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Body size- and season-dependent diel vertical migration of mesozooplankton resolved acoustically in the San Diego Trough

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Abstract

Diel vertical migration (DVM) is a common behavior among marine organisms to balance the trade-off between surface feeding opportunities and predation-related mortality risk. Body size is a master trait that impacts predation risk to both visual and nonvisual predators. Acoustic measurements from the autonomous *Zooglider* revealed size-dependent DVM behaviors in the San Diego Trough. Dual frequency (200 and 1000 kHz) backscatter, in conjunction with physical properties of the ambient water and optical imaging of zooplankton, were recorded during 12 *Zooglider* missions over 2 yr. Acoustic size-categories were identified based on the theoretical scattering properties of dominant taxonomic groups identified optically by the Zoocam. Acoustic modeling suggests that the measured acoustic backscatter in this region is largely dominated by copepods, with appreciable contributions from other taxa. We found that larger organisms migrated deeper (245–227 m) and faster (> 20 m h⁻¹) compared to smaller organisms (156 m, > 15 m h⁻¹). Larger organisms entered the upper layer of the water column later in the evening (0.2–1.5 h later) and descended into deeper water earlier in the morning (0.4–3.7 h earlier) than smaller-bodied organisms, consistent with body size-dependent visual predation risk. The variability in daytime depths occupied by small, intermediate, and large-bodied backscatterers was related to the depth of the euphotic zone, again consistent with light-dependent risk of predation.

Diel vertical migration (DVM) is a common behavior performed by many zooplankton taxa in the world ocean and freshwater lakes. Larger organisms that perform DVM commonly move deeper in the water column during the day and rise closer to the surface under the darkness of night to feed (Pinti et al. 2019). The benefits of DVM can be manifold, including predator avoidance (De Robertis et al. 2000), retention in favorable habitats (Batchelder et al. 2002) or dispersal, maximization of mate encounter (Madin and Purcell 1992), or avoidance of ultraviolet light penetrating into shallow waters (Williamson et al. 2011). DVM more generally represents a trade-off between feeding opportunities and elevated mortality risk near the surface (Aksnes and Ohman 1996).

The risks and benefits of DVM are mediated by the traits of the organisms involved (Litchman et al. 2013). Body size is considered a master trait that impacts the feeding, growth, reproduction, and survival of an organism (Litchman et al. 2013; Ohman and Romagnan 2016). DVM is more prevalent in larger bodied copepods (Hays et al. 1994). Smaller, less conspicuous euphausiids spend more time in surface water, rising earlier and descend later than larger conspecifics (De Robertis et al. 2000). The depth at which organisms of different body sizes reside can also reflect their predation risk (Ohman and Wood 1996; Hirst and Kiørboe 2002). The sizedependent mortality risk from visual predators in surface waters is modulated by the availability of light (De Robertis et al. 2000; Pinti et al. 2019).

The first descriptions of DVM date back over a century (Forel 1878), with the first acoustic observations published in 1948 (Johnson 1948). Active acoustic techniques allow measurements in large volumes of water at high temporal resolution when compared to traditional sampling methods (Simmonds and MacLennan 2008). Despite this advantage, active acoustic methods contain inherent ambiguities of interpretation. Among these are the variability of acoustic target strength. Target strength (TS [dB re m²]) is the log scaled amount of acoustic energy a single organism scatters back to the sound emitting and receiving device (transducer). An organism's TS is largely dictated by its material properties, orientation (relative to the sound source), size or biovolume

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(Demer and Martin 1995; Chu and Wiebe 2005), shape (Bairstow et al. 2021), and the physical characteristics of the sound source (including frequency; Jech and Michaels 2006). If properly constrained, differences in TS and in the received backscattered acoustic signal at different acoustic frequencies can be exploited to classify the received acoustic energy into biologically meaningful groups such as species groups or size classes (Greenlaw 1977; Holliday and Pieper 1980; Holliday et al. 1989). However, the rapid attenuation of sound energy with increasing acoustic frequency (Francois and Garrison 1982*a*; Macaulay et al. 2020) limits the utility of traditional downward looking, near-surface mounted multi-frequency acoustic systems for the monitoring of mesozooplankton. Submersible acoustic systems can mitigate this limitation (Guihen et al. 2014; Powell and Ohman 2015*a*; Whitmore et al. 2019).

