Vertical Distribution of Daily Migrating Mesopelagic Fish in Respect to Nocturnal Lights

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ABSTRACT

Vertical distribution of dielly migrating mesopelagic fish in respect to nocturnal lights

Perdana Karim Prihartato

The nighttime distribution of vertically migrating mesopelagic fish in relation to nocturnal light was studied during a circumglobal survey, in the Red Sea, and in a fjord at high latitude. The study was based on data derived from ship borne echo sounders (circumglobal and the Red Sea) as well as using upward looking echo sounders mounted on the bottom (Masfjorden, Norway). We also applied a numerical model for analyzing diel vertical migration patterns. The effect of the lunar cycle was the focus in studies at low latitudes, while seasonal changes in nocturnal light climate was in focus at high latitude. Lunar phase significantly affected the distribution of mesopelagic fish at the global scale and in the Red Sea. During nights near full moon, scattering layers of mesopelagic fish distributed deeper than during darker phases of the moon. At high latitude, mesopelagic fish switched its behavior along with seasonal changes in nocturnal lights. In autumn, the population of the studied fish (*Maurolicus muelleri*) formed separated layers. Juveniles performed normal diel vertical migration followed by midnight sinking, with midnight sinking mainly related to temperature minima and also for avoiding predators. Meanwhile the adults did not migrate vertically, reducing foraging but increasing the adult survival. From late winter to mid-Spring, interrupted ascents behavior was noted in the afternoon. Predator avoidance, satiation, and finding temperature optimum might be the reason behind interrupted ascents. At lighter nights in mid-summer, *M. muelleri* took on schooling behavior, likely as an anti-predator behavior permitting access to the upper waters in the absence of darkness.
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I would like to dedicate this thesis to my family, especially my mom, for her enduring support in during my study at KAUST. I would like to see you happy mom, I love you! 😊.
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<td>Diel vertical migration</td>
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<td>GAM</td>
<td>Generalized additive model</td>
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<td>MP</td>
<td>Moon phase</td>
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<td>NDVM</td>
<td>Normal diel vertical migration</td>
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<td>NoDVM</td>
<td>No diel vertical migration</td>
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<td>PAR</td>
<td>Photosynthetically active radiation</td>
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<td>SA</td>
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SUMMARY

The main objective of this dissertation was to unveil the nocturnal habitat selection of dielly migrating mesopelagic fish. Variations in nocturnal light comprised various phases of moon light at lower latitudes in the global ocean or seasonal changing light intensities with lights summer nights at high latitudes. The studies at low latitudes addressed bulk acoustic backscatter, while the high-latitude studies addressed *Maurolicus muelleri* (pearlside) in Masfjorden, Norway. Main focus was on distribution of acoustic backscatter in relation to measured or estimated nocturnal light conditions, supplemented by sampling and numerical model simulations to analyze the diel vertical migration (DVM) behavior of the mesopelagic fish.

Mesopelagic fish is ubiquitous in the world’s ocean with higher biomass than the better-known fish of economic value. Mesopelagic fish likely play an important role for transferring carbon from the upper productive layers to food-deprived waters at mesopelagic depths (200-1000 m). Mesopelagic fish also act as trophic link between zooplankton and piscivorous fish that has more economical values such as tuna, herring and cod.

The DVM patterns of mesopelagic fish vary, with the most common pattern called normal DVM (NDVM). In NDVM, the fish typically ascend to forage in surface layers during night followed by descent to mesopelagic depths (200-1000 m) during the day. The role of nocturnal lights and its variation related to lunar phase is important in determining the distribution and the behavior of mesopelagic fish. This may particularly be the case in tropical regions often characterized by clear skies and clear waters. At higher latitudes, seasonal patterns are more pronounced both in terms of light-conditions
and an ever-changing environment with respect to temperature, prey, and predators. Therefore DVM behavior of the mesopelagic fish is expected to vary seasonally. Studies addressing the nocturnal distribution of the mesopelagic fish throughout the seasons are still scarce.

In this study, we address the distribution of vertically migrating scattering layers from the circumglobal Malaspina expedition, two expeditions in the Red Sea, and from a long-term study in a Norwegian fjord (Masfjorden). For Masfjorden, we also use a numerical model in evaluating the DVM patterns.

Chapter I describes and analyses the nocturnal distribution of mesopelagic fish around the globe in relation to the moon phase (interpreted as an effect of nocturnal lights from the moon) and other environmental parameters such as dissolved oxygen, fluorescence, turbidity, temperature and salinity. A generalized additive model (GAM) revealed that moon phase and dissolved oxygen are among the significant factors affecting the distribution of mesopelagic fish at nighttime. During full moon, scattering layer (SL) of mesopelagic fish worldwide was distributed deeper compared to other moon phases. Our hypothesis is that anti-predation behavior is the dominant motivation determining habitat selection during different phases of moonlight especially during full moon. No significant difference was found in vertical distribution between darker moon phases. Additionally, oxygen levels appeared to influence the vertical distribution of nocturnal scattering layers with shallower depth of SLs at reduced oxygen levels. The GAM also revealed relations with between the vertical distribution of the SLs with fluorescence, turbidity and temperature, yet with unclear causation, if any.
Chapter II outlines the nocturnal distribution of mesopelagic fish in the Red Sea with respect to the lunar phase. While the approach is similar to Chapter I, this study provides information of nocturnal mesopelagic scattering layer in more restricted geographic space, but covering a longer time-span within one region. Most of the mesopelagic fish populations in the Red Sea were migrating to the surface at night. Apparent effects of the full moon on the SL were observed from echograms and a statistical analysis comparing results from 4 classifications according to moon-phase revealed the deepest distribution during the brightest nights, but no difference between other nights (moon phases). Results from the GAM-analysis revealed strong and significant effect of lunar phase only for the the upper part of the SL, with the SL weighted mean depths and the lower part not being significantly affected by lunar phase. The GAM analysis also depicted relations of the SL position with oxygen, salinity temperature and fluorescence, yet with unclear ecological explanation.

Chapter III analyzed seasonal difference in the nocturnal vertical migration behavior of the müller pearls ide mesopelagic fish (*Maurolicus muelleri*) for the upper 250 m of the water column. Continuous acoustic data obtained from upward facing echo sounders that were deployed on the bottom and floating at various depths in the water columns revealed four distinct nocturnal behaviors for pearlside associated with surface lights. From autumn to spring, juveniles formed a SL in the upper ~100-150 m at daytime, ascending to near surface at dusk followed by midnight sinking and a second ascent towards the surface at dawn. Midnight sinking became progressively deeper from autumn to winter. The adult part of the population stayed at ~150-250 m both day and night during this period. In late winter and until mid-Spring, interrupted ascent behavior was observed in
the afternoon, i.e. the ascending SL aborted the ascent at various depths. Corresponding interrupted ascents were never recorded at dawn.

From April, the entire population seemed to take part in DVM, with the pattern changing as nights became progressively lighter towards late spring and summer. The pearlside largely stopped midnight sinking when surface light reached above $10^{-3}$ \( \mu \text{mol m}^{-2} \text{s}^{-1} \) in mid-May. As nights became even lighter in June, the pearlsides took up schooling in upper layers at night, light levels were then 1-2 orders of magnitude higher than at the termination of midnight sinking. Midnight sinking was resumed when surface light decreased in mid-August. We suggest that seasonally changing nocturnal lights at high latitude affected the trade-offs between avoiding predators and foraging on zooplankton. In this way, both the nocturnal light levels and the duration of the summer night lead to variation in time spent at the near surface for feeding.

In Chapter IV we simulated seasonal variations in DVM behavior of *Maurolicus muelleri* linked to different environmental setting using dynamic programming. The model predicts specific nocturnal behaviors associated with seasons. Midnight sinking occurred in autumn mainly because *M. muelleri* sank to waters with temperature minima. Interrupted ascent was reproduced in early spring, related to a combination of factors such as surface light, temperature and turbidity. Midnight sinking also occurred in early spring, at this time to depths with temperature maxima. During summer, when surface light at night increased, permitting foraging throughout the night, *M. muelleri* did not perform midnight sinking. Also high temperature and turbidity motivated the fish to stay at the near surface water during the nights, providing enhanced growth and safe conditions to hide from predators.
This thesis has revealed dynamic nocturnal behavior of mesopelagic fish related to environmental settings, geographical regions and seasonal differences. Acoustic sampling and numerical modeling proved to be a feasible approach to unveil how mesopelagic fish choose their nocturnal habitat.
SYNTHESIS

1.0 INTRODUCTION

The terminology “mesopelagic fish” is referring to fish that live in the mesopelagic zone (200-1000 m) where light may permit detection of prey but not sufficient for phytoplankton to perform photosynthesis (Marshall 1951, Salvanès & Kristoffersen 2001, Robinson et al. 2010). Mesopelagic fish is ubiquitous in the world’s oceans (Gjøsæter & Kawaguchi 1980, Lam & Pauly 2005), from tropical to temperate oceans, inland fjords and (to a lesser extent) Polar Regions. The biomass of mesopelagic fish has recently been estimated at 10 billion tones, which are two orders of magnitude higher than the yearly outcome of commercial fisheries (Irigoien et al. 2014).

After World War II, acoustic methods were applied for biological studies, and the presence of a worldwide deep scattering layer (DSL) was established. The constituents of this DSL were debated, but appeared to be made of both mesopelagic invertebrates and fish (e.g. Moore 1950, Barham 1966). It has become increasingly clear that mesopelagic fish were a prevalent cause of the acoustic reverberation thanks to their swim bladder and large abundance (Dietz 1948, Tucker 1951, Barham 1966, Koslow et al. 1997, Kloser et al. 2009, Godø et al. 2009).

Mesopelagic fish currently has little economic importance (Catul et al. 2011). However, with the depletion of global fisheries catch due to overfishing, several attempts have been made to exploit the vast mesopelagic fish resource (Balu & Menon 2006, Mahato et al 2010). Fishing efforts on the targeted mesopelagic fish have been known since 1960s, especially on the myctophids species *Diaphus coeruleus* and *Gymnoscopelus nicholski* conducted by the former Soviet nations (FAO 1997). Trial
attempts have focused on exploiting the high biomass of mesopelagic fish in the Oman Sea, northern part of Arabian Sea, where mesopelagic fish from the myctophidae family appeared to be dominant (Gjøsæter & Kawaguchi 1980, Valinassab et al. 2007). Mesopelagic fish is known to avoid trawls (Kaartvedt et al. 2012), and trawl catches of mesopelagic fish have been too low to be economically feasible (Valinassab et al. 2007). Also high body contents of wax found in myctophids have discouraged the harvest of mesopelagic fish resources (Mahato et al 2010). Better trawling gear and extraction machinery perhaps may increase the potential for mesopelagic fish on an industrial scale in the future.

Mesopelagic fish play a role as trophic link between zooplankton and predatory fishes of commercial values (Giske et al. 1990, Potier et al. 2007, Shreeve et al 2009, as well as dolphins (Døksæter et al. 2008), sharks (Waller & Baranes 1994), squids (Silas et al 1985), and sea birds (Cherel et al. 2010).

Mesopelagic fish performed diel vertical migration (DVM), staying at mesopelagic depth at daytime and migrating to near surface at nighttime (Marshall 1951, Gjøsæter & Kawaguchi 1980, Kaartvedt et al. 2008). In this way, they are also important players for the active vertical carbon pump (Hernandez-Leon et al. 2010). Calculated active carbon transport from vertical migrants (including mesopelagic fish) is 15-40% of the total carbon flux globally (Bianchi et al. 2013b), even though carbon transport driven by mesopelagic fish will vary with spatial and seasonal differences.

The DVM patterns of mesopelagic fish can vary (Dypvik et al. 2012a, b, Staby 2010, Staby et al. 2011), but the fish normally perform some variety of normal DVM, characterized by shallower distribution at night than at day. Hypotheses presented for
organism performing DVM normally entail some trade-off between predator avoidance and foraging (Clark & Levy, 1988, Neilson & Perry 1990, Loose & Dawidowicz 1994, Tarling et al. 2002, Pearre 2003), but also involve relations to temperature, either preference for warmer waters to speed up digestion and thereby growth rates under conditions without food limitation (Wurtsbaugh & Neverman 1988, Dawidowicz & Loose 1992), or preference for colder waters to reduce metabolism with food limitation (Wohlschlag 1964, Killen 2014). Migration amplitudes can be affected by water clarity (Dodson 1990), oxygen levels (Kinzer et al. 1993, Kaartvedt et al. 2010), bottom effects (Gjøsæter & Kawaguchi 1980), and salinity (Bennett et al. 2002, Lougee et al. 2002). Among environmental factors, light is believed to act as cue for the diel vertical migrations (DVM) (Kampa & Boden 1954, Kampa 1970). DVM behavior could relate to the absolute value of light or isolume (Sweatt & Forward 1985, Baliño & Aksnes 1993), the relative change in the light intensity (Ringelberg 1995), or range of light intensities (Staby & Aksnes 2011).

Many DVM studies have focused on vertical distribution in relation to daylight. However, nocturnal light levels do also vary. Moonlight is the dominant source of light at night in most of the worlds’ oceans and its effect on the distribution of vertically migrating animals has been noted (Kampa 1970, Gliwicz 1986, Hernandez-Leon et al. 2002). Mesopelagic fish is known to avoid shallow water during full moon (Benoit-bird et al. 2009a). Even the behavior of predators on mesopelagic fish (dolphins) has been found to follow the lunar phase when foraging (Benoit-bird et al. 2009b). However, animal responses to lunar phase will vary related to species. For example, the mesopelagic fish *Hygophum macrochir* and *H. taaningi* stayed in deep water during new
moon, a moon phase when fishes otherwise would be expected to search to shallow waters (Linkowski 1996). Behavioral response of mesopelagic fish to lunar phase might expectedly be particularly strong in oligotrophic water with little or no clouds.

At higher latitudes, there are strong seasonal patterns in nocturnal light, while lunar phase might be less important due to in general more cloudy weather. This is the case for one of the study sites of this investigation. Masfjorden (~60 N) is characterized by increasingly lighter (and shorter) summer nights through spring and summer, and this location is also one of the rainiest sites in Norway, with clear prevalence of overcasts nights.

The main objective of this study was to unveil the nocturnal habitat selection of dielly migrating mesopelagic fish. Vertical distribution in nocturnal light as related to various phases of moonlight at lower latitudes in the global ocean or seasonal changing light intensities with lights summer nights at high latitudes.

2. STUDY ORGANISM AND STUDY SITES

2.1. STUDY ORGANISM (MESOPELAGIC FISH)

Myctophidae and Gonostomidae are the dominant families of mesopelagic fish in the world’s ocean (Gjøsaeter & Kawaguchi 1980), with Cyclothone sp (Gonostomidae) being the most abundant mesopelagic fish from a single genus (Nelson 2006). The studies at low latitudes carried out in this thesis addressed bulk acoustic backscatter as measured during the circumglobal Malaspina expedition and during cruises in the Red Sea. The high-latitude studies addressed seasonal changes in the DVM pattern and nocturnal
distribution of *Maurolicus muelleri* (pearlside) from a long-term, acoustic study in Masfjorden, Norway.

In Norwegian fjords, mesopelagic fish from *Maurolicus muelleri* (Gmelin) or pearlside from Sternoptychidae is the dominant species in the upper 200 m. *Maurolicus muelleri* is a family member of hatchetfish (*Sternoptychidae*), has silvery body color with ventral photophores along the bottom of its stomach (Fig. 1). The genus *Maurolicus* is reported to consist of fifteen allopatric species across world’s ocean (Parin & Kobyliansky 1996), of which *M. muelleri* is believed to be the most widely spread (Gjøsaeter & Kawaguchi 1980), although many early studies referring to *M. muelleri* likely entail other species.

*M. muelleri* is the prevailing acoustic target of the upper 200 m in Masfjorden (Gjøsaeter 1981, Giske et al 1990, Bjelland 1995, Rasmussen & Giske 1994, Staby et al. 2011). The life span of *M. muelleri* varies geographically (Goodson et al. 1995). The age can be 3-5 years and size up to 70 mm in the Norwegian Sea (Gjøsaeter 1981, Bjelland 1995, Kristoffersen & Salvanes 1998). In Japanese water, *M. muelleri* is known to grow until 42-47 mm (Nishimura 1959, Okiyama 1971, Yuuki 1982). In the Red Sea, *M. muelleri* (likely *Maurolicus* sp.) life span is 1 year and the size is smaller than any other region (Dalpadado & Gjøsaeter 1987). The length female matures also varies geographically, in Norwegian fjords this is between 24-30 mm (Rasmussen & Giske 1994, Bjelland 1995). Although the life span varies, age to maturity for *M. muelleri* is about 1 year across geographical region (Gjøsaeter 1981). In Norwegian seas and fjords, spawning seasons for *M. muelleri* strated in April and lasted until October (Gjøsaeter
1981, Kristoffersen & Salvanes 1998). Multiple batches of eggs were released, thus *M. muelleri* is categorized as clutch manipulators (Giske et al. 1990).

Figure 1. Mesopelagic fish study species. A. *Maurolicus muelleri* (*Sternopychidae*) is a dominating mesopelagic fish species for the upper 200 m in Masfjorden, Norway also spread across the globe. B. *Benthosema pterotum* (*Myctophidae*) is a dominating mesopelagic fish species in the Red Sea. C. A bucket of *M. muelleri* from trawl catches in Masfjorden, Norway.

2.2. STUDY SITES

2.2.1. OCEAN BETWEEN 40 N TO 40 S

The Malaspina expedition in December 2010 – July 2011 covered areas between 40 N to 40 S (Cózar et al. 2014, Fernandez-Castro et al. 2014, Irigoien et al. 2014, Fig. 2). The expedition passed five regions of the oceans: North and South Atlantic Ocean, Indian Ocean, West and East Pacific Ocean. Each of these regions characterized with its own water current system and environmental characteristics. A general characteristic of all oceans is the presence of oxygen minimum zone at depth of 300-700 m, but there is
particularly a suboxic region in the eastern tropical Pacific Ocean (Stramma et al. 2008, Irigoien et al. 2014). Average temperature from the surface to depth of ~1000 m for the region between 40 N to 40 S (during the Malaspina cruise) is ~9°C (Irigoien et al. 2014). In general, this region is dominated by oligotrophic water or case 1 water, characterized with low abundance of phytoplankton (Longhurst et al. 1995). However, episodic upwelling also occurred thus providing opportunity for phytoplankton grazers to increase their abundance i.e. major upwelling zone in Canary current systems (between 12 N to 42 N; Barton et al. 2004, Aristegui et al. 2009).

2.2.2. THE RED SEA

The Red Sea is a semi-enclosed elongated water body, ~1600 km long and ~240 km wide, stretching from 12.5 N to 30 N (Fig. 2). The southern part has sill depth of ~125 m (Neumann & McGill 1961, Yao et al. 2014a, b). The Red Sea is known to have particularly warm deep water, which is stable at ~22°C from 200 m down to the bottom. The surface temperature varies between ~21-31°C (Klevjer et al. 2012, Dypvik & Kaartvedt 2013, Yao et al. 2014a, b). There is an oxygen minimum zone between ~300-600 m (Klevjer et al. 2012). The Red Sea is known as oligotrophic with low phytoplankton concentrations (Wishner 1980, Weikert 1982, Böttger-Schnack 1990, Böttger-Schnack et al. 2008). There is some seasonality in the production cycle, with concentration of chlorophyll-a reaching meso-trophic levels during a spring bloom (Raitsos et al. 2013).

Mesopelagic fish in the Red Sea is dominated by the myctophid Benthosema pterotum or skinny-cheek lantern fish, Maurolicus sp and Vinciguerra mabahiss. These
species are considered to be important components constituting acoustic scattering layers in this region (Dalpadado & Gjøsæter 1987, Dypvik & Kaartvedt 2013). Mesopelagic fish in the Red Sea mainly feed on copepods (Dalpadado & Gjøsæter 1987, Dypvik & Kaartvedt 2013). Their feeding seems to be restricted to upper waters at night, with no daytime feeding in deep water (Dypvik & Kaartvedt 2013), the latter in contrast to what has been found among mesopelagic fish in other part of the world (Dypvik et al. 2012b, Staby et al. 2011).

2.2.3. MASFJORDEN

Masfjorden is located in Western Norway (~60°52’ N, ~5°24’ E) with length and width of 20 km and 1 km, respectively (Fig. 2). The sill at the entrance to the fjord has a depth of 75 m (Aksnes et al. 1989). Physical environmental variables (temperature, oxygen and salinity) below the sill are mainly stable irrespective of season (Aksnes et al. 1989, Giske et al. 1990). Above sill level, temperature and salinity change seasonally from 5-16°C and 30-34 psu (Aksnes et al. 1989, Bjelland 1995, Bagøien et al. 2001, Chapter IV). Zooplankton abundance and biomass vary seasonally (Balino & Aksnes 1993, Rasmussen & Giske 1994, Bagøien et al. 2001, Staby et al. 2011, Dypvik et al. 2012a,b). In autumn and winter, zooplankton biomass at the surface is lower than at depth of 150-300 m which mainly is dominated by the overwintering copepod *Calanus* spp. (Baliño & Aksnes 1993, Bagøien et al. 2001). In spring and summer, meso-zooplankton is most abundant in near surface waters ~0-50 m (Rasmussen & Giske 1994).
Figure 2. Maps depicting study areas: A. Ocean between 40 N to 40 S, B. Red Sea, and C. Masfjorden. Green, yellow, and red circles are the nocturnal acoustic data: green for Malaspina expedition in 2010, yellow for Red Sea survey 2010, and red for Red Sea survey 2011 respectively. Meanwhile blue circle depicting the location of bottom mounted echo sounder attached to the bottom.
3.0. OBJECTIVES

The main objective of this work is to address diel vertical migration (DVM) of mesopelagic fish with particular focus on vertical distributions at night as related to nocturnal lights conditions. Variations in nocturnal light have been related to lunar phase in waters between 40 N and 40 S, and seasonally changing lights at high latitudes (60 N), characterized by light summer nights. The main objective in *Chapter I* was to investigate distribution of nocturnal scattering layer composed of mesopelagic fish in respect to lunar phase worldwide, integrating both geographic and seasonal changes. The study was based on acoustic record by hull-mounted echo sounder on a vessel that circumnavigated the world. Measurements of environmental variables were also made alongside with the acoustic record. In *Chapter II* the objective was almost similar to *Chapter I*, the study was conducted in the Red Sea, largely eliminating the geographic variable, while including a temporal variable in the same environment. In *Chapter III* effects of seasonal variations in nocturnal lights were studied in a Norwegian fjord, representing a high latitude environment (60 N) with a strong seasonal component in the light climate. The study was based on continuous acoustic records using submerged echo sounders cabled to shore. This provided 11 months of acoustic record from October to August, encompassing both the darkest and lightest period. Diel vertical migration patterns of the mesopelagic fish in relation to light levels were also assessed using a numerical model in *Chapter IV*.

