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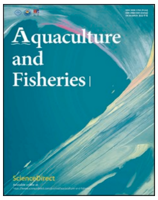

The response of mesopelagic organisms to artificial lights

Melanie J. Underwood*, Anne Christine Utne Palm, Jan Tore Øvredal, Åsmund Bjordal

Institute of Marine Research, PO Box 1870, Nordnes, NO-5817, Bergen, Norway

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ABSTRACT

Though mesopelagic fish respond to natural light (e.g., diurnal vertical migration), few studies have looked at how they respond to artificial light and if artificial lights could be used in commercial operations to improve catchability of mesopelagic fish. Here we present a preliminary study on how mesopelagic organisms respond to blue and green spotlights, as well as red and white diffuse lights in Masfjorden (Norway; max depth of 480 m). The response of organisms in each of the three sound scattering layers (SSLs) was observed when a) artificial lights were positioned in a layer or b) moved with a constant speed (generally 0.03 ms^{-1}) towards a layer. The artificial lights were attached to a rig with a self-contained echosounder, which recorded the vertical and horizontal avoidance of organisms in each SSL to different artificial lights. Net hauls (MIC-net) and video footage confirmed that *Maurolicus muelleri* and siphonophores were present in the upper layer (100–150 m), while *Benthosema glaciale* were present in the deeper layers (~200 m and ~300 m to seabed). Our findings suggest that *M. muelleri* (SSL1) horizontally avoid blue spotlight and white diffuse light, while *B. glaciale* (SSL2 and SSL3) mainly avoid the same lights downwards and can be herded downwards over 250 m. Though this study should be regarded as preliminary, the observed avoidance/herding response suggests artificial lights could be applied to improve existing fish capture methods for mesopelagic fish.

1. Introduction

With a growing world population, the demand for seafood is expected to increase. The supply from traditional capture fisheries has been rather stagnant around 85 million tons over the last 30 years, while aquaculture production has been steadily increasing (FAO, 2018). However, to meet the future demand for seafood, potential new resources should be explored. Among different candidates are mesopelagic fish – either for direct human consumption or as ingredients for aquaculture feed production.

Mesopelagic fish are found globally in the mesopelagic zone between 200 and 1000 m depth. They are mainly distributed in relatively scattered layers while in some waters, like the Arabian Sea and the Gulf of Oman, they occur in more dense concentrations (Gjøsæter, 1984). The global biomass of mesopelagic fish has earlier been estimated at about 1000 million tons (Gjøsæter & Kawaguchi, 1980; Lam & Pauly, 2005). However, a recent acoustic study suggests that the biomass could be ten times higher (Irigoien et al., 2014). Over the last 50 years mesopelagic fishes have been suggested as target for fisheries and fishing trials have been conducted (e.g., in the Gulf of Oman, South Africa and Iceland; MRI, 2016; Remesan, Prajith, Raj, Joseph, & Boopendranath, 2016; Shilat & Valinassab, 1998; Valinassab, Pierce, & Johannesson, 2007). However, few promising results regarding catches at commercial level have been recorded with traditional fishing gears. Given the scattered distribution and small size of mesopelagic fish, they are normally caught using long hauls with small meshed large pelagic trawls, that increases fuel cost as well as bycatch. Artificial lights could be used to herd or attract mesopelagic fish to increase catchability and selectivity in mesopelagic fisheries.

The use of artificial light has long traditions in capture fisheries, mainly to attract and concentrate the target species in order to increase catch rates (Ben-Yami, 1976; Gabriel, Lange, Dahm, & Wendt, 2008). In recent years, artificial light has also been tried with various fishing gears, either to increase catches of target species or improve the gear selectivity (Nguyen & Winger, 2019). From earlier studies we know that mesopelagic fishes respond to artificial white light by moving away from the light source (Barham, 1966; Blaxter & Currie, 1967; Kaartvedt, Røstad, Opdal, & Aksnes, 2019; Kampa & Boden, 1954; Peña, 2019). Warrant and Locket (2004) showed that the eyes of deep sea fishes are adapted to locate point source biolumineсence images. Thus, one could expect mesopelagic fish to respond particulary strongly to artifical spotlight (point source light) of wavelengthes that are similar to the

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* Corresponding author.
E-mail address: Melanie.Underwood@hi.no (M.J. Underwood).

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most common bioluminnecent colours of blue and green (Haddock & Case, 1999; Kampa & Boden, 1954). The natural behavior of mesopelagic fishes has been studied for decades in the Norwegian fjords, due to the great basin depths that have natural populations of mesopelagic organisms. The characteristic diurnal vertical migration with the variation in natural light level has been studied in the Masfjorden (Giske et al., 1990; Røstad, Kaartvedt, & Aksnes, 2016). In Masfjorden there are two dominant mesopelagic fish species: *Maurolicus muelleri* and *Benthosema glaciale*. Staby, Røstad, and Kaartvedt (2011) studied the diel vertical migration of these species across seasons. This revealed that both *B. glaciale* and *M. muelleri* have a diverse vertical migration behavior. *M. muelleri* usually distributes in a layer (<150 m depth) above the deeper scattering layers (around ~200 m and ~300 m), where *B. glaciale* is the dominate mesopelagic fish species (Kaartvedt, Røstad, Klevjer, & Staby, 2009). Therefore, Masfjorden is a perfect sheltered experimental location for studying the behavior of mesopelagic fish.

The present paper describes an initial study in Masfjorden of the responses (no response, attraction or avoidance) of mesopelagic organisms to different types of artificial light. The main aim was to investigate how mesopelagic fish (*M. muelleri* and *B. glaciale*) respond when exposed to artificial light of shorter wavelengths (blue and green) and general white light. In addition, we aimed to clarify possible differences between the two species in their behavioral response to light and if *M. muelleri* and *B. glaciale* can be herded by a slowly approaching light. Based on observed responses of mesopelagic fish to artificial light we suggest possible use of light to improve catchability and selectivity in fisheries for these species.

2. Materials and methods

2.1. Study site and environment

This study was conducted 18–24 January 2019, in Masfjorden - a fjord in western Norway approximately 60 km north of Bergen from the 25-m RV "*Hans Brattstrøm*" (60° 52′ N, 5° 25′ E, Fig. 1). All experiments and samples were conducted during daytime hours (between 9:00 and 17:30, UCT time). Salinity, temperature and oxygen profiles were measured in the middle of the experimental period (22nd of January) by a conductivity, temperature and depth profile (CTD; SD208-CTD/STD; SAIV AS, Bergen, Norway) equipped with an oxygen sensor. Behavior

Fig. 1. The study area, Masfjorden is north of Bergen, Norway. The X denotes the position the vessel was anchored and the position the MIC-net was conducted (60° 52′ N, 5° 25′ E).

observations of mesopelagic organisms to artificial light were conducted when the vessel was anchored at 480 m bottom depth. A submersible metal frame, fitted to the research vessel's hydrographic winch, was used to mount the different artificial lights, camera and echosounder (hereafter called "the rig"; see Fig. 2). The rig was lowered/hoisted by the hydrographic winch. During the experiment the depth of the rig was measured by the vessel's hull-mounted echosounder (see Acoustics below). A depth logger (RBR Solo^3, RBR Ltd, Ottawa, Canada) on the rig verified the depth of the rig during the deployment. All acoustic instruments, cameras and sensors were synchronized to UTC time.