Here, we test the hypothesis of body-size dependence of mesozooplankton DVM behavior in the San Diego Trough, a 1200-m-deep feature located in the southern sector of the California Current System. We utilize a dual-frequency (1000 and 200 kHz), single-beam echosounder system (Zonar) designed to resolve mesozooplankton acoustic backscatter, together with a shadowgraph imaging Zoocam, both mounted on the fully autonomous Zooglider (Ohman et al. 2019). We illustrate how concurrent in situ optical imaging provides important information on the taxonomic composition, body size, and shapes of the ensonified zooplankton that helps constrain acoustic scattering models. We then test for differences in the DVM behavior of large (> 3 mm), intermediate (1–3 mm), and small (< 1 mm) mesozooplankton, addressing daytime depths occupied, vertical migration velocities, and timing of migration based on year-round Zooglider missions.

Methods

Zooglider was deployed over the San Diego Trough, 30–35 km west of La Jolla, California, centered at 32.87° N, 117.63°W, on 12 missions from July 2017 to May 2019 (Table S1). Water depth at our study site was approximately 1000 m. Full *Zooglider* engineering details are described in Ohman et al. (2019). *Zooglider* followed a pre-programmed route, which was updated via two-way communication. Generally, *Zooglider* dove to 400 m, completing a dive approximately every 3 h, recording data only during each dive ascent. Dives in transit to/from the study site over the San Diego Trough (i.e., dives shallower than 385 m) are not considered here. Ascent and descent angles were ~ 17° and vertical velocities ~ 0.1 m s⁻¹.

Sensors mounted on *Zooglider* include a custom Zonar, consisting of single beam 200 kHz (3 dB beam angle $\theta_{3 \text{ dB } 200 \text{ kHz}} = 9.8^{\circ}$) and 1000 kHz ($\theta_{3 \text{ dB } 1000 \text{ kHz}} = 4^{\circ}$) transducers manufactured by the Instrument Development Group at the Scripps Institution of Oceanography (Table S2). Both transducers used a 5 kHz sampling rate with a 6 ms pulse duration. In every 4 m of depth during the glider ascent, a

four-ping burst ensemble was emitted sequentially at each of the two frequencies (four pings at 200 kHz, followed by four pings at 1000 kHz). The inter-ping interval was 200 ms (ping rate = 5 Hz) for the 200 kHz and 100 ms (ping rate = 10 Hz) for the 1000 kHz. A 1-ms blanking time for both (Table S2), which extends further than the theoretical nearfield zone of the transducers, was applied. For the present study, only data within a range of 3-6 m from the transducer face were considered. Zooglider is also equipped with an optical shadowgraph imaging system (Zoocam) with red light illumination (Ellen et al. 2019; Ohman et al. 2019), a pumped conductivity, temperature and depth unit (CTD, SeaBird CP41), and a chlorophyll a (Chl a) fluorometer (Seapoint mini-scf). Fluorometers were calibrated regularly using standardized dilutions of pure Chl a (Sigma Life Sciences) dissolved in 90% acetone as described by Powell and Ohman (2015a). Each calibration provided a slope value (mg Chl $a L^{-1} V^{-1}$) allowing the translation of measured fluorescence voltage counts into concentrations of Chl a (C) expressed in standardized fluorescence units (SFU) (Powell and Ohman 2015b). Diffuse attenuation coefficient (k) was approximated as $k = 0.121 C^{0.428}$ (Powell and Ohman 2015*a*). The euphotic depth ($Z_{1\%}$) was calculated as the depth at which light availability was 1% relative to the surface, following the Beer-Lambert law.

The Zoocam and Zonar sampled different parcels of water based on their configuration on *Zooglider* (*see* Ohman et al. 2019). Small particles of two size classes, 0.25–0.45 mm in equivalent circular diameter (ECD) and > 0.45 mm ECD were extracted from the optical data as a proxy for prey availability and an alternative descriptor to Chl *a* concentrations. These small particles were assumed to be mainly composed of marine snow (Ohman et al. 2019; Briseño-Avena et al. 2020; Fakhraee et al. 2020; Whitmore and Ohman 2021).

Acoustic data pre-processing

Zonar calibration largely followed procedures for single beam transducers in Demer et al. (2015), using a 10-mm tungsten carbide sphere with cobalt binding. Calibrations were completed on a regular basis in a purpose-built pool at the Scripps Institution of Oceanography. Transducers were mounted on a plate, which was then rotated and adjusted vertically to detect the position of maximum backscatter.

