The potential role of turbulence in modulating the migration of demersal zooplankton

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Abstract
Despite suggestions that turbulence can affect the migration of zooplankton, field observations of such effects are scarce. This is especially the case for bottom-associated (demersal) zooplankton that reside in the typically turbulent near-bottom environment. Using moored sensors deployed at two coastal sites in the North Pacific and the Red Sea, we present observations of the effects of turbulence on the nocturnal emergence of demersal zooplankton. A cabled observatory consisting of a plankton camera, an acoustic current profiler and environmental sensors, was deployed near bottom in 20 m of water near Oshima Island, Japan. Observations were also obtained from a second site near a coral reef in 16 m of water in the Red Sea. Acoustic backscatter data obtained from current profilers at both sites provided a proxy for zooplankton density. Combined with simultaneous estimates of turbulence intensity, the observations suggest that the nocturnal emergence of demersal zooplankton was hindered by elevated levels of turbulence. While our findings are inferred from acoustic data, agreement between the two different sites supports our hypothesis that demersal zooplankton may remain near the bed during times of strong turbulence.

Diel vertical migration of zooplankton is thought to be the greatest animal migration on the earth (Brierley 2014; Behrenfeld et al. 2019). Those migrations substantially affect key processes in the ocean, including predator–prey interactions (Ringelberg 2010), dispersal (Ayón et al. 2008), and vertical fluxes of organic matter (Steinberg and Landry 2017). Understanding the processes that control diel vertical migrations is thus of great importance.

Turbulence, a ubiquitous characteristic of the oceanic environment, greatly affects swimming behavior, feeding, and escape of zooplankton (Kiørboe 2008). While enhanced microscale turbulence may increase encounter rates of zooplankton with their prey and mates (Rothschild and Osborn 1988; Yamazaki et al. 1991; MacKenzie and Kiørboe 2000), an exposure to high turbulence can prevent zooplankton from detecting approaching predators, hence increasing their predation risk (Gilbert and Buskey 2005). Based on biophysical simulations, Visser et al. (2009) concluded that an avoidance of regions of strong turbulence should be the most advantageous for zooplankton reproduction. Indeed, substantial reductions of zooplankton density have been often observed in turbulent layers of a few to tens of meters in thickness, suggesting that zooplankton actually exhibit turbulence avoidance strategies in the field (Visser et al. 2001; Maar et al. 2006; Tanaka 2019).

Previous studies on the effects of turbulence on zooplankton migration have largely been confined to zooplankton in the energetic upper ocean, rendering unknown the effect of turbulence on another important group, the demersal zooplankton. This group consists of bottom-associated zooplankton that usually seek shelter in the seabed during the day and emerge to the water column during the night (Alldredge and King 1980; Vereshchaka 1995; Yahel et al. 2005). In shallow, complex habitats such as coral reefs, demersal zooplankton comprise a substantial proportion of the total zooplankton biomass found in the water column during the night (Yahel et al. 2005).

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Turbulence is created across the boundary layer by a variety of physical processes, including internal gravity waves, wind stresses, and sea surface cooling (Fig. 1). Turbulent Kinetic Energy (TKE) dissipation rate, a proxy for the intensity of microscale turbulence, ranges from $10^{-9}$ to $10^{-4}$ W kg$^{-1}$ in shallow coastal waters (Fig. 1). In the open ocean, the levels of turbulence away from the surface and bottom boundary layers are generally low (Fig. 1).

In this study, we examined the effect of turbulence on the emergence of demersal zooplankton in two different types of habitats, a subtropical rocky bottom in the North Pacific and a coral reef in the Red Sea. We found that zooplankton abundances were reduced during times of strong turbulence.

Methods
Cabled observatory

Our first site was located in a coastal area near Oshima Island, Japan (Fig. 2a), ~30 km offshore mainland Japan, ~100 km north of the Kuroshio Current. The sea around the island is oligotrophic (Takahashi et al. 1980). Typhoons typically pass near or over the island during summer and fall.