Subjects that are covered in this thesis are as follows:

- Vertical migration in relation to lunar phase across seasonal and geographical differences (*Chapter I & II*)
• DVM variations in relation to seasonal changing nocturnal lights (Chapter III)
• Other factors that related to vertical distribution of mesopelagic fish during nighttime (Papers I, II, III, and IV)

4.0. MATERIALS AND METHODS

Diel vertical migration (DVM) of mesopelagic fish was studied by acoustic methods, accompanied with sampling of environmental data, and the use of a numerical model. The acoustic methods provided non-intrusive measurements at large spatial (Chapters I & II) and long temporal (Chapter III) scales. Summary of approaches on each chapters is presented in Figure 3.

Data in this study were collected from a vessel that circumnavigated the world’s ocean (Chapter I) and a vessel surveying The Red Sea in two different years (Chapter II). Long-term data from one location were collected from stationary echo sounders in a Norwegian fjord (Chapter III), where also previous long-term continuous records to study the behavior of mesopelagic fish have been carried out (Kaartvedt et al. 2009, Staby et al. 2011, Dypvik et al. 2012b). Located at high-latitude (~60°N), Masfjorden provided a deep, semi-enclosed water body in close proximity to shore that facilitates these types of studies (Kaartvedt et al. 2009). In this study, three upward-looking echo sounders were applied; one mounted on the bottom (~390 m; 38 kHz), and two in moorings floating in the water column (90 m & 250 m; 200 kHz & 120 kHz respectively). The echo sounders were cabled to shore for electricity and continuous data transmission for 11 months (Chapter III).
Animal behavior whether as individuals or populations has been studied extensively through numerical models aiming to reveal behavioral patterns and their motivation (DeAngelis & Mooij 2003, Grimm & Railsback 2005). There are several ways to study behavior of animal both as populations and individuals: life history theory approach (Cole 1954), genetic algorithm (Strand et al. 2002), ideal free distribution (Iwasa 1982) and dynamic programming (Houston et al. 1988, Mangel & Clark 1986, 1988, Rosland & Giske 1994, 1997, Rosland 1997, Mangel 2014). We use dynamic programming due to its capability to take into consideration complexities in nature along with changes in environmental properties. A numerical model in the form of dynamic programming was used to assess diel vertical migration patterns of mesopelagic fish in relation to nocturnal light levels. The model is used as a tool for explaining the mesopelagic fish behavior recorded from the echo sounders (Chapter IV). Stochastic dynamic programming was used to represent how fish choose its habitat during vertical migration with attention given to optimal depths, stomach fullness, growth and mortality.

Figure 3. Summary of approaches on each chapter. Chapter I & II focused on lunar phase effect on the distribution of mesopelagic fish scattering layers which covered study site between 40 N and 40 S and the Red Sea respectively. Chapter III is focused on the nocturnal distribution of mesopelagic fish in respect to seasonally changing nocturnal lights and Chapter IV is focus on the modeling simulation of the diel vertical migration.

5.0. ABSTRACTS OF PAPERS

Chapter I:
The impact of moon phase on the global nocturnal vertical distribution of mesopelagic scattering layers (SLs) was studied during the Malaspina expedition that circumnavigated the world. Acoustic data were obtained from a 38 kHz echo sounder throughout nearly eight lunar cycles and more than 32,000 nautical miles of cruise track. We assessed the nocturnal weighted mean depths and the vertical extension of the SL (the upper twenty-fifth percentile and the lower seventy-fifth percentile of the backscatter) and used a generalized additive model to reveal the relationship between the nocturnal vertical distribution of the SL and moon phase as well as with other environmental factors. Moon phase and dissolved oxygen significantly affected the SLs distribution on a global scale, overriding any other factor during the large geographic coverage. Full moon caused a deepening effect on the nocturnal SL. Contrary to expectations, the shallowest distribution was not observed during the darkest nights (new moon) and there was no difference in vertical distribution between other moon phases. At dissolved oxygen concentrations less than 1 ml l\(^{-1}\) the SL moved shallower. Temperature, fluorescence and turbidity had significant effect on the deeper part of the SL. Particularly when turbidity increased, the lower SL moved considerably shallower. We conclude that the trend of SL’s deepening during ~full moon (bright nights) is a global phenomenon related to anti-predator behavior.

**Chapter II:**

Acoustic scattering layers (SL) of dielly migrating mesopelagic fish in the Red Sea were studied in the upper 200 m at night using an echo sounder operating at 38 kHz. The study was conducted during ~3 months of cruises in 2010 and 2011, coinciding with two lunar cycles. We hypothesized that lunar illumination would affect the nocturnal vertical
distribution of SL, with the deepest distribution in the proxy of the brightest night (full moon) and the shallowest at the darkest night at new moon. In accordance with expectations, the SL was distributed deeper during full moon. However, SLs distribution at other lunar phases was not significantly different from each other. Moonlight - particularly during full moon - possibly affects both the foraging success of the mesopelagic fish and their predators. We suggest that vertical habitat selection is chosen according to the anti-predation window theory, representing a trade-off between detecting own prey and at the same time avoiding predators.

Chapter III:

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 a SL in the upper ~100-150 m at day, characterized by migration to near-surface water near dusk, subsequent “mid-night sinking”, followed by dawn ascent before return to the daytime habitat. Light levels were about one order of magnitude lower during the dawn ascent than for ascent in the afternoon; with the latter terminating before fish reaching upper layers on ~1/3 of the nights from late Nov 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 $10^2$ to $10^1 \mu\text{mol m}^{-2}\text{s}^{-1}$ at the surface. Nocturnal schooling ceased in early July, and mid-night sinking reappeared as nights became darker in mid-August. We suggest that the strong variation in nocturnal light intensity at high latitudes provide changing trade-offs between visual foraging and avoiding predators, and hence varying time budgets for feeding in the upper, productive layers.

Chapter IV:

Diel vertical migration (DVM) of juvenile and adult Müller’s pearlside (Maurolicus muelleri) differs seasonally. We assessed environmental impacts and the state of the organism on depth selection in a western Norwegian fjord during night by sensitivity analyses of the output of a dynamic optimization model. The model predicts the optimum depth, stomach fullness and growth of the fish. In autumn, adult and juvenile fish were vertically separated. Adults formed a non-migrating layer at depths of 150-200 m, while juveniles performed normal DVM with midnight sinking behavior. Midnight sinking was mainly driven by temperature advantage for metabolic processes. In spring, ascents were interrupted at intermediate depths in the afternoon. Combinations of environmental factors such as temperature, turbidity, prey density and size could be linked to the interrupted ascents, but stomach fullness and perceived predation risk could also interrupt the normal ascent behavior. In summer, increased surface light led to increased nocturnal predation risk. Still, pearlsides made coherent nocturnal migrations to upper layers as a consequence of enhanced feeding opportunities. At daytime, feeding in summer
benefitted from increased light at depths while higher turbidity levels reduced risk of predation.

6.0. RESULTS AND DISCUSSION

6.1. GENERAL PATTERN OF DVM IN RESPECT TO LUNAR PHASE

Light is believed to be the most important proximate factor governing mesopelagic fish habitat selection during diel vertical migration (Murray & Hjort 1912, Kampa & Boden, 1954, Balino & Aksnes 1993, Rasmussen & Giske 1994). However, most studies on light intensity affecting vertical distributions have been for daytime. The aim of this thesis is to reveal variation in the distribution of mesopelagic fish scattering layers during nighttime in respect to lunar phase and seasonally changing nocturnal lights. Since mesopelagic fish is a dominating constituent of scattering layer detected from echo sounder at 38 kHz worldwide (Gjøsaeter & Kawaguchi 1984, Klevjer et al. 2012, Dypvik & Kaartvedt 2013, Irigoien et al. 2014, Chapter I & II), the use of echo sounders has been a central approach to study the behavior of these fishes.

Our studies cover the upper 200 m of the water column (Chapter I, II, & III) as most dielly migrating mesopelagic fish would stay at this depths during nighttime (Staby et al. 2011, Klevjer et al. 2012, Dypvik & Kaartvedt 2013, Irigoien et al. 2014,). We found that during full moon, mesopelagic fish was distributed deeper than during other lunar phases. This was the case both from the circumglobal cruise and in the Red Sea (Chapter I & II). Deeper mesopelagic fish distribution during full moon is likely explained in terms of increased predation risk during the illuminated phase of the moon (Luecke & Wurtsbaugh 1993, Benoit-Bird et al. 2009a, Rechencq et al. 2011). With deeper distribution of mesopelagic fish, their predators also have to reach deeper. Dolphins, which locates their
prey by echo location, has to swim deeper while predating on myctophids (Benoit-Bird et al. 2009b). Other predators that depend on visual detection of prey are expected to take an advantage of full moon to predate on mesopelagic fish. Yet, somewhat surprisingly, the distribution in the darkest nights at new moon was not shallower than at intermediate moon phases (Chapters I & II).

Full moon could provide both increased foraging opportunity for mesopelagic fish as well as hamper foraging due to the increasing risk of being predated by piscivorous. The first effect has been documented by high death rates of zooplankton due to efficient predation by a freshwater sardine in moon light (Gliwicz 1986). The sardines were forming shoals in upper waters (Gliwicz 1986), which might be a sufficiently efficient antipredator strategy to take advantage of the light nights for foraging without unacceptable high predation risk. This might represent a parallel to what was observed for the pearlside *Maurolicus muelleri* in the light summer nights at high latitude (*Chapter III*).

On the contrary, zooplankton abundance in the open ocean was reduced during the dark phase of the moon due to predation by dielly migrating mesopelagic fish, which in darker nights might avoid their own predators (Hernandez-Leon et al. 2002). In this case, zooplankton abundance and biomass was substantially higher during full moon, mostly explained by increased ability of piscivores to prey upon the plankton eaters. Feeding activities of the dielly migrating mesopelagic fish increased during dark nights, as also found in the case of herring larvae (Blaxter, 1968).

Surface light levels during full moon is roughly at $10^3$ to $10^{-4} \mu\text{mol m}^{-2} \text{s}^{-1}$ (Glass et al. 1986, Luecke & Wurtsbaugh 1993). Light levels needed for foraging will vary depending
on species and prey type (e.g. Rickel & Genin 2005), examples include reports on visual predators which are able to forage on their prey at depth of 70 m during full moon and 40 m with only starlight or no moon (Clarke & Denton 1962). Gadoids can see at light levels of $10^{-7}$ $\mu$mol m$^{-2}$ s$^{-1}$ (Ryer & Olla 1999), i.e. at $\sim$3 orders of magnitude less than surface light during full moon. The deeper distribution of mesopelagic fish during full moon reported by Benoit-Bird (2009a) did not distribute according to an isolume, and light levels at the top of SL varied by 4 orders of magnitude throughout the lunar cycle. Light levels at top of the acoustic scattering layer of *M. muelleri* in the Norwegian fjord also ranged 4 orders of magnitude ($10^{-4}$ to 1.6 $\mu$mol m$^{-2}$ s$^{-1}$; the latter being surface value when the fish reached their shallowest distribution) (*Chapter III*).

Effects of the lunar phase on vertical migration of animal have been recorded also to deeper depths (more than 1000 m), with endogenous rhythms synchronized to lunar phase believed to be the main reason (Van Haren 2007). Endogenous rhythm in fish vertical migration has been associated to tidal forcing especially in the intertidal zone (Sato & Jumars 2008); i.e. a relation to moon phase that does not involve the nocturnal illumination. At bathypelagic depth tidal forces are minimized, but also lunar light is too week to be detected, with a of $\sim10^{-15}$ that of midday surface lights (Ochoa et al. 2013). One hypothesis is that surface irradiance during night could indirectly affect bathypelagic depth by synchronized depth-tiered population migrations (Ochoa et al. 2013). These authors further suggested that the active vertical carbon transport from surface to bathypelagic depth might be affected by lunar phase, through what they called the “bucket brigade” model of depth-tiered population migrations (Ochoa et al 2013).
6.2. DVM PATTERNS IN RELATION TO SEASONALLY CHANGING NOCTURNAL LIGHTS

Mesopelagic fish is the dominant prevailing acoustic targets in Masfjorden with *Maurolicus muelleri* composing the scattering layer at the upper 200 m and *Benthosema glaciale* for the lower parts during daytime (Giske et al. 1990, Staby et al. 2011, Dypvik et al. 2012). This thesis included long-term continuous acoustic studies on the variation of DVM behavior of *M. muelleri*, particularly addressing relations between nocturnal behaviors of mesopelagic fish observed from the echo sounders with measured nocturnal lights (*Chapter III*). The nocturnal distribution of *M. muelleri* varied with seasons; including normal DVM (NDVM) with, and without interrupted ascents in the afternoon, with and without mid-night sinking and nocturnal schooling during summer (*Chapter III*). We found that *M. muelleri* during migrations followed preferred ranges of light intensities (*Chapter III*), as also found by Staby & Aksnes 2011). During the daily migrations, *M. muelleri* ascended in the afternoon at light levels one order of magnitude higher than dawn ascent (Staby & Aksnes 2011, *Chapter III*).

Midnight sinking was performed by *M. muelleri* from winter to mid-spring. Giske et al (1990) reported midnight by juvenile *M. muelleri* when light was too dark for visual detection of prey. Minimum surface light levels during midnight sinking between autumns to mid-spring were below the instrument’s threshold ($< 10^{-4}$ µmol m$^{-2}$ s$^{-1}$). Midnight sinking became progressively deeper from autumn to winter, but was reduced in mid-May when the darkest light at the surface was above $10^{-3}$ µmol m$^{-2}$ s$^{-1}$. In early spring, when the darkest hour of night at the surface reached values that could be measured and *M. muelleri* still performed midnight sinking; we estimated that the light
intensity at the upper SL (~60 m) was less than $10^{-6}$ µmol m$^{-2}$ s$^{-1}$ (*Chapter III*). Gadoid fishes are main predators of *M. muelleri* in Masfjorden (Giske et al. 1990), and it has been reported that juvenile gadoids at this light level can still be able to forage on zooplankton (Ryer & Olla 1999). We agree with Staby et al (2011) who suggested that midnight sinking was performed by *M. muelleri* in order to avoid predators. Midnight sinking ceased in mid-May when minimum detectable surface lights were above $10^{-3}$ µmol m$^{-2}$ s$^{-1}$. Although increased light intensity translated into increased predation risk (Aksnes & Giske 1994, Utne & Aksnes 1997, Rosland & Giske 1994, Staby et al. 2013), increased light level could also increase foraging opportunity for *M. mueleri*. Accordingly, in early summer, without midnight sinking, Rasmussen & Giske (1994) reported on the highest stomach fullness of *M. muelleri* during nighttime.

Vertical migrations that were arrested at various depths during the ascent in the afternoon were observed for *Maurolicus muelleri* from late winter to spring. Estimated light levels at depths during such events ranged between $10^{-3}$ to $10^{-1}$ µmol m$^{-2}$ s$^{-1}$. Increased predation risk associated with increased light intensities is hypothesized to cause such interrupted ascents behavior (*Chapter III*), although there were no consistent records of predators during arrested ascents and this issue remains to be resolved. Staby et al. (2011) proposed that *M. muelleri* performed interrupted ascents when encountering *Calanus* at intermediate depths during, thus satiation after feeding was the main cause for the interrupted ascent by the fish. Satiation is expected to be an individual response rather than the whole population gets satiated (Pearre 2003). This explanation was supported by the model (*Chapter IV*).
Nocturnal schooling behavior occurred at depths of 5-20 m in summer from early June until mid-July when light intensity during the darkest hour at night was above $10^{-2}$ µmol m$^{-2}$ s$^{-1}$ (Chapter III). We interpret schooling behavior conducted by *Maurolicus muelleri* as an anti-predator strategy when nights became too light to provide sufficient protection from predators. Schooling has been proven effective to reduce predation risks for fish (Magurran 1990,), including for mesopelagic fish for avoiding tuna predation (Alverson 1961, Marchal & Lebourges 1996). We were unable to incorporate schooling behavior in the model since density dependent processes are beyond the ability of dynamic programing method (Chapter IV).

### 6.3. DVM PATTERNS IN RESPECT TO OTHER ENVIRONMENTAL FACTORS: DISSOLVED OXYGEN, TEMPERATURE, AND PREY ABUNDANCE

During vertical migration, mesopelagic fishes encounter environmental changes in term of light intensity, dissolved oxygen, temperature, food abundance and predators (Neilson & Perry 1990, *Chapters I-IV*). Light intensity alone could not explain the dynamic behavior of DVM of mesopelagic fish. Therefore we assessed other environmental factors affecting vertical distributions of mesopelagic fish during nighttime. Among environmental parameters that were tested in this thesis are dissolved oxygen, temperature, prey abundance, fluorescence, turbidity, and salinity (*Chapters I-IV*).

The global study covering both geographical and seasonal changes revealed that the nocturnal distributions of scattering layer, presumably dominated by mesopelagic fish,
were also related to other factors than lunar phase (dissolved oxygen, temperature and turbidity) (*Chapter I*). Dissolved oxygen plays a pivotal role in determining the limit of expansion for animal performing DVM, although mainly at daytime (LaRow 1970, Kramer 1987, Kaartvedt et al. 2010, Bianchi et al. 2013a, *Chapter I*). Oxygen minimum zones (OMZs) are common in the world oceans (Longhurst 1967, Helly & Levin 2004, Stramma et al. 2008). Mesopelagic fish predators have larger body size and need more oxygen to support their metabolic requirement than their smaller prey (Prince & Goodyear 2006). Thus, water column with low oxygen level may prevent predators to enter and thus providing safe place to hide, although also some mesopelagic predators can utilize hypoxic water (Jorgensen et al. 2009). Several studies have reported that mesopelagic fish can adapt to conditions with low oxygen levels where they seek refuge from predators (Kinzer et al. 1993, Stramma et al. 2008, 2012, Seibel 2011, Catul et al. 2011, Torres et al. 2012, Klevjer et al. 2012). During nighttime, mesopelagic fish migrated to surface enriched oxygenated water to recompense insufficient oxygen during daytime (Kramer 1987, Torres & Somero 1988, Kinzer et al. 1993, Childress & Seibel 1998, Seibel 2011).

The Malaspina expedition traversed waters with low oxygen concentrations at mesopelagic depths, and in the Eastern Pacific region values were < 1 ml/L, in accordance with previous studies (Longhurst 1967, Stramma et al. 2008, Bertrand et al. 2010). In this region, both daytime and nighttime distribution of mesopelagic fish was shallower than any other region, possibly forced by limited oxygen supply (Irigoien et al. 2014). In the Red Sea, we found a weak relationship between average depths of mesopelagic fish during nights with dissolved oxygen level (*Chapter II*). Low oxygen
level was detected in the Red Sea at depth of 300-600 m (Weikert 1982, Halim 1984, Böttger-Schnack 1990, Dypvik & Kaartvedt 2013) and could limit the extent of daytime distribution for mesopelagic microneckton or providing safe place to avoid predators. At nighttime, large portions of mesopelagic fish in the Red Sea migrated to the upper 200 m, which was not affected by low oxygen levels (Klevjer et al. 2012, Dypvik & Kaartvedt 2013, Chapter II). The statistical significant relation between oxygen level and distribution of the nocturnal scattering layer found in the Red Sea is difficult to explain ecologically, and may be a correlation without representing cause-effect. In Masfjorden, waters are generally well oxygenated (Aksnes et al. 1989, 2009) so that we exclude the possibility of oxygen as a factor affecting for the vertical migration of mesopelagic fish in this habitat.

Oxygen minimum zones are expanding in the world’s oceans, mainly due to anthropogenic pressure (Rabalais & Turner 2001, Mee 2001) and climate change effect (Keeling & Garcia 2002, Stramma et al. 2008, 2012). It is expected that mesopelagic fish will stay shallower limited by the availability of oxygen. We suggest that in the future, during full moon mesopelagic fish might be more exposed to predation, thus reducing their abundance and causing tropical food web cascades. However, oxygen depleted waters on the other hand has proved to increase light absorption (Sørnes & Aksnes 2006), so that relations are not easy to predict.

Temperature may play an important role for animals choosing habitat during diel vertical migrations (Wurtsbaugh & Neverman 1988, Levy 1990, Neverman & Wurtsbaugh 1994, Sogard & Olla 1996). Mesopelagic fish stayed in deep and cooler water during daytime; thus as consequences their metabolic rates was reduced. When
migrating to near surface thus warmer temperature at nights, their digestion and potential growth is enhanced (Rosland & Giske 1994, 1997). There will be variation in DVM behaviors within mesopelagic fish populations based on ontogenetic differences and individual motivations (Sameoto 1989, Dypvik et al. 2012a, Chapter III-IV). Juvenile *M. muelleri* performed midnight sinking in autumn, apparently into temperature minima (Chapter IV). While in early spring, when *M. muelleri* has grown into larger size, midnight sinking depth coincides with temperature maxima (Chapter IV). Sensitivity analysis conducted for juvenile *M. muelleri* in autumn showed that reduced temperature affected mesopelagic fish to distribute shallower during midnight sinking (Chapter IV). The opposite effect was observed when temperature increased; midnight sinking depth was then deeper. A similar response was observed during spring, when midnight sinking depths of mesopelagic fish became deeper when temperature increased (Chapter IV). The inconsistency of temperature preference during midnight sinking for juvenile *M. muelleri* in autumn and more grown *M. muelleri* in spring is in accordance with findings that temperature preferences for dielly migrating fish may vary by season (Mehner et al. 2007).