2.2. *Acoustics*

A hull-mounted echosounder (EK60) operating at 38 kHz was used to record the distribution of the acoustically visible organisms at the research site throughout the experimental period. Responses observed by the 38 kHz were assumed to be caused by organisms with gas-filled organs, such as mesopelagic fish or siphonophores. This frequency has previously been used to study mesopelagic fish at this location (Kaartvedt et al., 2019; Kaartvedt, Staby, & Aksnes, 2012; Røstad et al., 2016; Staby et al., 2011). The initial acoustic observations showed three sound scattering layers (SSL), hereafter denoted as SSL1 (100–150 m), SSL2 (~200 m) and SSL3 (~300 m and down; see Fig. 3 and S1a).

To track the behavior of mesopelagic organisms close to the rig (2 m–100 m) in the horizontal and vertical planes, we used a Wide-Band Autonomous Transceiver (WBAT; SIMRAD Kongsberg Maritime AS, Horten, Norway) with two transducers mounted to the rig (Fig. 2). The transducers were a 120 kHz and a 70 kHz (ES120-7CD and ES70-7CD, respectively; SIMRAD Kongsberg Maritime AS, Horten, Norway) operating in continuous wave (CW) mode (alternating 100 pings each transducer) with a ping interval of 0.460 s and the pulse duration of 0.256 s were connected to the transceiver. The 120 kHz transducer recorded horizontally, while the 70 kHz transducer recorded vertically (downwards). A pressure sensor (SIMRAD Kongsberg Maritime AS, Horten, Norway) was added to the WBAT powered the unit once it was at a depth of 8 m.

2.3. *MIC-net sampling of sound scattering layers (SSL)*

To confirm previous findings of *M. muelleri* and *B. glaciale* distributions and other gas-bearing organisms, we trawled through SSL1 and SSL2 with a large plankton net (MIC-net; opening Ø 2 m, length of bag 13 m, mesh 500 μm). The MIC-net was towed at a speed of 1.2–1.8 knots for 30 min, during daylight hours (between 10:00–14:00, UTC) on the 19th and 23rd of January at the study site. At daytime the SSL1 layer was positioned between 115 and 145 m and the SSL2 layer between 180 and 220 m depth, the MIC-net was towed at mid layer depth (130 m and 200 m respectively). To make a representative sample of the more diffuse SSL3 layer we would have needed a larger sampling gear (for example a krill trawl), which the research vessel was not able to operate.

2.4. *Introduction of artificial lights*

2.4.1. *Choice of light sources and their properties*

All light sources were light-emitting diodes (LED). We used diving torches with white diffuse and custom-made wavelengths (red diffuse, green spotlight and blue spotlight; Brinyte DIV01; Hongkong Yeguang Co., Ltd, Shenzhen, China). In addition, we used a custom-made stronger white diffuse light (SWD) in an underwater housing (Nautilux custom; Group B Distribution Inc, Florida, USA) with a 11.5 mm white plexiglass diffuser. The blue - and green spotlights were made to match bioluminescence light (Haddock & Case, 1999; Kampa & Boden, 1954) and the visual pigments of *M. muelleri* (see Fig. 3b in de Busserolles et al., 2017) and *Benthosema* spp. (Douglas & Partridge, 1997). Accordingly, the two white lights had the same wavelength compositions, of which peak intensity overlaps with the visual pigments of *M. muelleri* and *Benthosema* spp. While, the red diffuse light was chosen to be an offset to the sensitivity of the two fish species visual sensitivity (Fig. 4). Intensity, wavelength and beam angle of the different lights used were measured by a Trios Ramses, vector irradiance sensor, at a 1-m distance in a dark room (TriOS Mess-und Datentechnik GmbH, Rastede, Germany), see Table 1. More detailed descriptions of the properties of the different artificial lights used are in Fig. S2 and the related text. The artificial lights were positioned on the rig so that they pointed either downwards, sidewards (horizontally) or upwards (Table 1).

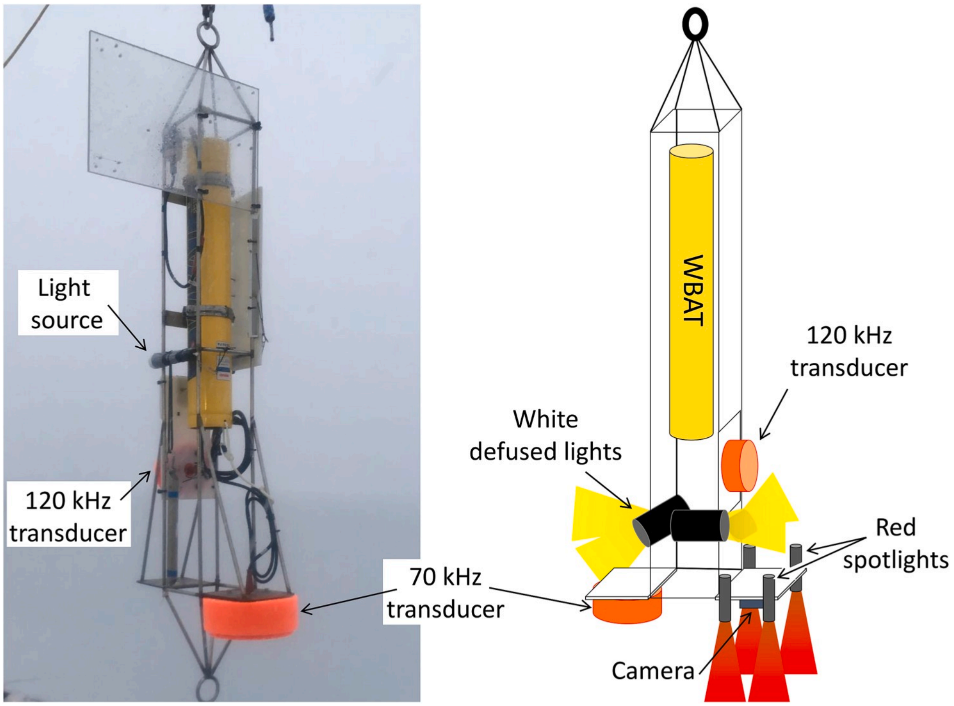

Fig. 2. The rig used during the study. The image on the left shows the rig with the WBAT and two transducers (120 kHz facing horizontally and 70 kHz facing vertically) and sidewards pointing lights. A drawing (not to scale) of the setup for station 9 is illustrated on the right. This included the WBAT, two transducers, strong white diffuse lights (SWD) pointing sidewards and the camera system (four red diffuse lights and GO Pro camera) to record the behavior of organisms. (For interpretation of the references to color in this figure legend, the reader is referred to the Web version of this article.)

