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Note

Light comfort zones of mesopelagic acoustic scattering layers in two contrasting optical environments

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ABSTRACT

We make a comparison of the mesopelagic sound scattering layers (SLs) in two contrasting optical environments; the clear Red Sea and in murkier coastal waters of Norway (Masfjorden). The depth distributions of the SL in Masfjorden are shallower and narrower than those of the Red Sea. This difference in depth distribution is consistent with the hypothesis that the organisms of the SL distribute according to similar light comfort zones (LCZ) in the two environments. Our study suggest that surface and underwater light measurements ranging more than 10 orders of magnitude is required to assess the controlling effects of light on SL structure and dynamics.

1. Introduction

Mesopelagic sound scattering layers (SLs), also called deep scattering layers, are ubiquitous features of the oceans. SLs have received increased attention in recent years as they might contain much higher biomass of mesopelagic fishes than previously assumed (Kaartvedt et al., 2012; Irigoien et al., 2014). Since the first observations of SLs in the late 1940s (see references in Fornshell and Tesei (2013)) it has been known that their characteristic diel vertical migrations (DVM) are related to variations in the surface light. A common interpretation is that organisms of the SL feed in the epipelagic at night and descend to mesopelagic depths to hide at daytime. The daytime depth position, however, and consequently the vertical range of these migrations, varies widely between locations. Bottom depth is one obvious constraint for the daytime depth and its associated migration amplitude, but also hypoxia (Bianchi et al., 2013), temperature, and density (Cade and Benoit-Bird, 2015) have been associated with SL distributions. Several previous studies also suggest that the SL organisms might have preference for a range of light intensities that typically span some orders of magnitude (Roe, 1983; Staby and Aksnes, 2011; Prihartato et al., 2015). Here, we elaborate this idea and present the first evidence that this might apply to the observed SLs in two very different optical environments.

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2. Theory and expectations

Organisms that have the ability to actively avoid too strong and too low light intensities can be said to occupy a light comfort zone, LCZ (Dupont et al., 2009). This differs somewhat from the isolume concept where organisms are assumed to be attracted by a specific light intensity (Cohen and Forward, 2009). It might be speculated that the ultimate mechanism giving rise to a LCZ, e.g. for mesopelagic fishes, represents the evolutionary solution to the trade-off conflict between visual foraging opportunities and predation mortality (Clark and Levy, 1988; Rosland and Giske, 1994; Giske et al., 2013). Nevertheless and regardless of the ultimate cause, if SL organisms do distribute according to a LCZ, two simple testable predictions emerge (Fig. 1): a murky water column (i.e. high light attenuation) is expected to have a shallower, and also narrower, SL depth distribution than a clear water column. Here, we test these expectations by comparing the SLs during a day in the clear Red Sea (clear water) with that of a murkier Norwegian coastal location, Masfjorden.

3. Methods

3.1. Study locations

The DVM patterns of the organisms constituting the SLs of Masfjorden are dynamic and change throughout the year in

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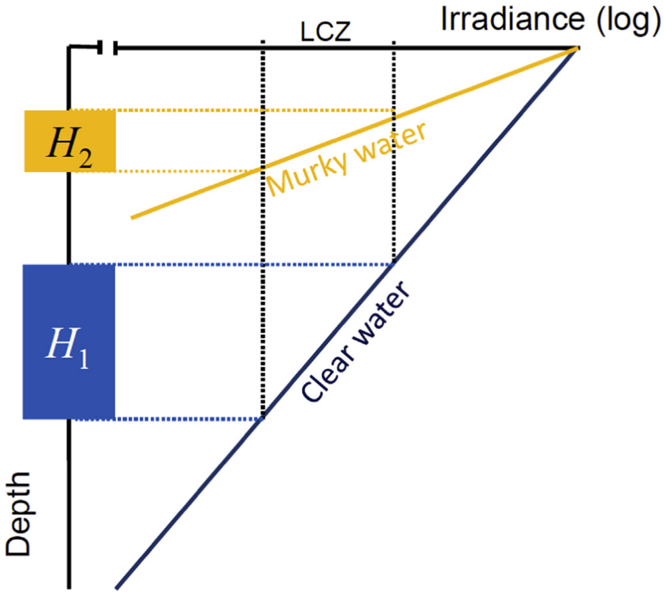

