Seasonal dynamics of the vertical migration behaviour of mesopelagic fish

Arved Staby

Dissertation for the degree philosophiae doctor (PhD)

At the University of Bergen, Norway

2010

ACKNOWLEDGEMENTS

I want to use the opportunity and thank the people who were either indirectly or directly involved in making this work possible. My friends Andre and Kirsten Reckeweg, Torolf Myklebust, Monica Mannelqvist, Jon Ødegård, and Carl von Bach, with whom I shared much needed relaxation time in between.

I am also thankful to colleagues in the aquatic behavioural research group for helpful discussions during the course of this study. Especially Anne Chrsitine Utne-Palm I am indebted to for organizing field trips to Masfjorden and making it possible to collect field data. The jogging sessions with my college Jon Egil Skjæraasen at lunch or after work provided much needed time-out from writing, reading and staring at my Dell 21“ screen.

I am indebted to Dag Aksnes for his support and guidance during the writing-up period of one of the papers.

I am grateful to my supervisors Anders Fernö, Anne Gro Vea Salvanes and Stein Kaartvedt for their support and guidance, and many fruitful discussions. I feel especially indebted to my co-supervisor Stein Kaartvedt, who together with Thor A. Klevjer and Anders Røstad made this study at all possible. Thank you for all your contributions.

And without the support, patience and commitment from my loving better-half Kjersti during the last years, as well as the inspiration and joy I got from my son Sondre and daughter Lise, I would not have managed. Thank you.

I want to dedicate this work to my mother Erika Gertrud Staby and my late father Hans Erik Staby. Ihr seid meine Vorbilder, und ohne eure Hilfe und Unterstützung wäre ich nicht dort wo ich jetzt bin. Vielen Dank für alles was ihr für mich getan habt.

Arved Staby

SUMMARY

This thesis focuses on the behavioural dynamics of mesopelagic fish in a fjordic environment. Acoustic data recorded with a stationary echosounder was used to primarily investigate the diel vertical migration behaviour of the mesopelagic fish *Maurolicus muelleri.* Particular emphasis was on the effect of daily and seasonal changes in surface light irradiance and the vertical distribution of large predator-like fish on *M. muelleri*. In addition the behaviour of the deeper distributed mesopelagic lantern fish *Benthosema glaciale* and large, individual fish were also investigated.

Diel vertical migrations (DVM) are vital in maintaining the energy flow in marine ecosystem food webs, and migrating organisms thus directly and indirectly provide food/nourishment to many non migrating animals. Typically, DVM are characterised by an ascent to surface waters from deeper day time depths at dusk, followed by a nocturnal period close to the surface and a subsequent descent to daytime depths at dawn.

M. muelleri and *B. glaciale* are abundant and ecologically important fish in several marine systems. They are part of the mesopelagic animal community that performs DVM - nature's largest migration in terms of biomass. In the Norwegian Sea and fjords *M. muelleri* forms acoustically visible scattering layers (SLs), while the deeper living *B. glaciale* appears acoustically more scattered and less dense, not aggregating in distinct SLs. Both species are challenged with seasonally changing gradients of environmental variables including light, temperature, salinity, food abundance and piscivorous predators.

Although several aspects of the behaviour and biology of *M. muelleri* and to a lesser extent of *B. glaciale* have been studied, our knowledge of short term and seasonal variation of individual fish and SL behaviour, as well as behavioural responses to seasonal changes in surface light irradiance and predator distribution is limited. To address these shortcomings we therefore utilised the fairly recent developments of stationary echosounder assemblages, located on fjord bottoms, which made it possible to collect continuous acoustic records of the entire water column over a 15 month period.

Here I present 4 papers covering the description of a stationary acoustic platform and its application in studying the temporal and spatial behavioural dynamics of *B. glaciale* individuals and layers as well as large individual fish (Paper 1), the monthly and seasonal variations in DVM behaviour of *M. muelleri* SL (Paper 2), the relationship between daily and monthly changes in surface light intensity and *M. muelleri* SL depth (Paper 3), and the vertical distribution of *M. muelleri* SL in relation to seasonally changing predator distribution (Paper 4). By collecting continuous acoustic data with an upward facing split beam echosounder located on the fjord bottom it was possible to observe biotic changes in the water column within the course of days, weeks, and months (Paper 1-4), as well as investigate the vertical distribution and swimming behaviour of individual fish by applying a target strength threshold and target tracking (Paper 1 and 3). Paper 1 specifically describes the reverse diel migrations during day time of the deeper distributed (> 200 m) lanternfish *B. glaciale* and its swimming behaviour, which was mostly passive and more active during stepwise vertical excursions. Paper 1 also deals with depth related differences in large fish swimming behaviour and target strength. Shallower distributed large fish (< 300 m) had both higher target strengths and swimming speeds than deeper distributed fish (> 300 m).

Paper 2 reports on novel behaviours of *M. muelleri* ontogenetic layers; early morning ascents, reverse diel migrations, and arrested migrations. Previous studies have shown that juvenile *M. muelleri* perform midnight sinking, i.e. the relocation to deeper waters after dusk, in January in addition to ordinary DVM between January and June. Adult fish on the other hand do not display DVM in January, and stayed in deep waters throughout the diel period, while migrating vertically between the surface and deeper day time depths in spring (May and June). In addition to these previous observations we found that a proportion of ascending juvenile *M. muelleri* arrested their migration between January and April. Further, adult fish displayed early morning ascents to the surface (in the absence of light) in September and October, and reverse migrations in November until January by migrating approximately 20-30 m upwards at dawn instead of descending. Adult fish ‘overwintered’ for approximately 6 months, whereas younger fish displayed midnight sinking between August and beginning of May. Paper 2 also demonstrated that when three SLs were present, the shallowest SL was composed of post-larvae ≈ 10mm long. The observed behavioural patterns are interpreted as responses to individual physiological state, hunger-satiation and condition, prey availability and predation risk at alternative depths.

Light affects many aspects of fish behaviour. The preferendum hypothesis states that organism change their depth during DVM because they follow a constant light level, i.e. an isolume. In Paper 3 the upper border depth of *M. muelleri* SLs was positively, linearly correlated to surface irradiance, which could suggest that *M. muelleri* follows an isolume. However, this assumes an invariant light attenuation coefficient. On the contrary we found that the light intensity of the isolume was not constant. It tended to vary with migration phase, whether fish were ascending or descending and it also changed with month. We therefore suggest that *M. muelleri* follow a preferred light range instead of a strict isolume, which reflects a more dynamic relationship. Differences in preferred light range also appear to be related to ontogeny and physiological state.

In paper 4 we applied target tracking to study the depth distribution of large, putative predatory fish. High numbers of predator-like fish at the surface at night during autumn and winter month, October – March, appear to cause juvenile *M. muelleri* to relocate deeper after dusk in order to avoid these predators. However, juveniles continued to decent at dawn in autumn and winter months despite the absence of pelagic daytime predators at this time. This suggests that *M. muelleri* has an innate (genetically fixed) behavioural response synchronised with the light cycle and triggered by a change in surface light intensity. The presence of high numbers of predators in shallow waters between dawn and dusk may explain why *M. muelleri* avoided the shallow waters at day time in spring and summer months. An increasingly deeper daytime distribution of predator-like fish in the course of summer may also have influenced the vertical distribution especially of the deeper SLs.

The overall findings in this thesis show that vessel independent acoustic observation platforms are well suited to detect and observe both short term and seasonal changes in the behaviour of both layers of fish and individuals. By combining acoustic data with environmental, biological and catch data, I have shown that the DVM behaviour of mesopelagic individuals and SLs is much more complex than previously believed, with fish displaying hitherto undescribed temporally varying behavioural patterns. My studies corroborate and supplement the current understanding of ecological interactions and processes that persist in fjordic environments. Behavioural aspects of *M. muelleri* have been used to model responses to environmental constraints and the life history of this species, and results presented in this thesis thus have the potential to improve such models. Due to their vital role as prey for commercially exploited fish species in marine ecosystems, mesopelagic fish species have in recent years been the focus of acoustic surveys to estimate their abundance and determine their distribution. A better understanding of their behaviour can aid in improving such estimates and contribute to the improved ecosystem based management of marine resources.

CONTENTS

INDIVIDUAL PAPERS

LIST OF PAPERS

Paper 1:

Kaartvedt, S., Røstad, A., Klevjer, T., **Staby, A.** (2009) Use of bottom-mounted echo sounders in exploring behavior of mesopelagic fishes. *Marine Ecology Progress Series* **395**: 109–118

Paper 2:

Staby, A., Røstad, A., Kaartvedt, S. (Manuscript) A full year study of diel vertical migration in the mesopelagic fish *Maurolicus muelleri* reveals novel and varied behavioural patterns

Paper 3:

Staby, A., Aksnes, D.L. (Manuscript) Follow the light – diurnal and seasonal variations in the vertical distribution of the mesopelagic fish *Maurolicus muelleri*

Paper 4:

Staby, A., Røstad, A., Salvanes, A.G.V., Kaartvedt, S. (Manuscript) Seasonal occurrence and vertical migration of potential predators of *Maurolicus muelleri*

INTRODUCTION

Habitat shifts among marine fish are common, and the motivations to do so can be multiple (Metcalf *et al.* 2008). The relocation to different habitats can have implications for the fitness of the migrating organism and is triggered by a) a change in the physical environment, e.g. temperature, oxygen, or light, or biotic factors like predator and food abundance of its immediate surrounding (Girsa 1973; Bohl 1980; McFarland 1986; Kramer 1987; Hamukuaya *et al.* 1998; Kaartvedt *et al.* 2009a; Utne-Palm *et al.* 2010), b) internal state, such as hunger level (Pearre 2003), or c) by a genetically fixed (innate) behaviour (Mehner *et al.* 2007; Huizinga *et al.* 2009). Typically the biotic and abiotic habitat of an organism can be described by a range of values. While a given set of values may be suitable for one population it need not be appropriate for another, which may be expressed in different behaviours, physiological adaptations and life histories (Hutchings 1993; Salvanes and Stockley 1996; Haugen and Vøllestad 2000; Salvanes *et al.* 2004). Within a population deviations from typical behavioural patterns due to ontogeny and phenotypic plasticity are not uncommon (Reebs 2002; van Damme *et al.* 2009).

A variety of organisms including zooplankton, mesopelagic nekton and planktivorous and piscivorous fish perform diel vertical migrations (DVM) (Roe 1983; Kaartvedt *et al.* 1988; Neilson and Perry 1990; Ringelberg 1991; Williams and Koslow 1997; Onsrud and Kaartvedt 1998; Frank and Widder 2002; Cohen and Forward 2009; Dupont *et al.* 2009). Two basic types of DVM patterns are identified: Type I migrations are the ascent of organisms to the surface at the onset of night (dusk) and down to daytime depths with day break (dawn), while the opposite takes place in Type II migrations (Neilson and Perry 1990). Nocturnal vertical relocations, like midnight sinking, can take place under low or absent light conditions between dusk and dawn (Giske *et al.* 1990; Tarling *et al.* 2002; Benoit-Bird *et al.* 2009). Light is considered an important proximate factor in DVM, with changes in both absolute and relative light intensity suggested to determine the depth distribution of organisms and the timing of their ascent to and descent from the surface (Neilson and Perry 1990; Baliño and Aksnes 1993; Widder and Frank 2001; Hays 2003; Cohen and Forward 2009). As light regimes and intensity vary markedly with season, especially at high latitudes, fish that are influenced by light are likely to adapt their behaviours accordingly.

Several hypotheses for vertical migrations on a population level have been proposed. Eggers (1978) proposed that the adaptive value of vertical migrations was to minimize predation mortality through predator avoidance. The predator avoidance hypothesis was later extended to include the optimization of foraging in the anti-predation window (Clark and Levy 1988; Scheuerell and Schindler 2003). The bioenergetic efficiency hypothesis states that organisms distribute at temperatures which maximize growth (Wurtsbaugh and Neverman 1988; Giske and Aksnes 1992; Bevelhimer and Adams 1993), while the foraging-opportunity hypothesis predicts that the depth distribution of the predator overlaps with depth changes of its prey (Levy 1990a; Neilson and Perry 1990). On an individual level the hunger-satiation hypothesis assumes that vertical movements of individuals are triggered by a change of its hunger or satiation state (Pearre 2003).

Fish can enhance their fitness in many ways and this often includes a trade-off between two or several traits such as growth, age and size at maturity, or current and future reproductive success (Stearns 1992). Mature fish on the verge of spawning may for instance opt to forsake foraging opportunities, which often entail an increased predation risk, for the benefit of future reproductive output. Migrating fish may enhance their fitness by optimizing growth or the build up of energy reserves, either by improving feeding conditions while minimizing predation risk, or by selecting a growth favourable environment. While visually foraging planktivores depend on light to detect their prey, they themselves become more susceptible to visual predators with increasing light. Organisms may therefore position themselves at a preferred (optimal) light level, optimizing visual foraging and growth while minimizing predation risk (Clark and Levy 1988; Appenzeller and Leggett 1995; Scheuerell and Schindler 2003).

Both the lantern fish *B. glaciale* and the hatchetfish *M. muelleri* are common in Norwegian fjords (Kaartvedt et al. 1988; Salvanes 2004). *B. glaciale* is usually found below 250 m during day time and higher up in the water column at night (Giske et al. 1990). Lantern fish are more dispersed and do not aggregate as densely as *M. muelleri* and thus do not form distinct sound scattering layers at depth (SLs).

Ontogenetic stages of *M. muelleri* often aggregate in separate acoustically visible sound scattering layers (SLs) above 200 m depth (Giske *et al.* 1990). Typically the SL composed of adult *M. muelleri* displays DVM in Spring (between April and June; Rasmussen and Giske

1994; Goodson *et al.* 1995), whereas in early winter (January) adult fish remain in deeper waters while juveniles perform DVM as well as nocturnal midnight sinking after dusk (Giske *et al.* 1990; Baliño and Aksnes 1993; Goodson *et al.* 1995).

M. muelleri adjusts its vertical distribution and behaviour according to changes in light intensity (Baliño and Aksnes 1993; Kaartvedt *et al.* 1996; Kaartvedt *et al.* 1998). The variation in vertical predation risk and feeding opportunity (Rosland and Giske 1994; Rosland 1997; Rosland and Giske 1997) have been suggested to influence the ontogenetically and seasonally varying depth distribution of this species. Trawl samples from the pelagic fjord habitat contained gadoid fish, including blue whiting, saithe, pollack and haddock, from the large piscivore fish community (Salvanes 1991; Giske *et al.* 1990; Bjelland 1995). Cod is also present year round and particularly in January – March (unpublished landing statistics). The midnight sinking behaviour of juvenile *M. muelleri* to slightly deeper waters after short feeding bouts at the surface at dusk (Rasmussen and Giske 1994) has been hypothesized to be the result of juveniles distributing at the temperature maximum, thereby accelerating digestion and growth (Giske *et al.* 1990). The predator avoidance (Tarling *et al.* 2002) and hunger-satiation hypothesis (Pearre 2003) are two alternative hypotheses proposed for this behaviour. The predator avoidance hypothesis states that organisms migrate to deeper waters and thereby avoid predators feeding at the surface, while the hunger-satiation hypothesis proposes that once organisms are satiated from feeding at the surface, they move/sink to deeper waters. Most studies that investigated *M. muelleri* behaviour were generally based on a limited time window, and little is known about how fish respond to short term or seasonal changes in surface light intensity, temperature, abundance and distribution of food, and predators. In the present thesis we use detailed acoustic data to explore the applicability of these hypotheses for mesopelagic fish.

The generally dense and homogenous nature of *M. muelleri* SLs, as well as the fact that individuals have an air filled swimbladder (Figure 2), makes it possible to study the behaviour of this species acoustically at both the individual (Torgersen and Kaartvedt 2001; Kaartvedt *et al.* 2008) and the population,i.e. layer, level (Torgersen *et al.* 1997). Thus, in an easily accessible fjord short and long term (seasonal) changes of this species' DVM behaviour can be observed with vessel independent acoustic platforms collecting continuous data. Since *M. muelleri* is found in worldwide oceanic environments as well, descriptions of the behavioural dynamics may also be relevant to other marine environments. In our study site *B. glaciale* cooccur with *M. muelleri*. It is thus necessary to distinguish its distribution and behaviour (acoustic records) from that of *M. muelleri*. This is done at the start of this thesis (Paper I), which also provides information for comparing the biology of these two mesopelagic fishes.

BACKGROUND

Study site

Given that the field studies presented in this thesis focused primarily on *M. muelleri* at the same location, we chose Masfjorden as the study location. This is the natural choice, since *M. muelleri* SLs and the fjords´ fauna have received much attention during previous comprehensive ecosystem investigations. Masfjorden is a 20 km long, approximately 1 km wide and 490 m deep fjord on the west coast of Norway (Figure 1). The water exchange regime of the fjord is mainly wind driven (Asplin *et al.* 1999) and is influenced by its 70 m deep sill (Aksnes *et al.* 1989). Resulting currents above sill depth (10 - 20 cm·s-1) vary seasonally and can strongly influence the distribution of plankton (Aksnes *et al.* 1989; Baliño and Aksnes 1993) and eggs and larvae in upper layers (Asplin et al 1999). The physical environment is stable below 80 – 90 m regardless of season (Aksnes *et al.* 1989; Giske *et al.* 1990; Bjelland 1995), although dissolved oxygen <3 $ml \cdot l^{-1}$ below 300 m and salinity of 34 ppm at 200 m have been reported (Sørnes and Aksnes 2006). Above the sill depth temperature

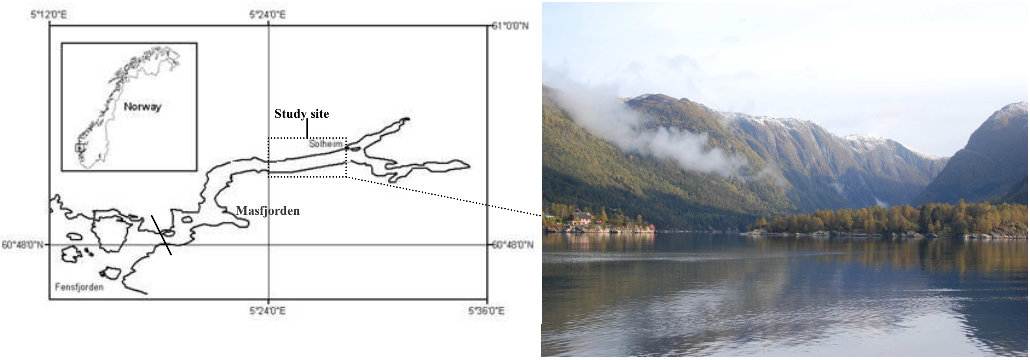


Figure 1: *Masfjorden on the west coast of Norway is like many fjords surrounded by high mountain ranges.*

and salinity vary seasonally ranging between 5 – 13^0C and 30 – 34 ppm respectively (Aksnes *et al.* 1989; Bjelland 1995; Bagøien *et al.* 2001).

In spring and summer zooplankton biomass is generally high in the upper 50 m at both day and night time (Aksnes *et al.* 1989; Bjelland 1995), while in October shallow zooplankton abundance may vary as this represents the end of the productive season (Aksnes *et al.* 1989; Bagøien *et al*. 2001). In late autumn and winter (November – February) zooplankton biomass at the surface is generally low, while large *Calanus* are abundant (overwinter) deeper than 150 m depth where they overwinter (Kaartvedt 1996; Bagøien *et al.* 2001). The species composition and abundance of piscivorous fish varies seasonally (Salvanes 1991). Density estimates of the commonly caught gadoids blue whiting and saithe, based on catch data published in Giske *et al.* (1990), Rasmussen and Giske (1994) and Bjelland (1995), ranged between 200-700 fish·nm^{-2}.

The study species *M. muelleri*

The pearlside *M. muelleri* is a member of the hatchetfish family (*Sternoptychidae*), which typically has silvery sides and latero-ventral photophores that vary in number ontogenetically (Figure 2). The species is common in all the worlds oceans (Gjøsæter and Kawaguchi 1980; Parin and Kobyliansky 1996), and has been the focus of recent acoustic surveys in various marine systems to estimate its abundance and map horizontal distribution (McClatchie and Dunford 2003, Coetzee *et al.* 2006). It has been studied in varying habitats, including oceanic (Linkowski 1983; John and Kloppmann 1989; Boehlert et al. 1994; Sassa et al. 2002), coastal shelf and slope (Clarke 1982; Young and Blaber 1986; Weiss *et al.* 1988; Prosch 1991; John and Kloppmann 1993; Landaeta and Castro 2002), and fjordic (Robertson 1976; Gjøsæter 1981; Giske *et al.* 1990; Rasmussen and Giske 1994; Bjelland 1995; Salvanes and Stockley 1996; Kristoffersen and Salvanes 1998; 2001) environments.

The trophic importance of this species in these systems is reflected by the range of its predators, which include demersal fish (Salvanes and Nordeide 1993; Payne *et al.* 1987; Punt *et al.* 1992; Pillar and Barange 1997), sharks (Ebert 1992), pelagic fish (Nepgen 1979; Prosch 1986; Giske et al 1990), cephalopods (Lipinski 1992; Villanueva 1993), as well as birds (Jackson 1988) and seals (David 1987).

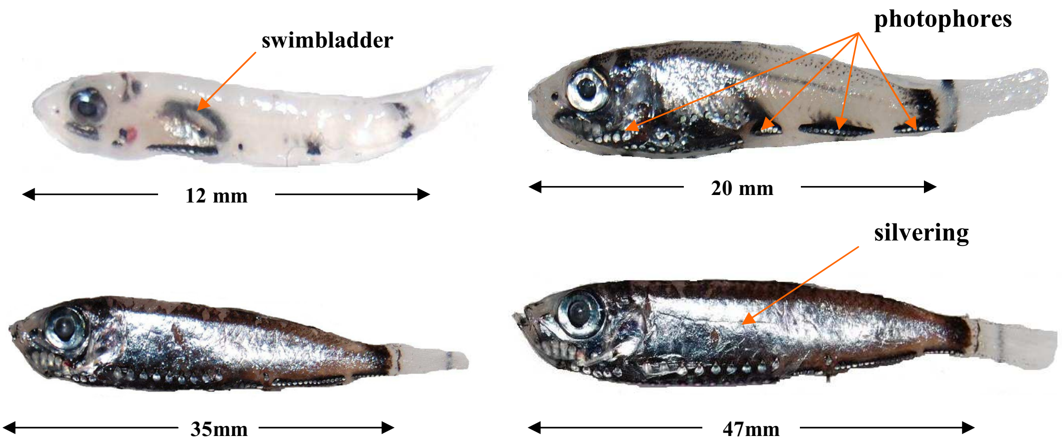


***Figure 2:** Different ontogenetic stages of M. muelleri showing varying degrees of silvering and transparency, and number of ventral photophores.*

The main preys of pearlside are copepods and cladocerans, but it also feeds on fish eggs, gastropod larvae and copepod larvae (Rasmussen and Giske 1994; Bjelland 1995; Bagøien *et al.* 2001).

The life history of this species seems to vary geographically. Age estimates of *M. muelleri* from Norwegian fjords and the Norwegian Sea suggest a longevity of 3 – 5 years in these waters (Gjøsæter 1981; Bjelland 1995; Kristoffersen and Salvanes 1998; Hamre 1999). Irrespective of the marine system pearlsides seem to mature within the first year (Clarke 1982; Rasmussen and Giske 1994; Prosch 1986). The length at which 50% of females mature (L_{50}) varies geographically (Young *et al.* 1987; Prosch 1991), and is estimated at 24 – 30 mm in Norwegian fjords (Rasmussen and Giske 1994; Bjelland 1995). *M. muelleri* is a batch spawner (Melo and Armstrong 1991) and has a length dependant fecundity of 100 – 2000 eggs ind^{-1} (Rasmussen and Giske 1994). Depending on the marine system it spawns at varying depth and over varying time periods (Robertson 1976; Lopes 1979; Prosch 1991; Weiss *et al.* 1988; John and Kloppmann 1989, 1993; Olivar *et al.* 1992). In Masfjorden pearlside spawn between April-August, with egg and larvae density maximum between 50-100 m (Lopes 1979).

Genetic variation between oceanic and fjordic samples indicates that only a small proportion of eggs and larvae are advected out of Masfjorden (Suneetha and Nævdal 2001). Once fully grown *M. muelleri* can achieve swimming speeds of 2 - 7 body lengths (approximately 8 - 30 cm $\cdot s^{-1}$; Torgersen and Kaartvedt 2001), and due to a prominent swimbladder (Figure 2) even the youngest ontogenetic stages can be acoustically detected.

ACOUSTICS AS A TOOL IN BEHAVIOURAL STUDIES

Historically the main application of hydro acoustics in marine science has been to assess the distribution of fish and estimate their biomass (Johannesson and Mitson 1983; Torgersen *et al.* 1997; McClatchie and Dunford 2003). However, in the last two decades hydro acoustics has increasingly become an integral tool for aquatic ecologists to observe the *in situ* behaviour and distribution of individual (Huse and Ona 1996; Torgersen and Kaartvedt 2001; Klevjer and Kaartvedt 2003; Mehner 2006; Kaartvedt *et al.* 2008) and groups or layers of marine organisms (Baliño and Aksnes 1993; Kaartvedt *et al.* 1998; Benoit-Bird and Au 2004, 2006). Typically acoustic observations for studying behaviour are made from moving or stationary vessels with hull mounted and / or submerged echo sounders (Huse and Ona 1996; Klevjer and Kaartvedt 2003; Kaartvedt *et al.* 2007), although floating devices have also been used (Handegard *et al. 2005*). Only fairly recently have upward facing echo sounders, positioned on the sea floor and connected to a vessel or land via cable, been used to observe the behaviour of marine organisms (Figure 3; Axenrot *et al.* 2004; Onsrud *et al.* 2005; Didrikas and Hansson 2009).

Echosounders produce pings, i.e. pulses of sound waves, with a set intensity (energy) travelling at approximately 1500 m s^{-1}. Various sized organism – zooplankton, shrimp or fish – inside the cone shaped beam of a sound wave will reflect (backscatter) varying proportions of the initial energy back to the echosounder (MacLennan and Simmonds 1992). Backscattered energy is integrated and then visualized in a two dimensional echogram, displaying the depth and intensity of individual and more aggregated (layers, schools) organisms (Figure 3; MacLennan and Simmonds 1992). The backscattered energy of individual fish, i.e. target strength (TS), with swimbladders is usually higher than the TS of fish lacking swimbladders (Foote 1987; Misund and Beltestad 1996). TS can also vary with fish size, swimming behaviour (tilt angle), physiological state (maturity state and condition factor), time of day and also distance to the echsounder (MacLennan and Simmonds 1992; Røstad 2006; Pedersen 2007). Nonetheless differences in TS can be used to acoustically distinguish between different sized individuals and species (Axelson 2007). Additionally, when using a split beam transducer and applying differences in TS as well as additional criteria such as minimum fish track length, maximum number of missing pings, and vertical gating, individual fish tracks can be identified and information about their swimming direction, tilt angle, swimming speeds or descriptions of swimming patterns and behaviour can be obtained (Brede *et al.*1990; Huse and Ona 1996; Torgersen and Kaartvedt 2001; Onsrud *et al.* 2005; Kaartvedt *et al.* 2008).

The species and size composition of acoustic observations, often referred to as acoustic targets, is verified with trawling. The interpretation of acoustic echograms is difficult without corresponding ground-truth data, i.e. information on species composition and biology of individuals (size, weight and maturity stage). Trawling speed, gear selectivity and avoidance, and that trawls also catch fish during setting and hauling will influence the catch composition, and thereby the interpretation of echograms. In the absence of concurrent catch historical catch data may be helpful in assessing acoustic targets should these have characteristic features, behaviour and TS.

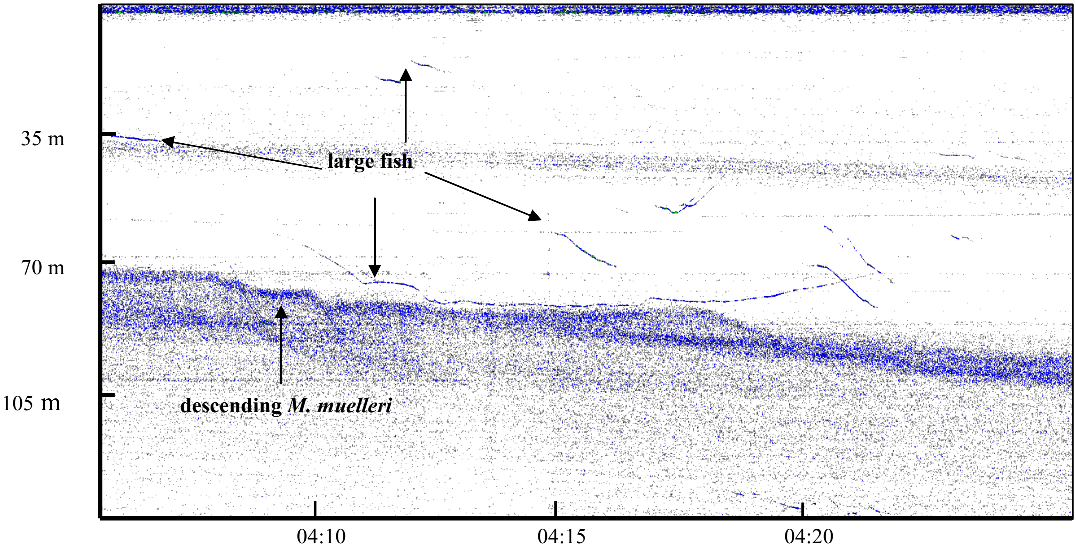


Figure 3: *Echogram from a 38 kHZ splitbeam echosounder placed on the bottom showing migrating M. muelleri and several large fish tracks with a Ts between -30 and -35dB dB in Masfjorden. The distance of these acoustic targets from the echosounder is between 250 and 390 m.*

AIMS AND OBJECTIVES

Previous studies in Masfjorden have focused primarily on the vertical distribution of *M. muelleri* SLs and other mesopelagic species, but were only based on a limited number of days and during certain months and thus without any knowledge from the long intermittent periods. The primary objective of this study was therefore to investigate how the timing and extension of diel vertical migration patterns of individual fish and of the SLs changes throughout the year by collecting continuously recorded acoustic data. The objectives of Paper 1 were to investigate the feasibility of using a stationary acoustic platform to describe fish behaviour in Masfjorden, and in the context of this thesis to distinguish the acoustic records displaying the behaviour of *B. glaciale* from those of *M. muelleri*. In Paper 2 acoustic recordings covering 15 successive months were used to investigate behavioural responses of *M. muelleri* on a weekly, monthly, seasonal and annual basis. By combining acoustic data and corresponding environmental data seasonal behavioural responses may be explained. Since light strongly influences SL DVM behaviour the objective of Paper 3 was to investigate whether daily and seasonal changes in surface light intensity influences the vertical depth distribution of *M. muelleri.* Predator-prey interaction studies can aid in testing the predator avoidance hypothesis and whether the behaviour of certain prey, in this case *M. muelleri*, thus result from changes in predator distribution (Paper 4).

MATERIALS AND METHODS

The recent advances in the development of stationary, vessel independent echosounder rigs have opened up new possibilities to study fish behaviour and ecological processes (**Paper 1-4**). The deployment of a stationary acoustic platform in Masfjorden enabled us to collect continuous acoustic data over a 15 month period. This data forms the basis of all four papers presented in this thesis.

An acoustic study covering a time period of 15 months inherently suffers from temporally irregular sampled ground-truth data, i.e. trawl catch data, due to the limited availability and costs of ships time. In Masfjorden the species composition of SLs above approximately 200 m is with all likelihood homogenous throughout the year and is dominated by *M. muelleri* (**Paper 2**), while separate SLs contain different ontogenetic stages of *M. muelleri* (Giske *et al.* 1990; Balino and Aksnes 1993; **Paper 2**). Although the mesopelagic species composition is less homogenous below 200 m the less dense acoustic targets are none the less mainly assigned to *B. glaciale* (**Paper 1**). While in previous studies ordinary pelagic trawls, which could not be closed, were used to assess the species composition of SLs and deeper acoustic targets, a multisampler system with three separate cod-ends (Engås *et al.* 1997) was used during two field campaigns in this study. The advantage of this system compared to ordinary trawls is that much cleaner samples (catches) from specific depths can be obtained. An opening and closing mechanism of the cod-ends, which is acoustically controlled, prevents undesirable sampling during the setting and heaving of the trawl. In Masfjorden trawling > 200m depth was carried out to assess the species composition and to collect biological information. Data on fish length, weight, sex, stomach contents, and gonad maturity stage can aid in drawing conclusions about behavioural patterns which cannot be explained in terms of changes in surface light or predator distribution alone (**Paper 1 and 2**).

The vertical distribution and temporal variation of large fish in Masfjorden is less well studied (Salvanes 1991). We applied automated and manual target tracking (TT) to detect individual large predator-like fish (**Paper 1 and 4**; Balk and Lindem 2008). The analysis software assigns several consecutive echoes, which satisfy preset track criteria, to the same target. TS is related to the size of the insonified fish (MacLennan and Simmonds 1992), and tracks from large predator-like fish could thus be differentiated from the smaller *M. muelleri* and other mesopelagic nekton by applying a TS threshold of -45 dB (**Paper 4**) and of -50 db (**Paper 1**). Only tracks with a minimum of 15 (**Paper 4**) and 25 (**Paper 1**) consecutive pings, allowing a maximum of 5 missing pings, and a gating of 0.8 m were accepted (**Paper 4**). While automated TT is more objective than manual TT it may include tracks which are not from individual fish, but rather from multiple targets or a random string of pings, introducing an error when using counts of fish tracks to determine their vertical distribution (**Paper 4**). Additionally, consecutive tracks may result from a single fish, thereby overestimating the number of tracks within an analysed depth bin. However, the introduced errors are consistent throughout the analysis and should therefore not bias counts of fish from a particular time period or depth range. The number of tracks detected will also be influenced by the distance (range) form the echosounder, as the acoustic beam gets wider with increasing range and the likelihood of a fish swimming into a wider beam at the surface (long range) thus being much greater than close to the transducer (short range). Counting of targets was therefore restricted to the upper 150 m (**Paper 4**).

M. muelleri scattering layers (SLs) are composed of similar sized fish that apparently behave in unison and thus occupy a similar depth range (**Paper 1 – 3**), although different behaviours were also observed (**Paper 2**). Acoustically SLs can be detected because they produce much stronger backscatter, i.e. the averaged sum of energy reflected by individuals in a SL is much stronger than from their surrounding. The backscattered energy can be quantified as the volume backscattered strength (Sv) expressed in decibels (dB). With decreasing fish density the Sv of the SL gets weaker, especially towards the fringes, making it more difficult to determine the precise depth of the upper and lower edges. To determine the depth of the upper SL edge we applied a Sv threshold of -75 dB (**Paper 3**), which relates to an approximate fish density of 0.04 per m^{-3}, assuming a TS of -59 dB. In comparison, the densest part of SLs had densities closer to 1 fish per m^{3}. The depth estimates obtained at a -75 db threshold fitted the upper SL edge visible on a -80 dB echogram well, adding confidence that with this method depth even small depth changes of the SL edge could be detected (**Paper 4**; Figure 5).

