



# Mesopelagic fishes in a hurry at low latitudes

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**ABSTRACT:** We studied mesopelagic fishes in the Red Sea (22° N), hypothesizing that the rapid shifts between day and night at low latitudes would translate into rapid vertical migration speeds and brief near-surface ‘antipredation windows’. Using a bottom-moored echosounder, we found that diel vertical migration speeds of acoustical scattering layers were up to double that of the global average. Visits to upper water by some of the layers were strikingly brief, around 10 min, and included unusual rapid ascent and descent (up to 22 cm s<sup>-1</sup>), apparently with a high degree of behavioral plasticity. We suggest that the behavior of mesopelagic fishes in upper waters relates to their respective light sensitivities but is controlled by the arrival of predators. Rapid shifts between day and night appear to be an inherent factor in structuring marine ecosystems at low latitudes.

**KEY WORDS:** Diel vertical migration · Antipredation window · Migration speed · Scattering layer · Red Sea

## 1. INTRODUCTION

The twilight zone is often used synonymously with the mesopelagic zone, i.e. depths from 200–1000 m, but has also been described relative to light intensities ranging between 10<sup>-1</sup> and 10<sup>-9</sup> μmol quanta m<sup>-2</sup> s<sup>-1</sup> (Kaartvedt et al. 2019). The lowest intensity corresponds to the visual threshold of lanternfishes (Myctophidae) (Turner et al. 2009), and the highest intensity corresponds to the upper light exposure of pearlshades *Maurolicus* spp. This genus is often the most shallow-living fish termed mesopelagic, having unique eyes that are adapted to higher light intensities than the lanternfishes (de Busserolles et al. 2017).

Mesopelagic organisms form acoustic scattering layers at depths of several hundred meters during the daytime and, to a varying degree, occupy upper waters at night. However, binary division into day and night is insufficient to categorize these movements. During daytime, the mesopelagic scattering layers distribute vertically in relation to variations in incoming sunlight and water clarity (Kampa 1975,

Aksnes et al. 2017). At night, there are also large variations in surface light, from 10<sup>-3</sup> μmol quanta m<sup>-2</sup> s<sup>-1</sup> during moonlit nights to 10<sup>-8</sup> μmol quanta m<sup>-2</sup> s<sup>-1</sup> in dark overcast nights (Denton 1990, Ryer & Olla 1999, de Busserolles et al. 2017). The range of nighttime light levels is further modified in higher latitudes, up to summer midnight sun.

Latitude affects the rate of light changes and the duration of the twilight periods at dawn and dusk. The fastest changes and shortest twilight periods occur at low latitudes, where sunrise and sunset are orthogonal to the sea surface. Rapid changes of incoming light may affect vertical migration velocities for organisms swimming at the same speed as moving isolumes (cf. Boden & Kampa 1967, Staby & Aksnes 2011). Moreover, the duration of twilight periods may be key for vertically migrating fish. Light-mediated behavior can theoretically be accounted for by a trade-off between feeding opportunities and predation risk, both involving visual search and thereby light (Clark & Levy 1988, Rosland & Giske 1997). According to such a trade-off, Clark &

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Levy (1988) suggested that planktivores, locating their prey by sight and in turn being subject to predation risk from predators that use sight to locate them, might exploit brief 'antipredation windows' at dusk and dawn for 'safe' foraging on abundant prey located in surface waters. Note that 'safe' is not used in an absolute sense but relative to the alternative involving foraging in daylight, providing both high visibility and high predation risk.

The observed migration patterns of *Maurolicus muelleri* at 61°N is consistent with this hypothesis (e.g. Giske et al. 1990, Rosland & Giske 1997). The associated interpretation is that fish occupy prey-rich surface waters around dusk and dawn when the risk of being visually spotted by predators is sufficiently low. The photoreceptors of *Maurolicus* spp. combine properties of both rods and cones into a single cell type specially tuned for dusk conditions (de Busserolles et al. 2017). For these fishes, it is too dark at night for visual prey detection, and they spend the nighttime hours at subsurface depths, except for light summer nights at high latitudes (Prihartato et al. 2015).

On the other hand, the dark-adapted lanternfishes might find sufficient light in upper waters even throughout dark nights (cf. Turner et al. 2009). There is an exceptional diversity in both optical and retinal specialization among deep-sea teleosts (de Busserolles et al. 2020). Therefore, we expect varied responses to the wide range of nocturnal light conditions related to eye sensitivity. However, light per se is not the only ecological driver; therefore, both the distribution and abundance of prey and responses to predators may modify migration patterns (e.g. Dypvik et al. 2012, Urmy & Benoit-Bird 2021).

