



Diel vertical migration and individual behavior of nekton beyond the ocean's twilight zone

Stein Kaartvedt^{a,*}, Anders Røstad^b, Svenja Christiansen^a, Thor A. Klevjer^c

^a Department of Biosciences, University of Oslo, 0316, Blindern, Norway

^b Red Sea Research Center, King Abdullah University of Science and Technology, Thuwal, 23955-6900, Saudi Arabia

^c Institute of Marine Research, 5817, Bergen, Norway

ARTICLE INFO

Keywords:

Diel vertical migration
Bathypelagic
Swimming patterns
Submerged echosounder
Red sea

ABSTRACT

Diel vertical migration (DVM) is normally limited to the upper 1000 m. However, the use of ship-borne and stationary submerged echosounders in the Red Sea unveiled consistent formation of daytime patches extending to 1200–1300 m, the patches dissolving at night when individuals migrated shallower. The diel vertical migration was not synchronized, and in the evening 4–5 h passed from the first to the last individual leaving their continuously dark daytime habitat. The mean ascent and descent speeds were $\sim 15 \text{ cm s}^{-1}$. Individuals were active upon return to deep water in the morning, some swimming rapidly up and down at speeds of up to $\sim 25 \text{ cm s}^{-1}$, with abrupt changes in swimming direction. Patch formation was swift, in spite of dilute overall population density, suggesting remote signaling to team up with conspecifics. Vertical swimming subsided as patches became established and persisted at $2\text{--}3 \text{ cm s}^{-1}$ within patches. The acoustic target strength of the individuals peaked at $\sim -55 \text{ dB}$ (38 kHz) and was constant regardless of vertical swimming directions. Based on the behavioral and acoustic evidence squids (*Sthenoteuthis* sp) are likely acoustic targets.

1. Introduction

The lower boundary of the mesopelagic- or twilight zone is defined as the depth without remaining surface light, generally set at 1000 m (Denton, 1990; Warrant and Locket, 2004). Yet, there are reports on vertically migrating acoustic scattering layers descending into bathypelagic waters below 1000 m in daytime and ascending at night (Van Haren, 2007; Van Haren and Compton, 2013; Ochoa et al., 2013). No detailed information on the behavior is available for such deep-living organisms and target identities are unknown.

The northern Red Sea is an oligotrophic ocean with optically clear waters, where scattering layers ascribed to mesopelagic fish extend down to 700–800 m in daytime (Klevjer et al., 2012; Dypvik and Kaartvedt, 2013). We here report on additional vertically migrating acoustic targets descending past the depths of the main scattering layers and even beyond the twilight zone during daytime. We deployed scientific echo sounders in deep waters to unveil details on their diel vertical migration (DVM) pattern and swimming behavior in the apparently continuously dark daytime habitat below 1000 m (Denton, 1990; Warrant and Locket, 2004).

2. Material and methods

2.1. Study sites

We made acoustic studies in the central and northern part of the Red Sea in November 2011 and April 2013, using the RV *Aegaeo*. In 2011 the study sites were located above and near the Kebrit (24.43° N, 36.16° E) and the Atlantis II (21.21° N, 38.04° E) brine pools, situated along the central axis of the Red Sea (Antunes et al., 2011). The brine/seawater interface is at 1470 and 2000 m depth, respectively, representing the effective bottom depth for the pelagic fauna at these locations. In 2013, studies were made east of Atlantis II (21.57° N, 38.18° E), at bottom depths of $\sim 1400\text{--}1500 \text{ m}$.

Warm surface waters and unusually warm deep water characterize the Red Sea. At our study sites (2011), the temperature and salinity were constant by depth below $\sim 300 \text{ m}$, being 21.7°C and 40.6, respectively (Dypvik and Kaartvedt, 2013; see also Fig. 3 c). There is an oxygen minimum zone (OMZ) at depths of 350–450 m, with values ranging from above 1 ml l^{-1} in northern parts of the Red Sea to about 0.5 ml l^{-1} further south (Klevjer et al., 2012). The oxygen minimum was most pronounced at the southern site Atlantis II, being less than 1 ml l^{-1} . Both

* Corresponding author.

E-mail address: stein.kaartvedt@ibv.uio.no (S. Kaartvedt).

at Kebrit and Atlantis, the oxygen contents increased slowly by depth beneath the OMZ to about 2 ml l^{-1} below 1000 m (Dypvik and Kaartvedt, 2013).

2.2. Acoustic studies

A shipborne Simrad EK60, 38 kHz echosounder provided records with acceptable signal to noise ratios in the upper 1100 m–1200 m when the ship was stationary. We applied a submersible echosounder to get high-resolution data in deep water. The submersible system consisted of Simrad EK60, 38 kHz and 200 kHz transceivers mounted in a pressure proof casing together with a PC. We here use results only at 38 kHz due to electrical noise at the higher frequency. Batteries in another casing powered the system. The echosounders had been calibrated at the surface using standard methods (Foote et al., 1987).