Temperature correlated with the distribution of nocturnal scattering layers both in the global data set and the Red Sea (Chapter I & II). However, the explanation of this relation was rather unclear. Worldwide, temperature at mesopelagic depth (600-700 m) ranged between 6 to 12°C with an average of 9°C (Irigoien et al. 2014). Increased temperature was correlated with deeper distribution of mesopelagic fish SL (Chapter I, II, & IV). In the Red Sea, temperatures are unusually warm (~22°C) at, and even below mesopelagic depths (200-1000 m) (Weikert 1982, Böttger-Schnack et al. 2008, Klevjer et
al. 2012) High temperature at mesopelagic depths in the Red Sea increases the metabolism thus possibly forcing the whole mesopelagic fish community to migrate to the surface for feeding every night (Klevjer et al. 2012, Dypvik & Kaartvedt 2013).

Mesopelagic fish perform normal DVM when epipelagic zooplankton abundance is high (Weikert 1982, Böttger-Schnack 1990, Rasmussen & Giske 1994, Staby et al. 2012, Dypvik & Kaartvedt 2013). In the Red Sea there are low concentrations of zooplankton at mesopelagic depths (Weikert 1982, Böttger-Schnack 1990, 1995, Dypvik & Kaartvedt 2013) and mesopelagic fish forage in upper waters throughout the night (Dalpadado & Gjøsæter 1987; Dypvik & Kaartvedt 2013). Along with limited seasonality on zooplankton abundance in the Red Sea, it is expected that feeding behavior of mesopelagic fish will be constrained to nighttime only (Dalpadado & Gjøsæter 1987, Van Couwelaar 1997, Klevjer et al. 2012, Chapter II).

At high latitude, zooplankton abundance and biomass vary between seasons (Balino & Aksnes 1993, Rasmussen & Giske 1994, Bagøien et al. 2001, Staby et al. 2011, Dypvik et al. 2012a, b). In winter, adult mesopelagic fish distribute corresponding to zooplankton distribution, staying at depth corresponding to distribution of overwintering copepods (Giske et al. 1990, Balino & Aksnes 1993, Bagøien et al. 2001, Dypvik et al. 2012a, b). Simulation on adult mesopelagic fish staying at depth gave high correlation with zooplankton abundance and biomass at corresponding depth (Chapter IV). Although, actual feeding was not observed, our model showed feeding rate was rather low for adult during daytime, while some dusk feeding was observed (Chapter IV). Migrating to the surface is proven to be effective for mesopelagic fish, both for juvenile and more mature fish, as they exploit near-surface anti-predation window to forage on epipelagic
zooplankton, with feeding constrained to dusk and dawn (Rosland & Giske 1994, *Chapter IV*).
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CHAPTER I

Global effects of moon phase on nocturnal acoustic scattering layers

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(manuscript)
Global effects of moon phase on nocturnal acoustic scattering layers

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Abstract
The impact of moon phase on the global nocturnal vertical distribution of mesopelagic scattering layers (SLs) was studied during the Malaspina expedition that circumnavigated the world. Acoustic data were obtained from a 38 kHz echo sounder throughout nearly eight lunar cycles and more than 32,000 nautical miles of cruise track. We assessed the nocturnal weighted mean depths and the vertical extension of the SL (the upper twenty-fifth percentile and the lower seventy-fifth percentile of the backscatter) and used a generalized additive model to reveal the relationship between the nocturnal vertical distribution of the SL and moon phase as well as with other environmental factors. Moon phase and dissolved oxygen significantly affected the SLs distribution on a global scale, overriding any other factor during the large geographic coverage. Full moon caused a deepening effect on the nocturnal SL. Contrary to expectations, the shallowest distribution was not observed during the darkest nights (new moon) and there was no difference in vertical distribution between other moon phases. At dissolved oxygen concentrations less than 1 ml l^{-1} the SL moved shallower. Temperature, fluorescence and turbidity had significant effect on the deeper part of the SL. Particularly when turbidity increased, the lower SL moved considerably shallower. We conclude that the trend of SL’s deepening during ~full moon (bright nights) is a global phenomenon related to anti-predator behavior.
Introduction

Mesopelagic acoustical scattering layers (SLs) comprising organisms carrying out diel vertical migration (DVM) are ubiquitous in the oceans (Marshall 1951, Barham 1966, Gjøsaeter & Kawaguchi 1980, Irigoien et al. 2014). Light intensity has been established as cue for mesopelagic animals to perform DVM (Kampa & Boden, 1954, Roe 1984, Frank & Widder 1997). Mesopelagic fish may follow fixed thresholds of light intensity called isolumes (Balino & Aksnes 1993), or be associated with ranges of light intensities (Staby & Aksnes 2011). Migrations may also possibly be initiated by the rate of change in the light intensity, as shown in the case of mesopelagic krill (Ringelberg 1995).

The anti-predation window theory suggests that planktivorous fish exploit periods with limited light intensities to forage on food-enriched surface layers while at the same time avoiding visually searching piscivorous fish (Clark & Levy 1988, Rosland & Giske 1994, Scheuerell & Schindler 2003). Short periods near sunset and sunrise are examples of time-windows when mesopelagic fishes find appropriate light for localizing near-surface food while at the same time being relatively safe for predators. As the light intensity decreases at night, foraging ability of piscivorous fish is hampered by reduced reaction distance and extended searching time (Aksnes & Utne 1997, Staby et al. 2013). In concordance, mesopelagic organisms may forage in the upper water column whilst the predation risks are being reduced (Clark & Levy 1988, Iwasa 1982, Staby et al. 2013), although nights may also become too dark for foraging for planktivores detecting their prey by sight (Giske & Aksnes 1992).
There are many records that pelagic organisms adjust their behavior in relation to nocturnal light levels and that the trade-offs between risk of predation and foraging opportunity will vary (Kampa & boden, 1954, Kampa 1970, Gliwicz, 1986, Benoit-bird et al. 2009a, Prihartato et al, 2014). In light summer nights at high latitudes, dielly migrating fish may choose to avoid surface layers (Sameoto 1989, Fortier et al. 2001, Kaartvedt 2008), or – depending on light level - may rather benefit from the extended periods of dusk that may provide foraging opportunities in upper waters throughout night (Kaartvedt et al. 1998, Prihartato et al, 2014).

Moonlight is a dominant source of nocturnal light and may affect the behavior of vertically migrating species (Kampa 1970, Alldredge & King 1980, Luecke & Wurtsbaugh 1993, Benoit-Bird et al. 2009a, b). Examples from nights with lunar eclipse suggest that copepods and krill may immediately respond to sudden changes in the light level (Tarling et al. 1999). Behavioral responses to moon light may be particularly pronounced in oligotrophic, clear waters in regions with little cloud cover (Dodson 1990, Hernandez-Leon et al. 2001).

Monthly patterns in mortality and population structure amongst zooplankton have been related to the state of the moon (Hernandez-Leon et al. 2001, 2010). In this case, recurrent monthly declines and increase in zooplankton standing stock have been explained with high predation rate at new moon when mesopelagic fish migrated all the way to the surface, and low mortality of zooplankton in moon-lit nights, when mesopelagic fish were assumed to avoid the upper layers where zooplankton reside, minimizing their own predation risk (Hernandez-Leon et al. 2001, 2010). Moonlight is
hypothesized to have global effects on dielly migrating mesopelagic fish (Hernandez-Leon 2008), yet no large-scale, global study has been carried out to date.

The Malaspina expedition circumnavigated the world’s ocean (www.expedicionmalaspina.es). The vessel was equipped with a 38 kHz echo sounder; enabling analyses of how nocturnal SLs in different environmental settings are behaving in the different light regimes following varying lunar cycles. Irigoien et al. (2014) concluded that the majority of the mesopelagic backscatter recorded during the Malaspina expedition originated from mesopelagic fish. This assumption is in accordance with many other studies of mesopelagic scattering layers (references in “Discussion”), even though also other taxa will contribute to the backscatter (e.g. Barham 1966). We here take benefit from the acoustic data from the Malaspina expedition to analyze whether the moon phase has a global effect on DVM. In this large-scale exercise, any measured global effects of moon phase (interpreted in terms of moon light) will override potential significant factors like varying taxonomic and ontogenetic compositions of the SLs (Linkowski 1996), cloud cover (Boden & Kampa 1967, Balino & Aksnes, 1993), distribution of food (Shreeve et al 2009, Dypvik et al. 2012), presence of predators (Kaartvedt et al. 2012), water clarity (Kaartvedt 1996, Widder & Frank 2001, Frank & Widder 2002), temperature (Wurtsbaugh & Neverman 1988, Giske & Aksnes 1992) and oxygen level (Torres et al. 1979, Childress & Seibel 1998), all known to be important for the vertical distribution and DVM of mesopelagic fish (and other taxa).

We aimed at addressing three hypotheses: First, moonlight effect on the distribution of mesopelagic SLs is a worldwide phenomenon. Second, we hypothesized that moonlight during the brightest phase (full moon) will hamper migrations to upper layers
due to increased danger of predation from visually searching piscivorous so that mesopelagic fish deepen their nocturnal distribution. Finally, we hypothesized that the shallowest distribution would occur during the darkest nights (new moon).

**Material and Methods**

Data were collected during the Malaspina expedition (*R/V Hespérides*) that circumnavigated the world from 14 Dec 2010 to 15 Jul 2011. Acoustic records that encompassed nearly eight lunar cycles and covered more than 32,000 miles of ship track were recorded (Fig. 1). An EK60 echo sounder operating at 38 kHz was used to collect the data. The data were cleaned from noises in several steps. First, moving average sliding window (9 x 1 bins) was applied to smooth the data. Second, additional visual examination of echograms was performed to ensure that bubbles and bottom effects did not affect the echoes. This procedure was performed using the large scale surveying system software (LSSS) (Korneliussen et al. 2009). Noise was particularly prominent in the nocturnal data due to periodic interference from the ships navigation system at night, leaving 106 nights of “cleaned” data from a total of 206 days sailing time. For exporting purpose, data were integrated at 2 min x 2 m depth for the upper 200 meters water column, apart from the upper 15 m that were deleted (the acoustic dead zone and near field). The depth range was selected as it basically encompassed the nocturnal distribution of the dielly migrating mesopelagic organisms. The extracted nautical area scattering coefficient (\(S_A; \text{dB re m}^2 \text{ nmi}^{-2}\)) was used as an estimate of acoustic biomass (Knudsen 1990).
In this study, only nocturnal acoustic data were used, here defined as data from 2 hours after sunset until 2 hours before sunrise at local time. Information on the sunrise and sunset along with the moon phase (percentage illuminated phase of the moon) were obtained from http://aa.usno.navy.mil/data/. Scattering layer density center estimated as weighted mean depths (SL_{WMD}) was calculated for each night. SL_{WMD} is a value of $S_A$ at each integrated depth multiplied by depth index ($d_i$) and divided by the total $S_A$ for the respective date (Eq. 1).

$$SL_{WMD} = \frac{\Sigma(S_A \cdot d_i)}{\Sigma S_A}$$  \hspace{1cm} (Eq. 1)

$$SL_C \% = \frac{\Sigma S_{Ac}}{\Sigma S_{Ac}}$$  \hspace{1cm} (Eq. 2)

The vertical extension of the SL was evaluated by estimating the daily upper limit of the $S_A$’s twenty-fifth percentile (SL_{P25}) and the lower limit at seventy-fifth percentile (SL_{P75}). Each of the characteristics for SL depths were tested against daily means of environmental parameters for the upper 200 m using generalized additive model regressions (GAM) (Hastie & Tibshirani 1990, Swartzman 1997). GAM is a non-parametric test with ability to analyze the relation between response and predictor variables without limiting the form of the relationships. We used the ‘mgcv’ package (version 1.7-28) of the R program (Wood 2006) with cubic smoothing spline functions (Hastie & Tibshirani 1990). In order to better visualize the GAM result, we multiplied the depth index by -1 so that the effects on the SL visualize shallowing trends as positive and deepening trends as negative.

The vertical extension of the SL (SL_{C}) was calculated as the sum of $S_A$ at each integrated depth divided by the total $S_A$ at each Moon phase (MP) category (Eq. 2). We
categorized moon phase into four different groups: C₁ (0-25%; 47 days), C₂ (25.1-50%; 21 days), C₃ (50.1-75%; 13 days), and C₄ (75.1-100%; 27 days). Analysis of variance (ANOVA) with post-hoc Tukey was applied to reveal which of those categories distributed deeper or shallower.

Environmental parameters were measured using a CTD, also equipped with turbidometer, oxygen sensor and fluorometer. Only CTD data coinciding with nocturnal acoustic records were used. Data were imported into MATLAB for visualization. A global coverage of water clarity was also presented in the form of downwelling attenuation coefficient irradiance at 490 nm (K₄⁹₀) retrieved from the 4 km-monthly Aqua-MODIS (www.oceancolor.gsfc.nasa.gov).

**Results**

**Water properties**

Sea surface temperatures varied from 18.1-29.3°C throughout the voyage. The depth of the thermocline ranged from ~20-140 m with temperature at ~20°C often delineating the mixed layer depth. Surface salinity varied between 33.4-37.6 psu with high salinity detected on the verge of Gulf of Panama (mid-June to July). Florescence values generally peaked between depths of 25 and ~90 m. The maximum recorded value was 3.55 (Fig. 2). There was a distinct oxygen minimum zone (< 1 mL/L) near 50-200 m in the Eastern Pacific Ocean (May-June; Fig. 2). In general, turbidity values were below 1 NTU (Tab. 1). This was also shown by the surface Kₖ(490) of Aqua MODIS satellite over 6 months period of the cruise with an average Kₖ₄⁹₀ at near surface of 0.04 m⁻¹ ± 0.064 SD (Fig 1).
Acoustic analyses and GAM model of scattering layer and environmental factors

The weighted mean depth of the nocturnal scattering layer for the upper 200 m (SL$_{WMD}$) varied from the shallowest at ~31 m to the deepest at ~130 m. The average nocturnal SL$_{WMD}$ for the whole cruise was 74.7 m, with 95% confidence interval 43.8 – 108.6 m (Fig. 3 and Fig. 4).

Moon phase had significant effects on the SL$_{WMD}$ and SL$_{P25}$ and to a lesser extent on the SL$_{P75}$ (Tab. 2). In general, a deeper distribution of the SL (negative effect) occurred when the values were 0.75 to 1 (full moon) (Fig. 6). The acoustic results from the four moon phase categories showed that the deepest occurred at C$_4$ (Kruskall-Wallis box plot, $p < 0.001$, Fig. 5). During the three darker periods (C$_1$, C$_2$, C$_3$) the mean depths were not different from each other (ANOVA with post-hoc Tukey). Most of the backscatter were confined at ~40-80 m during dark period (C$_1$, C$_2$, and C$_3$), while at brighter night (C$_4$), SLs were dispersed deeper at ~40-140 m (Fig. 5).

The distribution of the SL also was significantly related to other environmental factors than the moon phases (Tab. 2). The GAM model expected that the SLs depths were shallower with integrated dissolved oxygen (DO) less than 2.4 ml/L, with the influence of DO on SL$_{P25}$ being less than for SL$_{WMD}$ and SL$_{P75}$, i.e. being most pronounced for the deeper part of the SL (Fig. 6). The nocturnal SLs shallowed with increasing fluorescence. This was particularly evident for the lower part of the SL, with SL$_{P75}$ moving 100 m toward the surface with increasing fluorescence subsequent to the integrated values reached 0.12 (Fig. 6). Along with fluorescence, turbidity also significantly affected SL$_{P75}$, with increased turbidity, the SL would move shallower toward the surface (Fig. 6). Temperature was significantly affecting SL$_{P75}$, although it
seemed that the effect was the signature of the water mass. It appeared that salinity did not give large effect on the SL. Even so, salinity was linearly related $SL_{P25}$, while the lower SLs showed no significant relation (Tab. 2; Fig. 6).

**Discussion**

Here we present the first study of the effect of moon phase on the distribution of nocturnal scattering layer (SL) worldwide, documenting consistent effects for the habitat choice of the vertical migrants. We could not identify the species constituting the SL, since no trawling was carried out during the cruise. However, as outlined in Irigoien et al. (2014), we conclude that the backscatter largely is made up of mesopelagic fish. This concurs with a multitude of studies from throughout the worlds’ oceans that mesopelagic SLs at 38 kHz echo is dominated by mesopelagic fish; Arabian sea (Gjosaeter 1984, Kinzer et al. 1993), Red Sea (Dalpadado & Gjosaeter 1987, Klevjer et al. 2012, Dypvik & Kaartvedt 2013), Japan Sea (Sweatt & Forward 1985), Hawaiian water (Clarke 1978), Northeastern Atlantic Ocean (Roe 1984), Tasman Sea (Kloser et al. 2009) and the Mediterranean sea (Olivar et al. 2012).

The GAM-model showed that moon phase significantly affected the nocturnal SL ($SL_{P25}$ and $SL_{WMD}$), particularly in causing a deeper distribution when moon phase was above 0.75 (Fig. 6). The pattern was consistent throughout the voyage, even though the data were collected at large geographic scale, encompassing regions characterized by different environmental conditions, which each independently to some extent was correlated with the vertical distribution. Also consistent along the cruise track was the
similarity of the vertical distribution in the darker, yet still variable periods with respect to moonlight (C1, C2, and C3).

A relatively deep nocturnal distribution during full moon is most likely explained in terms of predator avoidance. This explanation would be in accordance with several previous studies addressing different taxa in various pelagic environments (Gliwicz 1986, Luecke & Wurtsbaugh 1993, Tarling et al. 1999). Hernandez-Leon et al. (2001) concluded that oceanic meso-zooplankton biomass and abundance peaked at full moon since planktivorous mesopelagic fish then avoided the upper layers at night to reduce vulnerability to piscivorous, thereby alleviating predation pressure on the plankton. Benoit-Bird et al. (2009b) concluded that a predator-prey relationship between dolphins and mesopelagic fish in Hawaiian waters was synchronized to the lunar cycle, dolphin diving deeper to forage on the mesopelagic fish during full moon in contrast to shallow foraging depth during new moon. Similar behavior was also observed for other mesopelagic fish predators, when during full moon they have to search mesopelagic fish deeper than during other lunar phases; cod (Giske et al. 1990), octopus (Villanueva 1993) and seabirds (Connan et al. 2007).

While a deeper nocturnal distribution during full moon was in accordance with our initial hypothesis, we did not find the shallowest distribution during the darkest night at new moon, as we had initially expected. An example of a parallel, seemingly counterintuitive response to moonlight is the myctophidae Hygophum macrochir and Hygophum taaningi which apparently ceased their migration during new moon and rather stayed at 400 m depth (Linkowski 1996).
We suggest that moonlight would provide sufficient light to forage on zooplankton enriched surface layer at night, at the same time with sufficiently reduced mortality risk during most phases of the moon. Such trade-offs between visual foraging and predator avoidance would be in accordance with the anti-predator window theory (Clark & Levy 1988, Rosland & Giske 1994, Scheurell & Schindler 2003). The presence of shallow anti-predation windows for mesopelagic fish foraging in upper layers has mostly been related to short periods of intermediate light at dusk and dawn (Staby et al. 2013), but also to less dark summer nights at high latitudes (Kaartvedt et al. 1998, Prihartato et al. 2014). These studies have focused on the more shallow-living components of the mesopelagic fauna (the pearlside Maurolicus muelleri). The deeper-living myctophids that prevail among mesopelagic fish in the world’s ocean (Catul et al. 2011) have more dark-adapted vision (cf. Warrant & Locket 2004), with other trade-offs between foraging and predator avoidance. Clear oligotrophic oceanic waters likely provide appropriate anti-predation windows throughout the night for dark-adapted fishes, possibly enhancing nocturnal foraging opportunities compared to more productive regions.

Among other environmental factors, dissolved oxygen (DO) was the most significant affecting the nocturnal distribution of SL (SL_{P25}, SL_{WMD}, and SL_{P75}). Oxygen plays a vital role for the habitat selection of migrating animals, particularly in regions with oxygen minimum zones (OMZ; oxygen values < 1.4 ml/L) (Childress & Seibel 1998). Regions of hypoxic waters, particularly in the marked OMZ of the eastern tropical pacific (Gilly et al. 2013) will affect the vertical extension of DVM (Longhurst 1967, Stramma et al. 2008, Bianchi et al. 2013). This clearly relates to daytime depth, but may cascade into
nocturnal distributions as well, and (Irigoiien et al. 2014) recorded shallower nocturnal distributions in regions of hypoxic waters than elsewhere.

Fluorescence values as proxy for chlorophyll suggest the level of available food for zooplankton, which in turn may translate into potential prey for mesopelagic fish located above the thermocline. There was limited variation in the depth of the fluorescence maximum throughout the survey (Fig. 2), with mean ± SD at 67.7 ± 11.82 m, while absolute fluorescence values varied considerably. The deeper parts of the SL (SL_{WMD} and SL_{P75}) were significantly related to fluorescence values, suggesting a causative relation to the shallower distribution of the mesopelagic fish in regions with high fluorescence. Increased fluorescence values in the surface may reflect increased food abundance for zooplankton, in turn causing the migrating mesopelagic fish to stay near surface. Increased fluorescence will also cause increased shading (cf. also the turbidity; Fig. 2), affecting the nocturnal light conditions. We cannot distinguish between these two possibilities.