A cabled observatory system, Oshima Coastal Environment data Acquisition Network System (hereafter OCEANS), was deployed near the southeastern tip of the island in 20-m water depth (34°4′10″N, 139°26.7′E) (Fig. 2c,e). The configuration of OCEANS is described in Yamazaki et al. (2016). The observatory system was attached to a large flat block (1 m in height) placed on the bottom and carried a plankton camera (Continuous Plankton Imaging and Classification System; hereafter CPICS) to observe the in situ zooplankton community. An Aquadopp acoustic current profiler, (400 kHz, Nortek AS) was also used to quantify zooplankton abundance. Additionally, OCEANS was equipped with an Acoustic Doppler Velocimeter (ADV, Nortek AS), a pressure sensor, and Photosynthetically Active Radiation (PAR) sensor.

CPICS’s image volume was $11.0 \times 15.0 \times 2.0$ mm in size (0.33 mL), and images were acquired at 3 Hz with the smallest detectable object being 100 μm in diameter. Zooplankton in the images were manually classified down to the order level. The emergence rate of each taxon (individuals h$^{-1}$) was converted to density (individuals L$^{-1}$) based on the hourly sampling volume (~3.6 L). As a white-light strobe was used for illumination of CPICS, it likely attracted phototactic zooplankton toward the strobe during the night, rendering overestimation of zooplankton densities (Tanaka et al. 2019). Therefore, we used the acoustic backscattering intensity measured with the Aquadopp to estimate zooplankton abundance.
at this site. Range-normalized acoustic backscatter intensity (dB) was obtained based on acoustic-spreading and water-absorption models as in Lohrmann (2001). The Aquadopp was set to record in ensemble intervals of 10 min (60 pings per ensemble) in 1-m bins in the vertical water column above (Fig. 2c). Demersal zooplankton typically show complicated distribution patterns at scales of several meters, and their behavioral patterns can differ among layers at different depths (Allardige and King 1985; Holzman et al. 2005). Therefore, two layers were analyzed: one was the closest to the bottom (4–5 m above bottom, hereafter “MAB”) and the other at the center of the water column (10–11 MAB). Acoustic data were continuously recorded from 12 August to 30 November 2014. Due to technical problems, CPICS images were recorded only from 20 September to 30 October 2014.

**Eilat observatory**

Our second study site was a tropical coral reef in the Gulf of Aqaba, Red Sea (29°30.0′N, 34°55.0′E) (Fig. 2b). Sea conditions were typically calm, with <0.3-m surface wave heights, <1-m tidal range, and 0.1 m s⁻¹ average current speeds (Reiss and Høttinger 1984; Reidenbach et al. 2006). The gulf is semi-oligotrophic, with surface chlorophyll concentrations ranging from 0.05 μg L⁻¹ during summer to >0.5 μg L⁻¹ during the spring bloom. This dynamic is driven by an unusually deep (300–800 m) convective mixing during the winter (Genin et al. 1995; Zarubin et al. 2017). Sea surface temperature ranges from 21°C in winter to 28–29°C in summer. Our study site was located at the fringing coral reef on the Nature Reserve of Eilat. The bottom topography at this site is steep, with water depth reaching 500-m depth ~3 km offshore. A description of the flourishing reef at the study site is found in Yahel et al. (2005) and references therein. The diverse reef is dominated by stony and soft corals, and high abundance of mollusks, echinoderms, ascidians, and sponges (Yahel et al. 2005). Benthic algae are sparse during the warm month with seasonal increase during winter–spring, depending on the depth of the mixed layer during the winter (Genin et al. 1995).

The zooplankton assemblage at this study site was dominated (70–80%) by copepods during day and by demersal amphipods, decapods and myids during the night (Echelman and Fishelson 1990; Yahel et al. 2005). The total zooplankton biomass found above the reef during the night was 5–10 times higher than that found during the day (Yahel et al. 2005), especially among large zooplankters (body length >710 μm).

