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NOTE

Changing weather causes behavioral responses in the lower mesopelagic

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ABSTRACT: Mesopelagic acoustic scattering layers at a 700 m deep location in the Red Sea ascended 70 to 80 m during a passing rain storm that reduced light levels at the surface by more than 2 orders of magnitude. The changes in vertical distribution were observed down to the deepest part of the water column and were interpreted as a response to sudden dark weather. However, light measurements suggest that the mesopelagic targets (fish) did not fully compensate for the reduction in ambient light, and the calculated light levels in the scattering layers were ~1 order of magnitude lower during the passage of the storm. The results show that fluctuating weather conditions may affect pelagic ecosystems even towards the lower parts of the mesopelagic zone.

KEY WORDS: Light · Behavior · Vertical distribution · Mesopelagic · Scattering layer

INTRODUCTION

Stormy weather affects marine ecosystems through varying mechanisms, comprising impacts on, for example, microbial populations (Zhang et al. 2013), sedimentation of algal blooms (Jackson 1990), damage to coral reefs (Mumby & Steneck 2008) and behavioral responses among macrofauna (Udyawer et al. 2013). Animal movements in shallow waters interpreted as flight reactions from physical disturbances have been reported for invertebrates, teleosts, marine reptiles and elasmobranchs (references in Udyawer et al. 2013).

Surface light may vary by about 1 order of magnitude between a sunny day and a day with dark clouds (Denton 1990). The mesopelagic zone is defined both relative to depth (200 to 1000 m) and light level. This 'twilight zone' is characterized by too little light for photosynthesis, but still enough light for organisms with very sensitive eyes to detect the downwelling irradiance (Warrant & Locket 2004). Mesopelagic organisms appear to have preference for a range of light intensities that typically span several orders of magnitude (Roe 1983, Staby & Aksnes 2011, Prihartato et al. 2015). Recently, Røstad et al. (2016a,b) suggested that organisms forming mesopelagic scattering layers inhabit a light comfort zone (LCZ) by actively avoiding too strong and too low light intensity. Accordingly, they react to changes in downwelling irradiance by adjusting their depth.

There are several reports on pelagic organisms changing their vertical distribution relative to varying surface light on scales other than diel; for example, weather (Hersey & Moore 1948, Baliño & Aksnes 1993), snow cover on ice (Vestheim et al. 2014), solar and lunar eclipses (Kampa 1975, Tarling et al. 1999, Strömberg et al. 2002), and state of the lunar cycle (Prihartato et al. 2016). Reports are mainly from the upper 100 to 200 m, but also include responses to solar eclipse at mesopelagic depths (Backus et al. 1965). The functional definition of the mesopelagic (dysphotic) zone, combined with the concept of LCZs

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*Corresponding author: stein.kaartvedt@ibv.uio.no of mesopelagic organisms, suggests that varying weather might lead to behavioral responses throughout the upper ~1000 m, mediated by fluctuation in the surface irradiance. Variation of 1 order of magnitude in surface light would correspond to an isolume depth variation of about 75 m in clear oceanic water (Denton 1990). However, reports on responses to weather changes appear to be wanting for the deep mesopelagic, and the extent to which deep-living organisms respond in accordance with short-term weather fluctuations remains to be established.

A heavy rain storm passed the Jeddah area in Saudi Arabia in November 2014, causing a strong drop in surface irradiance in the middle of the day. Concurrent measurements of mesopelagic acoustic scattering layers and surface light levels, together with data on vertical light extinction, provided a unique opportunity to assess the extent to which the rain storm affected distribution patterns in the lower mesopelagic zone relative to changes in ambient light. We hypothesized that the mesopelagic scattering layers would adjust their vertical distribution during passing of the rain storm, so that they would remain within the same LCZ throughout the event.