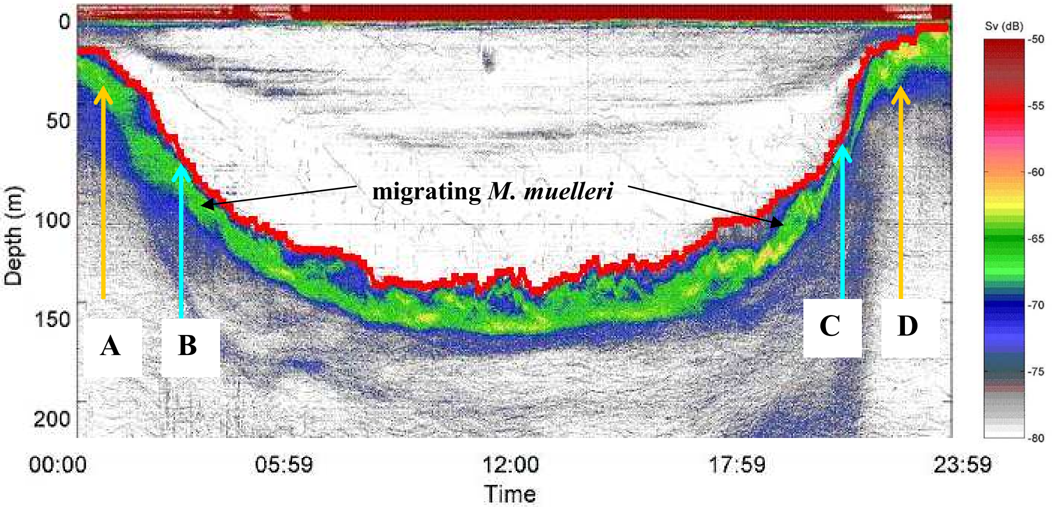


Figure 4: *Estimated depth of the upper edge of a M. muelleri scattering layer (red line) fitted on an echogram (10th July 2008) showing the M. muelleri scattering layer at a Sv threshold of -80 dB. a) start civil twilight, b) sunrise, c) sunset, d) end civil twilight.*

ABSTRACTS OF PAPERS

Paper 1: We deployed an upward-facing echo sounder mounted on the bottom and cabled to shore in a ~400 m fjord location for long-term studies of small mesopelagic fish and their potential predators. The population of the myctophid *Benthosema glaciale* displayed diverse diel vertical migration (DVM) behaviours, including normal DVM to surface waters at night, reverse DVM in the lower part of the water column in which fish ascended to ~200 m at day, as well as nonmigration of some individuals. The relative prevalence of these behavioural modes varied with season. Acoustic target tracking of individuals in deep water showed that *B. glaciale* was conspicuously inactive and drifted back and forth with weak tidal currents, essentially acting as plankton. Swimming was largely restricted to infrequent short bouts. More active swimming occasionally occurred in the vertical direction, and then in a stepwise pattern. Potential predators in deep water were swimming at speeds of <0.5 body length s^{-1}, with maximum speeds of ~1 body length s^{-1}. These results show that submerged echo sounders provide a means of non-intrusively studying both individual and population behaviour of deep-living organisms.

Paper 2: We studied the temporal dynamics of the vertical distribution of *Maurolicus muelleri* Scattering Layers (SL) by examining acoustic recordings from a stationary echosounder over a 15 month period (July 2007 – October 2008) in Masfjorden, Norway, complemented by intermittent sampling campaigns. Several novel behaviours were identified. The basic migration pattern of a shallow SL consisting of juvenile fish comprised ascent in the evening, "midnight" sinking shortly after dusk, ascent at dawn with subsequent descent to their daytime depth. However, fish in this layer displayed 'arrested migrations' during its dusk ascent in the period January to March 2008. Instead of completing a full migration to the surface, groups of fish interrupted their ascent at random intervals, returning to deeper waters. The midnight sinking individuals reached progressively deeper depths between dusk and dawn in the course of autumn and early winter. Adult fish constituting a deeper SL carried out normal diel vertical migrations (DVM) in summer, but modified their migration pattern conspicuously during the first autumn of the studies. Most individuals then suspended their migration in the evening, yet ascended toward the surface in the latter part of the night to reach upper layers during dawn, before returning to their daytime depth. This pattern was not observed during the second fall of the studies. Adult *M. muelleri* suspended the nocturnal ascent completely by mid-end November. During the subsequent period a fraction of adult *M. muelleri* performed limited reverse migrations, leaving the main SL and slightly shifting their vertical distribution upwards during the first part of the day. The width of the deep SL was narrowest during summer months June – August, and was broader with a deeper lower border during the period September – May. Our study suggests a range of adaptive, flexible behaviours of *M. muelleri*, which we explain as a result of ontogeny, state (satiation and hunger), and seasonality in light levels and changes in predation risk.

Paper 3: Previous one day studies of the mesopelagic fish *Maurolicus muelleri* suggest that their vertical distribution changes as if they were following a constant light intensity, sometimes denoted isolume. Here we investigate whether such behaviour is consistent under varying light conditions and over an extended time period. We analyse acoustical observations of ontogenetically varying Scattering Layers (SL) versus surface irradiance from selected days during a 9 month period (January – September 2008). Our results suggest that the SLs of *M. muelleri* have a restricted range of preferred light intensities rather than a very precise isolume. This tendency was found regardless of season and migration phase, i.e. during dawn descent, dusk ascent, and daytime. The light intensity estimated at the top of the upper SL for consecutive days, regardless of migration phase, varied on average by less than 1 order of magnitude, while the average monthly estimates for the descent, ascent and daytime periods varied from 0.004 – 0.39 $\mu E \cdot m^{-2} \cdot s^{-1}$, 0.08 – 2.35 $\mu E \cdot m^{-2} \cdot s^{-1}$and 0.02 – 0.68 $\mu E \cdot m^{-2} \cdot s^{-1}$ respectively. During their ascent fish experienced up to 9 times higher light intensities than during the descent, which might be explained in terms of different physiological states (e.g. hunger level). Our study suggests that the vertical migration of *M. muelleri* emerges as a result of a vertical habitat selection that can be characterized by the preference of a restricted range of light intensities and that these intensities might be state (e.g. hunger related) and age dependent.

Paper 4: The diel vertical migration behaviour (DVM) of pearlside (*Maurolicus muelleri*) Scattering Layers (SL) has been hypothesized to be caused by a response to predation risk, yet this has not been investigated. Here we present acoustic data on both pearlside and their potential predators from 224 days (over a 14 month period) registered with an upward facing split-beam transducer in Masfjorden, Norway. These data were complemented with catch data from a field campaign and landing statistics of gadoids from the region. We applied acoustic target tracking to study the diel vertical distribution of individual large fish (TS < -45 dB), and concurrently explore the behaviour of pearlside SLs. In autumn and winter echo counts of large fish at night time were high in the upper 30 m, and at day time low throughout the upper 70 - 100 m but higher between the deep and shallow pearlside SLs. In the same period juvenile *M. muelleri* avoided shallow distributed predators at night by performing midnight sinking shortly after dusk, while adult fish suspended DVM entirely. Juvenile *M. Muelleri*, after a predawn rise to the surface, descended to day time depths at dawn despite the near absence of large fish, suggesting a genetically fixed predator evasion behaviour. In spring and summer large fish occurred largely in the upper 120 m at day and night time, however with fewer night time observations in the upper 30 m than in autumn and winter. Midnight-sinking of *M. muelleri* was absent from the end of spring throughout summer, suggesting sufficient light levels for feeding in the anti-predation window. *M. muelleri* SLs displayed crepuscular DVM, and as large fish stayed deeper at day time towards the end of summer, the depth range of the deepest *M. muelleri* SL increased towards end of summer. The study suggests that different ontogenetic stages of *M. muelleri* are subjected to seasonally and dielly varying predation pressure.

RESULTS AND DISCUSSION

M. muelleri is a visually foraging planktivore and its feeding behaviour should thus be influenced by light intensity (Batty *et al.* 1990; Eiane *et al.* 1999; Ryer and Olla 1999; Meager *et al.* 2010). However, the ability to stay undetected from visually hunting predators while foraging in an environment without shelter is also a function of light, and decreases with increasing light intensity (Rosland and Giske 1994; Thetmeyer and Kils 1995; Johnsen and Sosik 2003). Thus, living in a fluctuating light environment fish are likely to strive to maximize the trade off between foraging success and predation risk, which could theoretically be achieved by seeking a constant light environment.

The results in this thesis suggest that *M. muelleri* do follow a preferred light range, which may span one to two orders of magnitude in the vertical extent of the SL. Different ontogenetic stages, i.e. SLs, seem to follow different light ranges, while the intensity of the preferred light range during the ascent could be slightly higher than during the descent. The vertical migrations at dusk and dawn of especially younger fish take place in the absence of predator-like fish, suggesting a genetically fixed response initiated by changes in light intensity. In contrast we believe that juvenile fish migrate to deeper waters at night (midnight sinking) after they have been at the surface in order to avoid shallow distributed piscivores (large predator-like fish). Our results also suggest that light and predation risk do not seem to be the only factors affecting the vertical distribution and habitat selection of *M. muelleri*. Arrested ascent migrations as well as early morning ascents of adult fish either occur in the absence of light or do not seem to be governed by changes in absolute light intensity. These observations suggest that other possibly internal factors like hunger and satiation also influence individual depth. Overwintering adult fish do not migrate to the surface, and during the same period display only a limited vertical response to changes in surface light intensity. Since adults start spawning shortly after their overwintering period, it is probable that by overwintering they trade off higher foraging rates against reproductive success in the upcoming spawning season.

WHY DO FISH UNDERTAKE DIEL VERTICAL MIGRATION (DVM)?

Vertically migrating fish are likely to experience steep gradients in light, temperature, salinity and oxygen, as well as changes in the distribution of prey and predators (Neilson and Perry

1990; **Paper 1-4**), and many hypotheses have been presented for the organisms's motivation perform DVM. The energetic efficiency hypothesis predicts that fish distribute at a temperature that stimulates digestion and minimizes energetic costs (Wurtsbaugh and Neverman 1988; Bevelhimer and Adams 1993). Migrating planktivores have been observed to stay at the thermocline (Levy 1990b) as well as the temperature maximum at night (Giske *et al.* 1990), in addition fish may have seasonal temperature preferences (Mehner *et al*. 2007). The findings in this thesis suggest that different ontogenetic *M. muelleri* stages generally did not distribute at a specific temperature range or the thermocline during the two sampling campaigns (**Paper 2**). However, due to the restricted coverage of the environmental sampling during this study, the effect temperature may have, especially on the night time distribution of juvenile *M. muelleri* during winter (e.g. Giske *et al.* 1990), cannot be dismissed. The environment below 80 – 90 m appears to be thermodynamically stable regardless of season, with temperatures between 7 – 8 ^{0}C (Bjelland 1995; Bagøien *et al.* 2001). It therefore seems unlikely that the overwintering depth of adult *M. muelleri* is due to a temperature preference.

Novel behaviours – early morning ascent, reverse DVM and arrested migrations

Several behaviours described in this study take place either in apparently complete absence of light, such as early morning ascents and midnight sinking (discussed in more detail in the predator-prey section), do not appear to be strictly governed by changes in light intensity, such as arrested migrations (**Paper 2**). Reverse diel migrations involve a shift from a darker to a lighter environment, and changes in light thus appear to influence this behaviour (**Paper 1 and 2**), although in *M. muelleri* this behaviour did not strictly correspond with either sunrise (ascent) or sunset (descent). *B. glaciale* displayed reverse DVM in August and November, with a proportion of fish ascending to approximately 200 m in the morning and descending after sunset (**Paper 1**). This behaviour takes both migrating species into in a lighter environment, and is thus explained by visual feeding on plankton distributed in midwater, including seasonally migrating plankton (*Calanus*; Bagøien et al. 2001), as well as organisms such as krill performing normal DVM.

In the period September through October adult *M. muelleri* displayed early morning ascents in one of the two years with studies during fall, while from November through January a proportion of adult fish performed reverse DVM at daytime. In the first period most fish migrated to the surface after midnight and descended to daytime depths shortly before the start of civil twilight. Only a few fish ascended to the surface at dusk, so that the majority of adults remained at daytime depth after the end of civil twilight (**Paper 2**). In the second period some *M. muelleri* migrated upwards before noon, clearly separating from the lower SL, before merging again with the deeper fish. Such behaviours may be related to the hunger/satiation state of the fish (Pearre 2003) or the condition of individuals. The hunger/satiation hypothesis states that individuals regulate their vertical depth as a result of hunger or as a result of satiation and the need to digest (Pearre 2003). Adult fish build up energy reserves (lipids) in spring and summer (Falk-Petersen *et al.* 1986; Prosch 1991) before commencing their overwintering period, which may persist for five to six months, below 125 m depth (**Paper 2**). At this depth feeding on overwintering *Calanus* is probably light limited, yet adult *M. muelleri* to some extent feed on these copepods at day (Bagøien et al. 2001). Hunger may set in after feeding seizes at dusk and ingested prey is digested during the course of night time. Hunger in the morning might motivate for foraging on near-surface prey during the dawn period as long as prey are reasonably abundant in upper waters, i.e. this mechanism may explain the morning ascent. In order to survive the long overwintering period, fish need to have sufficient lipid reserves and be in good condition. Fish in poor condition may adapt their behaviour and seek and exploit opportunities to improve their fitness and thus likelihood of survival. Such state-dependent behaviours may explain the reverse diel migrations, only carried out by a fraction of the population. This behaviour might increase the exposure to predators, and higher numbers of large predator-like fish were observed between the reverse migrating layer and the deeper *M. muelleri* SL in some months (December and January; **Paper 4**).

An inverse migration was also observed by part of the population of the deeper living *B. glaciale* (Paper 1). This species is likely adapted to foraging at lower light levels than *M. muelleri*, and as for *M. muelleri* we ascribe this behaviour to foraging on mid-water overwintering copepods at day (**Paper 1;** Dypvik 2010**).**

With regard to the adaptive value of DVM for the migrating organism several hypotheses have been suggested, one of which is the foraging opportunity hypothesis (Levy 1990a). This hypothesis assumes that fish follow their prey to increase feeding and subsequently improve their fitness (Janssen and Brandt 1980; Levy 1990a). As seasonally migrating zooplankton terminate their dormancy at depth at the middle of winter, beginning of spring (Visser and Jónasdóttir 1999), their ascent towards the surface may influence the vertical migration behaviour of shallower juvenile fish. Between January and March juveniles *M. muelleri* arrested their ascent migrations (**Paper 2**). Previous studies have suggested that organisms arrest their ascent to the surface to avoid shallow distributed predators (Onsrud and Kaartvedt 1998) or unfavourably bright surface waters (Kaartvedt *et al.* 1998). It is more likely that juvenile *M. muelleri* displayed such behaviour as a result of satiation, after having fed on the seasonally ascending copepods. Typically arrested migrations occurred at random depths and intensities, suggesting varying degrees of feeding efficiency of groups of fish. Kaartvedt et al. (2009) observed sprat leaving the migration after a short time during the dusk ascents and suggested that arrested migrations may extend the feeding period of sprat in the anti-predation window (Clark & Levy 1988) while foraging on mid-water *Calanus*.

Light as a governing and initiating factor of DVM

It is generally accepted that light influences and acts as a cue for DVM, with either relative or absolute changes in light intensity influencing the behaviour and distribution of migrating organisms (Neilson and Perry 1990; Hays 2003; Cohen and Forward 2009; Paper **1 and 3**). The northern krill (*Meganyctiphanes norvegica*) for example arrives at and departs from the surface approximately 30 min after sunset and before sunrise respectively, regardless of season (Tarling 2003). Changes in light intensity also influenced the behaviour of *B. glaciale* as it ascended to midwater at sunrise and descended at sunset (**Paper 1**). As is apparent from Figure 4 and 5, the descents and ascents of *M. muelleri* SLs correspond largely with the start and end of civil twilight (when the sun is 6^0 below the horizon), which is seasonally consistent (Figure 5). Preliminary investigations indicate that the light level when *M. muelleri* were at the surface before the descent at dawn ranged between 0.002 – 0.05 $\mu E \cdot m^{-2} \cdot s^{-1}$ (average 0.023 $\mu E \cdot m^{-2} \cdot s^{-1}$), while it ranged between 0.002 and 0.3 $\mu E \cdot m^{-2} \cdot s^{-1}$ (average 0.076 $\mu E \cdot m^{-2} \cdot s^{-1}$) at the surface arrival during dusk. Such surface light measurements are expected to vary with weather and also the ontogeny of the *M. muelleri* SL studied, since younger fish seemingly stay at the surface longer than older fish. It is also clear that neither sunrise nor sunset seem to govern the exact timing of migrations as both occur while the migrations are in progress, i.e. the start of descent from the surface does not occur at sunrise, while the ascent from deep waters does not match the time of sunset (Figure 4). However, the effect daily and seasonal variation in surface irradiance may have on the vertical depth distribution of *M. muelleri* is not clear, and was the main objective of **Paper 3**.

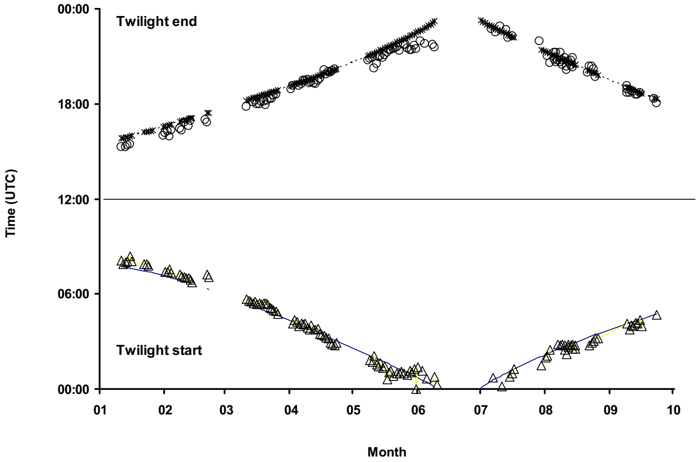


Figure 5: *The arrival at (upper panel) and departure from (lower panel) of M. muelleri at the surface (5 m depth) at civil twilight end and civil twilight start respectively. Lines indicate the timing of end and start of civil twilight, while symbols indicate the timing of M. muelleri.*

Light intensity decreases with increasing depth. Season, time of day and weather can influence the intensity of downwelling light below the sea surface (McFarland 1986), but also shading from organisms staying shallower may reduce light levels entering deeper waters. Surface light irradiance is up to ten times higher during summer months compared to winter months (Giske *et al.* 1990; Rasmussen and Giske 1994; **Paper 3**), while sudden cloud cover can cause substantial decreases in light intensity (McFarland 1986; Baliño and Aksnes 1993). Light intensity decreases with increasing depth due to seasonally varying scattering and absorbance (Kirk 1994; Frette *et al.* 2004). During spring and summer months scattering and absorbance tend to be higher than in autumn and winter (Frette *et al.* 2004), as a result of increased phytoplankton production and freshwater runoff into the fjord, which may reduce the high surface irradiance such that light intensity at depth is similar as during the darker winter months. Typically the spectral distribution of light tends to become narrower with increasing depth and also at dusk and dawn periods (McFarland 1986; Kirk 1994).

Several studies indicate that vertically migrating fish change their depth by following a preferred light level (Eggers 1978; Baliño and Aksnes 1993; Appenzeller and Leggett (1995); **Paper 3**). Rainbow smelt descending from surface waters at dawn stayed below a specific isolume as day light increased (Appenzeller and Leggett 1995) while a mesopelagic krill followed the decreasing depth of an isolume during its ascent (Widder and Frank 2001). In contrast the large majority of studies on zooplankton suggest that these organisms orientate according to relative changes in downwelling light (Cohen and Forward 2009).

We correlated daily upper SL depth and surface irradiance, hypothesising that a linear relationship would be indicative of fish following an isolume, i.e. preferred or optimal light level. For the majority of linear regressions more than 90% of variation in SL depth could be explained by changes in surface light irradiance (**Paper 3**). Applying a similar methodological approach in a study of trout smelt Appenzeller and Leggett (1995) obtained coefficients of determination of 0.78 – 0.83. In my study high coefficients of determination ($R^2 > 0.9$) were observed regardless of month, suggesting that the behavioural response of *M. muelleri* to changes in surface light intensity was consistent over time and probably independent of age. Light level estimates from consecutive days, regardless of migration phase, varied on average by less than 1 order of magnitude, while the average monthly light intensity estimates for the descent, ascent and daytime periods varied from 0.004 – 0.39 $\mu E \cdot m^{-2} \cdot s^{-1}$, 0.08 – 2.35 $\mu E \cdot m^{-2} \cdot s^{-1}$and 0.02 – 0.68 $\mu E \cdot m^{-2} \cdot s^{-1}$ respectively. *M. muelleri* thus did not seem to follow a constant light level throughout its daily migration, and they preferred different light levels during the descent and ascent periods (**Paper 3**). During the upward migration at dusk fish followed an average 9 times higher light level than when they descend at dawn. The higher light level may indicate that the ascending fish are hungry and thus take greater risks than descending, satiated fish. Monthly estimates of the preferred light level varied, suggesting that the age and state of fish may influence the light level fish choose to follow. Young developmental stages are more transparent than larger fish, which have numerous photophores and silver sides (Figure 2). Silvering and counter-illumination may be more efficient in making larger *M. muelleri* less conspicuous in a deeper homogenous (vertically symmetric) light environment, while transparency can be advantageous in a shallower pelagic habitat (Warrant and Locket 2004). Differences in preferred light level thus probably also reflect the ontogenetic (developmental) stage. By selecting a light environment that may also be affected by the state and ontogeny of the fish, migrating *M muelleri* may experience a constant ‘anti-predation window, thereby optimizing the balance between visual foraging and minimizing predation risk (Clark and Levy 1988)

Piscivore-planktivore interaction

Schooling *M. muelleri* have been observed under high surface light intensities on bright summer nights (Kaartvedt *et al.* 1998). This is considered an anti-predation behaviour (Pitcher 1993). *M. muelleri* does not possess any skeletal or morphological defences such as spines or amour, structures which in other fish species aid in preventing capture in the event of a predator attack (Figure 2; Fuiman and Magurran 1994; Wootton 1999). Large priscivores are likely to have a larger reaction distance than *M. muelleri* (Wootton 1999), and one may thus assume that once a potential predator encounters and detects an individual *M. muelleri*, the probability of it escaping would be low. For *M. muelleri* minimizing predator encounters would thus be beneficial. In a shelterless pelagic environment, with transparency, silvering and counter illumination as its primary predator defences (Figure 2; Wootton 1999), *M. muelleri* can reduce predation risk by migrating to larger depths at day as well as night time (midnight sinking) and thereby avoid shallow distributed predators (**Paper 2 and 4**).

Studies that have investigated DVM within a predator-prey context were done at the planktivore-plankton level, and suggest that DVM in zooplankton is the result of predator avoidance by seeking shelter in darker daytime depths (Hays 2003; Cohen and Forward 2009). Zooplankton DVM behaviour can furthermore be modified and amplified in the presence of planktivorous fish or fish kairomones (Hays 2003). A number of studies have also related DVM of planktivores to avoidance of larger predatory fish (Eggers 1978; Clark & Levy 1988; Scheuerell & Schindler 2003; Hrabik et al. 2006; Mehner *et al.* 2007).

We studied the vertical and temporal (24 hours) distribution of large predator-like fish, i.e. potential predators of *M. muelleri*, (TS > -45 dB) by obtaining monthly averages of occurrence for every 10 m depth and 1 hour time bin (**Paper 4**). Saithe (*Pollachius virens*), blue whiting (*Micromesistius poutassou*), haddock (*Melanogrammus aeglefinus*), pollack (*Pollachius pollachius*) and mackerel (*Scomber scombrus*) are the main predators of *M. muelleri* (Giske *et al.* 1990; Rasmussen and Giske 1994; Bjelland 1995; Kaartvedt *et al.* 1998; Paper 3).

According to the predator avoidance hypothesis *M. muelleri* would be expected to perform DVM only when a real predation risk by shallow distributed piscivores existed. This was however not the case in some months of the analysed period (July 2007 to September 2008; Paper 3). In the period October 2007 to March 2008 relatively few large fish were distributed above the shallowest *M. muelleri* SL, composed most probably of juvenile fish (**Paper 4**). Still juvenile *M. muelleri* performed DVM even in the absence of shallow distributed predators, suggesting that the presence of predators is not a requirement for DVM to be initiated. Ringelberg and Van Gool (1995) observed a similar reaction in *Daphnia* in the absence of kairomones, and suggested that such behaviour may be genetically fixed. Similarly Mehmer *et al.* (2007) proposed that the seasonal stability of DVM in coregonid fish, also in the absence of pelagic predators, indicated a genetically fixed behaviour.

Fischer (2004) suggested that such behaviour may occur in anticipation of rather than the observed predation risk itself. This may also apply here, since the results in **Paper 4** show that the majority of large predator-like fish had left the upper 30-50 m before juvenile *M. muelleri* had started their descent without a perceivable predation threat. Although juveniles could continue feeding in the shallow food rich layer during day time, reducing predation risk is traded off against potential foraging opportunities.

Midnight sinking, downward migration after visiting surface layers at dusk, of juvenile *M muelleri* SLs was most apparent between October and March (**Paper 4**). This is a common behaviour in *M. muelleri* (Giske et al.1990; Balino & Aksnes 1993; Torgersen *et al.* 1997), and has also been observed in different other zooplankton species (Tarling *et al.* 2002; Pearre 2003). Pearre (2003) proposed that satiation may function as a signal for midnight-sinking in individual zooplankton. Juvenile *M. muelleri* can ingest up to 80 copepods at dusk, suggesting a high degree of satiation (Srisomwong 2009). However, feeding efficiency in terms of ingested copepods varied (Srisomwong 2009), and in most months midnight sinking occurred mostly as a structured and well defined layer, suggesting limited variation in individual feeding efficiency or fullness of stomachs. Satiation may thus act as a mediator synchronised by light changes as well as a confounding factor in midnight sinking. By descending simultaneously with satiated conspecifics hungry individuals may benefit from a reduced predation risk while forsaking feeding.

Tarling *et al.* (2002) observed *Calanus finmarchicus* displaying midnight sinking, and suggested that this behaviour was a response to the arrival of krill at the surface layer, a predator of the copepod. After dusk descents were particularly apparent during the darker winter months (October to March) and corresponded with high average counts of large fish in the upper 50 m (**Paper 4**). Ryer and Olla (1999) showed that the gadoid walleye pollock (*Theragra chalcogramma*) successfully foraged at very low light levels ($5 \times 10^{-7}\ \mu\text{mol m}^{-2}\ \text{s}^{-1}$), while Hunter (1968) found that jack mackerel were able to forage on artemia down to a light level of approximately 1 x 10 $^{-5}$ µ mol m^{-2} s^{-1}. Light measurements suggest that juvenile *M. muelleri* on selected days (n = 9) in the first three months in 2008 arrived at the surface at dawn when surface irradiance (PAR) was < 2 x 10 $^{-3}$ µ mol m $^{-2}$ s $^{-1}$ and descended at dusk when surface irradiance was < 4 x 10 $^{-3}$ µ mol m $^{-2}$ s $^{-1}$. Prevailing light levels could thus facilitate visual foraging by piscivores on *M. muelleri* at the surface well before and after the dawn and dusk periods respectively. During this period the reduction in light intensity after dusk feeding may also function as a cue for *M. muelleri* to descend, while the ultimate response is likely to be predator avoidance (**Paper 4**).

Concluding Remarks

Studying fish behaviour in their native environment can be challenging, with costs and time often limiting the amount of data that can be collected. There are several advantageous with having a stationary transducer setup such as ours compared to using vessel mounted echosounders when studying fish behaviour. The running costs of such a system are much lower, while data can be collected non-intrusively and independently of weather conditions and continuously over much longer time periods with relatively limited work effort. This study has shown that this observational tool is suitable in describing the distribution and behaviour of individual fish (**Paper 1**), as well as short term and long term dynamics of SLs (**Paper 2**) with regard to changing light levels and predator distribution (**Paper 3 and 4**). This could beneficially be applied to other migrating species as well.

As with most acoustic studies, our study would have benefited from a more rigorous biological and environmental data collection campaign. Without comparisons with field observations, vital ground-truth data, acoustic interpretations of behavioural observations can become speculative. Due to the difficulty in securing ships time as well as the costs involved with research surveys, we collected data on only two field campaigns that overlapped with the observation period. For future studies it is recommended that biological and environmental data is collected at even time intervals to obtain a better temporal coverage.

Our results supplement and support the current understanding of *M. muelleri*, but likewise raise additional questions. The described behavioural patterns are complex and possibly involve mechanisms which need to be further investigated, such as the importance of state, i.e. satiation, hunger and maturity, as well as ontogeny. Also, how counter illumination functions during DVM is poorly understood. Scattering layers are aggregations of individuals, and our understanding of the benefits of migrating as a layer is also not clear.

REFERENCES

Aksnes, D.L., Aure, J., Kaartvedt, S., Magnesen, T., and Richard, J. (1989) Significance of advection for the carrying capacities of fjord populations. *Marine Ecology Progress Series* **50**: 263-274

Appenzeller, D.R., Heggett, W.C. (1995) An evaluation of light mediated vertical migration of fish based on hydroacoustic analysis of the diel vertical movements of rainbow smelt *Osmerus mordax*. *Canadian Journal of Fisheries and Aquatic Science* **52**:504-511

Asplin, L., Salvanes, A.G.V., and Kristoffersen, J.B. (1999) Nonlocal wind-driven fjord-coast advection and its potential effect on plankton and fish recruitment. *Fisheries Oceanography* **8**:255-263

Axelson, B.E. (2007) Acoustic identification and abundance estimation of horse mackerel, jellyfish and mesozooplankton in the Benguela Ecosystem". *PhD. thesis*, University of Bergen, 40 pages

Axenrot, T., Didrikas, T., Danielsson, C., and Hansson S (2004) Diel patterns in pelagic fish behaviour and distribution observed from a stationary, bottom-mounted, and upward-facing transducer. *ICES Journal of Marine Science* **61**:1100-1104

Bagøien, E., Kaartvedt, S., Aksnes, D.L., and Eiane, K. (2001) Vertical distribution and mortality of overwintering *Calanus*. *Limnology and Oceanography* **46:**1494-1510

Baliño, B.M. and Aksnes, D.L. (1993) Winter distribution and migration of the sound scattering layers, zooplankton and micronekton in Masfjorden, western Norway. *Marine Ecology Progress Series* **102:**35-50

Balk, H., and Lindem, T. (2008) Sonar4 and Sonar5-Pro post processing systems. Operator manual. Lindem Data Acquisition,Oslo

Batty, R.S., Blaxter, J.H.S., and Richard, J.M. (1990) Light intensity and the feeding behaviour of herring. *Marine Biology* **107**:383-388

Bevelhimer, M.S., and Adams, S.M. (1993) A bioenergetics analysis of diel vertical migration by Kokanee salmon, *Oncorhynchus nerka*. *Canadian Journal of Fisheries and Aquatic Science* **50**:2336-2349

Benoit-Bird, K.J., and Au, W.W.L. (2004) Diel migration dynamics of an island associated sound-scattering layer. *Deep Sea Research (Part I)* **51**:707-719

Benoit-Bird, K.J., and Au, W.W.L. (2006) Extreme diel horizontal migrations by a tropical nearshore resident micronekton community. *Marine Ecology Progress Series* **319**:1-14

Benoit-Bird, K.J., Au, W.W.L., and Wisdom, D.W. (2009) Nocturnal light and lunar cycle effects on diel migration of micronekton. Limnology and Oceanography **54**: 1789-1800

Bjelland, O. (1995) Life-history tactics of two fjordic populations of Maurolicus muelleri. *Cand. Scient. thesis*, University of Bergen, 79 pages

Boehlert, G.W., Wilson, C.D., and Mizuno, K. (1994) Populations of the sternoptychid fish *Maurolicus muelleri* on seamounts in the central north Pacific. *Pacific Science* **48**:57-69

Bohl, E. (1980) Diel pattern of pelagic distribution and feeding in planktivorous fish. *Oecologia* **44**: 368-375

Brede, R., Kristensen, F.H., Solli, H., and Ona, E. (1990) Target tracking with a split-beam echo sounder. *Rapports et Proces-verbaux des Reunions – Conseil International pour l'Explorations de la Mer* **189**:254–263

Clark, C.W., and Levy, D.A. (1988) Diel vertical migrations by juvenile sockeye salmon and the antipredation window. *American Naturalist* **131**:271-290

Clarke, T.A. (1982) Distribution, growth, and reproduction of the lightfish *Maurolicus muelleri* (Sternoptychidae) off south-east Australia. *CSIRO Marine Laboratories Report* No. 145, 11 pp

Coetzee, J., Krakstad, J.-O., and Stenevik, E.K. (2006) Acoustic survey of the mesopelagic resources of the Benguela region. *BENEFIT Surveys* RWG 2006-05, 66 pp.

Cohen, J.H., and Forward, R.B. (2009) Zooplankton diel vertical migration — a review of proximate control. *Oceanography and Marine Biology* **47**:77-110

David, J.H.M. (1987) Diet of the South African fur seal (1974-1985) and an assessment of competition with fisheries in southern Africa. *South African Journal of Marine Science* **5**:693-713

Didrikas, T., and Hansson, S. (2009) Effects of light intensity on activity and pelagic dispersion of fish: studies with a seabed-mounted echosounder. *ICES Journal of Marine Science* **66**:388–395

Dupont, N., Klevjer, T.A., Kaartvedt, S., and Aksnes, D.L. (2009) Diel vertical migration of the deep-water jellyfish *Periphylla periphylla* simulated as individual responses to absolute light intensity. *Limnology and Oceanography* **54**:1765–1775

Dypvik, E. (2010) Invers døgnvandring og fødebiologi hos nordlig lysprikkfisk (*Benthosema glaciale*) i Masfjorden. *Master thesis*, University of Oslo, 69 pages

Ebert, D.A., Compagno, L.J.V., and Cowley, P.D. (1992) A preliminary investigation of the feeding ecology of squaloid sharks off the west coast of southern Africa. *South African Journal of Marine Science* **12**:601-609

Eggers, D.M. (1978) Limnetic feeding behavior of juvenile sockeye salmon in lake Washington and predator avoidance. *Limnology and Oceanography* **23**:1114-1125

Eiane, K., Aksnes, D.L., Bagøien, E., and Kaartvedt, S. (1999) Fish or jellies - a question of visibility? *Limnology and Oceanography* **44**:1352-1357

Engås, A., Skeide, R., and West, C.W. (1997) The 'MultiSampler': a system for remotely opening and closing multiple codends on a sampling trawl. *Fisheries Research* **29**:295-298

Falk-Petersen, I.-B., Falk-Petersen, S., and Sargent, J.R. (1986) Nature, origin and possible roles of lipid deposits in *Maurolicus muelleri* (Gmelin) and *Benthosema glaciale* (Reinhart) from Ullsfjorden, northern Norway. *Polar Biology* **5**:535-540.