We used the data obtained by a coastal observatory system (hereafter “Eilat Observatory”), described by Yahel et al. (2005). Briefly, an upward-looking ADCP (600 kHz, RDI) was mounted on the coral bottom on a tripod in a water depth of 16 m (Fig. 2d). Backscatter counts were converted to acoustic backscatter intensity using models (Lohrmann 2001). The difference between the 600 kHz used for Eilat Observatory and 400 kHz used for OCEANS could result in difference in detectable zooplankton size ranges. Assuming a typical sound speed ~1500 m s⁻¹, the theoretical sound wavelengths can be calculated as 2.5 and 3.75 mm for 600 and 400 kHz, respectively. While such wavelengths could be associated with the minimum detectable zooplankton size, relationship between acoustic frequency and the detectable size rage is not well defined. However, the acoustic frequencies of 400 and 600 kHz are high enough to observe dynamics of subcentimeter zooplankton (Flagg and Smith 1989). We thus assume that the size ranges detectable by those current profilers were the same. The ADCP was set to record in ensemble intervals of 10 min (1000 pings per ensemble) and 1-m bins. Data recording lasted for over 2 months (16 February to 4 May 2000) (fig. 5e in Yahel et al. 2005). Two layers, one at 2–3 MAB and the other at middle of the water column (7–8 MAB) were analyzed to compare with the OCEANS data.

A comparison of the acoustic backscatter intensity with observed zooplankton density was carried out at our study site in Eilat during 13–16 October 2002 (Yahel et al. 2005). A multibeam 1.6 MHz echo sounder “FishTV” (Fig. 2d), designed for acoustic counting of in situ zooplankton (Jaffe et al. 1995; Genin et al. 2005), was used for this comparison. A significant linear relationship was found between the acoustic backscatter intensity and zooplankton density ($r^2 = 0.48, p < 0.01$) from measurements made at 2–3 MAB (fig. 4 in Yahel et al. 2005).

**Turbulent kinetic energy dissipation rate**

We estimated TKE dissipation rates ε (W kg⁻¹), a parameter typically used to quantify turbulence intensity (Smyth and Moum 2019). While there is a variety of direct and indirect methods to estimate ε, the “law of wall” method was applied to our data sets. In the bottom mixed layer where the mean velocity field is greatly affected by the no-slip bottom boundary condition, ε may be expressed as follows (e.g., Thorpe 2005):

$$
\varepsilon = \frac{u_*^3}{\kappa h}
$$

where $u_*$ is the friction velocity (m s⁻¹), $\kappa$ is the von Karman constant (~0.41), and $h$ is the height above the bottom (m). Here, the friction velocity $u_*$ is a representative velocity scale associated with bottom friction, calculated from the mean velocity measured by the ADV or ADCP for each site. For OCEANS, significant wave height $H_s$ (Rychlik 1996), estimated from the pressure sensor, was incorporated into the calculation of $u_*$ as the water body was strongly affected by both waves and mean currents. Procedures for calculating $u_*$ under this combined action of surface waves and mean currents are detailed in Drost et al. (2018). In general, high levels of tidally driven currents and high $H_s$ will result in high levels of ε. TKE dissipation rate ε as well as the other parameters were calculated and averaged over 1-h periods.

However, for the North Pacific site, acoustic records were substantially contaminated by acoustic reflection from mineral grains resuspended during typhoon events with $H_s$ larger.
than 1 m (Supporting Information Figs. S1, S2, and S3). As the focus will be kept on zooplankton, acoustic backscatters and camera records acquired with $H_s > 1$ m were not included in the statistical analyses for this site.