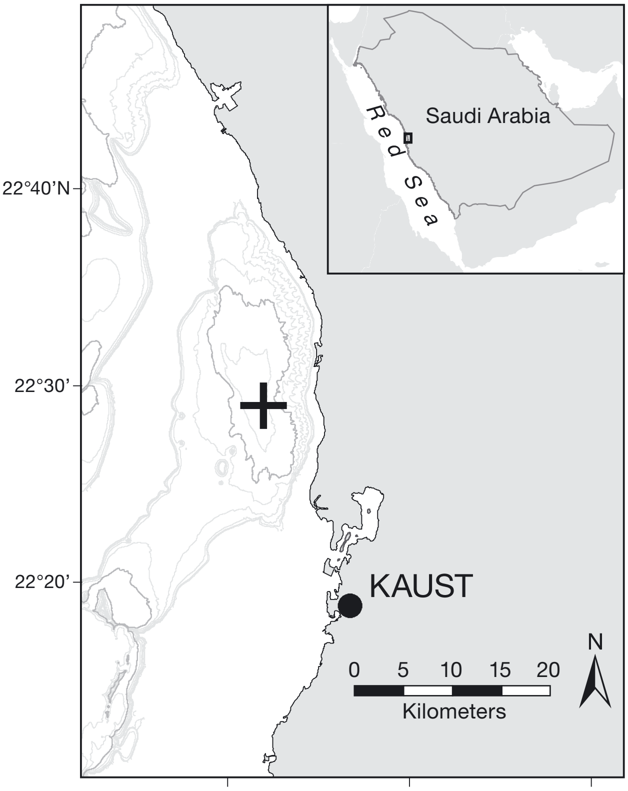

Fig. 1. Study area. Depth contours are separated by 100 m, with the 600 m isobaths highlighted. Locations for an upward-looking echosounder deployed at the bottom and measurements of vertical light extinction are depicted (+). Continuous measurements of surface light were made at King Abdullah University of Science and Technology (KAUST)

MATERIALS AND METHODS

Study location

The study was carried out at a ~700 m deep location (22.3° N, 39.03° E) near the King Abdullah University of Science and Technology (KAUST) campus, Saudi Arabia (Fig. 1). A more detailed description of the study location is provided in Røstad et al. (2016a,b) and Wiebe et al. (2016). There are relatively small seasonal variations at this low latitude, with some change in day length. The weather is mostly sunny, with 9 mo per year that are normally without any precipitation.

Mesopelagic scattering layers, apparently dominated by fish, are prominent in the Red Sea (Klevjer et al. 2012, Dypvik & Kaartvedt 2013, Røstad et al. 2016a). Previous studies suggest species compositions (Dypvik & Kaartvedt 2013), and we here also draw on unpublished results (A. Røstad & S. Kaartvedt) from the use of a 2.5 m^2 Tucker trawl and filming using a remotely operated vehicle in suggesting taxonomic compositions.

Light measurements

A meteorological station measured downward solar broadband irradiance (W m^{-2}) at KAUST, located ~25 km south of the study site (Fig. 1), with a temporal resolution of 1 min. Measurements of underwater downwelling irradiance were made down to 275 m (limitation by cable) at around midday the day before the storm event, as reported in Røstad et al. (2016a,b). To convert the broadband irradiance above the surface into the amount of visible (400 to 700 nm) light just below the surface, those authors reported a conversion factor of 1.16 µmol quanta s^{-1} W^{-1}. This factor has also been applied here. We applied their underwater irradiance observations to estimate the light attenuation coefficients (400 to 700 nm) shallower and deeper than 100 m. The attenuation coefficient was estimated by the slope of the linear regression model, $\ln(E_z/E_0) = -Kz + b$, where E_z and E_0 are the measured irradiances at depth z and just below the surface, respectively, K is the attenuation coefficient (m^{-1}) for the selected depth interval and b is the intercept.

Acoustic measurements

A rig with Simrad EK60 echosounders operating at 38 and 200 kHz was deployed at the bottom with the transceivers housed in a pressure-proof container and attached to upward-looking transducers. Data at 38 kHz are used for this paper (Simrad 38 kHz ES38DD transducer). The autonomous rig held a PC built into the same container as the acoustic transceiver and was powered by batteries in a separate pressure-proof container (system provided by METAS AS). The rig was equipped with syntactic foam for flotation and was anchored with heavy concrete weights. It was retrieved with the help of an acoustic release.

Echograms were visualized using MATLAB. We here present 24 h echograms for the day prior to the storm event (for comparison) as well as for the day with the passing storm. The ping rate was 1 ping per 2 s, and data for the ecograms were averages over 30 s. Acoustic values are given as calibrated mean volume backscattering strength, S_v (dB re 1 m^{-1}).