Fig. 1. Predictions from the LCZ hypothesis. If mesopelagic organisms distribute according to a light comfort zone (LCZ), the depth distribution of the organisms in a murky water column will be shallower and also narrower (H_2) than that of a clear water column (H_1). Both the depth location and the extension of the vertical distribution are proportional to the reciprocal light attenuation coefficient for downwelling irradiance which is given by the slope of the irradiance curve (log-scale). Modified from Dupont and Aksnes (2013).

concordance with seasonal changes in light conditions and possibly the distribution of prey (Staby et al., 2011; Dypvik et al., 2012a; Prihartato et al., 2015). Temperature varies in upper waters, but is basically stable below 100 m (∼7.5–8 C) throughout the year. High latitudes are characterized by dusk summer nights with light intensities that can be higher than the ambient day-time light of the SLs.

In contrast to Masfjorden, DVM patterns of the SLs in the Red Sea appear more or less invariant throughout the year (cf. also Klevjer et al. (2012) and Dypvik and Kaartvedt (2013)). This is not surprising given the relatively small seasonal variations at this low latitude. Also, the Red Sea is unique among the worlds' oceans in having very warm waters at depth (∼21.5 °C all the way to the bottom). Combined with presumably low prey concentrations, high metabolic rates related to such warm waters appear to force the entire population of mesopelagic fish to make feeding excursions to upper layers every night (Dypvik and Kaartvedt, 2013).

Here we present acoustic observations from the two locations at dates where light measurements also were available; August 16, 2011 in Masfjorden (60°50′N 5°30′E) and November 15, 2014 in the Red Sea (22°29′N, 39°02′E).

3.2. Acoustic measurements

In both locations, moorings with upward looking SIMRAD EK60 echosounders were deployed on the bottom with the transceivers housed in pressure proof containers attached to a SIMRAD 38 kHz ES38DD transducer. Bottom depths at these locations were ∼370 m in Masfjorden and ∼700 m in the Red Sea. In Masfjorden, the system was powered by cable to land, which also transferred digitized data to a computer on shore. The cable was attached to a rope, which secured retrieval of the rig at completion of the study (see Prihartato et al. (2015) for details).

The mooring deployed in the Red Sea was autonomous with a PC built into the same pressure proof container as the acoustic transceiver and being powered by batteries in a separate pressure proof container (system provided by METAS AS). The mooring was equipped with syntactic foam for flotation and was deployed with a heavy concrete weight. The system was retrieved by help of an acoustic release.

Echograms were visualized using Matlab. We made standard 24 h echograms as a function of depth, but also as a function of the calculated ambient light (see Section 3.3). Acoustic values are given as calibrated mean volume backscattering strength, S_v (dB re 1 m^{-1}).

3.3. Light measurements

At both locations measurements of underwater downwelling irradiance were obtained by a Trios RAMSES ACC hyperspectral radiometer around mid-day down to depths of 275 m and 90 m for the Red Sea and Masfjorden respectively. These measurements provided spectral resolution, with 3.3 nm bin size, of downwelling irradiance and were used to calculate ambient irradiance and to estimate photon capture rate for a model organism at mid-day (see Section 3.4). At depths below the deepest irradiance observation, we extrapolated by using attenuation coefficients (for each wavelength bin) that were estimated from depths deeper than 100 and 50 m for the Red Sea and for Masfjorden respectively.

In Masfjorden, measurements of total irradiance of the PAR band (400–700 nm) just above the surface were available from a LI-190 quantum sensor (at 15 minutes interval throughout day and night. This sensor had sufficient sensitivity to measure night sky irradiance at this high latitude in August and was, in combination with the estimated attenuation coefficient for PAR, used to calculate underwater total irradiance through day and night in the 400–700 nm band, i.e. without spectral resolution.