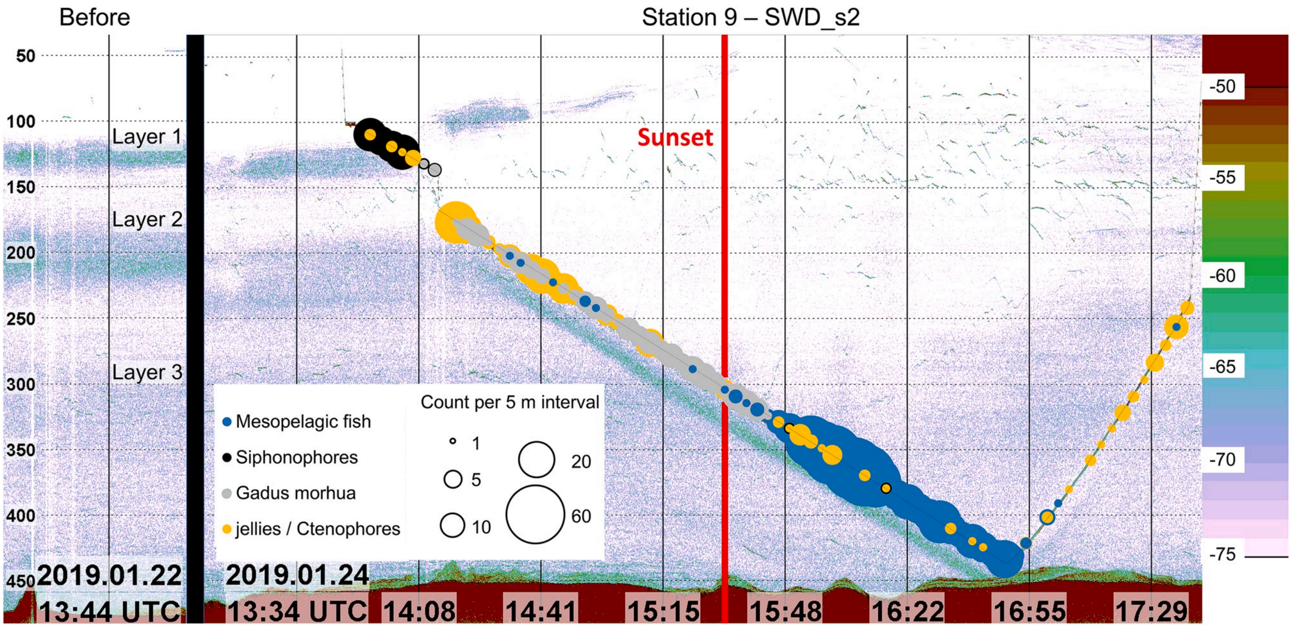

Fig. 3. The density and vertical distribution of the main mesopelagic organisms observed from the downward camera footage in station 9, shown as circle plots. The area of the circles represents the number of individuals observed per ~5 m depth interval. Sound scattering layers recorded from the hull-mounted echosounder before (left) and while the rig was lowered towards the layers (right). The Four strong white diffuse lights were placed on the rig in four sideward directions (St. 9; see Table 1). The red line indicates the time of sunset. (For interpretation of the references to color in this figure legend, the reader is referred to the Web version of this article.)

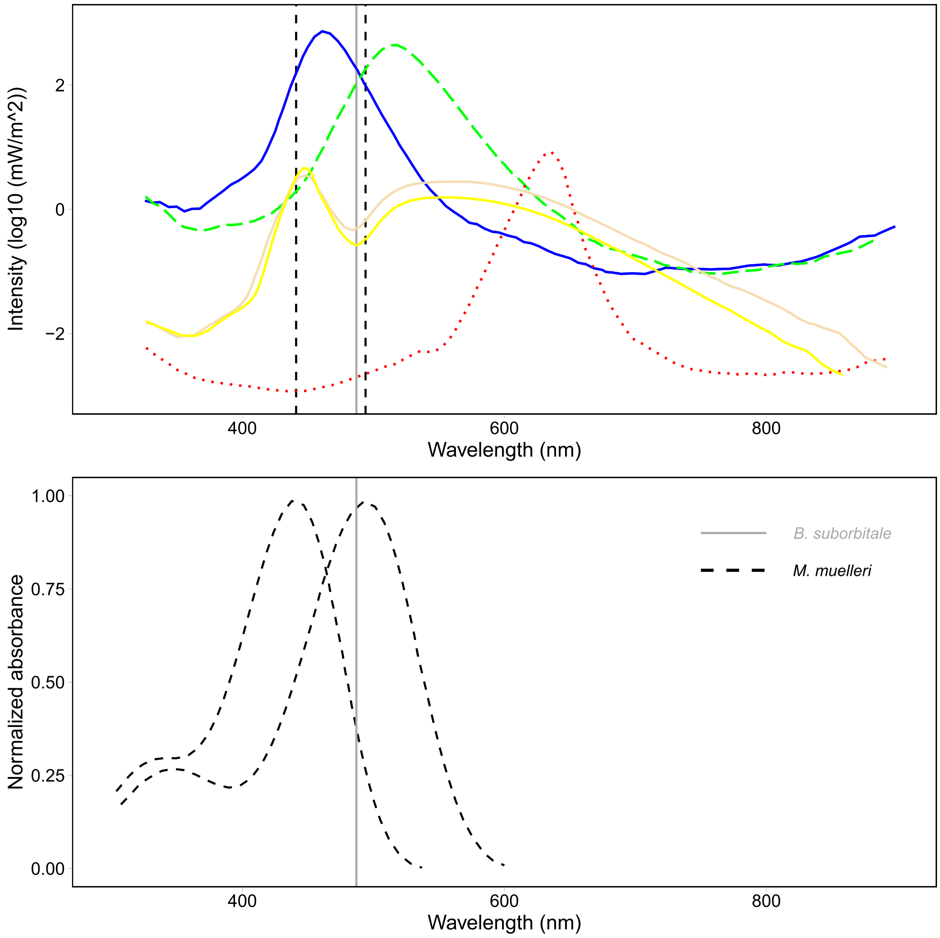

Fig. 4. The intensity across wavelengths of the artificial lights (upper figure) used in relation to the peak sensitivity of *Maurolicus muelleri* (black dotted vertical lines; de Busserolles et al., 2017) and *Benthosema suborbitale* (λ_{max} 487 nm, see Douglas & Partridge, 1997) marked with a grey vertical line. *B. suborbitale* is the closest relative to *Benthosema glaciale* based on visual properties (see Fig. 15 in de Busserolles, Marshall, & Collin, 2014). The lower figure indicates the spectra absorption curves for *M. muelleri* (black dotted lines; redrawn from de Busserolles et al., 2017) and the peak sensitivity of *B. suborbitale* (grey vertical line). To our knowledge the spectral absorption curve of *Benthosema* spp. is not available. The white artificial lights: white diffuse (WWD; yellow line) and stronger white diffuse lights (SWD; tanned/wheat line). Their peak intensities are at 447 nm (±5 nm) and 551 nm (±5 nm). The wavelength compositions of the colored diving torches were blue spotlight (BS; blue line), green spotlight (GS; green dashed line) and red diffuse (RD; red dotted line), which have their peak intensities at: 462 nm; 516 nm and 633 nm respectively. Artificial lights were measured by a Trios Ramses, vector irradiance sensor, at a 1-m distance in air in a dark room. Intensity is log (10) transformed, for better comparison. (For interpretation of the references to color in this figure legend, the reader is referred to the Web version of this article.)

Table 1
Station overview and response of sound scattering layers (SSL) to different artificial lights. The light intensity, beam angle and peak wavelength (Peak wavel.) were measured in air at a 1-m distance. From which, beam angle under water and intensity at 360° were estimated (for more details see Supplementary Fig. S2 and related text). Speed: is the speed of rig when approaching and passing at the depth of an SSL. No speed means that the rig was moved quickly to an SSL where it was kept in position. The average vertical (V) and/or the horizontal ((H) distance (± standard deviation) between the rig for each SSL is in the three last columns. Significant differences to the control (rig with no light) are given in parenthesis (Statistical test, Wilcoxon rank sum test). Minimum distance was limited to 2 m due to the narrow beam angle of the WBAT transducers (7°).

