

Seasonal patterns in the nocturnal distribution and behavior of the mesopelagic fish *Maurolicus muelleri* at high latitudes

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ABSTRACT: Acoustic scattering layers (SL) ascribed to pearlside *Maurolicus muelleri* were studied in Masfjorden, Norway, using upward-looking echo sounders cabled to shore for continuous long-term measurements. The acoustic studies were accompanied by continuous measurements of surface light and supplemented with intermittent field campaigns. From autumn to spring, young *M. muelleri* formed an SL in the upper ~75 to 150 m in the daytime, characterized by migration to near-surface water near dusk, subsequent 'midnight sinking', followed by a dawn ascent before a return to the daytime habitat. Light levels were ~1 order of magnitude lower during the dawn ascent than for ascent in the afternoon, with the latter terminating before fish reached upper layers on ~1/3 of the nights from late November to mid-April. Adults showed less tendency of migration during autumn and winter, until the SLs of young and adults merged in late spring, and thereafter displayed coherent migration behavior. The midnight sinking became progressively deeper from autumn to winter but was strongly reduced from mid-May when the darkest nocturnal light intensity (PAR) at the surface was above $10^{-3} \mu\text{mol m}^{-2} \text{s}^{-1}$. The pearlside took on schooling in upper waters during the even lighter nights in early June, with minimum light of $\sim 5 \times 10^{-3}$ to $10^{-1} \mu\text{mol m}^{-2} \text{s}^{-1}$ at the surface. Nocturnal schooling ceased in early July, and midnight sinking reappeared in mid-August. We suggest that the strong variation in nocturnal light intensity at high latitudes provides changing trade-offs between visual foraging and avoiding predators and hence varying time budgets for feeding in the upper, productive layers.

KEY WORDS: Behavior · Diel vertical migration · Light levels · Mesopelagic · Acoustics

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INTRODUCTION

Mesopelagic fish are widely distributed in the world's oceans (Gjøsæter & Kawaguchi 1980, Dalpadado & Gjøsæter 1988, Irigoien et al. 2014). These fish act as a trophic link between zooplankton (Shreeve et al. 2009) and commercially valuable and other predators (Giske et al. 1990, Potier et al. 2007, Doksæter et al. 2008). They may also play a significant role in the carbon transport from productive upper layers to food-deprived deeper layers (Hernández-León et al. 2010, Bianchi et al. 2013, Irigoien et al. 2014). Diel vertical migration (DVM) is common

among both zooplankton and fish, usually explained as trade-offs between avoiding predators and foraging (Rosland & Giske 1994, Pearre 2003). Various studies have shown that light acts as proximate initiator for DVM (Kampa & Boden 1954, Kampa 1970), and whether DVM behavior relates to the preference for a specific absolute intensity or isolume (Sweatt & Forward 1985), the rate of change in the light intensity (Ringelberg 1995, Cohen & Forward 2009), or the preference for a range of light intensities (Staby & Aksnes 2011) has been debated.

Most focus on the mesopelagic fish DVM in relation to light has been on light conditions during the

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day (Baliño & Aksnes 1993) or differences between day and night (O'Driscoll et al. 2009, Klevjer et al. 2012). However, light levels also vary at night. Fish vertical distribution, predation, and foraging activities can significantly be affected by nocturnal lights in relation to moonlight (Gliwicz 1986, Benoit-Bird et al. 2009) but also by seasonal cycles in the nocturnal light climate (Sameoto 1989, Rasmussen & Giske 1994, Kaartvedt 2008). Masfjorden, Norway, is located at a high latitude ($\sim 60^\circ$ N) and represents a relatively deep, protected, semi-enclosed water body, providing a natural laboratory to study mesopelagic fish. *Maurollicus muelleri*, or pearlside, which is the focus species of this study, is the prevailing acoustic target in the upper ~ 200 m of Masfjorden during daytime, being distributed shallower during the night (Giske et al. 1990, Baliño & Aksnes 1993, Rasmussen & Giske 1994, Kaartvedt et al. 1998, Aksnes et al. 2004, Staby & Aksnes 2011, Staby et al. 2011). However, not all parts of the population appear to take part in DVM at all times (Staby et al. 2011).

Several studies have indicated that the vertical distribution of pearlside is related to a certain range of light levels (Baliño & Aksnes 1993, Kaartvedt et al. 1996, Staby & Aksnes 2011). Pearlside appear to take advantage of the so-called anti-predation window (Clark & Levy 1988) and forage in upper waters at dusk and dawn. Particularly juveniles migrate to the surface in the afternoon and spend a short period near the surface, followed by midnight sinking and a subsequent dawn rise before returning to their daytime depth (Giske et al. 1990, Baliño & Aksnes 1993, Rasmussen & Giske 1994, Staby et al. 2011, 2013).

According to the anti-predation window hypothesis (Clark & Levy 1988), small planktivorous fish seek out intermediate light levels that are sufficient for obtaining food while at the same time being sufficiently low to be relatively safe from visually searching piscivores. 'Midnight sinking' follows as it becomes too dark for foraging at night. However, at high latitudes, the timing of the anti-predation window in upper waters may change, as nights get much lighter during spring and summer. This pattern may prevent vertically migrating fish from entering surface layers for feeding if there is too much light (Sameoto 1989, Kaartvedt 2008). On the other hand, the dusky light levels of summer nights might cause an extended, shallow anti-predation window, permitting foraging in likely food-rich upper waters throughout the night. Some previous studies in Norway have suggested that midnight sinking may be skipped entirely in summer (Rasmussen & Giske

1994, Kaartvedt et al. 1998, Staby et al. 2011). *M. muelleri* may even initiate schooling in upper layers during light summer nights (Kaartvedt et al. 1998). However, such reports are mostly from short-term observations, and light levels associated with switches between the different behaviors have not been established.

In this study, we take advantage of the unique opportunity for a long-term study of *M. muelleri* offered by a deep locality in close proximity to land. We applied upward-looking echosounders cabled to shore that provided continuous data on vertical migration behavior from autumn throughout the subsequent summer. This research was accompanied with continuous measurements of surface light and intermittent field campaigns, including measurements of water-column light extinction. We here address the seasonal patterns in DVM behavior of *M. muelleri*, emphasizing the nocturnal distribution, particularly focusing on the relatively light summer nights.

