagic domain CSNSBF S_a was greater at night (-54.3 dB, SD: 0.8) than during the day (-56.1 dB, SD: 1.1). CSNSBF had a lower dispersion during the day relative to the night (Table 2) and the CM shifted shallower by approximately 7 m from day to night.

In contrast to the epipelagic domain, upper mesopelagic S_a was more than two-fold greater (4 dB) during the day (-58.4 dB, SD: 1.9) than night (-62.4 dB, SD: 0.8) and the CM shifted 45 m shallower during the night. Within the lower mesopelagic domain, CM and I shifted between day and night, suggesting that CSNSBF moved deeper during the night by approximately 65 m.

3.4.2. Swimbladdered fishes (SBF)

S_a for SBF was more than an order of magnitude greater in the epipelagic at night (-59.2 dB, SD: 0.9) than during the day (-74.8 dB, SD: 3.0). In addition to increased S_a , SBF exhibited a greater P_{occ} , being more broadly distributed through the water column at night as compared to the daytime (Table 2). The CM of the layer was shallower (56.8 m, SD: 18.0 m) during the day and moved deeper during the night (62.1 m, SD: 5.5 m). Indices of dispersion (I and AI) in the upper mesopelagic found and increased distribution of biomass during the day compared to the night (Table 2). Within the upper mesopelagic domain, S_a , AI , and I were greater during the day, indicating reduced biomass and a more uniform distribution of fish during the night. Additionally the CM of SBF was deeper during the day (430.6 m, SD: 30.2) and migrated to shallower depths at night (318.9 m, SD: 5.5). Only small variations among indices were observed in the lower mesopelagic domain between night and day (Table 2).

3.4.3. Large non-swimbladdered fishes (LNSBF)

In the epipelagic domain, LNSBF showed more than a four-fold increase in S_a at night (-55.9 dB, SD: 0.5) (-63.9 dB, SD: 1.4) and shifted slightly shallower (~ 5 m change in CM) as compared to the day. The LNSBF also occupied a slightly greater portion of the water column during the night than the day (Table 2). The upper mesopelagic domain was characterized by a four-fold increase in

S_a during the day (difference of 5.9 dB), yet was more dispersed in the water column (greater P_{occ}) at night. Moreover the CM shifted approximately 100 m shallower during the night (Table 2). The lower mesopelagic domain had slightly greater S_a during the day (-66.1 dB, SD: 1.3) than the night (-67.6 dB, SD: 1.2) and was centered approximately 40 m shallower during the day (717.7 m) than the night (757.3 m).

3.4.4. Unclassified category

In the epipelagic domain the mean S_a of the unclassified category was an order of magnitude (11.54 dB) greater at night (-57.1 dB, SD: 0.6) than in the day (-68.7 dB, SD: 1.8) with no discernible difference in the CM between night and day (Table 2). However, organisms distributed at night showed a lower AI and a higher P_{occ} (Table 2) indicating that, when scattering intensity increased, the distribution became more uniform and the measured biomass tended to occupy a larger proportion of the epipelagic domain relative to the day. As with other scattering categories in the upper mesopelagic, mean S_a was approximately 5 dB greater during the day than the night, although the CM of biomass in the upper mesopelagic domain was 115 m shallower during the night (Table 2). The only slight variation observed within the lower mesopelagic domain occurred in the CM and I , with a tendency for a shallower and more dispersed distribution during day than the night.

4. Discussion

The approach of classifying water-column scattering data into taxonomic categories highlighted the ubiquitous vertical movement of multiple categories of organisms throughout the course of the study. The most conspicuous patterns emerged at night with a significant redistribution of acoustic backscatter from the lower and upper mesopelagic into the upper epipelagic (shallower than ~ 100 m), and additional insights can be found when comparing categories simultaneously (Fig. 2). Among the organisms

Table 2.
Mean values and standard deviations by scattering category, domain (E=epipelagic, UM=upper mesopelagic, LM=lower mesopelagic)/time of day (TOD).