Fischer P (2004) Nocturnal foraging in the stone loach (*Barbatula barbatula*): fixed or environmentally mediated behaviour? *Journal of Freshwater Ecology* **19**:77-85

Frank, T.M., and Widder, E.A. (2002) Effects of a decrease in downwelling irradiance on the daytime vertical distribution patterns of zooplankton and micronekton. *Marine Biology* **140**:1181-1193

Frette, Ø., Erga, S.R., Hamre, B., Aure, J., and Stamnes, J.J. (2004) Seasonal variability in inherent optical properties in a western Norwegian fjord. *Sarsia* **89**:276–291

Foote, K.G., Aglen, A., and Nakken, O. (1986) Measurement of fish target strength with a split-beam echo sounder. Journal of the Acoustical Society of America **80**:612-621

Fuiman, L.A., and A.E. Magurran (1994). Development of predator defences in fishes. *Reviews in Fish Biology and Fisheries* **4**:145-183

Girsa, I.I. (1973) Alteration in the behaviour and vertical distribution of certain juvenile cyprinids in relation to illumination intensity and the presence of a predator. *Journal of Ichthyology* **13**:449-454

Giske, J., and Aksnes, D.L. (1992) Ontogeny, season and trade-offs: Vertical distribution of the mesopelagic fish *Maurolicus muelleri*. *Sarsia* **77**:253-261

Giske, J., Aksnes, D.L., Balino, B.M., Kaartvedt, S., Lie, U., Nordeide, J.T., Salvanes, A.G.V., Wakili S.M. and Aadnesen, A. (1990) Vertical distribution and trophic interactions of zooplankton and fish in Masfjorden, Norway. *Sarsia* **75:**65-81

Gjøsæter, J. (1981) Life history and ecology of *Maurolicus muelleri* (Gonostomatidae) in the Norwegain waters. *Fiskeridirektoratets Skrifter, Serie Havundersøkelser* **17**:109-131

Gjøsæter, J., and Kawaguchi, K. (1980) A review of the world resources of mesopelagic fish. *FAO Fisheries Technical Paper* 193, 151 pages

Goodson, M.S., Giske, J., and Rosland, R. (1995) Growth and ovarian development of *Maurolicus muelleri* during spring. *Marine Biology* **124**:185-195

Hamre, L.A. (1999) *Growth and mortality of Maurolicus muelleri (Gmelin): Do parasites matter? Cand Scient thesis,* University of Bergen, 87 pages

Hamukuaya, H., O'Toole, M.J. and Woodhead, P.M.J. (1998) Observations of severe hypoxia and offshore displacements of Cape Hake over the Namibian shelf in 1994. *South African Journal of Marine Science* **19,** 57-59.

Handegard, N.O., Patel, R., and Hjellvik, V. (2005) Tracking individual fish from a moving platform using a split-beam transducer. *Journal of the Acoustical Society of America* **118**: 2210-2223

Haugen, T.O. and Vøllestad, L.A. (2000) Population differences in early life-history traits in grayling. *Journal of Evolutionary Biology* **1:**897-905.

Hays, G.C. (2003) A review of the adaptive significance and ecosystem consequences of zooplankton diel vertical migrations. *Hydrobiologia* **503**:163-170

Hrabik, T., Jensen, P.P., Martell, S.J.D., Walters, C.J., and Kitchell, J.F. (2006) Diel vertical migration in the Lake Superior pelagic community. I. Changes in the vertical migration of coregonids in response to varying predation risk. *Canadian Journal of Fisheries and Aquatic Science* **63**:2286-2295

Huizinga, M., Ghalambor, C.K., and Reznick D.N. (2009) The genetic and environmental basis of adaptive differences in shoaling behaviour among populations of Trinidadian guppies, *Poecilia reticulate*. *Journal of Evolutionary Biology* **22**:860–1866

Huse, I., and Ona, E. (1996) Tilt angle distribution and swimming speed of overwintering Norwegian spring spawning herring. *ICES Journal of Marine Science* **53**:863–873

Hutchings, J. (1993) Adaptive life histories effected by age-specific survival and growth. *Ecology* **74,** 673-684.

Jackson, C.S. (1988) Diets of the white-chinned petrel and sooty shearwater in the southern Benguela region, South Africa. *Condor* **90**:20-28

Janssen, J., and Brandt, S.B. (1980). Feeding ecology and vertical migration of adult alewives (*Alosa pseudoharengus*) in Lake Michigan. *Canadian Journal of Fisheries and Aquatic Science* **37**:177-384

Johannesson, K.A., and Mitson, R.B. (1983) Fisheries acoustics: a practical manual for biomass estimation. *FAO Fisheries Technical Paper* no. **240**, 249 pages

John, H.C., and Kloppmann, M. (1989) Ontogenetic changes in the vertical distribution of larval *Maurolicus muelleri* (Gmelin, 1789). *Archiv für Fischereiwissenschaften* **39**: 79-93

John, H.C. and Kloppmann, M. (1993) The vertical distribution of eggs of *Maurolicus muelleri*. *South African Journal of Marine Science* **13,** 161-174

Johnsen, S., and Sosik, H.M. (2003) Cryptic colouration and mirrored sides as camouflage strategies in near-surface pelagic habitats: implications for foraging and predator avoidance. Limnology and Oceanography **48**:1277-1288

Kirk, J.T.O. (1994) Light and photosynthesis in aquatic ecosystems. 2nd Edition. Cambridge University Press, Cambridge

Klevjer, T.A., and Kaartvedt, S. (2003) Split-beam target tracking can be used to study the swimming behaviour of deep-living plankton in situ. Aquatic Living Resources **16**:293-298

Kramer, D.L. (1987) Dissolved oxygen and fish behaviour. *Environmental Biology of Fishes* **18,** 81-92.

Kristoffersen, J.B., and Salvanes, A.G.V. (1998) Life history of *Maurolicus muelleri* in fjordic and oceanic environments. *Journal of Fish Biology* **53:**1324-1341

Kristoffersen, J.B., and Salvanes, A.G.V. (2001) Sexual size dimorphism and sex ratio in Müllers pearlside (*Maurolicus muelleri*). *Marine Biology* **138**:1087-1092

Kaartvedt, S., Aksnes, D.L., and Aadnesen, A. (1988) Winter distribution of macroplankton and micronekton in Masfjorden, western Norway. *Marine Ecology Progress Series* **45:**45-55.

Kaartvedt, S., Melle, W., Knutsen, T., and Skjoldal, H.R. (1996) Vertical distribution of fish and krill beneath water of varying optical properties. *Marine Ecology Progress Series* **136:**51-58

Kaartvedt ,S., Knutsen, T., and Holst, J.C. (1998) Schooling of the vertically migrating mesopelagic fish *Maurolicus muelleri* in light summer nights. *Marine Ecology Progress Series* **170**:287-290

Kaartvedt, S., Torgersen, T., Klevjer, T., Røstad, A., and Devine, J.A. (2008) Behaviour of individual mesopelagic fish in acoustic scattering layers of Norwegian fjords. *Marine Ecology Progress Series* **360**:201-209

Kaartvedt, S., Røstad, A., and Klevjer, T. (2009a) Sprat *Sprattus sprattus* can exploit low oxygen waters for overwintering. *Marine Ecology Progress Series* **390**:237-249

Landaeta, M.F., and Castro, L.R. (2002) Spring spawning and early nursery zone of the mesopelagic fish *Maurolicus parvipinnis* at the coastal upwelling zone off Talcahuano, central Chile. *Marine Ecology Progress Series* **226**:179-191

Levy, D.A. (1990a) Reciprocal diel vertical migration behaviour in planktivores and zooplankton in British Columbia lakes. *Canadian Journal of Fisheries and Aquatic Science* **47**:1755-1764

Levy, D A (1990b) Sensory mechanism and selective advantage for diel vertical migration in juvenile sockeye salmon, *Oncorhynchus nerka*. *Canadian Journal of Fisheries and Aquatic Science* **47**:1796-1802

Linkowski, T.B. (1983) Some aspects of the biology of *Maurolicus muelleri* (Sternoptychidae) from the South Atlantic. Council Meeting of the International Council for the Exploration of the Sea, Gothenburg, Sweden . ICES, Copenhagen, Denmark

Lipinski, M.R. (1992) Cephalopods and the Benguela ecosystem: trophic relationships and impact. *South African Journal of Marine Science* **12**:791-802

Lopes, P.C. (1979) Eggs and larvae of *Maurolicus muelleri* (Gonostomatidae) and other fish eggs and larvae from two fjords in western Norway. *Sarsia* **64**:199-210

MacLennan, D.N., and Simmonds, E.J. (1992) Fisheries acoustics. Chapman & Hall, London

McFarland, W.N. (1986) Light in the sea – correlations with behaviour of fishes and invertebrates. *American Zoologist* **26**:389-401

McClatchie, S., and Dunford, A. (2003) Estimated biomass of vertically migrating mesopelagic fish off New Zealand. *Deep-Sea Research I* **50**:1263-1281

Meager, J.J., Moberg, O., Strand, E., and Utne-Palm, A.C. (2010) Effects of light intensity on visual prey detection by juvenile Atlantic cod (*Gadus morhua* L). *Marine and Freshwater Behaviour and Physiology* **43**:99-108

Mehner T (2006) Individual variability of diel migrations in European vendance (*Coregonus albula*) explored by stationary vertical hydroacoustics. *Ecology of Freshwater Fish* **15**:146-154

Mehner, T., Kasprzak, P., and Hölker, F. (2007) Exploring ultimate hypothesis to predict diel vertical migrations in coregonid fish. *Canadian Journal of Fisheries and Aquatic Science* **64**:874-886

Melo, Y.C., and Armstrong, M.J. (1991) Batch spawning behaviour in lightfish *Maurolicus muelleri*. *South African Journal of Marine Science* **10**:125-130

Metcalfe, J.D., Righton, D., Eastwood, P., Hunter, E. (2008) Migration and habitat choice in marine fishes. In: *Fish Behaviour* (Eds. C. Magnhagen, V.A. Braithwaite, E. Forsgren, B.G. Kapoor) Science Publishers, Enfield, pp.187-234

Misund, O. A. and Beltestad, A. K. (1996) Target-strength estimates of schooling herring and mackerel using the comparison method. *ICES Journal of Marine Science Symposia*, **53**:281–284

Nepgen, C.S.D.V. (1979) The food of the snoek *Thyrsites atun*. *Fisheries Bulletin (South Africa)* **11**:39-42

Neilson, J.D., and Perry, R.I. (1990) Diel vertical migrations of marine fishes: an obligate or facultative process? *Advance in Marine Biology* **26**:115-167

Olivar, M.P., Rubies, P. and Salat, J. (1992) Horizontal and vertical distribution patterns of ichthyoplankton under intense upwelling regimes off Namibia. *South African Journal of Marine Science* **12**:71-82

Onsrud, M.S.R., and Kaartvedt, S. (1998) Die1 vertical migration of the krill *Meganyctiphanes norvegica* in relation to physical environment, food and predators. *Marine Ecology Progress Series* **171**:209-219

Onsrud, M.S.R., Kaartvedt, S., and Breien, M.T. (2005) In situ swimming speed and swimming behaviour of fish feeding on the krill *Meganyctiphanes norvegica*. *Canadian Journal of Fisheries and Aquatic Science* **62**:1822-1832

Parin, N.V., and Kobyliansky, S.G. (1996) Diagnosis and distribution of fifteen species recognized in genus *Maurolicus* cocco (Sternoptichydae, Stomiiformes) with a key to their identification. *Cybium* **20**:185-195

Payne, A.I.L., Rose, B., and Leslie, R.W. (1987) Feeding of hake and a first attempt at determining their trophic role in the South African west coast marine environment. *South African Journal of Marine Science* **5**:471-501.

Pearre, S. Jr. (2003) Eat and run? The hunger satiation hypothesis in vertical migration: history, evidence and consequences. *Biological Reviews* **78**:1-79.

Pedersen, G. (2007) Methodology for in situ target strength measurement of fish. *Ph.D. thesis*, University of Bergen

Pillar, S.C., and Barange, M. (1997) Diel variability in bottom trawl catches and feeding activity of the cape hakes off the west coast of South Africa. *ICES Journal of Marine Science* **54**:485-499.

Pitcher, T.J. (1993) Functions of shoaling behaviour in teleosts. In: *Behaviour of Teleost Fishes*, Vol. (eds T.J. Pitcher), 1st edn. Chapman and Hall, London, pp. 363-411

Prosch, R.M. (1986) The biology, distribution and ecology of Lampanyctodes hectoris and Maurolicus muelleri along the South African coast. *MSc thesis*, University of Cape Town, 197 pages

Prosch, R.M. (1991) Reproductive biology and spawning of the myctophid *Lampanyctodes hectoris* and the sternoptychid *Maurolicus muelleri* in the southern Benguela ecosystem. *South African Journal of Marine Science* **10**:241-252

Punt, A.E., Leslie, R.W., and Du Plessis, S.E. (1992) Estimation of the annual consumption of food by Cape hake *Merluccius capensis* and *M. paradoxus* off the South African west coast. *South African Journal of Marine Science* **12**:611-634.

Rasmussen, O.I., and Giske, J. (1994) Life-history parameters and vertical distribution of *Maurolicus muelleri* in Masfjorden in summer. *Marine Biology* **120:**649-664

Reebs, S.G. (2002) Plasticity of diel and circadian activity rhythms in fishes. *Reviews in Fish Biology and Fisheries* **12**: 349–371

Ringelberg, J. (1991) A mechanism of predator-mediated induction of diel vertical migration in *Daphnia hyaline*. *Journal of Plankton Research* **13**:83-89, 1991

Ringelberg, J., and Van Gool, E. (1995) Migrating daphnia have a memory for fish kairomones. *Marine and Freshwater Behaviour and Physiology* **26**:249-257

Robertson, D.A. (1976) Planktonic stages of *Maurolicus muelleri* (Teleostei: Sternoptychidae) in New Zealand waters. *New Zealand Journal of Marine and Freshwater Research* **10**:311-328

Roe, H.S.J. (1983) Vertical distributions of euphausiids and fish in relation to light intensity in the north-eastern Atlantic. *Marine Biology* **77**:287–298

Rosland, R. and Giske, J. (1994) A dynamic optimization model of the diel vertical distribution of a pelagic planktivorous fish. *Progress in Oceanography* **34**:1-43

Rosland, R. (1997) Optimal responses to environmental and physiological constraints: evaluation of a model for a planktivore. *Sarsia* **82**:113-128

Rosland, R. and Giske, J. (1997) A dynamic model for the life history of *Maurolicus muelleri*, a pelagic planktivorous fish. *Fisheries Oceanography* **6**:19-34

Ryer, C.H., and Olla, B.L. (1999) Light-induced changes in the prey consumption and behaviour of two juvenile planktivorous fish. *Marine Ecology Progress Series* **181**:41-51

Røstad, A. (2006) Fish behaviour and implications for acoustic abundance estimates and ecological research. *Ph.D. thesis*, University of Oslo, 29 pages

Salvanes, A.G.V. (1991) Structure and dynamics of the cod population and trophic interactions in Masfjorden: A contribution to a large-scale cod enhancement experiment. *Dr. Scient. thesis*, University of Bergen, 140 pages

Salvanes, A.G.V., and Nordeide J.T. (1993) Dominating sublittoral fish species in a west Norwegian fjord and their trophic links to cod (*Gadus morhua* L.). Sarsia **78**:221-234

Salvanes, A.G.V., and Stockley, B.M. (1996) Spatial variation of growth and gonadal developments of *Maurolicus muelleri* in the Norwegian Sea and in a Norwegian fjord. *Marine Biology* **126**:321-332

Salvanes, A.G.V. (2004) Mesopelagic fish. In: *The Norwegian Sea Ecosystem* (eds H.R. Skjoldal, R. Saetre, A. Fernø, O.A. Misund and I. Roettingen), Tapir Academic Press, Trondheim, pp. 301-314.

Salvanes, A.G.V., Skjæraasen, J.E. and Nilsen, T. (2004) Sub-populations of coastal cod with different behaviour and life-history strategies. *Marine Ecology Progress Series* **267,** 241-251.

Sassa, C., Kawaguchi, K., Kinoshita, T., and Watanabe, C. (2002) Assemblages of vertical migratory mesopelagic fish in the transitional region of the western north Pacific. *Fisheries Oceanography* **11**:193-204

Scheuerell, M.D., and Schindler, D.E. (2003) Diel vertical migration by juvenile sockeye salmon: empirical evidence for the antipredation window. *Ecology* **84**:1713-1720

Srisomwong, J. (2009) Diel vertical migration and feeding pattern of *M. muelleri* in Masfjorden in late autumn. *Master thesis*, University of Bergen, 36 pages

Stearns, S.C. (1992) *The Evolution of Life Histories*. Oxford University Press, Oxford.

Suneetha, K.B., and Nævdal, G. (2001) Genetic and morphological stock structure of the pearlside, *Maurolicus muelleri* (Pisces, Sternoptychidae), among Norwegian fjords and offshore area. *Sarsia* **86**:191-201

Sørnes, T., and Aksnes, D.L. (2006) Concurrent temporal patterns in light absorbance and fish abundance. *Marine Ecology Progress Series* **325**:181-186

Tarling, G.A., Jarvis, T., Emsley, S.M., and Matthews, J.B.L. (2002) Midnight sinking behaviour in *Calanus finmarchicus*: a response to satiation or krill? *Marine Ecology Progress Series* **240**:183-194

Tarling, G.A (2003) Sex-dependent diel vertical migration in northern krill *Meganyctiphanes norvegica* and its consequences for population dynamics. *Marine Ecology Progress Series* **260**:173–188

Thetmeyer, H., and Kils, U. (1995) To see and not be seen: the visibility of predator and prey with respect to feeding behaviour. *Marine Ecology Progress Series* **126**:1-8

Torgersen, T., Kaartvedt, S., Melle, W., and Knutsen, T. (1997) Large scale distribution of acoustical scattering layers at the Norwegian continental shelf and the eastern Norwegian Sea. *Sarsia* **82**:87-96

Torgersen, T., and Kaartvedt, S. (2001) In situ swimming behaviour of individual mesopelagic fish studied by split-beam echo target tracking. *ICES Journal of Marine Science* **58:**346-354

Utne-Palm, A.C., Salvanes, A.G.V., Currie, B., Kaartvedt, S., Nilsson, G.E., Braithwaite, V.A., Stecyk, J.A.W., Hundt, M., van der Bank, M., Flynn,B., Sandvik, G.K., Klevjer, T.A., Sweetman, A.K., Brüchert,V., Pittman, K., Peard, K.R., Lunde, I.G., Strandabø, R.A.U., Gibbons, M.J. (2010) Trophic structure and community stability in an overfished ecosystem. *Science* **329**:333-336 van Damme, C.J.G., Dickey-Collas, M., Rijnsdorp, A.D., and Kjesbu, O. (2009) Fecundity, atresia, and spawning strategies of Atlantic herring (*Clupea harengus*). *Canadian Journal of Fisheries and Aquatic Sciences* **66**:2130-2141

Villanueva, R. (1993) Diet and mandibular growth of *Octopus magnificus* (Cephalopoda). *South African Journal of Marine Science* **13**:121-126.

Visser, A.W., Jonasdottir, S.H. (1999) Lipids, buoyancy and the seasonal vertical migration of *Calanus finmarchicus. Fisheries Oceanography* **8**:100-106

Warrant, E.J. and Locket, N.A. (2004) Vision in the deep. *Biological Reviews of the Cambridge Philosophical Society* **79**:671-712.

Weiss, G., Hubold, G., and Bonecker, A.C. (1988) Eggs and larvae of *Maurolicus muelleri* (Gmelin, 1789) (Teleostei, Sternoptychidae) in the southwest Atlantic. *Meeresforschung* **32**:53-60

Widder, E.A., and Frank, T.M. (2001) The speed of an isolume: a shrimp's eye view. *Marine Biology* **138**:669-677

Williams, A., and Koslow, J.A. (1997) Species composition, biomass and vertical distribution of micronekton over the mid-slope region off southern Tasmania, Australia. *Marine Biology* **130**:259-276

Wootton, R.J. (1999) *Ecology of Teleost Fishes*, Kluwer Academic Publishers, Dordrecht.

Wurtsbaugh, W.A., Neverman, D. (1988) Post-feeding thermotaxis and daily vertical migration in a larval fish. *Nature* **333**:846-848

Young, J.W., and Blaber, S.J.M. (1986) Feeding ecology of three species of midwater fishes associated with the continental slope of eastern Tasmania, Australia. *Marine Biology* **93**:147-156

Young, J.W., Blaber, S.J.M. and Rose, R. (1987) Reproductive biology of three species of midwater fishes associated with the continental slope of Eastern Tasmania, Australia. *Marine Biology* **95**:323-332

Paper 1

Use of bottom-mounted echo sounders in exploring behavior of mesopelagic fishes

Kaartvedt, S., Røstad, A., Klevjer, T.A., **Staby, A.**

Marine Ecology Progress Series **395**: 109–118

Vol. 395: 109–118, 2009
doi: 10.3354/meps08174

MARINE ECOLOGY PROGRESS SERIES
Mar Ecol Prog Ser

Published December 3

Contribution to the Theme Section 'Acoustics in marine ecology'

Use of bottom-mounted echo sounders in exploring behavior of mesopelagic fishes

Stein Kaartvedt[1,2,*], Anders Røstad[1], Thor A. Klevjer[1], Arved Staby[2]

[1]Department of Biology, University of Oslo, PO Box 1066 Blindern, 0316 Oslo, Norway
[2]Deparment of Biology, University of Bergen, PO Box 7800, 5020 Bergen, Norway

ABSTRACT: We deployed an upward-facing echo sounder mounted on the bottom and cabled to shore in a ~400 m fjord location for long-term studies of small mesopelagic fish and their potential predators. The population of the myctophid *Benthosema glaciale* displayed diverse diel vertical migration (DVM) behaviors, including normal DVM to surface waters at night, reverse DVM in the lower part of the water column in which fish ascended to ~200 m at day, as well as nonmigration of some individuals. The relative prevalence of these behavioral modes varied with season. Acoustic target tracking of individuals in deep water showed that *B. glaciale* was conspicuously inactive and drifted back and forth with weak tidal currents, essentially acting as plankton. Swimming was largely restricted to infrequent short bouts. More active swimming occasionally occurred in the vertical direction, and then in a stepwise pattern. Potential predators in deep water were swimming at speeds of <0.5 body length s^{-1}, with maximum speeds of ~1 body length s^{-1}. These results show that submerged echo sounders provide a means of non-intrusively studying both individual and population behavior of deep-living organisms.

KEY WORDS: Mesopelagic · Diel vertical migration · Swimming behavior · Target tracking · *Benthosema glaciale* · Moored echo sounders

INTRODUCTION

The most common application of echo sounders in marine biological research has been in stock assessments of fish, in which volume backscatter is converted into fish biomass (Dragesund & Olsen 1965). It has also been documented that organisms constituting deep acoustic scattering layers carry out diel vertical migration (DVM) (Moore 1950, Hersey & Backus 1954), and acoustic studies of such migrations have become a field of research (e.g. Boden & Kampa 1967). Subsequent applications comprised assessments of plankton abundance and size distribution (e.g. Holliday & Pieper 1980, Greene et al. 1989, Everson et al. 1990). Echo sounders are now increasingly used for behavioral studies of plankton (DeRobertis et al. 2000, Genin et al. 2005, Kaartvedt et al. 2007) and fish (Huse & Ona 1996, Handegard & Tjøstheim 2005, Mehner 2006) and for *in situ* studies of predator–prey relationships (e.g. Zamon et al. 1996, Nøttestad et al. 2002, Kaartvedt et al. 2005).

Acoustic studies have normally been conducted from moving vessels, using hull-mounted transducers. As compact echo sounders that can be kept submerged in pressurized housings are now available, acoustics can be used in telling quite new stories. Stationary split-beam echo sounders can reveal the movements of individuals traversing the acoustic beam both horizontally and vertically (Ehrenberg & Torkelson 1996), and submerged echo sounders make it possible to establish the *in situ* swimming behavior of fish in deeper waters (Huse & Ona 1996). Autonomous systems may be battery powered and left at sea (Thomson & Allen 2000, Trevorrow 2005, Brierley et al. 2006), or they can be cabled to land for power and transmission of data (Patel 2007). Simple, moored and cabled systems enable detailed, long-term and relatively low-cost studies, in contrast to studies made from research vessels.

---

[*] Email: stein.kaartvedt@bio.uio.no

Understanding ecosystem functioning and managing marine resources properly require knowledge of individual behavior, since activity levels and swimming behavior affect the distribution of organisms, the interactions between predators and prey (Gerritsen & Strickler 1977, Wright & O'Brien 1984, O'Brien et al. 1990) and bioenergetic budgets (Torres & Childress 1983, Huse & Ona 1996). The remote and inaccessible nature of mesopelagic and deep-sea habitats has largely precluded direct observations of their inhabitants. Here, we show that submerged, stationary echo sounders may provide detailed information on the behavior of small mesopelagic fish and their potential predators in their natural environment. We present data from a bottom-mounted, upward facing echosounder that was cabled to shore in a Norwegian fjord. This approach provides a stable platform; the procedure is non-intrusive and imposes virtually no limitation on operation time and data storage capacity.

MATERIALS AND METHODS

A mooring with an upward-facing, calibrated echo sounder (Simrad EK 60, 38 kHz, 7.1° beam width) was deployed at 390 m depth in Masfjorden, Norway. The transceiver was housed in a glass sphere (pressure proof to 3000 m) next to an oil-filled transducer (Simrad ES38DD, 38 kHz; pressure proof to 1500 m), which was mounted in a steel frame with gimbal couplings to ensure horizontal orientation of the transducer surface. The echo sounder was connected to land with 1200 m of cable that provided electricity and transmitted data to a PC on shore. We used an input voltage of 220 V, but applied a 12 V transformer that was installed next to the transceiver within the glass sphere, as it appeared that this voltage gave less electrical noise in the acoustic records. Standard industrial modems were used to transmit data. The temporal resolution of data (ping rate) was 1 s^{-1}, and the pulse length was 0.512 ms. All raw data were stored for later analyses.

The mooring was deployed in July 2007 and was retrieved after 15 mo of measurements. Upon retrieval, the echo sounder was immediately redeployed at 300–400 m depth together with a standard copper sphere target to verify if the system was calibrated at the operation depth.

Here, we present results from three different periods (22–23 July, 29–30 August and 5–6 November 2007) to illustrate different types of information that were obtained using this approach. Results are given at 3 levels of resolution. Echograms display records from the entire water column for three 48 h periods, focusing on acoustic scattering layers, which verified that that display population behavior. Due to the large amount of data obtained, each pixel was based on the average of 15 pings when the echograms were visualized in Matlab. 'Echo traces' refer to records from single organisms (seen as a 'line') in a normal echogram. Acoustic 'tracks' are based on targets for which both horizontal and vertical position, as well as target strength (TS, a proxy for size) are known. In this case, the criteria for accepting echoes are stricter, so that some or all echoes that are seen in an echo trace may become rejected by the tracking algorithms. In all presentations, time is in UTC (coordinated universal time), which is one hour after standard local time.

Target tracking (TT) was used to assess the behavior of individual fish by grouping sequential echoes into tracks. In this procedure, subsequent echoes were merged to make up the swimming path and speed of an individual, or to assess the TS. Tracking can be performed automatically, using algorithms utilizing information on the proximity of sequential echoes in determining the tracks, or manually, with the researcher visually selecting which echoes to include in the tracks. Results from both types of procedures are presented here. The advantage of the automatic tracking algorithms is its objectivity, but the downsides are that longer trajectories typically get fragmented (Xie 2000), or trajectories of different organisms may become combined into a single track. In manual tracking, on the other hand, echo traces that evidently originate from single organisms are subjectively selected from the echogram. Raw data making up a trace are imported into tracking software and can then be used to estimate the swimming paths, speed and target strength of that particular individual (Balk & Lindem 2002).

Swimming velocities of small mesopelagic fish were assessed by automatic tracking, using the cross-filter detector of the Sonar5-Pro post-processing system at standard settings (Balk & Lindem 2002). Individuals with TS between –52 and –62 dB were tracked within a range of 20 to 70 m from the transducer (320 to 370 m depth). At shorter range, the acoustic beam was too narrow to obtain many successive pings, and further away, the numbers of targets became too high to be properly resolved. This is because the volume of the cone-shaped acoustic beam increases with range, and resolution of individuals requires that only 1 acoustic target is present at a given range (pulse volume). If this condition is violated, multiple targets composed of echoes from >1 organism may cause corrupted records (Soule et al. 1997). A minimum of 25 echoes were required to make up a track, accepting a maximum of 5 missing pings. The majority of small mesopelagic fish were inactive most of the time; thus, echo traces that displayed vertical swimming were selected in additional manual tracking to assess vertical velocities.

Targets with TS of >–50 dB were tracked separately. The single target echoes were detected in Sonar5-Pro using respective minimum and maximum echo lengths of 0.8 and 1.2, with a maximum phase deviation of 0.8. A minimum of 10 echoes were required to make up a track, with maximally 1 ping missing. These less numerous, larger fishes could be studied at longer range. Two size classes appeared to be present at different distances from the bottom, and results are presented for the 20–90 and 90–190 m range respectively (i.e. 300–370 and 200–300 m depth). The shallowest mode performed DVM during summer and then came within reach for TT when the fish descended in daylight. These fish had the strongest TS, and since the risk of recording multiple (hence larger) targets increases with range, we visually scrutinized echo traces of individual fish to make sure that only 1 fish was included in each track.

Correct swimming speed depends on correct measurements of positions in the acoustic beam. Errors introduced by the system's angular resolution (Brede et al. 1990) and erroneous angle measurements (Mulligan & Chen 2000) will add artificial movements to the targets and therefore overestimate swimming speeds. This bias will increase with range. Such errors can be reduced by smoothing. Handegard et al. (2005) and Røstad (2006) eliminated this range dependency (at a range of up to 125 m) by using linear regression to smooth the estimated echo positions, and we used the same approach in this study. Also in our case, this smoothing appeared to be successful, as no clear effect of range was recorded for fish tracked between 90 and 190 m ($R^2_{Jul} = 0.01$; $R^2_{Aug} = 0.07$, $R^2_{Nov} = 0.11$). In July, there was an effect of range on swimming speed within the deepest interval ($R^2_{20-90m} = 0.29$), which we ascribe to inclusion of some larger faster swimming targets at long range.

Acoustic studies are normally accompanied by sampling to identify and obtain biological information on acoustic targets. Because of its nature, continuous long-term acoustic records cannot be accompanied by an equivalent sampling resolution. Masfjorden was selected as the study site since its mesopelagic fish fauna is well established from previous sampling. Investigations over many years and from different seasons have shown a consistent presence of the lightfish *Maurolicus muelleri* that form conspicuous acoustic scattering layers in mid-waters, and the northern lanternfish *Benthosema glaciale* in lower layers (Kaartvedt et al. 1988, Giske et al. 1990, Baliño & Aksnes 1993, Bagøien et al. 2001). For this study, we carried out a sampling campaign with repeated trawling in the acoustic layers on 1 to 4 November 2007, i.e. with acoustics and sampling overlapping in time for one of the periods presented here (although we present acoustic data for the 2 days subsequent to the sampling campaign, since the ship's echo sounders interfered with records from the mooring). We used a Harstad trawl equipped with a multisampler cod end that can be remotely opened and closed during sampling (Engås et al. 1997), hence providing depth stratified catches. In total, 29 trawl samples were obtained from different parts of the water column during day and night.

RESULTS

Scattering layers and trawl catches

The echograms were dominated by a strong scattering layer, with daytime depths near 150 to 200 m, and carrying out DVM in July and August, but barely doing so in November (Fig. 1). Catches (Table 1) and previous studies identify this scattering layer as consisting of the lightfish *Maurolicus muelleri*, with juveniles of this species likely forming the weaker layer

Table 1. Trawl catches. Average catch (no. h^{-1}; #), average contribution to total catch in weight (%) and average lengths (L; mm) of the major taxa in day and night tows summarised by depth ranges (Masfjorden, November 2007). SDs of mean lengths are indicated in parentheses

		Depth range (m)																	
		<50			50–100			100–150			150–200			250–300			>300		
		#	%	L	#	%	L	#	%	L	#	%	L	#	%	L	#	%	L
Maurolicus muelleri	Day				3694	98.2	24 (3)	39 938	99.8	40 (4)				112	4.2	41 (6)	72	2.9	40 (4)
	Night	665	23.4	31 (8)	93	5.8	38 (5)				1159	61.1	38 (4)	49	1.2	41 (5)	0	0	
Benthosema glaciale	Day				0	0		0	0					494	71.7	59 (5)	536	65.7	59 (5)
	Night	62	18.0	55 (8)	29	4.8	53 (6)				85	9.1	54 (8)	1252	84.6	60 (5)	237	82.2	60 (5)
Pelagic shrimps	Day				2	1.7		0	0					374	23.9	74 (8)	388	31.4	66 (8)
	Night	257	42.2	65 (15)	507	89.2	71 (7)				244	28.8	75 (11)	413	14	62 (7)	97	17.1	68 (5)
Krill	Day				2	0	19	195	0.20	38 (3)				8	0.1	41 (3)	0	0	
	Night	562	16.2	40 (4)	3	0.20	39 (4)				41	0.9	40 (4)	35	0.2	41 (2)	17	0.7	38 (4)
Number of tows	Day					3			3						3			3	
	Night		7			3						3			3			1	

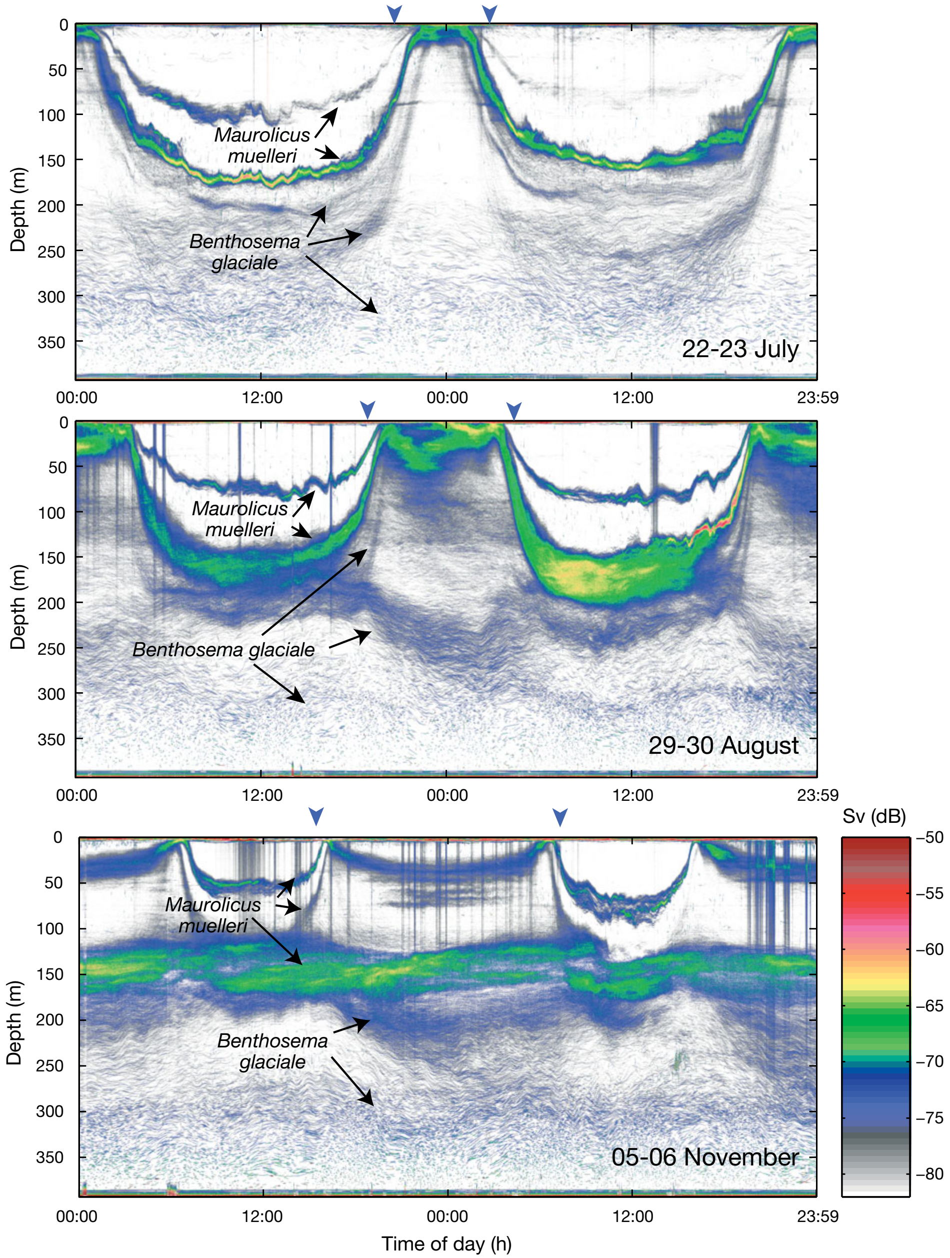


Fig. 1. Echograms for 22–23 July, 29–30 August and 5–6 November 2007. Color scale refers to backscattering strength (Sv) values (dB). Species of the fish making up scattering layers are indicated; additional vertical 'lines' (most prominent in November) are generated by rain. Blue arrowheads: times of sunset and sunrise

above. Here, we focus on the echoes below ~200 m, which we mainly ascribe to the lanternfish *Benthosema glaciale* based on the catches and previous studies. In November 2007, *B. glaciale* (average standard length of 6 cm) prevailed in catches below 250 m (Table 1), being numerically dominant in 8 of 9 samples taken. Also, pelagic shrimps (primarily *Sergestes arcticus*) were common in the deep catches. No *B. glaciale* were captured above 150 m during the day, while some individuals were captured in the upper 50 m at night (Table 1).