MATERIALS AND METHODS

Acoustic measurements

The study was carried out at a ~ 370 m deep location in Masfjorden, Norway ($\sim 60^\circ 50' \text{N}$, $\sim 5^\circ 30' \text{E}$), from 7 October 2010 to 15 August 2011. Continuous acoustic measurements were made near the location of former studies (Staby et al. 2011, Dypvik et al. 2012a,b; see Fig. 1a). We used 3 upward looking SIMRAD EK60 split beam echo sounders (7.1° beam widths), mounted on the bottom (38 kHz; ~ 370 m) and on rigs anchored to the bottom, floating at ~ 250 m (120 kHz) and ~ 90 m (200 kHz) (Fig. 1). Echo sounder depths were selected to give high-resolution data of different segments of the water column. The echo sounders were calibrated at the surface using standard methods (Foote et al. 1987). Pulse lengths and ping rates were $128 \mu\text{s}$ and 1 to 2 pings s^{-1} (200 kHz), $256 \mu\text{s}$ and 1 to 2 pings s^{-1} (120 kHz), and $512 \mu\text{s}$ and 1 ping s^{-1} (38 kHz), respectively.

The submerged transceivers were kept in pressure-proof casings and cabled to shore for power and transmittance of digitized signals to laptop computers, where data were stored in raw format for later analysis. The laptops were connected to the Internet for delivery of real-time echograms via web-based interfaces as well as to remotely control the echo sounders. This linkage allowed remote access for restarting the echo sounders after periods of power

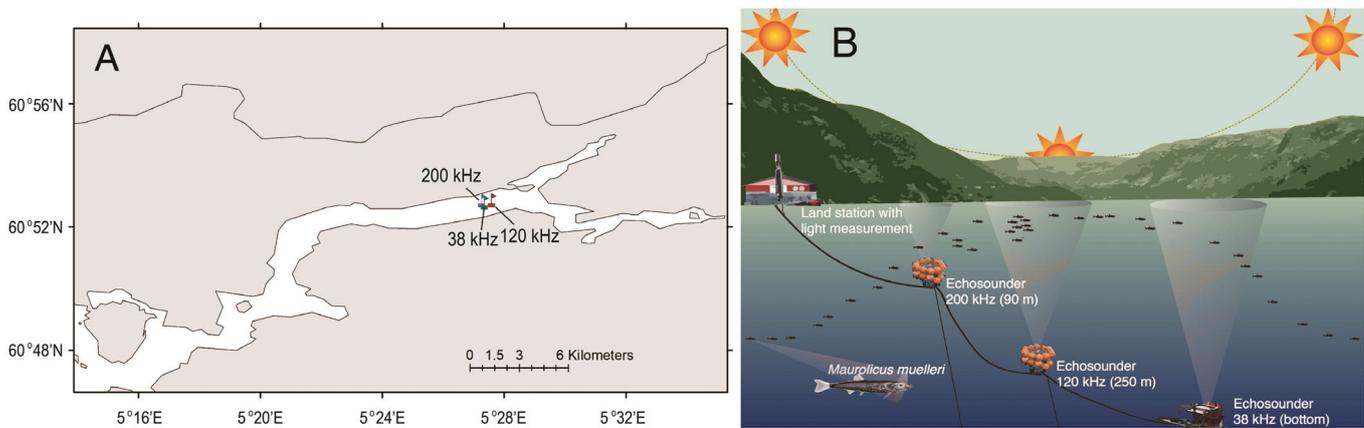


Fig. 1. (A) Map of Masfjorden depicting locations of the 3 echo sounders. The upward-looking echo sounders were mounted on the bottom ~370 m (38 kHz) and floating in the water column at ~250 m (120 kHz) and 90 m (200 kHz). (B) Sketch of the experimental set up

failures, which occurred due to a periodically unstable electrical line.

Observed DVM patterns were largely similar at 38 and 120 kHz. This similarity between the 2 frequencies suggests that the observed DVM patterns can be ascribed to fish because most plankton will not be detected at 38 kHz with the settings applied here (Kaarvedt et al. 2008). Moreover, *Maurolicus muelleri* mainly occurs in the upper ~250 m of the water column. Hence, we only present data from the floating echo sounders at 120 and 200 kHz, although we also refer to findings at 38 kHz. Data were obtained for 276 d and 269 d for 120 kHz and 200 kHz, respectively.

Processing and visualization of acoustic data

Echograms were visualized using MATLAB (version 2012b). Seasonal patterns of DVM were presented as monthly averaged daily 24 h echograms, with bin size of 2 min \times 5 cm, for the section of ~0 to 250 m. We organize the monthly echograms into 4 seasonal categories: autumn (October to November), winter (December to February), spring (March to May), and summer (June to August).

To display specific behavior patterns of organisms forming nighttime acoustic scattering layers (SLs), 4 high-resolution examples of SLs were chosen from both echo sounders to represent events that occurred in the course of the registration period: interrupted ascent (6 to 8 January), termination of midnight sinking (14 to 16 May), schooling behavior at light summer nights (18 to 20 June) and resumption of midnight sinking (14 to 16 August). This selection was

done for the whole days at 120 kHz, and with finer resolution for better visualization at 200 kHz.

The seasonal patterns of nocturnal scattering were visualized by importing all nocturnal data from 120 kHz and 200 kHz into respective echograms spanning the whole study period. Night was defined as the period after sunset and before sunrise at local time (UTC + 1 h; UTC + 2 h during daylight saving time from 28 March to 30 October 2011). Echo data were intermittently affected by different sources of noise, so prior to importing the data for final analysis, supervised noise removal was conducted to exclude 'bad echoes' using the LSSS software (Korneliusen et al. 2009). This process involved filtering of a 9-point moving average window to remove irregular spikes. The output value of this process was the scattering area (S_A), which was then translated into logarithmic value of backscattering volume (S_V ; Knudsen 1990). S_A was integrated at a resolution of 15 min \times 2 m. The upper 0–4 m was deleted to avoid surface-generated noise.

Composition of scattering layers

SLs in Masfjorden corresponding to those referred to in this paper have repeatedly been ascribed to *M. muelleri*. Previous studies conclude that the young-of-the-year form SLs in the upper 100 m from autumn to spring, and the adults stay at greater depths (Baliño & Aksnes 1993, Rasmussen & Giske 1994, Staby et al. 2011). Results from extensive trawling with a 100 m² pelagic trawl at the start (7 October 2010) and end (15 August 2011) of the present study were in accordance with these previous findings, with daytime

catches in the upper 150 m being completely dominated by *M. muelleri*. As the identity of these SLs is already well documented through previous work, details of trawl catches are not presented for the purpose of this paper. Additional plankton targets were apparent, mostly at 200 kHz.