Similarly, for the Red Sea hourly integrated values of total broadband irradiance (W m^{-2}) were available at a weather station located about 21 km from the location of acoustical registrations. Comparison of this broadband registration with the simultaneous underwater measurement just below the surface of the 400–700 nm band indicated a conversion factor of 1.16 μmol quanta s^{-1} W^{-1}, which was used to convert the total broadband irradiance measurements into total irradiance in the 400–700 nm band. Unfortunately, the broadband sensor did not provide reliable measurements of light intensity of the night sky.

3.4. Calculation of total photon capture rate

The brightness perceived by e.g. a fish can be approximated by total photon capture rates. We calculated such rates for different depths at the two locations according to the procedure described in Turner et al. (2009) for vision in lanternfish. This involved calculation of normalised absorbance spectra (according to the 3.3 nm resolution of the hyperspectral radiometer used for underwater light measurements) by the equations of Govardovskii et al. (2000, Eq. 1–2). These were converted into absolute spectral absorbance, by taking specific absorbance of rhodopsin (0.013 μm^{-1}) and photoreceptor outer-segment (50 μm) into account (see Turner et al. (2009)). These data were then recalculated as spectral absorptance (Eq. 6 in Turner et al. (2009)), which was multiplied by the estimated retinal irradiance (eq. 5 in Turner et al. (2009)) to give an estimate of the spectral photon capture rate at selected depths (see Table 1) at the two locations. Total photon capture rate was obtained by summing over the entire spectrum. We assumed a peak sensitivity of rod visual pigments of 487 nm which corresponds to an average of Mycthophidae listed in Douglas and Partridge (1997). This sensitivity was varied on the range 480–500 nm, but provided relatively small changes (less than 10%) in calculated photon capture for all depths at the two locations.

Table 1
Approximate daytime SL thickness and depth boundaries. Layer refers to the numbers defined in Figs. 3 and 4. Void refers to the depth span between layer 1 and 2 characterized by low acoustic backscatter. The ambient irradiance (total number of photons summed over the spectrum) is given for the depths that correspond to the indicated layer boundaries. Total photon capture is modelled (see Section 3.4) from the ambient irradiance and vision related parameters set according to a myctophid (Turner et al. 2009). Ratio is the value obtained for the Red Sea divided by that for Masfjorden.

Layer	Layer thickness (m)		Layer boundary (m)		Ambient irradiance (photons m^{-2} s^{-1})			Total photon capture rate (photons m^{-2} s^{-1})		
	Red Sea	Mas-fjorden	Red Sea	Mas-fjorden	Red Sea	Mas-fjorden	Ratio	Red Sea	Mas-fjorden	Ratio
			140	80	8.7×10^{16}	1.5×10^{16}	6	2.4×10^{16}	3.4×10^{15}	7
1	60	40								
			200	120	6.3×10^{15}	9.2×10^{14}	7	1.8×10^{15}	2.4×10^{14}	8
Void	120	50								
			320	170	4.5×10^{13}	3.6×10^{13}	1	1.3×10^{13}	1.0×10^{13}	1
2	160	80								
			480	250	6.7×10^{10}	2.6×10^{11}	0.3	2.0×10^{10}	7.5×10^{10}	0.3
3	200	130								
			680	380	2.1×10^{7}	1.0×10^{8}	0.2	6.2×10^{6}	3.0×10^{7}	0.2