Mesopelagic fish in the deeper part of the layer (SL_{P75}) moved shallower with increased turbidity, irrespective of moon phase (Fig. 6). Previous studies on mesopelagic fish also have documented shallower distribution with increasing turbidity (Kaartvedt et al. 1996, Wider & Frank 2001; Frank & Widder 2002). One potential mechanism is through reduced nocturnal light levels. Reduced nocturnal light related to overcast nights vs clear nights may affect the relationship, as mesopelagic fish is known to move shallower depth with presence of clouds in daytime (Balino & Aksnes 1993). We have not analyzed weather data along the cruise track, yet overcast versus clear nights would likely mainly have the effect of including noise in the data set as. Benoit Bird et al
(2009a) found that lunar phase actually accounted for more of the variability in migration of a scattering layer at the shelf than variation in nocturnal surface irradiance. They suggested that moonlight might be a cue for an endogenous lunar rhythm in the process of diel migration rather than a direct cause.

The nocturnal SL during the cruise was confined to depths above the thermocline except for ~ full moon (bright nights). Temperature gave significant effects for the deeper part of the SL (SL$_{P75}$). Temperature is known to play a role in nocturnal habitat selection for diellly migrating fish (Wurtsbaugh & Neverman 1988) and nocturnal habitat selection to speed up metabolism in warmer waters has also been suggested for mesopelagic fish (Giske & Aksnes 1992). However, we cannot conclude whether the correlation with temperature and SL$_{P75}$ in our data relate to the temperature per se, or rather reflects another water mass signature.

In conclusion, regardless of the many factors that can affect the nocturnal vertical distribution of diellly migrating mesopelagic organisms, the full moon caused a deepening effect on the nocturnal SL worldwide. The relation to moonlight appears to be a “step-function” with predator avoidance during full moon as an overriding effect.
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Table. 1. Summary of environmental parameters as mean and standard deviation (SD) for the upper 200 m.

<table>
<thead>
<tr>
<th></th>
<th>Dissolved oxygen (ml/l)</th>
<th>Temperature (°C)</th>
<th>Salinity (psu)</th>
<th>Turbidity (NTU)</th>
<th>Fluorescence</th>
</tr>
</thead>
<tbody>
<tr>
<td>Mean ± SD</td>
<td>3.58±0.61</td>
<td>17.26± 2.46</td>
<td>35.37±0.68</td>
<td>0.014 ± 1.03</td>
<td>0.075±0.048</td>
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</table>
Table 2. Results of Generalized additive models (GAM) regression for the effect of environmental factors on the scattering layer parameters. Values are degrees of freedom (d.f.) with p-levels in parentheses.

<table>
<thead>
<tr>
<th>Scattering layer (SL) parameters</th>
<th>Environmental factors</th>
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<tr>
<td></td>
<td>Moon phase</td>
<td>Dissolved oxygen</td>
<td>Temperature</td>
<td>Salinity</td>
<td>Turbidity</td>
<td>Fluorescence</td>
</tr>
<tr>
<td>SL&lt;sub&gt;P25&lt;/sub&gt;</td>
<td>2.768</td>
<td>8.472</td>
<td>1 (0.71)</td>
<td>1 (0.03336)</td>
<td>2.956</td>
<td>6.698</td>
</tr>
<tr>
<td></td>
<td>(&lt;0.0001)</td>
<td>(&lt;0.0001)</td>
<td></td>
<td></td>
<td>(0.2772)</td>
<td>(0.0648)</td>
</tr>
<tr>
<td>SL&lt;sub&gt;WMD&lt;/sub&gt;</td>
<td>5.073</td>
<td>7.46</td>
<td>8.72</td>
<td>8.183</td>
<td>5.697</td>
<td>1 (0.0001)</td>
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<td></td>
<td>(&lt;0.0001)</td>
<td>(&lt;0.0001)</td>
<td>(0.0541)</td>
<td>(0.204)</td>
<td>(0.0603)</td>
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<tr>
<td>SL&lt;sub&gt;P75&lt;/sub&gt;</td>
<td>2.329</td>
<td>6.63</td>
<td>8.8 (0.0005)</td>
<td>7.166</td>
<td>4.853</td>
<td>4.442</td>
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<td></td>
<td>(0.0753)</td>
<td>(&lt;0.0001)</td>
<td>(0.0771)</td>
<td>(0.00076)</td>
<td>(&lt;0.0001)</td>
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</tr>
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</table>
Figure 1. Map of cruise track with color symbols referring to moon phase (C₁; black, C₂; blue, C₃; red and C₄; yellow). Background shading shows 6 months average of K₄₉₀ as retrieved from Aqua-MODIS Level 3 satellite at 4 km resolution; darker color depicting water with increased K₄₉₀.
Figure 2. Hydrography along the cruise track (A) Temperature, (B) Salinity, (C) Fluorescence, (D) Turbidity, and (E) Dissolved oxygen. Color scale with red illustrating the highest and white the lowest value. Blanks represent gaps between measurements.
Figure 3. Nocturnal echogram for the upper 200 meter along the cruise track. The upper 10 m without data. The black triangles depicts borders between geographical regions; AT=Atlantic Ocean, IO= Indian Ocean, WP=Western Pacific, EP= Eastern Pacific. Color scale refers to acoustic backscatter (dB), with red as strongest and white as weakest values.
Figure 4. Daily averages of statistics representing the vertical distribution of the SL in relation to lunar illumination: $SL_{WMD}$ depicted by black line, area between $SL_{P25}$ & $SL_{P75}$ in grey. Second y-axis refers to moon phase (open circles). Dashed lines border the 95% confident interval for the whole study period.
Figure 5. Vertical extension of SL calculated based on $S_A$ for different moon phase categories; ($C_1$; black, $C_2$; blue, $C_3$; red, and $C_4$; yellow). The box-plots depict the distribution of $SL_{WMD}$ for each category (Kruskall-Wallis ANOVA tests, $p < 0.001$), showing median, 25 and 75 percentiles, and with whiskers representing 5 and 95 %. No data for upper 10 m.
Figure. 6. Generalized additive model. Effect on the statistics representing the vertical distribution of the SL (SL_{P25}, SL_{WMD} and SL_{P75}); the y-axis representing the spline functions effect on the statistics (in meter). Shaded grey areas indicate 95% confidence bounds. Note that the y-axis scale differs for SL_{P75}. Tick marks on the x-axis refer to observed data points.
CHAPTER II

Acoustic studies of lunar phase on nocturnal distribution of mesopelagic scattering layers in the Red Sea

Prihartato, PK & Kaartvedt, S

(manuscript)
Acoustic studies of lunar phase on nocturnal distribution of mesopelagic scattering layers in the Red Sea

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Abstract

Acoustic scattering layers (SL) of dielly migrating mesopelagic fish in the Red Sea were studied in the upper 200 m at night using an echo sounder operating at 38 kHz. The study was conducted during ~3 months of cruises in 2010 and 2011, coinciding with two lunar cycles. We hypothesized that lunar illumination would affect the nocturnal vertical distribution of SL, with the deepest distribution in the proxy of the brightest night (full moon) and the shallowest at the darkest night at new moon. In accordance with expectations, the SL was distributed deeper during full moon. However, SLs distribution at other lunar phases was not significantly different from each other. Moonlight - particularly during full moon - possibly affects both the foraging success of the mesopelagic fish and their predators. We suggest that vertical habitat selection is chosen according to the anti-predation window theory, representing a trade-off between detecting own prey and at the same time avoiding predators.
Introduction

Mesopelagic micronekton is distributed in all the worlds’ oceans (Gjøsaeter & Kawaguchi 1980, Irigoien et al. 2014). They commonly perform diel vertical migrations, foraging in shallow water at night and returning to depth at daytime. These migrations are generally explained as trade-offs between predator avoidance and feeding opportunity (Clark & Levy 1988, Rosland & Giske 1994), modified by hunger and satiation (Hays et al. 2001, Pearre 2003) or also affected by external stimuli such as temperature (Wurtsbaugh & Neverman 1988, Giske & Aksnes 1992, Giske et al. 1990) and light (Cohen & Forward 2009, Ringelberg 1995, Ringelberg & Van Gool 2003).

Acoustical scattering layers in the Red Sea are dominated by pearlside fish (Maurolicus muelleri; Vincegueria mabahiss) in the upper 500 m (daytime) and possibly also the skinny cheek lantern fish (Benthosema pterotum) (Dalpadado & Gjøsæter 1987, Klevjer et al. 2012, Dypvik & Kaartvedt 2013). The skinny cheek lantern fish prevail among acoustic targets in deeper waters; until about 700 m, bottom permitting (Klevjer et al. 2012, Dypvik & Kaartvedt 2013). Regardless of species, the entire population migrates to the upper 200 m at nighttime, to forage mainly on copepods (Dalpadado & Gjøsæter 1987, Dypvik & Kaartvedt 2013).

Moon is the dominant source of nocturnal light and several studies have indicated that moonlight significantly affects the distribution and behavior of vertical migrants (Gliwicz 1986, Benoit-Bird et al. 2009, Hernandez-Leon et al. 2001, 2002). For example the Tangayikan sardine (Limnothrissa miodon) forages efficiently on zooplankton at near surface during bright nights in comparison with darker nights (Gliwicz 1986). On the other hand, herring larvae utilize the dark period during new moon as the best time to
forage on zooplankton, in this way avoiding their predators (Blaxter, 1968). Hernandez-Leon (2008) documented cyclic fluctuations of zooplankton abundance in upper-layers in relation to the moon cycle, which he explains by fluctuating mortality in relation to varying effect of predation from mesopelagic fish. In that case, zooplankton mortality appeared lowest during full moon when mesopelagic fish avoided the uppermost layers where zooplankton resided.

Here we examined acoustic data from the semi-enclosed marine ecosystem of the Red Sea. The Red Sea is characterized with warm temperature at the surface from ~21-31°C as well as unusually warm deep waters; being uniformly distributed at ~22°C from ~200 m and down to the bottom, which may be deeper than 2000 m. Salinity is high (~39 psu at the surface). There is an oxygen minimum zone (< 1.4 ml/L) that expands from North to South. The depth of the lowest oxygen concentrations gets shallower from 450 m to 350 m, North to South respectively. Average minimum oxygen levels in the North is at ~1 ml/L while in the South at ~0.5 ml/L (Klevjer et al. 2012). The Northern half of the Red Sea is highly oligotrophic with clear waters, and low concentrations of zooplankton (Wishner 1980, Weikert 1982, Böttger-Schnack 1990, Böttger-Schnack et al. 2008). Skies are generally clear throughout the Red Sea.

The current study complements Prihartato et al. (2014a), which addressed nocturnal acoustic datasets from the circumglobal Malaspina expedition and the relation of scattering layers to moonlight. Here we make a similar analysis for a much more geographically restricted system where we expected limited seasonal and geographical variations. We investigate how lunar illumination will affect the vertical distribution of
mesopelagic fish in this clear and warm-water system, where trade-offs between feeding, digestion and predator avoidance may differ from other oceans.

**Methods**

Data were collected during two expeditions in the Red Sea (Fig 1) using R/V Aegaeo from 6 Mar – 23 Apr 2010 and 18 Sep - 17 Nov 2011. Temperature and salinities were measured with a SeaBird 9/11 CTD, also equipped with fluorescence and oxygen sensors. Echo data were recorded using a split beam Simrad EK60 echo sounder operating at 38 Khz. The echo sounder was not calibrated prior to sampling in 2010, so that adjustments of data for 2010 were later made based on calibration values from 2011. Acoustic data were affected by noise; therefore filtering was done to delete irregular spikes in the acoustic signals, as outlined in (Klevjer et al. 2012). Afterwards 9-point moving averages were applied to smooth the data. Supervised noise removal was conducted before importing the data for later analysis using LSSS software (Korneliussen et al. 2009). For exporting purpose, data were integrated at 2 m x 1 min. Data from the upper 15 m of the water column were removed.

Previous studies on acoustic SLs in the Red Sea have revealed that the nocturnal SL is mainly distributed in the upper 200 m of the water column (Klevjer et al. 2012, Dypvik & Kaartvedt 2013), and this depth range is our focus on analyses of the nocturnal SL. We defined “nocturnal” to represent the period of 2 hours after sunset and before sunrise, respectively (local time; UTC+3) (http://aa.usno.navy.mil/data/). This period was chosen to avoid any influence of daylight. In this study, we use normalized values of weighted mean depth (SL_{wmd}; Eq. 1), calculated at every 1 min and integrated over 200 m water
column. Also that the vertical extension of the SL was assessed by measuring the depths where twenty-fifth and seventy-fifth percentiles of the SL lied, referred to the upper and lower limit of the SL based on the total area backscatter SA (SL_{P25} & SL_{P75}, respectively). These daily SL parameters (SL_{P25}, SL_{WMD}, and SL_{P75}) were tested as response variables against daily average environmental parameters for the upper 200 m using generalized additive models (GAM) (Hastie & Tibshirani 1990, Swartzman 1997). GAM has the ability to analyze relationships between response and parameters tested without limiting the form of the relation. The GAM package of ‘mgcv’ (version 1.7-28) was used in R programming (Wood 2006). A cubic spline function was used to smooth the predictor line (Hastie & Tibshirani 1990). The depth indexes were inversed in order to better visualize the GAM results so that the deepening effect would be negative on the Y-axis and vice versa.

The vertical extension (SL_{f}) at each lunar phase (M_{p}) based on the illumination level ranging from 0 to 100 % representing new moon to full moon was calculated as the sum of S_{A} at each integrated depth divided by the total S_{A} for the particular lunar phase (Eq. 2). The four lunar phase categories are: C_{1} (0 – 25%; 17 days), C_{2} (25.1 – 50%; 16 days), C_{3} (50.1 – 75%; 11 days), and C_{4} (75.1 – 100%; 18 days). Mann-Whitney U test was applied to test datasets from different years (2010 and 2011), i.e. whether the SL_{P25}, SL_{WMD}, and SL_{P75} were distributed in a similar fashion or not. ANOVA with post-hoc Tukey test was used to test whether the vertical extension of the SL differed between moon phases:

\[
SL_{WMD} = \frac{\sum_{i=200} S_{A} d_{i}}{\sum S_{A}} \quad \text{(Eq. 1)}
\]

\[
SL_{F} = \frac{\sum S_{A(c)}}{\sum S_{A(c)}} \quad \text{(Eq. 2)}
\]
Results

Hydrography

In 2010, CTD casts from northern to central Red Sea (~28°N to 22°N respectively) showed that surface temperature spanned from 24.3 to 26.4°C. The vertically averaged temperature over the upper 200 m spanned from 24.4°C to 22.5°C. Surface salinity ranged from ~38.9-42.8 psu from northern to central Red Sea with vertically averaged salinities spanning from ~38.5 to 40.5 from the surface to 200 m depth. There was a consistent fluorescence maximum at depth of 45-140 m, with fluorescence values ranging from 0.1-1.4. Vertically averaged oxygen levels from northern to central Red Sea ranged from 2.2 ml/L to 4.1 ml/L (Fig. 2).

In 2011, surface temperatures from North to South of the Red Sea (~28°N to 17°N respectively) ranged from 28°C to 31.5°C. Vertically averaged temperature profile over the entire casts showed temperature at the surface was 31°C and decreased to 21.2°C at depth of 200 m. Salinity at the surface ranged from 40.5 to 38.5 psu from North to South, while the deeper layer (~200 m) was fairly constant at ~41 psu. Fluorescence values peaked at depth of ~50-150 m, with fluorescence maxima depth becoming gradually shallower in the South. Fluorescence values ranged between 0.1-1.4 with an overall average of 0.28. Oxygen levels ranged from 2.2-4.1 ml/L. The depth where oxygen value reaches 2 ml/L became slightly shallower from 200 m in the northern part of ~22.5 N to 170 m at the Southern part (17 N). There were also oxygen values below 1.4 ml/L in a patchy layer in the South of the Red Sea, mainly occurring at ~50-100 m (Fig 3).
Distribution of acoustic backscatter in relation to environmental conditions

Composite echograms showing the nocturnal backscatter in the upper 200 m along the cruise track for both years are given in Fig. (4). The upper part of the SL was generally deeper distributed in 2011, and Mann-Whitney U-test showed that the daily data of SL_{P25} and SL_{WMD} from 2010 and 2011 differed significantly between years (p < 0.0001 and p = 0.01, respectively). However, the SL_{P75} was not difference between the two years.

Diel echograms showed that during new moon (examples given for 28-29 Mar 2010 and 26-27 Oct 2011) the SL was concentrated at the near surface respectively at ~20-30 m and ~40-60 m. Meanwhile during full moon (examples from 13-14 Apr 2010 and 10-11 Nov 2011), SL dispersed and distributed deeper respectively at ~40-100 m and ~50-150 m (Fig. 5). Combining results for both years showed that distribution at bright nights (~full moon) was the deepest in comparison to other moon phases (post-hoc Tukey, p < 0.001) (Fig. 6).

In both years, the generalized additive model (GAM) showed that distribution of the upper scattering layer (SL_{P25}) in the Red Sea was related to lunar phase (p < 0.0001, Table 1). The distributions of the deeper part of the SLs (SL_{WMD} & SL_{P75}) however were less related to lunar phase. The GAM predicted a deeper distribution of the upper SL (SL_{P25}) when lunar phase illumination level reached above 0.75 and during full moon SL_{P25} moved 20 m deeper.

The distribution of all SLs parameters (SL_{P25}, SL_{WMD}, and SL_{P75}) varied in concordance with dissolved oxygen (p < 0.01, Table 1), with the SLs moving shallower when dissolved oxygen reached above 4 ml/L (Fig. 7). The vertical distribution of the
SLs (SL_{P25}, SL_{WMD}, and SL_{P75}) also varied significantly with salinity (p < 0.0001, Table 1) and both SL_{P25} and SL_{P75} moved shallower when salinity reached above 40 psu (Fig. 7). The lower limit of the SLs was also related to both temperature and fluorescence (Table 1).

**Discussion**

This study has suggested that the nocturnal distribution of scattering layers in the Red Sea, dominated by mesopelagic fish (see Dalpadado & Gjøsæter 1987, Klevjer et al. 2012, Dypvik & Kaartvedt 2013), is related to lunar phase, with the distribution of the SL being deeper during full moon (C_{4}) than during other moon phases. These results are similar to those of Prihartato et al (2014b) from a much larger, but also much more diverse dataset, spanning for the whole globe. Our results were also in line with other studies suggesting common responses in respect to lunar phase regardless of species composition and different environmental variables (Hernandez-Leon et al. 2002, Benoit-Bird et al. 2009). We interpret this relation so that the level of moonlight is the proximate cause for the deeper distribution at full moon, with the increased exposure to visual predators being the ultimate cause for selecting a somewhat deeper habitat.

Also the GAM analysis showed a highly significant relation with lunar phase; with a deeper distribution of the upper part of the layer at full moon. However, there was a concurrent shallow trend of the lower part of the layer (although not significant; p = 0.055), giving a more compact SL at full moon.

A very high proportion of the animals forming the SL in the Red Sea migrate from daytime depth (~300-800 m) to near surface at nighttime (Klevjer et al. 2012, Dypvik &
This is in contrast to what is often found for SLs elsewhere, where significant proportions of the mesopelagic populations may remain at depth also during nighttime (Sutton et al. 2008, Kaartvedt et al. 2009b, Staby et al. 2011, Dypvik et al. 2012, Prihartato et al. 2014). While, mesopelagic fish elsewhere also may forage at their daytime depth, or exploit limited light during dusk and dawn as anti-predation window for relatively safe foraging in near surface waters (Rosland & Giske 1994, Staby et al. 2013), mesopelagic fish in the Red Sea may rather (or also) exploit the entire night for foraging (Dalpadado & Gjøsæter 1987, Dypvik & Kaartvedt 2013), thereby extend the anti-predation window. The generally clear skies and clear waters in the Red Sea suggest different trade-offs between nocturnal feeding and predator avoidance than e.g. at higher latitudes, underlining the importance of the lunar phase in the ecology of dielly migrating mesopelagic fish in tropical waters.

Our results only address the effect of lunar phase in the upper 200 m. Recent findings suggest that lunar illumination could also affect deeper waters via depth tiered migrations (Ochoa et al. 2013).

The distribution of the SL was also significantly related to other environmental parameters. However, to what extent these are causative relationships are uncertain. Low oxygen levels might hamper downward migrations (Kinzer et al. 1993, Kaartvedt 2010), but may also provide refuge from predator (Prince & Goodyear 2006, Kaartvedt et al. 2009a) and mesopelagic fish in the nearby Arabian Sea may enter oxygen levels < 0.2 ml/L (Morrison et al. 1999, Luo et al. 2000). The mesopelagic fish in the Red Sea are exposed to more oxygenated water than those living in the Arabian Sea. Our GAM result
on the shallower SL depths with increased oxygen level does not harmonize with oxygen being a limited factor for the vertical distribution.

Mesopelagic fish can encounter high ranges of salinity during diel migrations, e.g. as reported from Masfjorden (Staby et al. 2011, Dypvik et al. 2012). The Red Sea has overturning circulation and eddies that change with seasons, also with variations in salinity from North to South (Yao et al. 2014a, b, Zhan et al. 2014). However, salinity below 100 m is practically uniform. Even so, there was significant shallowing of the SLs in relation to increased salinity, which is hard to explain in ecological terms.

Our GAM results suggest the importance of fluorescence and temperature influencing the lower part of mesopelagic fish SL in the Red Sea. Similar results were observed also from a circumglobal study encompassing larger environmental gradients, incorporating both seasonal and geographical variations (Prihartato et al. 2014b). The Red Sea has very high temperatures from the surface down to mesopelagic depth, which is not commonly observed in other oceans. Our GAM predicts deeper distributions with temperatures above 25°C (the middle and lower part of SLs; SL\textsubscript{WMD}; p = 0.04 & SL\textsubscript{P75}; p = 0.01, respectively). If a causal relationship, it is not clear how temperature influences the deeper part of the SLs only. Higher temperatures lead to high metabolic rates; which may be beneficial when organisms are limited by rate of digestion (Wurtsbaugh & Neverman 1988), but may be an unfavorable cost with limited food.