RESULTS

Solar irradiance at KAUST

The day prior to the storm event was sunny with clear skies and the incoming irradiance at the meteorological station at KAUST followed a typical dome-shaped diel pattern (Fig. 2A). The same pattern was evident on the morning of the next day, but near to noon the light intensity declined abruptly to levels

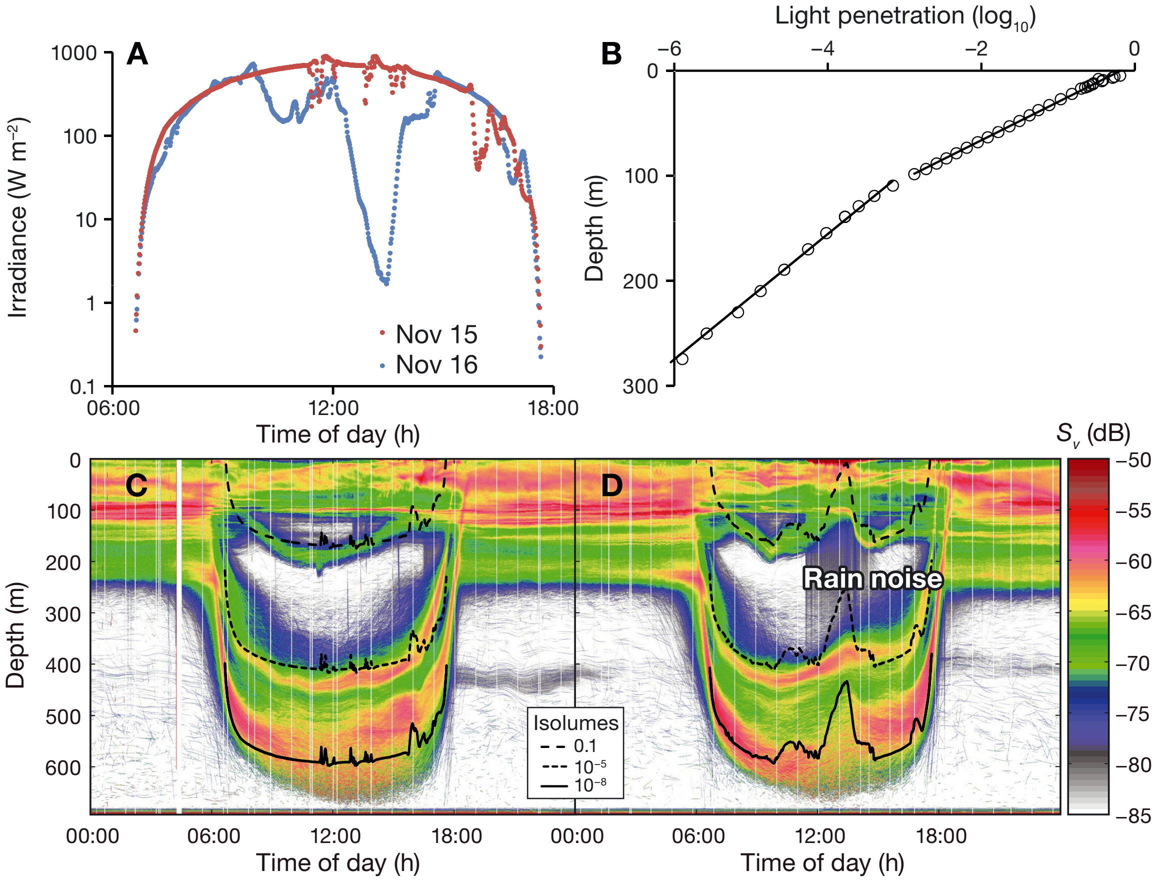

Fig. 2. (A) Observations of broadband irradiance at the meteorological station at KAUST the day before (15 November 2014; red) and the day of (16 November 2014; blue) the storm. (B) Light penetration according to measurements of underwater irradiance (400 to 700 nm) on 15 November. Light attenuation coefficients were estimated for the water column shallower and deeper than 100 m (see text). (C,D) Diel echograms for November 15 and 16, respectively, with calculated 0.1, 10^{-5} and 10^{-8} µmol quanta m^{-2} s^{-1} isolumes indicated. The passing rain storm is clearly indicated in the acoustic records (D; marked as rain noise). Color scale refers to echo intensity (S_v). Previous studies in the Red Sea suggest that the deepest scattering layer is primarily composed of the lanternfish *Benthosema pterotum* and the layer above of *Vinciguerria* sp. (Dypvik & Kaartvedt 2013), supported by our own unpublished results (A. Røstad & S. Kaartvedt) from sampling and the use of an ROV at the study site