4. Results

4.1. Light penetration

The light penetration of the Red Sea and Masfjorden is illustrated in Fig. 2 for the 470–500 nm band, which is relevant for deep see fish (Douglas et al., 1998). For the Red Sea the regression estimates of $K_{470\text{–}500}$ were 0.0534 ± 0.0008 and 0.0366 ± 0.0014 m^{-1} shallower and deeper than 100 m respectively. For Masfjorden the estimates were 0.1920 ± 0.0057, 0.0924 ± 0.0034, and 0.0596 ± 0.0011 m^{-1} for 0–25, 25–50, and below 50 m respectively (uncertainties are the estimated 95% c.i.). Thus, the light attenuation coefficients for the deepest layer were 61% higher in Masfjorden than in the Red Sea. Extrapolation indicates that the light penetrations at the bottom depths were similar, with a fraction of around 10^{-12} of the surface light, at the two locations. Thus, despite a shallower bottom depth, the water column of Masfjorden appears to offer a similar range of light intensities to the mesopelagic organisms as the Red Sea location.

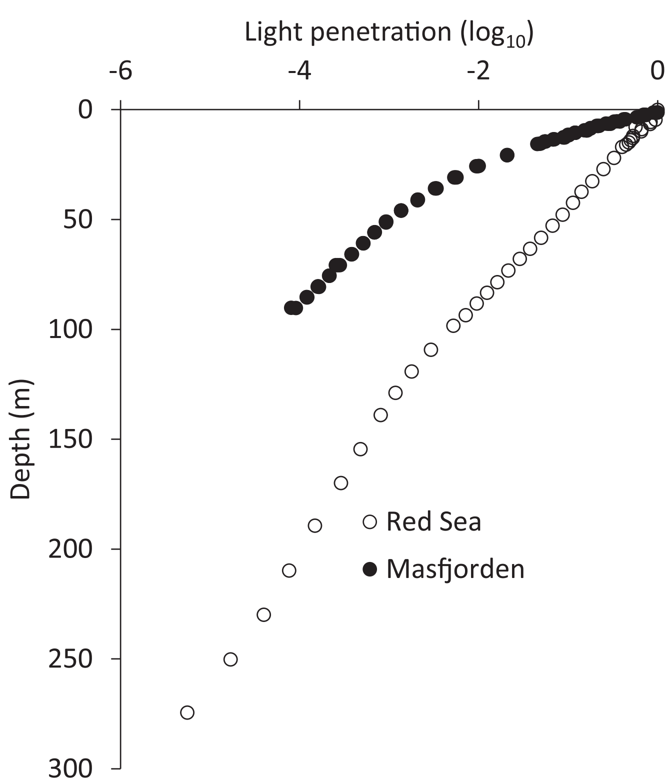

Fig. 2. Light penetration (given as the fraction of the irradiance just below surface) for the wavelength band 470 – 500 nm in the clear Red Sea compared with that of the murkier Masfjorden at the days of acoustic registrations; the Red Sea 15 November 2014 and Masfjorden 16 August 2011.

4.2. Acoustic registrations

The upper 100 m of the Red Sea had relatively strong acoustic scatter in daytime as well as in nighttime (Fig. 3A). Below this surface layer, we categorized the mesopelagic acoustic scatters into three layers (Fig. 4A and Table 1). Layer 1 is located around 200 m depth at mid-day and had a characteristic diel migration pattern (Fig. 3A). Below this layer there is a prominent acoustic void that spans from 200 to about 320 m at mid-day. Layers 2 and 3 are distributed between 320 and 480 m and 480–680 m depth respectively (Fig. 4A and Table 1). The depth locations of the three layers change slightly throughout the day, becoming progressively deeper until mid-day and shallower afterwards (Fig. 3A). In the afternoon the SL ascends rapidly into the upper 100–200 m, remaining in upper waters throughout the night and descending rapidly next morning. Only very few individual targets remained in the mesopelagic zone at night (layer 4 in Fig. 3A).

In Masfjorden the shallowest layer 1 is seen around 80–120 m depth at mid-day (Figs. 3A and 4B). The acoustic void extended from 120 to 170 m depth and layer 2 where located between 170 and 250 m. Nighttime depths were in the upper 25 m. A weaker layer 3, also migrating, occupied the depth interval 250–380 m at mid-day, thereafter becoming progressively shallower until ascending more rapidly to near-surface waters in the afternoon (Fig. 3B). Targets below 300 m mostly remained at depth day and night (layer 4 in Fig. 3B).

