



Complex sound scattering layer and water-column dynamics over a mesophotic coral ecosystem: Southwest Puerto Rico, U.S.A

Olivia M. Cheriton¹ · Curt D. Storlazzi¹ · Clark E. Sherman² · Kurt J. Rosenberger¹ · Nikolaos V. Schizas²

Received: 27 February 2025 / Accepted: 2 September 2025

This is a U.S. Government work and not under copyright protection in the US; foreign copyright protection may apply 2025, corrected publication 2025

Abstract A nearly 5-month record of high-resolution temperature and acoustic backscatter profiles from the upper insular slope off southwest Puerto Rico reveals complex sound scattering layer (SSL) dynamics over a mesophotic coral ecosystem (MCE). The SSLs exhibited both diel and reverse diel vertical migration, thin layer (< 5 m) and multiple layer formations, depth modulation due to internal waves, and vertical layering in the absence of water column stratification. The long-term observations also capture SSL and water column dynamics across changing seasons and two category five hurricanes, Irma and María. The SSLs, likely composed of zooplankton, represent an important food source for both the sessile (*e.g.*, corals and sponges) and mobile (*e.g.*, fish) MCE taxa, and their effective vertical mobility underscores their importance to trophic connectivity between the upper and lower slope MCEs, as well as the shelf. Our results also underscore the challenges in adequately resolving zooplankton aggregations using conventional sampling techniques.

Keywords Zooplankton · Mesophotic coral ecosystem · Diel vertical migration · Physical processes · Insular slope · Southwest Puerto Rico

Supplementary Information The online version contains supplementary material available at <https://doi.org/10.1007/s00338-025-02747-1>.

✉ Olivia M. Cheriton
oheriton@usgs.gov

¹ U.S. Geological Survey, Pacific Coastal and Marine Science Center, 2885 Mission Street, Santa Cruz, CA 95060, USA

² Department of Marine Sciences, University of Puerto Rico-Mayagüez, P.O. Box 9000, Mayagüez 00681, Puerto Rico

Introduction

Mesophotic coral ecosystems (MCEs, 30–150 m) are important marine habitats for a variety of species, but our understanding of these critical ecosystems is limited (Rocha et al. 2018). Zooplankton are a critical food source for many MCE organisms, including fish, sponges, and corals. Because of decreased photosynthetically active radiation at depth, corals in MCEs often utilize a mixotrophic feeding strategy, with the ability to switch to heterotrophy (Muscatine et al. 1989; Mass et al. 2007), although the relationship between heterotrophy with increasing depth is unclear (*e.g.*, Carmignani et al. 2023; Pérez-Rosales et al. 2024).

Little information is currently available on zooplankton composition, abundances, and behavior in MCEs. Two studies conducted at the MCE on the Bajo Frijol seamount in Colombia examined zooplankton collected from pump samples (Contreras-Vega et al. 2021; Criales-Hernández et al. 2021). Across seasons and multiple depths, the zooplankton assemblage of this size class was dominated by small copepods, nauplii, radiolarians, and tintinnids, and the abundances did not significantly differ between shallower and deeper depths of the water column. However, work at other sites has found variations in zooplankton assemblages across depth strata, particularly with regards to MCEs and shallow reefs. At the southern extent of the Mesoamerican Barrier Reef off Honduras, nocturnal light-trap samples showed greater zooplankton abundance at the MCE sites than the shallow reefs, although their overall species richness was roughly equal (Andradi-Brown et al. 2017). In contrast, light traps deployed in the Florida Keys reported the opposite: enhanced zooplankton abundance at the shelf reefs but greater species richness at the MCEs (Sponaugle et al. 2021). The deepest (~80 m) MCE site had an entirely distinct species assemblage, whereas the shallower (~60 m)

MCE contained a mix of the shallower and deeper zooplankton assemblage. Taken together, these studies indicate that the character of zooplankton assemblages at MCEs are likely distinct from those of shallower shelf coral reefs, and that the types, richness, and abundances of zooplankton from one MCE site to another can strongly differ.

Methods and field site

Study area

This study took place on the southwest upper insular slope off La Parguera, Puerto Rico, U.S.A. (Fig. 1a, b). Here, the shelf has a mean depth of approximately 20 m and extends roughly 10 km from shore to the shelf break at about 20–30 m depth. Beyond the shelf break, the insular slope hosts an MCE that has been the focus of several research studies. Our study site was at ‘Hole-in-the-wall’ (HW)—an established site that is part of the University of Puerto Rico at Mayagüez’s MCE research program. HW is located at approximately 55-m water depth, 10 km from shore, 150 m horizontally from the shelf break, and on a slope of 44° (Fig. 1b, c). The benthic communities here are composed of scleractinian corals, octocorals, macroalgae, crustose coralline algae, and sponges (Appeldoorn et al. 2021), and the primary seabed sediment between the benthic communities is sand (Sherman et al. 2010, 2016). In this region, from the insular shelf to mesophotic depths, the trophic web shifts to one based on plankton (García-Hernández et al. 2018). At HW, the fish abundances are 80% zooplanktivores, compared to only 18% over the nearby shelf (Appeldoorn et al. 2016). And one of the most abundant corals at these mesophotic