**Statistical analyses**

Potential role of near-bed turbulence on demersal zooplankton abundance was examined with generalized linear model (GLM). First, acoustic backscatter and $\varepsilon$ values were classified into two time categories (night and day) and two depth categories (lower and upper layers). By doing so, we can examine potential interactions among time and depth. However, autocorrelation within our time-series could violate the basic assumption of GLM. To overcome this problem, we averaged the observed acoustic backscatter within several $\varepsilon$ intervals for each combination of time and depth categories prior to applying GLM. The 14 $\varepsilon$ intervals were equally spaced using logarithmic scale between $10^{-11}$ and $10^{-4}$ W kg$^{-1}$. This division resulted in different sample sizes among the $\varepsilon$ intervals. Intervals with < 20 measurements, equivalent to 20 h, were omitted. The averaged acoustic backscatter was used as the response variable ($y$) for the GLM:

$$f(y) = \beta_1 + \beta_2 x + \beta_3 D + \beta_4 T + \beta_5 xD + \beta_6 xT + \beta_7 DT$$  \hspace{1cm} (2)

where $f$ is the link function, $\beta$ values are coefficients, $x$ is decimal logarithm of $\varepsilon$, $D$ is depth category, and $T$ is time category. For simplicity, $D$ and $T$ values were set as dummy variables, where $D = 0$ ($D = 1$) denotes lower (upper) layer, and $T = 0$ ($T = 1$) indicates nighttime (daytime). Submodels can be easily obtained by switching $T$ and $D$, expressing different conditions. For example, for the case “lower layer, nighttime”, the model of Eq. 2 is deformed into $f(y) = \beta_1 + \beta_2 x$ because the third to seventh terms become zero ($D = T = 0$). For error distribution, we employed Gaussian distribution with identity link function $f(y) = y$.

A similar GLM analysis was applied for zooplankton abundance (individuals h$^{-1}$), using the same $\varepsilon$ intervals and omitting intervals with < 20 measurements. We used gamma error distribution because zooplankton abundance is always positive. Zooplankton abundance was analyzed with logarithmic link function $f(y) = \ln(y)$ as well as identity link function $f(y) = y$. Results from the both link functions were compared.

**Results**

**OCEANS**

TKE dissipation rates $\varepsilon$ at the layer 4–5 MAB fluctuated within a range of $10^{-8}$ to $10^{-6}$ W kg$^{-1}$, and the average was $\varepsilon = 2 \times 10^{-7}$ W kg$^{-1}$ (Supporting Information Fig. S1b), typical for such near-bed layers (Fig. 1). Acoustic backscatter typically ranged from 55 to 65 dB (Supporting Information Fig. S1c) and showed a marked increase during the night at both the 4–5 and 10–11 MAB layers (Fig. 3a,b). A time lag in response of about 40 min between the two layers was found around dawn (Fig. 3b). Given the distance between the layers (~ 6 m), this implied a predawn descent speed of about 0.25 cm s$^{-1}$. An undetectable time lag around dusk indicates ascent speed was much faster than that for dawn period (Fig. 3a).

Over 3000 individuals belonging to 15 taxa were identified from the CPICS records (Fig. 4; Table 1). Nine of the taxa were observed only during the night, likely consisting of demersal zooplankton (hereafter, migrating taxa) (Fig. 4a–i; Table 1). Six taxa were observed during both night and day, likely consisting of a mixture of demersal and nondemersal species (hereafter, nonmigrating taxa) (Fig. 4j–o; Table 1). The dominant taxa were calanoid copepods during the day and ostracods and mysids during the night (Table 1). The mean (± SD) density of the migrating taxa during the night was 1.92 (± 2.91) individuals L$^{-1}$, more than five times larger than that of the nonmigrating taxa during the night (0.35 ± 0.68 individuals L$^{-1}$), and an order of magnitude higher than the density of the nonmigrating taxa during the day (0.18 ± 0.31 individuals L$^{-1}$). While the use of the white-light strobe may induce bias in zooplankton density during the night, the images clearly showed the emergence of typical demersal taxa around OCEANS (Fig. 4; Table 1).