In July, *Benthosema glaciale* undertook normal DVM (Fig. 1). However, part of the population (~30% of total acoustic backscatter) remained at depth. In August, the DVM patterns of *B. glaciale* changed. The upper part of the registrations allocated to this species continued to undertake normal DVM, but fish deeper in the water column now rather reversed their DVM (Fig. 1), with a component of the population ascending to ~200 m in the morning and descending in the evening. A third component of the population remained at depth (~40% of total backscatter). The daytime ascent persisted in November, with normal DVM of *B. glaciale* becoming inconspicuous in the acoustic records (Fig. 1). Approximately 50% of the population (in terms of acoustic backscatter) did not take part in the reverse migrations in November.

Individual behavior

Benthosema glaciale

Echo traces of individual *Benthosema glaciale* depicted slow internal waves with maximum vertical speeds of ~2 mm s^{-1} (Fig. 1, although this is not easily seen in these compressed plots). Long echo traces showed that *B. glaciale* remained within the stationary acoustic beam for prolonged periods, with many consecutive acoustic returns from the same individual. TT documented that this could be ascribed to low activity, and revealed that *B. glaciale* were drifting back and forth with weak tidal currents (Fig. 2). Currents were strongest in August and November, resulting in a ~6 h cyclic pattern in the population's net horizontal movements with peak velocities of ~3 cm s^{-1} and the direction being reversed between peaks (Fig. 2). Low population velocities (i.e. currents) were recorded in July (maxima of ~1.5 cm s^{-1}). Subtracting hourly population averages of the physical displacement from the individual tracks resulted in very slow individual movements (Fig. 3), with medians of 1.1 (median TS = –57.8 dB), 1.2 (median TS =–58.7 dB) and 0.8 cm s^{-1} (median TS = –58.4 dB) in July, August and November, respectively. Essentially, these fish were functionally

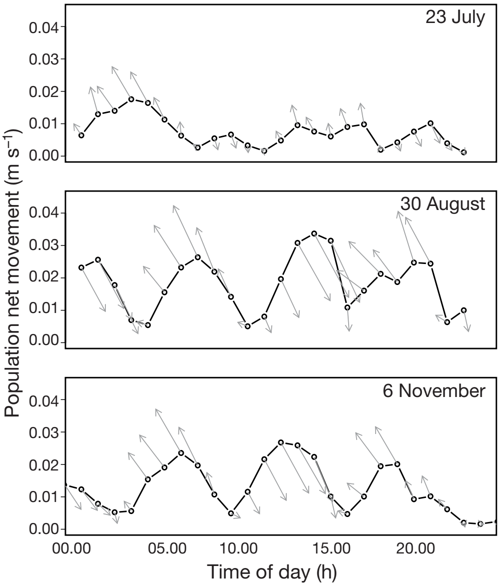


Fig. 2. Net horizontal population displacement of targets ascribed to *Benthosema glaciale* on 23 July (n_{track} = 7636; median TS = –57.8 dB), 30 August 2007 (n_{track} = 8012; median TS = –58.7 dB) and 6 November (n_{track} = 11520; median TS = –58.4 dB). Arrows depict relative direction and relative speed of displacement. The results are based on automatic tracking. Numbers of fish will be lower than numbers of tracks since automatic tracking tends to split long tracks into several shorter ones

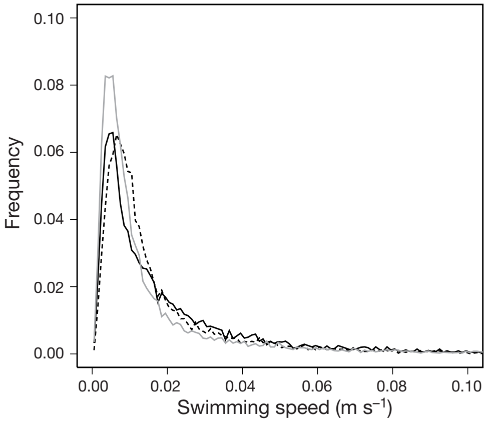


Fig. 3. Individual swimming speed (population net movement subtracted) of targets ascribed to *Benthosema glaciale*. (——) 23 July, (——) 30 August, (- - -) 6 November 2007

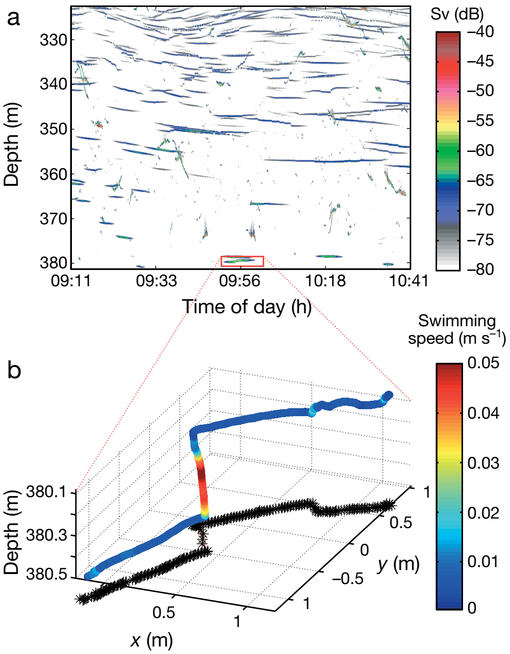


Fig. 4. (a) Echo traces of *Benthosema glaciale* (mostly blue or greenish) and larger fish (red, shorter-lasting traces). Color scale refers to Sv values (dB). (b) Example of 3-D relocation and swimming speed of a target ascribed to *B. glaciale* (framed in (a)) at 380 m depth on 30 August. Color scale refers to swimming speed (m s^{-1})

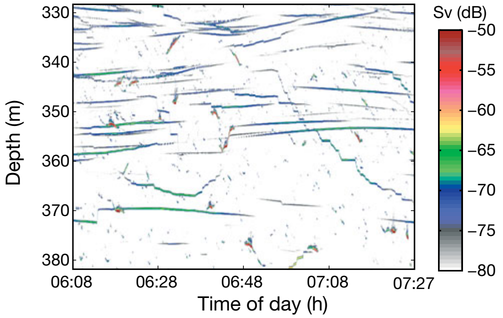


Fig. 5. Echo traces of individual fish on 23 July, showing both inactive fish and individuals swimming vertically in a stepwise fashion. The figure depicts echo traces both of *Benthosema glaciale* (mostly blue or greenish echo traces) and larger fish (red, shorter-lasting traces)

behaving like plankton even in very weak currents. Nevertheless, drifting individuals displayed infrequent small shifts in vertical position that were associated with short, horizontal swimming bouts (e.g. Fig. 4), before the fish came to rest again.

Some individuals exhibited more active swimming in the vertical direction, and their echo traces displayed a staircase-like stop-and-go pattern (e.g. Fig. 5). Fish that relocated in the vertical plane in one or more steps were selectively picked for assessing vertical swimming speeds and direction, using manual tracking during the vertical relocation. *Benthosema glaciale* generally shifted position at ~3–5 cm s^{-1}, both when ascending and descending, with maximum velocities of ~8 cm s^{-1} (Fig. 6). Individuals were swimming both upwards and downwards during both day and night. The TS appeared to be slightly lower during vertical relocation (~1–2 dB when ascending) than when drifting horizontally.

Potential predators

The acoustic analyses suggested 2 groups of larger fish (potential predators) in the lower parts of the water

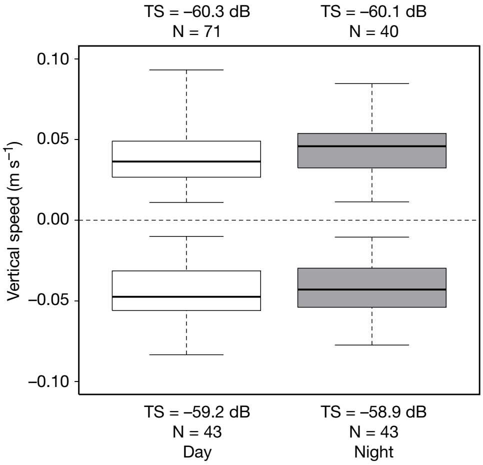


Fig. 6. Vertical speeds during relocation day (left) and night (right) of targets ascribed to *Benthosema glaciale*. The results are based on manual tracking of ascending (upper panel) and descending (lower panel) individuals, respectively (combined for July, August and November). The boxes encompass the 25th to 75th percentiles; whiskers denote maximum and minimum values, and the horizontal lines inside the boxes denote median swimming speeds. Median target strength (TS) and numbers of tracks are given

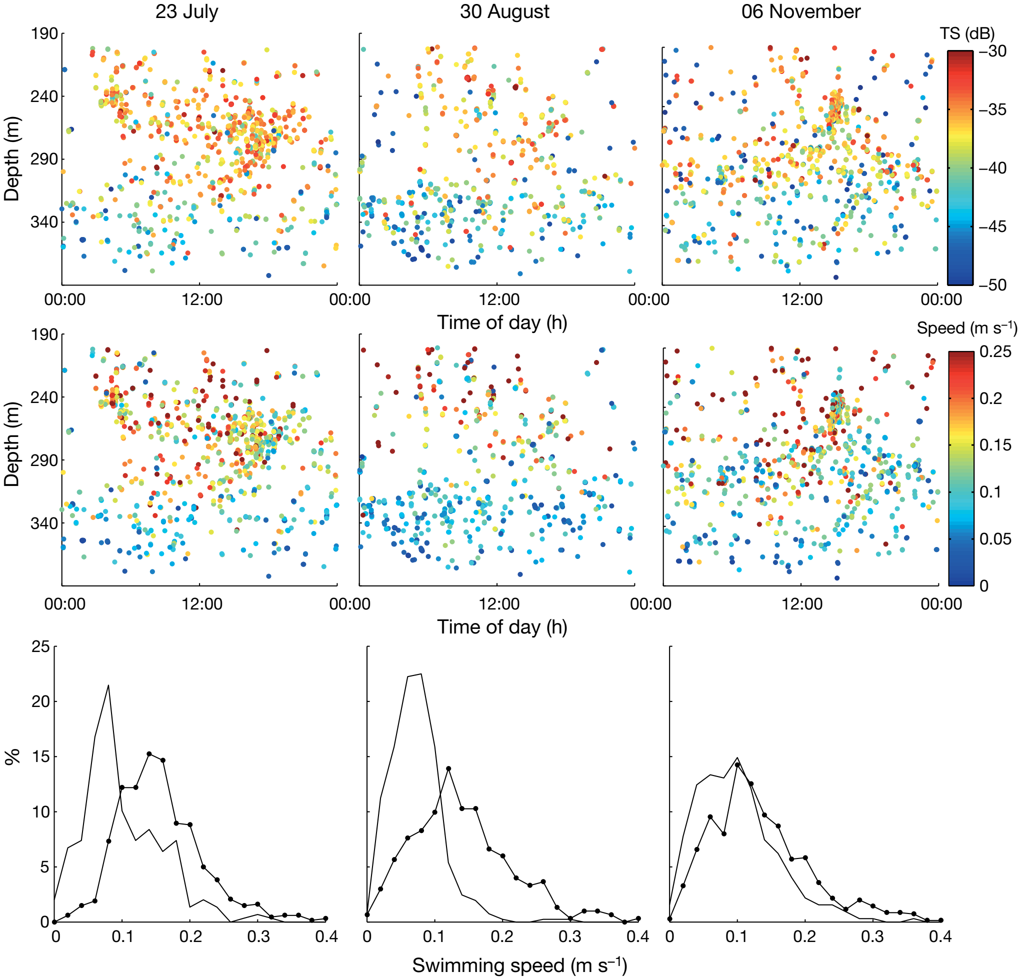


Fig. 7. Results from target tracking of fish with target strength (TS) >–50 dB for 23 July (left), 30 August (middle) and 6 November (right). Each dot represents an individual fish. Color scales in upper and middle panels are TS (dB) and swimming speed (m s^{-1}), respectively. Lower panel shows the distribution of swimming speeds for fish between 200–300 m (—●—: $n_{\text{trackJul}} = 681$; $n_{\text{trackAug}} = 301$; $n_{\text{trackNov}} = 685$) and below 300 m (——: $n_{\text{trackJul}} = 290$; $n_{\text{trackAug}} = 401$; $n_{\text{trackNov}} = 306$)

column (Fig. 7). There appeared to be a size shift at ~300 m depth (90 m above bottom), and fish above and below this depth are treated separately in the analyses. The near-bottom component (median TS = – 39.9 dB, –41.4 and –41.0 dB in July, August and November, respectively) was present during day and night. They were cruising at moderate speed (Fig. 7), with respective medians of 8, 7 and 9 cm s^{-1} in July, August and November, and maximum velocities of ~25 cm s^{-1}. Several such fishes can be seen in Figs. 4 & 5, as characterized by stronger (red in color) and shorter echo traces (due to their higher swimming speed) than that of *Benthosema glaciale*.

The fish above 300 m (median TS = – 36.0, 36.5 and –36.9 dB) were swimming with median speeds of 15, 13 and 12 cm s^{-1} for July, August and November respectively, with maximum velocities approaching 30 to 40 cm s^{-1} (Fig. 7).

DISCUSSION

Moored echo sounders facilitate non-intrusive, long-term studies of both individual and population behavior of deep-living organisms. Results for the 3 time-windows presented here exemplify types of findings obtainable using this approach. These examples provide new information on DVM behavior of mesopelagic fish and details on their individual swimming.

We are confident that the identity of the acoustic targets is correctly established. Results from sampling in this study concur with those from repetitive sampling over the years (see Material & Methods), and for all samples below 250 m combined, with *Benthosema glaciale* constituting 58% of the catches in terms of numbers. The other common group in the deep catches (pelagic shrimps, 32% of numbers in total) would make considerably weaker echoes (Benoit-Bird & Au 2001, 2006). The scattering layer focused on here is also recorded at 18 kHz (Kaartvedt et al. 2008), and scattering from mesopelagic fishes would be the predominant cause of acoustic reverberation at this frequency (Love et al. 2004).

The population of *Benthosema glaciale* displayed diverse DVM behavior, and comprised individuals carrying out normal DVM with ascent at night, individuals carrying out reverse DVM with ascent at day, as well as nonmigrating individuals. To our knowledge, documentation of reverse DVM is a novel finding for *B. glaciale* and for mesopelagic fish in general. We suggest that the reverse migrations at mesopelagic depths can be explained by visual foraging on mid-water plankton during the day, with a subsequent descent as feeding terminates in the deep, dark waters at night. Mesopelagic fish with dark-adapted eyes may be able to see their plankton prey at several hundred meters depth in daylight (Warrant & Locket 2004). Potential prey in mid-water comprises seasonally migrating copepods (*Calanus* spp.) which tend to be centered at ~150–250 m depth in this fjord during autumn (Bagøien et al. 2001), and which would be most easily spotted visually in the upper part of this range. Moreover, organisms carrying out normal DVM, like krill, may be spotted visually in mid-waters during daytime. Such hypotheses derived from the acoustic observations can be tested by sampling.

Normal DVM prevailed in July. Nocturnal ascent is normally ascribed to feeding on surface plankton at night (Roe & Badcock 1984, Pearre 2003), and plankton flourishes in upper layers during summer. Normal and reverse DVM of *Benthosema glaciale* co-occurred at the end of August. Only reverse migration was recorded acoustically for this species in November (when surface mesozooplankton populations are expectedly dilute), yet trawl catches documented some normal DVM.

There were always records of nonmigrating fish in the lower part of the water column. Since we could observe individual fish over long periods, we can conclude that the presence of fish in deep water throughout the diel cycle was not a result of asynchronous migrations (cf. Pearre 2003). Moreover, previous studies have concluded that populations of mesopelagic fish may separate into migrating and nonmigrating groups. Sutton & Hopkins (1996a,b) suggested that migrating individuals were feeding in upper layers at night, while individuals remaining at depth were in a digesting, or in a post-digestion state. Pearcy et al. (1979) suggested that a population of lanternfish split into nonmigrating individuals feeding at depth, and migrating individuals feeding in upper layers at night.

Individual fish likely adjust their migration pattern according to both external stimuli and internal state. It is well established that different parts of a population can behave differently due to factors like age (Giske & Aksnes 1992), stored resources (Hays et al. 2001), hunger (Pearre 2003) or parasites (Barber et al. 2000), or because the population may consist of both risk seeking and risk averse individuals (Wolf et al. 2007). More long-term acoustic observations will evidently document more variation in fish behavior than currently established, thus improving our understanding of behavioral flexibility and ecosystem functioning.

Benthosema glaciale displayed little swimming activity, passively of drifting back and forth with tidal currents. Such lethargic behavior concurs with observations from remotely operated vehicles (ROVs) and submersibles that show midwater fish hanging motionless in the water column (Barham 1966, 1970, Backus et al. 1968), but deviates from observations of myctophids undertaking extensive nocturnal horizontal migrations onto and off Hawaiian Islands shelf regions (Benoit-Bird & Au 2006, McManus et al. 2008). If *B. glaciale* were foraging during their tranquil state, the long duration of their trajectories, together with the intermittent, small shifts in their position, would suggest ambush feeding (cf. O'Brien et al. 1990). Kaartvedt et al. (2008) reported stepwise migration patterns for mesopelagic fish during DVM, as also shown for individual deep-living *B. glaciale* in this study. Such stop-and-go swimming concurs with saltatory search, in which fish scan the water for prey during the stationary phases, relocate and then scan a new volume (O'Brien et al. 1990).

Potential predatory fish were present in deep waters during both day and night. They were not allocated to species, but TSs of −40 and −36 dB correspond to sizes of 23 and 37 cm respectively, applying a standard conversion factor for gadoids (Foote 1987). For both groups, the median swimming speed would correspond to ~1/3 body length s^{-1}, as derived from the acoustic determination of size. Visual range is low in the dark, deep waters, and if these fishes were indeed predators on the lethargic *Benthosema glaciale*, slow swimming might be a way of minimizing hydrodynamic noise. Potential prey will be less able to note the approach of a 'silent' predator. Hydrodynamic silence would also facilitate prey detection for tactile predators in dark waters (Janssen et al. 1999).

PERSPECTIVES

In order to understand ecosystem functioning, it is necessary to unveil processes and interactions involving individual organisms (Kerfoot & Sih 1987, Williamson 1993). We have presented some examples of the usefulness of submerged, stationary echo sounders for providing information at the individual as well as the population level. This approach enables studies of even cm-sized organisms and their potential predators in their undisturbed natural environment at depths of several hundred meters and at time scales of seconds to years. Fjords are deep, their faunal composition resembles that of the adjacent ocean, and low advection provides good opportunities for target tracking. Such systems can be used as low-cost ocean laboratories to obtain high-resolution data for e.g. testing and parameterizing mechanistic predator–prey models.

Moored echo sounders have also proven their abilities in other environments, including freshwater (Cech & Kubecka 2002, Mehner 2006), coastal bays (Axenrot et al. 2004), coral reefs (Genin et al. 2005) and shelf ecosystems (e.g. Benoit-Bird & Au 2006), and acoustic moorings are becoming increasingly used for studies of the pelagic fauna even in remote and inaccessible environments (Brierley et al. 2006, Cottier et al. 2006). We are now on the verge of establishing large-scale cabled ocean observatories that are equipped with an array of environmental sensors on the bottom of the world oceans (e.g. Malakoff 2004). Echo sounders have the potential of contributing considerably to these endeavors to understand the physics of the oceans, their organisms and ecosystem functioning. Implementation of new and innovative infrastructure requires qualified researchers who know the possibilities and limitations of new techniques, and who can pose the right questions and handle the vast data streams. In parallel with the focus on logistics of new technologies like ocean observatories, there is a need to build competence among aquatic ecologists to exploit acoustic methods to their full benefit.

LITERATURE CITED

➤ Axenrot T, Didrikas T, Danielsson C, Hansson S (2004) Diel patterns in pelagic fish behaviour and distribution observed from a stationary, bottom-mounted, and upward-facing transducer. ICES J Mar Sci 61:1100–1104

➤ Backus RH, Craddock JE, Haedrich RL, Shores DL and others (1968) *Ceratoscopelus maderensis*: peculiar sound-scattering layer identified with this myctophid fish. Science 160:991–993

Bagøien E, Kaartvedt S, Aksnes DL, Eiane K (2001) Vertical distribution and mortality of overwintering *Calanus*. Limnol Oceanogr 46:1494–1510

➤ Baliño BM, Aksnes DL (1993) Winter distribution and migration of the sound scattering layers, zooplankton and micronekton in Masfjorden, western Norway. Mar Ecol Prog Ser 102:35–50

Balk H, Lindem T (2002) Sonar4 and Sonar5-Pro post-processing systems. Operator manual. Lindem Data Acquisition

➤ Barber I, Hoare D, Krause J (2000) Effects of parasites on fish behaviour: a review and evolutionary perspective. Rev Fish Biol Fish 10:131–165

➤ Barham EG (1966) Deep scattering layer migration and composition: observations from a diving saucer. Science 151: 1399–1403

Barham EG (1970) Deep-sea fishes lethargy and vertical orientation. In: Farquhar GB (ed) Proceedings of an international symposium on biological sound scattering in the ocean. Ocean Science Program, Washington, DC, p 100–118

➤ Benoit-Bird KJ, Au WWL (2001) Target strength measurements of Hawaiian mesopelagic boundary community animals. J Acoust Soc Am 110:812–819

➤ Benoit-Bird KJ, Au WWL (2006) Extreme diel horizontal migrations by a tropical nearshore resident micronekton community. Mar Ecol Prog Ser 319:1–14

Boden BP, Kampa EM (1967) The influence of natural light on the vertical migrations of an animal community in the sea. Symp Zool Soc Lond 19:15–26

Brede R, Kristensen FH, Solli H, Ona E (1990) Target tracking with a split-beam echo sounder. Rapp P-V Reùn Cons Int Explor Mer 189:254–263

Brierley AS, Saunders RA, Bone DG, Murphy EJ, Enderlein P, Conti SG, Demer DA (2006) Use of moored acoustic instruments to measure short-term variability in abundance of Antarctic krill. Limnol Oceanogr Methods 4:18–29

➤ Cech M, Kubecka J (2002) Sinusoidal cycling swimming pattern of reservoir fishes. J Fish Biol 61:456–471

Cottier FR, Tarling GA, Wold A, Falk-Petersen S (2006) Unsynchronised and synchronised vertical migration of zooplankton in a high Arctic fjord. Limnol Oceanogr 51: 2586–2599

DeRobertis A, Jaffe JS, Ohman MD (2000) Size-dependent visual predation risk and the timing of vertical migration in zooplankton. Limnol Oceanogr 45:1838–1844

Dragesund O, Olsen S (1965) On the possibility of estimating year-class strength by measuring echo-abundance of 0-group fish. Fiskeridir Skr Ser Havunders 13:47–75

➤ Ehrenberg JE, Torkelson TC (1996) Application of dual-beam and split-beam target tracking in fisheries acoustics. ICES J Mar Sci 53:329–334

➤ Engås A, Skeide R, West CW (1997) The 'multisampler': a system for remotely opening and closing multiple codends on a sampling trawl. Fish Res 29:295–298

➤ Everson I, Watkins JL, Bone DG, Foote KG (1990) Implications of a new acoustic target strength for abundance estimates of Antarctic krill. Nature 345:338–340

➤ Foote KG (1987) Fish target strengths for use in echo integrator surveys. J Acoust Soc Am 82:981–987

➤ Genin A, Jaffe JS, Reef R, Richter C, Franks PJS (2005) Swimming against the flow: a mechanism of zooplankton aggregation. Science 308:860–862

Gerritsen J, Strickler JR (1977) Encounter probabilities and community structure in zooplankton: a mathematical model. J Fish Res Board Can 34:73–82

Giske J, Aksnes DL, Ballno BM, Kaartvedt S and others (1990) Vertical distribution and trophic interactions of zooplankton and fish in Masfjorden, Norway. Sarsia 75:65–81

Giske J, Aksnes DL (1992) Ontogeny, season and trade-offs: vertical distribution of the mesopelagic fish *Maurolicus muelleri*. Sarsia 77:253–261

Greene CH, Wiebe PH, Burczynski J (1989) Analyzing zooplankton size distribution using high-frequency sound. Limnol Oceanogr 34:129–139

Handegard NO, Tjøstheim D (2005) When fish meet a trawling vessel: examining the behaviour of gadoids using a free-floating buoy and acoustic split-beam tracking. Can J Fish Aquat Sci 62:2409–2422

Handegard NO, Hjellvik V, Patel R (2005) Tracking individual fish from a moving platform using a split-beam transducer. J Acoust Soc Am 118:2210–2223

Hays GC, Kennedy H, Frost BW (2001) Individual variation in diel vertical migration of a marine copepod: why some individuals remain at depth when others migrate. Limnol Oceanogr 46:2050–2054

Hersey JB, Backus RH (1954) New evidence that migrating gas bubbles, probably the swim-bladders of fish, are largely responsible for scattering layers on the continental rise south of New England. Deep-Sea Res 1:190–191

Holliday DV, Pieper RE (1980) Volume scattering strengths and zooplankton distributions at acoustic frequencies between 0.5 and 3 MHz. J Acoust Soc Am 67:135–146

Huse I, Ona E (1996) Tilt angle distribution and swimming speed of overwintering Norwegian spring spawning herring. ICES J Mar Sci 53:863–867

Janssen J, Sideleva V, Biga H (1999) Use of the lateral line for feeding in two Lake Baikal sculpins. J Fish Biol 54: 404–416

Kaartvedt S, Aksnes DL, Aadnesen A (1988) Winter distribution of macroplankton and micronekton in Masfjorden, western Norway. Mar Ecol Prog Ser 45:45–55

Kaartvedt S, Røstad A, Fiksen Ø, Melle W, Torgersen T, Breien MT, Klevjer T (2005) Piscivorous fish patrol krill swarms. Mar Ecol Prog Ser 299:1–5

Kaartvedt S, Klevjer TA, Torgersen T, Sørnes TA, Røstad A (2007) Diel vertical migration of individual jellyfish (*Periphylla periphylla*). Limnol Oceanogr 52:975–983

Kaartvedt S, Torgersen T, Klevjer TA, Røstad A, Devine JA (2008) Behavior of individual mesopelagic fish in acoustic scattering layers of Norwegian fjords. Mar Ecol Prog Ser 360:201–209

Kerfoot WC, Sih A (eds) (l987) Predation: direct and indirect impacts on aquatic communities. University Press of New England, Hanover, NH

Love RH, Fisher RA, Wilson MA, Nero RW (2004) Unusual swimbladder behavior of fish in the Cariaco Trench. Deep-Sea Res I 51:1–16

Malakoff D (2004) John Delaney profile. Marine geologist hopes to hear the heartbeat of the planet. Science 303: 751–752

McManus MA, Benoit-Bird KJ, Woodson CB (2008) Behavior exceeds physical forcing in the diel horizontal migration of the midwater sound-scattering layer in Hawaiian waters. Mar Ecol Prog Ser 365:91–101

Mehner T (2006) Individual variability of diel vertical migrations in European vendace (*Coregonus albula*) explored by stationary vertical hydroacoustics. Ecol Freshwat Fish 15:146–153

Moore HB (1950) The relation between the scattering layer and the Euphausiaceae. Biol Bull 99:181–212

Mulligan TJ, Chen DG (2000) Comment on 'Can stationary bottom split-beam hydroacoustics be used to measure fish swimming speed *in situ*?' by Arrhenius et al. Fish Res 49: 93–96

Nøttestad L, Fernö A, Mackinson S, Pitcher T, Misund OA (2002) How whales influence herring school dynamics in a cold-front area of the Norwegian Sea. ICES J Mar Sci 59: 393–400

O'Brien WJ, Browman HI, Evans BI (1990) Search strategies of foraging animals. Am Sci 78:152–160

Patel R (2007) Surveillance of marine resources by use of stationary platforms and autonomous underwater vehicle (AUV). PhD thesis, Norwegian University of Science and Technology, Trondheim, Norway

Pearcy WG, Lorz H, Peterson W (1979) Comparison of the feeding habits of migratory and non-migratory *Stenobrachius leucopsarus* (Myctophidae). Mar Biol 51:1–8

Pearre S (2003) Eat and run? The hunger/satiation hypothesis in vertical migration: history, evidence and consequences. Biol Rev Camb Philos Soc 78:1–79

Roe HSJ, Badcock J (1984) The diel migrations and distributions within a mesopelagic community in the north east Atlantic. 5. Vertical migrations and feeding of fish. Prog Oceanogr 13:389–424

Røstad A (2006) Fish behavior and implications for acoustic abundance estimates and ecological research. PhD thesis, University of Oslo, Norway

Soule M, Barange M, Solli H, Hampton I (1997) Performance of a new phase algorithm for discriminating between single and overlapping echoes in a split-beam echosounder. ICES J Mar Sci 54:934–998

Sutton TT, Hopkins TL (1996a) The species composition, abundance, and vertical distribution of the stomiid (Pisces: Stomiidae) fish assemblage of the Gulf of Mexico. Bull Mar Sci 59:530–542

Sutton TT, Hopkins TL (1996b) Trophic ecology of the stomiid (Pisces: Stomiidae) fish assemblage of the eastern Gulf of Mexico: strategies, selectivity and impact of a top mesopelagic predator group. Mar Biol 127:179–192

Thomson RE, Allen SE (2000) Time series acoustic observations of macrozooplankton diel migration and associated pelagic fish abundance. Can J Fish Aquat Sci 57:1919–1931

Torres JJ, Childress JJ (1983) Relationship of oxygen consumption to swimming speed in *Euphausia pacifica*. 1. Effects of temperature and pressure. Mar Biol 74:79–86

Trevorrow MV (2005) The use of moored inverted echo sounders for monitoring meso-zooplankton and fish near the ocean surface. Can J Fish Aquat Sci 62:1004–1018

Warrant EJ, Locket NA (2004) Vision in the deep sea. Biol Rev Camb Philos Soc 79:671–712

Williamson CE (1993) Linking predation risk models with behavioral mechanisms: identifying population bottlenecks. Ecology 74:320–331

Wolf M, Van Doorn GS, Leimar A, Weissing FJ (2007) Life history trade-offs favour the evolution of animal personalities. Nature 447:581–584

Wright DI, O'Brien WJ (1984) The development and field test of a tactical model of the planktivorous feeding of white crappie (*Pomoxis annularis*). Ecol Monogr 54:65–98

Xie Y (2000) A range-dependent echo-association algorithm and its application in split-beam sonar tracking of migratory salmon in the Fraser River watershed. IEEE J Oceanic Eng 25:387–398

Zamon JE, Greene CH, Meir E, Demer DA, Hewitt RP, Sexton S (1996) Acoustic characterization of the 3-dimensional prey field of foraging chinstrap penguins. Mar Ecol Prog Ser 131:1–10

Submitted: February 12, 2008; Accepted: June 23, 2009

Proofs received from author(s): August 21, 2009

Paper 2

A full year study of diel vertical migration of the mesopelagic fish *Maurolicus muelleri* (Gmelin 1789) reveals novel and varied behavioural patterns

Staby, A., Røstad, A., Kaartvedt, S.