Volume backscatter was expressed as S_{ν} , computed from the raw voltage counts, following the sonar equation:

$$S_{\nu} = E(R) - \mathrm{SL} - 10\log_{10}\left(\frac{c\tau}{2}\right) - \Psi + 20\log_{10}(d_z) + 2\alpha d_z + G$$

with E(R) the recorded acoustic signal expressed in dB re 1 V, SL the source level in dB, c the sound speed in the ambient fluid medium (m s⁻¹), τ the pulse duration in s, Ψ the equivalent twoway beam angle expressed in steradians (sr or dB re 1 sr), d_z the range from the transducer face to the target (m), α the absorption coefficient, a metric of absorption loss in (dB re 1 m⁻¹), and G the

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on-axis calibration gain in (dB re 1 m). Ambient sound speed and absorption coefficients were computed directly from the *Zooglider* temperature, salinity, and pressure values following Mackenzie (1981) and Francois and Garrison (1982*a*,*b*). To improve data quality, ambient noise conditions and signal to noise ratio ($r_{\rm SN}$) were obtained from measurements of mission-specific dedicated passive ascents and minimum recorded S_v values at range (De Robertis and Higginbottom 2007).

Acoustic target simulations

We determined from Zoocam images that six taxonomic groups likely dominated the scattering of the mesozooplankton in our study site during these missions, namely copepods, chaetognaths, euphausiids, appendicularians, cnidarians, and doliolids/salps (Whitmore et al. 2019). The theoretical scattering properties of these taxonomic groups were approximated through simulations using the distorted wave born approximation (DWBA) (Stanton et al. 1998; Chu and Ye 1999; Stanton and Chu 2000) within the R (R Core Team 2020, v. 4.0.3) package ZooScatR (Gastauer et al. 2019). Key model input parameters for the DWBA are the shape of the target organism (Fig. 1, derived from optical images), length distribution (*L* in mm, also derived from optical data) (Table S3), length to radius ratio

distribution (L/a, derived from optical data) (Table S3) orientation distribution (θ in degree, where 0 is equal to broadside orientation, obtained from literature), ambient sound speed (c in m s^{-1} , calculated from in situ measurements), and sound speed and density contrast distributions (g and h, dimensionless, based on literature values) (Fig. 2; Table S4). A total of 100,000 simulations for each of the available frequencies and each taxonomic group (totaling 1.200.000 simulations) were computed, each drawing a set of parameters from the probability distribution of the given parameter (Fig. 2). Model input shapes were based on a representative group shape derived from an image selected from Zoocam recordings (Fig. 1). The basic shape x and y coordinates were extracted using ImageJ2 (Rueden et al. 2017) with calibrated pixel size. Shape files compatible with ZooScatR require the definition of the target midline coordinates as well as a tapering value, representing the radius of the circular element at each midline coordinate. Distributions of L and L/a were derived from a sample of 404,529 regions of interests (ROIs) from optical Zoocam recordings, identified manually by experts (Table S5). The majority of the ROIs were identified as marine snow (240,239, 59.4%; Whitmore 2019). No distinct category for marine snow was constructed because relatively little is known about the its scattering properties, although there is some



Fig. 1. Representative Zoocam ROIs and simplified shapes used within ZooScatR to simulate the TS of the six taxonomic groups: (a) euphausiids, (b) appendicularians, (c) copepods, (d) chaetognaths, (e) doliolids, and (f) cnidarians.



Fig. 2. Distributions of (a) g, (b) h (dimensionless; from literature), (c) L (mm, derived from optical recordings), (d) L/a (dimensionless, derived from optical recordings), and (e) θ (°, from literature), used as input parameters for the TS simulations for the distorted wave born approximation within ZooScatR. Colored lines designate the six dominant taxa in our study site.

indication that when considering size alone, marine snow should present scattering properties comparable to the presented groups (Briseño-Avena et al. 2018). Distributions of *g* and *h* were based on published values where available (Fig. 2; Table S4). Literature values for *h* were scaled to be valid for a mean observed ambient sound speed (*c*): $h = h_{\text{literature}} \times \frac{C_{\text{literature}}}{c_{\text{observed}}}$ and *g* values were scaled according to the mean observed ambient water density. Summary TS-L equations were established following the general equation $TS = a \log_{10}(L) + b$, where *a* and *b* are the slope and intercept of a linear regression, fitted in linear space (Fig. 3a).