Results from the GLM analyses showed the dependence of nocturnal acoustic backscatter on $\varepsilon$. The coefficient $\beta_2$ denotes...
Fig. 4. Images of zooplankton obtained with the plankton camera CPICS at the OCEANS site, Oshima Island (Fig. 2a,c,e). The migrating taxa consisted of ostracods (a), mysids (b), polychaetes (c), decapods (d), chaetognaths (e), monstrilloid copepods (f), amphipods (g), isopods (h), and cumaceans (i), whereas the non-migrating taxa consisted of calanoid copepods (j), larvaceans (k), harpacticoid copepods (l), cyclopoid copepods (m), poecilostomatoid copepods (n), and hydrozoans (o). Scale bar 4 mm for all images, except for the harpacticoid copepod (2 mm).

Table 1. Relative abundances of different zooplankton taxa at the OCEANS site, Oshima Island (Fig. 2a,c). The second column indicates the animal types: Holoplanktonic (H), demersal (D), and mixed (M). The third column indicates the relative abundance of each taxonomic group in the entire data set. The fourth column indicates the proportion appearing during the night. Number of records for each taxon is shown in the fifth column. Type definitions are based on the literature (Sale et al. 1976; Heidelberg et al. 2004; Melo et al. 2010). The use of white-light strobe may induce bias in our nocturnal camera records.

| Taxa                | Type | Relative abundance (%) | Night time appearance (%) | Number of records |
|---------------------|------|------------------------|---------------------------|------------------|
| Migrating taxa      |      |                        |                           |                  |
| Ostracod            | D    | 22.8                   | 100.0                     | 706              |
| Mysid               | D    | 20.0                   | 99.8                      | 620              |
| Polychaete          | M    | 8.6                    | 98.9                      | 266              |
| Decapod             | D    | 8.6                    | 100.0                     | 265              |
| Chaetognath         | M    | 5.6                    | 100.0                     | 172              |
| Monstrilloid copepod| M    | 4.5                    | 95.6                      | 138              |
| Amphipod            | D    | 4.3                    | 99.1                      | 133              |
| Isopod              | D    | 1.6                    | 95.7                      | 51               |
| Cumacean            | D    | 1.1                    | 96.3                      | 35               |
| Total               |      | 77.1                   | 99.4                      | 2386             |
| Nonmigrating taxa   |      |                        |                           |                  |
| Calanoid copepod    | H    | 11.1                   | 65.1                      | 345              |
| Larvacean           | H    | 4.2                    | 79.8                      | 130              |
| Harpacticoid copepod| M    | 2.7                    | 75.0                      | 84               |
| Cyclopoid copepod   | M    | 2.0                    | 59.2                      | 61               |
| Poecilostomatoid copepod | M | 1.8 | 68.3 | 57 |
| Hydrozoan           | H    | 1.0                    | 60.6                      | 32               |
| Total               |      | 22.8                   | 68.8                      | 709              |
the slope of acoustic backscatter against \( x = \log_{10} \varepsilon \) for the case “lower layer, nighttime” \((D = T = 0)\) (Fig. 5c). The coefficient was estimated as \( \beta_2 = -1.23 \) (Table 2). The theoretical probability that exceeds the absolute \( t \)-value of 3.96 was \( p = 0.002 \) (Table 2), indicating a negative effect of \( x \) on the nocturnal acoustic backscatter recorded at 4–5 MAB. Such negative effect is well visualized in Fig. 5c, showing the submodel \( f(y) = \beta_1 + \beta_2 x \) and the observed data.