Station #	Light:					Speed (ms^{-1}):			Average distance to rig (m (± SD); H = horizontally; V= Vertically) and Significant response (P; Wilcoxon rank sum test)		
	Number and color of light source (Abr.)	Direction of light	Peak wavel. (nm)	Intensity sum 360° (mWm^{-2})	Beam angle under water	SSL1 speed	SSL2 speed	SSL3 speed	SSL1	SSL2	SSL3
1	No light	–	–	–	–	0	0	0	V: 5.6 m (±1.5) H: 6.2 m (±1.7)	V: 4.8 m (±0.9) H: 5.9 m (±1.5)	
2	2 Red Diffuse (RD_s)	Sideward	633	900	90°	0	0	0	V: 7.4 m (±2.2) ($P > 0.05$) H: 6.8 m (±3) ($P > 0.05$)	V: 5.4 m (±2.5) ($P > 0.05$) H: 7.4 m (±2.6) ($P > 0.05$)	
3	2 Green Spot (GS_s)	Sideward	516	19 450	<15°	0	0	0	V: 6.7 m (±2.7) ($P > 0.05$) H: 7.2 m (±3.3) ($P > 0.05$)	V: 5.4 m (±2.4) ($P > 0.05$) H: 7.2 m (±3.0) ($P > 0.05$)	V: 6.6 m (±2.5) H: 10.5 m (±3.5)
4	2 Blue Spot (BS_s)	Sideward	462	22 000	<15°	0	0	0	V: 10.4 m (±1.5) ($P > 0.05$) H: 15.6 m (±5.0) ($P = 0.016$)	V: 8.9 m (±0.6) ($P = 0.008$) H: 10.6 m (±1.8) ($P = 0.015$)	
5	2 Weak White Diffuse (WWD_s)	Sideward	442 546	1230	60°	0	0	0	– H: 13.4 m (±3.5) ($P = 0.002$)	V: 12.8 m (±2.4) ($P = 0.015$) H: 7.8 m (±1.9) ($P > 0.05$)	V: 8.5 m (±3.3) H: 8.0 m (±1.5)
6	2 Weak White Diffuse (WWD_d)	Downward	442 546	1230	60°	0.03	0.03	0.03	V: 9.6 m (±1.5) ($P > 0.05$) H: 14.8 m (±2.1) ($P = 0.017$)	V: 27.4 m (±4.7) ($P = 0.001$) H: 23.6 m (±5.1) ($P = 0.002$)	V: 13.4 m (±1.9) H:11.9 m (±1.9)
7	2 Weak White Diffuse (WWD_u)	Upward	442 546	1230	60°	0.03	0.06	–	–	V: 7.4 (±1.6) ($P = 0.014$) H: 8 m (±2.5) ($P > 0.05$)	
8	4 Strong White Diffuse (SWD_s1)	Sideways 4 directions	442 556	3184	60° in 4 directions	0.03	0.03	0.03	V: 7.8 m (±2.9) ($P > 0.05$) H: 13.0 m (±4.9) ($P = 0.017$)	V: 8.8 m (±0.8) ($P < 0.001$) H: 13.8 m (±3.0) ($P = 0.002$)	V: 9.0 m (±1.7) H: 10.4 m (±3.4)
9	4 Strong White Diffuse (SWD_s2)	Sideways 4 directions	442 556	3184	60° in 4 directions	0.03	0.03	0.03	V: 7.4 m (±1.9) ($P > 0.05$) H: 28.7 m (±12.4) ($P = 0.016$)	V: 9.7 m (±1.2) ($P < 0.001$) H: 7.7 m (±1.9) ($P > 0.05$)	V: 7.9 m (±1.0) H: 8.1 m (±2.5)

2.4.2. *Control: the rig and red lights*

Two controls for organism responses were conducted for SSL1 and SSL2: Station 1, tested if there was any response to the rig alone, without any lights added, and Station 2, tested if there was any response to the rig when red diffuse (RD) lights were added. The rig was positioned in the SSLs to observe attraction, avoidance or indifferent responses. It was important to make sure that the presence of the rig alone had no effect, before including different light stimuli. The red light was used for video recording of organisms close to the rig, during the herding study (see station 9, below).

2.4.3. *Responses to different lights inside SSLs*

To study the mesopelagic organism's response to low wavelength lights, the rig was placed with lights pointing sidewards into the SSLs. The lights mounted on the rig included two green spotlights (GS; Station 3), two blue spotlights (BS; Station 4) and two weak white diffuse light (WWD; Station 5). The artificial lights' intensity, wavelength and beam angle are given in Table 1 and Fig. 4 (see also Fig. S2 for more detail).

2.4.4. Response to white lights approaching SSLs

Weak white diffuse (WWD) and strong white diffuse (SWD) lights were used to test if mesopelagic fish could be herded downwards and upwards (Stations 6 to 9; Table 1). For Station 6, two WWDs pointing downwards were mounted to the rig as it slowly (0.03 ms^{-1}) approached SSL1 and SSL2 from 30 to 50 m above. Station 7 had two WWDs pointing upwards, approaching SSL2 and SSL1 slowly (0.06 ms^{-1} and 0.03 ms^{-1}, respectively) from below. While Stations 8 and 9 had four strong white diffused lights (SWD), directed with a 90° angle to each other in the horizontal plane (Fig. 2). The four SWD lights formed a horizontal "light disc", which was lowered slowly (0.03 ms^{-1}) from 20 m above SSL1 to the bottom during Station 8. Due to time restraints, the rig was lowered to 20 m above SSL2 after moving through SSL1 and then to the bottom for Station 9.

2.5. Camera observations

A video camera, pointing downwards, was used to observe density and vertical distribution of the mesopelagic organisms, as we moved the rig slowly (0.03 ms^{-1}) down to the bottom and back up (station 9, Table 1 and Fig. 3). The camera was a GoPro HERO3+ black (GoPro Inc, San Mateo, USA) placed in a 2600 m depth-rated housing (Group B Distribution Inc, Florida, USA). Four diffuse red lights (RD, see above) were positioned around the camera, pointing in the direction of the camera's field of view, to aid camera vision without affecting the organisms (Fig. 2).

2.6. Analysis of the acoustics and video

WBAT acoustic data were viewed in the Large Scale Survey System software (LSSS; Korneliussen et al., 2006). The minimum vertical (70 kHz transducer) and the horizontal (120 kHz transducer) distances between the light source on the rig and organisms in the SSLs were recorded for each 100-ping section, and analyzed in R (R Core Team, 2018). Due to the narrow beam angle (7°), few individuals were observed within 2 m of the transducer and therefore the minimum range was limited to 2 m (minimum beam diameter of ~25 cm). Kruskal-Wallis test was used to see if the distance between the artificial light and the organisms were significantly different when a given light was introduced compared to the rig alone (control). The test was done for each of the SSLs and directions (i.e., SSL1 vertical, SSL1 horizontal, SSL2 vertical and SSL2 horizontal). There were no comparisons made for SSL3 as the control deployment stopped at the end of SSL2. However, we assume that SSL3 would react similarly to SSL2 as similar species composition has been recorded in both layers (Kaartvedt et al., 2009). Pairwise comparisons (light source vs the rig alone) were performed with the Wilcoxon rank sum test and Benjamini-Hochberg correction was used to account for multiple comparisons on the same data set (Benjamini & Hochberg, 1995).

