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Food for Thought

Enlightening the ocean's twilight zone

Stein Kaartvedt[1*,†], Tom J. Langbehn[2], and Dag L. Aksnes[2†]

[1]*Department of Biosciences, University of Oslo, PO Box 1066, Blindern, Oslo 0316, Norway*
[2]*Department of Biological Sciences, University of Bergen, Norway, Bergen 5020, Norway*

**Corresponding author: tel: + 47 22854739; e-mail:* stein.kaartvedt@ibv.uio.no.
[†]These authors contributed equally to this study.

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By definition, the mesopelagic twilight zone extends from 200 to 1000 m depth. Rather than confining the twilight zone to a certain depth interval, we here propose a definition that covers absolute light intensities ranging from 10^{-9} to 10^{-1} µmol quanta m^{-2} s^{-1}. The lowest intensity of this twilight habitat corresponds to the visual threshold of lanternfishes (Myctophidae). The highest intensity corresponds to the upper light exposure of pearlsides (*Maurolicus* spp.), which have a unique eye adapted to higher light intensities than the lanternfishes. By this definition, the daytime twilight habitat extends deeper than 1000 m in very clear oceanic water, while may even be largely located above 200 m in very murky coastal waters. During moonlit nights in clear water, the twilight habitat would still extend deep into the mesopelagic depth zone, while becoming compressed toward the surface in dark nights. Large variation in night light, from 10^{-3} µmol quanta m^{-2} s^{-1} during moonlit nights to 10^{-8} µmol quanta m^{-2} s^{-1} in dark overcast nights, implies that division of light into night- and daylight is insufficient to characterize the habitats and distributional patterns of twilight organisms. Future research will benefit from *in situ* light measurements, during night- as well as daytime, and habitat classification based on optical properties in addition to depth. We suggest some pertinent research questions for future exploration of the twilight zone.

Keywords: deep scattering layer, habitat classification, light levels, light measurements, mesopelagic.

Introduction

The mesopelagic zone and the organisms forming its sound scattering layers are currently receiving increasing attention due to high biomass and biodiversity, the potential role in biogeochemical cycling, and as a prey zone for charismatic macrofauna (Irigoien *et al.*, 2014; St John *et al.*, 2016). This part of the ocean furthermore is affected by reduced oxygen content, with implications for the mesopelagic biota (Breitburg *et al.*, 2018). The mesopelagic zone is defined as the depth between 200 and 1000 m, but is also referred to as the dysphotic zone or the twilight zone. The strong vertical light gradient likely represents an important selective force with consequences for the mesopelagic biodiversity, structure, and vertical dynamics as represented by the ubiquitous diel vertical migrations (Pearre, 2003). The daytime light of the mesopelagic zone spans around 10 orders of magnitude in clear waters (Warrant and Locket, 2004). However, this span can change greatly from one location to another due to spatial variations in water clarity (Kampa, 1971; Røstad *et al.*, 2016a, b; Aksnes *et al.*, 2017). Furthermore, mesopelagic light intensities vary temporarily with diel cycles in the incoming sun-, moon-, and starlight, which are modulated with variation in cloudiness, sea ice, and latitudinal differences in day length.

Much of our knowledge of the vertical structure of the mesopelagic biota originates from remote observations of sound scattering layers, i.e. the acoustic signature of macroplankton and micronekton. Mesopelagic sound scattering layers were first discovered during World War II (Duvall and Christensen, 1946; Johnson, 1948), and were referred to as the deep scattering layers (DSL). Because the vertical location of these layers varies with surface light intensity, as well as with water column light penetration, they are not always located particularly deep. Being an acoustical signature, it should also be noted that DSL characteristics will vary with the acoustical method and that different studies might not be directly comparable.

The daily variation in depth location, recognized by the first DSL explorers, provided the first evidence that these layers are not a physical phenomenon, but rather caused by living organisms (Duvall and Christensen, 1946; Dietz, 1948; Johnson, 1948; Boden, 1950; Carson, 1951). Subsequent studies included measurement of *in situ* light (Kampa and Boden, 1954; Clarke and Backus, 1957, 1964; Clarke and Kelly, 1965). More than six decades ago, Clark *et al.* developed a light metre enabling the direct measurements of daylight at more than 900 m depth and moon light at several hundred metres depth (Clarke and Kelly, 1965). Such high sensitivity matches that of e.g. mesopelagic fishes, which are an important component of the sound scattering layers. These fishes hold diverse visual adaptations that optimize light collection and can exploit very faint light (Warrant and Locket, 2004).

Even though the mesopelagic zone is identified relative to light and characterized by a huge span in light intensities, *in situ* light is seldom measured in present-day mesopelagic studies. Accordingly, recent global biogeographic classifications of the mesopelagic zone did not include light among the environmental parameters used to identify the vertical and spatial delineation of mesopelagic provinces (Proud *et al.*, 2017; Sutton *et al.*, 2017; Reygondeau *et al.*, 2018). In spite of huge technological progress and improvements in development of oceanographic instrumentation during the last decades, there has been surprisingly little methodological focus to improve our understanding of the light climate for the inhabitants of the twilight zone (but see Widder *et al.*, 1992; Frank and Widder, 2002; Haag *et al.*, 2014). Lack of standardized and commercially available light metres with required sensitivity is likely the reason why mesopelagic light characterization is commonly not included in contemporary studies. Thus, recent analyses of the global mesopelagic sound scattering distribution (e.g. Bianchi *et al.*, 2013; Irigoien *et al.*, 2014; Klevjer *et al.*, 2016; Proud *et al.*, 2017) involve correlations with routinely monitored variables such as temperature, dissolved oxygen, and fluorescence. Other studies have extrapolated mesopelagic light intensities from *in situ* measurements in the epipelagic (Røstad *et al.*, 2016a, b; Aksnes *et al.*, 2017) or from ocean colour (e.g. Bianchi *et al.*, 2013; Netburn and Koslow, 2015).