Here, we analyzed vertical migration behavior of mesopelagic fishes during rapid shifts between day and night at low latitudes, using acoustic data recorded at 22°N in the Red Sea. Common to the antipredation window scenario in Clark & Levy (1988), mesozooplankton proliferates in upper waters during both day and night (Weikert 1982, Dypvik & Kaartvedt 2013). In contrast to other tropical waters, the mesopelagic fauna of the Red Sea contains very few fish species (Johnson & Feltes 1984), which form distinct acoustic scattering layers (Dalpadado & Gjøsaeter 1987, Klevjer et al. 2012, Røstad et al. 2016). We hypothesized that varied light comfort zones (cf. Røstad et al. 2016), as expressed by the daytime vertical distributions of the scattering layers, would translate into varied behavior and distributions at the light levels found during dusk, dawn and night. We expected that the rapid shift between day and night

would instigate rapid vertical swimming and temporally constrain the existence of near-surface antipredation windows. We tested these predictions by scrutinizing echograms made through continuous registrations for 10 d during the spring equinox.

## 2. MATERIALS AND METHODS

We studied mesopelagic scattering layers at an 885 m deep station in the Red Sea (22.08°N, 38.71°E) from 18–28 March 2014. We obtained sunrise, sunset and twilight times and definitions/explanations from <https://www.timeanddate.com> for Thuwal, Saudi Arabia. At the equinox on 20 March, the period from start/end of nautical twilight (i.e. sun 12–6° below the horizon; horizon still being visible) and sunrise/sunset lasts for 46 min. Civil twilight (i.e. sun 6° below the horizon to sunrise/sunset; artificial light not necessary for normal outdoor activities) lasts for 22 min. In comparison, at a site for extensive mesopelagic studies at 61°N (Norwegian fjord), the same periods last for 93 and 42 min, respectively. Except for some passing or scattered clouds, days were sunny and nights were clear throughout the study period (<https://www.timeanddate.com/weather/@409682/historic?month=3&year=2014>), suggesting little short-term variation in irradiance. No clouds were recorded between 21 and 26 March 2014. We calculated moon rise and set based on lunar altitude obtained with the Matlab function 'LunarAzEl' (Koblick 2022). We further obtained lunar illumination from <https://aa.usno.navy.mil/data/MoonFraction>. The full moon was on 16 March, and moon rise was between 20:16 h (18 March) and 05:54 h (30 March) local time.

We deployed an upward-facing 38 kHz autonomous EK 60 echosounder (system provided by METAS) at the bottom of the sea. The transceiver, housed in a pressure-proof container, was connected to an oil-filled transducer with a 7.1° beam width (Simrad ES38DD; pressure-proof to 1500 m). The ping rate was one ping every 2 s. We retrieved the positively buoyant rig using an acoustic release. The echosounder had been calibrated at the surface, using a tungsten carbide calibration sphere and standard methods (Foote et al. 1987).

We used MATLAB (R2021b) to visualize echograms, with acoustic values presented as mean volume backscattering strength (dB re 1 m<sup>-1</sup>). For echograms showing longer periods (see Fig. 1), we gridded the data into 0.5 m and 90 s intervals. We used 2 different methods for obtaining estimates of vertical velocities. (1) We applied a method similar to the one described

in Bianchi & Mislan (2016) to obtain migration speeds of the 2 deepest scattering layers (termed L2 and L3; see Fig. 1). This approach provided information on the fastest part of the diel vertical migration (DVM) below the epipelagic layer (see Text S1 in the Supplement at [www.int-res.com/articles/suppl/m694p149\\_supp.pdf](http://www.int-res.com/articles/suppl/m694p149_supp.pdf)). (2) For the uppermost layer (L1) and L2 (see Fig. 1), we assessed vertical swimming speeds in upper waters at dusk and dawn directly from the echogram by selecting apparent start and end points (depth and time) and calculating the change in depth of scattering layers over time. We also used this approach to calculate the speed of individual echo traces at depth.

### 3. RESULTS

Three mesopelagic scattering layers were evident (Fig. 1). All layers relocated throughout the day, with their deepest distribution at noon.

At the start of the registration period, L1 reached depths of  $\sim 200$  m at noon (Fig. 1). It halted the afternoon ascent at 60–80 m, moving down to  $\sim 150$  m at night. A slow ( $< 1$  cm s $^{-1}$ ) morning ascent was initiated at sunrise (i.e. towards stronger light), with the fishes reaching  $\sim 100$ –80 m 1 h later (Figs. 2a & 3a,b), subsequently migrating downwards until noon. On

Day 5, schooling targets—not recorded during the previous days—appeared in upper layers in the afternoon (Fig. 2a).