Scattering Categories	Domain/TOD	Sa		CM		Inertia		AI		Pocc	
		Mean	StDev	Mean	StDev	Mean	Stdev	Mean	StDev	Mean	StDev
Crustacean/Small NSBF	<i>E</i>										
	Dawn	−55.86	1.48	62.67	6.59	44.22	9.78	0.06	0.01	0.95	0.02
	Day	−56.11	1.08	70.75	7.52	36.05	5.07	0.06	0.01	0.94	0.01
	Dusk	−54.88	1.02	60.71	17.66	43.39	16.17	0.07	0.02	0.93	0.02
	Night	−54.28	0.76	64.03	6.75	64.53	7.04	0.08	0.01	0.95	0.02
	<i>UM</i>										
	Dawn	−57.36	1.23	425.05	34.39	162.89	101.32	0.04	0.01	0.78	0.04
	Day	−58.37	1.94	459.40	17.21	109.70	40.22	0.04	0.01	0.77	0.03
	Dusk	−59.98	3.38	393.23	35.45	112.59	93.81	0.06	0.03	0.73	0.05
	Night	−62.43	1.83	413.76	24.20	130.87	182.36	0.07	0.01	0.71	0.02
	<i>LM</i>										
	Dawn	−67.00	5.26	714.56	20.19	31.24	21.25	0.10	0.09	0.66	0.03
Day	−68.13	5.71	670.70	36.54	58.13	46.30	0.15	0.15	0.66	0.04	
Dusk	−73.60	3.99	717.81	38.93	75.90	121.39	0.29	0.15	0.62	0.03	
Night	−67.57	5.86	735.41	22.91	24.41	12.81	0.14	0.15	0.66	0.04	
Large NSBF	<i>E</i>										
	Dawn	−59.74	2.06	58.30	7.14	52.71	21.19	0.06	0.01	0.98	0.02
	Day	−63.85	1.43	64.50	7.46	54.24	14.32	0.07	0.03	0.96	0.02
	Dusk	−59.58	1.89	67.19	9.45	74.47	19.96	0.06	0.01	0.97	0.03
	Night	−55.89	0.47	60.26	2.36	55.40	6.30	0.06	0.01	1.00	0.01
	<i>UM</i>										
	Dawn	−60.63	1.58	399.09	41.15	242.28	67.90	0.03	0.01	0.95	0.03
	Day	−60.24	1.25	444.32	9.98	139.90	43.60	0.03	0.01	0.89	0.05
	Dusk	−62.07	3.33	359.62	47.85	247.36	58.92	0.03	0.01	0.88	0.05
	Night	−66.11	0.89	343.52	15.99	316.54	70.08	0.03	0.01	0.93	0.05
	<i>LM</i>										
	Dawn	−66.93	1.14	743.49	15.48	156.02	38.05	0.03	0.01	0.86	0.05
Day	−66.12	1.27	717.70	14.87	186.63	48.52	0.04	0.08	0.86	0.06	
Dusk	−65.83	1.61	725.72	21.52	165.80	52.57	0.03	0.01	0.84	0.05	
Night	−67.60	1.21	757.26	11.21	170.18	40.38	0.03	0.00	0.89	0.04	
SB fish	<i>E</i>										
	Dawn	−68.69	5.24	57.95	20.50	54.38	38.70	0.14	0.07	0.91	0.05
	Day	−74.78	2.98	56.82	18.02	62.22	34.29	0.19	0.10	0.88	0.03
	Dusk	−66.73	5.60	86.79	22.31	75.66	31.47	0.13	0.07	0.91	0.04
	Night	−59.20	0.95	62.09	5.49	31.04	6.46	0.08	0.02	0.97	0.02
	<i>UM</i>										
	Dawn	−67.58	2.27	358.28	27.21	150.34	56.65	0.06	0.02	0.79	0.06
	Day	−66.95	1.53	430.62	30.23	119.80	54.96	0.08	0.06	0.76	0.06
	Dusk	−66.57	2.80	343.40	50.24	187.25	148.39	0.08	0.03	0.75	0.06
	Night	−69.31	0.97	318.94	8.45	76.05	36.48	0.05	0.01	0.80	0.05
	<i>LM</i>										
	Dawn	−69.23	1.89	806.79	5.55	84.91	31.85	0.04	0.01	0.81	0.06
Day	−69.33	1.53	795.85	11.23	111.25	54.25	0.04	0.01	0.81	0.06	
Dusk	−67.46	0.73	809.84	13.64	98.74	24.61	0.04	0.01	0.80	0.04	
Night	−69.10	1.32	810.38	11.84	101.78	20.69	0.04	0.01	0.84	0.03	
Unclassified	<i>E</i>										
	Dawn	−63.24	3.04	58.45	14.11	57.60	29.99	0.08	0.02	0.96	0.03
	Day	−68.65	1.79	63.05	9.98	67.12	23.80	0.10	0.04	0.93	0.03
	Dusk	−62.58	3.01	79.92	16.33	81.84	22.16	0.10	0.10	0.95	0.04
	Night	−57.11	0.61	60.45	3.56	43.18	5.61	0.06	0.01	1.00	0.01
	<i>UM</i>										
	Dawn	−63.30	1.52	379.27	37.42	219.46	53.03	0.04	0.01	0.90	0.05
	Day	−62.60	1.27	434.79	18.16	135.69	49.77	0.04	0.01	0.85	0.06
	Dusk	−63.32	1.97	344.16	52.48	204.98	82.76	0.04	0.01	0.84	0.06
	Night	−67.24	0.64	319.94	10.82	172.27	57.85	0.03	0.01	0.88	0.05
	<i>LM</i>										
	Dawn	−67.10	1.23	777.86	8.10	140.84	39.04	0.03	0.01	0.86	0.06
Day	−67.02	1.45	760.74	11.85	184.05	52.48	0.03	0.02	0.88	0.06	
Dusk	−65.28	1.34	770.00	11.14	168.72	30.33	0.03	0.00	0.88	0.04	
Night	−67.32	0.86	783.90	6.35	157.40	22.24	0.03	0.00	0.89	0.03	