Video footage from station 9 was analyzed post-cruise. Station 9 was chosen as this was a station where we went with a constant speed (0.03 ms^{-1}) through the layer depths to the bottom and rose to 250 m. Video footage was collected in 15 min files and analyzed in a random order In VLC media player (VideoLAN Org., Paris, France). During the analysis, we counted the total number of identified organisms (to lowest phylogenetic level) passing through the visual field of the camera. Species were identified and quantified from the video footage in 3 min blocks (~5-m depth bins). When species identification was not possible, species were noted to the following organism groups: mesopelagic fish, Euphausiacea (krill), Decapoda (shrimp), Copepoda, Tomopteridae (Fig. S3f), Chaetognatha (Fig. S3g), Siphonophorae (Fig. S3a), and Ctenophora or jellies (Fig. S3b). After analyzing the video footage, the time at the start of each 3 min block was synchronized with the time and depth of the rig. Results were overlaid onto the vessel's EK60 echogram.

3. Results

3.1. Environment

Three SSLs were observed during the cruise (Fig. 3; Fig. S1a). The CTD profile showed that there was a pycnocline at 30 m depth, with a temperature maximum of 10 °C and a fast drop in salinity above 30 m depth (Fig. 5). At the depth of SSL1, the temperature decreased from 8.6 °C at 100 m to 8.2 °C at 150 m, while the salinity stayed constant (35 ± 0.15 psμ). There was also a reduction in oxygen saturation level from 76% at 100 m to 59% at 150 m. Thus, the SSL1 layer had a diel vertical migration across a temperature, salinity and oxygen gradient. The SSL2 and SSL3 layers generally had more constant temperature (8.5 ± 0.3 °C) and salinity conditions (35 ± 0.15 psμ) but experienced a declining oxygen level with depth. At 200 m, the oxygen saturation was 60%. Between 330 m and 440 m there was a drop from 40 to 30% oxygen saturation, therefore the lower SSL (SSL3) experienced very low oxygen levels.

3.2. MIC-net samples from SSL1 and SSL2

There was a large variation in sample size and number of species between the two replicate hauls from SSL1 and SSL2 (Table 2). Thus, the samples gave only a picture of species present in the two layers and not their abundance. *M. muelleri* was found in the upper layer (SSL1) together with siphonophores, jellies, arrow-worms (Chaetognatha), pelagic polychaetes (*Tomopteris* spp.) and amphipods. In the second layer (SSL2), there were both *M. muelleri* and *B. glaciale*, though more of the latter. Krill (*Meganyctiphanes norvegica*) and shrimp (*Sergestes arcticus*) were also present in this layer, in addition to siphonophores, chaetognaths, jellies and *Tomopteris* spp.

3.3. Acoustic observations

Horizontal and/or vertical avoidance (i.e., keeping an increased distance from the rig) was seen when some artificial lights were used. (Table 1, Fig. 6). SSL1 showed significant horizontal avoidance (Kruskal-Wallis; $P < 0.001$), but not significant vertical avoidance (Kruskal-Wallis; $P = 0.17$), while SSL2 showed both significant horizontal and vertical avoidance (Kruskal-Wallis; $P < 0.001$ for both). However, no mesopelagic organisms were observed acoustically moving towards the artificial lights (attraction).

3.3.1. Control: the rig and red lights

No response to the rig or red artificial lights was observed with the hull-mounted echosounder (Figs. S1b–c). SSL1 and SSL2 did not dissipate or keep a distance from the rig. The WBAT analysis also showed no horizontal or vertical avoidance (keeping distance from the rig) by the organisms in SSL1 and SSL2 when the rig was deployed without any lights or with red lights (i.e., individuals were observed close to the submerged rig, Fig. 6a). No control was conducted for SSL3.

3.3.2. Responses to different lights inside SSLs

Sidewards-pointing green and blue spotlights, as well as weak white diffuse lights were introduced into the SSLs. By the hull-mounted echosounder, we observed that organisms in SSL1 dissipated when the green spotlight, blue spotlight and weak white diffuse lights encountered the layer (St. 3–5; Figs. S1d–f). This was verified with the WBAT data, which showed a significant increase in the horizontal distance organisms kept from the rig when blue spotlights and weak white diffuse lights were used compared to the rig alone (Table 1; BS_s, WWD_s, Fig. 6a). However, the WBAT data did not record a similar response seen in the hull-mounted echosounder with the sideward-pointing green spotlight (GS_s, Fig. 6a).

The hull-mounted echosounder showed that organisms in SSL2 also responded when the blue spotlight and white diffuse light were placed

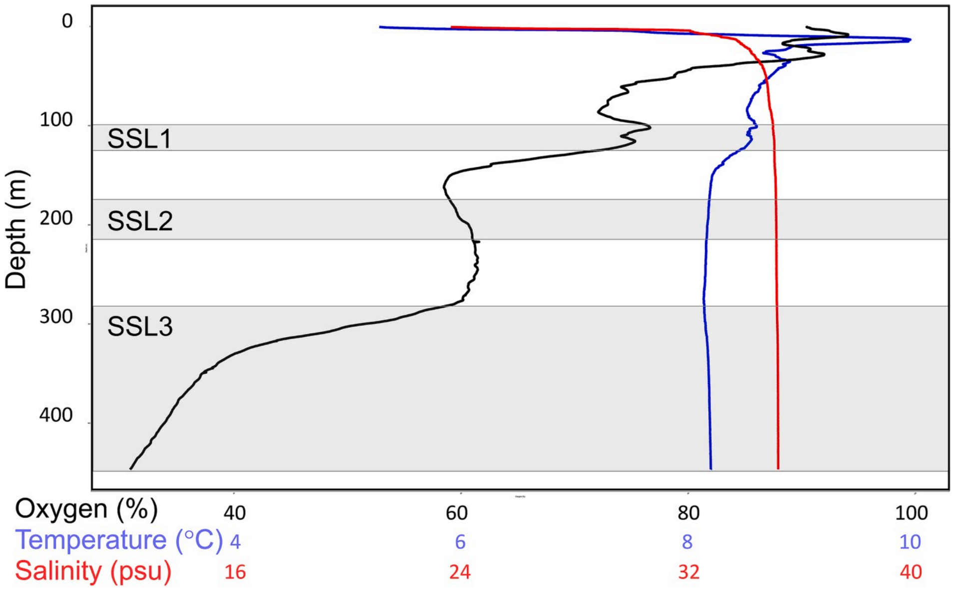

Fig. 5. Oxygen saturation (black line), salinity (red line) and temperature (blue line) recorded from a CTD profile conducted on the 22nd of January 2019. The grey areas indicate the depth of the sound scattering layers recorded from the hull-mounted echosounder. (For interpretation of the references to color in this figure legend, the reader is referred to the Web version of this article.)

Table 2
Samples from the MIC-net (large plankton net). Haul one and three were samples from the upper sound scattering layer (SSL1), while haul two and four from the second sound scattering layer (SSL2). For the first haul, only mesopelagic fish were counted and all other species/families present in the catch were noted as "present".