In 2011, we kept the submerged acoustic package suspended in a winch wire, transducer facing downwards. The ship remained at a fixed position during deployments, in this way allowing many repetitive echoes from individual targets. At Kebrit, we deployed the echosounder at 900 m for 3 h during the transition from night to day (6–9 h local). At Atlantis II, it was deployed at 900 m at two nights/days for in total 15 h (5–9 h and 23–10 h local), and at 1500 m for 10 h (02–12 h local).

In 2013, the submersible echosounder was mounted in a rig with the transducer facing upward. We deployed the positively buoyant rig at the sea floor (1460 m depth), with concrete blocks as anchors. We retrieved the rig after recording for 5 days, using an acoustic release.

Target strength (TS) and vertical swimming speeds were measured by analyzing individual tracks obtained by target tracking in the post-processing software Sonar5-Pro (Version 6.04; Balk and Lindem (2017)). We manually tracked available targets between 10 and 300 m range (910–1200 m depth) in 2011 and between 50 and ~500 m range (~960–1410 m depth) in 2013. The target tracking provided depth, time and TS information for each echo of a track, as well as the mean/median TS for the whole track.

We further analyzed the tracks in Matlab (R2017b): During post-processing, depth outliers were removed and the depths were smoothed (running mean with window size of 10 echoes). We calculated net vertical velocity (depth change over time; cm s^{-1}) between the first and last echo of each track. In order to analyze potential changes in swimming speed and TS with behavior, each track was visually classified into one of three types of behaviors (V-shaped swimming outside aggregations, other outside aggregation, inside aggregation,; see Fig. 1). In the V-shaped tracks, the mean upwards and downwards velocities were calculated separately by first calculating velocities between all individual echoes and then averaging all negative and positive velocities, respectively.

We additionally estimated swimming velocities by visually scrutinizing the echograms and marking the beginning and end of straight echo traces, an approach with lower requirements to the quality of the acoustic data. This was the method applied in assessing DVM in 2013 due to poor quality of data related to electrical noise and long range to individuals. A further consequence of long ranges in 2013 was range-dependent TS (Fig. 2). Below, we therefore use TS values only from 2011, which we consider reliable although the range of TS scatter suggests some inclusion of mixed targets.

To get a rough overview of the abundance of acoustic targets at depth we used echo integration from the submerged 38 kHz echo sounders in combination with *in situ* TS measurements. This was done for 2011 in the depth interval 1100–1250 m. The SED (Single Echo Detection) threshold was set at -62 dB. The “sv/ts scaling” method of Sonar5-Pro was applied, which integrates the TS distribution obtained from the SED echogram and the backscatter distribution of the normal (amp) echogram to calculate the numerical densities.

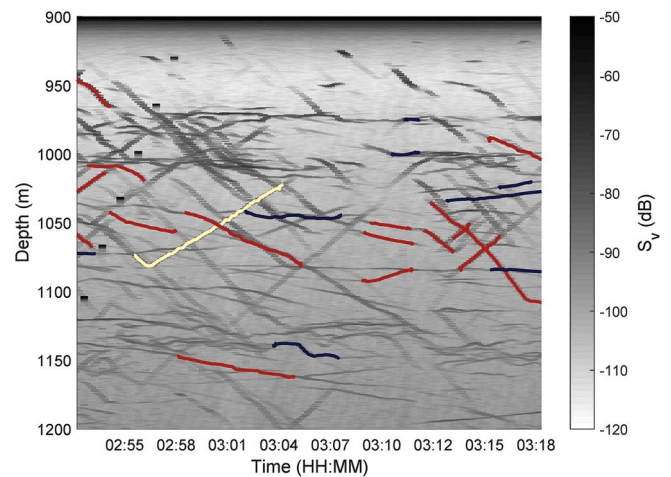


Fig. 1. Echogram from submerged echosounder (900 m) at Atlantis II on 15th November 2011 (time is UTC; 3 h earlier than local). Tracks obtained during target tracking are marked with superimposed lines, the color of the lines indicating type of behavior. Red: individuals swimming outside aggregations, blue: individuals in an aggregation and yellow: V-shaped tracks. The grey lines represent acoustic targets that did not pass the criteria for tracking. (For interpretation of the references to color in this figure legend, the reader is referred to the Web version of this article.)