4.3. SL distribution in relation to variation in the surface light intensity

In the lower panel of Fig. 3, we have replaced the depth axis with the total ambient irradiance as calculated from the observed variations in surface PAR (see Section 3.3). While the SLs were more shallowly distributed and more vertically compressed in Masfjorden, the ambient light of the SLs and the acoustic void largely concurred (orders of magnitude) with that in the Red Sea (Table 1). In association with the upward migration in the afternoon it appears as if ambient light of layer 2 and 3 increases two orders of magnitude in both locations (Fig. 3C and D). This might indicate that the layers move upward faster than the reduction in incoming light. At dawn a similar, although less pronounced,

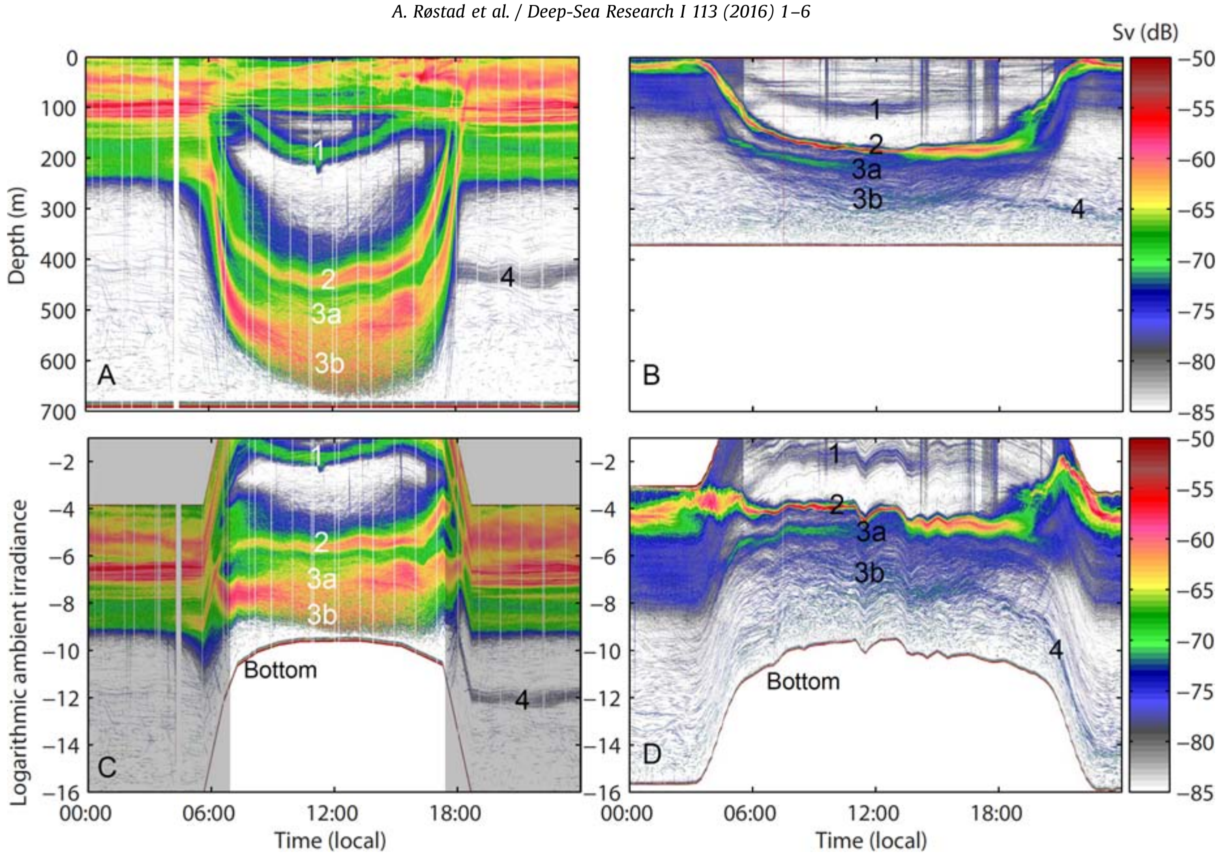

Fig. 3. Depth distribution of the acoustic scattering layers in the Red Sea on 15 November 2014 (A) and in Masfjorden on 16 August 2011 (B). The lower panels are based on the same observations, but instead of depth show the calculated ambient irradiance ($\log_{10}$) of the acoustic scatters for the Red Sea (C) and Masfjorden (D). The ambient irradiance (μmol quanta $m^{-2}\,s^{-1}$) was calculated from the surface broadband (Red Sea) and PAR (Masfjorden) and the corresponding K_{PAR} that were estimated from the underwater measurements at mid-day. We did not have observations of surface irradiance at night for the Red Sea and this period is indicated by grey shading in C.

pattern is indicated. We note, however, that our calculations of ambient irradiance are inaccurate, particularly during dusk and dawn. We assumed time-invariant light attenuation and surface reflectance coefficients. In nature these coefficients are higher at low sun angles and might therefore account for part of the increase in calculated ambient irradiance during dusk and dawn. Finally, the organisms of the SLs might be sensitive for variations in light at particular wavelengths that are not well reflected by variation in PAR.

At night time the combined layers 2 and 3 in Masfjorden occupied depths (upper 100 m, Fig. 3B) with ambient light similar to those observed at mid-day i.e. on the range 10^{-8}–10^{-4} μmol quanta $m^{-2}\,s^{-1}$ and with the strongest acoustic scatter (layer 2) on the range 10^{-5}–10^{-4} μmol quanta $m^{-2}\,s^{-1}$ (Fig. 3D).