(To be submitted to *Marine Ecology Progress Series*)

A full year study of diel vertical migration of the mesopelagic fish *Maurolicus muelleri* reveals novel and varied migration patterns

Arved Staby [1], Anders Røstad [23] and Stein Kaartvedt [23]

[1] Department of Biology, University of Bergen, P O 7803, 5020 Bergen, Norway
[2] Department of Biology, University of Oslo, P O Box 1066 Blindern, 0316 Oslo, Norway
[3] King Abdullah University of Science and Technology, Saudi Arabia

Abstract

We studied the temporal dynamics of the vertical distribution of *Maurolicus muelleri* Scattering Layers (SL) by examining acoustic recordings from a stationary echosounder over a 15 month period (July 2007 – October 2008) in Masfjorden, Norway, complemented by intermittent sampling campaigns. Several novel behaviours were identified. The basic migration pattern of a shallow SL consisting of juvenile fish comprised ascent in the evening, "midnight" sinking shortly after dusk, ascent at dawn with subsequent descent to their daytime depth. However, fish in this layer displayed 'arrested migrations' during its dusk ascent in the period January to March 2008. Instead of completing a full migration to the surface, groups of fish interrupted their ascent at random intervals, returning to deeper waters. The midnight sinking individuals reached progressively deeper depths between dusk and dawn in the course of autumn and early winter. Adult fish constituting a deeper SL carried out normal diel vertical migrations (DVM) in summer, but modified their migration pattern conspicuously during the first autumn of the studies. Most individuals then suspended their migration in the evening, yet ascended toward the surface in the latter part of the night to reach upper layers during dawn, before returning to their daytime depth. This pattern was not observed during the second fall of the studies. Adult *M. muelleri* suspended the nocturnal ascent completely by mid-end November. During the subsequent period a fraction of adult *M. muelleri* performed limited reverse migrations, leaving the main SL and slightly shifting their vertical distribution upwards during the first part of the day. The width of the deep SL was narrowest during summer months June – August, and was broader with a deeper lower border during the period September – May. Our study suggests a range of adaptive, flexible

behaviours of *M. muelleri*, which we explain as a result of ontogeny, state (satiation and hunger), and seasonality in light levels and changes in predation risk.

Introduction

The small mesopelagic fish *Maurolicus muelleri* (Gmelin 1789) displays Diel Vertical Migration (DVM) behaviour for the largest part of its life (3 -5 years; Gjøsæter 1981; Kristoffersen and Salvanes 1998; Hamre 1999). However, in Norwegian fjords the vertical distribution behaviour of this species varies with ontogeny and season (Giske et al 1990; Baliño and Aksnes 1993; Rasmussen and Giske 1994; Bjelland 1995; Goodson et al. 1995; Kaartvedt et al. 1998). Juveniles perform DVM in winter (Giske et al. 1990; Goodson et al. 1995) and feed on shallow distributed zooplankton during dusk and dawn periods (Bagøien et al. 2001). When feeding during the crepuscular periods, juveniles seemingly exploit the antipredation window by foraging at light levels which optimize the trade-off between feeding and minimizing predation risk (Clark & Levy 1988; Rosland 1997). In winter and the beginning of spring juveniles display midnight sinking behaviour after dusk (Giske et al. 1990; Goodson et al. 1995), distributing at deeper depths which may correspond with the temperature maximum (Giske et al. 1990, Giske & Aksnes 1992). During the productive season (March – September; Lopes 1979; Goodson et al. 1995), adult fish carry out DVM (Rasmussen and Giske 1994; Goodson et al. 1995), but remain in deeper waters and suppress DVM in winter (Giske et al 1990; Balino & Aksnes 1993; Goodson et al. 1995). By overwintering at deeper depths adults most likely reduce predation risk in order to increase survival until the next spawning season (Rosland and Giske 1994; Rosland 1997). On light/dusky summer nights dielly migrating *M. muelleri* avoid the uppermost layers and may reduce predation risk by schooling (Kaartvedt et al. 1998).

Although the DVM behaviour of *M. Muelleri* is well understood especially in the winter and autumn periods, with behaviours explained in terms of its ontogeny and a trade off between feeding predation risk, most field studies of *M. muelleri* have only covered time spans of a few days. Consequently, there is little data on short term (weeks) and long term variations (months or years) in behaviour, apart for the main seasonal patterns outlined above.

The lack of long-term data can now be accommodated by new methodological approaches. Increasingly, acoustic data obtained with stationary echosounders are being used to study the behaviour of aquatic organisms (Axenrot et al. 2004; Mehmer 2006; Didrikas & Hansen 2009; Kaartvedt et al. 2009). As *M. muelleri* forms acoustic scattering layers which normally are easily identified, and since it occurs in fjords (i.e. close to land) which greatly simplify logistics, the use of relatively simple, autonomous acoustic setups for uninterrupted observations over long time periods is achievable (Kaartvedt et al. 2009).

In this study, we apply an upward facing echosounder, mounted on the bottom at 400 m depth in Masfjorden, Norway. The system was cabled to shore for continuous power supply and transfer of data, and was operated for a 15 month period. The continuous acoustic measurements were supplemented with intermittent field campaigns with time and depth stratified trawl sampling to assess the composition of the sound Scattering Layers (SL). This approach provided new insights into the migration dynamics and behaviours of the *M. muelleri* population, and we describe here several novel behavioural patterns of *M. muelleri* scattering layers.

Materials and method

The study site was a deep basin in Masfjorden ($60^0$52’77N; $5^0$27’07E), Norway (Figure 1; Kaartvedt et al. 1988). Hydro acoustic data was collected at a 392 m deep location (Figure 1) between 1st July 2007 and 7th October 2008, apart for periods where the system stopped due to power failures (226 complete days were recorded in total). An upward facing Simrad EK60 38 kHz split beam echosounder, rigged on a stainless steel frame, was positioned on the fjord bottom and connected to a land-based laptop via a 1200 m long cable, which also supplied electricity and supported real time data transfer. The pinging rate was set at 0.9 sec^{-1} and the pulse duration was 0.512 ms. A detailed description of the set up is provided in Kaartvedt et al. (2009).

Acoustic data was post processed in MATLAB (The Mathworks) to obtain daily 24 hour echograms. The minimum post processing Sv threshold in MATLAB echograms was set at -80 dB, and the resulting echograms were analysed with regard to the number of visibly discernible SLs during day and night time, and the DVM behaviour of identified SLs. In most months two different *M. muelleri* SLs could be distinguished, and for simplicity reasons we will refer to the deepest SL as DSL and the shallowest SL as SSL. Sporadically a third layer was observed above the SSL, which we identified as consisting of *M. muelleri* post-larvae.

To compile a picture of the yearly midday and midnight depth distribution of the *M. muelleri* SLs, composite echograms of the midday period at 11:30 – 12:30 (9:30 – 10:30 UTC) and midnight period at 23:30 – 00:30 (21:30 – 22:30 UTC) were produced from all recorded days. The composite echograms were made in MATLAB by merging the selected hour for each day the data were collected during the 15 month registration period.

Field campaigns

The continuous acoustic measurements were accompanied by two field campaigns for sampling acoustic scattering layers and collecting environmental data. Acoustic target identification was done with trawling in close proximity of the echo sounder. During 1 – 4 November 2007 the *R.V. Håkon Mosby* (University of Bergen, IMR) and 3 – 7 October 2008 the *R.V. Trygve Braarud* (University of Oslo) collected depth and time stratified samples with pelagic trawls. The trawls were equipped with a remotely controlled Multisampler codend (Engås et al. 1997), which permitted depth-stratified sampling in three intervals. Trawling from *R.V. Håkon Mosby* was done with a Harstad trawl and from *R.V. Trygve Braarud* with a somewhat smaller young-fish trawl. Since the trawls could be opened and closed on demand from the vessel, contamination of the catch as a result of the net fishing while descending and ascending is eliminated, ensuring more representative samples from the targeted acoustic layer. Trawling speed varied between 2 and 3 knots, while trawl duration for each net varied between 5 and 15 minutes. Trawling depth was monitored by Scanmar sensors during sampling. Catches from the three codends were emptied into separate baskets, weighed and sorted according to species. Individual large fish were not included in the weight of the total catch. When possible the standard length of approximately 100 *M. muelleri* was measured. Trawls were grouped into day and night time trawls - in 2007 sunrise and sunset was at 7:00 and 15:30 and in 2008 at 06:00 and 17:00 (UTC). The trawl coverage during both periods was extensive (n = 65), and covered the entire water column between the surface and the bottom at 400 m in both diel periods.

Oceanographic data

Salinity (ppm), temperature (^{0}C), and dissolved oxygen (ml·l^{-1}) were measured with a Seabird 911 CTDO in November 2007 and a Falmouth Scientific, Inc. CTD in October 2008.

Results

Environment

Temperature, salinity and oxygen plots from 2007 and 2008 are shown in Figure 2. In both years temperature (8.6 ^{0}C) and salinity (34.9) below 90 m depth were similar and showed little variation by depth. Above 80 m depth temperature and salinity were less homogenous. Both the thermo- and halocline were more pronounced in 2007 than in 2008. In November 2007 temperature in the upper 60 m varied marginally (10.4 ^{0}C – 11.3 ^{0}C), while over the same depth range in October 2008 it decreased gradually from 14 ^{0}C to 8.5 ^{0}C. Similarly salinity in 2007 varied little above the halocline at 70 m depth (32 to 33), while in 2008 it increased steadily from 31 to 34.9 at 80 m. Oxygen concentrations at the surface (5 – 5.5 $ml \cdot l^{-1}$) decreased to 3.5 – 4 $ml \cdot l^{-1}$ and 2.5 – 3.5 $ml \cdot l^{-1}$ below 100 m in 2007 and 2008 respectively.

Trawl sampling and acoustics during field campaigns

The multisampler generally performed satisfactory during both occasions, adding confidence that catches reflected the species composition of targeted acoustic regions. With the exception of one tow in 2008, which was made at approximately 80 m depth and only had many small transparent *M. muelleri* post-larvae entangled in the netting in front of the multisampler unit and no catch in the cod end, trawls in scattering layers generally contained one or several of the major mesopelagic fish species.

During the two field campaigns, two SLs (SSL at 50 – 75 m and the DSL at 115 – 175 m) were present at daytime in November 2007 (Figure 6), while three SLs (post-larvae at 70 – 90 m, SSL at 110 – 125 m, and the DSL at 155 – 215 m) were observed in October 2008 (Figure 6). In the following section trawl sampling data is cross referenced with these SLs and their corresponding depth intervals.

2007 field campaign

M. muelleri catch rates in the upper 200 m were high (Figure 3) and clearly dominated the species composition of SLs above 200 m depth, irrespective of diel period (Figure 4). During the trawl sampling campaign in November 2007 day time catches at 100 - 150 m (corresponding to DSL depth) were dominated by large (40 mm) *M. muelleri* (Figure 4, 5). Also at 50 – 100 m (corresponding to SSL depth) catches were dominated by *M. muelleri*, but catches were smaller and consisted of smaller individuals (Figures 3, 4, 5). Catches of *M.*

muelleri (20 – 45mm) during night time at 25 – 50 m were low but still higher than any of the other identified mesopelagic fish species (Figures 3, 5), containing 38 % and 23 % *M. muelleri* in terms of numbers and weight respectively (Figure 4). Krill (*M. norvegica*; 19 % of number and 18 % of weight) and shrimp (*P. multidendata*; 38 % of number and 30 % of weight) were, however, caught in corresponding numbers. Night time catch rates of large *M. muelleri* at 150 – 200 m were high (Figure 3, 5).

2008 field campaign

Similar to 2007 high catch rates of *M. muelleri* dominated the species composition of SLs above 250 m depth, irrespective of diel period (Figures 3, 4). The SL at 70 – 90 m in Figure 6l consisted of *M. muelleri* larvae (≈ 11 mm; Figure 5), while trawls at 100 – 150 m (corresponding to SSL depth) and 150 – 200 m (corresponding to DSL depth) caught juvenile (21 mm) and adult (43 mm) *M. muelleri* respectively and contained > 95 % *M. muelleri* in terms of weight and numbers (Figures 4, 5). Similarly, night time trawls at 0 – 25 m had high catch rates of juvenile and adult *M. muelleri* (Figures 3, 5) and contained 74 % and 71 % *M. muelleri* in terms of number and weight respectively (Figure 4). Below 250 m catches were generally dominated by the *B. glaciale* and the shrimp *S. arcticus*, irrespective of diel period (Figure 3). Krill (*M. norvegica*) was the other species, besides *M. muelleri,* caught in large numbers in the upper 25 m during night time (19 % of the catch in terms of weight and number).

Behaviour of shallow scattering layer (SSL)

The SSL ascribed to juvenile *M. muelleri* was present between November and May (Fig. 6). Fish from the SSL performed DVM and displayed midnight sinking between dusk and dawn throughout this period (Figure 6; Figure 7). The depth fish descended to when displaying midnight sinking varied between months, showing an increasing trend until January and a decreasing trend until the beginning of May (Figure 6; Figure 7). Arrested migrations, in which groups of fish arrested their ascent at dusk, were first apparent in mid January and increased in intensity throughout February and stopped beginning of April (Figure 6). Arrested migration fish seized their migration at random depths and descended to deeper depths, spreading over a wide depth range and creating a near continuous layer between 50 – 150 m at night time (Figure 6). Towards April individual SLs increasingly overlapped, with fish from migrating SLs seemingly spreading out at different depths during night time (Figure

6). Prior to the firm establishment of the SSL in October/November, a shallower layer, likely *M. muelleri* post-larvae, was variably present from July/August until October (Figure 6).

Behaviour of the deep scattering layer (DSL)

In both years the DSL displayed normal DVM behaviour during spring and summer months – ascending from ~150 – 200 m at day to the surface in the evening and returning to depth in the morning (Figure 6). The DVM behaviour of the DSL changed in the course of September both years, with an increasing number of fish suspending their dusk migration. By the beginning of October most fish from the DSL stayed at approximately daytime depths after dusk both years (Figure 6). Yet, in 2007 the majority of the population rather ascended during the latter part of the night, starting the ascent already around mid-night, with the fish spending the dawn period in surface waters (Figure 6). This type of behaviour was not recorded in 2008. Also, among the relatively low number of fish migrating to the surface at dusk in October 2007, many returned to depth after a short stay at the top. In October 2008, on the other hand, the small proportion of fish that undertook DVM remained at the surface after dusk and did not descend to deeper depths until the morning (Figure 6).

At the beginning of November only a hazy ascent from and descent to the DSL was observed. At this stage the majority of fish remained at approximately the same depth during day and night time, dispersing in a broad continuous layer (Figure 6). In late November DSL fish seized to undertake normal DVM to upper waters entirely, although the distribution at daytime for the majority of targets was slightly deeper than at night. However, some individuals at this stage started migrating upwards (20 – 30 m) at day time and were clearly separated from the deeper part of the DSL, which simultaneously migrated deeper (Figure 6). After midday, the ‘reverse DVM’ fish merged again with the ascending deeper layer. This behaviour was observed until end of January. By the beginning of February the ‘reverse migrating’ layer increasingly overlapped with the progressively deeper migrating shallower SSL and DSL (Figure 6). Within a two week period, between end of March and beginning of April, the behaviour of the DSL changed, with the large majority of DSL fish performing a complete DVM cycle, migrating to the surface at dusk and back to deeper waters at dawn (Figure 6; Figure 7). In the following spring months the generally dispersed nature of SLs made it difficult to identify individual layers, but it seemed that the DSL and SSL had merged into a single layer by June (Figure 6).

Depth variation of DSL.

As evidenced in Figure 6, the upper and lower boundary as well as vertical extent (thickness) of the DSL varied within and between months. In Figure 7, data from the entire registration period is compiled to assess these patterns for both day and night. The upper border depth of the DSL at mid-day generally varied less than the lower boundary depth, and ranged between 145 – 160 m. The lower border displayed more pronounced seasonal variation. It was shallowest in summer months (< 180 m) and > 200 m in all other months (average depth 215 m). The DSL was narrower (14 – 28 m) during spring and summer months (June – August) compared to all other months (47 – 62 m). The vertical extent of the DSL at night varied slightly between months and ranged between 40 – 60 m (Figure 7). The depth of the upper border ranged between 110 – 150 m and the lower border was mostly between 150 – 190 m (Figure 7). In early autumn 2008 the DSL was deeper distributed (150 – 220 m) than in other months (Figure 2).

Discussion

The present study describes several novel behaviours of SLs observed in a fjord environment over a 15 month period. We have used selected days from different months (periods) to portray the temporal complexity of *M. muelleri* behaviour as single day echograms give superior resolution compared to e.g. long-term averages. However, the results presented here are representative for the selected periods, as documented by Staby et al. (2010), who presented acoustic data from the same investigation as averages for entire months. A comparison of single day echograms with composite monthly echograms (Staby et al. 2010) reveals the same overall patterns.

Layer composition

During the course of this study different Ss throughout the water column were sampled on two occasions, November 2007 and October 2008. Results from these field campaigns are in full concordance with a great number of earlier studies from different parts of the year, identifying the SSL as juvenile *M. muelleri* and the DSL as adult *M. muelleri*. (Kaartvedt et al. 1988; Giske et al. 1990; Baliño & Aksnes 1993; Rasmussen & Giske 1994; Bjelland 1995; Goodson et al. 1995; Bagøien et al. 2001). In addition we for the first time sampled post-larvae *M. muelleri* in the autumn, which likely constituted the shallowest SL at that time when three separate day time SLs were observed. This has not been reported elsewhere. *M. muelleri* has a gas filled swim bladder and resultantly a much higher target strength than invertebrate targets like krill and shrimps (Torgersen & Kaartvedt 2001; Klevjer & Kaartvedt 2006). We are confident therefore that the largest part of acoustic backscattering from the SSL and DSL represent *M. muelleri* throughout the acoustic registration period. The main uncertainty in target identification relates to the lower edge of the DSL. The abundance of the mesopelagic lanternfish *B. glaciale* increased below 200 m, as outlined in Kaartvedt et al. (2009) from this same study, and which was also observed in previous studies (Kaartvedt et al. 1988; Bagøien et al. 2001). Since the lower border of the DSL was often not clearly defined, with the exception in June and July, it is likely that *Benthosema glaciale* to some extent contributed with backscatter in its lower edge at about 200 m and was the dominant target below (Kaartvedt et al. 2009).

Relation to Hydrography

In both years the position of the shallow SLs with regard to the thermo and halocline suggests that hydrography does not strongly influence the vertical distribution of juvenile and post-larvae *M. muelleri*. With the exception of the day time SSL in November 2007, the distribution of juveniles and post-larvae did not seem to correspond with the thermocline and halocline, which are generally located at approximately sill depth between 70 – 90 m (Kaartvedt et al. 1988; Aksnes et al. 1989; Baliño & Aksnes 1993, Bagøien et al. 2001). Shallow SLs more likely change their depth distribution according to changing surface light intensity (Baliño & Aksnes 1993; Staby & Aksnes 2010) than the location of the halo – or thermocline.

Arrested migration

Juvenile *M. muelleri* constituted the SSL between November and April 2008. Arrested migrations in which groups of organisms left this layer and returned to depth in the course of the afternoon ascent were recorded from January to mid-March. Arrested dusk migrations of entire scattering layers have been linked to high surface light intensity on bright summer nights (Kaartvedt et al. 1998). This explanation does not apply here since, in contrast to summer nights, light intensities in winter months are below 0.0001 $\mu E \cdot m^{-2} \cdot s^{-1}$after civil twilight ends (Staby unpublished data). It is also unlikely that this consistent behaviour is affected by the lunar phase or nocturnal light, which can influence the nocturnal depth distribution of micronekton (Benoit-Bird et al. 2009). Juvenile fish however consume copepods in winter months (Srisomwong 2009), and findings from Heath (1999) showed that

Calanus, the most abundant prey for juvenile *M. muelleri* in Masfjorden (Bagøien et al. 2001), ascends from overwintering depths in the Norwegian Sea in mid February, with the ascent lasting several weeks (depending on the initial migration depth). Kaartvedt et al. (2009) observed sprat leaving the migration after a short time during the dusk ascents and suggested that arrested migrations may extend the feeding period of sprat in the anti-predation window (Clark & Levy 1988) while foraging on mid-water *Calanus*. Similarly juvenile *M. muelleri* may forage on seasonally ascending copepods distributed above their daytime depth while following a preferred light level during their ascent (Staby & Aksnes 2010). After becoming satiated fish return to deeper depths. Not all fish displayed this behaviour, but continued their migration to the surface, suggesting possible differences in feeding efficiency.

Midnight sinking

Juvenile *M. muelleri* displayed night time descents (midnight sinking) between October and April. Similarly Giske et al. (1990) observed in January that the night time distribution of juveniles corresponded with the temperature maximum. Distributing at higher temperatures might result in increased fitness (growth) due to higher digestion rates (Giske & Aksnes 1992). However, during the sampling campaign in November 2007 the temperature was relatively constant by depth in the upper 60 m, while the temperature in this layer decreased monotonically by depth in October 2008 (Fig. 2). Juvenile *M. muelleri* nevertheless performed mid-night sinking, so that the temperature does not seem to be the primary factor for this behaviour. We rather suggest that mid-night sinking took place to evade shallow foraging predators by migrating to deeper depths during periods when they do not feed themselves (Staby et. al. 2010). This does not negate that the temperature can modify the nocturnal distribution. The acoustic records demonstrated a deepening nocturnal distribution of the SSL in winter (Fig. 7), which would be in accordance with an expected progressive cooling of the upper waters (e.g. Bagøien et al. 2001). Levy (1990b) showed that the seasonally varying nocturnal distribution of planktivorous juvenile sockeye salmon coincided with changing thermocline depth, and suggested that such behaviour may optimize the metabolic efficiency.

Unlike adult fish juvenile *M. muelleri* presumably have limited lipid reserves, which could be used as an energy source during periods of reduced foraging activity in winter months. Additionally, in contrast to adult fish juveniles may benefit from performing DVM by maintaining growth to reach maturity. The benefits of early maturation could outweigh the greater predation risks associated with this behaviour (Rosland and Giske 1997). Juvenile migrations during the autumn and winter period seem to take place regardless of changes of seasonal factors in the environment as well as energetic state (Rosland and Giske 1997).

Behaviour of adult M. muelleri (DSL)

Adult *M. muelleri* performed DVM between April and September/October, consistent with findings from earlier studies (Rasmussen & Giske 1994; Bjelland 1995; Goodson et al. 1995). During this period, fish feed extensively on shallow distributed zooplankton during the crepuscular periods (Bjelland 1995; Rasmussen & Giske 1995), investing energy in gonad development and build up of its energy (lipid) reserves before the onset of the next winter period (Falk-Peterson et al. 1986). In spring and summer the vertical extent of the DSL was narrower than in other months. Surface irradiance is highest in the period June to August (Staby and Aksnes 2010), and thus by reducing their vertical spread, i.e. and forming a denser layer, adult fish may reduce predation risk during day time. The alternative of descending deeper might expose them to predators below, specialized to forage at the low light intensities at depth (Kaartvedt et al. 2009). Yet light conditions depend both on surface light and the water light extinction, underlining the need for *in situ* light measurements in evaluating light responses for deep-living fish.

Early morning vertical migrations

From latter half of September to the end of October 2007 a large proportion of adult *M. muelleri* did not migrate to the surface at dusk, but remained at depth during night time, only to migrate to be at the surface the following morning. This is to the best of our knowledge a novel observation. A possible explanation for the general lack of an evening ascent might be that adult fish this year had foraged adequately enough on deep-living prey at day to suppress a hunger sensation past dusk, restraining fish from migrating to surface waters to feed. According to this argument, food conditions at the daytime depth of *M. muelleri* would have been poorer the subsequent fall, when *M. Muelleri* performed normal DVM in the evening. Results from plankton tows support this hypothesis. The concentrations of overwintering *Calanus* in midwaters are at a seasonal high in the fall, and they occur in maximum abundance at depths inhabited by the DSL (Bagøien et al. 2001). Srisomwong (2009) found relatively high concentrations (> 100 ind m^{-3}) of copepods at 150 – 200 m depth early November 2007; while numbers of deep-living copepods were about an order of magnitude lower early October the subsequent fall (e.g. only 4 *Calanus* m^{-3}; Dypvik 2010). As *M. muelleri* does not feed at night time (Giske et al. 1990; Srisomwong 2009), hunger would motivate ascent in the morning, as long as there is sufficient food in the surface layer for taking the risk. Fish migrated to the surface after midnight within an approximately three hour long window, reaching the surface before civil twilight start. Since at the time of departure light is absent, this behaviour cannot be linked to any increase or change in light intensity and is more likely the result of endogenous rhythmicity. We suggest therefore that hunger could be a possible cause for such night time vertical ascents (Pearre 2003).

Overwintering at depth and reverse DVM

Between the end of November 2007 and mid March 2008 adult *M. muelleri* from the DSL suspended their migration to the surface at dusk entirely. By remaining at depth, as opposed to performing DVM, adult *M. muelleri* may reduce predation risk during periods with scant surface concentrations of zooplankton. By avoiding shallow foraging predators (Staby et al. 2010), they increase the likelihood of survival and thus future reproductive output during the next spawning season (Giske & Aksnes 1992; Rosland & Giske 1994; Rosland & Giske 1997). This change in behaviour implies that adult fish are able to survive at depth through feeding on deep distributed overwintering copepods at day time (Giske et al. 1990; Bagøien et al. 2001) and / or by using lipid reserves (Falk-Petersen et al. 1986; Hulley & Prosch 1987). Yet, the proportion of overwintering adults feeding on copepods at daytime and the number of copepods ingested is probably relatively low (Bagøien et al. 2001; Srisomwong 2009), with feeding rates at best sufficient to maintain zero growth (Giske & Aksnes 1992; Rosland & Giske 1997).

During this winter period without normal DVM, a proportion of adults displayed reverse DVM by moving approximately 20 – 30 m higher up in the water column before mid-daytime and down again after noon. This behaviour has not been described for *M. muelleri* before and generally few studies have described reverse diel vertical migrations among fish (Levy 1990a; Neilson and Perry 1990; Kaartvedt et al. 2009). While a short ascent into a brighter environment might increase the predation risk (Rosland & Giske 1997, Staby et al. 2010), feeding conditions can be improved with enhanced visibility and higher encounter rates with deep distributed copepods (Giske & Aksnes 1992; Vogel & Beauchamp 1999; Bagøien et al. 2001). Kaartvedt et al. (2009) suggested that deep distributed *B. glaciale* displayed reverse DVM during daytime in order to improve light conditions for feeding on *Calanus,* which typically overwinter at 150 – 200 m (Giske et al.1990, Kaartvedt 1996, Bagøien et al. 2001). Reverse diel migrations of some *M. muelleri* may thus be the result of improved feeding on the upper fringe of the overwintering population of *Calanus*. It should be noted that during the same period high counts of large fish seemingly performing DVM were observed between the reverse migrating fish and the deeper *M. muelleri* layer (Staby et al. 2010), suggesting that reverse migrating fish may take greater risks associated with their feeding.

In summary, this study has unveiled more flexible diel vertical migration patterns of *Maurolcius muelleri* than previously reported. It underlines the strength and possibilities offered by continuous measurements from acoustic moorings and gives ground for formulating future sampling programs that will further aid in interpretations of the results.

Acknowledgements

This study would not have been possible without the support of the Institute for Maine Research at Matre, which kindly made their infrastructure at Solheim (Masfjorden) available to us for this study, Jan Olav Fosse, Thor A. Klevjer, as well as the crew and students from the Universty of Bergen and University of Oslo onboard the *RV H. Mosby* and *RV T. Braarud.*

References

Aksnes DL, Aure J, Kaartvedt S, Magnesen T, Richard J (1989) Significance of advection for the carrying capacities of fjord populations. Mar Ecol Prog Ser 50: 263-274

Axenrot T, Didriakas T, Danielsson C, Hansson S (2004) Diel patterns in pelagic fish behaviour and distribution observed from a stationary, bottom-mounted, and upward-facing transducer. ICES J Mar Sci 61:1100-1104

Bagøien E, Kaartvedt S, Aksnes DL, Eiane K (2001) Vertical distribution and mortality of overwintering *Calanus*. Limnol Oceanogr 46:1494-1510

Baliño BM, Aksnes DL (1993) Winter distribution and migration of the sound scattering layers, zooplankton and micronekton in Masfjorden, western Norway. Mar Ecol Prog Ser 102: 35-50

Benoit-Bird KJ, Au WWL, Wisdom DW (2009) Nocturnal light and lunar cycle effects on diel migration of micronekton. Limnol Oceanogr 54:1789-1800

Bjelland O (1995) Life-history tactics of two fjordic populations of *Maurolicus muelleri*. Cand Scient thesis, University of Bergen, 79 pages

Clark CW, Levy DA (1988) Diel vertical migrations by juvenile sockeye salmon and the antipredation window. Am Nat 131:271-290

Didrikas T, Hansson S (2009) Effects of light intensity on activity and pelagic dispersion of fish: studies with a seabed-mounted echosounder. ICES J Mar Sci 66:388–395

Dypvik E (2010) Invers døgnvandring og fødebiologi hos nordlig lysprikkfisk (*Benthosema glaciale*) i Masfjorden. Master thesis, University of Oslo, 69 pages

Falk-Petersen I-B, Falk-Petersen S, Sargent JR (1986) Nature, origin and possible roles of lipid deposits in *Maurolicus muelleri* (Gmelin) and *Benthosema glaciale* (Reinhart) from Ullsfjorden, northern Norway. Polar Biol 5:535-540

Giske J, Aksnes DL, Balino BM, Kaartvedt S, Lie U, Nordeide JT, Salvanes AGV, Wakili SM, Aadnesen A (1990) Vertical distribution and trophic interactions of zooplankton and fish in Masfjorden, Norway. Sarsia 75:65-81

Giske J, Aksnes DL (1992) Ontogeny, season and trade-offs: Vertical distribution of the mesopelagic fish *Maurolicus muelleri*. Sarsia 77:253-261

Gjøsæter J (1981) Life history and ecology of *Maurolicus muelleri* (Gonostomatidae) in the Norwegian waters. Fiskeridirektoratets Skrifter, Serie Havundersøkelser 17:109-131

Goodson MS, Giske J, Rosland R (1995) Growth and ovarian development of *Maurolicus muelleri* during spring. Mar Biol 124:185-195

Hamre LA (1999) Growth and mortality of *Maurolicus muelleri* (Gmelin): Do parasites matter? Cand Scient thesis, University of Bergen, 87 pages

Heath MR (1999) The ascent migration of *Calanus finmarchicus* from overwintering depths in the Faroe-Shetland Channel. Fish Oceanogr 8:84-99

Hulley PA, Prosch RM (1987) Mesopelagic fish derivatives in the southern Benguela upwelling region. S Afr J Mar Sci 5:597-611

Kaartvedt S, Aksnes DL, Aadnesen A (1988) Winter distribution of macroplankton and micronekton in Masfjorden, western Norway. Mar Ecol Prog Ser 45:45-55

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

Kaartvedt S, Knutsen T, Holst JC (1998) Schooling of the vertically migrating mesopelagic fish *Maurolicus muelleri* in light summer nights. Mar Ecol Prog Ser 170:287-290

Kaartvedt S, Røstad A, Klevjer T, Staby A (2009) Use of bottom-mounted echo sounders in exploring behavior of mesopelagic fishes. Mar Ecol Prog Ser 395:109-118

Klevjer TA, Kaartvedt S (2006) In situ target strength and behaviour of northern krill (*Meganyctiphanes norvegica*). ICES J Mar Sci 63:1726-1735

Kristoffersen, J.B. Salvanes, A.G. (1998) Life history of *Maurolicus muelleri* in fjordic and oceanic environments. J Fish Biol 53:1324-1341

Levy DA (1990a) Reciprocal diel vertical migration behaviour in planktivores and zooplankton in British Columbia lakes. Can J Fish Aquat Sci 47:1755-1764

Levy DA (1990b) Sensory mechanism and selective advantage for diel vertical migration in juvenile sockeye salmon, *Oncorhynchus nerka*. Can J Fish Aquat Sci 47:1796-1802

Lopes PC (1979) Eggs and larvae of *Maurolicus muelleri* (Gonostomatidae) and other fish eggs and larvae from tow fjords in western Norway. Sarsia 64:199-210

Mehner T (2006) Individual variability of diel migrations in European vendance (*Coregonus albula*) explored by stationary vertical hydroacoustics. Ecol Freshw Fish 15:146-154

Neilson JD, Perry RI (1990) Diel vertical migrations of marine fishes: an obligate or facultative process? Adv Mar Biol 26:115-167

Pearre S Jr (2003) Eat and run? The hunger satiation hypothesis in vertical migration: history, evidence and consequences. Biol Rev 78:1-79

Rasmussen OI, Giske J (1994) Life-history parameters and vertical distribution of *Maurolicus muelleri* in Masfjorden in summer. Mar Biol 120:649-664

Rosland R, Giske J (1994) A dynamic optimization model of the diel vertical distribution of a pelagic planktivorous fish. Progr Oceangr 34:1-43

Rosland R (1997) Optimal responses to environmental and physiological constraints: evaluation of a model for a planktivore. Sarsia 82:113-128

Rosland R, Giske J (1997) A dynamic model for the life history of Maurolicus muelleri, a pelagic planktivorous fish. Fish Oceanogr 6:19-34

Srisomwong J (2009) Diel vertical migration and feeding pattern of *M. muelleri* in
Masfjorden in late autumn. Master thesis, University of Bergen, 36 pages

Staby A, Aksnes DA (2010) Follow the light - the vertical distribution of the mesopelagic fish *Maurolicus muelleri* (Gmelin 1789) with regard to diurnal and seasonal variations in surface irradiance. Manuscript

Staby A, Røstad A, Salvanes AGV, Kaartvedt S (2010) Seasonal occurrence and vertical migration of potential predators of *Maurolicus muelleri* (Gmelin 1789). Manuscript

Torgersen T, Kaartvedt S (2001) In situ swimming behaviour of individual mesopelagic fish studied by split-beam echo target tracking. ICES J Mar Sci 58:346-354

Vogel JL, DA Beauchamp (1999) Effects of light, prey size, and turbidity on reaction distances of lake trout (*Salvelinus namaycush*) to salmonid prey. Can J Fish Aquat Sci 56:1293-1297

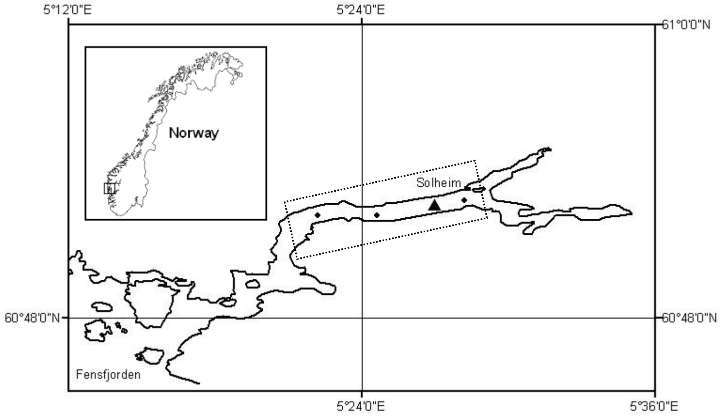


Figure 1: Figure 1: Masfjorden on the west coast of Norway, showing the position of the 38 kHz transducer (▲) at approximately 400 m depth, and oceanographic stations (•). Trawl sampling of the mesopelagic community was done within the dotted rectangle.