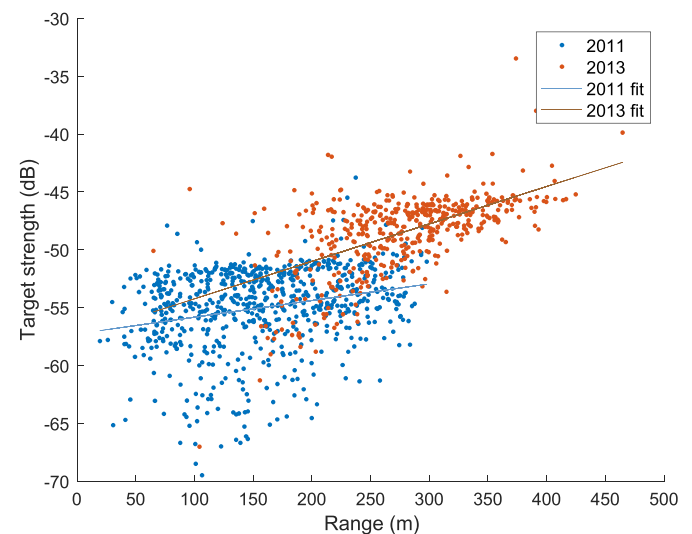


Fig. 2. Target strength with range in 2011 and 2013; the lines indicating the respective linear relationships.

2.3. Assessing the identity of the acoustic targets

We sampled using a Hamburg plankton trawl with 7 m^2 opening and $500 \mu\text{m}$ mesh size throughout, towed at 2.5 knots. This was the largest towing gear available. However, even with many hours of sampling in the deep acoustic structures catches were negligible and did not provide any reliable information on the acoustic targets. We therefore reason on target identity based on behavior and acoustic characteristics, as outlined in the Discussion.

3. Results

3.1. Shipborne echosounder

Mesopelagic scattering layers (SLs) ascended to the upper 200 m at night and descended in the morning. The deepest SL reached down to

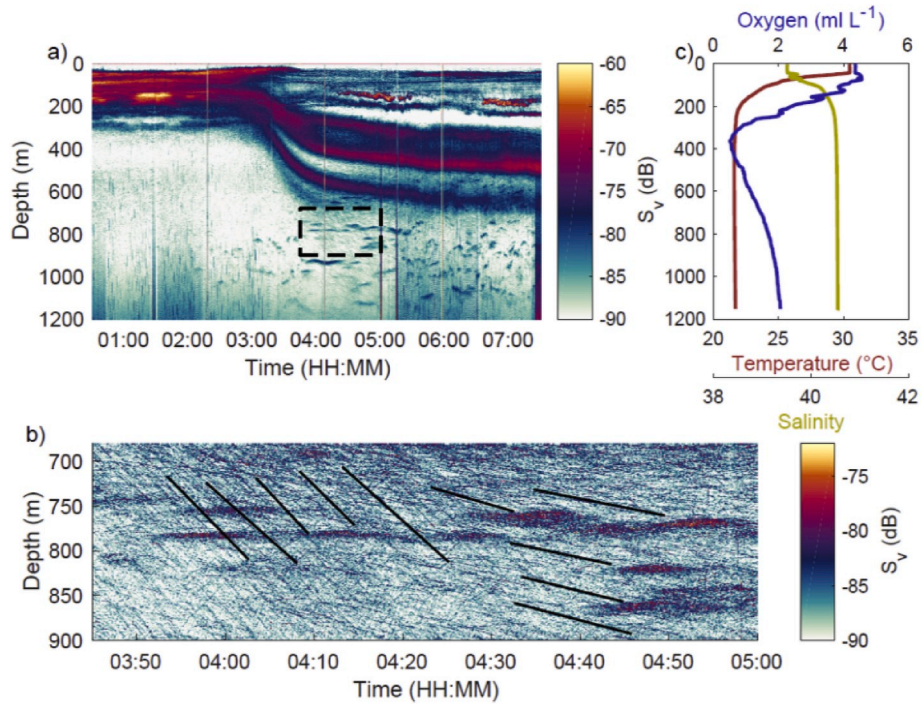


Fig. 3. a) Formation of deep patches below the DSL at Atlantis II as recorded by a 38 kHz hull-mounted echosounder on 13th November 2011 (time is UTC; sunrise at ~03:37). b) The superimposed lines in the lower panel (box depicted in a) highlight selected individuals representing fast (14–17 cm s⁻¹) and slower (3–5 cm s⁻¹) descent. c) Profiles of temperature, salinity and oxygen measured during preceding leg (26 September).