Fluorescence maxima depths in the Red Sea varied from 40-150 m with decreasing depths from North to South. Fluorescence maxima depths may be associated with high biomass of zooplankton, as shown for example in the nearby Arabian Sea (Ashjian et al. 2005). Also, maximum abundance of mesopelagic fish preys (copepods, gastropods and
ostracods) was found at depths of 50-100 m (Dypvik & Kaartvedt 2013), which is in accordance with the depths of fluorescence maxima observed from our study. Given that mesopelagic fish in the Red Sea mainly fed on herbivorous prey (copepods; Dypvik & Kaartvedt 2013) a relation between fluorescence values and scattering layers depths might be expected. However, the GAM only predicts ‘good’ fluorescence influence on the upper and lower SLs (SL_{WMD} and SL_{P75}, respectively) resulted in deeper distribution with increased fluorescence value (p= 0.03 and p=0.02, respectively). These patterns might be explained as the fish exploited increased phytoplankton abundance to avoid its predators (Giske et al. 1994, Fiksen et al. 2002). Increased concentrations of algae can also cause shading in deeper waters. However, none of these factors suggest why the SL should go deeper with increased fluorescence.

Zooplankton abundance in the Red Sea is low compared to other systems, particularly in deep waters (Wishner 1980, Weikert 1982, Böttger-Schnack 1990, Böttger-Schnack et al. 2008, Dypvik & Kaartvedt 2013). During daytime, mesopelagic fish in the Red Sea did not feed (Dypvik & Kaartvedt 2013). Thus, in accordance with hunger-satiation hypothesis (Pearre 2003), mesopelagic fish in the Red Sea is forced to forage at the near surface at night. The feeding activity with respect to lunar illumination was not addressed in this study, but fluctuations in zooplankton abundance have been related to the lunar phase elsewhere, with high abundance near full moon and low abundance at new moon (Gliwicz 1986, Pinot & Jansá 2001, Hernandez-Leon et al. 2001, 2002). Our acoustic study is in accordance with such observations, suggesting that during full moon dielly migrating mesopelagic fish may arrest their migrations at sub-surface depths, possibly not getting access to zooplankton populations, which they can harvest at other lunar phases.
(Benoit-Bird et al. 2009, Hernandez-Leon et al. 2001, 2002). An anticipated result would be increased zooplankton concentrations in near surface waters during full moon due to reduced predation by mesopelagic fish (Hernandez-Leon et al 2001), yet this remains to be established.
References


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Prihartato PK, Kaartvedt S, Irigoien X (2014b) A global study of lunar illumination effects on the distribution of diel migrating scattering layer. (manuscript)


Table 1. Results of GAM regression for the relation of environmental factors with the scattering layer parameters. The values given in the table are the degree of freedom (d.f.) and p-level inside the parentheses.

<table>
<thead>
<tr>
<th>Covariate</th>
<th>Lunar phase</th>
<th>Dissolved oxygen</th>
<th>Temperature</th>
<th>Salinity</th>
<th>Fluoresence</th>
</tr>
</thead>
<tbody>
<tr>
<td>SLP25</td>
<td>2.99(&lt;0.0001)</td>
<td>4.27(&lt;0.0001)</td>
<td>2.99(0.09)</td>
<td>3.76(&lt;0.001)</td>
<td>1 (0.03)</td>
</tr>
<tr>
<td>SLWMD</td>
<td>2.65(0.06)</td>
<td>3.77(&lt;0.001)</td>
<td>2.51(0.04)</td>
<td>8.38(&lt;0.001)</td>
<td>7.5(0.28)</td>
</tr>
<tr>
<td>SLP75</td>
<td>2.09(0.06)</td>
<td>2.36(0.001)</td>
<td>2.60(0.01)</td>
<td>2.552(&lt;0.001)</td>
<td>1 (0.02)</td>
</tr>
</tbody>
</table>
Fig. 1. Maps showing cruise tracks of R/V Aegaeo, (A) 2010 and (B) 2011. Boxes with coloration show the nocturnal acoustic record from EK60 marked according to lunar illumination where black is $C_1$ (0-25%), blue is $C_2$ (25.1-50%), red is $C_3$ (50.1-75%) and red is $C_4$ (75.1-100%). Green dots show locations of CTD casts for both years.
Fig. 2. Temperature, salinity, fluorescence and oxygen level from North (28°N) to South (22°N) in the Red Sea based on CTD casts in March-April 2010 as depicted in Figure 1A.
Fig. 3. Temperature, salinity, fluorescence and oxygen level from North (28°N) to South (17°N) in the Red Sea based on CTD casts in Sept-Nov 2011 as depicted in Figure 1B.
Fig. 4. Echograms from hull-mounted 38 kHz echo sounder displaying nocturnal backscatter from North to South in the Red Sea. Upper and lower panel is respectively 2010 and 2011 data. Coloration of echograms refers to volume backscattering (Sv), with red as the strongest and white the weakest backscatters.
Fig. 5. Daily 24 hours echogram in the upper 200 m from hull mounted 38 kHz echo sounder. (A) 28-29 Mar 2010 and (C) 26-27 Oct 2011 at new moon (SL\textsubscript{WMD} respectively is at 88.74 m and 112.69 m). (B) 13-14 Apr 2010 and (D) 10-11 Nov 2011 exemplify full moon (SL\textsubscript{WMD} respectively is at 83.98 m and 105.51 m). Black and red triangles depict sunset and sunrise. The coloration refers to volume backscattering (Sv), where red is the strongest and white the weakest backscatter. Electrical noise has been deleted. Time is presented as local time (UTC + 3).
Fig. 6. Vertical distribution of SL (SL$_F$), categorized based on lunar phase (fraction of illuminated moon): C$_1$ (0-25%), C$_2$ (25.1 – 50%), C$_3$ (50.1 – 75%) and C$_4$ (75.1 – 100 %).

The upper 15 m was deleted to avoid surface generated noise.
Fig. 7. Generalized additive model functions on the influence of moon phase and environmental parameters on scattering layers of mesopelagic fish in the Red Sea with P25, WMD and P75 are the upper limit, middle and lower limit of the scattering layer. Environmental variables are dissolved oxygen, temperature, salinity, and fluorescence. Grey shaded area indicates 95% confidence bounds.
CHAPTER III

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

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

Perdana K Prihartato, Dag L Aksnes, and Stein Kaartvedt

**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 a SL in the upper ~100-150 m at day, characterized by migration to near-surface water near dusk, subsequent “mid-night sinking”, followed by dawn ascent before return to the daytime habitat. Light levels were about one order of magnitude lower during the dawn ascent than for ascent in the afternoon; with the latter terminating before fish reaching upper layers on ~1/3 of the nights from late Nov 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 $10^{-2}$ to $10^{-1} \, \mu\text{mol m}^{-2}\text{s}^{-1}$ at the surface. Nocturnal schooling ceased in early July, and mid-night sinking reappeared as nights became darker in mid-August. We suggest that the strong variation in nocturnal light intensity at high latitudes
provide changing trade-offs between visual foraging and avoiding predators, and hence varying time budgets for feeding in the upper, productive layers.

**Introduction**

Mesopelagic fish are widely distributed in the world’s oceans (Gjøsaeter & Kawaguchi 1980, Dalpadado & Gjøsaeter 1988, Irigoien et al. 2014). They act as trophic link between zooplankton (Shreeve et al. 2009) and commercially valuable and other predators (Giske et al. 1990, Potier et al. 2007, Doksaeter et al. 2008). They may also play a significant role in the carbon transport from productive upper layers to food-deprived deeper layers (Hernandez-Leon 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), 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 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...
Masfjorden, Norway, is located at high-latitude (~60˚N), and represents a relatively deep, protected, semi-enclosed water body, providing a natural laboratory to study mesopelagic fish. *Maurolicus muelleri* or pearlside, which is the focus species of this study, is the prevailing acoustic target in the upper ~200 meter of Masfjorden during daytime, being distributed shallower during night (Giske et al. 1990, Balino & 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 (Balino & Aksnes 1993, Kaartvedt 1996, Staby & Aksnes 2011). Pearlside appears 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, spend a short period near surface followed by midnight sinking, a subsequent dawn rise, before returning to their daytime depth (Giske et al. 1990, Balino & Aksnes 1993, Rasmussen & Giske 1994, Kaartvedt et al. 1998, Staby et al. 2011, Staby et al. 2013).

According to the anti-predation window hypothesis (Clark & Levy 1988), small planktivorous fish seek out intermediate light levels which are sufficient for obtaining food, while at the same time being sufficiently low to be relatively safe for visually searching piscivores. “Mid-night 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 may prevent vertically migrating fish from entering surface layers for feeding if too light (Sameoto
1989, Kaartvedt 2008). On the other hand, dusk 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 mid-night 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 in 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 *Maurolicus 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 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**

The study was carried out at a ~ 350 m deep location in Masfjorden, Norway (~ 60° 50’ N, ~5° 30’ E), from 7 Oct 2010 to 15 Aug 2011. Continuous acoustic measurements were made near the location of former studies conducted by (Staby et al. 2011, Dypvik et al. 2012a, b) see map in Fig. 1. We used three calibrated upward looking SIMRAD EK60 split beam echo sounders (7.1° beam widths), mounted on the bottom (38 kHz) and in rigs
anchored to the bottom, floating at ~250 m (120 kHz) and ~90 m (200 kHz) (Fig. 2). Echo sounder depths were selected to give high-resolution data of different segments of the water column. Observed DVM patterns were largely similar at 38 and 120 kHz. This similarity between the two frequencies suggests that the observed DVM patterns can be ascribed to fish as most plankton will not be detected at 38 kHz with the settings applied here (Kaartvedt 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 also referring to findings at 38 kHz.

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 Internet for delivery of real-time echograms via web-based interfaces as well as to remotely control the echo sounders. This allowed remote access for restarting the echo sounders after periods of power failures, which occurred due to a periodically unstable electrical line. Data were obtained for 276 days and 269 days for 120 kHz and 200 kHz, respectively.

Echograms were visualized using MATLAB. Seasonal patterns of *Maurolicus muelleri* DVM were presented as monthly averaged daily 24 hours echograms, with bin size of 2 min x 5 cm, for the section of ~0-250 m. We organize the monthly echograms into four seasonal categories; autumn (Oct-Nov), winter (Dec-Feb), spring (Mar-May) and summer (Jun-Aug).

In order to display specific behavior patterns of nighttime scattering layers (SLs), four 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 (6-8 Jan),
termination of mid-night sinking (14-16 May), schooling behavior at light summer nights (18-20 Jun) and resumption of mid-night sinking (14-16 Aug). This was done for the whole days at 120 kHz, and with more short-term resolution for better visualization at 200 kHz.

The patterns of nocturnal scattering for the whole study period were visualized by importing all nocturnal data from 120 kHz and 200 kHz into respective composite echograms. Night was defined as the period after sunset and before sunrise at local time (UTC+1 h; UTC+2 h during daylight saving time/DST from 28 Mar to 30 Oct 2011). Echo data were intermittently affected by different source of noises, so prior to importing the data for final analysis, supervised noise removal was conducted in order to exclude “bad echoes” using the LSSS software (Korneliussen et al. 2009). This process involved filtering of 9 points moving average window to remove irregular spikes. Output value of this process was 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 x 2 m. The upper 0-4 m was deleted to avoid surface generated noise. The nocturnal vertical distribution of *Maurolicus muelleri* for each month was also investigated by summarizing the integrated $S_A$ in each of three depth segments (0-30 m; 31-60 m; 61-90 m) recorded by the 200 kHz echo sounder, and divided by the total sum of $S_A$.

Photosynthetically active radiation (PAR, 400 to 700 nm) was continuously recorded about 2 m above the surface (referred to as surface irradiance) from 10 Dec 2010 to 15 Aug 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 µmol m$^{-2}$ s$^{-1}$. The surface irradiance at the darkest period at night
(minimum nocturnal light levels) was higher than this sensitivity threshold from 28 Apr until records ended on 15 Aug 2011. Prior to Apr 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 as ascribed to artificial lighting at the shore station where the logging was made.

We used the measurements of surface irradiance to characterize the irradiance at the top of the SL (as visible in the high-resolution 200 kHz echogram when using $S_V$ threshold of -75 dB) when 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 Jan, 22 Feb, 11 Apr, 16 Jun, and 16 Aug 2011. These measurements were taken at 1, 5, and 10 m, and then for each tenth meters depth down to ~90 m depth. For each of these depth we calculated the attenuation coefficient ($K_z$) for downwelling irradiance (PAR) between the surface (i.e. one meter depth) and the depth ($z$) in question according to the expression $K_z = -\ln(E_1/E_z)/(z-1)$, 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: $E_{TSL} = E_0 \exp[-KZ_{TSL}]$, 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 *Maurolicus 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 for surface light values being between $10^{-3}$ and 1 μmol m$^{-2}$ 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* scattering layer at any time of day and year by Staby & Aksnes (2011).

Scattering layers in Masfjorden corresponding to those referred to in this paper have repeatedly been ascribed to *Maurolicus muelleri*. Previous studies conclude that the young-of the year form SL in the upper 100 m from autumn to spring and the adults staying at larger depths (Balino & Aksnes 1993, Rasmussen & Giske 1994, Staby et al. 2011). Results from extensive trawling with a 100 m$^2$ pelagic trawl at the start (7 Oct 2010) and end (15 Aug 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.

Results

Nocturnal light

Surface light could be detected even during the darkest part of the night from 28 Apr to the end of the registration period (15 Aug 2011). The minimum measured nocturnal irradiance spanned two orders of magnitude, from 0.00016 µmol m$^{-2}$ s$^{-1}$ on 28 April to 0.061 µmol m$^{-2}$ s$^{-1}$ on 22 June. Thereafter it decreased to 0.0002 µmol m$^{-2}$ s$^{-1}$ at the end of the acoustic records 15 Aug 2011 (Fig. 3).

Light at top of the scattering layer at dusk and dawn are shown in Fig. 4 and appeared to differ significantly between dusk and dawn (Mann-Whitney U test, $p << 0.001$) regardless of season. On average, the surface light at initiation of descent in the morning was relatively stable at 0.032 µmol m$^{-2}$ s$^{-1}$. This was an order of magnitude lower than the average light level when fish reached the surface layers in the evening (0.21 µmol m$^{-2}$ s$^{-1}$).

Behavioral pattern of Maurolicus muelleri scattering layers (SLs)

In autumn and winter, at least two SLs ascribed to Maurolicus 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 is masked by the monthly average presented in (Fig. 5). The DSL was situated at 150 - 200 m day and night, with some, but only 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 *Maurolicus muelleri*, which formed the SSL, stayed at depths of ~75-125 m during daytime, but were located progressively deeper through the registration period, so that daytime depth reached 150 m in spring (Fig. 5). These *M. muelleri* always carried out DVM, ascending to the surface at dusk followed by “mid-night 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 ~30-50 m early in the registration period towards 70-100 m at the end of winter and in early spring (Fig. 5 - Fig. 6). Based on echo integration for 30 m-intervals in the upper 90 m (200 kHz), about 84 % of the backscatter (*M. muelleri*) occupied the upper 30 m in October, with 13 % and 3% residing in the 31-60 m and 61-90 m interval, respectively (Fig 7). Later the proportion backscatter decreased in upper layers and increased in the deeper layer so that about 60 % of the nocturnal backscatter was located in the deepest interval from January through March, thereafter reversing to a shallower distribution (Fig. 7).

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 afternoon ascent at various depths (mean = 24.6 ± 17.4 m) before reaching upper layers (e.g. Fig 8A). Such interrupted ascents were recorded on 46 out of the 158 dates from 27 Nov 2010 to 18 Apr 2011, particularly frequently in March. 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 night (Fig 8B). The minimum surface irradiance at night at the time of initiation of this behavior was about $10^{-3}$ µmol m$^{-2}$ s$^{-1}$ (Fig 9, A, B, C, and D). The structure of the nocturnal scattering layers subsequently changed in early June. 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 (Fig 8C). During this time, minimum nocturnal surface irradiance was between $10^{-2}$ and $10^{-1}$ µmol m$^{-2}$ s$^{-1}$, while the fishes reached upper waters at levels of about $1$ µmol m$^{-2}$ s$^{-1}$ (Fig. 9, E, F, G and H). Schooling subsided in early July. Fish thereafter continued to stay in upper layers throughout night until mid-August (Fig 8D), when mid-night sinking reappeared as nocturnal surface irradiance apparently (irregular light-data at this time) again dropped towards $10^{-3}$ µmol m$^{-2}$ s$^{-1}$ (Fig. 9, I and J).

The duration of periods with nocturnal surface light between $10^{-3}$ and $1$ µmol m$^{-2}$ s$^{-1}$ (i.e. a coarse proxy for the nocturnal extension of the anti-predator window in upper layers) varied through the year (Fig. 10) and roughly comprised the time fish resided in upper waters. It was relatively short (about 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 5-6 hours in late May/early June. The period thereafter became shorter as night became shorter towards the end of June (about 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 ascribed to *Maurolicus muelleri* (sampling from this study and previous sampling, see references in Material and Methods section) 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 (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 appear from previous studies (Giske et al. 1990, Staby & Aksnes 2011), and different behavior in juveniles and adults has been interpreted as different trade-off between foraging and predator avoidance in the two groups (Rosland & Giske 1994). Adults seem to have no, or negative growth during winter (Rosland & Giske 1997), yet may forage in their daytime depth on plankton like overwintering copepods (Bagøien et al. 2001). By largely remaining in deep water, adult pearlside’s 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 also was 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 scattering layers 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’s SL is related to light intensity in daytime and during diel vertical migrations (Balino & Aksnes 1993, Rasmussen & Giske 1994). We here unveil how also changes in nocturnal light levels 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 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 registration period, estimated light intensity at the top of the scattering layer typically spanned 4 orders of magnitude ($10^{-4}$ to $1.6 \mu$mol m$^{-2}$ s$^{-1}$; the latter being surface value when the fish reached their shallowest distribution), with particularly low values during interrupted ascents. To this adds the extra extinction from the top to the bottom of the scattering layers. Therefore, although the vertical positioning of *Maurolicus muelleri* is tightly related to light, this is not a fixed light value. In line with Staby & Aksnes (2011), our results suggest that pearlsides are following preferred ranges of light intensity rather than a constant fixed isolume, and that this range spans several orders of magnitude.

At shorter time scales, the vertical distribution appears to be coupled to a narrower range of light levels (Balino & Aksnes 1993, Staby & Aksnes 2011), although there were notable variations also from day-to-day, particularly related to afternoons with interrupted ascents. However, some of this variation might reflect methodological
constraints, as interpretations from echograms were subjective (like time for start of
descent), and light intensity changes rapidly at dusk and dawn. Finally our calculation of
underwater light intensity has not accounted for variations in $K$ caused by variations in
the radiant field, i.e. 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 about one order of magnitude
weaker when the SL reached the surface during the morning ascent than during the
 corresponding ascent in the afternoon. This 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. On the
other hand, 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 is more efficient
in detecting prey at low light levels in the morning than in the evening (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 has been
suggested as one possible explanation for small planktivorous coral fishes emerging from
their nocturnal shelter in the morning at lower light levels than when returning 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 most safe 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, on the other hand, rather rely on hiding in dim light.

**Interrupted ascent**

Interrupted ascent behavior was frequently recorded from late winter to mid-March yet at different depths. In spring, the estimated underwater irradiance at the top of the SL during interrupted ascent ranged between $10^{-3}$ and $10^{-1}$ µmol m$^{-2}$ s$^{-1}$ and were about 1-2 orders of magnitude lower than during the afternoons they continued to the surface (Fig. 3). This might suggest some relation to predator avoidance behavior. Previous studies have shown instantaneous diving responses among mesopelagic fish to presence of predators (Kaartvedt et al. 2012), and such responses were also recorded for *Maurolicus muelleri* during this study (not shown). 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 a population response as 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**

*Maurolicus 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 9; I and J). The nocturnal distribution became deeper through fall and winter (Fig. 6). Giske and Aksnes (1992) suggested that pearlsides were 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 would be in accordance with the observations. Results from Staby et al. (2011) did not fully support the importance of temperature profiles for pearlside’s that perform mid-night 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 3-5 orders of magnitude less than surface light (based on measurements of extinction), i.e. \(< 10^{-8} \text{ µmol m}^{-2} \text{s}^{-1}\). In early spring, when nocturnal surface light could be detected, midnight sinking occurred when this light decreased to about \(10^{-3} \text{ µmol m}^{-2} \text{s}^{-1}\); then translating into \(< 10^{-6} \text{ to } \mu\text{mol m}^{-2} \text{s}^{-1}\) 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 and Olla (1999) showed that juveniles of the gadoid walleye pollack could forage successfully on *Artemia* at very low light intensities (5×10⁻⁷ μmol m⁻² s⁻¹). This suggests that mid-night sinking of *M. muelleri* actually may be warranted to get away from nocturnal predators.

**Termination of mid-night sinking**

From mid-May to mid-August, *Maurolicus muelleri* remained in upper layers throughout the nights, with limited evidence of mid-night sinking. This occurred when the minimum nocturnal surface light exceeded 10⁻³ μmol m⁻² s⁻¹. We interpret the shift in behavior so 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, about a tripling when this behavior first appeared in mid-May (Figs. 8-10). This suggests that summer may be a particularly important period for growth, not only due to higher plankton concentrations and warmer waters in 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 and 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 mid-night sun.
Schooling in light summer nights

As nights became even lighter towards mid-summer, *Maurolicus muelleri* took on schooling in upper layers. This occurred from early June until ceasing in mid-July concordant with minimum nocturnal surface light above $10^{-2}$ µmol m$^{-2}$ s$^{-1}$ (Figs. 8-9). The pearlside often schooled at 5-20 m depth, so that light intensities at these depths were one to two orders of magnitude lower than at the surface. Schooling is well acknowledged as an anti-predator strategy (Magurran 1990, Kaartvedt et al. 1998). 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 *Maurolicus muelleri*. However, there are likely limitations for the seasonal variation in light conditions that the mesopelagic fish can handle as 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 mid-night sun will prevent the fish to seek upper layers in cover of darkness, while total darkness in winter hamper their feeding during that season.