Although mesopelagic light attenuation might correlate with attenuation in upper water, early on it was recognized that to extrapolate absolute light intensity from measurements in shallower water introduced large uncertainties (Kampa, 1955, 1971). Thus it appears pertinent to repeat the message of Kampa (1971): "… it is now time to measure, rather than calculate, conditions at the depths of any sonic scatterers that appear to be photo oriented before drawing conclusions about their behavior". With the renewed interest in exploration of life in the twilight zone, we find it timely to summarize and synthesize current knowledge on the association between the mesopelagic sound scattering layers and the light environment. We here consider natural downwelling light, which becomes diffuse at twilight depths, although recognizing that moonlight and starlight might be perceived as beam light by twilight organisms occupying the upper water column at night and responses to light beams (point sources) might differ from those to diffuse light (Blaxter and Currie, 1967; Warrant and Locket, 2004). We search for general patterns on how such downwelling light affects the DSL organisms. From this we outline hypotheses and research questions that we believe future research of the twilight zone can benefit from. Such research questions span from twilight effects on global distributional patterns of the DSL organisms to distribution in oxygen minimum zones and microbial hot spots (see Table 1).

Variations in the vertical extent of the twilight zone

Rather than confining the mesopelagic twilight to a metric depth interval, we will here demarcate the twilight zone as a fixed range of light intensities. The depth and the vertical extent of this zone is determined by the incoming light at the sea surface (i.e. bioluminescent sources are not considered) and the water column light attenuation. The downwelling irradiance (E_z) of a particular wavelength (λ) at depth (z) is given according to:

$$E_z(\lambda) = E_0(\lambda)e^{-K(\lambda)z}, \quad (1)$$

where $E_0(\lambda)$ is the downwelling irradiance just below the sea surface. $K(\lambda)$ is the attenuation coefficient of downwelling irradiance, which is here represented by the attenuation coefficient for the depth range between the surface and the depth z. Note, however, that $K(\lambda)$ varies with the angular distribution of light and the optical constituents of the water. Consequently, attenuation varies with depth, particularly in upper waters, but this is not elaborated here. In marine ecological studies underwater light is often measured by a PAR sensor (photosynthetically active radiation within 400–700 nm), and attenuation (K) is calculated according to PAR attenuation. Below, we will refer to such quantities although we emphasize that future mesopelagic twilight studies should ideally involve wavelength-resolved measurements. This is essential in studies addressing vision and associated quantities like eye photon capture (Turner *et al.* 2009).

When the sun is high in the sky, the downwelling irradiance just below surface is of the order of 10^3 µmol quanta m^{-2} s^{-1} in the PAR band. In very clear oceanic water ($K = 0.025\,m^{-1}$, approximated for the PAR band), the intensity has fallen to about 10^{-8} µmol quanta m^{-2} s^{-1} at 1000 m. The distribution of these quanta is more narrow than the surface light, with peak intensity typically around 480–490 nm. Denton (1990) considered a threshold depth of around 1000 m at which a fish can see downwelling sunlight in the clearest ocean water. Turner *et al.* (2009) assessed the photon catch rate of a lantern fish (Myctophidae) retina containing the most sensitive visual pigment at 1000 m in the Sargasso Sea as the visual threshold limit. They calculated this threshold to be 10^9 photons m^{-2} s^{-1} or 1.6×10^{-9} µmol quanta m^{-2} s^{-1}. This corresponds to the light level calculated for the lower edge of DSL in the relatively transparent Red Sea (Røstad *et al.*, 2016a, b). This level appeared to be actively chosen by the deepest living DSL organisms, as evidenced by instantaneous upwards shift in distribution following the darkening by a passing storm (Kaartvedt *et al.*, 2017). If 10^{-9} µmol quanta m^{-2} s^{-1} is taken as the lowest light intensity of the twilight zone, the deepest twilight depth (T_D) is:

$$T_D \approx -\ln\ (10^{-9}/E_0)/K \quad (2a)$$

Note that this approximation [as well as Equation (2b)] ignores depth and wavelength resolution and that this is required in a more precise treatment.

The pearlsides (*Maurolicus* spp.) are small fishes inhabiting the upper mesopelagic zone and have evolved a unique type of eye that operates at higher light intensities than e.g. the myctophids (de Busserolles *et al.*, 2017). The ambient light of the shallowest scattering layer of the youngest age group of *Maurolicus muelleri*

Table 1. Hypotheses related to the ocean twilight.