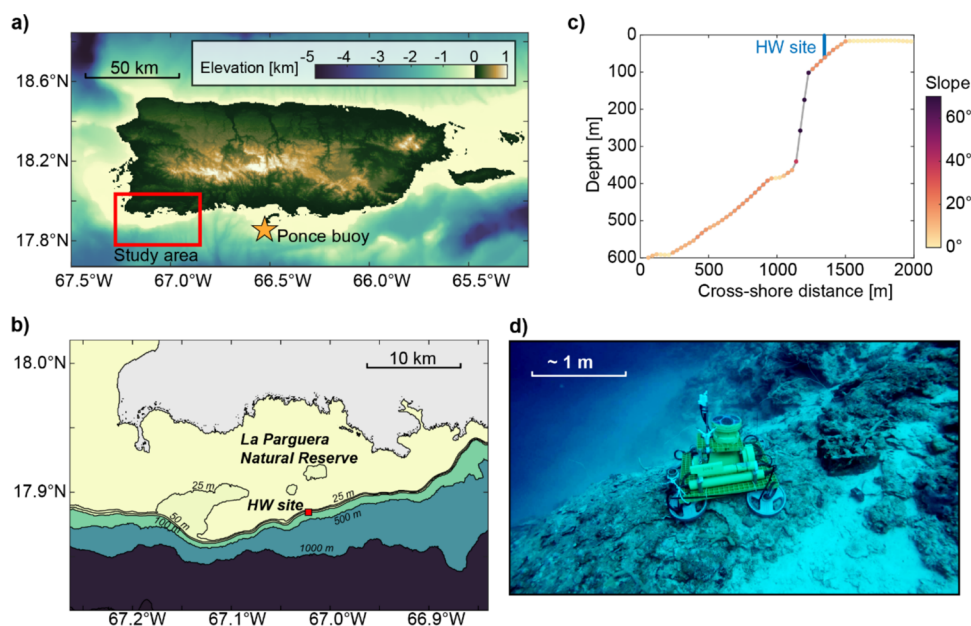
depths is *Agaricia lamarcki* (Sherman et al. 2010; Appeldoorn et al. 2016; García-Hernández et al. 2018), a species known to rely on heterotrophic feeding across a broad range of depths (Crandall et al. 2016).

Deployment

The nearly 5-month set of observations spans 27 July through 7 December 2017. The study objectives were to resolve water-column dynamics in support of a shelf sediment transport investigation (Cheriton et al. 2019a, 2021). A benthic instrument package was installed at HW, on a small, relatively flat terrace at 55-m water depth (Fig. 1d). On this package was an upwards-looking 300-kHz RD Instruments acoustic Doppler current profiler (ADCP), which collected 2-min profiles in 1-m bins, from about 4–49 m above the bed (6–51 m depths). The currents were strongly along-isobath, so the principal component was used to represent upcoast (west–northwest) and downcoast (east–southeast) flow. The along-isobath currents were depth-averaged according to above (< 20 m) and below (> 30 m) the shelf break, and then, to focus on tidal and subtidal variability we applied a - h low-pass filter.

Approximately 15 m downslope from the benthic package, a vertical thermistor chain was deployed at 62-m depth that consisted of 1 SeaBird SBE-56 thermistor at 57-m depth that logged every 30 s, and 8 RBR SoloT thermistors mounted every 5 m from 52 to 17 m depth that sampled every 5 s, and a SeaBird Electronics SBE-37 TS sensor that sampled once every 2 min at a depth of 12 m. Temperature was interpolated to a 1 m depth interval. In order to identify the mixed layer depth (MLD), the interpolated temperature was also smoothed in the vertical dimension using a digital

Fig. 1 **a** Location of the study area on the southwest coast of Puerto Rico (red box). **b** Deployment site on the upper insular slope directly offshore of the La Parguera Natural Reserve, at the ‘Hole-in-the-wall’ (HW) mesophotic coral ecosystem research location (red square). **c** Approximate profile of the insular slope, with the slope (color ramp) and the HW mooring location overlaid. **d** Photo of the upwards-looking acoustic Doppler current profiler (ADCP) installed at the HW site (55-m depth)



5-m low-pass filter. Then the MLD was identified by finding the shallowest depth at which the vertical rate of change of the smoothed temperature exceeded 1° m^{-1} .

Wind velocity and atmospheric pressure were measured by the Caribbean Integrated Coastal Ocean Observing System's (<https://www.caricoos.org/>) Ponce buoy, which is located at the outer shelf, in 19 m depth, approximately 50 km east of HW (Fig. 1a). Sunrise and sunset times were obtained from the U.S. Naval Observatory (<https://aa.usno.navy.mil>).

Sound scattering layer identification

Echo strength in the ADCP profiles was converted to absolute volume scattering strength, Sv (Deines 1999; Gostiaux and van Haren 2010). Due to the range-dependent increase in background noise, the background Sv values were determined by finding the minimum Sv at each depth bin and performing a linear fit (Fig. 2a). This background profile was subtracted from the Sv record to produce corrected volume scattering, Sv_c , which represents an above background scattering strength (Fig. 2b). For each Sv_c profile, sound scattering layers (SSLs) were identified by first smoothing the profile using a low-pass, 5th-order, zero-phase forward and reverse filter, then identifying distinct peaks with magnitudes greater than 25 dB (Fig. 2b). Though the minimum peak value was 25 dB, the SSL peak magnitudes could reach up to 45 dB, with 40% of SSL peaks having $Sv_c > 29$ dB. For a single peak in the profile, the upper and lower extents were the depths at which the peak dropped to below 22 dB. If the lower extent was below the deepest bin, the peak was flagged and excluded from analyses regarding SSL vertical thickness. For profiles with multiple distinct peaks, the peaks were first sorted according to peak magnitude, to prioritize the strongest peaks. Then, if a secondary peak overlapped with previous (*i.e.*, stronger) peaks, those layers were consolidated. Isolated scattering peaks that did not comprise a coherent (in time and space) layer were manually removed. In addition, the scattering patterns during the passage of Hurricane María were excluded from the analyses, as the surface scattering was most likely bubbles, and the near-bed signal was likely contaminated by suspended particulate material from the shelf and seabed (refer to Supporting Information).