Light measurements

Photosynthetically active radiation (PAR, 400 to 700 nm) was continuously recorded about 2 m above the surface (referred to as surface irradiance) from 10 December 2010 to 15 August 2011 with a calibrated LI-190 quantum sensor and data stored on a LI-1400 data logger. Measurements were averaged and stored every 15 min. The lower threshold of the sensor was $0.0001 \mu\text{mol m}^{-2} \text{s}^{-1}$. The surface irradiance at the darkest period at night (minimum nocturnal light levels) was higher than this sensitivity threshold from 28 April until records ended on 15 August 2011. Prior to April 28, the sensitivity of the sensor was not adequate to measure light during night. A few incidences of relatively high nocturnal light measured during winter were removed from the dataset because these incidents were ascribed to artificial lighting at the shore station where the logging was conducted.

We used the results of surface irradiance as a proxy for the irradiance at the top of the SL (as visible in the high-resolution 200 kHz echogram when using an S_V threshold of -75 dB) when the SL approached the surface in the morning (right before dawn descent) and evening (dusk ascent). However, sometimes interrupted ascents of the SL were observed in the afternoon, i.e. the top of the SL was then located well below the surface. In these cases, results from underwater light measurements were used to approximate the ambient irradiance at the top of the SL (explained below).

Underwater irradiance was measured using a RAMSES ACC hyper-spectral radiometer (Trios-optical sensors, Oldenburg, Germany) around noon on 26 January, 22 February, 11 April, 16 June, and 16 August 2011. These measurements were taken at 1, 5, and 10 m and then every 10 m down to ~ 90 m depth. For each of these depths, we calculated the attenuation coefficient (K_z) for downwelling irradiance (PAR) between the surface (i.e. 1 m depth) and the depth (z) in question according to the following expression:

$$K_z = -\ln(E_1/E_z)/(z - 1) \quad (1)$$

where E_1 and E_z are the measured downwelling irradiance at 1 and z m respectively. Simultaneous registration of surface irradiance was obtained for each of the underwater measurements so that the K_z estimates were based on simultaneous measurements of E_1 and E_z . As noted above, for the interrupted ascents, we approximated the ambient irradiance (E_{TSL}), on the order of magnitude, for the depth (Z_{TSL}) where the upward migration of the SL halted according to Eq. (2):

$$E_{\text{TSL}} = E_0 \exp[-KZ_{\text{TSL}}] \quad (2)$$

where E_0 is the measured surface irradiance at the time of the interrupted ascent, and K is the estimated attenuation coefficient at the date closest to the interrupted ascent and for the depth closest to Z_{TSL} .

In accordance with the anti-predation window hypothesis (and previous studies on pearlside), we hypothesize that *M. muelleri* will exploit dim light to forage while concurrently avoiding visually searching piscivores (Clark & Levy 1988, Rosland & Giske 1994, Staby et al. 2013). The extension of the anti-predation window (by migration) is according to this hypothesis important for their foraging and survival success. *M. muelleri* (particularly juveniles) appear to mainly forage in upper waters during dusk and dawn (Staby et al. 2011), and we used the time during which surface light values were between 10^{-3} and $1 \mu\text{mol m}^{-2} \text{s}^{-1}$ as a rough proxy to assess how the duration of potential foraging in near-surface waters would vary throughout the year. These values were selected based on the ranges measured in the course of this investigation and also encompassing the values given for the top of the *Maurolicus* SL at any time of day and year by Staby & Aksnes (2011).

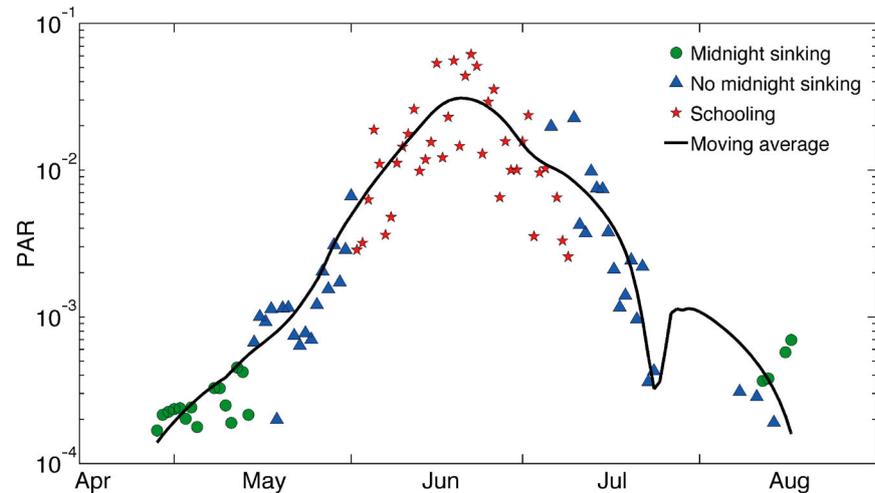
RESULTS

Nocturnal light

Surface light could be detected even during the darkest part of the night from 28 April to the end of the registration period (15 August 2011). The minimum measured nocturnal irradiance spanned 2 orders of magnitude, from $0.00016 \mu\text{mol m}^{-2} \text{s}^{-1}$ on 28 April to $0.061 \mu\text{mol m}^{-2} \text{s}^{-1}$ on 22 June. Thereafter, it decreased to the end of the records, yet with some variation between nights (Fig. 2).

Surface light was always above the registration threshold when the upper SL of *Maurolicus muelleri* appeared close to the surface at dusk and dawn (Fig. 3). Due to the shallow distribution, these light

Fig. 2. Minimum nocturnal surface irradiance (PAR) as measured with a LiCor quantum meter and fish behavior derived from echograms. There are no light measurements prior to 28 April due to insufficient sensitivity of the PAR sensor. Dots are measured minimum light values, with the line representing the moving average ($n = 23$). Color and symbol depict fish behavior on the respective nights



levels approximately represent light at the top of the near-surface scattering layer (SL), although the migrations sometimes stopped at a few meters depth, apparently hampered by a pycnocline (acoustically visible and likely related to low-salinity surface layer). Light levels proved to differ significantly between dusk and dawn (Mann-Whitney U test, $p \ll 0.001$), regardless of season. On average, the surface light at initiation of descent in the morning was relatively stable at $0.032 \mu\text{mol m}^{-2} \text{s}^{-1}$. This was an order of magnitude lower than the average light level when fish reached the surface layers in the afternoon ($0.21 \mu\text{mol m}^{-2} \text{s}^{-1}$). However, as will be outlined below, on a number of nights, fish interrupted their ascents in the afternoon and did then not experience these high light intensities (Fig. 3B).