During the last 5 d, L1 split in 2 (Figs. 1–3), with apparent interchange of individuals (marked with an arrow in Fig. 3d). We continued to focus on the deeper part. Concurrently, behavior in the morning changed conspicuously, visualized here by increasing the temporal resolution (Fig. 3). From one day to the next, the slow upward relocation following sunrise on 23 March was substituted on 24 March with an earlier and faster morning ascent to shallower waters than the previous mornings (Figs. 2 & 3). This earlier dawn rise started during early nautical twilight ( $\sim 30$  min before sunrise), with the fishes ascending at up to  $\sim 22$  cm s $^{-1}$  and the layer reaching 45–35 m at the start of civil twilight. The fishes only spent  $\sim 10$  min at such shallow depths, then started to descend  $\sim 10$  min before sunrise with the first individuals returning to  $\sim 70$  m at sunrise, i.e. at the time the slow upward swimming towards increasing light was initiated the preceding days.

The intermediate layer (L2) had its daytime core at about 400–450 m depth, with migration all the way to the surface evident in the evening. Vertical migrations were fast, with average ( $\pm$ SD) ascent velocities of  $10 \pm 4$  cm s $^{-1}$  based on all dates. Shortly after arriving in surface waters  $\sim 30$  min after sunset, the fishes

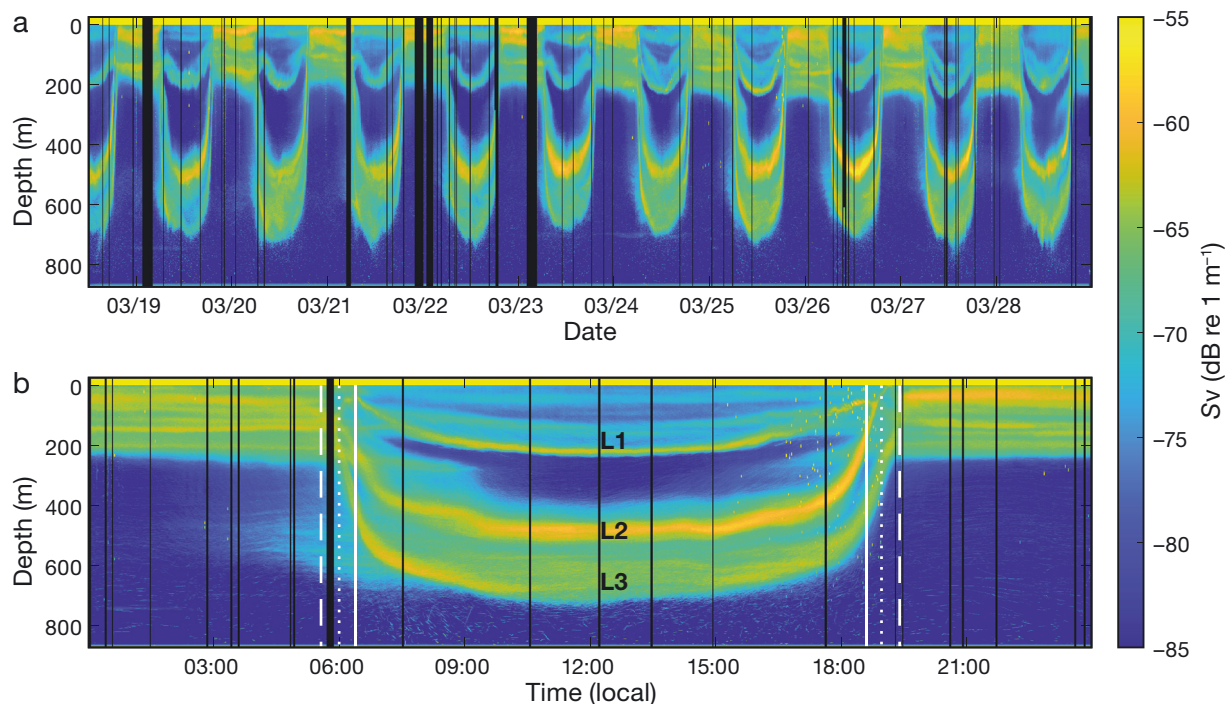


Fig. 1. Echograms for (a) the whole registration period and (b) one day (25 March 2014). The main acoustic scattering layers are denoted by L1–L3. White vertical lines: sunrise and sunset; dashed vertical lines: nautical twilight; dotted lines: civil twilight; black vertical bands: periods without records. Color scale refers to volume backscatter ( $S_v$ )