To examine diurnal SSL patterns, the SSL vertical thicknesses and depths were binned by daytime and night-time periods, which were defined as the time periods 1 h after sunrise to 1 h before sunset (daytime) and 1 h after sunset to 1 h before sunrise (night-time). In addition, the overall SSL intensity of the day and night periods was expressed as the sum of the SSL peak magnitudes, normalized by the number of hours (n_{hr}) in the time period: $\sum Sv_c / n_{hr}$.

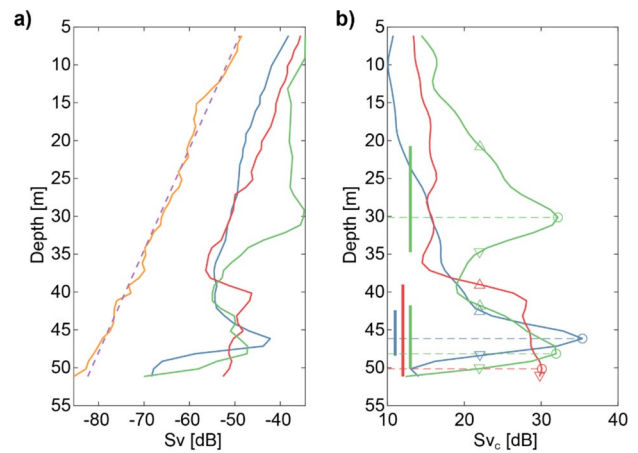


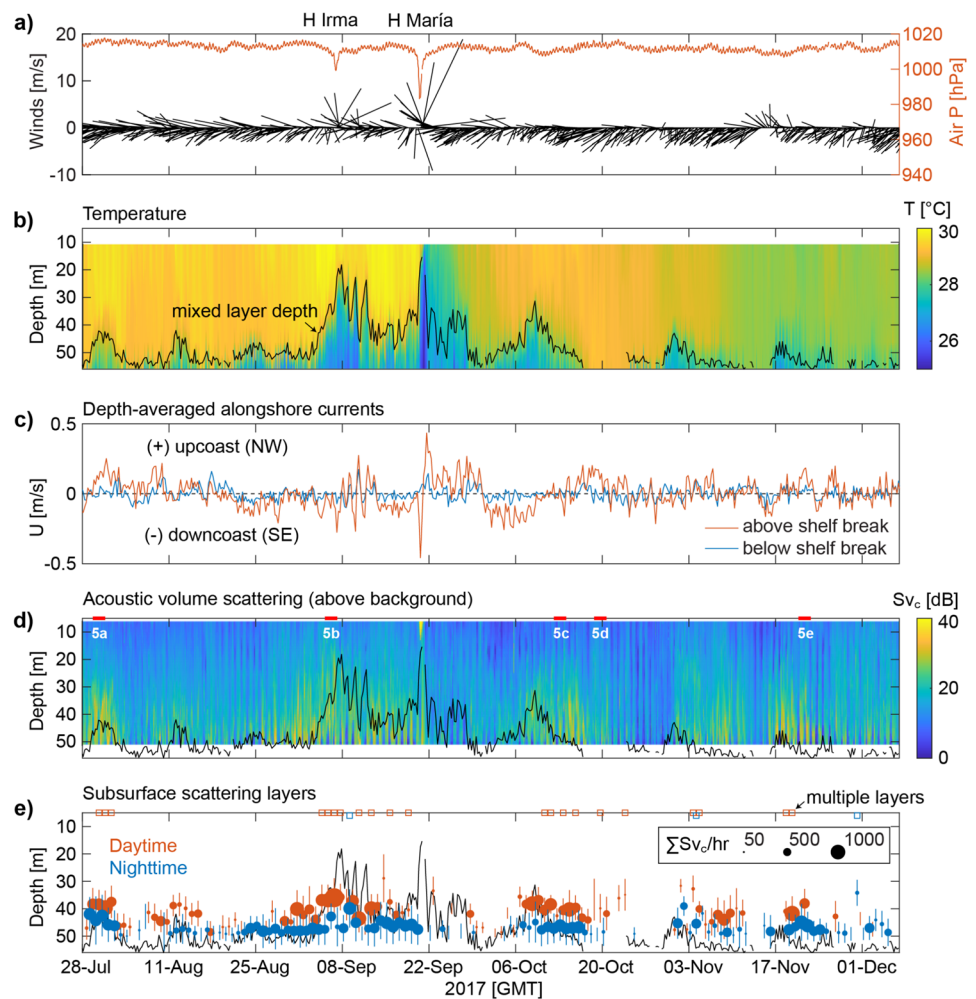
Fig. 2 Three example profiles of acoustic volume backscatter (Sv) and their layer characteristics. **a** The original Sv profiles (red, blue, green lines) shown with the minimum value for each depth across the entire record (orange line) and the linear fit (purple dashed line) that was subtracted from Sv to generate the corrected, “above background” acoustic backscatter (Sv_c) profiles shown in **(b)**. **b** The three example Sv_c profiles, showing the identified layer peaks (circles) and associated depth (horizontal dashed lines), the upper (triangles) and lower extents (upside-down triangles), and the resulting vertical thickness (thick vertical lines). In the case of the red example profile, the lower extent is not captured (*i.e.*, it is below the profiling range), and this profile would be flagged by the identification algorithm. In the case of the green profile, two distinct layers are identified