Acoustic data classification

dB differencing is a common method used to partition the received acoustic signal into different groups (Korneliussen 2018). Based on the simulated target strength (TS) values at 1000 and 200 kHz, a synthetic variable TS_{Δ} defined as $TS_{1000 \text{ kHz}} - TS_{200 \text{ kHz}}$ was introduced to explore the frequency dependent relationship of TS and length of the simulated acoustic targets. Three organism size classes were defined: small (0–1 mm), intermediate (1–3 mm), and large (> 3 mm). A probability map (pmTS) for any $TS_{\Delta i}$ ranging from

-15 to 28 dB at 0.5 dB intervals describing the chance that $TS_{\Delta i}$ falls within a particular size class was computed as $P(\text{size class}_i) = \frac{\sum TS_{ji}}{\sum TS_j}$ where $\sum TS_{ji}$ is the sum of TS simulations at a given TS interval *j* within the size class *i*, and $\sum TS_j$ is the sum of TS simulations at a given TS interval *j* (Fig. 3b).

The synthetic variable $S_{\nu\Delta} = S_{\nu 1000 \text{ kHz}} - S_{\nu 200 \text{ kHz}}$ was computed and the pmTS, describing the chance that any given single target contributing to the overall S_{ν} is within a given size class, was applied as a mean proportion. The S_{ν} of the single-beam echosounder is composed of a multitude of unresolvable single targets. While we do not identify single organisms, this method uses probability to evaluate the likely size composition of the multitude of unresolvable single targets with the S_{ν} of the single-beam echosounder.

DVM detection

Each *Zooglider* mission was summarized as a composite echogram with bin sizes of 1 dive by 1 m of depth. Each dive was allocated a time of the day according to the median dive ascent time. GPS location and time of the day were used to split the composite data into day and night sections, based on



Fig. 3. (a) Modeled $TS_{1000} - TS_{200}$ for body lengths ranging from 0.1 to 10 mm, for different taxonomic groups (colored lines) and for the overall mean (black line). 95% confidence intervals indicated by the shaded area. The dashed vertical lines mark the size thresholds for small, intermediate, and large organisms. (b) Percentage contribution of different size classes of acoustic backscatterers to the target strength (TS) at 1000 kHz, as a function of the difference in TS between 1000 and 200 kHz, $TS_{1000} - TS_{200}$.

the local timing of nautical dusk and dawn (12° below/above the horizon). S_{ν} data were then averaged by season (Fig. S1). In order to extract the vertically migrating portion of the scattering organisms from the nonmigrant organisms, we calculated absolute difference in backscattering strength between day and night ($\Delta S_{\nu \text{ Day/Night}}$ [dB re m⁻²]). For each season, a mean daytime S_{ν} ($\overline{S_{\nu \text{ Day}}}$) and a mean nighttime S_{ν} ($\overline{S_{\nu \text{ Night}}}$) value was calculated at 1 m depth intervals, averaged in the linear domain.

 $\Delta S_{\nu \text{ Day/Night}}$ was computed as:

$$\begin{cases} \Delta S_{\nu \text{ Day/Night}} = S_{\nu \text{ Day}} - \overline{S_{\nu \text{ Night}}} \text{ for daylight hours} \\ \Delta S_{\nu \text{ Day/Night}} = S_{\nu \text{ Night}} - \overline{S_{\nu \text{ Day}}} \text{ for nighttime hours} \end{cases}$$

where $S_{\nu Day}$ includes all data between nautical sunrise and nautical sunset, while $S_{\nu Night}$ includes all data between nautical sunset and nautical sunrise. The depth of the vertically migrating layer was detected as the 45th percentile of the cumulative sum from the surface to 400 m, where $\Delta S_{\nu Day/Night}$ >0. $\Delta S_{\nu Day/Night}$ was computed for small, intermediate, and large components of the overall data and corresponding DVM depths were obtained. The 45th percentile was chosen through an iterative process, providing the best fit to the data, based on visual inspection. To reduce bias originating from strong scatterers only present for a brief period of time, $\Delta S_{\nu Day/Night}$ >12 (i.e., 15.8 times the acoustic energy in the linear domain) were set to 12.