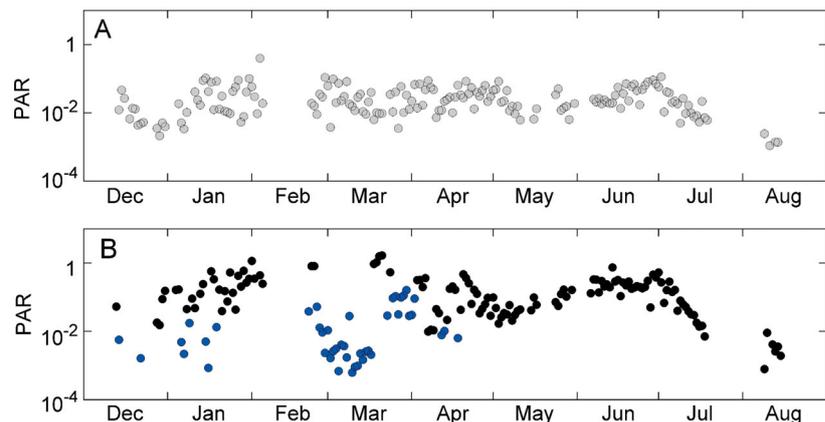
Behavioral pattern of *M. muelleri* scattering layers

In autumn and winter, at least 2 SLs ascribed to *M. muelleri* were recorded, referred to here as the deep scattering layer (DSL) and shallow scattering layer

(SSL), often structured into several sub-layers, which to some extent are masked by the monthly average presented in Fig. 4. The DSL was situated at 150 to 200 m day and night, with some but only a limited range of vertical migration subsequent to October and until March/April. Thereafter, all prevailing acoustic scatter in the upper ~ 200 m performed coherent DVM until records ended in August.

The younger *M. muelleri*, which formed the SSL, stayed at depths of ~ 75 to 125 m during daytime but were located progressively deeper through the registration period, so that daytime depth reached 150 m in spring (Fig. 4). These *M. muelleri* always carried out DVM, ascending to the surface at dusk followed by 'midnight sinking' with a subsequent ascent at dawn before descending to their daytime depths. The nocturnal distribution of the SSL subsequent to the descent from near-surface waters at dusk deepened throughout autumn to winter, from the upper ~ 30 to 50 m early in the registration period toward 70 to 100 m at the end of winter and in early spring, thereafter reversing to a shallower distribution (Figs. 4 & 5).

Fig. 3. Downwelling irradiance at the surface when the upper SL of *Maurolicus muelleri* is located closest to the surface. (A) Prior to descent in the morning; (B) after ascent in the afternoon. Blue points represent the calculated underwater light intensity at the top of the SL during interrupted ascent



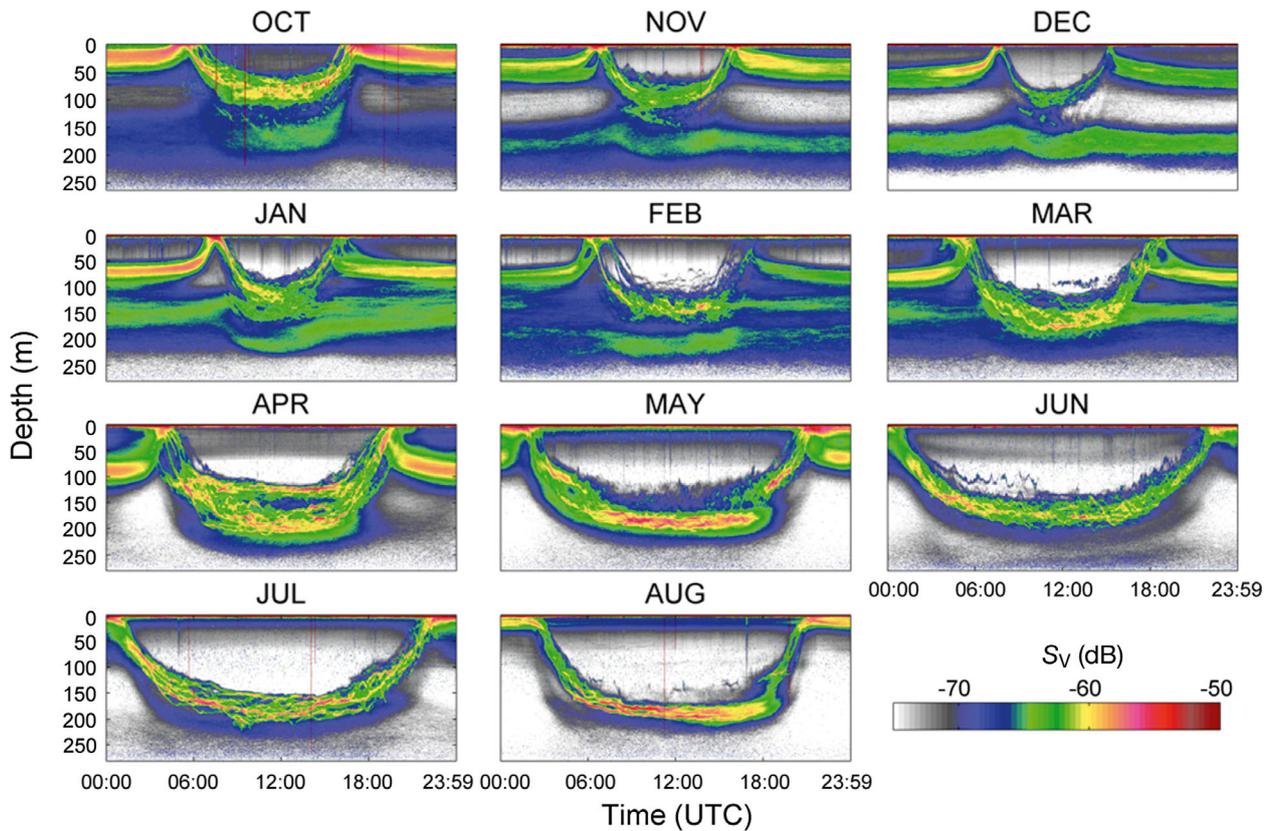


Fig. 4. Monthly averaged echograms at 120 kHz, displaying 24 h images for the upper ~280 m. Averages are based on the following numbers of days: Oct (26 d), Nov (30 d), Dec (21 d), Jan (29 d), Feb (19 d), Mar (30 d), Apr (30 d), May (29 d), Jun (30 d), Jul (17 d), and Aug (15 d). Color scale refers to backscattering strength (S_V) values (dB). Time is given in UTC (local standard time – 1 h)