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References


Fig 1. Map of Masfjorden depicting locations of the three echo sounders. The upward looking echosounders were mounted on the bottom ~395 m (38 kHz), and floating in the water column at ~ 250 m (120 kHz) and 90 m (200 kHz).
Fig. 2. Sketch of the acoustic set up in Masfjorden.
Fig. 3. The minimum nocturnal surface irradiance (PAR) as measured with a LiCor quantum meter. There are no measurements prior to 28 April due to insufficient sensitivity of the PAR sensor. Grey dots are the observations and the red line is the moving average.
Fig. 4. Downwelling irradiance at the surface when the upper SL of *Maurolicus muelleri* is located closest to the surface. (A) Prior to descent; (B) After ascent. Blue points represent the calculated light intensity during interrupted ascent.
Fig. 5. Monthly averaged echograms at 120 kHz, displaying 24 hours images for the upper ~ 280 m. Averages are based on the following numbers of days: Oct (26 days), Nov (30 days), Dec (21 days), Jan (29 days), Feb (19 days), Mar (30 days), Apr (30 days), May (29 days), Jun (30 days), Jul (17 days), and Aug (15 days). Color scale refers to backscattering strength (Sv) values (dB). Time is given in UTC (local standard time -1 h).
Fig. 6 Echograms depicting the nocturnal backscatter for the whole study period at 120 kHz (A) and 200 kHz (B). Gaps in the datasets are from periods without records. Color scale refers to backscattering strength (Sv) values (dB).
Fig. 7. Monthly values of relative vertical distribution of nocturnal acoustic backscatter for the upper 90 m (200 kHz). Grey, white and black bar is the integrated $S_A$ for the upper 30 m, 31-60 m and 61-90 m, respectively.
Fig 8. Selected echograms for three consecutive days representing different diel migrations patterns. (A) Interrupted ascent in winter (6-8 Jan 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 (Sv) values (dB).
Fig. 9. Echograms of the upper 40 m showing nocturnal SL (200 kHz) with corresponding surface light intensities depicting termination of midnight sinking (15-16 May; A-D), schooling behavior (18-19 June; E-H) and resumption of midnight sinking (15 August; I, J). Color scale refers to backscattering strength (Sv) values (dB).
Fig. 10. The nocturnal extension of the duration of the anti-predation window with grey circles depicting observations and red line indicates the moving average.
CHAPTER IV

A sensitivity analysis of seasonal dynamics in nighttime behavior of a mesopelagic planktivore (*Maurolicus muelleri*)

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(manuscript)
A sensitivity analysis of seasonal dynamics in nighttime behavior of a mesopelagic planktivore (*Maurolicus muelleri*)

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**Abstract**

Diel vertical migration (DVM) of juvenile and adult Müller’s pearlside (*Maurolicus muelleri*) differs seasonally. We assessed environmental impacts and the state of the organism on depth selection in a western Norwegian fjord during night by sensitivity analyses of the output of a dynamic optimization model. The model predicts the optimum depth, stomach fullness and growth of the fish. In autumn, adult and juvenile fish were vertically separated. Adults formed a non-migrating layer at depths of 150-200 m, while juveniles performed normal DVM with midnight sinking behavior. Midnight sinking was mainly driven by temperature advantage for metabolic processes. In spring, ascents were interrupted at intermediate depths in the afternoon. Combinations of environmental factors such as temperature, turbidity, prey density and size could be linked to the interrupted ascents, but stomach fullness and perceived predation risk could also interrupt the normal ascent behavior. In summer, increased surface light led to increased nocturnal predation risk. Still, pearlsides made coherent nocturnal migrations to upper layers as a consequence of enhanced feeding opportunities. At daytime, feeding in summer benefitted from increased light at depths while higher turbidity levels reduced risk of predation.
Introduction

Mesopelagic fish is ubiquitous in the world’s ocean with recent estimates suggesting that their biomass could be larger than 10 billion tones (Irigoien et al. 2014). Mesopelagic fish is abundant also in Norwegian fjords with Müller’s pearlside (*Maurolicus muelleri*) being the main acoustic target forming scattering layer (SL) in the upper 200 m and glacier lanternfish (*Benthosema glaciale*) below (Giske 1990, Goodson 1995, Kaartvedt 1998 Staby et al. 2011, Dypvik et al. 2012, Prihartato et al. 2014). Pearlsides perform diel vertical migration (DVM). Normally, the SL ascends to the surface at dusk, followed by “midnight sinking” with a subsequent dawn ascent to surface waters, before returning to deeper waters (Rosland & Giske 1994, Staby et al. 2011). However, the DVM varies in respect to ontogenetic stages and light regime (Staby & Aksnes 2011, Staby et al. 2011). In late autumn until early spring, adults mainly stay at depth throughout the diel cycle (Staby et al. 2011, Prihartato et al. 2014) while juveniles perform normal DVM (NDVM), yet with some variations in the patterns. Midnight sinking is common in autumn, winter and early spring, until ceasing in concordance with increasing nocturnal light intensities in late spring (Rasmussen & Giske 1994, Prihartato et al. 2014). Interrupted ascent has been recorded in winter and spring (Staby et al. 2011, Prihartato et al. 2014), and schooling behavior becomes apparent in light summer nights (Kaartvedt et al. 1998, Prihartato et al. 2014).

Ultimately, depth selection is a means to maximize expected future reproductive rate (McLaren 1963, Clark & Levy, 1988). A series of proximate factors have been proposed, such as finding temperature optimum to maximize growth (Wurtsbaugh & Neverman, 1988, Dawidowicz & Loose, 1992, Ward et al. 2010), driven by hunger or satiation state.
of the fish (Pearre 2003, Ward et al. 2010), following light cues (Balino & Aksnes 1993, Staby & Aksnes 2011, Prihartato et al. 2014) or predatory avoidance behavior (Loose & Dawidowicz 1994). These motivations could interact with each other and may change through time.

*Maurolicus muelleri* has been shown to exploit the anti-predation window (Rosland & Giske 1994, 1997, Rosland, 1997) defined by the light-dependent ratio between food availability and the predation risk (Clark & Levy 1988). Increased light intensity could improve prey detection rate but also predation risk (Aksnes & Giske 1990, Giske & Aksnes, 1992, Aksnes & Utne 1997, Staby et al. 2013). Different exposure to light in respect to changing season therefore could contract/expand the anti-predation window associated with migrations to upper layers at night (Prihartato et al. 2014), thus creating dynamic trade-offs between the pearlsides’ visual search for prey and avoidance of piscivores.

Most studies of vertical migration of planktivorous fish have focused on the daytime situation when the sound scattering layers are clearest and light intensity can be measured. In this study we will evaluate the dynamic DVM behavior of *Maurolicus muelleri* in different seasons, focusing on the nighttime. We use dynamic programming as optimization method due to its extensive ability to combine environmental conditions with the internal physiological states of the organism (Mangel & Clark 1986, McNamara & Houston 1986, Mangel 2014). We further modify previous models by (Rosland & Giske 1994, Rosland 1997) on winter behavior in year classes of *M. muelleri* to simulate the DVM in different seasons characterized by specific nocturnal behaviors as revealed
from acoustic studies (Prihartato et al. 2014): autumn (midnight sinking), winter/spring (interrupted ascent) and summer (no midnight sinking).

**Methods**

**Acoustic, Biological and Environmental Data Collection**

Data sampling was conducted in Masfjorden, Norway (60°50’N, 5°30’E; Fig. 1). Acoustic data were extracted from an upward looking echo sounder operating at 120 kHz and floating at ~250 m depth, further described in Prihartato et al. (2014). Three behavioral DVM modes of *Maurolicus muelleri* observed from the acoustic studies were selected to represent seasonal difference: midnight sinking in autumn (exemplified with echogram from 26 Oct 2010; field data available from own sampling), interrupted ascent in spring (exemplified with echogram from 15 Mar 2011, environmental data from literature), and DVM without midnight sinking in summer (exemplified with echogram from 10 Aug 2011, field data available from own sampling). Biological and environmental data were collected 8 Oct and 14 Aug 2011 from R/V *Trygve Braarud*, University of Oslo. Previous and current trawling results suggested that the SL observed in this study is mainly composed of *M. muelleri*. The depth of the SL (upper, middle and lower SL) was obtained by averaging acoustic backscatter volume (*S*<sub>V</sub>) for every 30 minutes horizontal bin and 1 m vertical depth with *S*<sub>V</sub> threshold of -75 dB m<sup>-1</sup>. These results were used to compare with the model results.

Vertical temperature profiles measured using CTD 8 Oct 2010 and 14 Aug 2011 were used to represent the autumn and summer environmental condition respectively. Temperature from spring was obtained from previous CTD measurement in the nearby
Herdlefjorden (Rosland 1997). Surface irradiance (photosynthetically active radiation, 400-700 nm) was continuously measured using a calibrated LI-190 quantum sensor and recorded on a LI-1400 data logger. These data were later averaged into 15 min intervals. Own light data were not available for autumn, as light measurements first started 10 Dec 2010. Therefore we digitized surface light irradiance and coefficient of extinction at PAR for autumn (2 Nov 2007) from Staby et al. (2013). Underwater irradiance was measured using RAMSES ACC hyper-spectral radiometer down to 90 m. Coefficient of extinction at 500 nm (K) was derived from these measurements. Summer surface and underwater lights were retrieved from 16 Aug 2011 measurements meanwhile winter measurement was on 10 Dec 2010. We use the winter measurement to represent coefficient of extinction in autumn. Coefficient of extinction in spring was derived from the nearby Herdlefjorden (Rosland 1997).

Zooplankton abundance and vertical distributions were assessed from samples taken day and night during autumn (7 October 2010) and summer (16 August 2011) using a WP2 net with an opening of 0.25 m$^2$ and mesh size of 200 µm and being equipped with a messenger operating to close the net. Samples were taken in five depth intervals throughout the water column (0-50, 50-100, 100-200, 200-300 and 300-400 m). Due to time constraints, only the upper 50 m were sampled at night. Samples were weighted to calculate wet weight (mg/m$^3$). For spring, zooplankton abundance and biomass were created in such manner so that during night the fish would stay at the upper 25 m preceded with interrupted ascents. In order to do that zooplankton abundance and biomass were reconstructed at the upper 25 m, the abundance will exceed those of summer (14000 ind m$^{-3}$). Also that in order to forge the fish to perform interrupted
ascent, zooplankton abundance at the 50-100 m and 101-150 m was modified to be more than 5000 ind m$^{-3}$. For all seasons in order to calculate the zooplankton biomass, only dominating species of zooplankton, mostly consisting of *Calanus sp* (CV 5), *Oithona sp*, and *Microcalanus sp*) were used as input for the model.

**Overview of the model**

**Purpose**

The purpose is to study the combined effects of environment and the state of the organism on optimum nighttime distribution of *Maurolicus muelleri* at different seasons. The interaction between environmental factors (e.g. zooplankton biomass and abundance, temperature, and light) and physiological state of the fish (growth and stomach process) were analyzed also and formulated as realistically as possible.

The description of the model follows the ODD protocol (Overview, Design concepts, Details) as outlined by (Grimm et al 2006, 2010). Schematic overall simulation is summarized in Fig. 2. However, as most of the main model has been explained in Rosland & Giske (1994) and Rosland (1997), we will only focus on the model development that particularly relates to this study.

**Entities, State Variables and Scales**

The model entities are environment and the state of individual/population of *Maurolicus muelleri*. The model environment resembles a one dimensional water column (MASFjorden, Norway) divided into 25 discrete depths representing in total 250 m. Each depth interval is characterized with temperature, prey biomass and numerical abundance,
and the light irradiance for each season. All parameters vary with time interval. The model is set to represent 24 hours cycle at 15 minutes time interval. Therefore our model is constructed with 25 x 96 bins (one day simulation). We also extend the model into three-days simulation to assess the behavior of the model.

The states variables for *Maurolicus muelleri* are: growth in terms of structural weight of the fish in ash free dry weight (*G*), stomach fullness of the fish (*ST*) and optimum depth (*Z*) (Tab. 3). We run different cohorts of *M. muelleri* (juveniles and adults) in autumn. In spring and summer, we consider that the population is homogenous, consisting only of adult *M. muelleri*.

**Process Overview and Scheduling**

Each time step, variables in the model is updated by a series of processes (See schematic diagram in Fig. 2). The basis of this model is the relationship of fitness, growth and survival of *Maurolicus muelleri* that will eventually maximize reproductive output. At each time step, feeding involves visual prey detection. Prey encounter rate depends on the prey abundance, swimming speed (Eggers 1977) and visual range of the fish. Growth rate is determined by prey encounter rate, digestion rate, and metabolic rate. Competition between conspecifics in terms of feeding is neglected in this model. In Masfjorden, *M. muelleri* is being preyed upon by gadoids like blue whiting and saithe (Giske et al. 1990). We here assume that predation risk is only from visual predators.

The environment is set to change at each time step in the vertical plane as related to light, zooplankton abundance and biomass, and temperature. Simulation for winter has
been given in Rosland & Giske (1994). Therefore we will focus on the DVM simulation in autumn, spring and summer.

**Design Concepts**

Optimal behavioral decisions at each time step are determined by how behavior impacts expected fitness. Commonly, fitness is defined as a function of survival and maximizing reproductive output. In order to reproduce, *Maurolicus muelleri* has to reach a certain age, size and physiological conditions. Therefore growth is needed. Survival depends on physiological state (e.g. feeding) and anti-predation behavior. Therefore optimum depth is chosen by *M. muelleri* in order to maximize fitness; regarded as a balance between avoiding predators and increasing fecundity. However, since our model only comprises short-term behavior (one to three days), modification on the fitness function is needed.

Stochastic dynamic programming (SDP) started with backward iteration to find the optimal strategy for an individual, and assuming that individuals always decide the optimum choice based on states (depth, stomach, and growth). After finding basic solution, the model will start to test the optimal solutions with changing time using forward iteration until reaching the ultimate solution at terminal time (Mangel & Clark 1986, Houston et al. 1988, Clark, 1993, Rosland & Giske 1994, 1997, Rosland 1997). For simplicity, the modeled fish did not breed in spring and summer so that all resources are allocated only to growth.
**Fitness**

As mentioned earlier, the model output relies heavily on the predefined terminal fitness function. Table 1 provides the processes that are involved in the tuning of the terminal function. Terminal fitness at the end of the simulation was then formulated as a function of growth \((G)\) under the assumption that growth would eventually increase future reproductive output (Eq. 1). We have assigned numerical frames for growth compartment with a cap function \((0 < G < G_{cap})\). The growth cap function is assigned so that growth would not fall outside the cap function during the backward and forward iteration.

The fitness function is incremented by shape. The function shape depends on the fitness function tuner \((\gamma)\). The shape of the function would be concave if \(\gamma \geq 1\) meaning that motivation to grow were increased exponentially at the early simulation and became stable at certain growth size near terminal time, linear \(\gamma = 1\) where motivation to grow gained would be constant, and convex \(\gamma \leq 1\) which gave low motivation for the fish until certain growth level where the fish could exponentially be motivated to increase the growth (Eq. 2, Table 1, Fig. 3). Adult and juvenile cohorts were entitled to different fitness shape in the sensitivity test in order to find their actual natural growth pattern. For \(\gamma < 1\) the function was scaled using terminal fitness scale \((\Delta_c)\) Eq. 3, the terminal fitness function then would be as in Eq. (4).
Details

Initialization of the environment

Prey density was obtained from zooplankton catches in the unit of individual m$^{-3}$ (see biotic parameters) and then linearly interpolated throughout the time horizon of the model. Zooplankton body mass was calculated in terms of ash free dry weight (AFDW; µg ind$^{-1}$), and radius was calculated from the relation of zooplankton body mass and its shape assuming that zooplankton and *Maurolicus muelleri* have spherical shapes (Giske et al. 1990). If surface light irradiance were below the instrument threshold (< 0.0001 µmol m$^{-2}$ s$^{-1}$) then the light irradiance would not be incorporated into the model. The light at depth was calculated using Eq. 5 along with applying downwelling irradiance from the surface light measurements. The light at depth was then interpolated for 0-200 m of the water column for the whole model duration (one and three-days).

Input Data

Acoustic observations and model basic layer information

Acoustic data from autumn (26 Oct) unveiled two SLs during daytime; SL1 stayed at daytime depth of 110-180 m and SL2 stayed at depth of 150-240 m during day and night (Fig 4). At night, midnight sinking was observed for SL1 at depth of ~20-50 m. The two SLs in the echogram were used as reference for the model, referred to as juveniles (24 mm) and adults (39 mm) respectively. In spring (represented by echogram on 15 Mar 2011; Fig 4), interrupted ascent behavior was recorded at depth of ~70 m on recurrent nights (the weaker echoes [depicted by blue color code in Fig 4] migrating all the way to the surface are likely represented by krill). We assume that individuals of this SL have
grown into pre-adults of 35 mm and performing NDVM. Midnight sinking still appears and reached deeper depth than in the autumn (70-100 m). The non-migrating SL, which is composed of adults, remained day and night at depths of 150-200 m (Fig. 4). In summer (represented by echogram on 10 Aug 2011), *Maurolicus muelleri* formed one dense SL and carried out NDVM. Daytime distribution was at depth of 175-225 m while they stayed in near-surface water throughout the night (Fig. 4).

**Environmental parameters**

Surface light irradiance in autumn (data from 2 Nov 2007) had maximum value at noon (174 µmol m$^{-2}$s$^{-1}$) and nocturnal lights below the instrument threshold. In spring (15 Mar 2010), surface light irradiance at noon was 731 µmol m$^{-2}$s$^{-1}$; with nocturnal lights ranging in the order of 10$^{-3}$ to below instrument’s threshold (< 10$^{-4}$ µmol m$^{-2}$s$^{-1}$). In summer (10 Aug 2011), maximum surface irradiance occurred at noon (1250 µmol m$^{-2}$s$^{-1}$) (Fig. 5A) and surface light was detectable at the same light level in spring.

The coefficient of extinction at 500 nm ($K$) was highest at the surface, being maximal in autumn (0.282 m$^{-1}$), intermediate in summer (0.253 m$^{-1}$), and lowest in spring (0.176 m$^{-1}$). The coefficient of extinction drastically decreased below 20 m, decreasing further down to 140 m and then stabilized at ~0.05 m$^{-1}$ until reaching 250 m (Fig. 5B).

Temperature in autumn was 14.2°C at the surface and then gradually decreased until reaching 7.9°C at 45-250 m (Fig. 5B). In spring, the surface temperature in Herdlefjorden was 4.9°C then gradually increased to 8°C from 140-250 m. In summer, the surface temperature was 15.9°C decreasing to 7.2-8.2°C at depth of 250 m (Fig. 5B).
The highest numbers of zooplankton were found in the upper 25 m for all seasons. The highest zooplankton density was recorded for night time in spring with about 14000 ind m\(^{-3}\) followed by summer at 13000 ind m\(^{-3}\) and autumn with 1000 ind m\(^{-3}\). Somewhat lower concentrations of zooplankton were found at daytime, with abundance in the upper 25 m during summer (4500 ind m\(^{-3}\)) and autumn (900 ind m\(^{-3}\)). Secondary peaks in zooplankton abundance were detected at 150-175 m (300 ind m\(^{-3}\)) and 50-100 m (5000 ind m\(^{-3}\)) for autumn and spring respectively. Zooplankton radius (ZR) in autumn ranged from 1.1-4.1 mm. Meanwhile in spring and summer, ZR size was smaller and ranged from 0.16-0.68 mm (Fig. 5C, D, and E).

**Sub models**

**Visual foraging model**

The fish was assumed to detect prey only by vision; thus the possibility of detection by olfaction and the lateral line organ were excluded from the model. The visual foraging model described by (Aksnes & Utne 1997) was used to calculate predation reaction distance (Eq. 10, Table 3). Parameterization is given in Table 4. Visual foraging was calculated both for planktivores (\(V_{pl}\)) and piscivores (\(V_{pc}\)) as functions of ambient light intensity (\(I_d\)), beam attenuation (\(B_d\)), inherent contrast of the prey against its background (\(C\)), zooplankton and fish radius (\(R_d\)) following Eq. 9 in Table 2. Furthermore, the visual foraging model incorporates light processing capacity at the retina (\(I_{\text{max}}\)), half saturation coefficient for light entering the lens (\(k_1\)), and light sensitivity threshold of the eye for both planktivores and piscivores (\(\Delta T\)). The light sensitive thresholds were determined by sensitivity constant (\(K_s\)) divided by the focal length of the fish (\(f_1\)), where standard for \(M\).
muelleri’s eye sensitivity threshold \((K_s)\) is \(5 \cdot 10^{-5}\) for and for the predators \((K_p)\) is \(1 \cdot 10^{-5}\) \((\Delta T = K_s/f_i)\). The eye’s focal length of the fish was set \((f_i)\) with formulation \(f_i = 1.18 l_d\) (Charman & Tucker 1973). The fish lens diameter \((l_d)\) was calculated in respect to fish length \((L)\), where \(l_d = 0.26 + 0.04L\) (Giske et al. 1992).