Median daytime depths were compared between size classes using a Kruskal–Wallis with Dunn test and Bonferroni correction. Pearson product–moment correlations were used to test for a relationship between the amplitude of DVM and the depth of light penetration (as euphotic zone depth, $Z_{1\%}$ irradiance) or concentration of potential prey. Potential prey concentration was estimated from optically counted ROI (0.25–0.45 mm). We utilize ROIs < 0.45 mm as a proxy for prey availability rather than Chl *a* for two reasons. First, Chl *a* values are already incorporated into the estimate of euphotic zone depth, so the two would not be independent. Second, evidence suggests that the particles detected by *Zooglider* in the water column are a better proxy for food availability to zooplankton in this region than Chl *a*, especially for particles within the euphotic zone (Whitmore 2019; Whitmore and Ohman 2021).

Vertical migration velocities were computed as the variation in depth over time as summarized by a 12° polynomial regression. Timing of DVM descent and ascent was assessed as the time of passage of the 45^{th} percentile layer past 100 m, the approximate midpoint of day and night depths, for each of the three size classes in each season.

Results

Water column properties

Mean water column properties in the upper 150 m of the San Diego Trough (Fig. 4) illustrate a seasonal warming, accompanied by appearance of reduced salinity waters in summer and autumn. This salinity signature indicates intrusion of water from the California Current, via the seasonally developed Southern California Eddy (Lynn and Simpson 1987; Strub and James 2000). At 100 m, the average temperatures fluctuated by less than 1.3°C inter-seasonally with rather stable standard deviation of 0.2-0.5°C. Chl a concentrations were maximal at 40-65 m for all seasons, with the highest concentrations observed in summer and lower concentrations in autumn and winter. The concentration of small particles (0.25 - 0.45 mm)and particles > 0.45 mm ECD were both maximal in summer, with Gastauer et al.



Fig. 4. Seasonal oceanographic descriptors for the San Diego Trough *Zooglider* missions binned by 1 m depth intervals from the surface to 150 m: (**a**) temperature (°C), (**b**) diffuse attenuation coefficient (m⁻¹); dots indicate mean euphotic zone depth, (**c**) salinity, (**d**) Chl *a* (SFU), (**e**) ROIs 0.25–0.45 mm (no. L⁻¹), (**f**) ROIs > 0.45 mm (no. L⁻¹).

peaks at slightly shallower depths than the corresponding Chl *a* maximum, and minimum values in autumn. The larger-sized particles were relatively rare in spring. The

diffuse attenuation coefficient increased in spring and summer, corresponding to the changes observed in Chl a and smaller particles (Fig. 4).

TS-simulations

Target strength varied with body length with taxon-specific differences (Figs. 3a, 5). Consistently steeper slopes (*a*) and lower intercepts (*b*) were found at 1000 kHz for all taxa (Table S6; Fig. 5). All constants *a* and *b* entered the linear model with high significance (p < 0.01) with standard errors < 5%. In the region where $kL_{ac,max} << 1$ (k=wavenumber $=\frac{2\pi}{c}f$ and $L_{ac,max}$ is the extent of the maximum acoustically detectable dimension), Rayleigh scattering is the dominant scattering mechanism, with negligible influence of orientation and shape, with the amplitude proportional to the square of the wavenumber and the volume. At 200 kHz $kL_{ac,max}$ approaches 1 at $L_{ac} \sim 1.20$ mm and at $L_{ac} \sim 0.24$ mm at 1000 kHz. For larger targets, Mie or geometric scattering becomes the dominant process with complex phase variability.

The length-stratified categories of small and intermediate organisms were dominated by copepods, both in terms of numerical densities, as observed by Zoocam (small: 56.2%, intermediate: 49.0%; Table S5) and contributions weighted by

TS at 1000 kHz (small: 96.8%, intermediate: 90.0%; Table S5; Fig. S2a). Differences in contributions between the numerical and TS weighted proportions can be explained by the relatively strong scattering by copepods, compared to the other categories. Large organisms were dominated by chaetognaths in terms of numerical densities, derived from Zoocam images (61.2%) while contributions weighted by TS at 1000 kHz were dominated by cnidarians (73.4%). Cnidarians are stronger scatterers at 1000 kHz when compared to chaetognaths (Figs. 5, S1b; Table S5). TS_{Δ} across the entire range considered of -15 to 28 dB was dominated or showed a strong contribution by the scattering of copepods (Fig. S2b), which can be explained by their high numerical abundance, paired with their relatively strong acoustic scattering at 1000 and 200 kHz when compared to the other groups, with the exception of euphausiids (Figs. 3a, 5). Small scatterers dominated regions where $TS_{\Delta} > 23$ dB, while large scatterers mainly contributed to the scattering for $TS_{\Delta} < -10$ (Fig. 3b). Intermediate-sized targets dominated the TS_{Δ} between small and large.