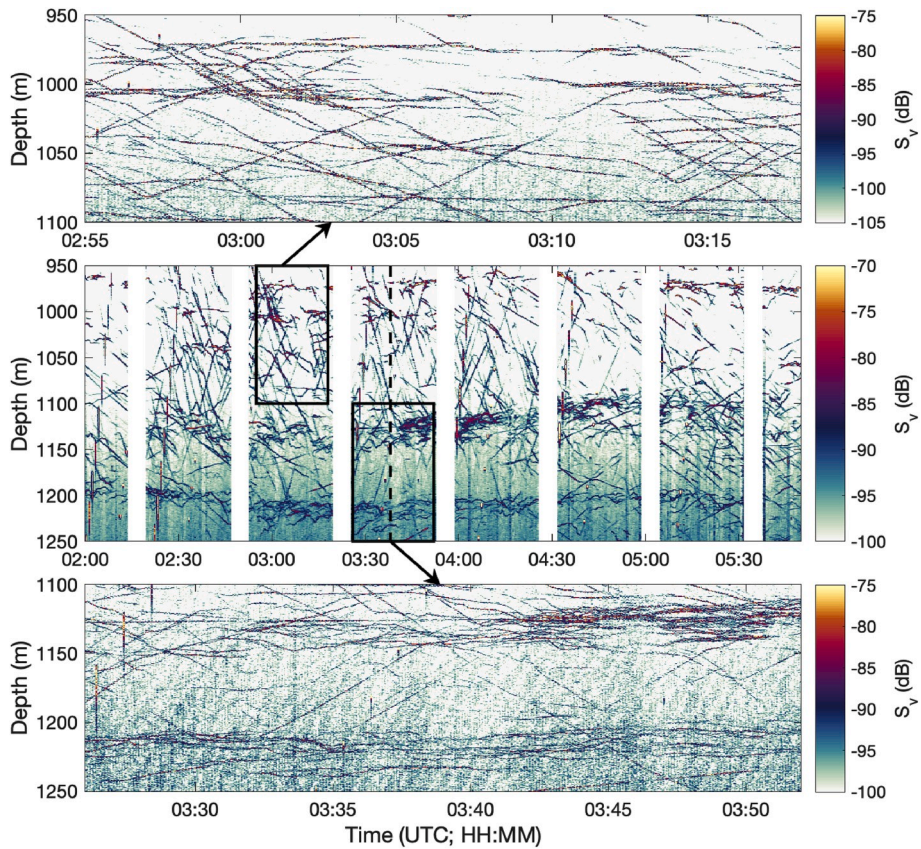


Fig. 4. Deep patch formation in the morning at Atlantis II as observed from a down-looking 38 kHz echosounder, deployed at 900 m depth on the 15th November 2011. The dashed black line at ~03:40 UTC indicates sunrise. The upper and lower panels represent zooms for periods and depth as depicted in the mid panel. No data recorded during white periods.

700–800 m during daytime. Additional acoustic targets were migrating below the deepest SL (Fig. 3). Individual descent speed for the fastest of these targets, as derived from the echogram, was $\sim 15 \text{ cm s}^{-1}$. Deep patches emerged at the end of the night/early morning. They started to form $\sim 1 \text{ h}$ prior to sunrise and subsequently became more prominent. Patches were recorded from the lower part of the mesopelagic SLs and down to the maximum recording depth of $\sim 1200 \text{ m}$ (Fig. 3). The patches vanished in the afternoon (not shown due to noisy echogram caused by ROV-operation).

3.2. Submerged echosounder 2011

Few acoustic targets occurred in deep water during the first part of the night. Small patches started emerging at depth $\sim 1 \text{ h}$ before sunrise (Fig. 4), subsequently becoming more prominent. Most records were at 1100–1300 m, but a few individuals descended beyond 1400 m (not shown). Almost no acoustic targets appeared in the echogram with the downward facing echo sounder located at 1500 m (not shown), suggesting that distributions were restricted to shallower depths.

Vertical swimming at depth was prominent in the morning (Fig. 5). Echo traces reflected individuals swiftly changing between descent and

ascent, forming characteristic V-shaped patterns. In one case, an individual was recorded for 11 min, first descending 45 m, followed by a rapid ($\sim 25 \text{ cm s}^{-1}$) 70 m ascent (Fig. 5A). Steadily ascending or descending individuals recorded outside patches had swimming speeds around 15 cm s^{-1} . Vertical swimming was much less prominent among individuals assembling in apparent shoals, with mean speed of 2–3 cm s^{-1} (Fig. 5). Vertical velocities were not significantly different in up- or downwards swimming trajectories.

TS distributions at 38 kHz peaked at $\sim -55 \text{ dB}$ (for both locations) in 2011 (Fig. 5 D). TS was in essence unrelated to behavior. Values were similar when individuals were descending and ascending as well as when apparently swimming horizontally (Fig. 5). The estimated numerical abundance at 1100–1250 m was 1 individual $10\,000 \text{ m}^{-3}$.

3.3. Upward looking seafloor mounted echosounder (2013)

As in 2011, deep patches started appearing about 1 h before sunrise, becoming more prominent as more individuals returned to depth. Patches dissolved in the afternoon, with individual ascent clearly depicted by individual echo traces (Fig. 6). Ascending individuals abruptly left their group and swam upward at a speed of $\sim 15 \text{ cm s}^{-1}$ (15