Hypotheses	Arguments	Action
Light exposure of the daytime DSL is largely similar between geographic regions.	Available data show a correlation between water clarity and vertical distribution of the DSL. It is not known to what extent outliers from predictions relate to methodological constraints or biological variability.	Measure mesopelagic light and extend the geographic coverage of observations to include very clear and very murky waters.
Light exposure during day and night is comparable in vertically migrating organisms.	Preliminary data suggest that vertically migrating organisms forming the DSL expose themselves to a limited range of light intensities throughout the diel cycle, yet documentation of relation to nocturnal light is largely lacking.	Establish ambient wavelength resolved light measurements for day and night.
Light climate in polar regions hampers success of mesopelagic fish.	The extreme photoperiod in the Arctic hampers the access to upper waters in summer and visual foraging at depth in winter. Huge ocean areas in Antarctica become ice covered during long winter periods, causing a dark under-ice environment that may hamper visual prey detection.	Establish DSL distribution and its components relative to photoperiod (latitude). Assess under-ice light environment.
Trophic transfer efficiency from phytoplankton to mesopelagic fish is particularly high in clear oligotrophic oceans.	Clear waters afford visual planktivores longer sighting distance and an extended vertical habitat.	Add water clarity as factor in studies of trophic structure and production.
Hypoxia results in darker waters with an upward shift in the twilight zone causing shallower distribution of the DSL.	The distribution of DSL organisms is shallower in the OMZs, but still penetrates into the low oxygen waters. Release of CDOM from microbial heterotrophic degradation of particulate organic matter may result in elevated light attenuation in oxygen-depleted waters.	Measure transparency relative to hypoxia. Assess the hypothesized association between hypoxia and CDOM.
Light conditions (water clarity) determine depths of mesopelagic microbial hot spots.	Excretion by mesopelagic micronekton with a light-dependent vertical distribution stimulates microbial activity.	Assess microbial processes relative to vertical DSL distributions along gradients of water clarity.

DLS, deep scattering layers; OMZ, oxygen minimum zone; CDOM, coloured dissolved organic matter.

is around 10^{-1} µmol quanta m^{-2} s^{-1} which amounts to a daytime depth shallower than 100 m, and consequently within the epipelagic, in murky coastal water (Staby and Aksnes, 2011). In more transparent water, however, 10^{-1} µmol quanta m^{-2} s^{-1} is found at daytime depths of 370 m and 230 m for a K of 0.025 and 0.04 m^{-1} respectively (assuming surface irradiance of 10^3 µmol quanta m^{-2} s^{-1}), which are within the mesopelagic. If 10^{-1} µmol quanta m^{-2} s^{-1} is taken as the upper light level of the twilight zone, the shallowest twilight depth is (T_S):

$$T_S \approx -\ln(10^{-1}/E_0)/K \tag{2b}$$

Equations (2a) and (2b) illustrate how the twilight zone varies with surface light intensity and water column light attenuation. For example with $K = 0.025\ m^{-1}$, the daytime twilight zone is around 370–1100 m, while with $K = 0.1$ the majority of the metrically defined mesopelagic zone lays in bathypelagic darkness (Figure 1).

The transparency of the upper 200 m determines the fraction of the surface light that enters the upper boundary of the mesopelagic zone. In oceanic waters, this transparency depends to a large degree on the water column productivity and the light attenuation caused by phytoplankton. Within the mesopelagic zone, the variation in transparency is much less than in the epipelagic zone (Jerlov, 1976). Nevertheless, the mesopelagic transparency is not homogenous, and variations in mesopelagic light attenuation appear to affect the depth of the sound scattering layers (Kampa, 1971; Aksnes *et al.*, 2017) and individual mesopelagic organisms (Frank and Widder, 2002). To our knowledge, only a few studies have measured light penetration in the mesopelagic (e.g. Kampa, 1971; Roe, 1983; Frank and Widder, 2002). Kampa (1971) compared attenuation of downwelling irradiance (K) at depths greater than 200 m in different coastal regions of the Atlantic and Pacific Oceans. She found a span from 0.024 m^{-1} (at 480 nm) for mesopelagic waters off Tenerife to 0.06 m^{-1} in the San Diego Trough. About the same span was found, with a proxy method based on direct measurements, for open-ocean areas between 40° N and 40° S in the Atlantic, Indian, and Pacific Oceans (Aksnes *et al.*, 2017). This span might appear modest compared to the much larger variation of K in the euphotic zone, but causes large variations in location of the twilight zone. For example the daytime twilight zone, 370–1 100 m, in clear water ($K = 0.025\ m^{-1}$) shoals