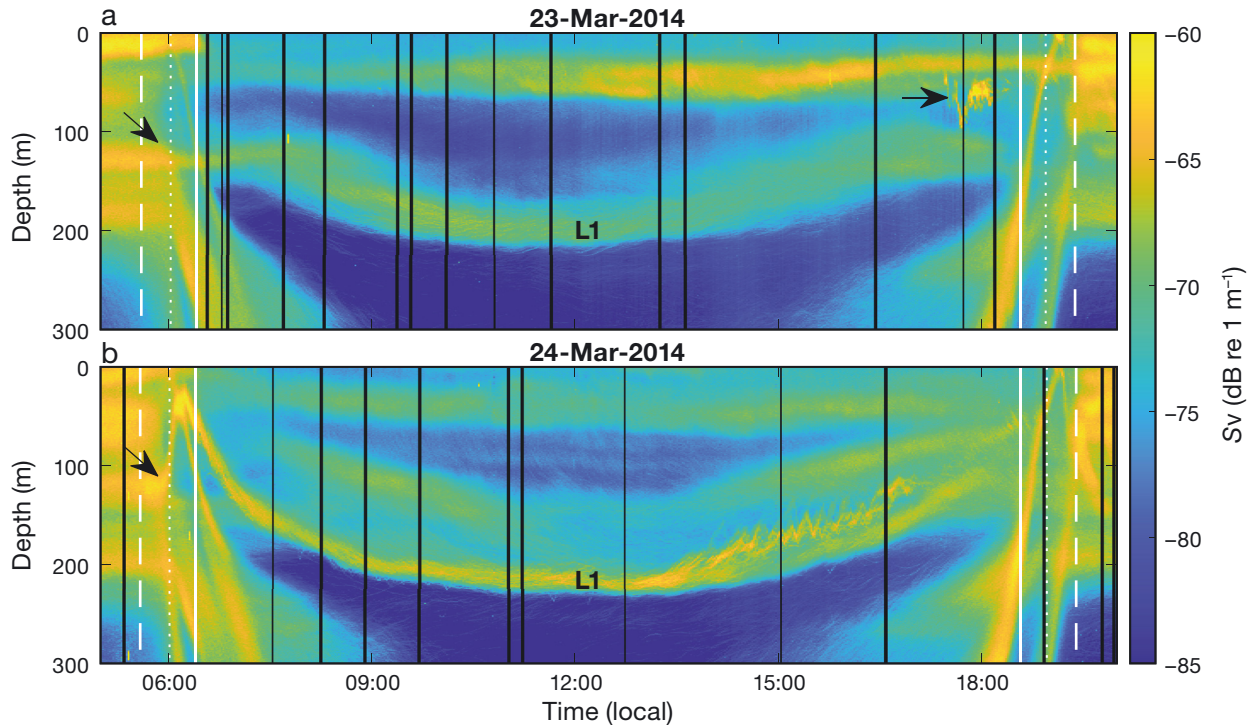


Fig. 2. Echograms for (a) 23 and (b) 24 March 2014. Arrows to the left in the figures highlight changing behavior of the uppermost acoustic scattering layer (L1) between the subsequent mornings; arrow in the upper right of (a) highlights a fish school. White vertical lines: sunrise and sunset, respectively; dashed vertical lines: nautical twilight; dotted lines: civil twilight; black vertical bands: periods without records. Color scale refers to volume backscatter ( $S_v$ )