**Prey encounter rate**

Prey encounter rate \((E_N)\) was calculated as function of the visual predation reactive field angle of the fish \((\theta)\), swimming speed \((v)\), visual reactive distance of planktivores \((V_{pl})\) and zooplankton density \((N_d)\) (Eq. 11 Table 3). Prey encounter rate and zooplankton density were then used to calculate feeding rate \((e)\) along with prey handling time \((h)\) (Eq. 12 Table 3). The subsequent step was to calculate mass encountered \((m)\) from feeding rate and zooplankton biomass through time interval of the model. Probability of finding prey at each depth \(P_z(m)\) was calculated from mass encountered and assumed to follow Poisson distribution (Eq. 14). The iteration was limited by stomach capacity \((X)\), which for adult and juvenile *Maurolicus muelleri* was estimated to be 20 copepods d\(^{-1}\) and 15 copepods d\(^{-1}\) respectively (Giske et al. 1992)

**Individual fish physiology**

Different ontogenetic stages of the fish were considered in the model. For autumn, fish lengths were set for juvenile and adults at 24 and 39 mm, respectively. We assume that the juvenile fish has grown into pre-adults (35 mm) in spring and adults (39 mm) in summer. *Maurolicus muelleri* body mass was calculated based on weight to length
relationships following Staby et al. (2013) in Eq. 6 and later on converted into ash free dry weight (AFDW) in (Eq. 7 & Eq. 8, Table. 2).

Fish metabolism was represented by stomach index from $x$ until reaching maximum capacity at $X$ (Table 4), where maximum stomach (X) means that stomach can hold up to 20 copepods. Stomach weight was assumed to be 4 % of the body (AFDW). Stomach evacuation rate ($\sigma_m$) depended on enzymatic processes controlled by Arrhenius temperature function ($T_D$) and changed with stomach dynamic (Eq. 18, Table 3). The Arrhenius temperature function is depended on the calculation of lower and higher boundaries of the tolerance temperature ranges ($T_L$ and $T_H$) and Arrhenius temperature for the rate of decrease at lower and higher boundaries ($T_{Al}$ and $T_{Ah}$) (Eq. 17, Table 3). We do not have information about parameters needed to calculate Arrhenius temperature for Maurolicus muelleri; therefore we applied parameters from blue mussels (Mytilus edulis) that lived in a nearby fjord (Rosland et al. 2009). The depth dependent environment was obtained from the CTD ($T_K$) and the optimum temperature were set at 20°C ($T_1$). Metabolic cost is calculated by the mass accumulated during time interval reduced by exponential function of respiration cost at temperature optimum (Eq. 19, Table 3).

**Migration cost**

Migration is energetically costly and could affect the optimal depth chosen by Maurolicus muelleri. Optimum depth range by M. muelleri was constrained by the migration distance ($\delta$), which was a function of vertical migration rate of M. muelleri and the time needed to adjust the pressure in the swim bladders (Eq. 16, Table 3). Previous
study by Balino & Aksnes (1993) suggested that the vertical migration rate for *M. muelleri* is $2.78 \times 10^{-2} \text{ m s}^{-1}$ (Table 4).

**Mortality by predation**

Mortality is calculated based on predation probability of *Maurolicus muelleri* ($\varphi_2$) that depend on the visual range model by predator ($V_w$) and daily mortality constant ($k_M$) through time intervals (Eq. 15, Table 3). The value of $k_M$ at each day was unknown for *M. muelleri*. Therefore we assume that $k_M$ is constant throughout seasons.

**Dynamic equations**

Dynamic state variables of the fish in this model were previously developed in (Rosland & Giske 1994) where growth ($G$), and stomach fullness ($ST$) change as result of feeding gains and metabolic costs for the fish that choose the optimum depth ($Z^*$) throughout time interval ($t-T$). Growth itself was defined as mass accumulated (AFDW) during time interval deducted by gut absorption coefficient assimilation process ($\alpha$) and stomach evacuation rate ($\sigma_m$) constrained with daylight feeding ($K_d$) and migration cost ($\varepsilon$) (Eq. 23, Table 3). We set up a cap function of upper growth ($G_u$) and lower growth ($G_l$), with the assumptions that *Maurolicus muelleri* can only grow inside this range. The state of the stomach ($ST$) follows Eq. 22 where stomach index is transformed into AFDW. Dynamic changes of the stomach state at terminal time $ST$ ($T$) depends on the state of stomach contents at the start of the run $ST$ ($t$) added with feeding probability at depth ($P_2$) and subtracted by stomach evacuation rate ($\sigma_m$) (Eq. 24, Table 3).
The optimal solution of SDP model is found by backwards induction from a goal function at the terminal time ($T$). Thereafter the population optimal strategy is to follow calculated temporary optimum strategy from the backward iteration. Then this strategy is tested using forward iteration with changing environmental parameters until it reaches terminal time resulted in the ultimate optimum strategy. We here displayed the forward iteration only, where state change from time $t$ to $t+1$ is a probabilistic calculation considering all potential meal sizes ($m$), starvation, and predation risk (Eqs 25-27, Table 3). Interpolation was conducted to avoid states falling in between the discrete steps in the state variable arrays during backward and forward iteration. The optimum depth choice also considers the probabilistic state change from time $t$ to $t+1$ for each available depth, choosing depths ($z$) that most likely will maximize the value of the goal function in the final time step (Eq. 28, Table 3).

**Sensitivity analysis**

Sensitivity tests were conducted for the model according to Eq. 29, representing the fraction of deviation from basic run; model outputs ($Y_i$) divided by basic runs ($Y_0$).

$$S = \frac{Y_i}{Y_0}$$  \hspace{1cm} (29)

Only parameters that could change the model output more than 0.2 (20 %) were categorized as significant parameters. Except for adult in autumn, if changes in model output are 50% from the basic run then the parameter involved in the change is categorized as significant parameter. If parameter changed in both directions (decreased or increased) resulted in significant changes (20% or 50% for adult autumn), then we will neglect the parameter as sensitive because no matter what changes in the parameters the
model output will change anyway. The optimum depth choice, feeding rate and predation risk by vision were used as model output variables. Parameters tested and variables involved for autumn, spring and summer are displayed in Table 5, 6 and 7 respectively.

Results

Optimum depth on basic run at different seasons

Autumn

Model results for 24 hours simulations showed that juveniles were distributed at 40-60 m depth at midnight while at midday they distributed at 110-155 m (Fig. 6A). When the model time horizon increased into 72 hours, juveniles still carried out NDVM subsequently followed by midnight sinking. The adult part on the other hand distributed at 130-220 m both day and night. The three-days simulations for autumn were in accordance with the observed acoustic SLs, including depths of the midnight sinking (Fig. 6A). The juvenile layer furthermore split in two parts during daytime. This daytime bimodal distribution was observed also from the acoustic (Fig. 4). However, we did not possess trawling data on the exact date to identify organisms constituting these sub-layers. Therefore we could not conclude if these layers were made up of juveniles or a component of migrating adults Maurolicus muelleri.

Spring

The optimum depth produced by the model in spring was based on the assumption that Maurolicus muelleri has grown to mature size at 35 mm. Simulation output produced
interrupted ascents in the afternoon, with some part of the population migrating to the surface. Midnight sinking was also shown, reaching depths of 60-90 m. During daytime, the average midday depth from the one-day simulation was 30-40 m shallower than the acoustic observation (Figs 4B & 6B), while three-days simulation gave midday depths ~50 m deeper than the one-day simulation (Fig. 7B). There was a notable split of the SL with a shallow component at 90-110 m during the first half day of three-days simulation. This pattern was not observed from one-day simulation or the observation (Fig. 6B). In general, the model result was in good agreement with the observed SL from the acoustic.

**Summer**

In summer, we assume that *Maurolicus muelleri* has grown into adult size at 39 mm. Midday depths from one-day simulation ranged from 130 to 225 m, yet with a deeper midday depths in comparison with three-days simulations (Figs. 6C & 7C). Our result fits well with the acoustic data, only that the midday SL depths from acoustic observation were distributed at 175-225 m. The nocturnal depths from the model were similar to the acoustic observation (Figs 4C & 6C). The model reproduced the lack of midnight sinking which characterized the nocturnal summer behavior of *M. muelleri*.

**State dynamic of stomach and growth at different seasons**

The highest stomach contents occurred in summer, followed by spring and the lowest stomach content occurred for juveniles in autumn (Fig. 8). Daytime feeding took place during all seasons and for all sizes so that stomachs never emptied during daytime. For adults in autumn, maximum stomach content occurred during daytime and was depleted
afterward. Juveniles had the highest stomach fullness during crepuscular periods. Stomach contents became depleted during midnight sinking both in autumn and spring. Furthermore in spring, interrupted ascent in the afternoon created temporary stomach depletion for *Maurolicus muelleri*. Feeding was resumed by some part of *M. muelleri* population that performed NDVM (Fig 10A & B).

Growth pattern for *Maurolicus muelleri* in different seasons is presented in Fig. 9. In autumn, average growth rate at terminal time for juvenile is at 0.0311 g g\(^{-1}\) d\(^{-1}\). Meanwhile, adult (derived from first day simulation of the three-days simulation) displayed negative growth at terminal time (-0.002 g g\(^{-1}\) d\(^{-1}\)). In spring and summer, growth rate at terminal time for *M. muelleri* was 0.04 and 0.05 g g\(^{-1}\) d\(^{-1}\) respectively (Tables 5, 6, and 7).

**Feeding rate at different seasons**

Ontogenetic differences in autumn were expected to give variation in feeding rate (FR) for juveniles and adults. FR for juveniles increased during crepuscular periods. FR during midnight sinking was low, similar to daytime FR. Both simulations for one and three-days showed that juvenile FR at dawn is about three times that of daytime. Meanwhile adult FR was considerably higher than juveniles with highest FR noted during crepuscular periods for the one-day simulation (Fig. 10A) i.e. for the simulation where adults performing normal DVM. For three-days simulation, feeding rate at dawn was lower for non-migrating adults but still higher than for the juveniles.

In spring, crepuscular feeding was still dominant, yet interrupted ascent reduced FR to almost half of its dawn value. In summer, FR was highest during nights (Fig. 10A &
B). In comparison to fall, average FR in summer was higher. However, the value was lower than in spring.

**Mortality at different seasons**

Mortality rate was highest during summer (6.69e\(^{-4}\) d\(^{-1}\)) followed by spring (3.19e\(^{-4}\) d\(^{-1}\)) and autumn (1.26e\(^{-4}\) d\(^{-1}\)) (Tables 5, 6, and 7). In autumn, adults were exposed to higher predation risk than juveniles (Fig. 10C & D).

**Ratio of mortality over feeding rate**

The ratio of mortality over feeding rate (M/FR) as average of 250 m model depths was lowest during nighttime for all seasons. One-day simulation revealed that daytime M/FR was lowest during summer in comparison with other seasons whiles juveniles in autumn experienced the highest risk (Figs. 10E & F). All simulations agreed that nighttime provided relative safety towards predators.

**Sensitivity tests**

Due to the inconsistency of adult behavior derived from one-day model simulation, for example if compared to acoustic observation. We use the first-day result from three-days simulations to represent the DVM behavior of *Maurolicus muelleri* in autumn. Parameters tested in the sensitivity test were: terminal fitness tuner (\(\gamma\)), eye sensitivity threshold for *M. muelleri* and predator (\(K_s\) & \(K_p\), respectively), daily mortality constant (\(K_M\)), zooplankton density and radius (\(N_D\) & \(R_D\), respectively), surface light (\(I\)), coefficient of extinction that represent turbidity (\(K\)), and temperature (\(T\)).
Sensitivity test on the optimum depths

In autumn, temperature gave a major effect on the optimum depth choice during midnight sinking for juveniles. The same temperature profile, but reducing the temperatures by a factor of 0.5 C led to shallower depth and vice versa. The adults tended to be more risk avert than the juveniles. Reducing each of these parameters: *Maurolicus muelleri*’s eye sensitivity threshold ($K_s$), mortality rate ($K_M$), and turbidity ($K$) resulted in shallower distribution of adults *M. muelleri*. However these changes did not alter adult’s behavior from non-migrating (NoDVM) into normal DVM (NDVM) (Tables 5 & 6).

In spring, shallower interrupted ascent depths in the afternoon were observed by reducing parameters: terminal fitness function ($\gamma$), piscivorous’s eye sensitivity threshold ($K_p$), zooplankton radius and density ($R_D$ & $N_D$, respectively). Similar shallower distribution of interrupted ascents was found also when planktivorous’s eye sensitivity threshold ($K_s$) and temperature ($T$) were increased. Deeper interrupted ascents depths were found when those parameters were changed in the opposite direction. Daytime depths were more stable, with turbidity ($K$) being the only parameter that could alter the depth output. Reduced turbidity ($K$) leads to deeper depth and vice versa (Table 6).

In summer, nighttime depths were deeper when temperature ($T$) was increased. Daytime depth could only change when introduced to changes in turbidity ($K$) (Table 7).

Sensitivity test on the feeding rate

In autumn, juvenile feeding rate decreased by reducing the parameters: terminal fitness ($\gamma$), *Maurolicus muelleri*’s eye sensitivity threshold ($K_s$), zooplankton radius ($R_D$)
and temperature \((T)\). Increased feeding rate for juvenile was observed when turbidity \((K)\) increased. For adult, sensitivity test that is significant has to be redefined, since changes in both directions (increased and reduced) of some parameters resulted on model output to change 20\%. Therefore we set the definition of significant change into 0.5 (50\%) and if changes in both directions resulted in significant model output thus we neglect the parameter as significant. Adult feeding rate increased by reducing parameters: terminal fitness \((\gamma)\), *Maurolicus muelleri*’s eye sensitivity threshold \((K_s)\), daily mortality rate \((K_M)\), and temperature \((T)\). Meanwhile, if these parameters were increased then model output was increased: predator’s eye sensitivity threshold \((K_p)\) and zooplankton radius \((R_D)\).

In spring and summer, turbidity is the only parameter influencing the model output, with decreased turbidity lead to decreased feeding rate.

**Sensitivity test on the mortality rate**

Mortality rate increased significantly in all seasons if predator’s eye sensitivity threshold \((K_p)\), constant daily mortality constant \((K_M)\), surface light \((I)\), and turbidity \((K)\) were increased (Tables 5, 6, and 7).

**Sensitivity test for growth**

Growth of juveniles in autumn was sensitive to change in zooplankton radius \((Z_R)\) and temperature \((T)\). Reduced zooplankton radius \((R_D)\) and temperature \((T)\) caused reduced growth and vice versa. For adults, most parameters (except reducing terminal fitness \((\gamma)\) and zooplankton radius \((R_D)\)) significantly affected growth. In spring, both
reduced turbidity \((K)\) and temperature \((T)\) resulted in reduced growth \((G)\). Increased temperature \((T)\) leads to increased growth during spring and summer (Tables 5, 6, and 7).

**Discussion**

Simulations from our model reproduced DVM patterns of mesopelagic fish that were coherent with acoustic observations. We are confident that the species constitute the scattering layer from the acoustic study is *Maurolicus muelleri* as repeatedly reported from previous studies (Giske et al. 1990, Balino & Aksnes 1993, Bjelland 1995, Staby et al. 2011). We successfully simulated three distinct nocturnal patterns: midnight sinking, interrupted ascent, and normal diel vertical migration along with introduced ontogenetic difference through the year. Our model also consider state dynamic of the fish including growth in term of weight changes, stomach fullness, and depth choices by the modeled fish. The modeled DVM patterns were also in accordance with previous modeling studies (Rosland & Giske 1994, 1997, Rosland 1997, Staby et al. 2013). Different ontogenetic behaviors in term of depth choice displayed by juvenile and adult *M. muelleri* were also successfully simulated in this model, again in accordance with previous acoustic observations (Staby et al. 2011, Prihartato et al. 2014).

**Behavior of *Maurolicus muelleri* in different seasons**

**Autumn**

**Ontogenetic differences**

The vertical distribution of *Maurolicus muelleri* generated by the model displayed different ontogenetic patterns in autumn, comprised of migrating juveniles and non-
migrating adults (Figs 6 & 7). For the 24-hour simulation, boundary effects affected the model vertical distribution. When the time horizon of the model was extended to 72 hours, adults were not migrating. The result was in good agreement with patterns observed from echo sounders use in this study and also previous studies (Rosland & Giske 1994, Staby et al. 2011, Prihartato et al. 2014).

Juvenile *Maurolicus muelleri* performed midnight sinking to subsurface depths. In fall, the nocturnal distribution coincided with temperature minima (~7.5°C). In spring, on the other hand, midnight sinking was progressively deeper found at similar temperature (~8°C), but at this time with colder temperatures at the surface. Our sensitivity test suggests that temperature play a significant role in determining optimum depths both for autumn and spring. It appears that *M. muelleri* may try to find optimum depth related to its metabolic needs. Previous studies conducted in winter have suggested that *M. muelleri* performed midnight sinking to depth where temperature maxima occurred (Giske et al. 1990, Giske & Aksnes, 1992). Wurtsbaugh & Neverman (1988) suggested that fish might seek warmer temperatures during night to maximize growth.

Tarling et al. (2002) suggested that midnight sinking in zooplankton was caused by predator avoidance behavior. However none of the parameters in the model that relates to predation risk such as surface lights (*I*), daily mortality constant (*K_m*) and predator’s eye sensitivity threshold (*K_p*) could alter midnight sinking depths.

The model output in this study included negative growth among adults during the non-migrating period, the result was in accordance with (Rosland & Giske 1994). Falk-Petersen et al. (1986) reported that adult *M. mulleri* use lipid to survive during winter at deep depths with no or limited growth.
Feeding rate for adults was higher than the juveniles, although the adults for the most part did not carry out DVM. That result contrasts previous studies (Rosland & Giske 1994, Staby et al. 2013). This discrepancy is probably due to a part of the population going to the surface for dusk/dawn feeding while in previous models the fish totally abandon vertical migration and rather stay at deep depth. In general, feeding rate is lower at night in comparison to daytime in autumn, as also reported in winter (Rosland & Giske 1994, Staby et al. 2013).

**Spring**

**Interrupted ascent**

We explored the potential cause of interrupted ascent behavior through simulation of DVM in spring. The model successfully reproduced interrupted ascents in the afternoon, as recorded from acoustic studies (Staby et al. 2011, Prihartato et al. 2014). We suggest that trade-offs between predation risks, feeding opportunity and metabolic needs were responsible causing interrupted ascent behavior.

We found that if zooplankton density and radius \((N_D \ & \ R_D, \ \text{respectively})\) were reduced in the model, shallower interrupted ascents or normal DVM will be observed. On the contrary, if zooplankton density and radius were increased, no afternoon ascents were observed. Hence the fish would stay at depths without migrating to the surface. This result concurs with explanations by Staby et al. (2011), who suggested that interrupted ascent of *Maurolicus muelleri* might be related to its prey (*Calanus sp*) ascending from its overwintering depths in winter/spring. After satiated, *M. muelleri* returned to deeper depths.
Temperature was also found to be a significant factor affecting interrupted ascent behavior. Increased temperature led to shallower depth of the interrupted ascent, and vice versa. Previous knowledge on the role of temperature has been limited on affecting nocturnal distribution especially midnight sinking depths of *M. mueleri* (Giske & Aksnes 1990, Prihartato et al. 2014). In spring, temperatures were low from surface to 60 m. Interrupted ascents mainly occurred at thermocline depths between 40-60 m. We suggest that finding optimum temperature (warmer) to support rapid digestion after encountering *Calanus sp* may be one of the reasons behind interrupted ascents.

Deeper interrupted ascent depth was observed in the simulation when turbidity was reduced. This concurred with predation risk being significantly increased (six folds) when turbidity was reduced into half. Both zooplankton and mesopelagic fish have been reported to move shallower with increased turbidity i.e. increased coefficient of light extinction (*K*) (Kaartvedt et al. 1996, Widder & Frank 2001, Frank & Widder 2002). Hence, also the light-related predation risk may have contributed to the interrupted ascents.

**Summer**

**Normal DVM with no midnight sinking**

In summer, nocturnal surface light was generally one order of magnitude higher than in spring (Prihartato et al 2014). During this time, *M. muelleri* stayed at near surface waters throughout the night, with both simulation and acoustic observations showing similar pattern. Increased surface light in summer favors increased feeding rate
throughout nights. Changes in other parameters of the model did not affect nocturnal depth distribution of nocturnal SL except when temperature was increased.

Shallower daytime depths were observed when turbidity increased. Turbidity impacts trade-offs between predation risk and feeding during daytime. By moving shallower to brighter environment, *M. muelleri* increases both feeding opportunities and risks of predation. However, *M. muelleri* will be less exposed with increased turbidity. Shading effect from phytoplankton reduces predation rates on zooplankton and fish larvae (Giske et al. 1994, Fiksen et al. 2002). The reaction distances of both planktivres and piscivores are significantly reduced with increasing turbidity (Aksnes & Utne 1997, Vogel & Beauchamp 1999, Staby et al. 2013), with piscivores got affected the most since they normally operates at longer reaction distances to spot their more dilute distributed prey (e.g. Clark & Levy 1988).

**Reliability of the model**

Feeding rate (*FR*) was high during crepuscular periods for all seasons. Similar findings on crepuscular feeding are reported in previous studies (Clark & Levy 1988, Rosland & Giske 1994, Rosland, 1997, Staby et al. 2011). Feeding in the model was limited to visual search for prey both for piscivorous and *Maurolicus muelleri*. The use of olfactory and lateral line in prey detection was neglected in the model. Yet the model depth showed good agreement with observations and we assume that our representation of prey search is acceptable (Rosland & Giske 1994, Rosland 1997, Staby et al. 2011). We neglected the possibility of *M. muelleri* producing offspring in spring and summer. However, we kept fitness motivation for the fish to enhance growth that indirectly related
to increasing reproductive output. Other anti-predation strategies such as counter illumination by silvering and transparency were excluded from the model so that in the model the vertical habitat selection was the only way *M. muelleri* could affect avoidance of predators. Yet again the simulated DVM depths in this study were in good agreement with observations from comprehensive acoustic studies. We also could not simulate schooling behavior in summer as an anti-predation strategy for *M. muelleri* since our model did not consider density dependent processes (schooling behavior was observed in the acoustic studies; Prihartato et al. 2014). The importance of terminal fitness function tuner on growth rate was considered, with the effect however was limited to adults in autumn only. By and large, this model study has successfully reproduced main patterns of the DVM behavior of *M. muelleri* as observed from acoustic studies and helped given insight into processes that may explain the observed patterns.