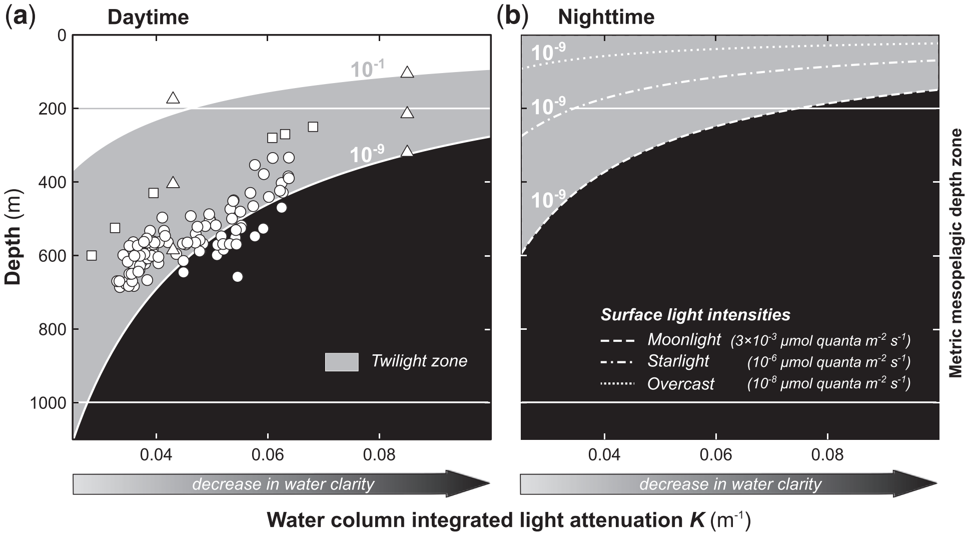

Figure 1. The vertical extension of the twilight zone, defined as the depth interval where the light intensity is between 10^{-9} and 0.1 μmol quanta m^{-2} s^{-1}, at daytime (a) and night-time (b) as a function of water column light attenuation. Daytime surface light intensity is assumed to be 1000 μmol quanta m^{-2} s^{-1}. Daytime data points correspond to the mean depth of the sound scattering layers reported for the circumglobal Malaspina Expedition (circles, Aksnes *et al.*, 2017), for regions in the North Atlantic and Gulf of California (squares, approximated from fig. 4 in Kampa, 1971), and for three different vertical sound scattering layers in the Red Sea and Masfjorden (triangles, Røstad *et al.*, 2016a, b). The light intensities of Kampa (1971) were converted to total irradiance by the use of an empirical relationship between PAR and irradiance at 480 nm that was derived from measurements below 100 m in the Red Sea (Røstad *et al.*, 2016a, b).

to 150–460 m in the less transparent water ($K = 0.06$ m^{-1}) (Figure 1). The daytime twilight zone is here shallower, but also narrower, than that calculated for bright moonlight and clear water. Hence—and noteworthy—increasing the light attenuation coefficient with a factor 2.4 has more impact on the shoaling of the twilight zone than a one million times decrease in surface light intensity.

High light attenuation can give rise to very pronounced compressions of the twilight zone. This is well illustrated by Lurefjorden, a Norwegian fjord that contains coastal water with a light attenuation coefficient slightly above 0.1 m^{-1} (at 500 nm) down to its maximum depth of 440 m (Bozman *et al.*, 2017). This gives a daytime twilight zone extending from about 90 to 280 m, which means that most of this compressed twilight zone is actually located in the epipelagic during daytime, and that the deepest part of this relatively shallow fjord always corresponds to that of the bathypelagic zone with regard to the light environment. The presence of a persistent and exceptionally large mass occurrence of the deep-water jellyfish, *Periphylla periphylla*, has been associated with the dark light regime of this fjord (Eiane *et al.*, 1999; Bozman *et al.*, 2017).

The light exposure of sound scattering layers

Above, we described how the vertical extent of a twilight zone, as defined according to a particular range in light intensity (from 10^{-1} to 10^{-9} μmol quanta m^{-2} s^{-1}), changed with temporal variations in surface light and spatial variations in light penetration. To what extent do such variations affect the organism of the twilight zone? A large number of studies have documented a tight correlation between the depth of the acoustic scattering layers and the surface light as seen on the daily scale in DVM (e.g. Pearre, 2003; Bianchi and Mislan, 2016). This also applies at shorter time scales in connection with variable cloudiness (Blaxter and Currie, 1967; Kaartvedt *et al.*, 2017) and solar eclipses (Backus *et al.*, 1965; Tont and Wick, 1973; Kampa, 1975). Although such correlations with surface light are well documented, less is known about the actual ambient light exposure of these layers. To what extent are they exposed to similar light intensities in different regions and across the global ocean, and is the light exposure at night similar to that of daytime? Below we evaluate available information that provides some insight into these questions.

Is light exposure of mesopelagic organisms similar across regions?

To our knowledge, Kampa (1971) was the first to compare ambient light of a mesopelagic sound scattering layer across regions. The upper daytime depth of a ubiquitous subtropical oceanic layer varied from a minimum of around 250 m in the Gulf of California to 600 m in the eastern North Atlantic (Figure 1). Still, the ambient light at the top of the scattering layer was similar (10^{-7}–10^{-6} W m^{-2} nm^{-1} at 480 nm). Variation in water column light penetration accounted for the variation in depth, with the murkiest and clearest water in the Gulf of California and in the North Atlantic respectively. In a comparison of the relatively transparent Red Sea with a murkier Norwegian fjord, Røstad *et al.* (2016a, b) also found that different depth distributions (Figure 1) were accounted for by different water column light penetration, and that the light exposure of the scattering layers in these two quite different environments was similar. Correspondingly, Dickson (1972) suggested that light penetration was a first-order factor determining daytime depth in the North Atlantic Ocean. This notion was based on a striking positive correlation between transparency as observed by Secchi depth and the depth of sound scattering layers. Similarly, Isaacs *et al.* (1974)

and Tont (1976) found that DSL daytime depth was correlated with transparency in the Californian Current and Peru Current. Kaartvedt *et al.* (1996) provided corresponding evidence from fronts in the Norwegian Sea where scattering layers shoaled with increased light extinction.

On the global scale, two recent studies Bianchi *et al.* (2013) and Irigoien *et al.* (2014) confirmed pronounced variation in the depth distribution of the mesopelagic scattering layers. Both Bianchi *et al.* (2013) and Klevjer *et al.* (2016) (analysing data from the Malaspina expedition; Irigoien *et al.*, 2014) found a correlation with dissolved oxygen, i.e. that hypoxic areas tended to have shallower sound scattering layers. Both studies found that the backscatter still appeared deep into the hypoxic and anoxic waters at daytime, indicating that oxygen limitation *per se* might not be the cause for the shallower distribution. In a further analysis of the Malaspina data, using *in situ* light measurements in the upper 150–280 m and an empirical light attenuation model for depths below, Aksnes *et al.* (2017) established the light regime throughout this circumglobal transect. Similar to Kampa (1971), variation in light penetration accounted for much of the depth variation (Figure 1). The average light intensity at the median depth of the sound scattering distribution was around 10^{-7} µmol quanta m^{-2} s^{-1}, with a span from10^{-9} to 10^{-6} µmol quanta m^{-2} s^{-1} at the 25% and 75% quartile depths, respectively (Aksnes *et al.*, 2017). This light exposure was similar for the hypoxic and the oxygenated stations. The correlation between the depth of the scattering layer and dissolved oxygen previously reported by Klevjer *et al.* (2016) was explained by another (negative) correlation, i.e. between light attenuation and dissolved oxygen potentially caused by elevated concentrations of light absorbing DOM in hypoxic water according to Aksnes *et al.* (2017). Thus, similar to the result of Kampa (1971), ambient light appears to be first-order factor determining daytime depth of the acoustic scattering layers observed across the circumglobal Malaspina Expedition transect.