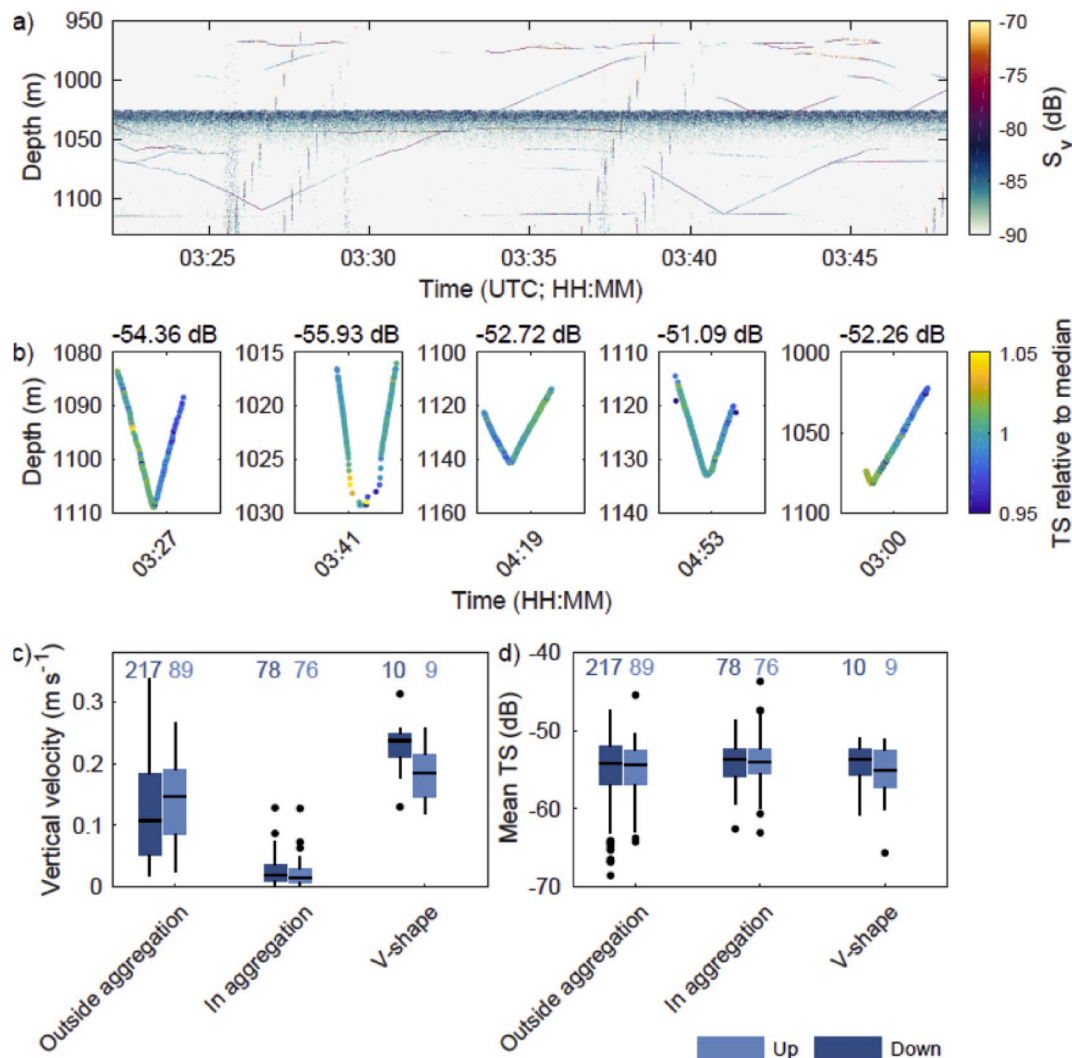


Fig. 5. Data on individuals from submerged echosounder (900m) 11–15 Nov 2011 (sum for Kebrit and Atlantis II). A) Examples of V-shaped echotraces in ordinary echogram. Horizontal “line” at $\sim 1030 \text{ m}$ and oblique, pulsed echo traces represent noise. B) Examples of V-shaped tracks with median TS as derived from acoustic target tracking (6 min periods); color scale depicts variation in TS relative to median; C) Vertical swimming speed relative to type of behavior, and D) Mean TS relative to swimming behavior. Digits atop C and D represent numbers of observations. (For interpretation of the references to color in this figure legend, the reader is referred to the Web version of this article.)

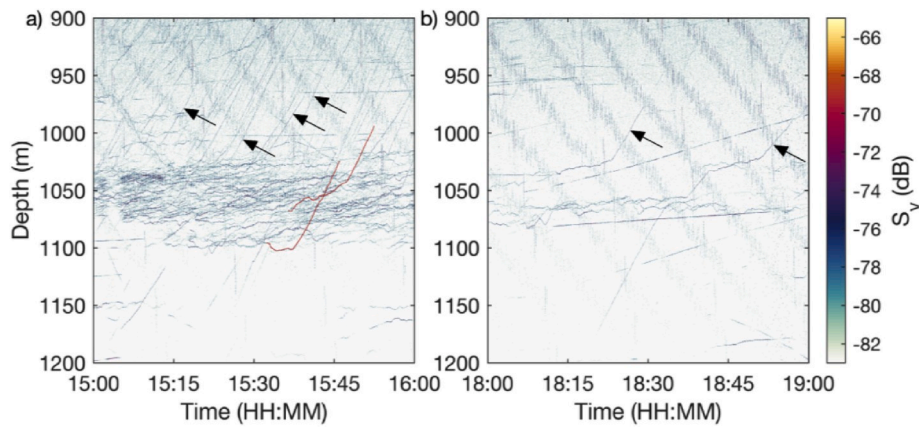


Fig. 6. Targets leaving a deep aggregation in the afternoon of the 9th April 2013 (time is UTC). Arrows depict examples of leaving individuals. Two echotracings with superimposed red lines depict individuals recorded both inside, and when leaving the patch. Oblique downward bands represent noise. Sunset at 15:44 UTC. (For interpretation of the references to color in this figure legend, the reader is referred to the Web version of this article.)