We then examined the difference in the effects of \( x \) on acoustic backscatter during the night and during the day by comparing the slopes for the case “lower layer, nighttime” and “lower layer, daytime”. Here the GLM was deformed into \( f(y) = \beta_1 + \beta_4 + (\beta_2 + \beta_6)x \) for the latter case \((D = 0 \text{ and } T = 1)\), with the coefficient \( \beta_6 = 1.04 \) indicating the difference in slopes between day and night. The \( p \)-value for \( \beta_6 \) was \( p = 0.013 \) (Table 2), indicating a significant difference of the slopes between day and night. Additionally, the positive \( \beta_6 \) value means compensation of the negative slope of \( \beta_2 = -1.23 \). The net slope for the case “lower layer, daytime” was \( \beta_2 + \beta_6 = -0.19 \) (Table 2). Such compensated slope can be seen in Fig. 5a.

Similarly, we examined the effect of depth on the slopes. The model becomes \( f(y) = \beta_1 + \beta_3 + (\beta_2 + \beta_5)x \) for the case “upper layer, nighttime” \((D = 1 \text{ and } T = 0)\). The coefficient \( \beta_5 \) means the difference in slopes between lower and upper layers (Fig. 5c,d). The coefficient \( \beta_5 \) was \( \beta_5 = -0.61 \), not statistically different from zero \((p = 0.112; \text{ Table 2})\).

Our GLM analysis was also applied for the migrating zooplankton taxa observed during nighttime (Fig. 4a–i; Table 1). Unlike for the acoustic backscatter, we only had a submodel \( f(y) = \beta_1 + \beta_2 x \) for this analysis since the migrating taxa were observed near the bottom at 2 MAB mostly during nighttime (Table 1). The observed data points, even though the sample size was only 4, looked well fitted with both the logarithmic and identity link functions (Fig. 6). While the observed trend was quite linear and well fitted with the identity link function (Fig. 6b), we speculated that a realistic error range was provided by the logarithmic link function (Fig. 6a). The \( \beta_2 \)
Table 2. Coefficients of the generalized linear model Eq. 2 for acoustic backscatter observed by OCEANS and Eilat Observatory. Variable \( x \) denotes decimal logarithm of turbulent kinetic energy dissipation rate \((x = \log_{10} \varepsilon)\). Variable \( D \) and \( T \) are dummy variables for depth and time categories, respectively. Here, \( D = 0 \) \((D = 1)\) denotes lower (upper) layer, and \( T = 0 \) \((T = 1)\) means nighttime (daytime). The coefficients are derived from the data in Fig. 5.

| Coefficient | Variable | OCEANS | Eilat Observatory |
|-------------|----------|--------|-------------------|
| \( \beta_1 \) | \((\text{Intercept})\) | 52.47 2.11 24.88 \(< 0.001\) | 95.55 4.24 22.56 \(< 0.001\) |
| \( \beta_2 \) | \( x \) | \(-1.23\) \(0.31\) \(-3.96\) \(0.002\) | \(-3.89\) \(0.58\) \(-6.75\) \(< 0.001\) |
| \( \beta_3 \) | \( D \) | \(-5.53\) \(2.54\) \(-2.18\) \(0.048\) | \(-8.69\) \(4.37\) \(-1.99\) \(0.058\) |
| \( \beta_4 \) | \( T \) | \(4.90\) \(2.44\) \(2.01\) \(0.066\) | \(0.82\) \(4.51\) \(0.18\) \(0.857\) |
| \( \beta_5 \) | \( x D \) | \(-0.61\) \(0.36\) \(-1.71\) \(0.112\) | \(-0.63\) \(0.57\) \(-1.12\) \(0.273\) |
| \( \beta_6 \) | \( x T \) | \(1.04\) \(0.36\) \(2.89\) \(0.013\) | \(1.58\) \(0.61\) \(2.60\) \(0.015\) |
| \( \beta_7 \) | \( D T \) | \(0.71\) \(0.54\) \(1.31\) \(0.211\) | \(2.96\) \(1.37\) \(2.15\) \(0.041\) |

**Fig. 6.** Turbulent kinetic energy dissipation rate \( \varepsilon \) vs. migrating taxa (individuals \( \text{L}^{-1} \)). Each dot denotes the summarized (averaged) data within each \( \varepsilon \) intervals. Thick lines denote the generalized linear model Eq. 2 for the case “lower layer, nighttime” \((D = T = 0)\), derived with (a) logarithmic link function \( f(y) = \ln(y) \) and (b) identity link function \( f(y) = y \), respectively. Shaded areas denote 95% confidence intervals estimated from gamma error distribution. Coefficients for the models are summarized in Table 3.