Summarizing available data on light extinction and vertical distribution of mesopelagic acoustic backscatter, distributions largely follow predictions relative to light conditions, though with some examples of deeper distributions than expected for the Malaspina data (Figure 1) where the establishment of mesopelagic light is based on proxies and not direct measurements. To what extent such deviations from predictions refer to biological variation or methodological factors remain to be established, underlining the need for measurements of mesopelagic light conditions. We are not aware of concurrent data on ambient light and vertical distribution of the DSL in very murky waters. However, Sassa *et al.* (2010) captured the lanternfish *Benthosema pterotum* at 40–90 m at the shelf region in the East China Sea, ascribing the particularly shallow distribution to greatly reduced light penetration caused by highly turbid waters.

Is light exposure similar day and night?

Moonlight and starlight are of no importance for photosynthesis, but play an important role in photoreception and vision. Bright moonlight intensity is about 3×10^{-6} that of sunlight (Denton, 1990), i.e. on the order 3×10^{-3} µmol quanta m^{-2} s^{-1}. This provides a full-moon night-time twilight zone extending from the surface down to 600 m depth in very clear water ($K = 0.025\ m^{-1}$; Figure 1). Thus, also at night-time, the vertical extent of a twilight zone can be quite wide and, at least in theory, provide conditions for e.g. visual foraging at large depths. In sole starlight, where the surface light is about 10^{-9} that of daylight (Ryer and Olla, 1999), i.e. 10^{-6} µmol quanta m^{-2} s^{-1}, the nocturnal twilight depths in clear waters extends from the surface to 280 m. During heavy cloudiness, light levels may be further reduced by ~1–2 orders of magnitude (de Busserolles *et al.*, 2017; Kaartvedt *et al.*, 2017). According to the definition introduced here, if the surface light falls below 10^{-9} µmol quanta m^{-2} s^{-1}, there will be no twilight habitat. Such dark conditions apparently may be restricted to night in ice-covered oceans.

Obviously, mesopelagic organisms that do not ascend at night (Klevjer *et al.*, 2016) will experience large daily variations in light exposure. For the migrating animals of the sound scattering layers, a key question is how light at night compares to that during the day. It is noteworthy that incoming light at night actually varies much more than fluctuating daylight. While the surface daylight may vary 1–2 order of magnitudes depending on weather, the light at night may vary up to 5 order of magnitudes, depending on weather and state of the moon (Figure 1; disregarding the special cases of bright summer nights and mid-night sun at high latitudes).

Day and night comparisons of the ambient, as well as the light perceived by migrating organisms, involve several methodological challenges. The spectral distribution of light at the surface is broader than at mesopelagic depths, where downwelling irradiance peaks narrowly around at ~480 nm (Widder and Frank, 2001; Palmer and Johnsen, 2015). This is close to the peak sensitivity of the rod visual pigments in e.g. myctophids and other mesopelagic fish taxa (Warrant and Locket, 2004). This sensitivity may also have evolved for maximum sensitivity to bioluminescence rather than to ambient light, as the amount of light from biological sources may override the light coming from above (Warrant and Locket, 2004; Turner *et al.*, 2009). Nevertheless, for an individual moving upwards in the water column, a successively larger fraction of the total ambient light is of less relevance for a visual system optimized at ~480 nm. A vertically migrating mesopelagic fish may have identical photon capture, i.e. perceive the same light intensity, in shallow waters at night as at deep waters at day, even if a PAR sensor summing photons from 400 to 700 nm indicates a higher light exposure at their shallow nighttime depths than at their deeper daytime depths. Note however that Warrant and Locket (2004) refer to an example of a myctophid apparently having additional pigments sensitive to wavelengths only experienced in upper layers. They speculate that this may contribute in nocturnal food search in upper layers. One way to estimate the perceived light in future studies would be to calculate the photon capture, which depends on the wavelength distribution of the ambient light as well as the spectral absorbance properties of the eye pigment and photoreceptor in question (Turner *et al.*, 2009; Røstad *et al.*, 2016a, b). Below we can only make tentative assessments of how the light exposure of migrating sound scattering layers compares from day (in deep water) to night (in shallow water).

Norheim *et al.* (2016) estimated the day and night light exposure for a vertically migrating DSL along a northward gradient in the Norwegian Sea in summer. Nights were relatively bright, although not with midnight sun. The night light increased several orders of magnitude as the ship moved toward higher latitudes. The sound scattering layer migrated successively less as the night light increased, i.e. the ascent toward surface at dusk halted at successively deeper depths. The mean depth of the sound scattering layer, which varied with more than 300 m, had approximately the same ambient light, 2×10^{-6} mW m^{-2}nm^{-1} (at 486 nm), during night-time as during daytime. Because ambient light was measured at a wavelength presumably relevant for the visual system of the migrators, the methodological challenges mentioned above were partly accommodated in this particular study. Integrated over all wavelengths, the ambient light corresponded to 1.9×10^{-7} μmol quanta m^{-2} s^{-1}. This value is similar to that reported for the median depth of the daytime sound scattering distribution observed during the Malaspina Expedition (Aksnes *et al.*, 2017).