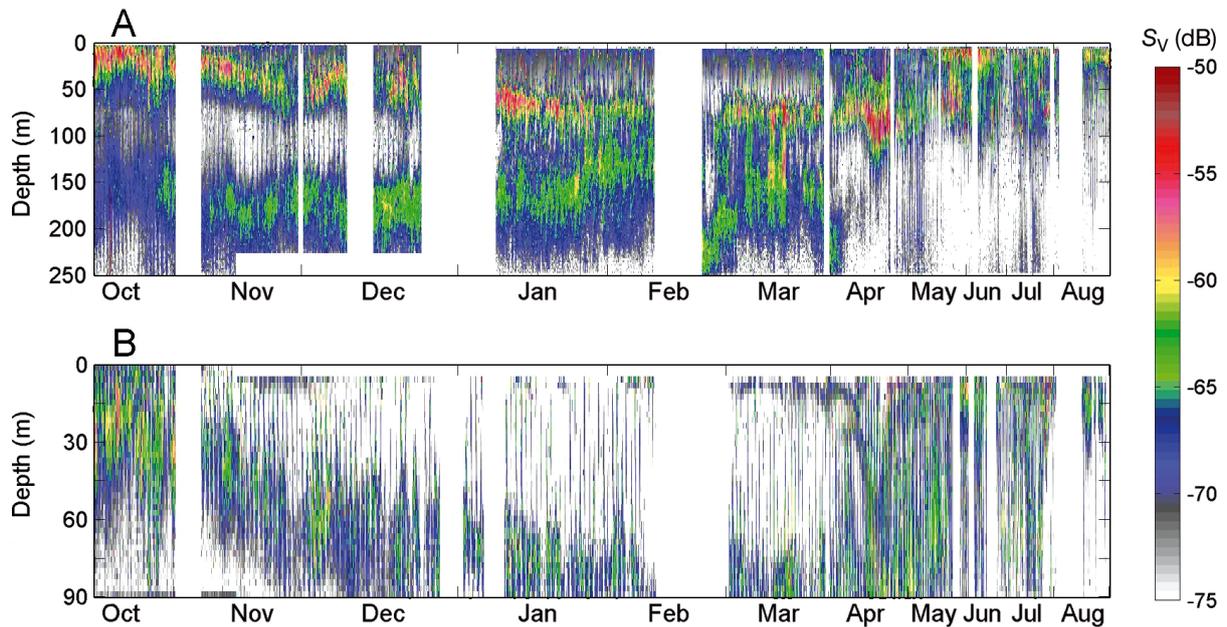


Fig. 5. Echograms depicting the nocturnal backscatter for the whole study period at (A) 120 kHz and (B) 200 kHz. Gaps in the datasets are from periods without records. Color scale refers to backscattering strength (S_V) values (dB)

From late autumn to spring, there was an asynchrony between the dusk and dawn ascent. In the afternoon, individuals forming the SSL repeatedly arrested their ascent at various depths (mean = 24.6 ± 17.4 m) before reaching upper layers (e.g. Fig. 6A). Such interrupted ascents were recorded on 46 of the 158 dates from 27 November 2010 to 18 April 2011, particularly frequently in March. The estimated underwater irradiance at the top of the SL during interrupted ascent ranged between 10^{-3} and $10^{-1} \mu\text{mol m}^{-2} \text{s}^{-1}$ and was about 1 to 2 orders of magnitude lower than during the afternoons they continued to the surface (Fig. 3B). Interrupted ascents were never recorded in the morning, so that dawn rise to surface waters was documented on every date during the same period.

A change in the nocturnal distribution took place from mid-May. The midnight sinking behavior then tended to cease, with a subsequently increased portion of the nocturnal SL inhabiting near-surface waters (upper ~25 m) throughout the night (Fig. 6B).

The minimum surface irradiance at night at the time of initiation of this behavior was $\sim 10^{-3} \mu\text{mol m}^{-2} \text{s}^{-1}$ (Figs. 2 & 7A,B). The structure of the nocturnal SLs subsequently changed in early June. On the first dates of the month, fish were schooling upon reaching the surface early at night, while schooling persisted throughout the short nights in mid-summer (Figs. 2, 6C & 7C,D). During this time, minimum nocturnal surface irradiance was mostly between $\sim 5 \times 10^{-3}$ and $10^{-1} \mu\text{mol m}^{-2} \text{s}^{-1}$, while the fishes reached upper waters at levels of $\sim 1 \mu\text{mol m}^{-2} \text{s}^{-1}$ (Fig. 7C,D). Schooling subsided in early July. Fish thereafter continued to stay in upper layers throughout night until mid-August (Fig. 6D), when midnight sinking reappeared as nocturnal surface irradiance apparently (irregular light-data at this time) again dropped toward $10^{-3} \mu\text{mol m}^{-2} \text{s}^{-1}$ (Figs. 2 & 7E).

The duration of periods with nocturnal surface light between 10^{-3} and $1 \mu\text{mol m}^{-2} \text{s}^{-1}$ (i.e. a coarse proxy for the nocturnal extension of the anti-predator window in upper layers) varied through the year