represented, the CSNSBF were the largest component of measured NASC throughout the water column, whereas swimbladdered fishes represented the smallest component during this study.

4.1. Vertical and temporal variation in sound scattering layers

The mean depth of acoustic backscatter for all categories during both day and night was consistently below the thermocline depth

(45 m) suggesting that the majority of the detected biomass may avoid the upper mixed layer in response to light intensity, reduced food supply near the surface, or for metabolic benefits associated with cooler temperatures. The depth of scattering layers has been shown to be a function of surface irradiance and/or lunar cycle (Clarke 1973; Gjøsaeter 1984; Kampa, 1970; Benoit-Bird et al., 2009), food (Gjøsaeter and Kawaguchi 1980) and thermal gradients (Tont, 1976; Yoon et al., 2007; Hazen and Johnston, 2010;

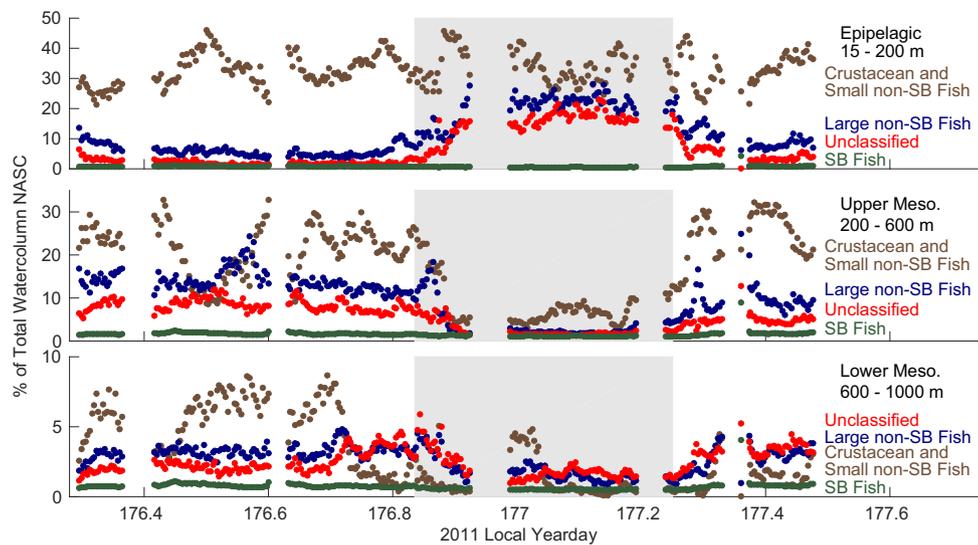


Fig. 6. Percentage of water column NASC for three different depth ranges (Epipelagic 15–200 m; Upper Mesopelagic 200–600 m; Lower Mesopelagic 600–1000 m) for the four scatterer categories. The grey regions represent the time between sunset and sunrise. Note that the y axis scale is variable.