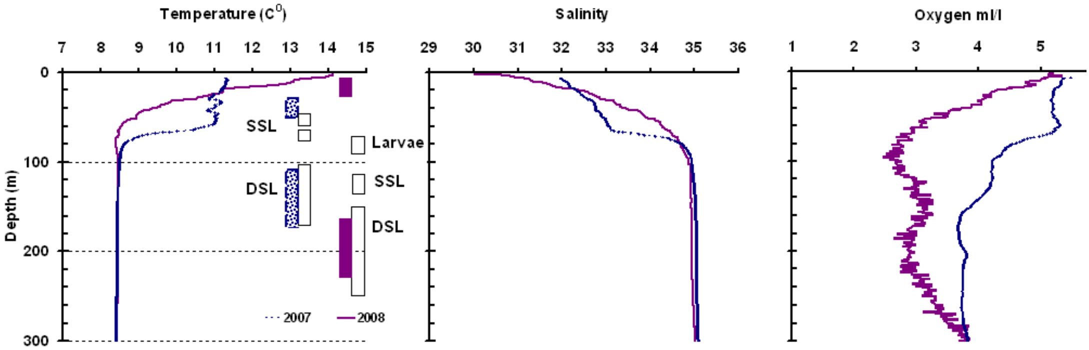


Figure 2: Temperature, salinity and oxygen profiles from Masfjorden November 2007 and October 2008. Bars (left 2007, right 2008) indicate approximate day time (open bars) and night time (filled bars) depth ranges of different (identified by abbreviations) *M. muelleri* scattering layers.

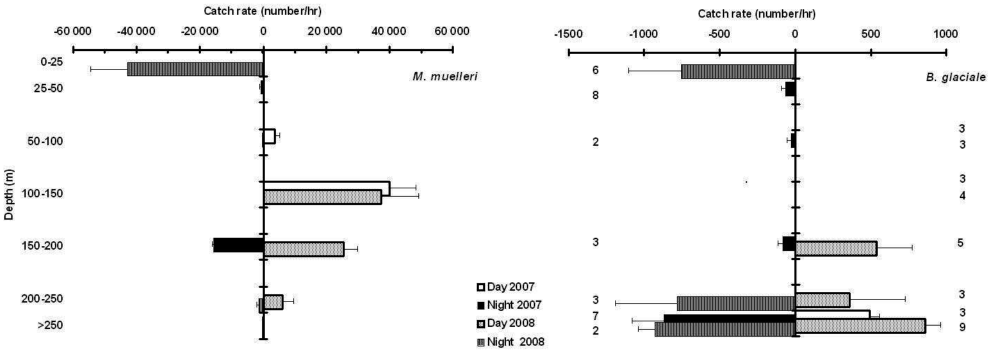


Figure 3: Average day and night time catch rates of *M. muelleri* and *B. glaciale* by depth range during November 2007 and October 2008 (the scale of catch rates varies between species). Error bars indicate the Standard Error of the average, while the number of trawls in each depth range is indicated on the left and right in the right hand graph.

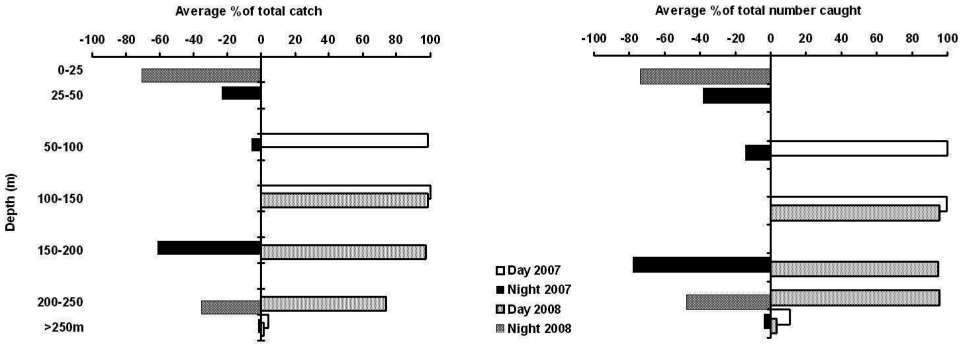


Figure 4: Average percentage *M. muelleri* of the total catch in a) weight and b) number per depth range.

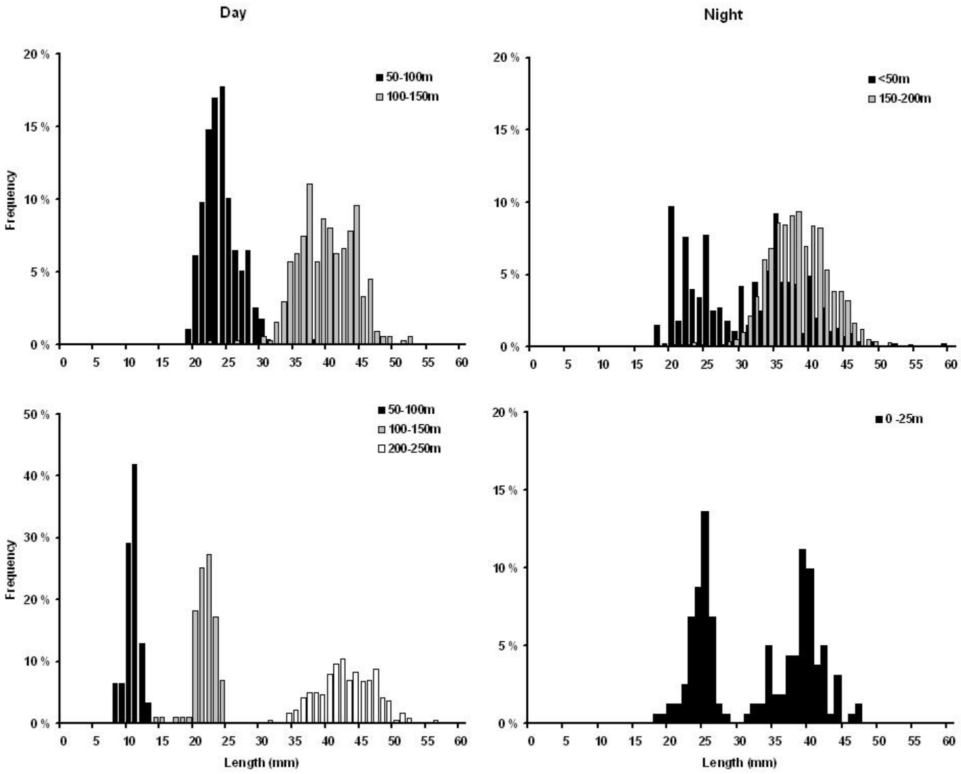
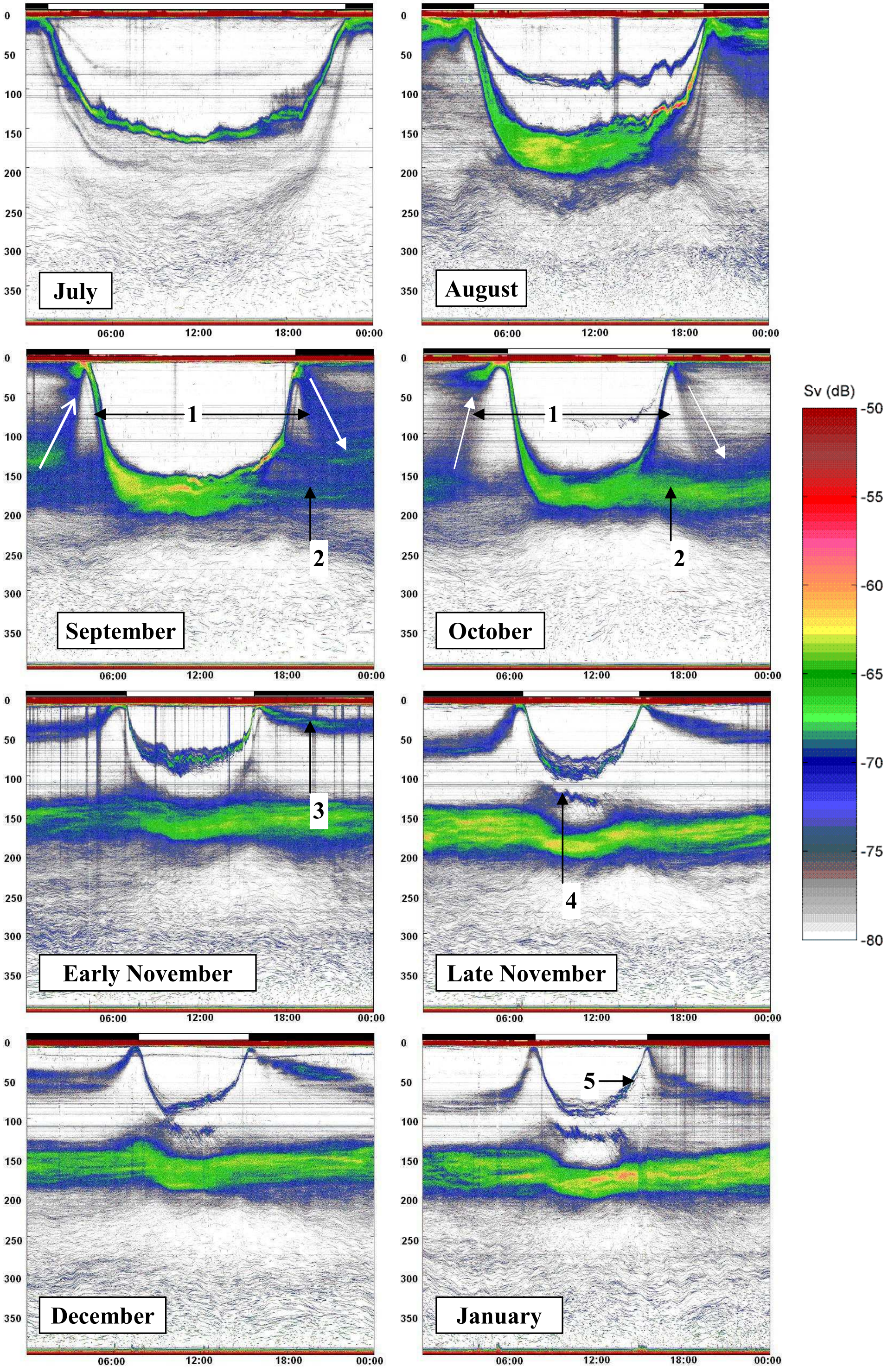
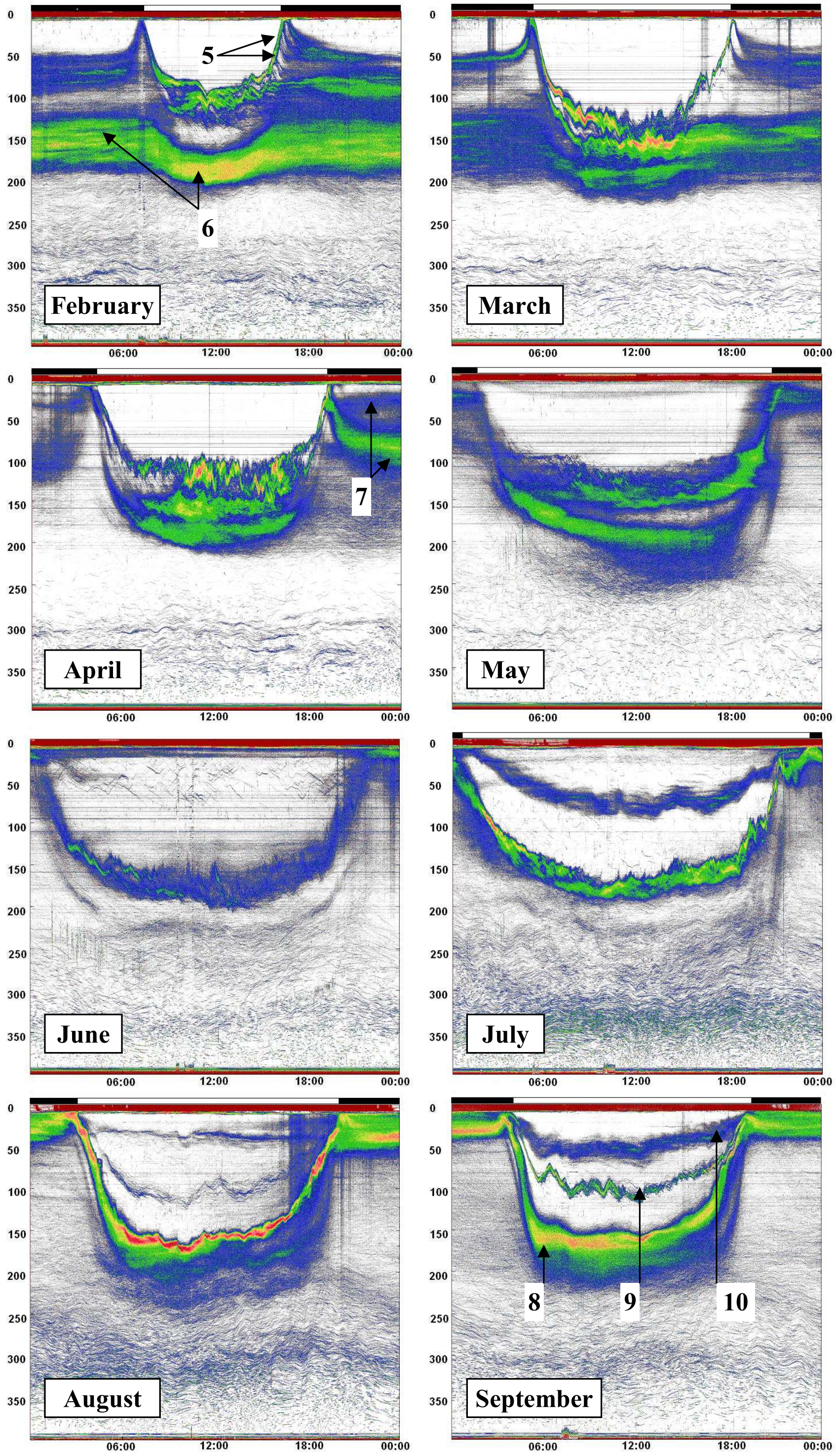


Figure 5: Length frequency distributions of *M. muelleri* during day (left) and night time (right) at different depth ranges in 2007 (top) and 2008 (bottom).


July
August
September
October
Early November
Late November
December
January
0
50
100
150
200
250
300
350
06:00
12:00
18:00
00:00
1
2
3
4
5
Sv (dB)
-50
-55
-60
-65
-70
-75
-80


February
March
April
May
June
July
August
September
0
50
100
150
200
250
300
350
06:00
12:00
18:00
00:00
5
6
7
8
9
10

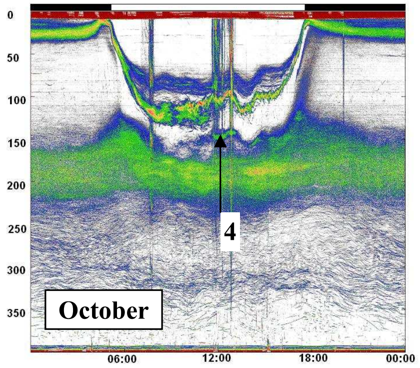


Figure 6: Daily echograms from selected months in 2007 (July to December) and 2008 (January to October). 1) Adult *M. muelleri* migrating to the surface long before dawn and descending after a short dusk stay, 2) non-migrators, 3) midnight sinking of juvenile *M. muelleri* between dusk and dawn, 4) reverse DVM, 5) arrested migration, 6) beginning of diel vertical migration, 7) midnight sinking to different depths, 8) adult pearlside layer, 9) juvenile layer, and 10) larvae layer (based on 2008 trawl data). At the top of each echogram corresponding dark and light hours (start and end of civil twilight) are indicated by dark and open bars respectively.

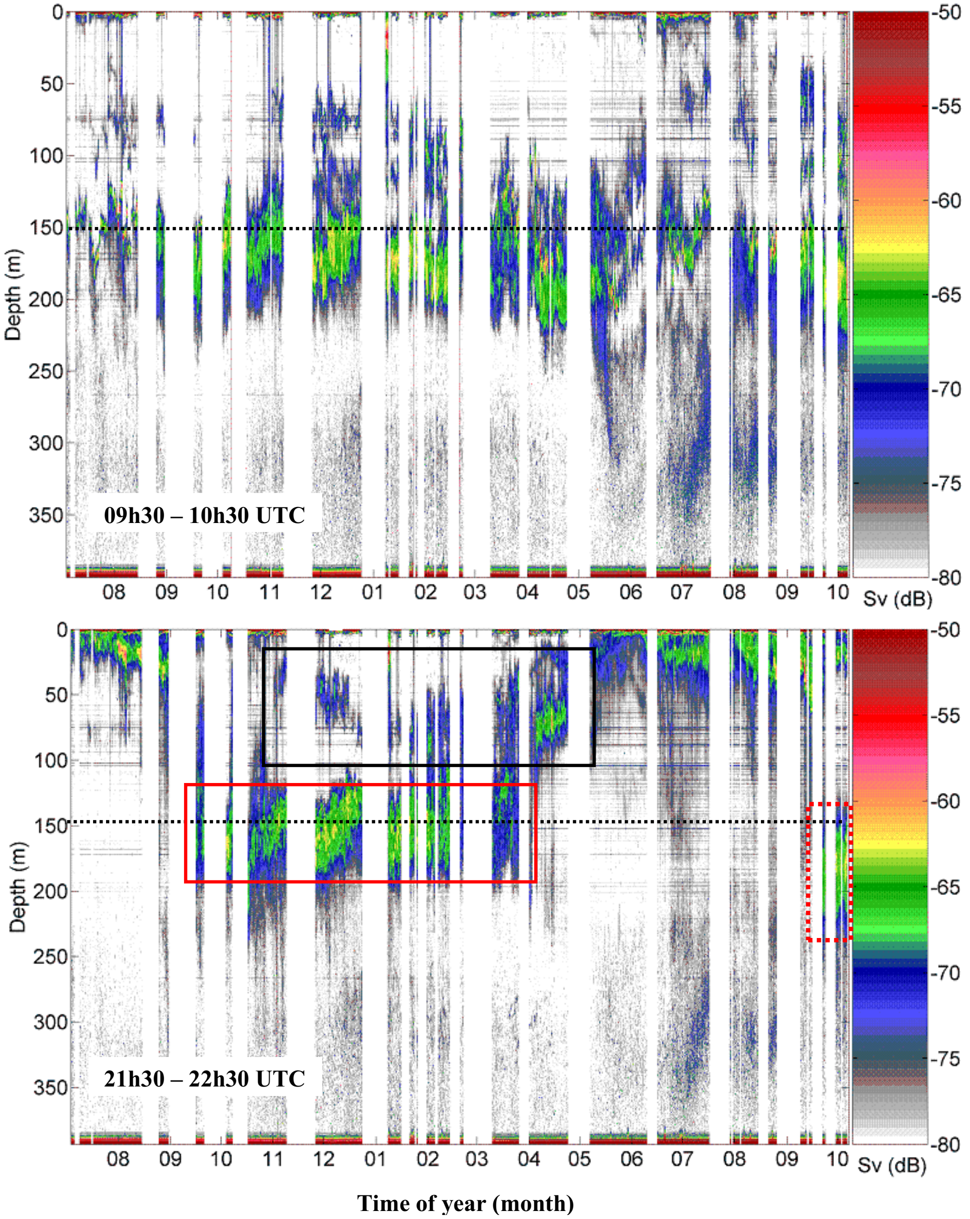


Figure 7: Composite echograms of the midday (09h30 – 10h30 UTC) and midnight (21h30 – 22h30 UTC) sections of all recorded days in 2007 (08 - 12) and 2008 (01 – 10). During the overwintering period from September 2007 until April 2008 (red rectangle) and the start of the overwintering period in September 2008 (dotted red rectangle) adult *M. muelleri* do not migrate to the surface at dusk but stay at deep depths at night time. Between November and May juvenile *M .muelleri* displayed midnight sinking (black rectangle). White regions indicate missing days where no acoustic data was recorded.

Paper 3

Follow the light – diurnal and seasonal variations in vertical distribution of the mesopelagic fish *Maurolicus muelleri*

Staby, A., Aksnes, D.

(To be submitted to *Marine Ecology Progress Series*)

3

Follow the light – diurnal and seasonal variations in vertical distribution of the mesopelagic fish *Maurolicus muelleri*

Arved Staby and Dag L. Aksnes

University of Bergen, Department of Biology, P O Box 7803, 5020 Bergen, Norway

Abstract

Previous one day studies of the mesopelagic fish *Maurolicus muelleri* suggest that their vertical distribution changes as if they were following a constant light intensity, sometimes denoted isolume. Here we investigate whether such behaviour is consistent under varying light conditions and over an extended time period. We analyse acoustical observations of ontogenetically varying Scattering Layers (SL) versus surface irradiance from selected days during a 9 month period (January – September 2008). Our results suggest that the SLs of *M. muelleri* have a restricted range of preferred light intensities rather than a very precise isolume. This tendency was found regardless of season and migration phase, i.e. during dawn descent, dusk ascent, and daytime. The light intensity estimated at the top of the upper SL for consecutive days, regardless of migration phase, varied on average by less than 1 order of magnitude, while the average monthly estimates for the descent, ascent and daytime periods varied from 0.004 – 0.39 $\mu E \cdot m^{-2} \cdot s^{-1}$, 0.08 – 2.35 $\mu E \cdot m^{-2} \cdot s^{-1}$ and 0.02 – 0.68 $\mu E \cdot m^{-2} \cdot s^{-1}$ respectively. During their ascent fish experienced up to 9 times higher light intensities than during the descent, which might be explained in terms of different physiological states (e.g. hunger level). Our study suggests that the vertical migration of *M. muelleri* emerges as a result of a vertical habitat selection that can be characterized by the preference of a restricted range of light intensities and that these intensities might be state (e.g. hunger related) and age dependent.

Introduction

Light is an environmental variable that together with abiotic (e.g. temperature or oxygen) and biotic factors (food abundance or predator density) determines the habitat fish occupy in the pelagic environment (McFarland 1986; Metcalf et al. 2008). Visually foraging fish require light to sustain feeding (Eggers 1978; Aksnes & Utne 1997; Ryer & Olla 1999), but also the anti predator behaviour of many fish appears to be affected by light (Ryer & Olla 1998; Kaartvedt et al. 1998). Changes in the vertical distribution of fish have thus been associated with concurrent changes in surface irradiance (Roe 1983; Baliño & Aksnes 1993; Rasmussen & Giske 1994; Kaartvedt *et al.* 1996; Frank & Widder 2002).

The pelagic environment offers few possibilities for fish to hide from predators. Small pelagic planktivorous fish may reduce the risk of predation by schooling, lessening their conspicuousness through camouflage, or by migrating into waters with reduced light intensity (Pitcher 1993; Appenzeller & Heggett 1995; Warrant & Locket 2004). This has also been suggested for the mesopelagic pearlside *Maurolicus muelleri*, which probably reduces predation risk by visually foraging predators by performing vertical migrations (Giske *et al.* 1990; Rosland & Giske 1997).

Different ontogenetic stages of *M. muelleri* form distinct homogenous sound Scattering Layers (SLs) at different depths during day and night time (Giske et al. 1990; Baliño & Aksnes 1993; Staby et al. 2010). The species inhabits deeper waters during day time, ascends to the surface at dusk to feed during the crepuscular periods (Bagøien et al. 2001), and descends again to day time depth as surface light intensity increases at dawn. *M. muelleri* possibly takes advantage of the ‘anti-predation window’ during the crepuscular hours, by foraging at a light level with reduced predation risk (Clark & Levy 1988; Appenzeller & Heggett 1995; Scheuerell & Schindler 2003).

Which aspect of changing light intensity is governing the migrations in fish? Whether it is the change in absolute light intensity (Widder & Frank 2001), the relative rate of change in light intensity (Ringelberg 1995; Ringelberg & van Gool 2003), a certain light threshold that is required to initiate a behavioural response (Sweatt & Forward 1985), or other unrevealed mechanisms is not entirely clear (Neilson & Perry 1990; Johnsen 2005). Several studies of planktonic organisms suggest that the relative rate of change in light intensity is the proximate cause and initiating cue of DVM (Ringelberg 1995; Cohen & Forward 2009), although a recent study of the deep water jellyfish *Periphylla periphylla* (Dupont et al. 2009) suggests that migration at the population level can be ascribed to a preference of a certain light range at the individual level. Studies of planktivores also suggest that fish follow a preferred light intensity during their migrations (Eggers 1978; Bohl 1980; Appenzeller & Leggett 1995).

M. muelleri is known to change its vertical position instantaneously with changing surface light levels, not only during dusk and dawn, but also during daytime (Giske et al. 1990; Baliño & Aksnes 1993; Rasmussen & Giske 1994; Kaartvedt et al. 1998). As has been hypothesized for *P. periphylla* (Dupont et al. 2009) this behaviour suggests that the individuals prefer a certain light range during daytime as well as during dusk and dawn. At the population level such behaviour might appear as if the individuals (i.e. the population average) follow a preferred light intensity, a so called isolume. To what extent the vertical distribution of *M. muelleri* can be characterized by such behaviour beyond the daily time scale is unknown.

In the present study we therefore investigate the relationship between variations in the depth distribution of *M. muelleri* and the variations of incoming surface irradiance beyond the daily time scale such as consecutive days with similar and dissimilar sky conditions. We hypothesize that the variations in the depth of the SL's of *M. muelleri* can be accounted for by proximate isolume behaviour, i.e. that *M. muelleri* relocate vertically to keep the ambient light intensity constant. If this applies the depth of the SLs is expected to be linearly related to the logarithm of the surface light intensity (See Methods). Here we test this expectation by analysing continuously recorded surface irradiance and acoustic data from selected days in a nine month period (January – September 2008).

Materials and Methods

The study location was Masfjorden ($60^0$50' N; $5^0$25' E) on the west coast of Norway (Kaartvedt et al. 1988). Surface irradiance (Photosynthetically Active Radiation (PAR) at 400 – 700 nm) was collected between January 2008 and September 2008, and was measured with a calibrated LI-190 quantum sensor (LI-COR Biosciences) and stored on a LI-1400 data logger (LI-COR Biosciences, Lincoln, Nebraska). Irradiance was sampled every 30 seconds and averages logged every 15 minutes. The sensor was mounted approximately 2 m above the sea surface with minimal obstruction (shadowing) from surrounding structures. During the same period acoustic data of the entire water column was recorded with an upward facing EK60 38 kHz split beam echosounder (SIMRAD) mounted at the bottom (392 m) and located approximately one kilometre away from the location of the quantum sensor. The echosounder settings are described in detail in Kaartvedt et al. (2009). In Masfjorden daytime SLs above 200 m are practically homogenous and dominated (> 95 % in terms of number and weight) by *M. muelleri* (Kaartvedt et al. 2009; Staby et al. 2010).

Scattering layer depth estimation

Data presented in this study is from selected paired (consecutive) days, which either had nearly identical (sunny or overcast) or dissimilar (sunny versus overcast) surface light intensity, as well as clearly distinguishable SLs from the period January to September 2008. SLs in June were generally hazy and diffuse, and it was thus not possible to obtain reliable depth estimates for this month. For all other months we obtained depth estimates of the upper border of different SLs, and estimated the depth of the shallowest SL (SSL) in January – April and the depth of the deep SL (DSL) in May – September. Acoustic data from the upper 250 m recorded in periods when surface PAR was higher than the threshold sensitivity for the irradiance sensor (0.0001 $\mu E \cdot m^{-2} \cdot s^{-1}$) was divided into 10 minute (horizontal) and 1 m (vertical) bins. The average volume backscattering (Sv) – the amount of acoustic energy reflected by 1 m^{-3} – was calculated for each bin using the biomass calculation setup in SONAR5-PRO (Balk & Lindem 2009). The upper boundary of a SL was then defined as the depth where the average Sv dropped below -75 dB. The depth estimates were plotted against time and superimposed on daily echograms to asses how well they corresponded with the SLs.

Data analysis

Although it is likely that fish have a preferred range of light intensities rather than a particular intensity, we simplify and assume a single value in our analysis, a so called isolume, and report on the variation in this estimate. The hypothesis that fish stay at a depth following an isolume (given as the downwelling irradiance, E_{iso}), can be expressed:

$$E_{iso} = E_0 e^{-KZ_{iso}} \qquad (1)$$

where Z_{iso} is the isolume depth, E_0 is surface irradiance, and K the attenuation coefficient for downwelling irradiance. Solving equation (1) for Z_{iso}

$$Z_{iso} = \frac{1}{K}\ln E_0 - \frac{1}{K}\ln E_{iso} \qquad (2)$$

Equation (2) is of the form $y = ax + b$, where the slope a equals $\frac{1}{K}$, x equals $\ln E_0$, and the intercept b equals $-\frac{1}{K}\ln E_{iso}$ which according to the above isolume hypothesis should be a constant (as long as K can be regarded constant). Thus the expectation is that changes in the depth of the SL (which is an assumed estimate of Z_{iso}) that were obtained from the acoustical observations should be linearly related to the changes in $\ln E_0$ that were obtained by the PAR sensor. This assumes invariant attenuation coefficient (the rate at which light is reduced as a result of absorption and scattering) and we therefore applied measurements of consecutive days to minimize possible variations in the inherent optical properties of the water column. Since K is an apparent property that is also affected by the angular distribution of light (e.g. affected by the sun elevation and cloudiness) some variations in K are expected. Based on previous observations of K in Masfjorden it appears fairly stable below 40 – 50 m depth (Giske et al. 1990; Baliño & Aksnes 1993), but the K in Eq. (2) represents the average attenuation between the surface and the actual depth and will therefore be somewhat affected by variations in angular distribution of light, e.g. as would be between a cloudy and sunny day. Despite these uncertainties concerning K, we investigated to what extent Eq. (2) could account for the observed variations in the depth of the SLs during entire day periods, as well as for limited periods during the observed dawn descents and dusk ascents. The analyses were limited to periods when $E_0 > 0.0001\ \mu E \cdot m^{-2} \cdot s^{-1}$ and the estimated Z_{iso} was deeper than 40 m.

The hypothesis of a preferred light intensity implies Z_{iso} to be similar on consecutive days with similar surface irradiance (e.g. two sunny days), and to be different on days with dissimilar surface irradiance (e.g. a sunny versus a cloudy day). The ascent and descent periods around dawn and dusk were defined as follows: fish descended / ascended as long as the difference of subtracted successive depth estimates was positive / negative, while the migration ended when either zero or negative / positive values were obtained.

Equation 2 can be rearranged such that:

$$\frac{b}{a} = \frac{-\frac{1}{K}\ln E_{iso}}{\frac{1}{K}} = -\ln E_{iso} \qquad (3)$$

Thus the light intensity of the isolume E_{iso} at depth Z_{iso} can be estimated according to:

$$E_{iso} = e^{-\frac{b}{a}} \tag{4}$$

It should be noted that an implicit assumption to this expression is invariant K during the period of observation.

Statistical analysis

Similarity of regression slopes was tested by applying an analysis of regression slope homogeneity in STATISTICA 8 (StatSoft 2010). In the homogeneity-of-slopes model the dependant variable was depth (Z_{iso}), the continuous predictor $\ln E_0$, and the categorical independent variable date (day).

Results

Consecutive days with similar light intensity

Maximum surface irradiance (1250 – 1500 $\mu E \cdot m^{-2} \cdot s^{-1}$) was 12 – 15 times higher on sunny days in April and May than on overcast days in January (< 100 $\mu E \cdot m^{-2} \cdot s^{-1}$; Figure 1). Irradiance increased until midday (11h30 – 12h00 UTC) and decreased in a similar pattern, with few irregular fluctuations in light intensity over the course of a day (Figure 1). The light intensity fell abruptly at 16h30 and 17h00 in April and May respectively, probably as a result of the sun disappearing behind mountains surrounding the fjord.

The depth variations of the SLs upper border reflected the variations in the logarithmic surface irradiance and were 50 – 70 m deeper at midday in April and May than in January (Fig 1). Depth estimates of the SL descents and ascents of consecutive days overlapped temporally, while the SL depth difference between consecutive days in May was at times 10 – 20 m.

Consecutive days with dissimilar light intensity

Consecutive days with different light intensities in February, March, and July to September are shown in Figure 2. Two partially overcast days in February had high irradiance variations with between day differences up to 400 $\mu E \cdot m^{-2} \cdot s^{-1}$. In March light levels were approximately five times higher on the 21st compared to the 20th. However, on 21st March irradiance did not follow the symmetrical dome-shaped distribution, which is typical for an entirely sunny day. The 10th July was an entirely sunny day (1500 $\mu E \cdot m^{-2} \cdot s^{-1}$ at midday), compared to the overcast 13th July (620 $\mu E \cdot m^{-2} \cdot s^{-1}$). The 8th August had some irregular irradiance measurements but was otherwise sunny, while the 13th September was an entirely sunny day (Figure 1c). Differences between average daily irradiance were 370 $\mu E \cdot m^{-2} \cdot s^{-1}$ and 425 $\mu E \cdot m^{-2} \cdot s^{-1}$ in August and September respectively.

With the exception of the deep scattering layers (DSL) in September (Figure 2e), SLs were deeper distributed when corresponding surface irradiance measurements were higher (Figure 2a – 2d). The average difference in depth of the upper SL edge on consecutive days (calculated as the average depth between the end of the descent and the start of the ascent) was approximately 15, 30, 20 and 20 m in February, March, July and August respectively.

Regressions

The estimated regression equations (see Eq. 2) for SL depth versus log transformed surface irradiance are summarized in Table 1. Most regressions were significant at the $p < 0.001$ level, with a coefficient of determination $R^2 > 0.9$, and all were significant at $p < 0.05$ level. Thus a strong effect of light on the daytime, dawn, and dusk depth distribution appears for all investigated dates. Slope (a) as well as intercept (b) estimates generally displayed less variation on consecutive days with similar irradiance (January, April and May) than on days with different surface irradiance (Table 1). Analysis of slope homogeneity showed that slope variation was highest on consecutive days with different surface light intensities and most significant in March and September (Table 2). Variations in the slope can have been caused by methodological weaknesses, SLs not strictly following a preferred light intensity or by variations in K due to variations in the angular distribution of light between e.g. cloudy and sunny days. According to Eq. (2) the slope is the reciprocal of K, and the observed slope variations in March and September correspond to variations in K (m^{-1}) in the range of 0.054 – 0.073 and 0.047 – 0.071 respectively. Alternatively, the slope variations for these two months might reflect a variation in preferred light intensity in the range of 0.31 – 1.046 and 0.057 – 0.185 $\mu E \cdot m^{-2} \cdot s^{-1}$.

Slopes of the descent and ascent periods from consecutive days were generally similar, with the exception of descents in February and May, and ascents in April and May (Table 2).

Estimated light levels at SL depth

According to Eq. (2) the light preference values or 'isolumes' (E_{iso}) can be estimated from the estimated slopes and the intercepts of the regression equations in Table 1, i.e. $E_{iso} = \exp(-b/a)$. As noted above such estimates of E_{iso} will also be affected by potential variations in K within the time period the regression coefficients are estimated for.

Estimated isolumes (E_{iso}), based on entire day as well as descent and ascent migrations, were similar on consecutive days, but varied between months (Figure 3). On consecutive days estimates of E_{iso} differed by an average factor of three during daylight periods, while E_{iso} from descents and ascents differed by an average factor of five and three respectively. On 13 out of 16 days E_{iso} was between 2 – 9 times higher during the ascent than the descent phase. Seasonal variation of E_{iso} was generally highest in the first five months (January – May), while the isolume intensity at the DSL depth seemed to be similar in July- September (Figure 3).