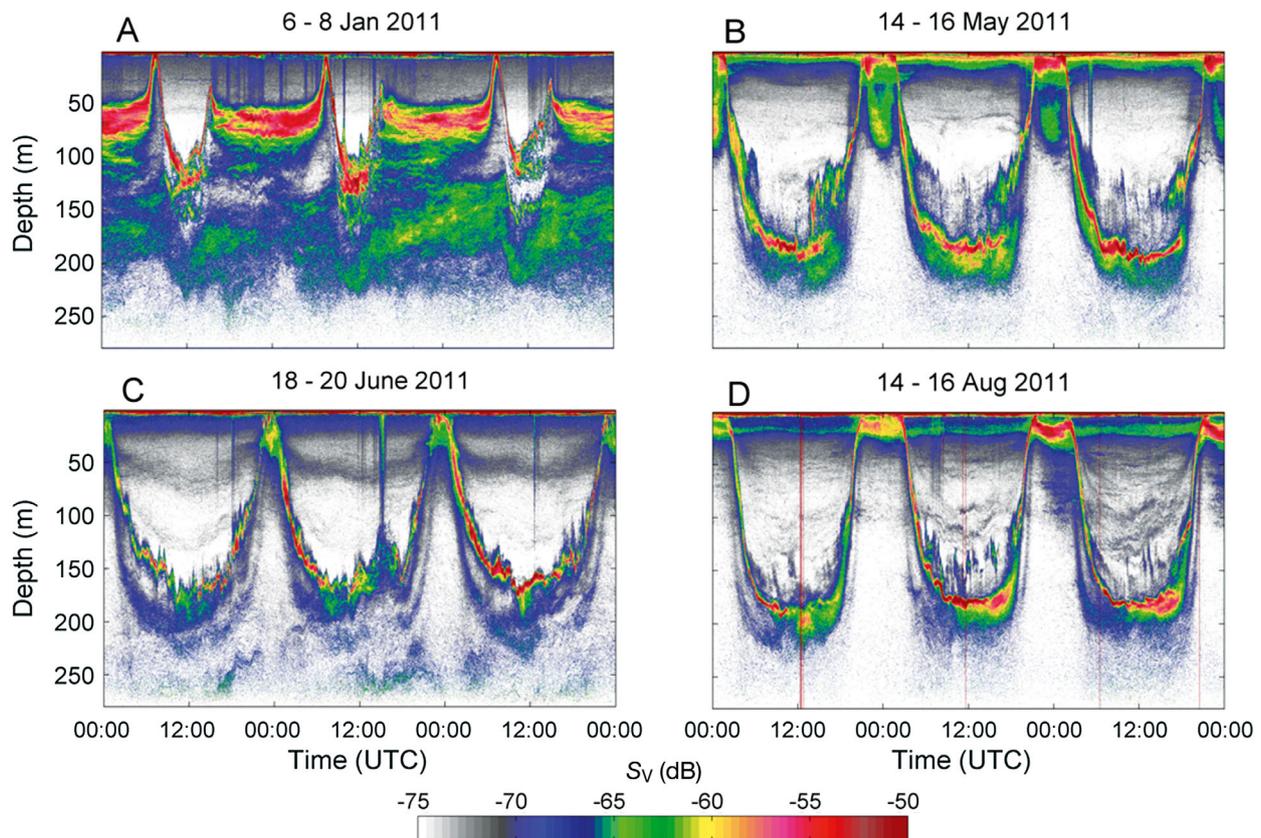


Fig. 6. Selected echograms for 3 consecutive days representing different diel migration patterns. (A) Interrupted ascent in winter (6–8 January 2011), (B) termination of midnight sinking in late spring (14–16 May), (C) schooling in mid-summer (18–20 June), and (D) resumption of midnight sinking in late summer (14–16 August). Color scale refers to backscattering strength (S_v) values (dB)