± 3.8 SD cm s^{-1} ; $n = 56$). Individuals started leaving deep water about 1 h prior to sunset, numbers of ascending individuals increasing in the subsequent hours, yet the last individuals did not seem to leave their deep habitat until about 3–4 h after sunset (Fig. 6). Thereafter, only rare targets appeared in deep water before starting re-appearing prior to sunrise the following morning.

Data were mostly of too low quality for target tracking in 2013, and we only have results on vertical swimming speed for a low number of individuals within shoals. These compared well with results from 2011, being a few cm s^{-1} (1.7 ± 0.8 SD cm s^{-1} ; $n = 10$).

4. Discussion

4.1. Individual behavior and possible identity of acoustic targets

We have documented diel vertical migrations reaching down into the continuously dark waters beyond the twilight zone. We have furthermore provided information on *in situ* behavior and TS of migrating organisms in deep water. Such deep diel migrations have previously been reported from deployments of Acoustic Doppler Current Profilers (ADCPs; Van Haren, 2007; Van Haren and Compton, 2013; Ochoa et al., 2013). These authors suggest zooplankton as the potential targets. We exclude zooplankton as acoustic targets in our case, the rapid individual swimming and the echo strengths at 38 kHz (TS) suggest nektonic organisms.

The rapid swimming and high maneuverability documented by the acoustic records upon forming of the shoals are in accordance with squid behavior (O'Dor, 1982; Jereb and Roper, 2010; Peña et al., 2018), and contrast with the normally torpid behavior of deep-sea fishes (Barham, 1970; but see reference to *Lestrolepis* sp. below). Also, the low variability in TS over the tracks are in accordance with Benoit-Bird and Gilly (2012), who found that changes in orientation did not affect TS (at 38 kHz) for the Humboldt squid *Dosidicus gigas*. However, the acoustic backscatter from squid is complex, and other authors have suggested strong dependence of squid TS on orientation and behavior (Lipinski and Soule, 2007; Soule et al., 2010). Other potential acoustic targets were the barracudina *Lestrolepis* sp. This fish may form schools in deeper waters of tropical seas (Harry, 1953) and individuals have been observed to move in vertical position making abrupt full turns from head-up to head-down positions (FAO, 1983). A few small specimens were captured in upper waters at night, and their presence in deep waters of the Red Sea at daytime was documented by attraction to the light of a ROV used in a parallel study by Kaartvedt et al. (2016). The main argument against *Lestrolepis* as the prevalent acoustic target is that these elongated, small fishes with no swim bladder (FAO, 1983) would expectedly have TS weaker than -55 dB during steep ascents and

descents.

During the current study, squids fished by the crew (jigging) in upper waters at night belonged to the genus *Sthenoteuthis*, which commonly occur in the Red Sea (Jereb and Roper, 2010). *Sthenoteuthis* (uncertain species complex; Jereb and Roper, 2010) are reported to aggregate in shoals at mesopelagic and upper bathypelagic depths during day (Shchetinnikov, 1992; Shulman et al., 2002; Jereb and Roper, 2010), being rather inactive while in their daytime shoals (Jereb and Roper, 2010). They ascend for foraging (primarily on myctophids) in upper layers at night (Shchetinnikov, 1992; Shulman et al., 2002; Jereb and Roper, 2010; Peña et al., 2018).

4.2. Diel vertical migration

The migrations to upper layers were nocturnal. However, ascent in the afternoon would not have been triggered by particular light levels (Widder and Frank, 2001; Frank and Widder, 2002) or relative change in light intensity (Ringelberg, 1995), as daylight apparently did not penetrate as deep as the habitat and there was no synchrony in timing. Migrations might rather relate to internal state (c.f. Pearre, 2003). Upward swimming from the continuously dark habitat appeared close to, or after sunset. However, the asynchronous ascent involved individuals leaving their daytime shoal one by one throughout a period spanning 4–5 h, as observed directly from the echograms (cf. Fig. 6).