The surface nightlight with a full moon and sole starlight are about 10^{-6} and 10^{-9} of daylight respectively, i.e. on the order of 10^{-3} and 10^{-6} μmol quanta m^{-2} s^{-1}. This suggests that light at full moon is ∼2 orders of magnitude higher than light levels at the upper part of the DSL in daytime. Evidence of the importance of moonlight for DSL vertical distribution is mostly circumstantial, primarily referring to the state of the moon. Early accounts noted that the vertically migrating scattering layers indeed tended to stay deeper in bright moonlight than on dark nights (Dietz, 1962). Based on net catches of myctophids, Clarke (1973) concluded that most species stayed 50–75 m deeper during the full compared to the new moon. However, this deeper distribution did not appear to compensate fully for the increased light (Clarke, 1970). Wang *et al.* (2014) and Prihartato *et al.* (2016) analysed acoustic datasets with extensive temporal and geographic coverage, respectively, and concluded that full moon caused deeper nocturnal scattering layers. In both cases, responses did not relate linearly to moon phase, with shifts toward deeper distributions first being evident following 65%–75% of full moon. This pattern may result since the brightness of the moon does not increase linearly, but exponentially with the moon phase (Lane and Irvine, 1973; Palmer and Johnsen, 2015). Brightness of the moon is also affected by the position of the moon in the sky (Lane and Irvine, 1973; Palmer and Johnsen, 2015) and lunar phase is an uncertain proxy for downwelling irradiance at the sea surface. This again underlines the need for *in situ* night measurements. Benoit-Bird *et al.* (2009) measured nocturnal light at sound scattering layer depths with a sensor having spectral peak sensitivity at 550 nm chosen to match the spectral peak of nocturnal light. They found that the scattering layers stayed deeper at full moon and furthermore that light levels were higher than would be experienced at daytime depth. Yet in their analysis, lunar phase appeared more important than lunar illumination *per se* and Benoit-Bird *et al.* (2009) suggested an endogenous lunar rhythm in the migration.

Results on predators foraging on vertically migrating mesopelagic prey represent another line of evidence that strong moonlight hampers vertical ascents. Nocturnal diving depth of various air-breathing predators such as seals, dolphins, and birds foraging on migrating mesopelagic prey is related to the lunar cycle, with deeper dives during full moon when their mesopelagic prey arrest upward migrations at deeper depths (e.g. Horning and Trillmich, 1999; Connan *et al.*, 2007). In Galápagos fur seals with limited diving capacities, reduction in foraging efficiency apparently results in weight loss during full moon when prey is out of reach (Horning and Trillmich, 1999). Such responses to light nights suggest reduced predation on the mesopelagic vertical migrators. Light nights potentially also cause reduced feeding for the mesopelagic vertical migrators in cases where their prey are concentrated in the upper waters. Hernandez-Leon *et al.* (2010) found that mesozooplankton biomass fluctuated according to the lunar cycle and peaked during full moon. They ascribed this pattern to reduced mortality in light nights when migrating mesopelagic fish avoided upper layers.

Surface light intensity of a starlit night (∼10^{-6} μmol quanta m^{-2} s^{-1}) roughly corresponds to the light levels of the shallowest part of the oceanic DSL reported in Norheim *et al.* (2016). It thus appears that starlight would commonly offer an upper water twilight habitat overlapping with shallow-living prey. In tropical waters foraging of vertically migrating myctophids has been documented throughout the night (Dypvik and Kaartvedt, 2013). Surface light levels on dark, overcast nights are about one order of magnitude higher than the sensitivity limit of myctophid eyes and the lower edge of the daytime DSL, which we here have used in demarcating the lower limit of the twilight zone. So, even dark nights might provide a thin upper layer with light that might be exploited by the most dark-adapted species. To what extent foraging success is related to weather conditions (i.e. cloudy vs. clear skies) is not known. Yet we expect that the nocturnal foraging conditions may differ between high pressure (clear nights) and low pressure (dark nights) regions. In ice-covered waters, there would not be any twilight at all during dark overcast nights.

The more shallow-living mesopelagic pearlside *Mauroliccus* spp. is adapted for life at intermediate (mesopic) light intensities (de Busserolles *et al.*, 2017). They form daytime acoustic scattering layers that are shallower than what is normally termed as the DSL. Moreover, *Maurolicus* inhabits upper waters throughout the relatively light summer nights at high latitudes (Rasmussen and Giske, 1994; Prihartato *et al.*, 2015). In darker nights, *M. muelleri* appears to stop feeding (Rasmussen and Giske, 1994), displaying "mid-night sinking" after migrating to surface waters at dusk and before a subsequent dawn ascent providing favourable light conditions (Prihartato *et al.*, 2015). So while e.g. myctophids appear hampered by bright nights due to exclusion from upper waters (Sameoto, 1989; Norheim *et al.*, 2016), upper water foraging of pearlsides is hampered in dark nights and appear to be favoured under dusk conditions.

Isolume attraction or light comfort zone?