**Acknowledgements**

We thank Thor Klevjer and Anders Røstad for help collecting acoustic studies. Rita Amundsen was helping with collecting and managing the zooplankton datasets.
References


Kaartvedt S (1996) Habitat preference during overwintering and timing of seasonal vertical migration of *Calanus finmarchicus*. Ophelia 44:145-156


Table 1. Tuned fitness function.

<table>
<thead>
<tr>
<th>Eq.</th>
<th>Process</th>
<th>Equation</th>
</tr>
</thead>
<tbody>
<tr>
<td>(1)</td>
<td>Expected fitness at terminal time (T)</td>
<td>$F(G,t,T) = \max E{\Phi(G)</td>
</tr>
<tr>
<td>(2)</td>
<td>Fitness in growth function with fitness function tuner</td>
<td>$\Phi(G) = \begin{cases} \frac{G^\gamma}{(Gcap)^\gamma} &amp; \text{for } \gamma \geq 1 \ \frac{G}{G + (Gcap \times \gamma)} &amp; \text{for } \gamma &lt; 1 \end{cases}$</td>
</tr>
<tr>
<td>(3)</td>
<td>Scaled fitness</td>
<td>$\Delta \varsigma = \exp(\varsigma) - 1$</td>
</tr>
<tr>
<td>(4)</td>
<td>Fitness function</td>
<td>$\Phi(G) = 1 + \Phi(G) \times \Delta \varsigma$</td>
</tr>
</tbody>
</table>
Table 2. Initialization of the model

<table>
<thead>
<tr>
<th>Eq.</th>
<th>Parameters</th>
<th>Equation</th>
</tr>
</thead>
<tbody>
<tr>
<td>(5)</td>
<td>Light at depth</td>
<td>( I_d = I_{d-1} \exp (-K_a(d - z)) )</td>
</tr>
<tr>
<td>(6)</td>
<td>Fish weight to length</td>
<td>( WW = 0.0082 L^{3.18} )</td>
</tr>
<tr>
<td>(7)</td>
<td>Ratio of fish wet weight to AFDW</td>
<td>( WW = 5 \text{AFDW} )</td>
</tr>
<tr>
<td>(8)</td>
<td>Ratio of zooplankton wet weight to AFDW</td>
<td>14</td>
</tr>
<tr>
<td>(9)</td>
<td>Zooplankton radius</td>
<td>( R_D = \frac{3}{4\pi} \left( \frac{3(Z_{AFDW})}{4} \right)^{1/3} )</td>
</tr>
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</table>
Table 3. Processes in the model

<table>
<thead>
<tr>
<th>Eq.</th>
<th>Process</th>
<th>Equation</th>
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<tr>
<td>(10)</td>
<td>Visual foraging radius for planktivorous and piscivorous ( (V_{pl} \text{ and } V_{pc}) )</td>
<td>[ V_{pl}^2 = I_d \exp \left( -B_d V_{pl} \right) \left</td>
</tr>
<tr>
<td>(11)</td>
<td>Encounter rate</td>
<td>( E_N = \pi (V_{pl} \sin \theta)^2 v N_d )</td>
</tr>
<tr>
<td>(12)</td>
<td>Feeding rate</td>
<td>( e = \frac{\left( N_d/h \right)}{1/(E_N) + N_d} )</td>
</tr>
<tr>
<td>(13)</td>
<td>Mass encountered</td>
<td>( m = e \times \tau \times N_b )</td>
</tr>
<tr>
<td>(14)</td>
<td>Feeding probability at depth</td>
<td>( P_z = \left( \frac{\lambda^i}{i!} \exp(-\lambda \times i) \right), \text{ Where } \lambda = \frac{i \times m}{s_T} \text{ and } I \in { i, I } )</td>
</tr>
<tr>
<td>(15)</td>
<td>Survival probability at depth</td>
<td>( \varphi_z = \exp \left( -V_{pc}^2 k_M \tau \right) )</td>
</tr>
<tr>
<td>(16)</td>
<td>Optimum depth as function of migration constraints</td>
<td>( d - (\delta \tau) \leq z \ast (S, w, d, t) \leq d + (\delta \tau) )</td>
</tr>
<tr>
<td>(17)</td>
<td>Arrhenius temperature (K)</td>
<td>( T_D = \exp \left( \frac{T_A}{T_1} - \frac{T_A}{T_K} \right) \times \left( 1 + \exp \left( \frac{T_{AL}}{T_K} - \frac{T_{AL}}{T_L} \right) + \exp \left( \frac{T_{AH}}{T_L} - \frac{T_{AH}}{T_K} \right)^{-1} \right) )</td>
</tr>
<tr>
<td>(18)</td>
<td>Stomach evacuation rate (( \mu \text{ g AFDW}))</td>
<td>( \sigma_m = ST (1 - \exp(k_c T_D)), \text{ Where } k_c = -\log(0.5) \times T_D )</td>
</tr>
<tr>
<td>(19)</td>
<td>Metabolism cost (( \mu \text{ g AFDW}))</td>
<td>( c_m = W (1 - \exp(RT_K)) )</td>
</tr>
<tr>
<td>(20)</td>
<td>Cap function of growth extremes ((\mu \text{ g AFDW}))</td>
<td>( G_u = W + (\alpha_{lim} \times \max(\alpha) \times H) - \max(c_m), \text{ and } G_l = W - \max(c_m) )</td>
</tr>
<tr>
<td>(21)</td>
<td>Growth index to AFDW</td>
<td>( G = G_l + (G_c - 1) \delta_g, \text{ Where } \delta_g = \frac{G_u - G_l}{G_c} )</td>
</tr>
<tr>
<td>(22)</td>
<td>Stomach index to AFDW</td>
<td>( ST = x S \frac{c}{X} )</td>
</tr>
<tr>
<td>(23)</td>
<td>State change in growth dynamic over time interval</td>
<td>( G(T) = G(t) + \alpha \times \sigma_m - c_m \left( \varepsilon \frac{</td>
</tr>
<tr>
<td>(24)</td>
<td>State change in stomach dynamic</td>
<td>( ST(T) = ST(t) + P_z - \sigma_m )</td>
</tr>
<tr>
<td>Equation</td>
<td>Description</td>
<td>Formula</td>
</tr>
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<td>----------</td>
<td>--------------------------------------------</td>
<td>-------------------------------------------------------------------------</td>
</tr>
<tr>
<td>(25)</td>
<td>Probabilities if the fish survive</td>
<td>( A_m(\text{ST}, G, z, t + 1</td>
</tr>
<tr>
<td>(26)</td>
<td>Probabilities if the fish dies</td>
<td>( S_m(\text{ST}, G, z, t + 1</td>
</tr>
<tr>
<td>(27)</td>
<td>Fraction of population alive at time ((t + 1))</td>
<td>( \eta(\text{ST}, G, Z, t + 1) = \sum_{\text{ST}, G, d, m} (A_m(\text{ST}, G, z, t + 1</td>
</tr>
<tr>
<td>(28)</td>
<td>The depth distributions of the population at all-time intervals</td>
<td>( U(z, t) = \sum_{s, g, d} (\eta(s, g, d, t)</td>
</tr>
</tbody>
</table>
Table 4. Parameters used in the model in the basic run at each season with initial for (w) winter, (sp) spring and (su) summer. Ontogenetic stage in the model is denoted by (A) adult and (J) juvenile.

<table>
<thead>
<tr>
<th>Name</th>
<th>Description</th>
<th>Value</th>
<th>Dimension</th>
<th>Source</th>
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<tbody>
<tr>
<td>(\alpha)</td>
<td>Assimilation coefficient</td>
<td>0.5</td>
<td>-</td>
<td>Kiørboe et al. (1987)</td>
</tr>
<tr>
<td>(\alpha_{lim})</td>
<td>Day length limited assimilation</td>
<td>1-24 hours</td>
<td>-</td>
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<tr>
<td>(\delta)</td>
<td>Migration rate</td>
<td>0.03 m s(^{-1})</td>
<td></td>
<td>Modified from Balino &amp; Aksnes (1993)</td>
</tr>
<tr>
<td>(\Delta T)</td>
<td>Eye sensitivity threshold scales</td>
<td>- m</td>
<td>-</td>
<td></td>
</tr>
<tr>
<td>(\gamma)</td>
<td>Terminal fitness coefficient</td>
<td>0-1.5</td>
<td>-</td>
<td></td>
</tr>
<tr>
<td>(\lambda)</td>
<td>Probability of finding prey</td>
<td>0-1</td>
<td>-</td>
<td>-</td>
</tr>
<tr>
<td>(\sigma_m)</td>
<td>Metabolic cost</td>
<td>-</td>
<td>-</td>
<td>-</td>
</tr>
<tr>
<td>(\theta)</td>
<td>Field angle for encountering prey</td>
<td>30 degrees</td>
<td>-</td>
<td></td>
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<tr>
<td>(\tau)</td>
<td>Time step of the model</td>
<td>900 s</td>
<td>-</td>
<td></td>
</tr>
<tr>
<td>(B_d)</td>
<td>Beam attenuation</td>
<td>3K(_D) m(^{-1})</td>
<td></td>
<td>(Giske et al. 1990)</td>
</tr>
<tr>
<td>(C)</td>
<td>Prey inherent contrast</td>
<td>0.5</td>
<td>-</td>
<td>Aksnes &amp; Utne (1997)</td>
</tr>
<tr>
<td>(d)</td>
<td>Water column</td>
<td>250 m</td>
<td>-</td>
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<tr>
<td>(D_d)</td>
<td>Depth of the scattering layer (SL)</td>
<td>0-250 m</td>
<td></td>
<td>Echo sounder 120 kHz</td>
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<tr>
<td>(g)</td>
<td>Growth</td>
<td>0</td>
<td>-</td>
<td>-</td>
</tr>
<tr>
<td>(G_{cap})</td>
<td>Growth cap function</td>
<td>20</td>
<td>-</td>
<td>-</td>
</tr>
<tr>
<td>(h)</td>
<td>Prey handling time constant</td>
<td>2 s</td>
<td></td>
<td>Eggers (1977)</td>
</tr>
<tr>
<td>(i)</td>
<td>Feeding level from (i) to (I)</td>
<td>1 to 20</td>
<td>-</td>
<td>Rosland &amp; Giske (1994)</td>
</tr>
<tr>
<td>(I_d)</td>
<td>Light irradiance at depth where fish SL is located</td>
<td>- (\mu) mol m(^{-2})s(^{-1})</td>
<td></td>
<td>LICOR instruments</td>
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<tr>
<td>(I_{max})</td>
<td>Maximum light irradiance processed at fish’s retina</td>
<td>- (\mu) mol m(^{-2})s(^{-1})</td>
<td></td>
<td>Aksnes &amp; Utne (1997)</td>
</tr>
<tr>
<td>(K_\sigma)</td>
<td>Time to evacuate half stomach stomach at temperature optimum</td>
<td>3 s</td>
<td></td>
<td>Rosland et al. (2009)</td>
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<tr>
<td>(K_d)</td>
<td>Extinction coefficient</td>
<td>- m(^{-1})</td>
<td></td>
<td>Measurements</td>
</tr>
<tr>
<td>(K_I)</td>
<td>Half saturation of light entering fish’s eye</td>
<td>0.5</td>
<td>-</td>
<td>Aksnes &amp; Utne (1997)</td>
</tr>
<tr>
<td>(K_M)</td>
<td>Daily mortality constant</td>
<td>5.10(^{-3}) s(^{-1})</td>
<td></td>
<td>Modified from</td>
</tr>
<tr>
<td>Symbol</td>
<td>Description</td>
<td>Value</td>
<td>Source</td>
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<td>--------</td>
<td>------------------------------------------------------------------------------</td>
<td>----------------------------------------------------------------------</td>
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<tr>
<td>$K_s$</td>
<td>Eye sensitivity constant</td>
<td>$5.10^{-5}$ $\mu$ mol m$^{-2}$s$^{-1}$</td>
<td>Aksnes &amp; Utne (1997)</td>
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<tr>
<td>$L$</td>
<td>Fish length</td>
<td>24-39 mm</td>
<td>Staby et al. (2011, 2013)</td>
<td></td>
</tr>
<tr>
<td>$N_D$</td>
<td>Prey density</td>
<td>- Ind/m$^3$</td>
<td>Net catches</td>
<td></td>
</tr>
<tr>
<td>$N_B$</td>
<td>Prey biomass</td>
<td>-</td>
<td>Net catches (Tab. 1)</td>
<td></td>
</tr>
<tr>
<td>$R$</td>
<td>Respiration cost for metabolic process at temperature optimum</td>
<td>-0.01 -</td>
<td></td>
<td></td>
</tr>
<tr>
<td>$R_D$</td>
<td>Zooplankton radius</td>
<td>- m</td>
<td>Eq. 9</td>
<td></td>
</tr>
<tr>
<td>$s$</td>
<td>Stomach weight ratio to bodyweight (AFDW)</td>
<td>5% from bodyweight</td>
<td>Ash free dry weight (AFDW)</td>
<td></td>
</tr>
<tr>
<td>$t$</td>
<td>Duration of time intervals from $t$ to $T$</td>
<td>1-192 intervals</td>
<td>15 minutes resolution for 24 hours</td>
<td></td>
</tr>
<tr>
<td>$T_D$</td>
<td>Temperature at depth</td>
<td>- Ceclius (C)</td>
<td>CTD data</td>
<td></td>
</tr>
<tr>
<td>$T_I$</td>
<td>Reference temperature</td>
<td>20 Ceclius (C)</td>
<td>Rosland et al. (2009)</td>
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<tr>
<td>$T_A$</td>
<td>Arrhenius temperature</td>
<td>7022 Kelvin (K)</td>
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<tr>
<td>$T_{AL}$</td>
<td>Rate of decrease at lower boundary</td>
<td>45430 Kelvin (K)</td>
<td>Rosland et al. (2009)</td>
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<tr>
<td>$T_{AH}$</td>
<td>Rate of decrease at upper boundary</td>
<td>31376 Kelvin (K)</td>
<td>Rosland et al. (2009)</td>
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<tr>
<td>$T_H$</td>
<td>Upper boundary of temperature tolerance range</td>
<td>296 Kelvin (K)</td>
<td>Rosland et al. (2009)</td>
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</tr>
<tr>
<td>$T_K$</td>
<td>Temperature at depth</td>
<td>- Kelvin (K)</td>
<td>CTD data</td>
<td></td>
</tr>
<tr>
<td>$T_L$</td>
<td>Lower boundary of temperature tolerance range</td>
<td>275 Kelvin (K)</td>
<td>Rosland et al. (2009)</td>
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<tr>
<td>$v$</td>
<td>Swimming speed of the fish</td>
<td>1 Body length of the fish</td>
<td>Eggers (1977)</td>
<td></td>
</tr>
<tr>
<td>$w$</td>
<td>Weight of the fish</td>
<td>- AFDW</td>
<td>Staby et al. (2013)</td>
<td></td>
</tr>
<tr>
<td>$WW$</td>
<td>Wet weight of the fish</td>
<td>- grams</td>
<td>Rosland &amp; Giske (1994), Staby et al. (2013)</td>
<td></td>
</tr>
<tr>
<td>$X$</td>
<td>Stomach level from x to maximum X</td>
<td>20 (A) 15 (J)</td>
<td>Giske et al. (1992)</td>
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<tr>
<td>$z$</td>
<td>Depth selected by the optimization</td>
<td>0-250 m</td>
<td>-</td>
<td></td>
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</tbody>
</table>
Table 5. Results from different runs given as fraction of the basic run in autumn both for juvenile (24 mm) and adult (39 mm). Basic run (BR) presented for comparison. Note that the adult simulation was using the first day from the three days simulation. Optimum depths ($Z^*$) at day (11:30-12:30) and night (22:30-23:30) are displayed. Feeding rate (FR) and mortality rate based on visual predation (M) are given as daily average. Growth (G) is given at the terminal time. Sensitivity variables are terminal fitness ($\gamma$), visual threshold for *Maurolicus muelleri* ($K_s$), visual threshold of predators ($K_p$), and daily mortality constant ($K_M$). Environmental variable are zooplankton radius ($R_D$), zooplankton density ($N_D$), surface irradiance ($I$), coefficient of extinctions at 500 nm ($K$), and temperature ($T$).

<table>
<thead>
<tr>
<th>Variable</th>
<th>CF</th>
<th>Juvenile</th>
<th></th>
<th></th>
<th></th>
<th>Adult</th>
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<td>$Z^*$</td>
<td>FR</td>
<td>M</td>
<td>G</td>
<td>$Z^*$</td>
<td>FR</td>
<td>M</td>
<td>G</td>
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<tr>
<td></td>
<td></td>
<td>Day</td>
<td>Night</td>
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<td>Day</td>
<td>Night</td>
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<td>$K_s$</td>
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<td>$K_p$</td>
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<td>$K_M$</td>
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<td>$N_D$</td>
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Table 6. Results from different runs given as fraction of the basic run in spring for the fish (35 mm). Basic run (BR) is presented for comparison. Note that the adult simulation was using the first day from the three days simulation. Optimum depth ($Z^*$) at day (11:30-12:30), interrupted ascent (18:30-19:30) and night (22:30-23:30) are displayed. Feeding rate (FR) and mortality rate based on visual predation (M) are given as daily average. Growth (G) is given at the terminal time. Sensitivity variables are terminal fitness ($\gamma$), visual threshold for *Maurolicus muelleri* ($K_s$), visual threshold of predators ($K_p$), and daily mortality constant ($K_M$). Environmental variable are zooplankton radius ($R_D$), zooplankton density ($N_D$), surface irradiance ($I$), coefficient of extinctions at 500 nm ($K$), and temperature ($T$).

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Table. 7. Results from basic run and changing in parameter value for summer for the fish (39 mm). Note that the adult simulation was using the first day from the three days simulation. Optimum depth (Z*) at day (11:30-12:30) and night (22:30-23:30) are displayed. Feeding rate (FR) and mortality rate based on visual predation (M) are given as daily average. Growth (G) is given at the terminal time. Sensitivity variables are terminal fitness (γ), visual threshold for Maurolicus muelleri (K_s), visual threshold of predators (K_p), and daily mortality constant (K_M). Environmental variables are zooplankton radius (R_D), zooplankton density (N_D), surface irradiance (I), coefficient of extinctions at 500 nm (K), and temperature (T).

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Fig. 1. Map of Masfjorden, Western Norway. The red dot marks the location of the echo sounder.
Fig. 2. Schematic diagram of the dynamic programming for *Maurolicus muelleri*.
Fig. 3. Example of variation in terminal fitness function (for summer only). Colored lines indicate different fitness function tuner (see method) thus resulted in different shape of motivation: red, pink, blue, and green lines indicate tuning numbers of 0.25, 0.5, 1, and 2 respectively.
Fig. 4. Selected echograms from the 120 kHz echo sounder depicting DVM at different seasons. Autumn is represented by 26 Oct 2010 echogram with two separated scattering layers (SL): juvenile (SL1) and adult (SL2). Spring is represented by 15 Mar 2011 echogram; for simplicity we only consider the single layer that performed interrupted ascend in the afternoon. Summer is represented by 10 Aug 2011 echogram displaying a singular SL without midnight sinking. Coloration refers to the volume backscattering (Sv) where red illustrates the strongest and white the weakest backscatter.
Fig. 5. Environmental parameters used for the modeling. (A) Surface light as PAR. (B) Coefficient of extinctions and temperature showed in solid and circles lines respectively with blue, green and red representing 26 Oct, 15 Mar and 10 Aug. (C, D, and E) zooplankton abundance (bars) and radius (lines). Day and night are represented with dark and lighter coloration.
Fig. 6. 24-hours DVM simulation by the model. (A) 26 Oct where juvenile (24 mm) occupies the upper layer and adults (39 mm) is the non-migrating layer, (B) 15 Mar with one uniform layer of 35 mm fish size and (C) 10 Aug with 39 mm fish size. Red plots are the SL depths observed from the echo sounder with upper caps showing the upper and lower SLs and the circles are the mean SL depths. Color bar indicates the probability of the population residing at chosen depths with black indicating the strongest probability and white with the lowest probability.
Fig. 7. 72-hours DVM simulation by the model. (A) 26 Oct where juveniles (24 mm) occupy the upper layer and adults (39 mm) is the non-migrating layer, (B) 15 Mar produces only one singular layer (35 mm) and (C) 10 Aug is also singular layer (39 mm). Color bar indicates the probability of population residing at chosen depths with black indicates the strongest probability and white the lowest probability.
Fig. 8. Stomach fullness of *Maurolicus muelleri* in percentage (%). A. 24-hours simulation and (B) 72-hours simulation. Color lines describe fish of different size and in different season with black and blue being juveniles (24 mm) and adults (39 mm) in autumn. Green line indicates fish (35 mm) in spring, while red line shows *M. muelleri* (39 mm) in summer.
Fig. 9. Growth dynamics of *Maurolicus muelleri* as percentage (%) increase from initial weight. A. 24-hours simulation and (B) 72-hours simulation. Color lines represent fish of different size and season, with black and blue being juveniles (24 mm) and adults (39 mm) in autumn. Green line indicates fish (35 mm) in spring, while red line shows *M. muelleri* (39 mm) in summer.
Fig. 10. Feeding rate and mortality. Feeding rate over time (A) 24-hours and (B) 72-hours. Predation risk shown by mortality rate (h⁻¹) for 24 hours (C) and 72 hours (D).

Ratio mortality/feeding rate over time: (E) 24-hours and (F) 72-hours. Black line represents juveniles in autumn (24 mm) and blue line represents the adults in autumn (39 mm). Green line represents fish in spring (35 mm) and red line for summer (39 mm).