Klevjer and Kaartvedt, 2011). The effect of light on the depth distribution can be rapid and occur over time periods much less than the diel cycle, as evidenced by fishes moving shallower during solar eclipses (Backus et al., 1965; Kampa 1975). High light intensity in the day as well as during some lunar phases at night may increase the risk of detection by predators causing the organisms to stay further from the surface and concentrate them in the mid-water (Benoit-Bird et al., 2009). Further, the effect of moonlight can alter the vertical distribution for many different mesopelagic organisms including sergestid shrimps, myctophids and predatory stomiids (Walters, 1976; Clarke, 1973; John, 1978; Drazen et al., 2011). However, in our study the importance of moonlight was likely negligible as the moon phase was a late-stage waxing crescent.

Apart from the potential importance of light intensity, observed acoustic backscatter distributions are likely also related to water temperature. Metabolic rates of mesopelagic fishes and crustaceans increase with temperature (Donnelly and Torres, 1988), thus these animals may select for more energetically-favorable conditions below the thermocline. In the Gulf of Mexico, the summer temperatures in the upper mixed layer are relatively high (29 °C), during both day and night, which may determine the upper limit of the vertical distribution of organisms. In previous studies, many myctophids and euphausiids in the Gulf of Mexico were found to avoid the higher temperature of the upper mixed layers (Moore, 1950; Gartner et al., 1987; Lancraft et al., 1988). In addition to the direct effect of temperature on animal metabolism, animals may benefit when they move to thermocline regions as these gradients may promote increased feeding opportunities (Ropke, 1993; Sassa et al., 2004), which may be a stronger driver for movement than physicochemical conditions. Rissik and Suthers (2000) reported that some myctophids were more successful at foraging near the thermocline than in surface waters as it offered a greater concentration of food resources relative to other parts of the water column. It is understood that zooplanktivorous micronekton migrate upward in the water column to forage on mesozooplankton while the mesozooplankton at the same time are migrating toward the surface to graze on the phytoplankton. Thus, higher order predators (invertebrates, fishes, marine mammals) may modify their own risk-averse behavior or poor metabolic conditions to pursue foraging opportunities to optimize the exploitation of migrating prey (Hays, 2003).

4.2. Movement of dominant scattering groups (or loss of groups)

Examination of the ΔS_V data provides context to the spatio-temporal shifts in community composition. The low variability in ΔS_V in the epipelagic domain during the day suggests that the species composition in this region was relatively stable. However, as expected, species composition can change abruptly during crepuscular periods and throughout the night, with the onset of vertical migration leading to a concomitant increase in biomass and variability in scattering profiles between 50 and 200 m. When considering the magnitude of changes observed among scattering categories, the LNSBF and SBF categories both have measured increases in S_a (by 8 and 15 dB, respectively) at night in the epipelagic domain. In contrast to the daytime, species composition was more variable at night, especially between 100 and 200 m, suggesting a nocturnal redistribution of biomass within this upper portion of the water column.

Evidence of vertical migration during the night has been reported most commonly for zooplankton and crustaceans. The nocturnal vertical behavior is known as “midnight sinking” and describes zooplankton and crustaceans ascending to the surface during twilight hours and sinking deeper in between dusk and dawn (Cushing, 1951). Although crustaceans (in particular euphausiids) and other zooplankton such as decapods can be a significant component of the deep scattering layers (Moore, 1950; Ressler, 2002), they are considered weak scatterers at 18 and 38 kHz compared to organisms with shells or air-inclusions (e.g., shelled pteropods and siphonophores, respectively) and therefore likely comprise a reduced proportion of the total backscatter at these frequencies. Thus changes in the acoustic composition during the night could be related to the sinking of other important components of backscatter at these frequencies, (e.g., pteropods or siphonophores), or a redistribution of the other nektonic components in relation to the dynamics of their prey (i.e., euphausiids).