Results

Our nearly 5-month-long dataset reveals high spatial and temporal resolution details of sound scattering layer (SSL) dynamics over an upper insular slope MCE. During the deployment, the area was affected by two major hurricanes, Irma (indirect impact) and María (direct impact), as well as a shift from warmer summer/fall conditions to cooler winter conditions (Fig. 3a, b). The MLD exhibited regular vertical fluctuations roughly every 14 d, likely driven by spring-neap tidal cycles, driving a 10–20 m rise above the HW seabed to 35–40 m water depth. Under hurricane conditions, the MLD could shoal to the shelf break (~20 m) or shallower, depending on the proximity of the storm. With the transition to winter (approximately mid to late October), the MLD deepened and cooled. The currents above the shelf break were stronger than those below (Fig. 3c), with the shallowest depth bin having a mean ± 1 -standard deviation current speed of $0.15 \pm 0.11 \text{ m s}^{-1}$, and that of the deepest depth bin $0.04 \pm 0.03 \text{ m s}^{-1}$.

Subsurface SSLs were common features throughout the study period, with SSLs detected over the MCE site 39% of the time, and SSL activity continuing into the winter months, even after the MLD had cooled and deepened (Fig. 3d and 4e). The SSLs were typically observed at depths > 40 m but were also found as shallow as the shelf

Fig. 3 Time-series from the entire 132-d deployment. **a** Wind velocity (black vectors, left axis), and barometric pressure (orange line, right axis) measured by the Ponce buoy; the timing of two major tropical cyclones (TC), Irma and María, are labeled and correspond to the sharp dips in barometric pressure. **b** Temperature with the approximate mixed layer depth (MLD) overlaid (black line). **c** 3-h-averaged along-isobath currents averaged over depths above (orange line) and below (blue line) the shelf break; positive values indicate upcoast (northwest-directed) and negative values indicate downcoast (southeast-headed). **d** Corrected acoustic volume backscatter (Sv_c), with MLD overlaid (black line); 2-d time periods shown in Fig. 5 panels are indicated by red lines and white text labels. **e** Subsurface scattering layer (SSL) characteristics aggregated by day- (dark orange) and night-time (blue) periods: the mean SSL depth and vertical thickness (vertical lines), intensity (size of circle), and occurrence of multiple layers (squares at top of axis); the MLD (black line) is also overlaid



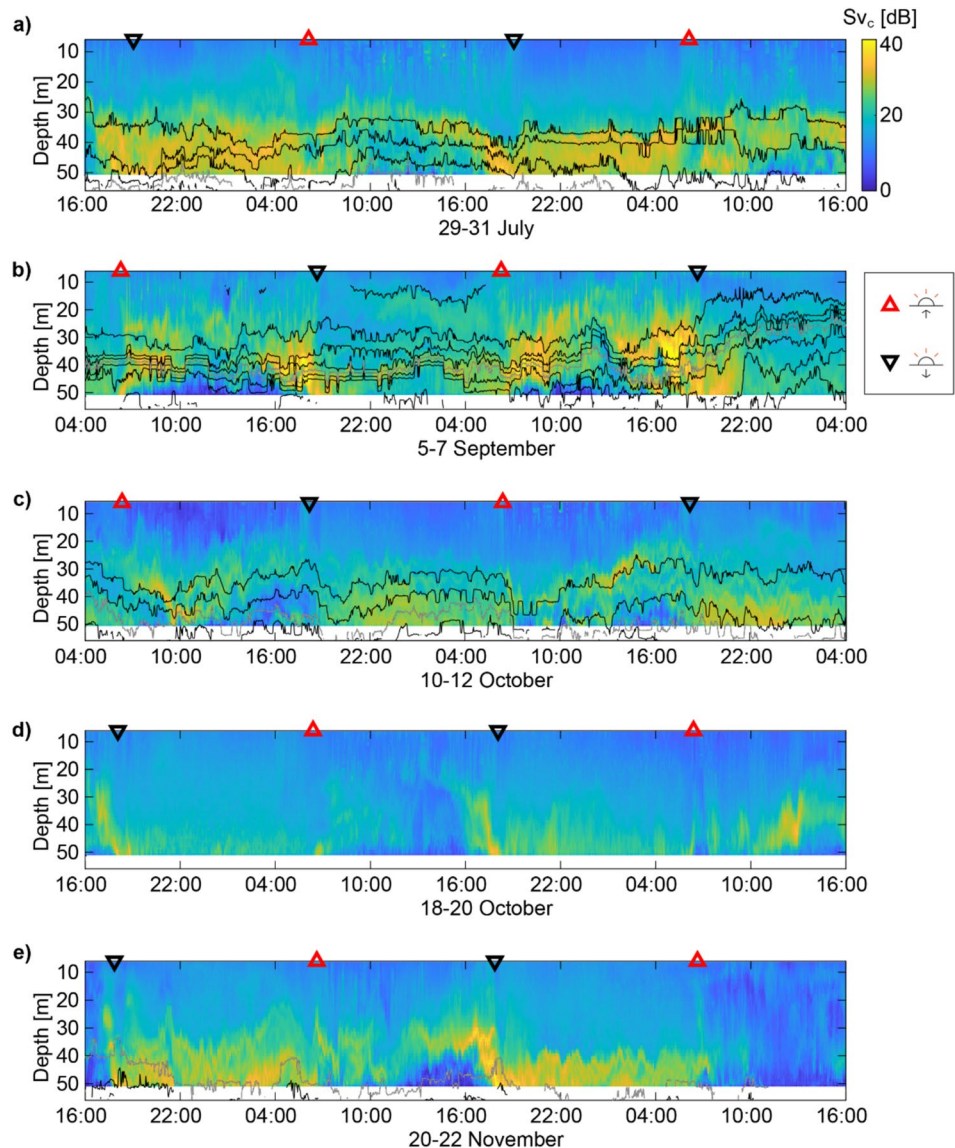
break. In general, the depth of the SSLs followed the MLD, and SSLs were most prevalent (within our ADCP profile range) when the MLD was also at least 5–10 m above the seabed. Correspondingly, the times when SSLs were absent were when the MLD was below the study site. After María, there was a 15-d period when SSLs were mostly absent from our study site. However, it is unclear if the absence of SSLs after María was due to storm effects, as a gap of a similar timespan (14 d) occurred roughly 2 weeks later, from 18 to 31 October.