Table 3. Coefficients of the generalized linear model Eq. 2 for the migrating zooplankton taxa with the logarithmic link function \( f(y) = \ln(y) \) and the identity link function \( f(y) = y \). Variable \( x \) denotes decimal logarithm of turbulent kinetic energy dissipation rate \((x = \log_{10} \varepsilon)\). We only have a submodel \( f(y) = \beta_1 + \beta_2 x \) for the case “lower layer, nighttime” \((D = T = 0)\) since the migrating taxa were observed near the bottom at 2 MAB mostly during nighttime (Table 1). The coefficients are derived from the data in Fig. 6.

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**OCEANS**

| Link function | Coefficient | Variable | Estimate | SE  | \( t \)-Value | \( p \)-Value |
|---------------|-------------|----------|----------|-----|--------------|--------------|
| \( f(y) = \ln(y) \) | \( \beta_1 \) | \((\text{Intercept})\) | \(-11.11\) | \(2.58\) | \(-4.30\) | \(0.050\) |
| | \( \beta_2 \) | \( x \) | \(-1.80\) | \(0.40\) | \(-4.55\) | \(0.045\) |
| \( f(y) = y \) | \( \beta_1 \) | \((\text{Intercept})\) | \(-16.94\) | \(1.14\) | \(-14.86\) | \(0.004\) |
| | \( \beta_2 \) | \( x \) | \(-3.00\) | \(0.20\) | \(-15.21\) | \(0.004\) |

Eilat Observatory

TKE dissipation rate \( \varepsilon \) typically ranged from \(10^{-9}\) to \(10^{-5}\) \(\text{W kg}^{-1}\) (Supporting Information Fig. S4a). The typical range of acoustic backscatter was \(100–150\) dB (Supporting Information Fig. S4b). Acoustic backscatter showed slight time lags of \(~10\) min between the layers at \(2–3\) and \(7–8\) MAB for both dusk and dawn (Fig. 3c,d). Given the distance between the layers \(\sim 5\) m, the implied bulk swimming speed was 0.83 cm s\(^{-1}\) for both periods.

The GLM analyses showed the relationship between acoustic backscatter and the environmental conditions (i.e., turbulence, depth, and time), and the results were similar to those from OCEANS. The coefficient \( \beta_2 \), which is the bulk slope of acoustic backscatter against \( x \), was \( \beta_2 = -3.89 \) (Table 2). The \( p \)-value for \( \beta_2 \) was \( p < 0.001 \) (Table 2). This clearly suggests a negative effect of \( x \) on the nocturnal acoustic backscatter recorded near the bed (Fig. 5g). Additionally, the coefficient \( \beta_6 \), which means the difference in slopes between daytime and nighttime, was \( \beta_6 = 1.58 \), where the \( p \)-value was \( p = 0.015 \) (Table 2). This suggests a significant difference in slopes between daytime and nighttime, while the case “lower layer, daytime” \((D = 0 \text{ and } T = 1)\) had a negative slope against \( x \) (Fig. 5e) unlike for OCEANS. Finally, the coefficient \( \beta_5 \), which indicates the difference in slopes
between different depths, was not statistically significant ($p = 0.273$; Table 2).

The key coefficients, $\beta_2$, $\beta_5$, and $\beta_6$, which are associated with the model slopes, were found to be similar for OCEANS and Eilat Observatory in terms of statistical significance (Table 2). The other coefficients, $\beta_1$, $\beta_3$, $\beta_4$, and $\beta_7$, are related to the model intercepts. Since the intercepts are affected by both backscatter levels and slopes, we speculate that those coefficients are less useful than slopes for understanding zooplankton dynamics.