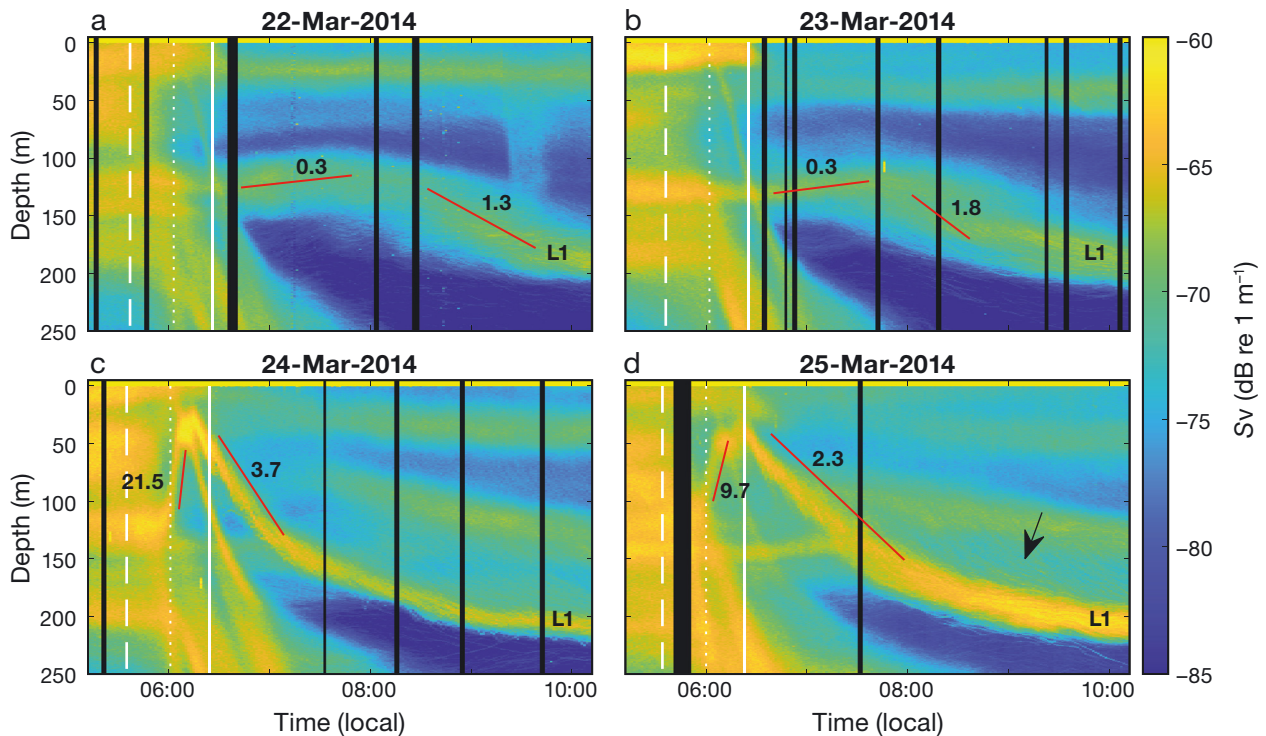


Fig. 3. Echograms showing down migrations on (a) 22 March, (b) 23 March, (c) 24 March and (d) 25 March 2014. The migration behavior of the uppermost scattering layer (L1) is drastically different between the first and last 2 days, with the initial slow upward relocation following sunrise substituted with an earlier and faster morning ascent to waters shallower than the previous mornings. Dashed vertical lines: nautical twilight; dotted lines: civil twilight; white lines: sunrise; red lines and text: migration speeds ( $\text{cm s}^{-1}$ ) obtained directly from the echogram. Arrow in (d) depicts individuals descending into L1. Black vertical bands: periods without records. Color scale refers to volume backscatter ( $S_v$ )

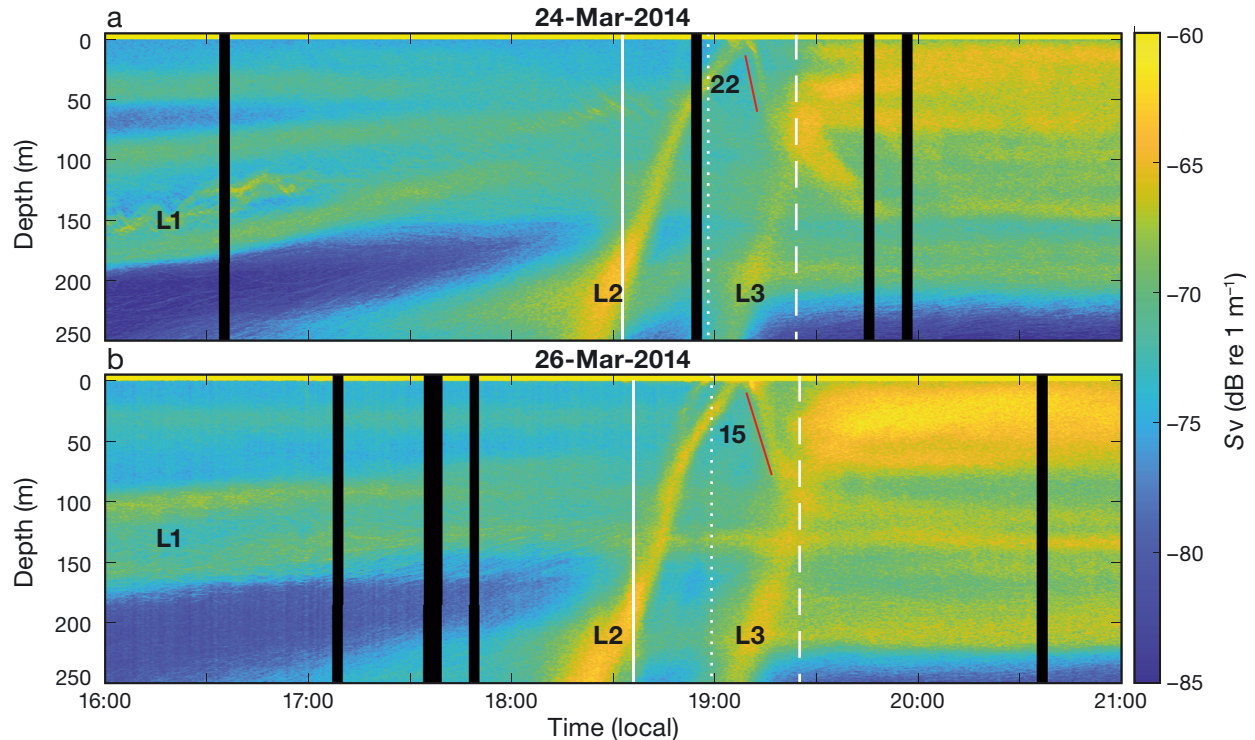


Fig. 4. Dusk migrations of the intermediate scattering layer (L2), showing very short stays in surface waters and rapid descents. The diving L2 intercepts the ascending L3 at around 100 m depth towards the end of civil twilight. White vertical lines: sunset; dotted lines: civil twilight; dashed lines: nautical twilight; red lines and text: migration speeds ( $\text{cm s}^{-1}$ ); black vertical bands: periods without records. Color scale refers to volume backscatter (Sv)