The SSLs typically followed isotherm depths and occasionally exhibited modulation by high-frequency internal waves (Fig. 4b, c). However, there were exceptions to this. For example, SSLs often persisted for 6–10 days over our study site even after the MLD had deepened (e.g., 9–17 October, 1–11 November, and 18–24 November time periods in Fig. 3d, e). Another exception was when the MLD shoaled to the shelf-break depth in response to Irma and the SSLs remained deeper (~7 September; Fig. 3). Comparing the depths of the SSL Sv_c peaks and the MLD, approximately 20% of the SSLs were > 10 m offset from the MLD.

There were several instances when the MLD was below the depth of our study site (55 m) and rapid vertical migrations were observed to start from just below the shelf-break depth (~30 m; Fig. 4d), with descent speeds of ~1–2 cm s⁻¹ (inferred from the SSL inclination; Supporting Information Fig. S2)—matching reported swimming speeds for common zooplankton such as copepods and euphausiids (De Robertis et al. 2003; Chen and Hwang 2018).

Cases of multiple SSLs present simultaneously in the water column were common and tended to occur several days after the shoaling of the MLD (Fig. 3e, 4e). Multiple SSLs were more likely to occur during the day, with 16% of daytime periods having sustained multiple SSLs present, compared to only 2% of night-time periods (Fig. 3e). There were periods when the night-time SSLs were stronger than the daytime ones (e.g., 23–29 August and 22 November to 5 December in Fig. 3e and 4a), as well as periods when daytime SSLs were stronger (e.g., 7–16 August and 6–10 October in Fig. 3e and 4b). But overall, the SSL vertical thicknesses and intensities had the same distributions regardless of time of day (Fig. 5a, b). The primary distinction

Fig. 4 Example 2-d time-series of corrected volume scattering (S_v) for 5 time periods (a–e), with isotherms overlaid (black and gray lines). All times are in local time. The isotherms have 0.5-°C steps, and the 28-°C isotherm is indicated by a gray line. The black upside-down triangles indicated sunset, and the red triangles indicate sunrise. Note that the time of day indicated by the x-axis labels is not uniform for all the time periods. The subsurface scattering layers (SSLs) exhibit different dynamics, such as stronger and broader SSL during the night (a) vs. during the day (b), short-lived SSLs (c), prominent SSL vertical migration with the mixed layer depth below the profile window (d), and strong SSLs even during winter months (e)



between daytime and night-time SSLs is that the daytime SSLs were shallower (mean depth 41.5 ± 4.2 m) than night-time (47.0 ± 2.4 m; Fig. 3e and 5c). The deeper night-time SSLs could be due to a variety of different factors, including reverse diel vertical migration (*i.e.*, deepening of daytime SSLs) or diel vertical migration from below our study site.