Species/family	# individuals	SSL	Haul
Maurolicus muelleri	33	1	1
Tomopteris spp.	Present	1	1
Chaetognatha	present	1	1
Siphonophorae	present	1	1
Amphipod	present	1	1
Maurolicus muelleri	16	2	2
Benthosema glaciale	66	2	2
Sergestes arcticus	38	2	2
Meganyctiphanes norvegica	99	2	2
Siphonophorae	15	2	2
Tomopteris spp.	75	2	2
Maurolicus muelleri	15	1	3
Siphonophorae	20	1	3
Chaetognatha	8	1	3
Amphipod	2	1	3
Maurolicus muelleri	3	2	4
Benthosema glaciale	15	2	4
Sergestes arcticus	42	2	4
Meganyctiphanes norvegica	25	2	4
Siphonophorae	15	2	4

inside the layer. However, the green spotlight barely weakened the layer with some of the layer above the rig dissipating (St. 3–5; Figs. S1d–f). The WBAT data showed that mesopelagic organisms increased their distance to the rig significantly in the horizontal and vertical plane for blue spotlight and in the vertical plane for weak white diffuse light (Table 1; BS_s, WWD_s, Fig. 6a).

The blue and green spotlights had ~100 times higher intensity than the white diffuse lights; however, this difference between spotlights and white diffuse lights was not observed in the distance of organisms to the rig both horizontally and vertically when the rig was in the SSLs. Organisms in SSL2 even kept a greater vertical distance with the lower intense white diffuse lights. For blue spotlight (BS, St. 4), the mesopelagic organisms kept at a maximum horizontal distance of ~16 m in SSL1, while the distance was ~30 m for SSL1 when stronger white diffused light was introduced (SWD, St. 9; Table 1). These distances correspond to a calculated intensity of ~20 mWm^{-2} and ~0.2 mWm^{-2} for the BS and SWD light accordingly (see Fig. S2 and including text).

The green spotlight and the weak white diffuse light were also introduced into SSL3 (St. 3 and 5; Figs. S1d and f). Organisms in SSL3 were observed in the hull-mounted echosounder to respond when the white diffuse light was placed inside the layer. However, little response was observed with the green spotlight. WBAT data showed that the organisms responded more in the vertical plane with weak white diffuse lights, compared to the green spotlight. Though organisms did respond horizontally with the green spotlight (Table 1; GS_s, WWD_s, Fig. 6a).

3.3.3. Response to white lights approaching SSLs

Two types of white diffuse lights (weak and strong) were slowly moved towards SSLs from above (St. 6, 8 and 9. Fig. S1g, i-j). SSL1 dissipated (i.e., no echoes were recorded in the hull-mounted echosounder) as the rig approached SSL1 with downwards and sidewards pointing white lights. This was also observed in the WBAT data with a significant increase in the horizontal distance for all white diffuse lights pointing sidewards and downwards when compared to the rig without any lights (Table 1; WWD_d, SWD_s1, SWD_s2, Fig. 6b). However, when approaching SSL1 from below with weak white diffuse lights pointing upwards, SSL1 dissipated earlier (~30 m prior to encountering the layer; Fig. S1h). SSL1 was gone before the rig was at the layer depth and therefore it was not possible to analyze the WBAT data.

When the rig was moved towards SSL2, white diffuse lights (i.e., weak downwards and strong sidewards) herded organisms downwards (echosounder observations, St. 6, 8 and 9; Fig. S1g, h-j). SSL2 organisms were herded downwards over 130 m with downward-pointing weak white diffuse lights before the rig was raised at the same speed (St. 6; Fig. S1g). The herded organisms did not rise with the rig when the rig was raised but maintained the depth (330 m) they were herded to (Fig. S1g). With sideward strong white diffuse lights, organisms were herded downwards over 250 m towards the seabed (450 m; St. 8–9. Figs. S1i–j). When SSL2 was lowered towards SSL3 (at 300 m depth), SSL3 appeared to be herded downwards as well (St. 8–9. Figs. S1i–j). While being herded downwards with white diffuse light, SSL2 kept a