Surface light at dusk and dawn

Light intensities at the surface before *M. muelleri* descended from the surface at dawn and arrived at dusk after ascent were compared with corresponding E_{iso} estimates from the descent and ascent phases (Figure 3). In the period January – May estimates of the preferred light intensity during descents and ascents often overlapped with the surface light recordings (Figure 3). In July – September the DSL could not be tracked all the way to the surface (See also Figure 2) and it was therefore not possible to obtain a time of surface arrival with a corresponding surface light recording

Discussion

The linear relationships we report between SL depth and the logarithmic surface irradiance indicate that changes in the vertical distribution of the SLs are greatly affected by changes in light. However, our study does not suggest that the two *M. muelleri* SL's are strictly attracted to invariant universal light intensities as suggested by the isolume concept. The term 'a preferred range of light intensities' seems more appropriate. The similarity between the actual measured surface light when *M. muelleri* were at the surface and the indirect estimates of the preferred intensity that were obtained by Eq (4) in the period January - May (Figure 3) suggest that the indirect estimates of the light preference appear relatively accurate.

The present results suggest that the ambient light level at *M. muelleri* SL depth is similar on consecutive days, when variation in *K* is likely to be small and similar. On successive days with different surface light intensity *M. muelleri* SLs were consistently distributed shallower on overcast days (with the exception of September), indicating that SLs adjusted their depth to a similar preferred light intensity on the two days with different surface irradiance. This adds to the within day observations of Baliño and Aksnes (1993) who observed that SLs rapidly adjusted their depths upward when surface light intensity dropped as a result of sudden cloudiness. Thus these observations suggest a preference for an absolute light intensity both within and between days.

We assumed an invariant light attenuation coefficient *K* when estimating preferred light intensities. However, *K* can vary as a result of variations in the light field above and below the air-water interface. Several studies have suggested that mesopelagic organisms moved shallower with increased turbidity, i.e. increases in *K* (Kaartvedt et al. 1996; Widder & Frank 2001; Frank & Widder 2002). Solar elevation (solar zenith angle) and sky conditions, however, also affect the angular distribution of light and thereby *K* (Zheng et al. 2002), and variations in solar elevation may affect *K* with 25 % (Jerlov 1968). Additionally, in contrast to sunny days, irradiance on overcast days is more diffuse than direct, which can result in altered *K* (Kirk 1984; Zheng et al. 2002). Our results indicate that this might have been the case, as our *K*-estimates were higher on overcast days compared to the sunnier days on three out of four occasions. Thus *K*-variations might explain some of the observed variation in our *a* and *b* estimates (Eq. 2) as well as the estimates of the preferred light intensity (Eq. 4). In future studies actual measurements of underwater irradiance should be conducted to eliminate this source of variation.

While a preferred range of light intensities probably involves ontogenetic variations, as evidenced by the different location of the two SLs, similar estimates of preferred light intensity for the DSL in July, August and September indicate that ontogenetically similar fish (according to Goodson et al. 1995 the lower SL is composed of adult fish > 30 mm, regardless of season) may follow a similar preferred range of light intensities over time.

The consistently lower preferred light level of the descent SL compared to the ascent SL suggests that *M. muelleri* might respond differently to light during dawn and dusk. Bjelland (1995) and Rasmussen and Giske (1994) reported that light levels *M. muelleri* SLs experienced at the surface were two to four orders of magnitude higher at dusk than at dawn, while our study suggests a corresponding one order of magnitude difference. After feeding at the surface at dawn fish are likely to be more satiated on their descent (Bagøien 2001). While ascending at dusk, after a prolonged day time period with lower foraging rates, fish might take greater risks to feed at higher light intensities (Appenzeller & Leggett 1995). Alternatively it might be hypothesized that the diurnal migration pattern of *M. muelleri* is controlled by internal clocks adjusted to diurnal and seasonal variations rather than by the instantaneous variations in light per *se*. However, such circadian rhythms cannot account for SLs responding to unpredictable light fluctuations caused by moving clouds (Baliño & Aksnes 1993). According to McFarland (1986) the sudden darkening of the sun by cloud cover can reduce the light intensity by as much as 75 % within seconds.

Recent studies of mesopelagic crustaceans (Onsrud & Kaartvedt 1998; Widder & Frank 2001; Frank & Widder 2002) not only suggest that these organisms followed an upper isolume during their ascents, but also that their swimming speeds were sufficiently high to keep track with the changing isolume depth (Widder & Frank 2001). Torgersen and Kaartvedt (2001) in a study of migrating individuals found that *M. muelleri* can achieve vertical swimming speeds of 10 – 20 cm s^{-1}during both descents and ascents, which is probably sufficiently fast to follow the speed of the vertically changing preferred light intensity during crepuscular periods.

We have estimated the light intensity at the top edge of SLs, but a SL extends over a depth range and consequently over a range of light intensities. Acoustic data suggests that individuals or groups of fish vary their depth within a SL, at times migrating between SLs and thereby experiencing varying ambient light levels (Staby, unpublished data). It was difficult to estimate the depth of the lower SL border during the first five months, either because SLs were not clearly separated from each other or the lower edge was not clearly defined. However in July – September depth estimates from the lower DSL border could be obtained on some days and the calculated light levels suggest that the light intensity between the upper and lower edge of a SL (20 – 80 m) may vary by several orders of magnitude (10^{-1}– 10^{-7}), depending on the vertical extension of the SL. This suggests a much higher variation in the ambient light of individuals within a SL at a particular time than the temporal variation in the ambient light at the top edge of the SLs. These observations also suggest that *M. muelleri* has a larger tolerance for moving into darker water than for moving into too illuminated water. This is reasonable if increased light means higher predation risk and decreased light only means lowered visual food intake. While food intake can be adjusted predation cannot.

It should be noted that our understanding of individual fish behaviour and the advantage of being in a SL and how this is achieved is poorly understood, although individual behaviour has been addressed in some recent studies (Torgersen & Kaartvedt 2001; Kaartvedt et al. 2008). Acoustic echograms show that the descent and ascent migration generally occur as narrow layers, which suggests that visual orientation among individuals may be important during these periods. Furthermore, on bright summer nights Kaartvedt et al. (1998) observed schooling *M. muelleri* in surface waters, which is commonly interpreted as a result of visual orientation among individuals

Ontogeny and variation of preferred light range

M. muelleri typically form vertically separate SLs according to their developmental stage, i.e. post-larvae, juveniles and adults (Goodson et al. 1995; Staby & Kaartvedt 2010). Based on findings by Goodson et al. (1995) we believe that the SSL in the period January – May was composed of varying sized fish (Goodson et al. 1995), although this cannot be said with certainty (due to the lack of catch data in the present study). In contrast according to the results of Goodson et al. (1995) the DSL in July – September probably contained similarly sized adult *M. muelleri*. Typically the ontogenetic stages can be characterised by their degree of transparency and lateral silvering, as well as number of ventral photophores. Post-larvae are transparent with little silvering and few photophores (Robertson 1976), while the more silvery juveniles are less transparent and have more photophores. Adults are entirely silver on their sides and have batteries of ventral photophores (Staby unpublished data). The efficiency with which transparency and silvering make various ontogenetic stages less conspicuous will depend on the light intensity and scattering properties of the water, i.e. depth (Johnsen & Sosik 2003). Additionally, counter-illumination, or the downwelling light produced by photophores, aids in braking up the silhouette of organisms against a brighter background (Widder 1999). The structure of *M. muelleri's* ventral photophores is similar to that of the related hatchet fish *Argyropelecus hemigymnus* (Cavallaro *et al.* 2004), which produces light with an angular distribution similar to that of downwelling light (Denton *et al.* 1972).

Kaartvedt et al. (2008) suggested that ascending *M. muelleri* minimize a reduction of optimal counter-illumination by having a stepwise saltatory swimming behaviour, with short vertical displacements and prolonged horizontal periods. However the intensity of counter-illumination will most likely differ with ontogeny due to different numbers of photophores, which may influence the light range post-larvae, juveniles and adults follow.

In summary our study suggests that the vertical migration of *M. muelleri* appears to emerge as a result of a vertical habitat selection that can be characterized by a preferred range of light intensities, and that these intensities might be state (e.g. hunger related) and age dependent.

Acknowledgements

We thank Anders Fernö, Anne Gro Vea Salvanes, and Jon Egil Skjæraasen for comments on earlier versions of the manuscript, as well as Helge Balk for helping with some acoustic analysis in Sonar5-Pro.

References

Aksnes DL, Utne ACW (1997) A revised model of visual range in fish. Sarsia 82:137-147

Appenzeller DR, Heggett WC (1995) An evaluation of light mediated vertical migration of fish based on hydroacoustic analysis of the diel vertical movements of rainbow smelt *Osmerus mordax*. Can J Fish Aquat Sci 52:504-511

Bagøien E, Kaartvedt S, Aksnes DL, Eiane K (2001) Vertical distribution and mortality of overwintering *Calanus*. Limnol Oceanogr 46:1494-1510

Baliño B, Aksnes DL (1993) Winter distribution and migration of the sound scattering layers, zooplankton and micronekton in Masfjorden, western Norway. Mar Ecol Prog Ser 102:35-50

Balk H, Lindem T (2009) Sonar4 and Sonar5-Pro post processing systems. Lindem Data Acquisition,Oslo

Bjelland (1995) Life history tactics of two fjordic populations of *Maurolicus muelleri*. Cand. Scient. thesis, University of Bergen, 79 pp

Bohl E (1980) Diel pattern of pelagic distribution and feeding in planktivorous fish. Oecologia 44:368-375

Cavallaro M, Mammola CL, Verdiglione R (2004) Structural and ultrastructural comparison of photophores of two species of deep-sea fishes: *Argyropelecus hemigymnus* and *Maurolicus muelleri*. J Fish Biol 64:1552-1567

Clark CW, Levy DA (1988) Diel vertical migration by juvenile sockeye salmon and the antipredation window. Am Nat 131:271-290

Cohen JH, Forward RB (2009) Zooplankton diel vertical migration – a review of proximate control. Oceanogr Mar Biol 47:77-110

Denton EJ, Gilpin-Brown JB, Wright Source PG (1972) The angular distribution of the light produced by some mesopelagic fish in relation to their camouflage. P Roy Soc Lond B Bio 182:145-158

Dupont N, Klevjer TA, Kaartvedt S, Aksnes DL (2009) Diel vertical migration of the deep-water jellyfish *Periphylla periphylla* simulated as individual responses to absolute light intensity. Limnol Oceanogr 54:1765–1775

Eggers DM (1978) Limnetic feeding behavior of juvenile sockeye salmon in lake Washington and predator avoidance. Limnol Oceanogr 23:1114-1125

Frank TM, Widder EA (2002) Effects of a decrease in downwelling irradiance on the daytime vertical distribution patterns of zooplankton and micronekton. Mar Biol 140:1181-1193

Giske J, Aksnes DL, Baliño B, Kaartvedt S, Lie U, Nordeide JT, Salvanes AGV, Wakili SM, Aadnesen A (1990) Vertical destribution and trophical interactions of zooplankton and fish in Masfjorden, Norway. Sarsia 75:65-81

Goodson MS, Giske J, Rosland R (1995) Growth and ovarian development of *Maurolicus muelleri* during spring. Mar Biol 124:185-195

Jerlov NG (1968) Optical Oceanography. Elsevier Publishers, New York.

Johnsen S, Sosik HM (2003) Cryptic colouration and mirrored sides as camouflage strategies in near-surface pelagic habitats: implications for foraging and predator avoidance. Limnol Oceanogr 48:1277-1288

Johnsen S (2005) Visual ecology in the high seas. Mar Ecol Prog Ser 287: 281-285

Kaartvedt S, Melle W, Knutsen T, Skjoldal HR (1996) Vertical distribution of fish and krill beneath water of varying optical distribution. Mar Ecol Prog Ser 136:51-58

Kaartvedt S, Knutsen T, Holst JC (1998) Schooling of the vertically migrating mesopelagic fish *Maurolicus muelleri* in light summer nights. Mar Ecol Prog Ser 170:287-290

Kaartvedt S, Torgersen T, Klevjer T, Røstad A, Devine JA (2008) Behaviour of individual mesopelagic fish in acoustic scattering layers of Norwegian fjords. Mar Ecol Prog Ser 360:201-209

Kaartvedt S, Røstad A, Klevjer T, Staby A (2009) Use of bottom-mounted echo sounders in exploring behavior of mesopelagic fishes. Mar Ecol Prog Ser 395:109-118

Kirk JTO (1984) Dependence of relationship between inherent and apparent optical properties of water on solar altitude. Limnol Oceanogr 29:350–356

McFarland WN (1986) Light in the sea – correlations with behaviour of fishes and invertebrates. Amer Zool 26: 389-401

Metcalfe JD, Righton D, Eastwood P, Hunter E (2008) Migration and habitat choic in marine fishes. In: *Fish Behaviour* (Eds. C. Magnhagen, V.A. Braithwaite, E. Forsgren, B.G. Kapoor) Science Publishers, Enfield, pp.187-234

Neilson JD, Perry RI (1990) Diel vertical migrations of marine fishes: an obligate or facultative process? Adv Mar Biol 26: 115-168

Onsrud MSR, Kaartvedt S (1998) Die1 vertical migration of the krill *Meganyctiphanes norvegica* in relation to physical environment, food and predators. Mar Ecol Prog Ser 171:209-219

Pitcher TJ (1993) Functions of shoaling behaviour in teleosts. In: Pitcher TJ (ed) Behaviour of teleost fishes. Chapman and Hall, London

Rasmussen OI, Giske J (1994) Life history parameters and vertical distribution of *Maurolicus muelleri* in Masfjorden in summer. Mar Biol 120:649-664

Ringelberg J (1995) Changes in light-intensity and diel vertical migration – a comparison of marine and freshwater environments. J Mar Biol Assoc 75: 15-25

Ringelberg J, Van Gool E (2003) On the combined analysis of proximate and ultimate aspects in diel vertical migration (DVM) research. Hydrobiol 491:85-90

Robertson DA (1976) Planktonic stages of *Maurolicus muelleri* (teleostei: Sternoptychidae) in New Zealand waters. New Zeal J Mar Fresh 10:311-328

Roe HSJ (1983) Vertical distributions of euphausiids and fish in relation to light intensity in the northeastern Atlantic. Mar Biol 77:287-298

Rosland R, Giske J (1997) A dynamic model for the life history of *Maurolicus muelleri*, a pelagic planktivorous fish. Fish Oceanogr 6:19-34

Ryer CH, Olla BL (1998) Effect of light on juvenile walleye Pollock shoaling and their interaction with predators. Mar Ecol Prog Ser 167: 215-226

Ryer CH, Olla BL (1999) Light-induced changes in the prey consumption and behaviour of two juvenile planktivorous fish. Mar Ecol Prog Ser 181:41-51

Scheuerell MD, Schindler DE (2003) Diel vertical migration by juvenile sockeye salmon: empirical evidence for the antipredation window. Ecology 84:1713-1720

Staby A, Røstad A, Kaartvedt S (2010) A full year study of diel vertical migration in the mesopelagic fish *Maurolicus muelleri* (Gmelin 1789) reveals novel and varied behavioural patterns (Paper 2 in this thesis)

Sweatt AJ, Forward RB (1985) Diel vertical migration and photoresponses of the chaetognath *Sagitta hispida* Conant. Biol Bul (Woods Hole) 168:18-31

Torgersen T, Kaartvedt S (2001) In situ swimming behaviour of individualmesopelagic fish studied by split-beam echo target tracking. ICES J Mar Sci 58:346-354

Warrant EJ, Locket NA (2004) Vision in the deep. Biol Rev 79:671-712

Widder EA (1999) Bioluminescence. In: Archer SN, Djamgoz MBA, Loew ER, Partridge JC (eds) Adaptive mechanisms in the ecology of vision. Kluwer Academic Publishers, Dordrecht

Widder EA, Frank TM (2001) The speed of an isolume: a shrimp's eye view. Mar Biol 138:669-677

Zheng X, Dickey T, Chang G (2002) Variability of the downwelling diffuse attenuation coefficient with consideration of inelastic scattering. App Opt 41:6477-6488

Table 1: Summary of linear regressions (Eq. 2) with data from entire day - and descent and ascent periods (defined in the materials and methods section). The regression slope (*a*) and the regression intercept (*b*) were used to estimate the light intensity of the isolume $E_{iso} = Exp^{(-b/a)}$ ($\mu E \cdot m^{-2} \cdot s^{-1}$) for each period. (SSL shallow scattering layer, DSL deep scattering layer). Regression significance levels: * $p < 0.001$; ** $p < 0.01$.

Month	Days	Weather	Scattering	Entire day period				Descent period				Ascent period			
			layer	*a*	*b*	R^2	E_{iso}	*a*	*b*	R^2	E_{iso}	*a*	*b*	R^2	E_{iso}
January	13	Overcast	SSL	14.3	13.8	0.93 *	0.38	14.7	15.4	0.98 *	0.35	16.1	5.5	0.97 **	0.71
	14	Overcats	SSL	14.7	11.3	0.94 *	0.46	15.4	12.7	0.99 **	0.44	16.6	3.5	0.98 *	0.81
February	12	Overcast	SSL	12.1	28	0.93 *	0.10	9.5	38.2	0.98 *	0.02	14.3	20.7	0.98 *	0.24
	13	Overcast	SSL	12.1	31	0.81 *	0.08	14.1	27	0.97 *	0.15	17.6	7.1	0.94 *	0.67
March	20	Overcast	SSL	13.7	16.05	0.79 *	0.31	14.1	17.9	0.99 *	0.28	18	-5	0.97 **	1.3
	21	Sunny	SSL	18.4	-0.83	0.96 *	1.05	15.5	12.8	1 *	0.44	24.9	-30.3	0.98 *	3.4
April	19	Sunny	SSL	10.9	40.9	0.92 *	0.02	9.2	44.6	0.91 **	0.01	14.9	30.4	0.96 *	0.13
	20	Sunny	SSL	11	43	0.93 *	0.02	7.2	54.2	0.94 **	0.001	11.6	42.6	0.93 *	0.03
May	24	Sunny	DSL	11.6	50.2	0.78 *	0.01	18.2	43	0.96 *	0.09	21.4	8.2	0.98 *	0.68
	25	Sunny	DSL	13	41.8	0.86 *	0.04	12.7	52.8	0.99 *	0.02	13.5	28.6	0.94 **	0.12
July	10	Sunny	DSL	13.7	30.7	0.96 *	0.11	11.8	36.1	0.98 *	0.05	16.4	20.7	0.93 *	0.28
	13	Overcast	DSL	11.9	38.2	0.88 *	0.04	13.8	40.2	0.99 *	0.05	15.2	18.4	0.95 *	0.30
August	7	Overcast	DSL	16	32.2	0.92 *	0.13	16.1	35.3	0.96 *	0.11	20	12	0.95 *	0.55
	8	Sunny	DSL	18.3	22	0.94 *	0.30	17.9	24.6	0.97 *	0.25	25.2	-7.1	0.87 *	1.3
September	10	Overcast	DSL	21.1	35.6	0.92 *	0.19	19.7	38.9	0.90 **	0.14	20.7	28.3	0.88 **	0.26
	13	Sunny	DSL	14.1	40.4	0.87 *	0.06	21.2	20.7	1 *	0.38	22.3	3.4	0.67 **	0.86

Table 2: Summary of slope homogeneity analysis based on data from entire day periods, as well as descent and ascent periods. (DSL deep scattering layer, SSL shallow scattering layer). Numbers are significance levels (* $p < 0.001$; ** $p < 0.01$; *** $p < 0.05$) and give an indication of similarity of regression slopes from consecutive days. Non-significant numbers imply similar (parallel) slopes. (O – overcast, S – sunny).

Month	Days	Weather	Scattering layer	Entire day period	Descent period	Ascent period
January	13 and14	O	SSL	0.731	0.576	0.778
February	12 and 13	O	SSL	0.993	**0.001** *	0.186
March	20 and 21	O and S	SSL	**0.001** *	0.136	0.054
April	19 and 20	S	SSL	0.818	0.342	**0.044** ***
May	24 and 25	S	SSL	0.149	**0.004** **	**0.006** **
July	10 and13	O and S	DSL	**0.004** **	**0.02** ***	0.588
August	7 and 8	O and S	DSL	**0.006** **	0.327	0.15
September	10 and 13	O and S	DSL	**0.001** *	0.715	0.812

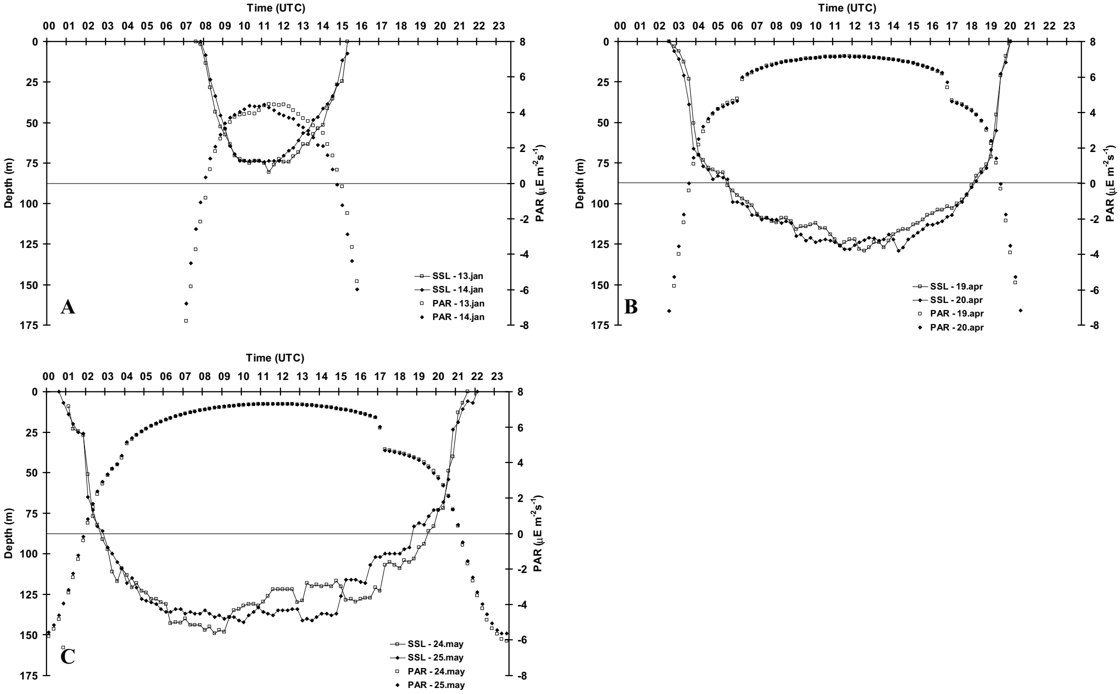


Figure 1: Estimated depth of the upper edge of the shallow scattering layer (SSL) and corresponding ln transformed surface irradiance (PAR) on days with similar surface light intensity (A – January, B – April, C – May 2008).

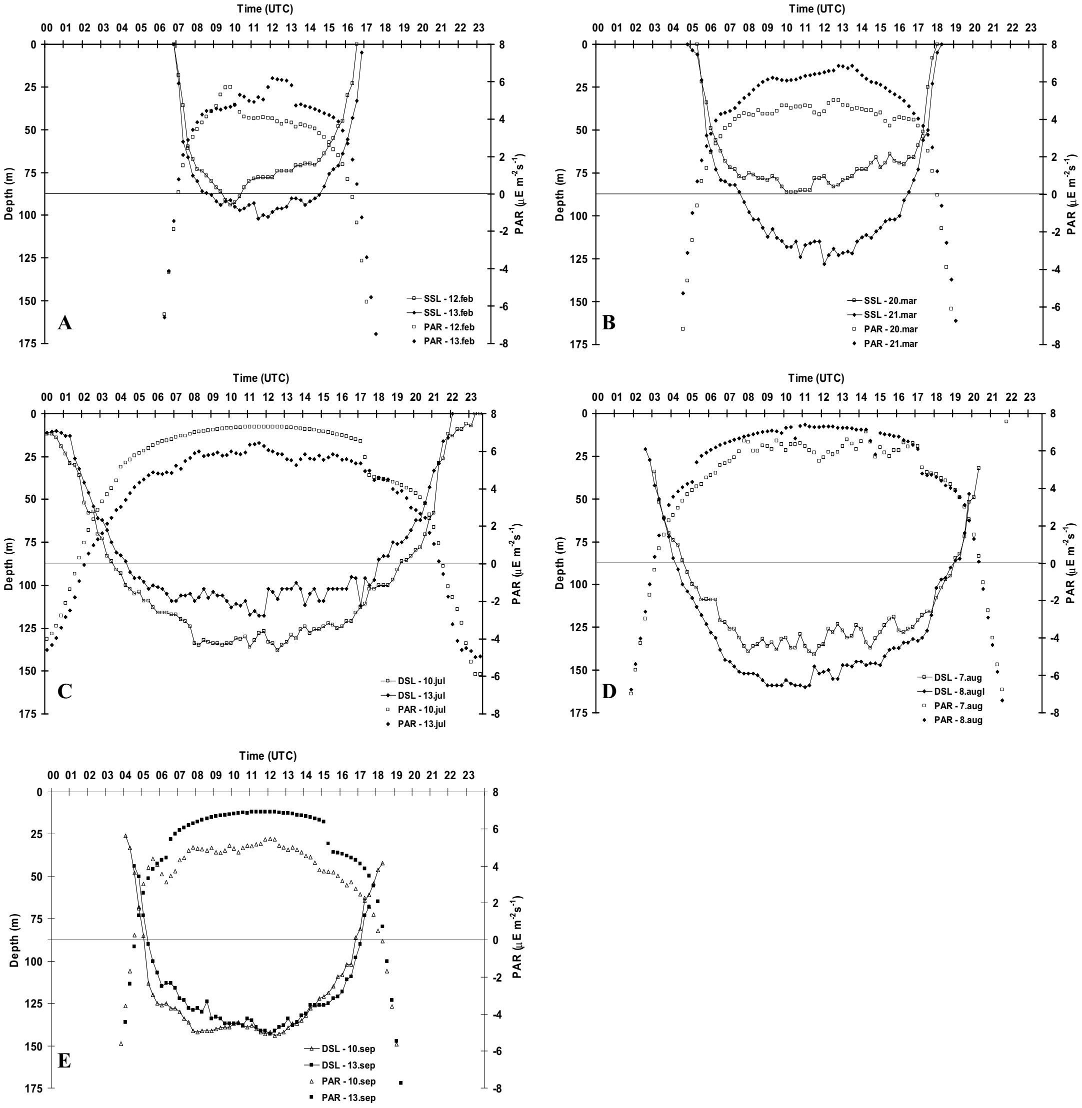


Figure 2: Estimated depth of the upper border of shallow scattering layers (SSL) and deep scattering layers (DSL), with corresponding ln transformed surface irradiance (PAR) on days with dissimilar surface light intensity. (A – February, B – March, C – July, D – August, E – September 2008). Note different depth scales.

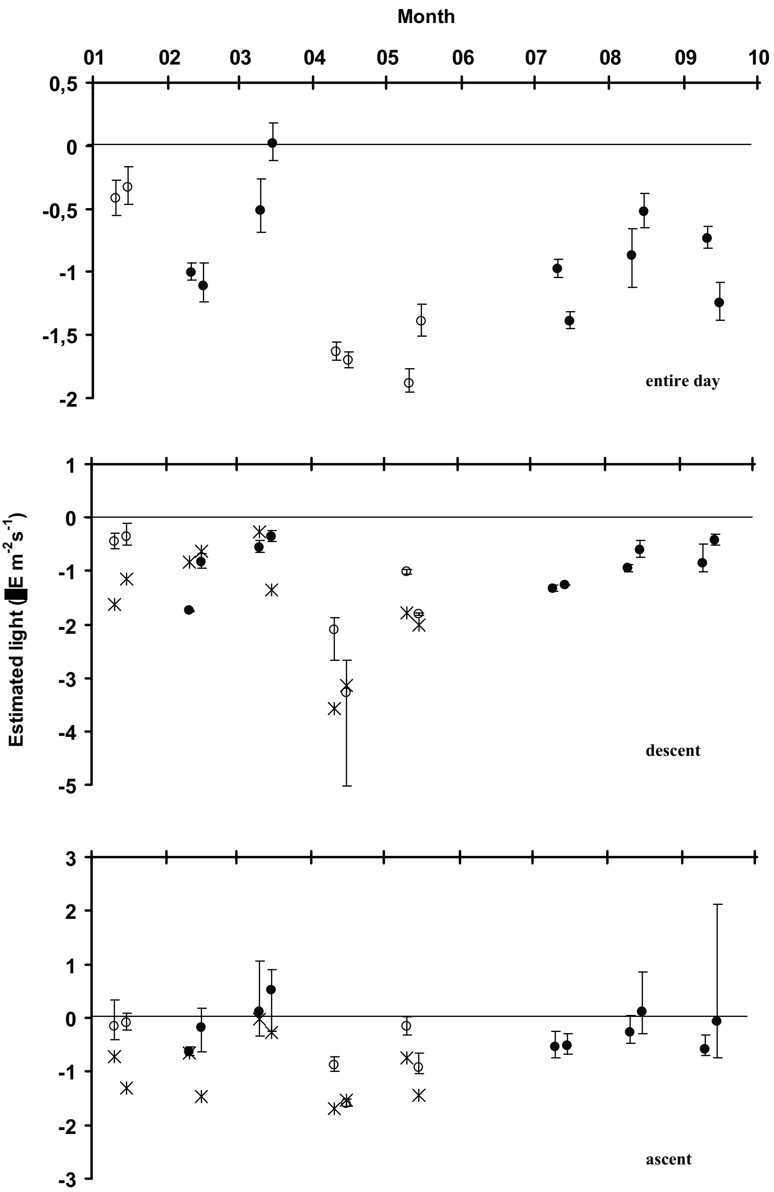


Figure 3: Estimated light intensity ($\log_{10}$ transformed) of the isolume E_{iso} at the upper border of SLs. Solid circles are consecutive days with dissimilar surface light intensity, while open circles indicate consecutive days with similar light intensity (Error bars show 95 % confidence intervals of the estimated light level). Crosses indicate measured surface light intensities when *M. muelleri* were observed at the surface at dawn (before descent) and dusk (after ascent).

Paper 4

Seasonal occurrence and vertical migration of potential predators of *Maurolicus muelleri* (Gmelin 1789).

Staby, A., Røstad, A., Salvanes, A.G.V., Kaartvedt, S.

(Manuscript)

Seasonal occurrence and vertical migration of potential predators of *Maurolicus muelleri* (Gmelin 1789)

Arved Staby [1], Anders Røstad [2 3], Anne Gro Vea Salvanes[1], and Stein Kaartvedt [2 3]

[1] *Department of Biology, University of Bergen, P O Box 7803, 5020 Bergen, Norway*

[2] *Department of Biology, University of Oslo, P O Box 1066 Blindern, 0316 Oslo, Norway*

[3] *King Abdullah University of Science and Technology, Saudi Arabia*

Abstract

The Diel Vertical Migration (DVM) behaviour of pearlside (*Maurolicus muelleri*) Scattering Layers (SL) has been hypothesized to be caused by a response to predation risk, yet this has not been investigated. Here we present acoustic data on both pearlside and their potential predators from 224 days (over a 14 month period) registered with an upward facing split-beam transducer in Masfjorden, Norway. These data were complemented with catch data from a field campaign and landing statistics of gadoids from the region. We applied acoustic target tracking to study the diel vertical distribution of individual large fish (TS < -45 dB), and concurrently explore the behaviour of pearlside SLs. In autumn and winter echo counts of large fish at night time were high in the upper 30 m, and at day time low throughout the upper 70 – 100 m but higher between the deep and shallow pearlside SLs. In the same period juvenile *M. muelleri* avoided shallow distributed predators at night by performing midnight sinking shortly after dusk, while adult fish suspended DVM entirely. Juvenile *M. Muelleri*, after a predawn rise to the surface, descended to day time depths at dawn despite the near absence of large fish, suggesting a genetically fixed predator evasion behaviour. In spring and summer large fish occurred largely in the upper 120 m at day and night time, however with fewer night time observations in the upper 30 m than in autumn and winter. Midnight-sinking of *M. muelleri* was absent from the end of spring throughout summer, suggesting sufficient light levels for feeding in the anti-predation window. *M. muelleri* SLs displayed crepuscular DVM, and as large fish stayed deeper at day time towards the end of summer, the depth range of the deepest *M. muelleri* SL increased towards end of summer. The study suggests that

different ontogenetic stages of *M. muelleri* are subjected to seasonally and dielly varying predation pressure.

Introduction

In the bright pelagic environment prey organisms are susceptible to visual predators and have resultantly evolved physiological and behavioural adaptations to reduce predation mortality (Pitcher 1993; Kaartvedt et al. 1998; Warrant & Locket 2004). Numerous previous studies in Norwegian fjords have shown that planktivore *M. muelleri* distributes into a "shallow" juvenile and "deep" adult fish Scattering Layer (SL), whose diurnal pattern of depth distribution is found to vary seasonally (Giske et al. 1990; Baliño & Aksnes 1993; Rasmussen & Giske 1994; Bjelland 1995; Staby et al. 2010). Yet the spatial and temporal distribution and composition of predatory fish have not been assessed as thoroughly.

M. muelleri is an abundant fish species worldwide, whose acoustically visible SLs carry out Diel Vertical Migration (DVM; Gjøsæter 1981; Clarke 1982; Landaeta & Castro 2002; McClatchie & Dunford 2003). An ultimate aspect of DVM is that organisms, descending to greater depths at dawn, avoid and thus reduce predation risk by pelagic predators during day time (Cohen & Forward 2009). Several studies have related DVM of planktivores to avoidance of larger predatory (piscivorous) fish (Eggers 1978; Clark & Levy 1988; Scheuerell & Schindler 2003; Hrabik et al. 2006; Mehner *et al.* 2007). Clark and Levy (1988) extended the predator avoidance hypothesis by stating that a vertically migrating planktivore during the crepuscular periods distributes at light levels which optimize feeding while at the same time reducing predation risk – termed antipredator window.

Adult *M. muelleri* suspend DVM in January, and instead remain at deeper depths throughout the entire diel period (Giske et al. 1990; Baliño & Aksnes 1993). While this behaviour may result in reduced feeding, adults may gain from a reduced predation risk (Rosland and Giske 1997).

In winter (January) juvenile *M. muelleri* relocate to deeper waters (midnight sinking) after spending a short period at the surface at dusk. Juveniles may benefit from increased digestion by distributing at the subsurface temperature maximum at night (Giske et al 1990; Giske and

Aksnes 1992). An alternative explanation for nocturnal descents is predator avoidance, as descending organisms avoid their shallow distributed predators (Tarling 2002).