A recurrent question is whether organisms adhere to a particular light intensity, sometimes referred to as an isolume (e.g. Kampa and Boden, 1954; Clarke and Backus, 1957; Ringelberg, 1995; Cohen and Forward, 2009). During dusk when sunlight diminishes, an isolume will ascend (i.e. move towards surface) while descend during dawn. Kampa and Boden (1954) observed that the DSL moved along with isolume movements, yet the light of the ascending scattering layer was more than 10 times higher than during descent. Clarke and Backus (1957) observed that the ascending DSL was exposed to more than 100 times higher light intensity when at shallower depth around sunset than at midday and concluded that other behaviour than the following of a certain light intensity was involved. These early observations, combined with the fact that scattering layers and species distributions have extended depth distributions and thereby considerable span in light exposure, clearly suggest that the organisms of a DSL are not attracted by one common light intensity. It is now usual to regard light-associated DVM as emergent and flexible (Clark and Levy, 1988; Giske *et al.*, 2013) rather than a hard-wired unconditional response such as implied by obligate attraction to a specific light intensity. Individual state (such as size, maturation level, hunger, parasites, etc.) and physiological adaptations to light levels (Myslinski *et al.* 2005) can control behaviour in synergy with environmental factors.

Studies of species known to constitute sound scattering layers (e.g. Roe, 1983; Frank and Widder, 2002) demonstrate that they distribute vertically across light intensities that span several orders of magnitude. The study of Frank and Widder (2002), who measured *in situ* light and animal distribution simultaneously, provides compelling evidence that several species of vertically migrating euphausiids, salps, and sergestids adjusted their depth distribution to remain within a range of preferred irradiance. Røstad *et al.* (2016a, b) used the term "light comfort zone" (LCZ) for the phenomenon that acoustic scattering layers in different locations occupied depths that were characterized by a certain range of light intensities. Rather than attraction, LCZ might imply avoidance, i.e. of too high as well as too low light intensity, and where the two intensities differ with several orders of magnitude. It might be hypothesized that a LCZ has emerged as the evolutionary solution to the trade-off conflict between visual foraging opportunities and visual predation risk (Clark and Levy, 1988; Pearre, 2003; Giske *et al.*, 2013), giving a light span that was termed the antipredation window by Clark and Levy (1988). In the words of Boden and Kampa (1967): "... diurnal vertical migration of animals where light is appreciable are directly controlled by light and represent the animals' effort to remain within a comfortable and/or useful photo environment".

In theory, a zooplanktivorous mesopelagic fish occupying a LCZ can be a visual predator at any time and any depth if zooplankton prey is present. Thus, the common general DVM explanation "feed at night and hide at day" is not always relevant if the LCZ concept applies. Mesopelagic fish foraging in their daytime habitat has repeatedly been documented, including predation on *Calanus* spp. copepods overwintering at mesopelagic depths (Pearcy *et al.*, 1977; Bagøien *et al.*, 2001; Dypvik *et al.*, 2012). Long-term acoustic studies of DSLs ascribed to the lanternfish *Benthosema glaciale* have documented persistent inverse diel vertical migration for part of the population in fall and winter, in which fishes ascend to ~200 m depth at day and descend 50–100 m at night (Dypvik *et al.*, 2012). The suggested interpretation is that the lanternfish forages at the upper fringe of overwintering *Calanus* in daytime, where light conditions provide the best trade-off between feeding and predator avoidance, i.e. a deep "antipredation window" or LCZ. In this situation the lanternfish do not follow a LCZ toward the surface at dusk, but rather sink into deeper and darker waters at night, corresponding to the upper-layer midnight sinking of the pearlside *M. muelleri*. Light appears to be the driver for the subsequent upward daytime migration. It might be speculated that successful daytime foraging at depth demotivates a nocturnal ascent (Pearcy *et al.*, 1977; Dypvik *et al.*, 2012), or that the potential gain does not justify an ascent as food in upper waters is less abundant during winter.

Can latitudinal variation in photoperiod explain variations in mesopelagic structure and dynamics?

The depth position of the ocean twilight zone depends on surface light, which holds a strong latitudinal component. The photoperiod becomes particularly extreme in the Arctic and Antarctica north of 67°N and south of 67°S (polar circle), with progressively longer and pronounced periods of midnight sun and winter darkness. Ice cover adds to the latter, but also affects light conditions in spring and early summer. Because of these photoperiod extremes, shortage of appropriate light habitat overlapping with concentrations of potential prey might explain why the Arctic Ocean is poor in mesopelagic fish and those present appear to be adult expatriates (Sameoto, 1989; Kaartvedt 2008).

Similarly in the Southern ocean, abundance of mesopelagic fishes decrease and their body sizes increase with increasing latitude (Saunders *et al.*, 2017; Escobar-Flores *et al.*, 2018). Moreover, the majority of myctophids in cold Antarctic waters appears to be expatriates (Saunders *et al.*, 2017). Much of the Southern Ocean has less extreme photoperiod than the Arctic due to lower latitudes. Yet Dietz (1962) found that "...near Antarctica, where the nights were reduced to a mere four hours, the [diel] migrations seemed to break up in confusion. The organisms of the shadows apparently could not cope with a 20-hour day". Moreover, vast areas south of the polar front become ice covered every winter (Zwally *et al.*, 1983). Arndt *et al.* (2017) found 4–5 orders of magnitude reduction in the light level under snow-covered Antarctic ice, and Ainley *et al.* (1986) concluded that the physical environment immediately beneath the Antarctic ice was reminiscent of the mesopelagic zone. They observed mesopelagic crustaceans in surface waters under ice, the same species only captured deeper than 300 m in ice-free waters. The abundance of mesopelagic fish appeared to decline with the ice (Ainley *et al.*, 1986). Consequently, evaluating consequences on the mesopelagic biota of a less dark ocean following projected reduced ice (Maksym, 2019) is a relevant topic associated with global warming (cf. Langbehn and Varpe, 2017).