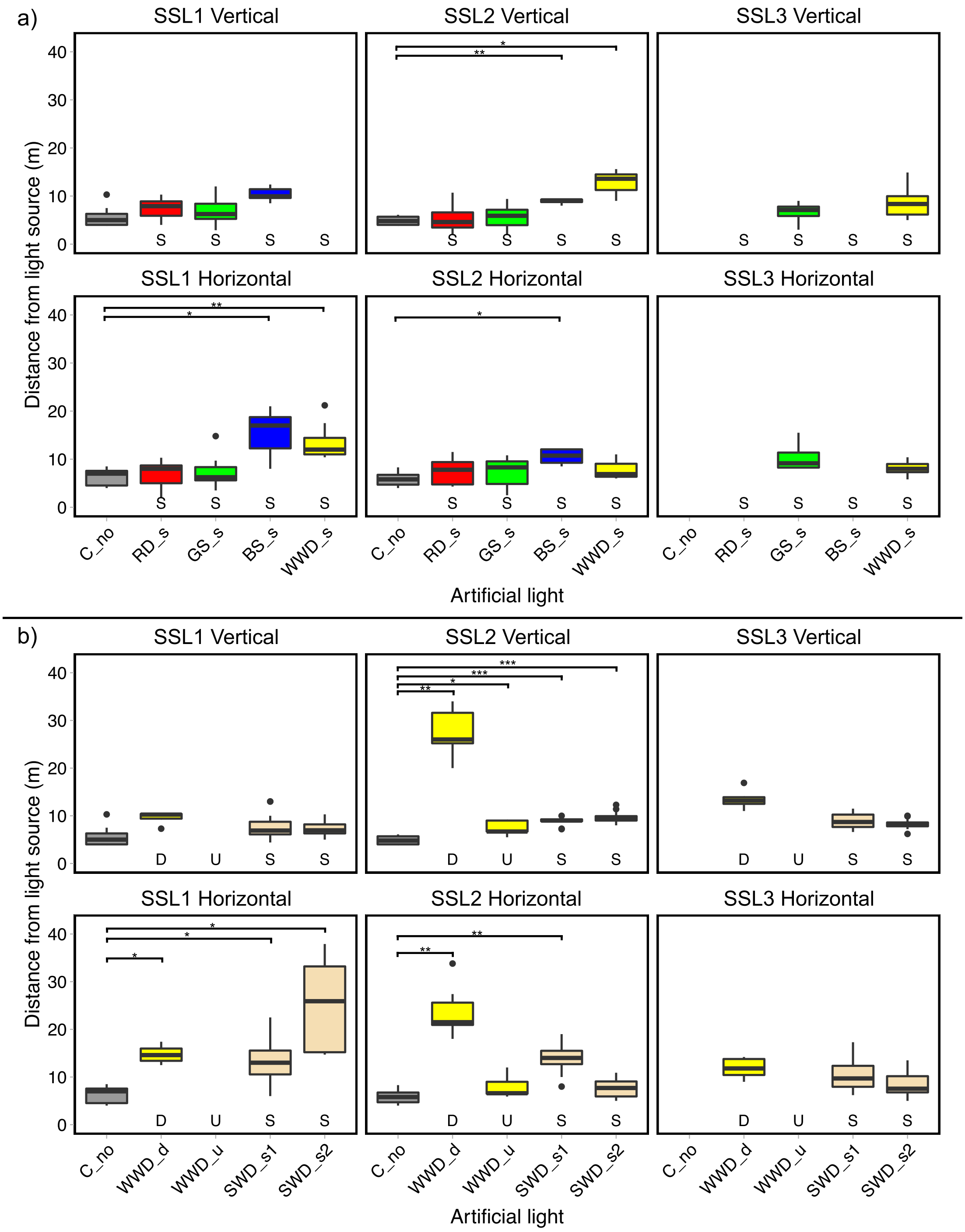

Fig. 6. The minimum horizontal and vertical distance of organisms in each layer (SSL1, SSL2 and SSL3) to the light source as observed by the WBAT (120 and 70 kHz, respectively). The upper graph (a) are boxplots of the artificial lights placed inside the layer compared to the control (C_no; no movement and no artificial lights), while the lower graph (b) are boxplots of the results from moving the artificial lights towards the layer compared to the control (C_no; no movement and no artificial lights). Artificial lights included red diffuse light (RD_s) green spotlight (GS_s), blue spotlight (BS_s), weak white diffuse lights (WWD_s, WWD_d and WWD_u) and strong white diffuse lights (SWD_s1 and SWD_s2). The rig was moving through the water column at 0.03 ms^{-1}, apart from WWD_u (0.06 ms^{-1} towards SSL2). Light direction is indicated below the boxplot ("S" for sidewards-, "D" for downwards- and "U" for upwards-pointing lights). Boxplots show the 25 and 75 percentiles with the median indicated by a black line. Significant differences between the light source and the control (no light) are illustrated by stars above the boxplot (*P = 0.1–0.5; **P = 0.001–0.1; ***P < 0.001). (For interpretation of the references to color in this figure legend, the reader is referred to the Web version of this article.)

significantly increased horizontal and vertical distance from most of the white lights (strong and weak downward pointing and strong sideward pointing) when compared to the rig without any lights (Table 1; WWD_s, SWD_s1, Fig. 6b). Variation in the horizontal distance to the rig was observed between replicate trials with strong white diffuse lights (St. 8–9; SWD_s1 and SWD_s2, Fig. 6b).

As the rig was raised towards SSL2 with weak white diffuse lights pointing upwards, herding of organisms upwards was not observed.

However, before the layer dissipated, organisms kept an increased vertical distance from the light when compared to the rig without lights (Table 1; WWD_u, Fig. 6b; Fig. S1h).

3.4. Camera observations

Camera observations during lowering and lifting of the rig at station 9 were analyzed, starting from the top of SSL1 (100 m depth) going all the way to the bottom (480 m) and back up to 250 m (Fig. 3). The visual distance was estimated as 1–1.5 m from the passage rate of jellyfish (easy to identify in the footage and moved slowly). Siphonophores (Fig. S3a) were the dominating group observed at the depth of SSL1 (from 110 to 150 m depth), with an average of 7 individuals observed per ~5 m depth interval. No mesopelagic fish were observed, however, a few Atlantic cod (*Gadus morhua;* 0.4 ind., per ~5 m) and some jellies (average 1.3 ind., per ~5 m) were observed at the depth of SSL1 (Table 3). At the depth of SSL2 (from 175 to 275 m depth), jellies and Ctenophores (Fig. S3b) dominated (average 5.4 ind., per ~5 m), and there were 23 cod observations (average 2 ind., per ~5 m), but only three observations of mesopelagic fish (Table 3). At the depth of SSL3 (from 275 to 450 m depth), the dominant group was mesopelagic fish totaling 591 individuals (95% of all mesopelagic fish observations) of which 10% were identified as male *B. glaciale* due to the dorsal caudal light organ (supracaudal organ) found on males. An average observation rate of 16 ind., per ~5 m depth was recorded (Table 3). A total of 166 observations were recorded of cod feeding around the rig from 105 m to 330 m (Table 3; Fig. S3c). Below 330 m the number of mesopelagic fish increased from 18 observations (above 330 m = 0.4 ind., per ~5 m) to 579 observations (below 330 m = 22.3 ind., per ~5 m; Table 3; Table S1). The mesopelagic fish were observed performing saltatory search swimming (i.e., glide/pause in between fast tailbeats; O'Brien, Browman, & Evans, 1990) previously concluded as a feeding behavior (Kaartvedt, Torgersen, Klevjer, Røstad, & Devine, 2008). Ctenophores and jellies dominated the deep layer on the way up, and only few fish were observed (Table 3; Fig. 3). From 330 m and down to the bottom we had the highest observation of mesopelagic fish (579 obs.) while hardly any mesopelagic fish (12 obs.) were observed in the same depth interval when the rig was lifted (Table 3; Fig. 3). Interestingly, some of the identified male *B. glaciale's* had 1-2 large copepod ectoparasites *Sarcotretes scopeli* (see Fig. S3e and Gjøsæter, 1971). Though *M. muelleri* have a pointier nose and a more flattened body than the myctophids (Fig. S3d) it was hard to distinguish *M. muelleri* from female *B. glaciale* in the video footage and therefore both species were grouped as “mesopelagic fish”. Few krill and copepods were noted as these were hard to distinguish from the marine snow. Number of Chaetognatha, Copepoda, and Tomopteridae by depth is shown in Table S1.

4. Discussion

This study showed that mesopelagic fish (and maybe siphonophores, see below) respond to blue, green and white artificial lights but not red artificial lights, nor the rig alone. The artificial light's wavelength and beam (diffuse light or spotlight/point light) affected the degree of avoidance or herding of the fish. However, light intensity, at the level tested here (two orders of magnitude), did not seem to influence the fish's avoidance behavior. No attraction to light was revealed by the acoustics. Mesopelagic fish were observed avoiding the lights by keeping distance from the light source horizontally and vertically. The fish in each sound scattering layer (SSL) responded differently in the way they avoided the artificial light. When the fish in SSL1 responded, they avoided by keeping a horizontal distance from the artificial light independent of wavelength, intensity or beam (diffuse or spotlight). In contrast, when fish in SSL2 and SSL3 responded, they always avoided by keeping a vertical distance, and in some cases also horizontal. No upwards avoidance was induced for neither of the SSLs when shining the light from below. The MIC-net samples showed that *M. muelleri* was the only mesopelagic fish in SSL1. It was also represented in SSL2, but this layer had more *B. glaciale*. The species distribution of the upper two layers, is in accordance with earlier studies from the same area (Kaartvedt et al., 2009), which have described *B. glaciale* to be dominate in SSL2 and SSL3. Our findings indicate that *M. muelleri* (SSL1) avoids artificial light horizontally, while *B. glaciale* (SSL2 and SSL3) avoid downwards.

Like the present study, previous studies with white artificial light also showed an avoidance (Blaxter & Currie, 1967; Gjøsæter, 1984; Kaartvedt et al., 2019; Peña, 2019), thus, our finding related to white light was expected. To our knowledge, the reaction of mesopelagic fish to different colored lights has not been tested before this study. Our study showed a significant avoidance to blue ($\lambda_{\max}$ 462 nm) spotlight at the depth of SSL1 (horizontal) and SSL2 (vertical and horizontal). The WBAT data showed no significant response in the layers to green spotlight, though on the vessel's echogram the fish in SSL1 dissipated after some time and a thinning of SSL2 was observed. Based on sensitivity of the visual pigments of *M. muelleri* (blue $\lambda_{\max}$ 441 nm and blue-green $\lambda_{\max}$ 494 nm; de Busserolles et al., 2017), and *Benthosema* spp. (blue-green $\lambda_{\max}$ 480–490 nm; Turner, White, Collins, Partridge, & Douglas, 2009), both should be able to see the blue (peak 462 nm) and green (peak 517 mm) spotlights. The stronger response to blue light could be explained by the natural response to sunlight at depth (i.e., sunlight gets increasingly blue by depth due to the water's absorption of the longer wavelengths (Jerlov, 1968).