Fig. 5. Taxonomic group-specific relationships of target strength vs. body length with linear regressions fitted through all simulated acoustic targets at 200 kHz (solid line), 1000 kHz (dashed line), and the difference between 1000 and 200 kHz (dotted line). Shaded regions represent the density of TS values scaled to 1 in each length bin.



Fig. 6. The difference in backscattering strength between day and night ($\Delta S_{\nu \text{ Day/Night}}$; see Methods section) for small, intermediate and large acoustic backscatterers (columns) with indication of DVM depth (lines) for the different seasons (rows). Positive $\Delta S_{\nu \text{ Day/Night}}$ was assumed to be part of a vertical migration. For the "small" size fraction a weakly migrating (dotted line) and a strongly migrating (solid line) layer were recognized.

Diel vertical migration

Size-dependent DVM behavior was detected for all *Zooglider* missions in the San Diego Trough (Figs. 6, S1). For the acoustically classified "small" organisms, two separate but consistent

DVM patterns were observed. One part of the small-bodied acoustic layer remained in the upper 20–40 m layer by day as well as by night, while an-other part showed increased volume backscatter in daytime depths near 150–200 m (Fig. 6). For



Fig. 7. Dependence of daytime depths of each size class (rows) on (left column) euphotic zone depths as a proxy for light availability and (right column) ROIs < 0.45 mm as a proxy for food availability, with accompanying linear regression lines, correlation coefficients, and *p* values.

both intermediate and larger sources of backscatter, the daynight differenced volume backscatter showed pronounced DVM at all seasons (Fig. 6). Median daytime depths for the different size classes and seasons (Table S7) showed that intermediate- and large-sized individuals consistently occurred at deeper average daytime depth (227 ± 4.4 and 245 ± 4.4 m, respectively; mean $\pm 95\%$) than smaller-sized organisms (156 ± 2.4 and 45 ± 1.4 m for small deep and small near-surface, respectively; p < 0.01, Kruskal–Wallis with Dunn test and Bonferroni correction).

Influence of euphotic zone depth and prey availability on daytime depths

We considered variations in euphotic zone depth and prey availability (represented by ROIs < 0.45 mm) as potential explanatory variables for seasonal variability in daytime

depths (Fig. 7). No association of daytime habitat depth of small shallow scatterers was found with either euphotic zone depth or ROIs < 0.45 mm (p > 0.3). In contrast, euphotic zone depth was consistently a significant explanatory variable for the daytime depths of larger backscatterers, with a negative relationship for small deep (R = 0.22, p < 0.01), and a positive relationship for intermediate (R = -0.33, p < 0.01) and large (R = -0.53, p < 0.01) acoustic backscatters (Fig. 7). Most importantly, the strength of the relationship between daytime depth and euphotic zone depth increased with increasing body size, suggesting a stronger dependence of daytime depth on light penetration for the largest organisms. Daytime depths of occurrence of acoustic backscatterers showed much weaker relationships with concentrations of suspended particles, a proxy for food availability (small: R = -0.21, p < 0.01, intermediate: R = 0.14, p = 0.02, and large: R = 0.14, p = 0.01; Fig. 7).

Vertical migration velocities

The velocity of vertical migration varied with time of the day, body size, and season (Fig. 8). Larger scatterers displayed slightly higher speeds of ascent $(-22.4 \pm 3.4 \text{ m h}^{-1}, \text{ mean } \pm 95\%)$ and descent $(25.2 \pm 3.8 \text{ m h}^{-1})$, compared to intermediate scatterers (ascent: $-22.1 \pm 3.5 \text{ m h}^{-1}$, descent: $24.0 \pm 3.7 \text{ m h}^{-1}$). Small deep migrating scatterers showed comparable average vertical migration speeds $(-14.4 \pm 2.2 \text{ m h}^{-1} \text{ and } 16.4 \pm 2.5 \text{ m h}^{-1}$, respectively). Small shallow scatterers showed slow average migration speeds of $-2.9 \text{ and } 2.9 \text{ m h}^{-1}$. Large, intermediate, and small deep migrating scatterers migrated at peak speeds of > 70 to almost 100 m h^{-1} (large: -70.6, 98.9 m h^{-1}; intermediate: -78.8, 94.8 m h^{-1} ; small deep -44.9, 70.4 m h^{-1} , for ascent and descent, respectively). Not surprisingly, the timing of onset of crepuscular ascent and descent varied directly with time of year and day length (Fig. 8).