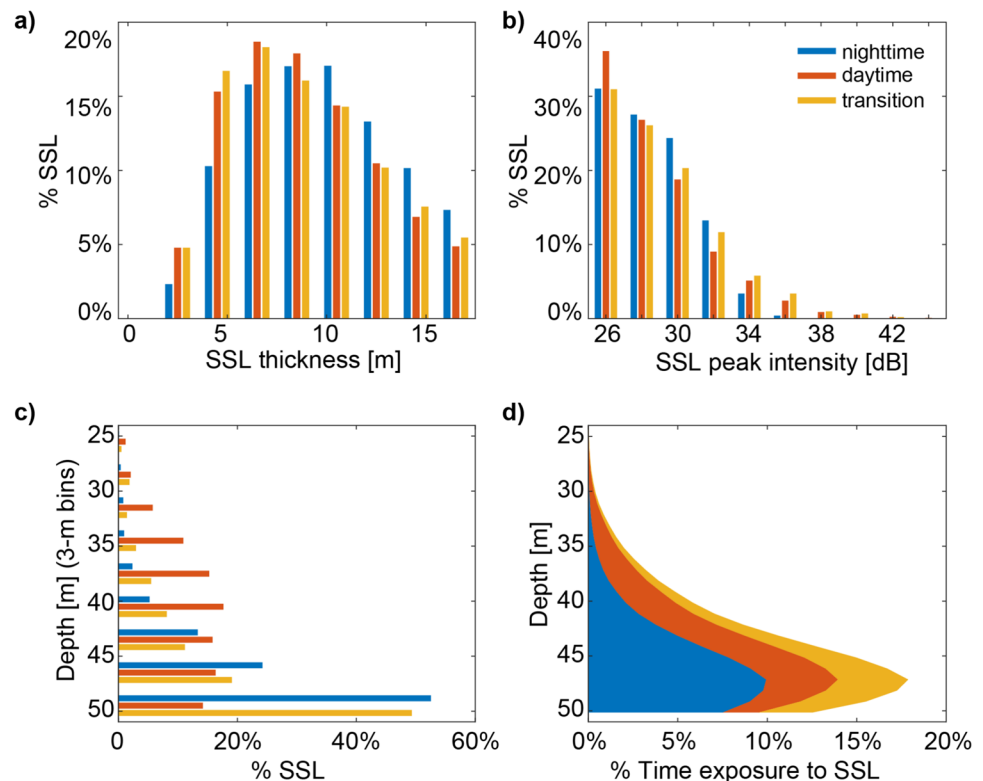
Over our observed depth range, the exposure to SSLs increased with depth to about 47 m (Fig. 5d). Taking these depths as a proxy for seabed depths (the slope here is steep), this suggests that MCE organisms at the HW site are exposed to SSLs roughly 13–18% of the time, equivalent to a daily average of about 3–4 h, and most of this exposure occurs at night. For depths shallower than 40 m, daytime exposure exceeds that of other times. This supports the theory that MCE corals might maximize energy production by taking advantage of the greater abundance of zooplankton at night

when phototrophic energy gains are unavailable (Lesser et al. 2009), similar to what has been suggested for shallow corals (Houlbrèque and Ferrier-Pagès 2009).

Discussion

The scatterers within the observed SSLs were probably primarily zooplankton, as it is unlikely that inorganic suspended particulates such as sediment could produce the sustained diurnal scattering patterns and complex vertical layering observed throughout the 5-month study. We would expect the strongest echo off scatterers whose size is roughly equivalent to the acoustic wavelength of our ADCP, $O(1$ mm), noting that target strength also depends on physiological factors such as shape and orientation (Holliday and

Fig. 5 Characteristics of sub-surface scattering layers (SSL) by percentage of SSLs during night-time (blue), daytime (dark orange), and the transition periods (light orange): **a** Vertical thickness, **b** Peak intensity (Sv_c), and **c** Depth (note: rotated axes). **d** Percentage of total time that different depths are exposed to SSLs, shown as cumulative contributions. Night-time SSLs tend to be deeper than those at other times; SSL vertical thickness and intensity distributions do not vary by time of day. Exposure to SSLs increases with depth, and most of this exposure occurs during night-time. Note: The decrease in exposure below 47 m is likely an artifact of our SSL identification (*i.e.*, elevated scattering at or near the deepest profile bin is less likely to be identified as a coherent SSL)



Pieper. 1980). Net tows collected offshore of our study site found the mesoplankton assemblage dominated by copepods, larvaceans, chaetognaths, amphipods, and euphausiids (Yoshioka et al. 1985; Pena 2006). These organisms have a size range matching the ADCP's target strength and swimming speeds on the order of the observed SSL layer migrations ($1\text{--}2\text{ cm s}^{-1}$). In addition, the complex SSL dynamics, with multiple layers, merging and bifurcating SSLs, and constantly changing vertical migration patterns, indicate these SSLs were composed of a multitude of species with differential behaviors and responses, and that there was a highly heterogeneous water-column partitioning of these species and behaviors.

Typical sampling techniques for zooplankton at MCE sites such as light traps, pumps, and net tows provide valuable species information, but they do not provide the spatial and temporal resolution necessary to resolve the layering dynamics shown in our observations. The SSLs were often vertically thin (Fig. 4c), with approximately 11% less than 5 m in vertical extent, and 50% less than 9 m (Fig. 5c). As observed in a wide variety of coastal ocean environments, zooplankton commonly aggregate into thin layers (McManus et al. 2005; Sevajian et al. 2010). Our observations show that thin layers also occur over the insular slopes of tropical islands and within MCEs.

Our intra-seasonal, high-resolution record of SSLs over an MCE provides several additive findings. First, SSLs were common features over the upper insular slope MCE even

through the seasonal transition, but they could also be absent for prolonged periods (~ 2 weeks) of time. The SSLs, which were likely composed of zooplankton, often followed the MLD, but were sometimes decoupled from water-column structure, highlighting the importance of behavior in determining these organisms' proximity and availability as a food source for benthic MCE organisms. Lastly, the SSLs appeared to be highly mobile—on daily timescales, these features can vertically traverse $O(100\text{ m})$ across slope depths and possibly up to the shelf depths. This mobility, coupled with their ecological importance, may serve as a form of vertical connectivity across MCE depths and possibly also to the shelf, supporting the biodiversity, health, and persistence of MCEs.