Measurements of night light were not available for the Red Sea (indicated with shaded area in Fig. 3C). The calculated ambient night light of the mesopelagic SL was similar to the daytime range when the surface irradiance was set constant at 10^{-4} μmol quanta $m^{-2}\,s^{-1}$ (indicated with shaded area in Fig. 3C). This value is about one order of magnitude lower than the light level of a full moon (Jensen et al., 2001). At November 15 the moon was above the horizon after midnight and was lit about 45%.

4.4. Modelled photon capture rate

The calculated photon capture rates reported in Table 1 indicate the brightness a lantern fish (Myctophidae) perceive at mid-day. As shown by the ratio (last column of Table 1), the estimated photon capture at the SL boundary depths are similar, i.e. within one order of magnitude, in the Red Sea and Masfjorden. Although the wavelength composition was different at the two locations (the Red Sea is "bluer", not shown), the percentage photons captured were similar with ranges of 28–30% and 23–30% for different depths in the Red Sea and Masfjorden respectively. Consequently, the variation in photon capture reflected largely the variation in the total ambient irradiance as shown in Table 1 and Fig. 4C and D. A visual pigment sensitivity of 487 nm was used for the values reported in Table 1. The exact value of this sensitivity, however, appears not to be critical for the calculations. When this sensitivity was varied between 480 and 500 nm the resulting photon captures varied less than 10% (not shown).

5. Discussion

The taxonomic compositions of the two systems have not been assessed for the days presented here, and we briefly refer to knowledge from previous studies. In the most studied location, Masfjorden, the lanternfish *Benthosema glaciale* is the prevailing acoustic target in layer 3 (Kaartvedt et al., 2009; Dypvik et al., 2012b). The upper layers 1 and 2 are mainly composed of juvenile and adult pearlside *Maruolicus muelleri* respectively (e.g. Giske et al., 1990; Staby et al., 2011). Also in the Red Sea a lanternfish, *Benthosema pterotum*, prevails at depth (layer 3) (Klevjer et al., 2012; Dypvik and Kaartvedt, 2013). Catches in the Red Sea have been very scant; likely due to avoidance (cf. Kaartvedt et al., 2012). Myctophids rapidly accumulate, however, in the light beams of ROVs documenting their presence (Dypvik and Kaartvedt, 2013). Compared to Masfjorden backscatter in the Red Sea is surprisingly strong, yet how this translates to numerical abundance and biomass is unsettled as individual target strength (and the contribution of possible resonance which may enhance the backscatter) remains to be established.