This study demonstrated how artificial light could be used to herd mesopelagic fish downwards. With slowly approaching white light, we were able to herd fish from a depth of 200 m down to 450 m. The herded organisms did not follow when the rig was raised and maintained the depth at which they were herded to (Figs. S1i–j). Herded organisms were most likely mesopelagic fish. This is based on the strong echoes from the hull-mounted echosounder and that few fish were observed in the video footage when the rig was lifted. Downwards avoidance of mesopelagic organisms to artificial light has been studied before. Blaxter and Currie

Table 3

Counts of identified organisms from the video footage. *Cod*: *Gadus morhua* (Fig. S3c), *Mesopelagic Fish (all)*: all mesopelagic fish observed, *B. glaciale (male)*: *Benthosema glaciale* males (Fig. S3e), *Siphonophorae* (Fig. S3a), *Jelly or Ctenophora* (Fig. S3b), *Euphausiacea*: krill and shrimp. Proportional distributions (%) and average number counted per ~5 m depth interval, were calculated within different depth intervals (105 down to 330 m, 330 down to 450 m, 450 m up to 250 m) and sounds scattering layers (*SSL1*, *SSL2* and *SSL3*). *Total:* is the total count of organisms as the rig traveled down and up (i.e., 105 m down to 450 m and 450 m up to 250 m). A detailed overview of counts in ~5 m depth intervals is given in Table S1.

Depth intervals	Cod		Mesopelagic fish (all)		B. glaciale (male)		Siphonophorae		Jelly or Ctenophora		Euphausiacea	
	%	~5 m	%	~5 m	%	~5 m	%	~5 m	%	~5 m	%	~5 m
SSL1 (105 to 150 m)	2	0.4	0	0	0	0	49	7	4	1.3	0	0
SSL2 (175 to 275 m)	23	2	0.5	0.2	0	0	8	0.5	40	5.4	11	0.5
SSL3 (275 to 450 m)	48	2.1	95	16	97	1.6	24	0.7	22	1.6	27	0.6
Down 105 to 330 m	100	3.7	3	0.4	0	0	82	2.1	77	4.6	78	1.5
Down 330 to 450 m	0	0	95	22.3	97	2.2	15	0.7	10	1.0	8	0.3
Up 450 to 250 m	0	0	2	0.3	3	0.05	2	0.07	13	0.8	14	0.3
Total	166		610		60		114		267		88	

(1967) found repulsion with downwards diving and Kaartvedt et al. (2019) recently published a study on herding mesopelagic fish by light. In the Red Sea they herded two layers of mesopelagic fish down to the bottom with a ROV equiped with to white LED light (40 W, 2520 lm). In the same study they showed acoustically that mesopelagic fish in the near range to the ROV (25 m ± 5 SD) were attracted to the spotlight. While they avoided the light at longer distance (>25 m (±5 SD) where the light became more diffuse. Barham (1966) showed also some attraction to light by mesopelagic fish. These findings are not in accordance with the present acoustic observations, as we found no clear attraction of mesopelagic organisms, even when using strong spotlights (21000 $\mathrm{mWm^{-2}}$). If any trend in these few deployments, fish kept at a longer distance with white diffuse light compared to the blue spotlight (Fig. 6).

Though our main findings showed that mesopelagic fish are significantly avoiding artificial light, we observed mesopelagic fish within 1.5 m of the rig (video footage) from 330 m and down. From here on, observations of mesopelagic fish increased drastically (from ~1 to ~46 ind. per 10 m depth interwall). The mesopelagic fish that became visible in the camera showed a saltatory swimming behavior, a typical swimming pattern for planktivory fish when feeding (O'Brien et al., 1990). This is previously described for mesopelagic fish as fast tailbeats followed by gliding (Barham, 1966; Kaartvedt et al., 2008, 2019). While gliding, the fish spots its prey by vision (O'Brien et al., 1990) or in the dark by lateral line (Janssen, 1997), the latter being less efficient. The light from the rig attracted copepods and krill, which the mesopelagic fish could feed on safely once the cod had withdrawn at 330 m (Table 3; Fig. 3). The depth at which cod stopped following the rig coincides with a sudden decrease in oxygen from 60% to 40% saturation (Fig. 5), which is close to the hypoxic threshold for cod (Plante, Chabot, & Dutil, 1998).

Our MIC-net data and video footage indicated that siphonophores were abundant at the depth of SSL1. These organisms are known for having a similar acoustic signal to mesopelagic fish (Barham, 1963; Stanton, Chu, Wiebe, Martin, & Eastwood, 1998), with a particular strong backscatter at 38 kHz (Knutsen et al., 2018). This is caused by gas-filed organs (pneumatophores), that aid them in their vertical migration. Interestingly, blue spotlight and white diffuse light moved all organisms in SSL1 recorded within the acoustic beam of the hull-mounted echosounder, which indicates that the siphonophores as well as *M. muelleri* avoid artificial light by moving away (seen in the hull-mounted Ek60 echogram; Fig. 3 and Fig. S1). The video footage supported this finding, as we registered lower density of siphonophores on the way up compared to on the way down. Some siphonophores have been found to prefer a particular light intensity range (Lučić et al., 2011).

The response of fish to artificial light has been used mostly to aggregate small pelagic fish for increased catchability with different fishing methods (Ben-Yami, 1976; Gabriel et al., 2008; Nguyen & Winger, 2019). However, our main observation with mesopelagic fish was a clear horizontal and downwards avoidance to different light qualities, particularly white diffuse and blue spotlight. In addition, diffuse light could be better for herding since it's wider beam will affect a larger water volume (see Fig. S2) and because it has similar characteristics to natural light (sun or moon light; Kaartvedt et al., 2009). The observed avoidance (downwards and sidewards) and herding responses to light might be used in commercial fisheries to improve catch rates and selectivity, and thus should be tested further. For example, blue or white light may be used to filter mesopelagic fish from a layer, increase the density of fish in front of the trawl, or reduce escapement from the trawl. Profitable catches with pelagic trawls have been obtained in recent (2019) trial fisheries for *M. muelleri* in the Norwegian trench (Bjordal & Thorvaldsen, 2020). However, significant fish escapement through the upper panel meshes was observed by video recordings. Application of white light in the upper panel and parts of the side panels of the trawl could be used to herd fish away from the trawl net, thus reducing escapement and increasing the catchability. Artificial white light could also be used in front of the trawl, (e.g., on the trawl warps, doors and sweeps) in order to herd mesopelagic fish into the trawl path, resulting in higher densities entering the trawl. Therefore, the above suggestions should be tested in commercial fishing operations.

CRediT authorship contribution statement

Melanie J. Underwood: Methodology, Formal analysis, Investigation, Resources, Data curation, Writing - original draft, Writing - review & editing, Visualization. **Anne Christine Utne Palm:** Conceptualization, Methodology, Formal analysis, Investigation, Resources, Data curation, Writing - original draft, Writing - review & editing, Visualization. **Jan Tore Øvredal:** Methodology, Investigation, Resources. **Åsmund Bjordal:** Conceptualization, Methodology, Investigation, Resources, Writing - original draft, Writing - review & editing, Supervision, Funding acquisition.

Declarations of competing interest

None.

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Appendix A. Supplementary data

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