swam rapidly downwards (marked with 15 and 22  $\text{cm s}^{-1}$  in Fig. 4). The time spent in near-surface waters was only about 10 min (Fig. 4). The rapid descent happened well before moon rise. The diving fish subsequently passed 100 m at the end of nautical twilight. Details in near-surface waters before dawn were not resolved, but at least some of the organisms from L2 started their descent from surface waters (Fig. 3), meaning they had reentered shallow waters at some time during the night.

The lower layer (L3) had a noon core distribution at 600–700 m, ascending towards the surface every night (Fig. 1). The layer reached upper waters after nautical twilight (Fig. 1b). Vertical migrations were fast, with ascents and descents at  $11 \pm 2$  and  $15 \pm 2 \text{ cm s}^{-1}$  respectively. Around 19:30 h (the end of nautical twilight), the ascending L3 intercepted the rapidly descending L2 at  $\sim 100$  m (Fig. 4).

An additional type of individual acoustic target spent daytime below the mesopelagic scattering layers. These targets became apparent in the afternoon when swimming straight upwards at high speed ( $10\text{--}20 \text{ cm s}^{-1}$ ) shortly after the ascent of L3 (Fig. 5). In the morning, these targets rapidly descended towards the bottom prior to the arrival of L3 in near-bottom waters.

#### 4. DISCUSSION

We documented rapid vertical migrations of mesopelagic scattering layers and strikingly brief stays in upper waters at dusk and dawn (summarized in Fig. 6). Moreover, we documented behavioral shifts from one day to the next. Vertical migration speeds during DVMs were up to double that of the global averages reported by Bianchi & Mislán (2016). The fast ascent and descent apparently relate to the rapid shifts between day and night, as the migrations of the Red Sea scattering layers closely track the vertically moving isolumines (Røstad et al. 2016, Kaartvedt et al. 2017). The temporally compressed ‘antipredation windows’ at sunrise and sunset appear central for conspicuous behavioral patterns in upper layers. However, light alone cannot explain these patterns.

We relied on previous work in assessing the constituents of the scattering layers. We ascribed the upper mesopelagic layer to *Maurollicus mucronatus* (Dalpadado & Gjøsæter 1987; at that time termed *M. muelleri*; de Busserolles et al. 2017). The behavior at dawn during the first part of the registration period compares with previous studies in the Red Sea. The fish ascend towards increasing light in the morning, turn when encountering light values  $>10^{-1} \mu\text{mol}$