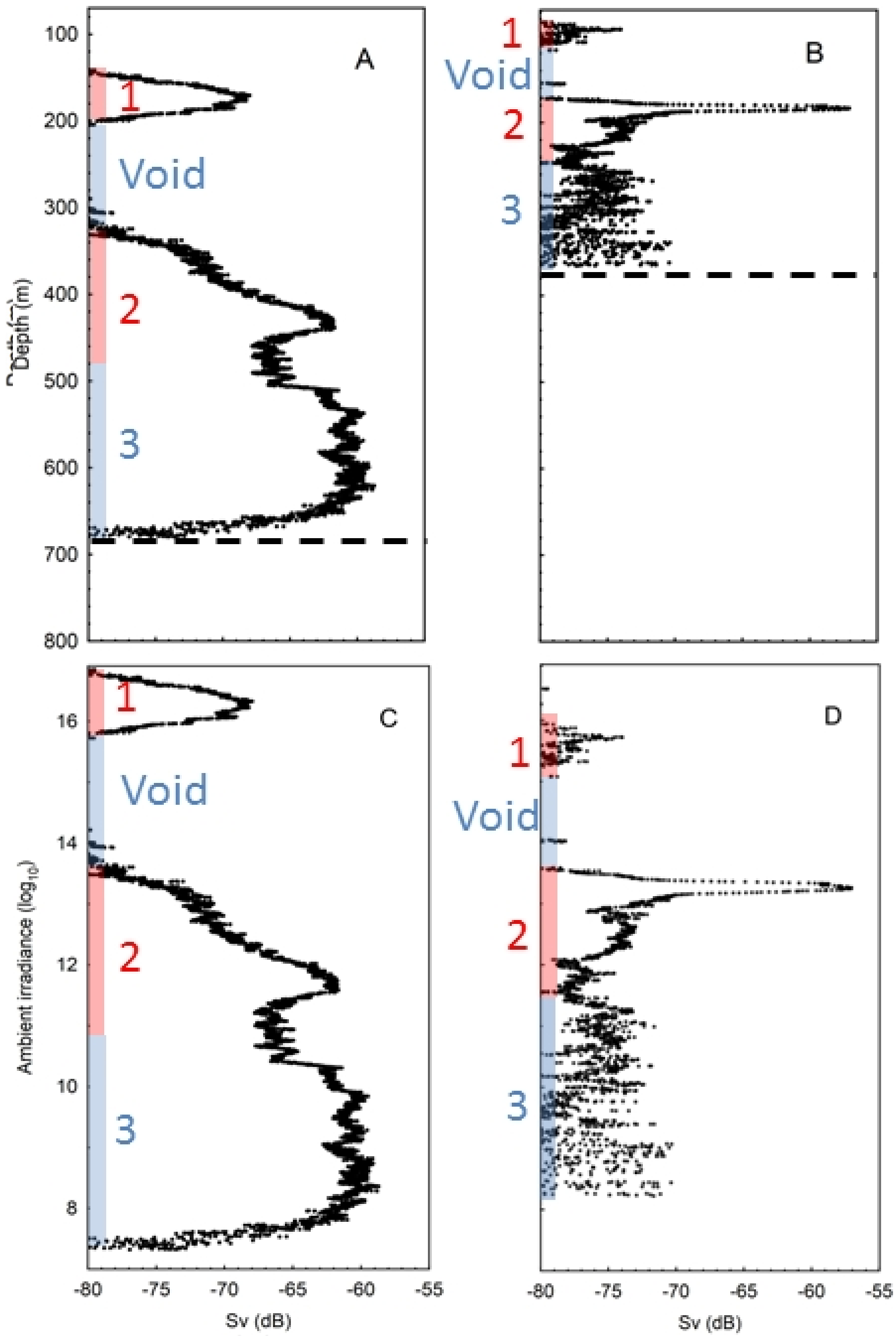

Fig. 4. Mid-day depth distribution of acoustic scatter in the Red Sea (A, 15 November 2014) and in Masfjorden (B, 16 August 2011). The lower panels are based on the same observations, but instead of depth show the total ambient irradiance (photons m^{-2} s^{-1}), i.e. obtained by summin over the measured spectrum, of the acoustic scatters of the Red Sea (C) and Masfjorden (D). Broken lines indicate location of bottom. The numbers correspond to the layers that are also indicated in Fig. 3 and Table 1.

5.1. Evidence of similar light comfort zones at the two locations

Given the physical and biological differences between the two systems it is striking that the calculated ambient irradiances of the acoustic layers, and also the estimated photon capture rates, were not that different (Table 1). The two LCZ predictions (Fig. 1) are: The murkier Masfjorden should have shallower, and also narrower, SL layers than the clear Red Sea. Quantitatively, this prediction can be expressed $H \propto K^{-1}$ where H (m) is either the depth of the SL or the vertical extension of the layer (Dupont and Aksnes, 2013). The reciprocal of the deepest $K_{470-500}$ (Fig. 2) were 27.3 and 16.7 m for the Red Sea and Masfjorden respectively. This provides the LCZ expectation that the SL of Masfjorden should be about 60% shallower, but also narrower, than the SL of the Red Sea. The depth localization and thickness of the layers (Table 1) appear consistent with this expectation. It is furthermore of interest that the thickness of the daytime “dead zone” that was observed, i.e. the acoustic void between layer 1 and 2, is also shallower and narrower in Masfjorden than in the Red Sea (Fig. 4 and Table 1).

The LCZ also implies that the daily SL variations within the two systems should disappear if the sound scatters are plotted as a function of their ambient light instead of depth. During periods around dusk and dawn, however, our results suggest that the ambient light of the organisms of the SL increases markedly in both locations (Fig. 3C and D), which is not consistent with the LCZ expectation. It has previously been speculated that such increased light exposure is governed by higher predation risk taking by the SL organisms in order to increase own visual food intake in a surface layer that is rich in prey organisms (e.g. Staby and Aksnes, 2011). As noted above, however, the apparent increase in light exposure might, at least in part, be due to inaccurate specification of underwater irradiance at low sun angles.