Acknowledgements This work was carried out in collaboration between the University of Puerto Rico—Mayaguez and the U.S. Geological Survey's (USGS) Coral Reef Project. It was funded by the USGS's Coastal Marine Hazards and Resources Program, with partial funding by the National Science Foundation OCE Award No. 1809878. We thank Josh Logan, Mark Buckley, Cordell Johnson, and Amy West (USGS), Milton Carlo, Bill Schmidt, Haibo Xu, and Evan Tuohy (UPRM) for field support. We are grateful to Nancy Prouty and Amanda Demopoulos (USGS) for early reviews, and two anonymous reviewers whose comments greatly benefited the manuscript. Any use of trade, firm, or product names is for descriptive purposes only and does not imply endorsement by the U.S. Government.

Author contribution CDS, OMC, KJR, CS, and NVS designed the field study; CDS, CS, and NVS secured funding. OMC and CDS developed the research question, and OMC performed the analyses,

prepared the figures, and wrote the manuscript. All authors contributed to data collection and field deployment. All authors reviewed the text and approved the final version.

Funding USGS's Coastal Marine Hazards and Resources Program, the National Science Foundation OCE Award No. 1809878.

Data availability Data used in this study are available at <https://doi.org/10.5066/P9IXOHID> (Cheriton et al. 2019b), except for auxiliary datasets, which are available via websites provided in the text.

Declarations

Conflict of interest The authors declare no conflict of interest.

Open Access This article is licensed under a Creative Commons Attribution 4.0 International License, which permits use, sharing, adaptation, distribution and reproduction in any medium or format, as long as you give appropriate credit to the original author(s) and the source, provide a link to the Creative Commons licence, and indicate if changes were made. The images or other third party material in this article are included in the article's Creative Commons licence, unless indicated otherwise in a credit line to the material. If material is not included in the article's Creative Commons licence and your intended use is not permitted by statutory regulation or exceeds the permitted use, you will need to obtain permission directly from the copyright holder. To view a copy of this licence, visit <http://creativecommons.org/licenses/by/4.0/>.

References

- Andradi-Brown DA, Head CEI, Exton DA, Hunt CL, Hendrix A, Gress E, Rogers AD (2017) Identifying zooplankton community changes between shallow and upper-mesophotic reefs on the Mesoamerican Barrier Reef, Caribbean. *PeerJ* 5:e2853. <https://doi.org/10.7717/peerj.2853>
- Appeldoorn RS, Ballantine D, Bejarano I, Ruiz H, Schizas N, Schmidt W, Sherman C, Weil E (2016) Mesophotic coral ecosystems examined: La Parguera, Puerto Rico, USA. In: Baker EK, Puglise KA, Harris PT (eds) *Mesophotic Coral Ecosystems—A Lifeboat For Coral Reefs?* The United Nations Environment Programme and GRID-Arendal, Nairobi and Arendal, pp 45–49
- Appeldoorn RS, Ballantine DL, Carlo M, Cruz Motta JJ, Nemeth M, Ruiz HJ, Schizas NV, Sherman CE, Weil E, Yoshioka PM (2021) Intra-annual variation in mesophotic benthic assemblages on the insular slope of Southwest Puerto Rico as a function of depth and geomorphology. *Front Mar Sci* 8:732926. <https://doi.org/10.3389/fmars.2021.732926>
- Carmignani A, Radice VZ, McMahon KM, Holman AI, Miller K, Grice K, Richards Z (2023) Levels of autotrophy and heterotrophy in mesophotic corals near the end photic zone. *Front Mar Sci*. <https://doi.org/10.3389/fmars.2023.1089746>
- Chen M-R, Hwang J-S (2018) The swimming behavior of the calanoid copepod *Calanus sinicus* under different food concentrations. *Zool Stud* 57:e13. <https://doi.org/10.6620/ZS.2018.57-13>
- Cheriton OM, Storlazzi CD, Rosenberger KJ, Sherman CE, Schmidt WE (2021) Rapid observations of ocean dynamics and stratification along a steep island coast during Hurricane María. *Sci Adv* 7:eabf1552. <https://doi.org/10.1126/sciadv.abf1552>
- Cheriton OM, Storlazzi CD, Rosenberger KJ, and C. Sherman C (2019). Controls on sediment transport over coral reefs off southwest Puerto Rico: seasonal patterns and Hurricane Maria. *Coastal Sediments 2019: Proc of the 9th Intl Conf*, 2019:903–915. https://doi.org/10.1142/9789811204487_0079
- Cheriton OM, Rosenberger KJ, Logan JB, Storlazzi CD (2019) Time series data of oceanographic conditions from La Parguera, Puerto Rico, 2017–2018 Coral Reef Circulation and Sediment Dynamics Experiment. U.S. Geological Survey data release. <https://doi.org/10.5066/P9IXOHID>
- Contreras-Vega L, Henao-Castro A, Navas-S GR (2021) Composition of the zooplankton community associated with mesophotic corals in “Corales de Profundidad” National Natural Park, Colombian Caribbean. *Rev Acad Colomb Cienc Ex Fis Nat* 45:747–760. <https://doi.org/10.18257/raccefyn.1396>
- Crandall JB, Teece MA, Estes BA, Manfrino C, Ciesla JH (2016) Nutrient acquisition strategies in mesophotic hard corals using compound specific stable isotope analysis of sterols. *J Exp Mar Biol Ecol* 474:133–141. <https://doi.org/10.1016/j.jembe.2015.10.010>
- Criales-Hernández M, Jerez-Guerrero M, Rodríguez-Rubio E, Benavides-Serrato M (2021) Zooplankton community associated with mesophotic coral reefs in the Colombian Caribbean Sea. *Reg Stud Mar Sci* 45:101843. <https://doi.org/10.1016/j.rsma.2021.101843>
- De Robertis A, Schell C, Jaffe JS (2003) Acoustic observations of the swimming behavior of the euphausiid *Euphausia pacifica* Hansen. *ICES J Mar Sci* 60:885–898. [https://doi.org/10.1016/S1054-3139\(03\)00070-5](https://doi.org/10.1016/S1054-3139(03)00070-5)
- Deines KL (1999) Backscatter estimation using broadband acoustic Doppler current profilers. In: *Proc IEEE 6th Work Conf Curr Meas*, pp 249–253
- García-Hernández JE, Sanchez PJ, Hammerman NM, Schizas NV (2018) Fish, coral, and sponge assemblages associated with altphtotic and mesophotic reefs along the Guanica Biosphere Reserve continental shelf edge, Southwest Puerto Rico. *Front Mar Sci* 5:303. <https://doi.org/10.3389/fmars.2018.00303>
- Gostiaux L, van Haren H (2010) Extracting meaningful information from uncalibrated backscattered echo intensity data. *J Atmos Ocean Technol* 27:943–949. <https://doi.org/10.1175/2009JTECH0704.1>
- Holliday DV, Pieper RE (1980) Volume scattering strengths and zooplankton distributions at acoustic frequencies between 0.5 and 3 MHz. *J Acoust Soc Am* 67:135–146
- Houlbrèque F, Ferrier-Pagès F (2009) Heterotrophy in tropical scleractinian corals. *Bio Rev* 84:1–17. <https://doi.org/10.1111/j.1469-185X.2008.00058.x>
- Lesser MP, Slattery M, Leichter JJ (2009) Ecology of mesophotic coral reefs. *J Exp Mar Biol Ecol* 375:1–8. <https://doi.org/10.1016/j.jembe.2009.05.009>
- Mass T, Einbinder S, Brokovich E, Shashar N, Vago R, Erez J, Dubinsky Z (2007) Photoacclimation of *Stylophora pistillata* to light extremes: metabolism and calcification. *Mar Ecol Prog Ser* 334:93–102. <https://doi.org/10.3354/meps33409>
- McManus MA, Cheriton OM, Drake PT, Holliday DV, Storlazzi CD, Donaghay PL, Greenlaw CF (2005) Effects of physical processes on structure and transport of thin zooplankton layers in the coastal ocean. *Mar Ecol Prog Ser* 301:199–215. <https://doi.org/10.3354/meps301199>
- Muscantine L, Porter JW, Kaplan IR (1989) Resource partitioning by reef corals as determined from stable isotope composition. *Mar Biol* 100:185–193. <https://doi.org/10.1007/BF00391957>
- Pena WR (2006) Characterizing Zooplankton and micronekton diel vertical migration at the western Puerto Rican shelf/slope break. MS Thesis, University of Puerto Rico Mayagüez
- Pérez-Rosales G, Rouzé H, Pichon M, Bongaerts P, Bregere N, Carlot J, Parravicini V, Hédouin L, Under the Pole Consortium (2024) Differential strategies developed by two light-dependent