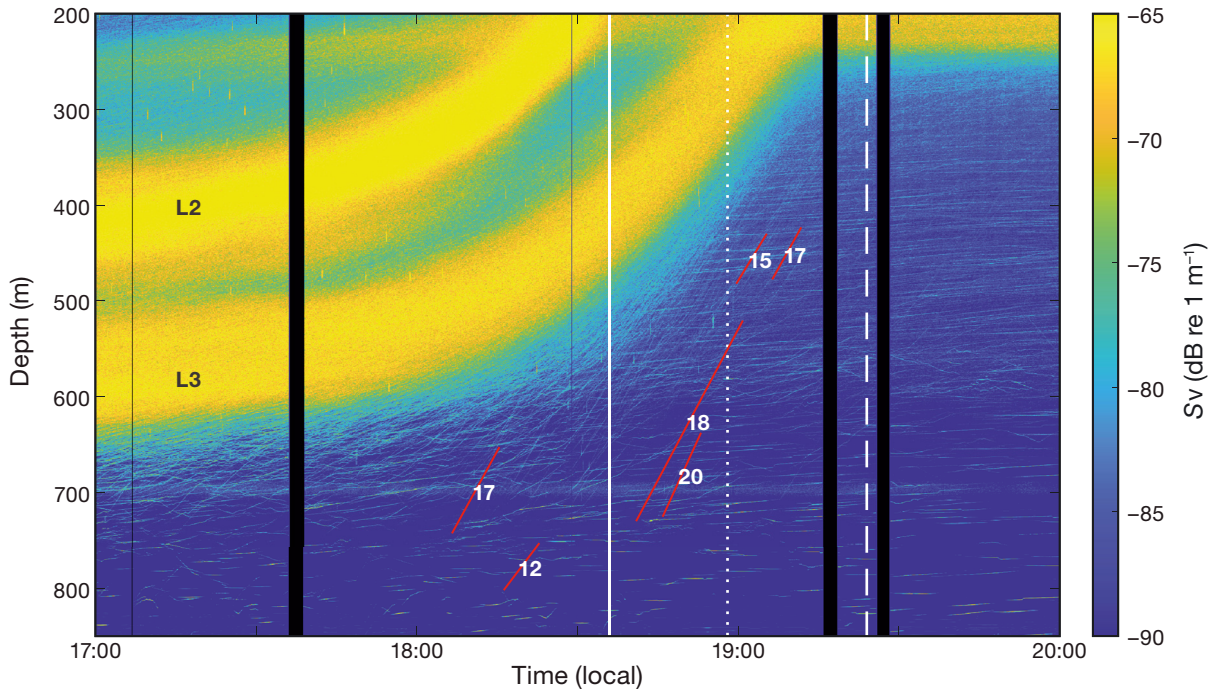


Fig. 5. Individual targets ascending from near-bottom waters. Red lines and text: migration speeds ( $\text{cm s}^{-1}$ ) obtained directly from the echogram; white vertical line: sunset; dotted line: civil twilight; dashed line: nautical twilight; black vertical bands: periods without records. Color scale refers to volume backscatter (Sv)

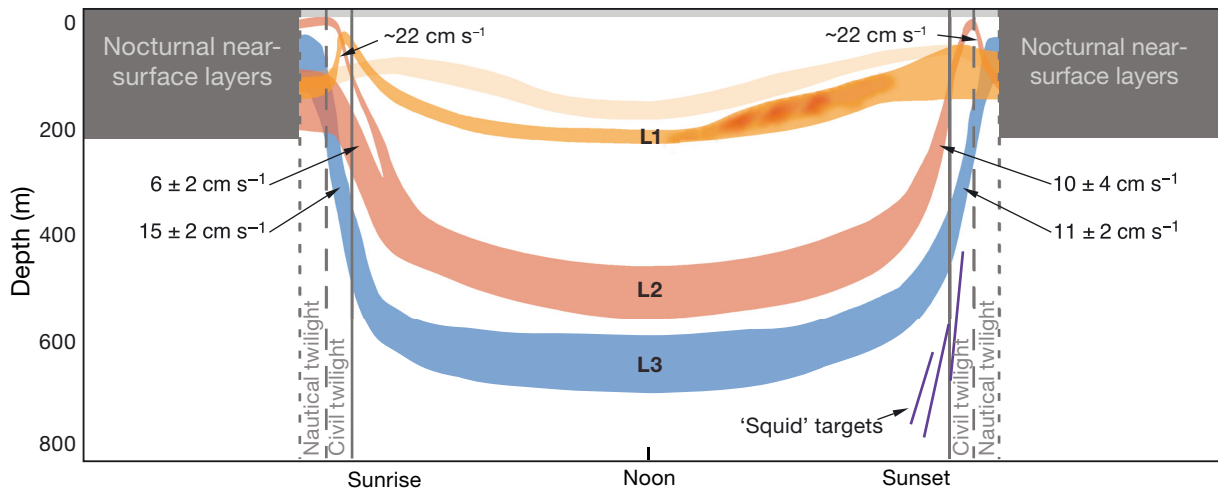


Fig. 6. Schematic summary of migration patterns and velocities. Migration velocities for the 2 deeper scattering layers (L2 and L3) during normal diel vertical migrations are based on all 10 d of records (means  $\pm$  SD). Upper water patterns at dawn and dusk changed during the course of the study, and migration velocities for L1 during rapid morning ascent and L2 during rapid dusk descent represent data from 24 March. In both cases, the times spent at the shallowest depths were about 10 min

quanta  $\text{m}^{-2} \text{s}^{-1}$ , subsequently descending with increasing light (Røstad et al. 2016, Kaartvedt et al. 2017). However, from one day to the next, they changed behavior, with altered timing and depth of dawn migrations implying very different responses to light in the morning. Moreover, the dawn ascent became extremely fast (up to  $22 \text{ cm s}^{-1}$ ). Such speeds

would have represented 5–10 body lengths  $\text{s}^{-1}$ , as Dalpadado & Gjørseter (1987) found size at first maturity of 19–20 mm, although individuals up to 4 cm were captured. For its northern counterpart *M. muelleri*, such high speeds were only observed with instantaneous diving upon encounters with predators (Christiansen et al. 2021).