In the upper mesopelagic (200–600 m), the scattering profiles were more variable during the day than at night, especially between 300 and 500 m, indicating changes in the daytime distribution of organisms. The daytime vertical movement of some species may explain part of the increased variability observed as some micronekton organisms (e.g., euphausiids, myctophids) have been reported to ascend in the morning and descend in the evening or early night, which is the opposite pattern generally observed with migrating animals (Moore, 1950; Cushing 1951;

Dypvik et al., 2012). At night, the acoustic backscatter attributed to the combined categories of the CSNSBF, LNSBF, SBF, and unclassified organisms moved toward the epipelagic domain, while a measurable amount remained within the mesopelagic domain. The CSNSBF migrated to 400 m whereas LNSBF, SBF and the unclassified category were observed moving into shallower depths between 300 and 350 m.

A clear shift in the *CM* was observed in the upper mesopelagic indicating a diel periodicity in the vertical distribution of acoustic backscatter. During the day all the categories were closely distributed between 400 and 460 m, forming a unique mixed layer. At night CSNSBF remained within that narrow interval (400–460 m), while the other categories were observed migrating to shallower depths between 300 and 350 m. Irrespective of scattering category, the mean biomass that remained in the upper mesopelagic during the daytime moved shallower at night, likely following the vertical migration of prey (Watanabe et al., 1999). In addition, a clear separation developed at night between the CSNSBF and the other acoustic groups, suggesting a differential use of habitat (i.e. resource partitioning) by specific taxonomic groups (Hopkins and Sutton, 1998).

In the lower mesopelagic (600–1000 m), the species composition was more variable during the day than at night, with increases in variability occurring mainly between 600 and 800 m. A decrease in total backscatter during the night suggests that LNSBF, the only category for which a decline in S_a was observed during the night, was moving out of the lower mesopelagic. *Photostomias* spp. (Stomiidae) which inhabits the lower mesopelagic was observed to have a deeper distribution at night than in the day (Sutton and Hopkins, 1996a), which may also explain the deeper *CM* of this group. A deepening in *CM* during the night was also observed for the CSNSBF. No changes in S_a or *CM* were observed for SBF or the unclassified category, suggesting that there may be some component or proportion of the deep biomass that remains resident at depth and does not undergo a measurable vertical migration. The absence of vertical migration has been observed for many myctophids, including small juveniles (Clarke, 1973; Willis and Percy, 1980). In addition to compositional variability, the changes in observed scattering profiles could be the result of a redistribution of intraspecific size classes with depth by dominant micronekton, where within a species, juveniles and adults may occupy different depth strata which may also change during a 24-h period (Hopkins 1982; Roe and Badcock 1984; Gartner et al., 1987).

4.3. Comparison of acoustic and net measures of biological organisms

The distributional patterns of organisms measured acoustically were not completely consistent with those derived from net tow data. The greatest incongruities were observed for LNSBF and SBF in the upper mesopelagic. The backscatter from these two acoustic categories suggested higher abundance in the day than at night with LNSBF contributing more than the SBF. However, net sampling found a very low abundance of LNSBF throughout the water column and the higher abundances that did occur at night within the upper mesopelagic.

The general lack of agreement between acoustic and trawl-based estimates of the numerical density of mesopelagic organisms is well known and has been reported across many regions (Kloser et al., 2009; Stanton et al., 2012; Davison et al., 2014) and there are many possible explanations for this. The possible depth dependence of TS for resonant SBF (Kloser et al., 2002) is largely a function of whether the fish is physostomous or physoclistous, and the ability for the fish to adapt to relatively rapid changes in pressure (i.e. depth) (Stanton et al., 2012). Changes in the swimbladder volume or shape as a function of depth could result in