In the morning, targets arrived over periods of several hours. Rapid reforming of patches suggests some remote signaling, as the population density at depth was dilute, here estimated as ~ 1 individual $10\,000\text{ m}^{-3}$ when the population had returned to depth. Bioluminescent signals are a likely means of locating conspecifics in these deep, dark waters. Bioluminescent flashes might work at distances up to several hundred meters given large eyes and bright flashes (Warrant and Lockett, 2004). The squid (*Sthenoteuthis* sp.) fished in the Red Sea has a large photophore on the dorsal side, which apparently would facilitate bioluminescent communication.

In contrast to our study, previous reports on deep DVM have found synchronous migrations in the afternoon, with populations leaving bathypelagic water coherently prior to sunset and the deeper residing targets starting the ascent earlier in the afternoon (Ochoa et al., 2013; Van Haren and Compton, 2013). Furthermore, previous reports concluded that these were short-range migrations. Vertical speed as estimated from the ADCPs used in these investigations were only a few cm s^{-1} ($\sim 1\text{--}4\text{ cm s}^{-1}$), too slow for migrators to reach the surface and even depths where surface light could be detected (Van Haren, 2007; Ochoa et al., 2013; Van Haren and Compton, 2013). We measured considerably higher and reliable migration speed directly from echo traces of vertically moving individuals. Moreover, enduring echo traces

of descending individuals in the morning (hull-mounted transducer; cf. Fig. 3) verified that the migrations extended through much of the water column.

Nocturnal migrations spanning ~1000 m evidently will represent costs, in terms of energy for swimming, but also in terms of reduced forage time, if foraging is restricted to upper layers. The acoustic targets addressed here stayed deeper than the vertically migrating mesopelagic scattering layers and apparently inhabited food deprived waters at day (Dypvik and Kaartvedt, 2013). The migration speed of about 15 cm s^{-1} suggests that >2 h are required for traversing the water column, both in the morning and evening, and some individuals started their ascent late in the evening. In sum, this suggests that >30% of a nocturnal foraging period is sacrificed to ensure a deep daytime distribution.

The costs associated with DVM should be countered with benefits. Deep daytime distribution of vertically migrating organisms is normally interpreted as a means to hide at depth from visually searching predators, but that would not explain migrations beyond the twilight zone. Yet, there are increasing numbers of reports of megafauna diving into the bathypelagic, apparently on foraging migrations, and echo locating predators can locate and capture their prey at depths of 1000 m and deeper (e.g. Tyack et al., 2006; Soto et al., 2008). While the overall concentrations of the acoustic targets in the deep Red Sea were low, they appeared to occur in aggregations that might be exploited by predators. The deep daytime descent brought the acoustic targets below the mesopelagic oxygen minimum zone, which might have been favorable, yet the deep-water of the Red Sea was still relatively hypoxic ($1.5\text{--}2 \text{ ml O}_2 \text{ l}^{-1}$) and warm ($\sim 22 \text{ }^\circ\text{C}$). Squids have one of the highest rates of energy metabolism among marine animals. However, *Sthenoteuthis* spp. are well adapted to live in very low oxygen conditions, with significant anaerobic protein utilization in energy metabolism (Shulman et al., 2002).

Regardless of motivation and target identity, our study documents DVM extending into bathypelagic waters. The methodological approach enabled assessment of individual behavior and unveiled that there was no synchronous behavior among individuals, even though there was a clear diel signal of the vertical migration at depths where no daylight remains. The assessment of individuals moreover unveiled conspicuous vertical swimming and high swimming speed at depth, apparently subsiding upon the formation of shoals. The study documents benefits of using submerged scientific echosounders for addressing the abundance and behavior of organisms in this otherwise difficult accessible domain of the ocean.

Declaration of competing interest

The authors declare that they have no known competing financial interests or personal relationships that could have appeared to influence the work reported in this paper.

Acknowledgement

The study was funded by King Abdullah University of Science and Technology (KAUST), Saudi Arabia.