Urmy & Benoit-Bird (2021) observed changes in mesopelagic DVM patterns upon the arrival of predators. Episodic appearance of fish schools altered migration behavior for days even after the potential predators disappeared, suggesting the prey animals were adjusting their position relative to risk rather than directly fleeing predators (Urmy & Benoit-Bird 2021). In the Red Sea, the behavioral change occurred following the appearance of fish schools the previous afternoon (Fig. 2a). We hypothesize that these near-surface schools represent predators whose arrival altered the migratory behavior of the small mesopelagic fishes.

The mid-water layer is primarily formed by *Vinciguerria mabahiss* (Dypvik & Kaartvedt 2013). The estimated light levels tracked by this layer ( $\sim 10^{-5}$ – $10^{-6}$   $\mu\text{mol quanta m}^{-2} \text{s}^{-1}$ ; Røstad et al. 2016) correspond to surface light on a clear starlit night (Ryer & Olla 1999). Time of night, state and position of the moon in the sky as well as changing cloudiness would provide varying opportunities and trade-offs for nocturnal near-surface visual foraging and predation risk. Our observation of an extremely short stay ( $\sim 10$  min) in surface waters after sunset appears novel for a mesopelagic fish. The subsequent very rapid descent (up to  $22 \text{ cm s}^{-1}$ ) does not resemble passive ‘mid-night sinking’ (cf. Pearre 2003); the diving fish apparently had an urgent need to enter deeper waters which was unrelated to moon rise or weather conditions.

*V. mabahiss* is endemic to the Red Sea (Johnson & Feltes 1984), but there is limited knowledge of its behavior. However, information for other species of *Vinciguerria* suggests flexible behavior. Vertically migrating *V. nimbaria* exhibits epipelagic foraging at dusk and dawn off Japan (Ozawa et al. 1977). In waters near the equator, the fish adjust their DVM patterns relative to food abundance, with rapid foraging at dusk and dawn in the rich zone of equatorial upwelling, while apparently being obliged to spend time foraging in upper layers during the day in poorer adjacent regions (Marchal & Lebourges 1996, Lebourges-Dhaussy et al. 2000). Unusual daytime surface aggregations of *V. lucetia* occur in equatorial waters associated with fronts accumulating their prey (Pitman & Ballance 1990). The silvery sides of fishes (like for *Vinciguerria* and *Maurolicus*) provide some cryptic function in upper, sunlit waters (Johnsen 2014). We suggest that extreme light conditions at low latitudes, only offering a very short antipredation window in the upper waters at dusk and dawn, might translate into unusual behavior during the day.

The deepest layer, ascribed to *Benthoosema pterotum* (Dypvik & Kaartvedt 2013), migrated regularly, apparently remaining in upper waters throughout the night. For this dark-adapted lanternfish, in daytime occurring within the  $\sim 10^{-6}$ – $10^{-9}$   $\mu\text{mol quanta m}^{-2} \text{s}^{-1}$  light interval in the Red Sea (Røstad et al. 2016), nocturnal light levels may always be sufficient for foraging in near-surface waters (though moonlight might be too bright, as it exceeds  $10^{-6}$  in upper waters). However, during rapid shifts between night and day, these fish might rely on a rapid descent to leave waters with light intensities that are too high. Tropical surface schools of *B. pterotum* chased by tuna have been reported (Alverson 1961).

A fourth group of acoustic targets left near-bottom waters just after the deepest scattering layer, returning before the mesopelagic fishes in the morning. They resemble the acoustic signatures we have previously ascribed to squid (Kaartvedt et al. 2020). We suggest that these targets represent nocturnal, dark-adapted visual predators of the mesopelagic fishes, reaching surface layers shortly after *Vinciguerria* left. The paths of these ascending potential predators and the rapidly descending fish would then cross in darker waters. The very short stay in surface waters at dusk by *Vinciguerria* may thus be a strategy to avoid the dark-adapted predators.

Nocturnal light spans 5 orders of magnitude, and there is high diversity in visual specialization among mesopelagic fishes. Water clarity, varying weather, lunar phase and latitude all contribute to shaping the abiotic nocturnal environment. This landscape of light is essential for interactions between prey and predators, which in turn vary in distribution, abundance and sensory capabilities. Mesopelagic fishes can display flexible behavior and respond accordingly. We assessed mesopelagic fish behavior for 10 d in one location. Yet we suggest that rapid shifts between day and night are key elements of low-latitude ecosystems with linked behavioral adaptations. Vertical migration velocities peak in tropical and subtropical regions (Bianchi & Mislán 2016). Our observations of strikingly brief darts towards upper waters at dusk and dawn were made possible by a methodological approach enabling continuous registrations with high temporal and vertical resolution throughout the water column and facilitated by the low diversity of the scattering layers. Patterns reported here might apply elsewhere and may not be specific to the Red Sea ecosystem.

**Data availability.** The data reported in this study are available at <https://doi.org/10.1594/PANGAEA.942966>

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