changes in the SBF acoustic scattering response and result in variable classification. Additionally, since a gas-bearing model was used to describe the scattering from SBF, other organisms containing gas inclusions (specifically siphonophores) may be categorized incorrectly as SBF. These may be important considerations as scattering at 18 and 38 kHz is much stronger for organisms with a gas inclusion than for those without (Warren et al., 2001; Lavery et al., 2007). Perhaps most important are the differences in capture efficiency of net systems for specific organisms. Some gas-bearing organisms (such as siphonophores) can be extruded by midwater trawls and thus be underrepresented in catch counts. Similarly larger, faster-swimming fishes are better able to avoid the net (Kaartvedt et al., 2012; Davison et al., 2014). This means that the capture efficiency and the taxonomic- and sized-based variation must be better understood in order to resolve the mismatch between trawl and acoustic estimates of mesopelagic fish abundance and biomass.

Erroneous acoustic classifications may also be the result of insufficient knowledge of organism physiology, morphology and ontogenetic changes in swimbladder inflation and body density of the midwater species of the Gulf of Mexico. For example, some mesopelagic species possess a functional swimbladder as juveniles that regress as the animal matures and can become filled with lipids instead of gas (Davison, 2011). Until we have better knowledge about the physiological changes that occur (and when they occur) for the SBF category, there will continue to be inherent uncertainties in using this type of classification approach. However, this approach produces unique and valuable (despite these uncertainties) information about the spatiotemporal distribution of mesopelagic organisms.

Acoustic measurements found that CSNSBF were the dominant nektonic/micronektonic components in the epipelagic during the day and in the upper mesopelagic in both day and night, with approximately two times greater acoustic backscatter than other categories. These findings agree with the net catch data for combined macrozooplakton, CSNSBF. However, several global studies conclude that mesopelagic fishes make up the majority of backscatter (Godo et al., 2009; Kloser et al., 2009). Two possible explanations exist for this discrepancy. The trawl efficiency for small non-swimbladdered fish is not 100%, and therefore animals which contribute to the acoustic backscatter may not be quantitatively represented in net catches (i.e., the net estimate is too low). Alternatively, aggregations of macrozooplankton (which generally are not considered to be significant scatterers at 18 and 38 kHz) may be large enough that their scattering is detected and incorrectly classified as CSNSBF (i.e., the acoustic estimate is too high). It is unlikely that SBF were incorrectly classified as CSNSBF, due to changes in the resonance peak of scattering, given that the ratio of backscatter values between day and night was very close to 1 ($S_{a_day}/S_{a_night}=0.96$), indicating biomass was not misclassified or 'lost'.

Further, several types of organisms are not included as distinct scatterer categories in this analysis either due to lack of length information (e.g., pteropods) or less well-developed scattering models (e.g., gelatinous zooplankton, cephalopods). These include organisms that can be important acoustic scatterers (e.g., pteropods), important prey resources (e.g., squid), or can occur in swarms (e.g., gelatinous zooplankton). The dB-difference windows that were created included an 'unclassified' category that likely includes a variety of these and other organisms. The dB-difference windows for the four acoustic categories cover the entire range of dB differences observed in the data such that all scattering observed in the water column is classified into one of the categories.

In summary, this is the first study in the Gulf of Mexico that uses spectral scattering characteristics to identify and discriminate layers to examine the spatial and temporal distribution among

scattering categories. This approach permitted the examination of variability in scattering groups throughout the water column and to quantify the redistribution of mesopelagic animals associated through the diel migration process. Based on the classification approach presented, we observed category-specific vertical movement during both the night and day with some groups displaying little or no vertical movement on a diel cycle. This study was focused at a relatively fine spatial and temporal scale in order to examine the identification and categorization method for application to deep scattering layers. Results suggest that this approach and improved estimates of spatio-temporal structure through further development of acoustic modeling approaches may be useful to acoustically describe the dynamics of the mesopelagic community over broader spatial and temporal scales. This type of analysis can contribute to providing a broad scale view of how the various components of the mesopelagic ecosystem respond to various physical and environmental drivers.

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Appendix A. Supplementary material

Supplementary data associated with this article can be found in the online version at <http://dx.doi.org/10.1016/j.dsr.2016.05.014>.

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