High trophic transfer efficiency in the clear oligotrophic ocean?

Irigoien *et al.* (2014) found that the energy transfer efficiency from phytoplankton to mesopelagic fishes in the clear oligotrophic ocean was higher than typically assumed. They proposed that this might be due to increased visual foraging opportunities by mesopelagic fishes in clear oceanic water. Clear waters afford visual predators longer sighting distance than in more productive and turbid shelf and coastal waters, but also an extended vertical habitat since light penetrates deeper (Irigoien *et al.*, 2014). To the extent that the LCZ and the antipredation window (Clark and Levy, 1988; Røstad *et al.* (2016a, b) applies, this means that the fishes can forage over a larger vertical habitat than in murkier water. The question if high transfer efficiency governed by water clarity can explain the apparently high mesopelagic fish biomass in the open ocean is of particular relevance since the oligotrophic ocean areas are expected to increase in size following enhanced stratification with global warming (Cabré *et al.* 2015).

Association between ocean twilight and hypoxia?

The oxygen content of the open ocean is declining at accelerating pace and the minimum zones of the worlds' oceans are expanding both horizontally and vertically (Breitburg *et al.*, 2018). One suggested consequence is that oxygen limitation will force mesopelagic organisms upward, thereby becoming more vulnerable to visual predators (Koslow *et al.*, 2011; Bianchi *et al.*, 2013; Netburn and Koslow, 2015). Results from the Malaspina expedition (Klevjer *et al.*, 2016; Aksnes *et al.*, 2017), however, showed that even with shallower distribution in hypoxic waters, the DSL light exposure was similar to that found in oxygen-rich water columns elsewhere.

The DSL actually was located deep into the hypoxic zone during daytime so, rather than low oxygen concentrations, low light penetration may cause the shallow DSL distributions found in hypoxic water columns (Aksnes *et al.*, 2017). Low light penetration appears to be associated with low oxygen concentration in the open ocean mesopelagic (Aksnes *et al.*, 2017) as well as in the mesopelagic of coastal systems (Aksnes *et al.*, 2009).

A possible mechanism involves the release of coloured dissolved organic matter (CDOM) from microbial heterotrophic degradation of particulate organic matter. The higher apparent oxygen utilization (AOU) of oxygen-depleted water suggest higher past microbial activity and thereby potentially higher concentrations of bio-refractory light absorbing DOM (Yamashita and Tanoue 2008, Aksnes *et al.*, 2009; Catalá *et al.*, 2015). A confounding factor concerning the effects of light and oxygen is that vision is particularly oxygen demanding, and that hypoxia in itself might alter vision in marine organisms, including higher light requirements (McCormick and Levin, 2017). Future research involving measurements of mesopelagic light *in situ* are required to resolve the relative contribution of hypoxia and light conditions for distributions in oxygen minimum zones.

Is a twilight-structured mesopelagic fauna an important regulator of microbial activity and biogeochemical cycling?

The vertically migrating mesopelagic fauna contributes to the vertical carbon flux in potentially significant ways (Hernandez-Leon *et al.*, 2010; Robinson *et al.*, 2010; Klevjer *et al.*, 2016). Bianchi *et al.* (2013) suggested that the daytime oxygen consumption by migrants might intensify oxygen depletion in poorly ventilated regions, and Irigoien *et al.* (2014) estimated that mesopelagic fish might respire ~10% of the global primary production in deep water. Their contribution to the vertical carbon flux, including excretion of dissolved organic carbon (DOC) at mesopelagic depth, affects microbial processes (Robinson *et al.*, 2010). Calleja *et al.* (2018) demonstrated a positive relation between the vertical DSL location and heterotrophic prokaryotic metabolisms, making the DSL daytime habitat a hot spot for heterotrophic prokaryotes. This relation apparently resulted from the supply of labile DOC fuelling the metabolisms of prokaryotic heterotrophs. In the context of the current article, the hypothesis for further studies is that the vertical distribution of central microbial mesopelagic processes may be governed by the light environment through the depth positioning of the twilight fauna and their production of the labile DOC.

Time for measuring twilight

The recurrent theme of this article is that twilight is a first-order environmental driver for mesopelagic organisms and ecosystems. Yet, twilight is seldom measured in contemporary studies and this calls for inclusion of *in situ* light measurements. We have previously referred to the pioneering work in the middle of the last century (e.g. Kampa and Boden, 1954; Clarke and Backus, 1957; Clarke and Kelly, 1965). Subsequent studies by Roe *et al.* characterized the light environment when sampling both invertebrates and fish (Roe and Harris, 1980; Roe, 1983). Widder *et al.* made further methodological developments for measuring downwelling light (as well as bioluminescence) and underlined the need to address both the spectral distribution of light and the spectral sensitivities of the eyes (Widder *et al.*, 1992; Frank and Widder, 1997; Widder and Frank, 2001; Frank and Widder, 2002). Huge improvements in development of oceanographic instrumentation during the last decades now set the stage for assessing the light conditions in our quest to unveil the ecology of the twilight zone (Haag *et al.*, 2014). We emphasize the need for also measuring the low, although highly relevant, light intensities at night as well as below sea ice. Nocturnal light levels appear sufficient to be utilized by mesopelagic organisms and vary ~5 orders of magnitude at the surface—with implied importance for foraging and predation risk.

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