- scleractinian corals to extend their vertical range to mesophotic depths. *Coral Reefs* 43:1375–1391. <https://doi.org/10.1007/s00338-024-02544-2>
- Rocha LA, Pinheiro HT, Shepherd B, Papastamatiou YP, Luiz OJ, Pyle RL, Bongaerts P (2018) Mesophotic coral ecosystems are threatened and ecologically distinct from shallow water reefs. *Science* 361:281–284. <https://doi.org/10.1126/science.aag1614>
- Sevadjian JC, McManus MA, Pawlak G (2010) Effects of physical structure and processes on thin zooplankton layers in Mamala Bay, Hawaii. *Mar Ecol Prog Ser* 409:95–106. <https://doi.org/10.3354/meps08614>
- Sherman C, Nemeth M, Ruíz H, Bejarano I, Appeldoorn R, Pagán F, Schärer M, Weil E (2010) Geomorphology and benthic cover of mesophotic coral ecosystems of the upper insular slope of southwest Puerto Rico. *Coral Reefs* 29:347–360. <https://doi.org/10.1007/s00338-010-0607-4>
- Sherman C, Schmidt W, Appeldoorn R, Hutchinson Y, Ruiz H, Nemeth M, Bejarano I, Cruz Motta JJ, Xu H (2016) Sediment dynamics and their potential influence on insular-slope mesophotic coral ecosystems. *Cont Shelf Res* 129:1–9. <https://doi.org/10.1016/j.csr.2016.09.012>
- Sponaugle S, Goldstein E, Ivory J, Doering K, D'Alessandro E, Guigand C, Cowen RK (2021) Near-reef zooplankton differs across depths in a subtropical seascape. *J Plankton Res* 43:586–597. <https://doi.org/10.1093/plankt/fbab043>
- Yoshioka PM, Owen GP, Pesante D (1985) Spatial and temporal variations in Caribbean zooplankton near Puerto Rico. *J Plank Res* 7:733–751. <https://doi.org/10.1093/plankt/7.6.733>

Publisher's Note Springer Nature remains neutral with regard to jurisdictional claims in published maps and institutional affiliations.