DVM timing

During morning descent, intermediate and larger backscatterers passed the mid-point of daytime diving depths (100 m) considerably earlier than smaller backscatterers, averaging -0.4 to -3.7 h difference depending on the season (Fig. 9). The timing of evening ascent showed the inverse pattern, with intermediate and larger organisms ascending 0.2–1.6 h later than the small backscatterers (Fig. 9). Hence, smaller migratory backscatterers had a longer residence time in surface waters, while intermediate and large backscatterers transited to surface waters later in the afternoon and transited to deeper water earlier in the morning.

Discussion

Modeling of acoustic scatterers

As acoustic targets, zooplankton generally are referred to as weak, fluid-like scatterers (Stanton et al. 1998; Stanton and Chu 2000). Our modeling shows that linking taxonomic composition or size classes with acoustic returns using only the two



Fig. 8. Vertical migration velocities as a function of time of day for the different seasons and size classes summarized by a polynomial regression (black lines; 95% Cl = colored area). Black shaded area indicates night in the given season, lighter gray shading indicates the transition to dusk or dawn. Solar noon is indicated by a black vertical line and the vertical velocity of 0 is shown as a dotted horizontal line.

present frequencies is challenging. However, the availability of independent, optical Zoocam assessments of the composition of the zooplankton in the water column helped constrain the problem. This information permitted us to simulate many acoustic targets, with varying model parameter values, assuming the phases from individual targets are random, and neglecting the effects of attenuation or multipath scattering. Assuming that the sum of the echo energy from individual scatterers (computed over a range of model input variables) is equal to the aggregation scattering (Lavery et al. 2007), we could then infer the most likely sources of backscatter at different dB-differenced levels of return. Accordingly, of the six dominant taxonomic groups in our system, we found that the Zonar acoustic backscatter in this study region is likely to be disproportionately dominated by the sound scattered by copepods (Fig. S2a,b), although other taxa also contribute (Table S5). Fast swimming species such as adult euphausiids could potentially have avoided the glider and therefore introduced a bias toward slower swimming organisms, although a previous study detected no evidence of avoidance by euphausiids or other organisms (Whitmore et al. 2019), perhaps due to the hydrodynamically efficient design of the glider hull and camera system, combined with the low detectability of red illumination (Ohman et al. 2019).

Behavioral differences between small and large scatterers

Daytime depths and vertical migration speeds of large, intermediate, and small scatterers differed, with progressively shallower depths, smaller DVM amplitudes, and slower migration speeds with diminishing size. The increased DVM amplitudes of larger-bodied organisms are in agreement with previous net-based studies (Steinberg et al. 2008; Ohman and Romagnan 2016) and model predictions (Pinti et al. 2019) for different sized copepods. In experimental mesocosms, copepods increased their daytime depth and amplitude with increasing developmental stage and size (Huntley and Brooks 1982).

The onset of the descent and ascent 1–2 h before sunrise and sunset is in accord with other observations (Cisewski et al. 2021). Daytime migration depths are also consistent with previous acoustic studies (Ursella et al. 2018; Guerra et al. 2019). Vertical migration speeds are in agreement with studies analyzing the vertical migration speeds of zooplankton mainly dominated by copepods (Wiebe et al. 1992; Heywood 1996; Cisewski et al. 2021). Previous studies in high latitudes have found a negative relationship between length of day and vertical migration speed and a positive relation to daytime depth (Tarling et al. 2002; Cisewski et al. 2021). We did not observe similar, clear seasonal patterns in vertical velocities, which may have



Fig. 9. Body size-dependent times of transit past the 100 m depth horizon for four seasons during the (**a**–**d**) descent and (**e**–**h**) ascent phase of DVM. The center line in the boxplots represents the median, the upper line is the 75% and the lower the 25% quantile, with whiskers indicating the smallest or largest value within 1.5 times the interquartile range above the 75th percentile.

been due to the more limited variations in duration of daylight and transition times from light to dark at the moderate latitude ($\sim 32.9^{\circ}$ N) of the present study.