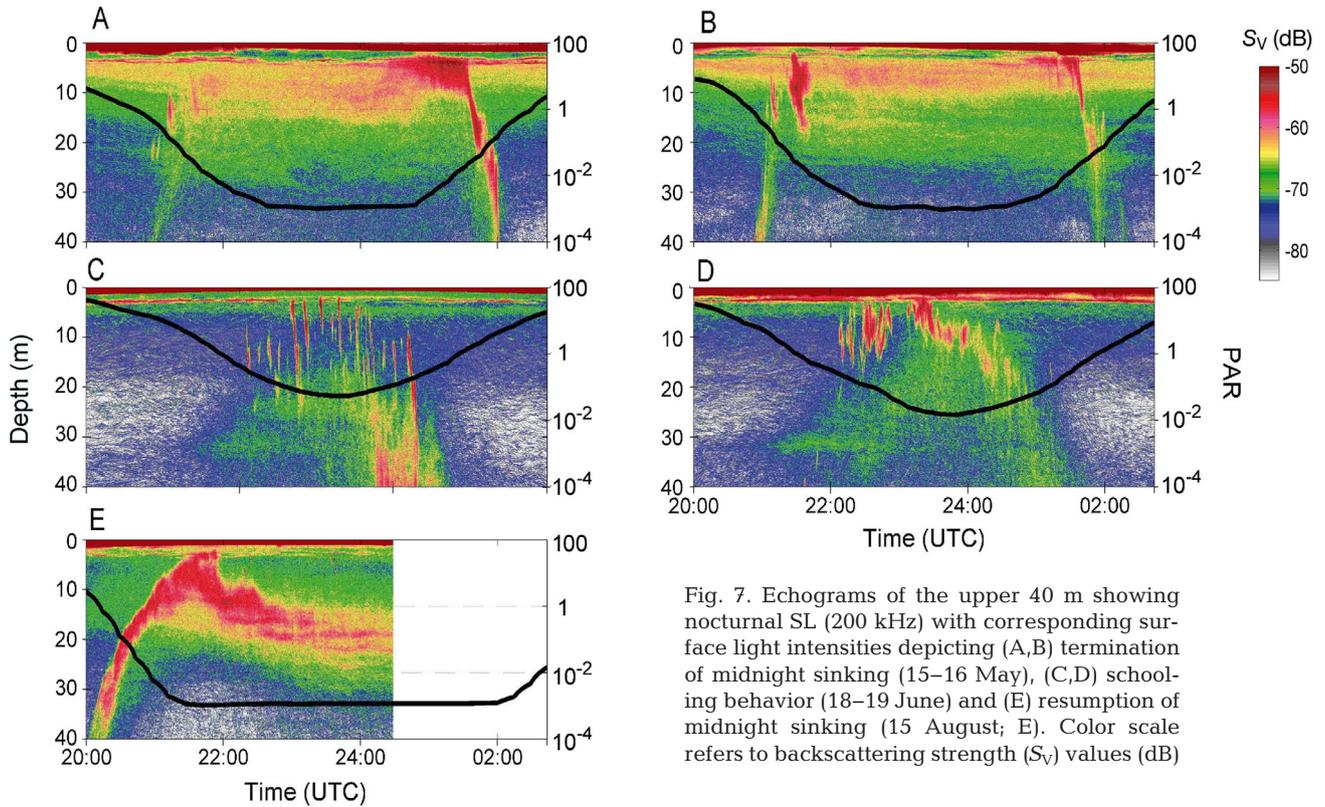


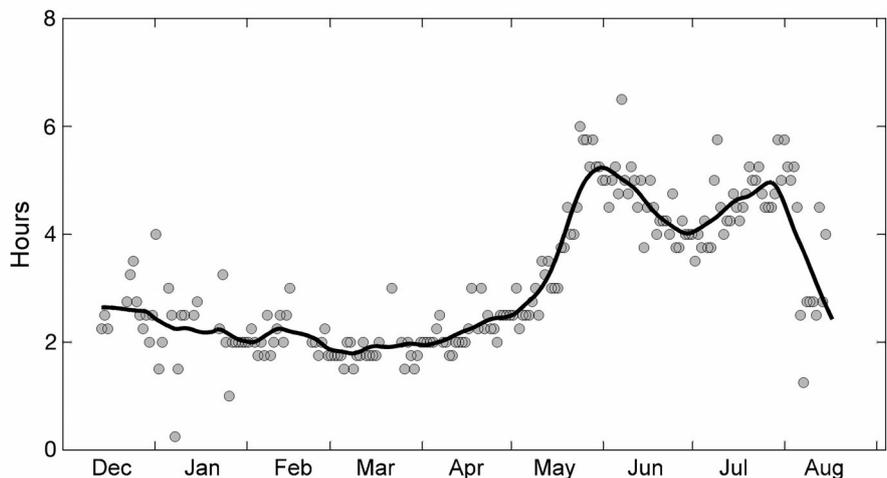
Fig. 7. Echograms of the upper 40 m showing nocturnal SL (200 kHz) with corresponding surface light intensities depicting (A,B) termination of midnight sinking (15–16 May), (C,D) schooling behavior (18–19 June) and (E) resumption of midnight sinking (15 August; E). Color scale refers to backscattering strength (S_v) values (dB)

(Fig. 8) and roughly comprised the time fish resided in upper waters. It was relatively short (~2 h) during winter and early spring, as confined to dusk and dawn periods. The time-window for this light range increased in mid-May, being 5 to 6 h in late May and early June. The period thereafter became shorter as night became shorter toward the end of June (~4 h), before subsequently increasing with increasing length of the night until the end of the registration period in mid-August, when the duration would drop due to resumption of midnight sinking.

DISCUSSION

We have unveiled seasonal variations in DVM-behavior of scattering layers (SLs) ascribed to *Maurolicus muelleri* (sampling from this study and previous sampling; see references in 'Material and methods') by exploring long-term, high-resolution acoustic data. Emphasis has been on the nocturnal vertical distribution in a high-latitude ecosystem where nocturnal light conditions vary strongly throughout the year. Individuals in the deeper SL

Fig. 8. Nocturnal extension of the duration of the anti-predation window, with grey circles depicting observations and the line indicating the moving average (n = 23). The antipredation window relates to intermediate light levels sufficient for obtaining food, while at the same time being sufficiently low to offer relative protection from visually searching piscivores. We selected the periods with surface light values being between 10^{-3} and $1 \mu\text{mol m}^{-2} \text{s}^{-1}$ based on the light ranges measured between *Maurolicus muelleri* reaching the surface in the afternoon and initiation of midnight sinking



(adult part of the population) did not appear to migrate extensively during fall and winter, yet the mid-water vertical distribution was somewhat shallower at night. Corresponding patterns emerge from previous studies (Giske et al. 1990, Staby & Aksnes 2011). Different behavior in juveniles and adults has been interpreted as different trade-off between foraging and predator avoidance in the 2 groups (Rosland & Giske 1994), as also found for other pelagic taxa (De Robertis 2002, Pearre 2003). Adults seem to have no or negative growth during winter (Rosland & Giske 1997) yet may forage in their daytime depth on plankton, such as overwintering copepods (Bagøien et al. 2001). By largely remaining in deep water, adult pearlside strongly increase their probability of survival to the spawning season in spring (Rosland & Giske 1997).

Individuals of the shallowest SL always carried out DVM, as was also the case for the adults during spring and summer, again in accordance with previous studies (Staby et al. 2011). However, the migration pattern varied and comprised migrations with and without midnight sinking, interrupted ascents in the evening and shifts from occurrence in diffuse nocturnal SL through most of the year to nocturnal near-surface schooling behaviors during the lightest part of the year.

Behavioral responses to nocturnal lights

It is well established that the vertical distribution of pearlside is related to light intensity in daytime and during diel vertical migrations (Baliño & Aksnes 1993, Rasmussen & Giske 1994). We here unveil how changes in nocturnal light levels also affect the vertical distribution and behavior of pearlside. We largely refer to surface light, and it must also be noted that the underwater light intensity we have estimated involves interpolation of the light attenuation coefficient over relatively large time periods. This interpolation has obviously reduced the accuracy of our estimates of underwater light but nevertheless provides useful information concerning the order of magnitude of the ambient light intensities experienced by the fishes.

For the whole period of measurements, estimated light intensity at the top of the SL typically spanned 4 orders of magnitude (10^{-4} to $1.6 \mu\text{mol m}^{-2} \text{s}^{-1}$; the latter being surface value when the fish reached their shallowest distribution). The additional light extinction from top to bottom of the SL should also be considered. Therefore, although the vertical positioning

of *M. muelleri* is tightly related to light, this is not a fixed light value. In line with Staby & Aksnes (2011), our results suggest that pearlside follow preferred ranges of light intensity rather than a constant fixed isolume and that these ranges span several orders of magnitude. This finding concurs with conclusions from studies of mesopelagic fish in other systems (Roe 1983, Benoit-Bird et al. 2009).

At shorter time scales, the vertical distribution appears to be coupled to a narrower range of light levels (Baliño & Aksnes 1993, Staby & Aksnes 2011), although there were notable variations from day to day. This variation particularly related to afternoons with interrupted ascents, but other aspects of the behavior also did not fully match the variation in light levels (e.g. Fig. 2). Some of this variation might reflect methodological constraints, as interpretations from echograms were subjective, but evidently other factors than light will also affect behavior. Finally, our calculation of underwater light intensity has not accounted for variations in K caused by variations in the radiant field, such as the change in the angle of incoming sunlight during the day, cloudiness, and wave action.

Within days, the surface light intensity was on average ~ 1 order of magnitude weaker when the SL reached the surface during the morning ascent than during the corresponding ascent in the afternoon. This pattern corroborates findings by Staby & Aksnes (2011). The weaker light when fish reached the surface in the morning would be in line with fish being motivated for early feeding after a long night without foraging. In contrast, this behavior is contrary to the assumption that hungry fish would be more prone to undertake risky behavior (Dill 1983) and therefore extend the duration of their dawn ascent in supposedly food-rich waters into higher light intensities. Alternatively, this behavior might have a pure physiological cause if dark-adapted fish are more efficient in detecting prey at low light levels in the morning than in the evening (this hypothesis might relate both to the pearlside and their predators). The dark-to-light adaptation in the retina is indeed much more rapid than the light-to-dark adaptation (Ferwerda et al. 1996). This hypothesis has been suggested as one possible explanation for the emergence of small planktivorous coral fishes from their nocturnal shelter in the morning at lower light levels than the levels at which they return to their shelter in the evening (Rickel & Genin 2005). Note however, that the trade-off between feeding and predator avoidance is very different in that setting. Small planktivorous fish on coral reefs are safest in bright light since they spot

their predators by sight and can retract to nearby shelters when threatened as well as when light decreases (Holbrook & Schmitt 2002). Mesopelagic fish, in contrast, rely on hiding in dim light.