The results from Masfjorden indicate that the SL organisms expose themselves to similar light intensities (Fig. 3D) day and night, i.e. the LCZ is the same. Whether this also applies for the Red Sea and elsewhere needs to be addressed in future studies that measure spectral night light that allows the assessment of photon capture rates.

5.2. Recommendations for future studies

The results reported here are based on a one day comparison. Future studies based on more extensive data set, including seasonality as well as larger spatial coverage, are needed for a general evaluation of LCZ behavior. Our study suggests that such studies require measurements of irradiance levels that are much lower than commonly measured in biological oceanography. Changes in irradiance at levels which are ten orders of magnitude lower than daylight, appear significant to the organisms of the deepest SL. Night is often equated with dark in ecological studies. As shown for Masfjorden, however, night light might provide the SL organisms with the same ambient light they experience at daytime. Thus accurate characterization of variations in night light, including spectral resolution enabling photon capture calculation, is needed to fully characterize and understand the light governed behavior of mesopelagic organisms. Furthermore, future studies should avoid the inaccuracies invoked in calculating underwater light from measurements made in air, and rather strive to make continuous underwater measurements ideally at the depths of the SL organisms. According to our results this requires sensors detecting light intensities as low as 10^7 photons $m^{-2}\,s^{-1}$.

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Appendix A. Supporting information

Supplementary data associated with this article can be found in the online version at http://dx.doi.org/10.1016/j.dsr.2016.02.020.

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