Particularly illuminating was the dependence of the timing of onset of upward and downward migrations on the body size of the acoustic scatterers. Benoit-Bird and Moline (2021) inferred that much larger, nektonic organisms detectable at low acoustic frequencies over a 6 d study also showed a sizedependent timing of DVM. In our study, the smallest migratory scatterers migrated toward surface waters earlier before dusk and migrated into deeper waters later in relation to dawn than the intermediate and large scatterers. This pattern held at all times of year. This body size-dependent pattern of migration timing was detected acoustically in a fjord population dominated by the euphausiid Euphausia pacifica (De Robertis et al. 2000) and numerically modeled by De Robertis et al. (2000). Our results, based on backscatterers dominated by copepods, are consistent with the overall pattern in De Robertis et al. (2000) and suggest that body size-dependent predation risk is a strong selective agent that influences the optimal migration timing for different types of zooplankton. The nearly continuous, autonomous measurements by Zooglider made it possible to acquire data at the high temporal resolution that is needed to resolve such timing offsets with body size.

Relationships with predictor variables

Daytime depths of all migrating size groups showed a significant correlation with depth of the euphotic zone, a metric of water clarity. Small migratory backscatters showed a weak negative relationship with euphotic zone depth, while intermediate and large scatterers exhibited a progressively stronger positive relationship with euphotic zone depth. We interpret the differences among size classes to again reflect differential susceptibility of different zooplankton size classes to the risk of predation by visual predators. Increasing optical clarity results in larger encounter distances with prey of a given size, which is particularly pronounced for larger-bodied zooplankton (Aksnes and Giske 1993). Hence, for the intermediate- and larger-bodied organisms, the daytime habitat depth deepens in clearer waters in order to diminish this risk. The smallbodied migrators also descend subsurface at depth, with no evidence of reverse DVM (Ohman 1990), suggesting a lightmediated predation risk but of lesser magnitude than for larger, more visually conspicuous prey. We find it somewhat surprising that, having selected a daytime depth, the specific depth chosen by smaller migrants varies weakly, but negatively with euphotic zone depth. This phenomenon probably reflects a nonlinear photo-tactic response, where smallerbodied organisms descend from illuminated surface waters to avoid predation risk, but are weakly attracted to diffuse irradiance once at depth (cf., Aksnes and Ohman 1996; De Robertis et al. 2000; Ohman and Romagnan 2016; Fakhraee et al. 2020). Experimental assessment of size- and taxonspecific light responses is needed to address this issue. Previous studies have found the optical attenuation coefficient (Ohman and Romagnan 2016; Pinti et al. 2019) and water clarity (Steinberg et al. 2008) to be related to DVM amplitude and residence depths.

Our use of particles < 0.45 mm ECD as a proxy for food available to particle-grazing and flux-feeding zooplankton is supported by recent results that this quantity is a better descriptor of mesozooplankton habitat depths—and presumably grazing activity—in this study site than is Chl a (Whitmore 2019; Whitmore and Ohman 2021). The optically resolved particles include microzooplankton and smaller marine snow, as well as living photoautotrophs, all of which can be important dietary constituents for suspension-feeding zooplankton.

Study limitations

Lacking direct sampling of the organisms detected acoustically, our scattering models are based on imperfect assumptions and do not reflect the full variability of species, shape, or body composition observed in nature (Chu et al. 2003; Bairstow et al. 2021). Beyond our general classification as predominantly large, intermediate, and small, we do not know the actual sizes of the organisms detected. In addition, zooplankton species composition could have departed from the mean for any specific dive or Zooglider mission. Furthermore, there are many exceptions to most body size-based rules, where other traits can modify DVM behavior. However, we found the behaviors for these acoustically resolved size classes to be surprisingly consistent across seasons. We believe that the modeling approach used here reinforces the importance of body size and illustrates how acoustic target strength models can be aided by in situ imaging. Further studies are needed to link taxonomic group and size information obtained from optical images with acoustic data. Acoustic inversion remains a challenging topic (Lavery et al. 2007).

Implications in relation to climate change

The factors identified here associated with the depth distributions of mesozooplankton are projected to themselves be altered by climate change. The southern California Current System has undergone long-term shoaling of the euphotic zone and increasing concentrations of Chl a (Aksnes and Ohman 1996; Kahru et al. 2018). Modeling predicts that despite limited changes in wind-driven upwelling in these latitudes, primary production is likely to increase in association with elevated nutrient concentrations on deeper isopycnal surfaces (Rykaczewski and Dunne 2010). Our results suggest that more productive waters associated with a shoaling of the euphotic zone will lead to a shallower depth distribution of

intermediate and larger-sized zooplankton, which tend to be disproportionately significant to zooplankton-mediated biogeochemical export (Kelly et al. 2019).

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Conflict of Interest

None declared.

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