Interrupted ascent

Interrupted ascent behavior was frequently recorded from late autumn to mid-March yet at different depths. In spring, the estimated underwater irradiance at the top of the SL during interrupted ascent was about 1 to 2 orders of magnitude lower than during the afternoons that the fish continued to the surface (Fig. 3). This pattern might suggest some relation to predator avoidance behavior. Previous studies have shown instantaneous diving responses among mesopelagic fish to the presence of predators (Kaartvedt et al. 2012), and such responses were also recorded for *M. muelleri* during this study (e.g. Godø et al. 2014). However, there were no systematic records of excessive numbers of predators associated with such events, and the interrupted ascents were recorded coherently by all echo sounders, located several hundred meters away from each other. Alternatively, as the copepod *Calanus* ascends from overwintering in winter and early spring, it is possible that satiation following feeding during the ascent reduces motivation for further migration during this time of the year (Staby et al. 2011). However, such reaction to satiation would expectedly be an individual response (Pearre 2003) and not the population response indicated in the echograms. Migrations might also be stopped by gradients in temperature and salinity, yet such gradients are not expected at depth and would not explain the consistent difference between dawn and dusk ascents. Overall, the most likely reason for the interrupted ascents in the afternoon seems to have some relation to perceived risk of predation, but this behavior is still poorly understood.

Midnight sinking

M. muelleri does not forage in darkness, and midnight sinking apparently takes place when the conditions are too dark for visual detection of prey (Giske et al. 1990). Accordingly, midnight sinking was initiated as nights became darker in late summer (Fig. 7E). Resumption of midnight sinking in August is also documented by Staby et al. (2011). In parallel to the darker nights in August, there may have been

changes in the distribution of potential prey, as the copepod *Calanus finmarchicus* tends to start descending for overwintering during this time of the year, with potential effects on the diel migration pattern of mesopelagic fish (Kaartvedt et al. 2009, Dypvik et al. 2012b).

The nocturnal distribution became deeper through fall and winter (Fig. 5). Giske & Aksnes (1992) suggested that pearlside was seeking warm temperature at night for more rapid digestion of the afternoon meal, in this way maximizing growth (cf. Wurtsbaugh & Neverman 1988). We do not have temperature profiles through winter to correlate with the observed distributions, but the subsurface temperature maximum will become progressively deeper due to cooling from above (Bagøien et al. 2001). This pattern would be in accordance with the observations. Results from Staby et al. (2011) did not fully support the importance of temperature profiles for pearlside that perform midnight sinking behavior, and these authors referred to predator avoidance from visually searching piscivores as an alternative explanation. We could not measure surface light during the dark winter nights due to lack of instrument sensitivity, but light intensities at the upper SL during midnight sinking would have been 3 to 5 orders of magnitude less than surface light (based on measurements of extinction), i.e. $<10^{-8} \mu\text{mol m}^{-2} \text{s}^{-1}$. In early spring, when nocturnal surface light could be detected, midnight sinking occurred when this light decreased to $\sim 10^{-3} \mu\text{mol m}^{-2} \text{s}^{-1}$, then translating into $<10^{-6} \mu\text{mol m}^{-2} \text{s}^{-1}$ at the depth of midnight sinking. Gadoids appear to be the most important predators on *M. muelleri* in Masfjorden (Giske et al. 1990, Staby & Aksnes 2011). Ryer & Olla (1999) showed that juveniles of the gadoid walleye pollock could forage successfully on *Artemia* at very low light intensities ($5 \times 10^{-7} \mu\text{mol m}^{-2} \text{s}^{-1}$). This result suggests that midnight sinking of *M. muelleri* actually may be beneficial to avoid nocturnal predators.

Termination of midnight sinking

From mid-May to mid-August, *M. muelleri* remained in upper layers throughout the nights, with limited evidence of midnight sinking. This time represents a period of the year when the concentration of zooplankton peaks in upper waters of Masfjorden (Aksnes et al. 1989, Rasmussen & Giske 1994). Seasonally fluctuating vertical distribution and abundance of zooplankton appear to affect the migration

patterns of the mesopelagic fish in this system (Staby et al. 2011, Dypvik et al. 2012b), yet as visual predators, *M. muelleri* need sufficient light to see their prey. The termination of midnight sinking occurred when the minimum nocturnal surface light exceeded $10^{-3} \mu\text{mol m}^{-2} \text{s}^{-1}$. We interpret the shift in behavior as a sign that the pearlside now had sufficient light for foraging throughout the night (Rasmussen & Giske 1994, Kaartvedt et al. 1998). The light summer nights therefore represented a marked increase in the time available for foraging in upper waters (Fig. 8). This result suggests that summer may be a particularly important period for growth, not only due to higher plankton concentrations and warmer surface waters at this time but also due to the seasonal light cycle. The importance of the seasonal light cycle at high latitudes has been reported for fish in other settings. Suthers & Sundby (1996) found enhanced growth rates of cod larvae at high latitudes in summer, which they ascribed to the long period for visual foraging at times with midnight sun.

Schooling in light summer nights

As nights became even lighter toward mid-summer, *M. muelleri* took on schooling in upper layers. This pattern occurred from early June until ceasing the first half of July concordant with minimum nocturnal surface light above $5 \times 10^{-3} \mu\text{mol m}^{-2} \text{s}^{-1}$ (Figs. 2, 6 & 7). The pearlside often schooled at 5 to 20 m depth, with light intensities at these depths being 1 to 2 orders of magnitude lower than at the surface. Schooling is well acknowledged as an anti-predator strategy (Magurran 1990), and mesopelagic fish taking up schooling behavior have previously been reported for fish being chased by tuna during daylight hours (Alverson 1961, Marchal & Lebourges 1996).

The change in nocturnal anti-predator behavior shows behavioral flexibility, which may permit extension of the oceanic habitat available for *M. muelleri*. However, there are likely limitations for the seasonal variation in light conditions that the mesopelagic fish can handle because they appear to be scarce in the polar regions. Kaartvedt (2008) suggested that this could relate to the extreme light climate at high latitudes; very light summer nights with midnight sun will prevent the fish from seeking upper layers in cover of darkness, while total darkness in winter hampers their feeding during that season.

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