References

- Antunes, A., Ngugi, D.K., Stingl, U., 2011. Microbiology of the Red Sea (and other) deep-sea anoxic brine lakes. *Environ. Microbiol. Rep.* 3, 416–433.
- Balk, H., Lindem, T., 2017. Sonar4 and Sonar5-Pro Post Processing Systems, Operator Manual Version 604. CageEye AS, Frysjaeveien 40, Entrance 7, 0884 Oslo, Norway.
- Barham, E.G., 1970. Deep-sea fishes: lethargy and vertical orientation. In: *Int Symp Biol Sound Scattering in the Ocean*. Ocean Science Program, Washington, DC, pp. 110–118.
- Benoit-Bird, K.J., Gilly, W.F., 2012. Coordinated nocturnal behavior of foraging jumbo squid *Dosidicus gigas*. *Mar. Ecol. Prog. Ser.* 455, 211–228.
- Denton, E., 1990. Light and Vision at Depths Greater than 200 Metres. *Light and Life in the Sea*, pp. 127–148.
- Dypvik, E., Kaartvedt, S., 2013. Vertical migration and diel feeding periodicity of the skinnycheek lanternfish (*Benthosema pterotum*) in the Red Sea. *Deep-Sea Res.* 172, 9–16.
- FAO species identification sheet, 1983. Paralepididae. Barracudinas.
- Foote, K.G., Vestnes, G., MacLennan, D.N., Simmonds, E.J., 1987. Calibration of Acoustic Instruments for Fish Density Estimation: a Practical Guide. *Coop Res Rep*, vol. 144. ICES, Copenhagen, Den.
- Frank, T., Widder, E., 2002. Effects of a decrease in downwelling irradiance on the daytime vertical distribution patterns of zooplankton and micronekton. *Mar. Biol.* 140, 1181–1193.
- Harry, R.R., 1953. Studies on the bathypelagic fishes of the family Paralepididae (order Inioi). 2. A revision of the North Pacific species. *Proc. Natl. Acad. Sci. Unit. States Am.* 105, 169–230.
- Jereb, P., Roper, C.F.E., 2010. *Cephalopods of the World: an Annotated and Illustrated Catalogue of Cephalopod Species Known to Date. Myopsid and Oegopsid Squids*, vol. 2. Food and Agriculture Organization of the United Nations, Rome, pp. 315–318.
- Kaartvedt, S., Antunes, A., Røstad, A., Kleivjer, T.K., Vestheim, H., 2016. Zooplankton at deep Red Sea brine pools. *J. Plankton Res.* 38, 679–684.
- Klevjer, T.A., Torres, D., Kaartvedt, S., 2012. Distribution and movement of mesopelagic scattering layers in the Red Sea. *Mar. Biol.* 159, 1833–1841.
- Lipinski, M.R., Soule, M.A., 2007. A new direct method of stock assessment of the loliginid squid. *Rev. Fish Biol. Fish.* 17, 437–453.
- Ochoa, J., Maske, H., Sheinbaum, J., Canedla, J., 2013. Diel and lunar cycles of vertical migration extending to below 1000 m in the ocean and the vertical connectivity of depth-tiered populations. *Limnol. Oceanogr.* 58, 1207–1214, 2013.
- O'Dor, R.K., 1982. The respiratory metabolism and swimming performance of the squid, *Loligo opalescens*. *Can. J. Fish. Aquat. Sci.* 39, 580–587.
- Pearre, S., 2003. Eat and run? The hunger/satiation hypothesis in vertical migration: history, evidence and consequences. *Biol. Rev.* 78, 1–79.
- Peña, M., Villanueva, R., Escáñez, A., Ariza, A., 2018. Opportunistic acoustic recordings of (potential) orangeback flying squid *Sthenoteuthis pteropus* in the Central Eastern Atlantic. *J. Mar. Syst.* 179, 31–37.
- Ringelberg, J., 1995. Changes in light intensity and diel vertical migration: a comparison of marine and freshwater environments. *J. Mar. Biol. Ass. UK* 75, 15–25.
- Shchetinnikov, A.S., 1992. Feeding spectrum of squid *Sthenoteuthis oualaniensis* (Oegopsida) in the eastern Pacific. *J. Mar. Biol. Ass. UK* 72, 849–860.
- Shulman, G.E., Chesalin, M.V., Abolmasova, G.I., Yuneva, T.V., Kideys, A., 2002. Metabolic strategy in pelagic squid of genus *Sthenoteuthis* (Ommastrephidae) as the basis of high abundance and productivity: an overview of Soviet investigations. *Bull. Mar. Sci.* 71, 815–836.
- Soto, N.A., Johnson, M.P., Madsen, P.T., Díaz, F., Domínguez, I., Brito, A., Tyack, P., 2008. Cheetahs of the deep sea: deep foraging sprints in short-finned pilot whales off Tenerife (Canary Islands). *J. Anim. Ecol.* 77, 936–947.
- Soule, M.A., Hampton, I., Lipinski, M.R., 2010. Estimating the target strength of live, free-swimming chokka squid *Loligo reynaudii* at 38 and 120 kHz. *ICES J. Mar. Sci.* 67, 1381–1391.
- Tyack, P.L., Johnson, M., Soto, N.A., Sturlese, A., Madsen, P.T., 2006. Extreme diving of beaked whales. *J. Exp. Biol.* 209, 4238–4253.
- Van Haren, H., 2007. Monthly periodicity in acoustic reflections and vertical motions in the deep ocean. *Geophys. Res. Lett.* 34, 1–5. <https://doi.org/10.1029/2007GL029947>. L12603.
- Van Haren, H., Compton, T.J., 2013. Diel vertical migration in deep sea plankton is finely tuned to latitudinal and seasonal day length. *PLoS One* 8 (5), e64435. <https://doi.org/10.1371/journal.pone.0064435>.
- Warrant, E.J., Locket, N.A., 2004. Vision in the deep sea. *Biol. Rev.* 79, 671–712.
- Widder, E.A., Frank, T.M., 2001. The speed of an isolume: a shrimp's eye view. *Mar. Biol.* 138, 669–677.