**Discussion**

A significant decrease in zooplankton densities with increasing TKE dissipation rates was observed during the night at our two study sites in the Pacific Ocean and the Red Sea. This observation, detected in the near-bottom layer (< 10 MAB), likely reflects an avoidance of emergence by demersal zooplankton under conditions of strong near-bottom turbulence. A similar trend found at two sites that markedly differ in their taxonomic composition (ostracods and mysids in the North Pacific site and amphipods, decapods, and mysids in the Red Sea site) may indicate that the observed hindrance of emergence under high turbulence levels is a general phenomenon.

Demersal zooplankton are typically associated with specific type of habitats, such as coral heads and patches of sandy bottom (Alldredge and King 1977). The avoidance of ascent into turbulent waters during the night minimizes the risk of being swept away toward undesirable habitats, as the individuals remain in viscous boundary layers (~ several millimeters in thickness) where both the turbulent and flow speeds are drastically reduced (Reidenbach et al. 2006). At the same time, such avoidance could be disadvantageous as the individual zooplankters remain in the food-depleted layer (Yahel et al. 1998). Ecological consequences of such turbulence avoidance are unknown. However, given that demersal zooplankton could be a key group for the trophic transfer throughout different trophic levels (i.e., from phytoplankton to pelagic fish) in coastal zones (Alldredge and King 1977; Vereshchaka 1995; Steinberg and Landry 2017), the effects of turbulence avoidance could be substantial.

Substantial descents of holoplankton triggered by near-surface turbulence have also been observed in the ocean (Lagadec et al. 1997; Incze et al. 2001; Visser et al. 2001; Maar et al. 2006; Tanaka 2019). Negative correlations between acoustic backscatter and $\varepsilon$ was also found during the day at the Eilat Observatory (Fig. 5e,f), where the source of acoustic backscatter was mainly copepod species (Echelman and Fishelson 1990; Yahel et al. 2005). Conversely, no significant trend was found in the layer at 4–5 MAB during the day in OCEANS (Fig. 5a), where the dominant taxon was calanoid copepod. A possible reason for the variability in the relationship between diurnal acoustic backscatter and $\varepsilon$ may be individual feeding modes. For example, an observational study reported that ambush feeders exhibited substantial descents in response to wind-induced turbulence, whereas suspension feeders did not (Tanaka 2019). Indeed, inhibition of ambush feeding in turbulent waters has been suggested by numerical (Visser et al. 2009) and analytic (Pécseli et al. 2019) studies.

The use of white light strobe at 3 Hz with CPICS was likely to bias the results of this camera system, as many zooplankters, especially demersal species, are attracted to artificial light. Due to the zooplankton’s limited swimming ability, strong turbulence likely hindered their ability to swim toward the light source, artificially leading to lower zooplankton densities in the volume illuminated by CPICS under conditions of strong turbulence (Fig. 6). Thereby, both this artifact and the avoidance of emergence would lead to records of lower zooplankton densities under conditions of higher turbulence. The degree to which the light-driven artifact contributed to the trend seen in Fig. 6 is unknown. Such an artifact was recently reported by Tanaka et al. (2019) who observed, based on laboratory and field experiments, that high turbulence intensity artificially lowered zooplankton abundance, and consequently the levels of turbidity recorded with fluorescence-turbidity sensors that emit blue light.

Our acoustic records, showing similar trends, were free of such artifact. Based on those acoustic records, we conclude that strong turbulence hinders the nocturnal emergence of demersal zooplankton. However, the observed trends were weakly supported by statistical tests. Our reliance only on acoustics should motivate future studies to reexamine the relationships between turbulence and demersal plankton using optics with infrared illumination and net sampling.

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Conflict of Interest
None declared.