more than 2 orders of magnitude lower than the previous day. The minimal surface broadband irradiance during the storm passage was 1.7 W m^{-2} compared to 654 W m^{-2} at the same time the day before (Fig. 2A). Irradiance subsequently increased, reaching normal levels in the afternoon. The estimated light attenuation coefficients (400 to 700 nm) of the upper 100 m and in the depth region of 100 of 275 m were 0.063 ± 0.001 ($r^2 = 0.997$, $p < 10^{-3}$, n = 28) and 0.038 ± 0.002 m^{-1} ($r^2 = 0.995$, $p < 10^{-3}$, n = 12), respectively (Fig. 2B) (uncertainties are the estimated 95% CI).

Acoustics

Three scattering layers all displayed diel vertical migration (Fig. 2). The day before the storm (Fig. 2C), an upper layer barely intercepted the upper boundary of the mesopelagic zone, with the deepest distribution at midday being at about 200 m. The core of a second layer occurred at about 400 to 450 m at midday, while the deepest layer reached down to ~680 m. The 2 deeper layers descended rapidly in the morning, followed by a continuous slow deepening until noon and subsequent slow shallowing before a rapid ascent to upper waters near sunset. The day before the storm, all mesopelagic scattering layers distributed according to rather constant light levels, although apparently at somewhat stronger light in the afternoon (Fig. 2C). Light level at the bottom of the deepest layer was calculated at ~10^{-9} µmol quanta m^{-2} s^{-1}.

On the day with the passing storm (Fig. 2D), a regular diel migration pattern appeared until late morning. However, near noon the vertical distribution of all mesopelagic scattering layers shifted abruptly ~70 to 80 m upwards, coinciding with the rapidly darkening weather, as shown by the superimposed isolumes. The passing weather system was also evidenced in the echogram. The echosounder picks up sound from rain at the surface, causing clear marks defining rain periods in the echogram (Fig. 2D), and increasing winds create waves and bubbles in surface waters that appear as strong echoes during the same period (very evident in the upper 15 m when addressing the data at finer vertical resolution than displayed in Fig. 2). Although all mesopelagic scattering layers responded by rapid and marked ascents upon arrival of the storm, the upward shifts in distributions did not appear to compensate fully for the darkening (Fig. 2D), and the calculated light levels in the scattering layers were ~1 order of magnitude lower during the passage of the storm.

DISCUSSION

Low latitude, generally sunny weather and enduring oligotrophic conditions make the light regime at the study site relatively constant with time. The yearly average rainfall in the nearby city of Jeddah is about 50 to 100 mm, with only a few rainy days a year, albeit with potentially heavy rainfall (Almazroui 2011). Thus the regular daily changes in solar radiance become the dominant source of variation for the underwater light intensity. In this context, the passing rain storm reported here represents a very rare event.

The storm caused rapid shoaling of the mesopelagic scattering layers, in accordance with the prediction of shallower vertical distribution due to reduced surface irradiance caused by the passing rain storm. However, even if ascending ~70 to 80 m, the upward vertical shifts did not fully compensate for the reduced incoming sunlight. Therefore, the behavior of the organisms did not fully adhere to the LCZ hypothesis on this short time scale, as the hypothesis would predict a stronger vertical response as evidenced by the isolumes superimposed on the echograms (Fig. 2D). It should be noted that there are uncertainties in the indicated isolume depths during the storm (Fig. 2D), as the attenuation coefficients underlying the isolume calculations were estimated under calm conditions the day before (Fig. 2B). The instantaneous response to the unpredictable and marked midday darkening evidently cannot be explained by endogenous rhythm (cf. Cohen & Forward 2009). Yet, clock genes may cause circadian rhythms among fish (Costa et al. 2016), and we cannot reject that fish are less prone to react with light-related upward swimming in the middle of the day than in the afternoon.

This study showed that changing weather affects marine life even to large depth. Fluctuating surface irradiance resonated down to the bottom of a 700 m water column, at light levels as low as 10^{-9} µmol quanta m^{-2} s^{-1}. The mesopelagic zone is inhabited by organisms with very light-sensitive eyes (Warrant & Locket 2004). We hypothesize that changing light in relation to varying weather may affect such deep-living organisms throughout the world's oceans, with implications for vertical distributions and trophic interactions.

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