The typical predators of *M. muelleri* in Masfjorden are gadoids, mostly blue whiting (*Micromesistious potassou*) and saithe (*Pollachius virens*), and to a lesser degree haddock (*Melanogrammus aeglefinus*) and pollack (*Pollachius pollachius*; Giske et al. 1990; Salvanes and Nordeide 1993; Rasmussen and Giske 1994; Bjelland 1995). It has been shown that the abundance of some of these predators varies seasonally (Salvanes 1991) and that in winter predator biomass varies with depth (Giske et al. 1990). Yet, the predators of *M. muelleri* that may explain the patterns of DVM of this prey fish have received less attention than *M. muelleri* acoustical SLs. Seasonal variations in predator abundance, patterns of vertical distribution and diel vertical migration are largely lacking.

The typical large and scattered predators of *M. muelleri* can be distinguished acoustically and separated from smaller and more abundant fish based on their generally higher target strength (TS; Foote et al. 1986; MacLannen & Simmonds 1992; Kaartvedt et. al 2009), and the distribution of their TS by depth can be obtained. Fish that remain in the acoustic beam of a stationary echosounder for a given time period are represented by successive single echoes (Brede 1990). Target tracking (TT) software sort these into “tracks”, which allows us to utilize counts of single fish tracks to obtain indices of abundance for predators in chosen depth bins of the water column throughout day and night (Josse et al. 1999; Kaartvedt et al. 2009).

In the present study we investigate the diel vertical distribution of large fish and their potential prey *M. muelleri* over a 14 month period, using continuously recorded acoustic data. We interpret these in view of fish data from a sampling campaign and average monthly catch data of predators from 7 years landings statistics reflecting all daily catches delivered by fishermen in the years during 1986 – 1992 from Masfjorden. We predict that *M. muelleri* stay deep during day to avoid shallower distributed pelagic predators, and that adult *M. muelleri* suspend their nocturnal ascent in winter (cf. Staby et al. 2010) since the trade-off between feeding and predator risk then is unfavourable. We furthermore predict that midnight sinking, which is a consistent feature of the DVM-behaviour of post-larvae/juvenile fish (Staby et al. 2010), is due to avoiding risk of predation of shallower distributed predators at the surface between dusk and dawn.

Materials and methods

Masfjorden lies on the west coast of Norway ($60^0$40’ N; $5^0$25’ E). The fjord is approximately 20 km long and 1 km wide, and opens via a 75 m deep sill into the adjacent Fensfjorden. At its deepest point the fjord is approximately 490 m deep.

Acoustic data

Acoustic data was recorded at a 390 m deep location over a 14 month period (July 2007 to October 2008). A stationary, upward facing SIMRAD EK60 echosounder with a SIMRAD ES38DD transducer (7^0 beamwidth) enclosed in a pressure proof casing and located on the fjord bottom was connected via a 1.2 km long cable to a laptop on land, transmitting real time data and providing electricity for the echo sounder. A detailed description of the set-up is given in Kaartvedt et al. (2009). The ping rate was set at 0.9 s^{-1} and the pulse duration 0.512 ms. Acoustic data was analysed using the Sonar5-Pro post processing software (Balk and Lindem 2009).

We could not use echo integration in assessing predator abundance, as the predator echoes were swamped by those of *M. muelleri*. We therefore used echo counting of individually recorded fish targets. This procedure introduces a bias in the estimate as the width of the acoustic beam is smallest close to the transducer and increases with increasing range. Therefore, the likelihood of a fish swimming into a wider beam at the surface (long range) is much greater than close to the transducer (short range) and fish farther away can also be tracked for a longer time period, depending on their swimming speed. The number of fish close to the transducer will be underestimated. We here compare average track counts limited to waters above 200 m depth, reducing the maximum theoretical correction factor that would need to be applied for the deepest records (closest to the transducer) to 3.9. On the other hand, quality of records in shallow water (long range) are poorer, particularly at the outer periphery of the acoustic beam, and targets at long range may not be recognized as valid tracks by the tracking software. Fish records at long range also have a higher probability of being rejected by the target tracking software due to so-called multiple echoes (Soule et al. 1996). We therefore have made no effort in correcting abundance of fish with range, so that data do not represent absolute values. Yet, we believe the data on the predatory fish reflect real patterns in vertical distribution and seasonal abundance, and that uncertainties are small enough as to not influence the overall conclusions.

To estimate predator occurrence and their depth distribution through time we recorded EK60 rawdata files were first converted at 40logR with parameters for single echo detections (SED) set at a minimum and maximum echolength of 0.6 and 1.4 respectively, as well as a maximum phase deviation of 0.5 and a maximum beam compensation of 3 dB. SEDs of fish with TS > -45 dB were automatically tracked with the 'track and classify' module in Sonar5-Pro (Balk and Lindem 2009). No manual post-tracking quality inspection was done due to the large number of tracks (n = 64824) and days (n = 224) analysed. The tracker accepted only tracks with a minimum track length of 15 pings, allowing for a maximum of 5 missing pings and a 0.8 m gating (vertical depth difference). Track data included the average TS, range and start time and was exported into MS Excel for further analyses. Tracks from the upper 5 m were discarded. Tracks were allocated to 10 m depth and hourly time bins. For each depth-time bin we calculated the weighted monthly average number of tracks for large predator-like fish by dividing their total number in each bin with the number of days used in the monthly analysis, and then multiplying with the proportion of days where a given bin contained tracks and the total number of days with records in each month

Composite monthly echograms to display monthly averages of the small prey fish *M. muelleri* distribution and DVM behaviour were processed in Matlab by combining data from all days of measurements, thus generating an average daily echogram for each month. The day was divided into 30 second intervals and all the pings in a month in each interval were averaged. Further, each interval was plotted in Matlab as a normal echogram creating the composite echograms. We then superimposed MS Excel bubble plots showing the average number of large fish per bin onto these echograms, which gave an indication of large fish distribution with regard to *M. muelleri* SLs. The monthly echograms basically consist of two scattering layers; the shallow most being ascribed to juvenile *M. muelleri* and the deeper to adult *M. muelleri* (see Staby et al. 2010).

Trawling performed during the acoustic registration period (Kaartvedt et al. 2009; Staby et al. 2010) did not catch piscivorous fish. We therefore also carried out trawling with the *RV Håkon Mosby* in October 2009, and deployed a pelagic Harstad trawl combined with a multisampler cod end unit (Engås et al. 1997) to obtain depth stratified samples from *M.*

muelleri SLs (0 – 200 m). Larger fish were additionally targeted at varying depths with a larger version of the Harstad trawl (12 m headline height). Trawl duration was 10 min for multisampler tows and 30 min for large pelagic trawl tows. Floaters were mounted on the headline and the top of the net to keep it from sinking when trawling at the surface (upper 15 m). Species specific length measurements as well as the weight of large fish were taken and the stomach contents analysed onboard. The number and standard length of intact *M. muelleri* in stomachs was also determined. In addition to trawling piscivores were fished from the side of the stationary vessel with rods and metal fish lures. We obtained an approximate depth of caught fish by identifying large fish tracks accumulated underneath the vessel on the acoustic echograms.

Landing statistics

The local fishermen delivered daily catches at the local fish delivery plant in Masfjorden and we have access to daily landings from each fisherman recorded from 1985 to 1992. We used data from subareas 1 and 2 (defined in Salvanes 1986), which cover the entire length of the fjord (22 km). Since the fjord is steep and small, the number of commercial fishermen is low and the landing statistics are scattered. We therefore pooled the monthly data from all years before estimating the average monthly catch by species. For each month the sum of all landings was used as one data point, and we only included the months with landings. The gadoid fish were targeted with set-nets at 15 – 100 m depth over night (Ingard Sandnes pers comm).

Results

Acoustic data

Large fish targets

A total of 64824 tracks fulfilled the defined criteria set for the target tracking analyses from July 2007 to September 2008. There is daily and monthly variation in presence of predators shallower than 200 m, both in acoustic intensity and in the depth distribution (Figure 1). From July 2007 to May 2008 the number of predators tracked were less than 300 individuals and ranged from 148 (April 2007) to 321 (August 2007). The densities in June – September 2008 were higher (> 400) than in 2007, and in most months nearly twice as many large fish were tracked. The spatial and temporal distribution of large fish varied between months (Figure 2).

Summer (July to September)

The 2007 summer period showed similar trends as the summer in 2008, and both periods are therefore described at the same time. In summer the distribution of large predator-like fish indicated DVM behaviour between dawn and dusk (Figure 2). Large fish distributed increasingly deeper at day time as summer progressed (Figure 3), with most fish found below 70 m, between the deepest (125 – 200 m) SL containing large *M. muelleri* and the somewhat shallower (80 – 90 m) SL composed of smaller fish. *M. muelleri* SLs performed vertical migrations at dawn and dusk, and showed signs of midnight sinking in September. Few large fish were found above the shallowest SL at day time and in the upper 50 m at night (Figure 2). A similar pattern was observed during the period July – September 2007, although not as pronounced.

Autumn (October to December)

Large predator-like fish did DVM in autumn and they were at day time mainly distributed at 100 – 150 m and between the two SLs of juvenile and adult *M. muelleri* (Figure 2). That the large predators stayed shallower than adult prey and deeper than juvenile prey was particularly pronounced in November and December. In the latter months most adult *M. muelleri* stayed deeper than 125 m at night. Few large predator-like fish were tracked above the shallowest SL at 70 m during day time (Figure 3), while at night the large proportion of piscivores were in the upper 50 m (Figure 3). Juvenile *M. muelleri* displayed midnight sinking behaviour at night, descending from the surface to deeper waters after dusk (Figure 2). The midnight sinking juvenile SL descended to increasingly deeper depths towards the end of autumn and distributed at 30 – 70 m in December. At night the majority of piscivores were in the upper 30 m after juvenile *M. muelleri* had arrived in the afternoon and left before *M. muelleri* had descended from the surface in the morning (Figure 4).

.

Winter (January to March)

The winter distribution of large fish was similar as in autumn. During daytime few large fish were present above the shallowest *M. muelleri* SL, and with the exception of January, the number of fish throughout the water column was conspicuously low. Juvenile *M. muelleri* performed ordinary DVM, while adult fish remained below 150 m depth during daytime and migrated approximately 30 – 40 m upwards after dusk. At night more than 50 % of piscivores were in the upper 50 m of the water column (Figure 2 and 3). During winter juvenile *M. muelleri* displayed midnight sinking and distributed deeper (50 – 100 m) than in autumn.

Most large fish had left the surface before *M. muelleri* had started their descent at dawn and arrived at the surface after *M. muelleri* was at the surface at dusk (Figure 4).

Spring (April to June)

April was different to all other months with a low number of large fish in the entire water column irrespective of time of day. Nonetheless results suggest a slight daytime increase in the number of large fish above the M. *muelleri* SL (100 – 200 m) in April 2008, with the distribution of large fish becoming increasingly denser and spread over a wider depth range (20 – 140 m) in May and June (Figure 2). During spring *M. muelleri* SLs displayed ordinary DVM (Figure 2). The vertical distribution of large fish was similar at day and night (Figure 3), but at night fewer large fish were present in the upper 50 m than in the autumn and winter period (Figure 3). *M. muelleri* performed midnight sinking in April and until the beginning of May (Figure 2).

Target strength frequency distribution

Average target strength (TS) frequency distributions of large fish showed small variations throughout the year, with regard to both depth and diel period. Generally 70 % – 90 % of the entire average track TS were between -28 and -37 dB (Figure 5).

Catches of large fish and stomach contents

In October 2009 a total 21 large pelagic trawls and 12 multisampler tows caught 42 large fish at the site where the acoustic data was collected. In addition one pollack and three saithe were caught with rod and reel at approximately 60 – 100 m depth (Table 1). 81 % of the predators had eaten *M. muelleri* (Table 1) and the average number of *M. muelleri* per predator stomach of gadoids and mackerel ranged between 15 and 21 (Table 1).

In the upper 10 m at night the horse mackerel, mackerel and lump sucker predators had consumed juvenile *M. muelleri* (20 mm; SD 3 mm; n = 15). Larger *M. muelleri* were also present in the stomach contents of haddock (39 mm; SD = 3 mm; n = 20) and pollack (40 mm; SD = 3 mm; n = 6) caught deeper than 150 m. Night catches of saithe were between 50 – 100 m and at 150 m during the day demonstrated feeding on a broad size range of *M. muelleri* (19 – 35 mm).

Landing statistics

Saithe, haddock, pollack and cod are large piscivorous predators that are known to overlap in depth distribution with *M. muelleri* prey, and typically present in Masfjorden. The abundance of these predators varies during the year as indicated from the landing statistics (Table 2). Cod is present throughout the year and in high quantities especially in February and March and in the period July to December. Saithe was mainly caught in March, July and between October and November, and haddock was numerous between February and April. Pollack was most abundant in April and October.

Discussion

This study gives insight into the seasonal variation of the vertical distribution of large fish in relation to the distribution of the mesopelagic planktivore *M. muelleri*. When counts of large fish, with a TS corresponding to that of gadoids, were high in the upper 50 m at night, presenting a real predation threat, juvenile *M. muelleri* invariantly performed midnight sinking, suggesting an antipredation response to nocturnally feeding predators. Concurrently adult *M. muelleri* suspended DVM entirely, the benefits of ascending to forage on scant surface winter population of plankton likely being outweighed by the danger of predation during the overwintering period. Even if large pelagic fish were absent at day time in autumn and winter, juvenile *M. muelleri* continued leaving the surface layers at dawn, suggesting an innate behavioural response probably triggered by changes in light levels.

The vertical distribution of large fish changed markedly in spring and summer. In spring increasing numbers of large fish were present between the surface and the deep prey SLs during daytime. Such increase in large fish in spring is in accordance with high landings of several gadoids at this time of the year (Table 2). In summer the number of large fish staying between the shallow and deep *M. muelleri* SL increased during day time. In addition, it was clear from the acoustic data that day time depth of large fish was increasingly deeper from June to September. Furthermore, the data suggests that *M. muelleri* responded to this by choosing even deeper daytime depth. In the summer period pollack, saithe and cod were frequently caught.

We have here demonstrated that several species in the epipelagic and pelagic zone feed on *M. muelleri*, and that these thus present a predation risk that varies in time and depth. Findings from previous studies indicate that the gadoids saithe and blue whiting are the most frequently trawled pelagic predators of *M. muelleri* in Masfjorden (Giske et al. 1990; Rasmussen and Giske 1994; Bjelland 1995), as are haddock and pollack. All these predators have a similar TS range (-28 and -37 dB; Table 1). In addition mackerel eat juvenile *M. muelleri* especially at the surface, but this species has a low TS (Table 2; Misund & Beltestad 1996), so it is unlikely that this species contributed markedly to large fish tracks in the acoustics data, even if it may be abundant in summer and autumn months (Iversen 2004). However a behavioural response such as predator avoidance may be elicited also by predators that do not show acoustically, while inherent behavioural traits are likely to occur irrespective of predator presence (see below).

DVM linked to predator-prey interactions is often interpreted in terms of a trade-off between feeding and predation risk (Rosland & Giske 1994; Rosland & Giske 1997). While DVM behaviour of fish is generally investigated in terms of fish – plankton interactions (Neilson & Perry 1990; Bertrand et al. 2004; Onsrud et al. 2004), a number of studies have interpreted vertical migration behaviour of planktivorous fish in terms of interactions with potential predators (Eggers 1978; Clark & Levy 1988; Neilson and Perry 1990; Hrabik et al 2006; Mehner et al. 2007). Eggers (1978) proposed that juvenile sockeye salmon migrated vertically to optimize short term feeding opportunities while minimizing predation risk, while Clark and Levy (1988) suggested that the vertical feeding excursions of juvenile sockeye salmon corresponded with the antipredation window during crepuscular hours, i.e. periods with some light for feeding, yet sufficiently low to reduce the risk of predation considerably. These studies thus also describe an important role to ambient light levels, which influence the vulnerability i.e. conspicuousness, of the prey fish, in our case *M. mulleri*. By adapting their vertical distribution to a preferred light level (isolume) (Baliño & Aksnes 1993; Staby & Aksnes 2010) they may be able to feed throughout their vertical migrations, whilst taking advantage of the antipredation window (Clark and Levy 1988; Scheuerell & Schindler 2003), also when feeding on shallow distributed zooplankton during the crepuscular periods (Srisomwong 2009), they could reduce predation risk.

The distribution of tracked predators suggests that in autumn and winter months as well as summer months these also performed DVM, which is a common behaviour in gadoids

(Stensholt et al. 2002; Espeland et al. 2010; Olsen et al. 2010). However the predator DVM did not always seem to overlap temporally with the DVM of juvenile and adult *M. muelleri*. The greater number of large predator-like fish left the surface waters at dawn before, and arrived at the surface at dusk after juvenile *M. muelleri* (Figure 5). Whether this behaviour of large fish is the result of satiation, following descending other prey species such as lanternfish *B. glaciale* and mesopelagic krill and shrimps, or is influenced by increasing and decreasing light levels, is uncertain.

Juvenile *M. muelleri* consistently performed DVM despite the daytime absence of potential predators. A plausible interpretation of this behaviour is that it is genetically fixed, and that it does not require the external stimulus, in this case the presence of predatory fish, to be executed. Mehner et al. (2007) found that coregonid fishes continued their DVM behaviour although the risk of predation was insignificant. Similarly stone loach did not shift their feeding behaviour from nocturnal to daytime feeding even though predators were absent (Fischer 2004). Such behaviour, it was hypothesized, could occur in anticipation of rather than the actual presence of a potential daytime predator (Fischer 2004). Also in *M. muelleri* it is likely that this behaviour has been manifested during the evolutionary development and is triggered by changes in light.

Midnight sinking of juvenile M. Muelleri

Several studies have observed midnight sinking in *M. muelleri* (Giske et al.1990; Baliño & Aksnes 1993; Kaartvedt et al. 2008; Staby et al. 2010). Giske and Aksnes (1992) explained the distribution of juvenile *M. muelleri* at the temperature maximum in terms of a gain in fitness brought about by higher digestion rates. An overlap between higher temperatures and night time distribution in other studies was not always apparent (Torgersen et al. 1997; Baliño & Aksnes 1993; Staby & Kaartvedt 2010) and Torgersen et al. (1997) suggested that this behaviour could instead be interpreted as predator avoidance behaviour. Alternatively satiation has been suggested as a signal in zooplankton midnight-sinking (Pearre 2003). After feeding at dusk the midnight sinking of *M. muelleri* in Masfjorden occurred mostly in a structured and well defined layer suggesting limited variation in individual feeding efficiency. However descending simultaneously with satiated conspecifics hungry individuals may benefit from reduced predation risk. After dusk descents were particularly apparent during the darker autumn and winter months (October to March) and corresponded with high average counts of large fish in the upper 50 m. Landings data suggests that the high counts of shallow predatory fish correlate with higher landings of gadoids including saithe, cod, and pollack in autumn and winter. Ryer and Olla (1999) showed that the gadoid walleye pollock successfully foraged at very low light levels (5 x 10^{-7} µmol m^{-2} s^{-1}), while Hunter (1968) found that jack mackerel were able to forage on artemia down to a light level of approximately 1 · 10^{-5} µmol m^{-2} s^{-1}. Light measurements suggest that juvenile *M. muelleri* on selected days (n = 9) in the first three months in 2008 arrived at the surface at dawn when surface irradiance (PAR) was < 2 · 10^{-3} µmol m^{-2} s^{-1} and descended at dusk when surface irradiance was < 4 · 10^{-3} µmol m^{-2} s^{-1}. Visually feeding predators could thus have fed on *M. muelleri* and other organisms at these light levels. Tarling et al. (2002) observed *Calanus finmarchicus* displaying midnight sinking, and suggested that this behaviour was a response to the arrival of krill, a predator of the copepod. While the ultimate aspect of midnight sinking is most likely to be predator avoidance, the proximate initiator for this behaviour may be the reduction in light intensity after dusk, functioning as a cue for *M. muelleri* to descend.

In contrast to dark winter nights, the anti-predation window is probably continuous between the crepuscular periods (21h30 – 03h00) on bright spring and summer nights. Surface irradiance was generally above 1 · 10^{-3} µmol m^{-2} s^{-1} (Staby unpublished data) between mid May and mid July. *M. muelleri* would gain from remaining in the ‘anti-predation’ window while taking advantage of optimal foraging conditions. However, if light intensity at the surface is above the anti-predation window intensity, *M. muelleri* may arrest their dusk ascent, avoiding surface waters and forming schools to reduce predation mortality (Kaartvedt et al. 1998). The commencement of the pre-dawn ascent occurred before light was measurable (Staby unpublished data) and when large fish were still present in the surface layer. Juvenile *M. muelleri* ascended in a seemingly dense layer and reached the surface consistently at the start of civil twilight. It could be argued that the timing of the pre-dawn ascent is internally controlled by a synchronized endogenous rhythm, and that the presence of potential predators did not hinder juveniles from ascending. What remains unclear though is whether the stimuli triggering this behaviour may be a change in light intensity, which would indicate a high photosensitivity, or alternatively a change in internal state, i.e. hunger (Pearre 2003).

In conclusion our results have shown that by by means of applying target tracking to long term acoustic data sets, the seasonal variation of the vertical distribution of large piscivores with diel period, probably influencing the vertical distribution of the prey *M. muelleri*.

References

Baliño B, Aksnes DL (1993) Winter distribution and migration of the sound scattering layers, zooplankton and micronekton in Masfjorden, western Norway. Mar Ecol Prog Ser 102:35-55

Balk H, Lindem T (2009) Sonar 4 and Sonar5-Pro post-processing systems. Lindem Data Acquisition, Oslo, Norway

Barange M, Hampton I (1994) Influence of trawling on *in situ* estimates of Cape horse mackerel (*Trachurus trachurus capensis*) target strength. ICES J Mar Sci 51:121-126

Bertrand A, Barbirie MA, Córdova J, Hernández C, Gómez F, Leiva F (2004) Diel vertical behaviour, predator-prey relationships, and occupation of space by jack mackerel (*Trachurus murphyi*) off Chile. ICES J Mar Sci 61:1105-1112

Bjelland O (1995) Life-history tactics of two fjordic populations of Maurolicus muelleri. *Cand. Scient. thesis*, University of Bergen, Bergen, Norway

Brede R, Kristensen FH, Solli H, Ona E (1990) Target tracking with a split-beam echo sounder. Rap Proces 189:254–263

Clark CW, Levy DA (1988) Diel vertical migrations by juvenile sockeye salmon and the antipredation window. Am Nat 131:271-290

Clarke TA (1982) Distribution, growth, and reproduction of the Lightfish *Maurolicus muelleri* (Sternoptychidae) off South-east Australia. CSIRO Marine Laboratories Report No. 145, 11pp

Cohen JH, Forward RB (2009) Zooplankton diel vertical migration — a review of proximate control. Oceanogr Mar Biol 47:77-110

Eggers DM (1978) Limnetic feeding behavior of juvenile sockeye salmon in lake Washington and predator avoidance. Limnol Oceanogr 23:1114-1125

Engås A, Skeide R, West CW (1997) The 'MultiSampler': a system for remotely opening and closing multiple codends on a sampling trawl. Fish Res 29:295-298

Espeland SH, Thoresen AG, Olsen EM, Stige LC, Knutsen H, Gjøsæter J, Stenseth NC (2010) Diel vertical migration patterns in young Skagerrak coastal cod. Mar Ecol Prog Ser 405:29-37

Fischer P (2004) Nocturnal foraging in the stone loach (*Barbatula barbatula*): fixed or environmentally mediated behaviour? J Freshwat Ecol 19:77-85

Foote KG, Aglen A, Nakken O (1986) Measurement of fish target strength with a split-beam echo sounder. J Acoust Soc Am 80:612-621

Giske J, Aksnes DL, Baliño BM, Kaartvedt S, Lie U, Nordeide JT, Salvanes AGV, Wakili SM, Aadnesen A (1990) Vertical distribution and trophic interactions of zooplankton and fish in Masfjorde, Norway. Sarsia 75:65-82

Giske J, Aksnes DL (1992) Ontogeny, season and trade-offs: vertical distribution of the mesopelagic fish *Maurolicus muelleri.* Sarsia 77:253-261

Gjøsæter J (1981) Life history and ecology of *Maurolicus muelleri* (Gonostomatidae) in the Norwegain waters. Fiskeridirektoratets Skrifter, Serie Havundersøkelser 17:109-131

Hrabik T, Jensen PP, Martell SJD, Walters CJ, Kitchell JF (2006) Diel vertical migration in the Lake Superior pelagic community. I. Changes in the vertical migration of coregonids in response to varying predation risk. Can J Fish Aquat Sci 63:2286-2295

Hunter JR (1968) Effects of Light on schooling and feeding of jack mackerel, *Trachurus symmetricus*. J Fish Res Board Can 25:393-407

Iversen (2004) Mackerel and horse mackerel. In Skjoldal HR, Saetre R, Fernö A, Misund OA, Roettingen I (eds) The Norwegian Sea ecosystem. Tapir Academic Press, Trondheim, pp. 289-300

Josse E, Bertrand A, Dagorn L (1999) An acoustic approach to study tuna aggregated around fish aggregating devices in French Polynesia: methods and validation. Aquat Living Resour 12:303−313

Kaartvedt S, Knutsen T, Holst JC (1998) Schooling of the vertically migrating mesopelagic fish *Maurolicus muelleri* in light summer nights. Mar Ecol Prog Ser 170:287-290

Kaartvedt S, Torgersen T, Klevjer TA, Røstad A, Devine JA (2008) Behaviour of individual mesopelagic fish in acoustic scattering layers of Norwegian fjords. Mar Ecol Prog Ser 360:201-209

Kaartvedt S, Røstad A, Klevjer T, Staby A (2009) Use of bottom-mounted echo sounders in exploring behavior of mesopelagic fishes. Mar Ecol Prog Ser 395:109-118

Landaeta MF, Castro LR (2002) Spring spawning and early nursery zone of the mesopelagic fish *Maurolicus parvipinnis* at the coastal upwelling zone off Talcahuano, central Chile. Mar Ecol Prog Ser 226:179-191

MacLennan DN, Simmonds EJ (1992) Fisheries acoustics. Chapman and Hall, London

McClatchie S, Dunford A (2003) Estimated biomass of vertically migrating mesopelagic fish off New Zealand. Deep-Sea Res I 50:1263–1281

Mehner T, Kasprzak P, Hölker F (2007) Exploring ultimate hypothesis to predict diel vertical migrations in coregonid fish. Can J Fish Aquat Sci 64:874-886

Misund OA, Beltestad AK (1996) Target-strength estimates of schooling herring and mackerel using the comparison method. ICES J Mar Sci 53:281-284

Neilson JD, Perry RI (1990) Diel vertical migrations of marine fishes: an obligate or facultative process? Adv Mar Biol 26:115-167

Olsen E, Aanes S, Mehl S, Holst JC, Aglen A, Gjøsæter H (2010) Cod, haddock, saithe, herring, and capelin in the Barents Sea and adjacent waters: a review of the biological value of the area. ICES J Mar Sci 67: 87-101

Onsrud MSR, Kaartvedt S, Røstad A, Klevjer TA (2004) Vertical distribution and feeding patterns in fish foraging on the krill *Meganyctiphanes norvegica*. ICES J Mar Sci 61:1278-1290

Pearre S Jr. (2003) Eat and run? The hunger satiation hypothesis in vertical migration: history, evidence and consequences. Biol Rev 78:1-79

Pitcher TJ (1993) Functions of shoaling behaviour in teleosts. In: Pitcher TJ (ed) Behaviour of teleost fishes. Chapman and Hall, London, pp. 363-411

Rasmussen OI, Giske J (1994) Life-history parameters and vertical distribution of *Maurolicus muelleri* in Masfjorden in summer. Mar Biol 120:649-664

Rosland R, Giske J (1994) A dynamic optimization model for the diel vertical distribution of a pelagic planktivorous fish. Prog Oceanogr 34:1-43

Rosland R, Giske J (1997) A dynamic model for the life history of *Maurolicus muelleri*, a pelagic planktivorous fish. Fish Oceanogr 6:19-34

Ryer CH, Olla BL (1999) Light-induced changes in the prey consumption and behaviour of two juvenile planktivorous fish. Mar Ecol Prog Ser 81:41-51

Salvanes AGV (1986) Preliminary report from a study of species composition, size composition and distribution of the fish in a fjord of western Norway based on regularly conducted experimental fishing and catch statistics during one year. ICES CM1986/G:70

Salvanes AGV (1991) Structure and dynamics of the cod population and trophic interactions in Masfjorden: A contribution to a large-scale cod enhancement experiment. *Dr. Scient. thesis*, University of Bergen, 140 pages

Salvanes AGV, Nordeide JT (1993) Dominating sublittoral fish species in a west Norwegian fjord and their trophic links to cod (*Gadus morhua* L.). Sarsia 78:221-234

Scheuerell MD, Schindler DE (2003) Diel vertical migration by juvenile sockeye salmon: empirical evidence for the antipredation window. Ecology 84:1713-1720

Soule M, Hampton I, Barange M (1996) Potential improvements to current methods of recognizing single targets with a split-beam echo-sounder. ICES J Mar Sci 53:237-243

Srisomwong J (2009) Diel vertical migration and feeding pattern of *M. muelleri* in Masfjorden in late autumn. Master thesis, University of Bergen, Bergen, Norway

Staby A, Aksnes DL (2010) Follow the light – diurnal and seasonal variations in vertical distribution of the mesopelagic fish *Maurolicus muelleri*. (Paper 3 in this thesis)

Staby A, Røstad A, Kaartvedt S (2010) A full year study of diel vertical migration in the mesopelagic fish *Maurolicus muelleri* reveals novel and varied behavioural patterns. (Paper 2 in this thesis)

Stensholt BK, Aglen A, Mehl S, Stensholt E (2002) Vertical density distributions of fish: a balance between environmental and physiological limitation. ICES J Mar Sci 59:679-710

Tarling GA, Jarvis T, Emsley SM, Matthews JBL (2002) Midnight sinking behaviour in *Calanus finmarchicus*: a response to satiation or krill? Mar Ecol Prog Ser 240:183-194

Torgersen T, Kaartvedt S, Melle W, Knutsen T (1997) Large scale distribution of acoustical scattering layers at the Norwegian continental shelf and the eastern Norwegian Sea. Sarsia 82:87-96

Warrant EJ, Locket NA (2004) Vision in the deep. Biol Rev 79:671-712

Table 1: Number of fish caught in pelagic trawls (PT) and with rod and reel (trawls that did not catch any large fish are not shown). Numbers in parenthesis indicate number of pearlside identified in stomachs and the mean length of pearlside in good condition.* not measured. Target strength (TS) estimates are based on the standard equation TS = 20LogL + b (L is length), except estimates for horse mackerel (TS = 10.9LogL-52.78).

Date	Gear type	Start time	Trawl depth	Saithe	Pollack	Haddock	Mackerell	Horse mackerell	Blue ling	Roundnose Grenadier	Greater silver smelt	Lump sucker
15.10.2009	PT	12:32	59	1 (1;19)								
	PT	19:26	10				2 (21;-)	1 (16;-)			2 *	
	PT	21:15	51	1 (14;-)								
	PT	22:17	75	10 (46;26)								
16.10.2009	PT	06:28	300	1 (0;-)								
	PT	14:38	350						1 (0;-)			
17.10.2009	PT	21:13	10				4 (63;22)	1 (0;-)			2 *	1 (7;-)
	PT	03:46	25								1 *	
	PT	07:12	147	1 (132;-)	1 (0;-)	1 (20;-)						
	PT	11:50	160		1 (11;40)							
	PT	13:01	10									2 *
	PT	14:10	112								1 (0;-)	
	PT	15:29	345						1 (0;-)	2 (0;-)		
	PT	20:35	99	1 (12;-)								
	PT	21:37	9				1 (25;18)					
18.10.2009	PT	00:48	60	1 (46;-)								
	PT	02:58	220			1 (21;39)						
16.10.2009	Rod		75		1 (7;-)							
	Rod		60	1 (0;-)								
	Rod		100	2 (21;35)								
	Length (cm)			66 – 97	56 – 69	55 – 61	20 – 21	10 – 45	88 – 89	7	47	35
	TS range (dB)			-26.1 – -29.4 [1]	-30.7 – -32.5 [1]	-32.2 – -33.1 [2]	-60.1 [3]	-34.8 – -41.9 [4]	-28.6	-	-34.6 [1]	-
	Vertical migrator			Yes [5]	Unknown	Yes [5]	Unknown	Unknown	No	No	Unknown	No

[1] Foote et al. 1986; [2] MacLennan & Simmonds 1992; [3] Misund & Beltestad 1996; [4] Barange & Hampton 1994; [5] Olsen et al. 2010

Table 2: Average monthly landings (headed and gutted weight in kg) of tusk, haddock, ling, pollack, cod and saithe in Masfjorden. For each species landings data is summed for each month and averaged over the period 1986 – 1992. Only months with 2 or more landings were used to calculate the average monthly landings.

	Month											
Species	1	2	3	4	5	6	7	8	9	10	11	12
Tusk					20	20	15			58		
Haddock		17	17	41			5			5	11	
Ling					32	30				21		
Pollack				51	3	3	2	7	5	32	8	
Saithe			164	9			16	3		93	65	
Cod	110	328	384	25	21	24	44	64	55	75	38	48

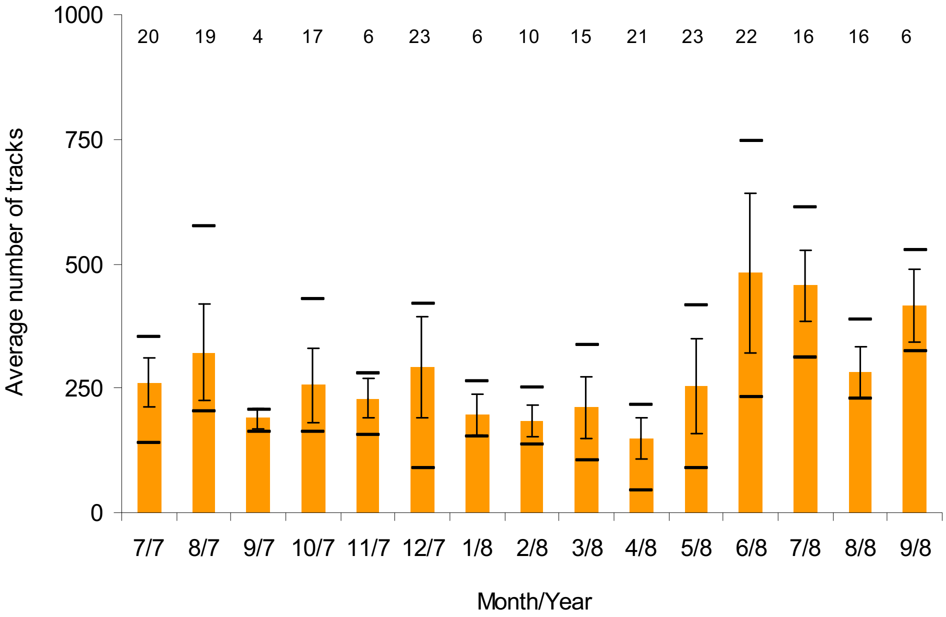
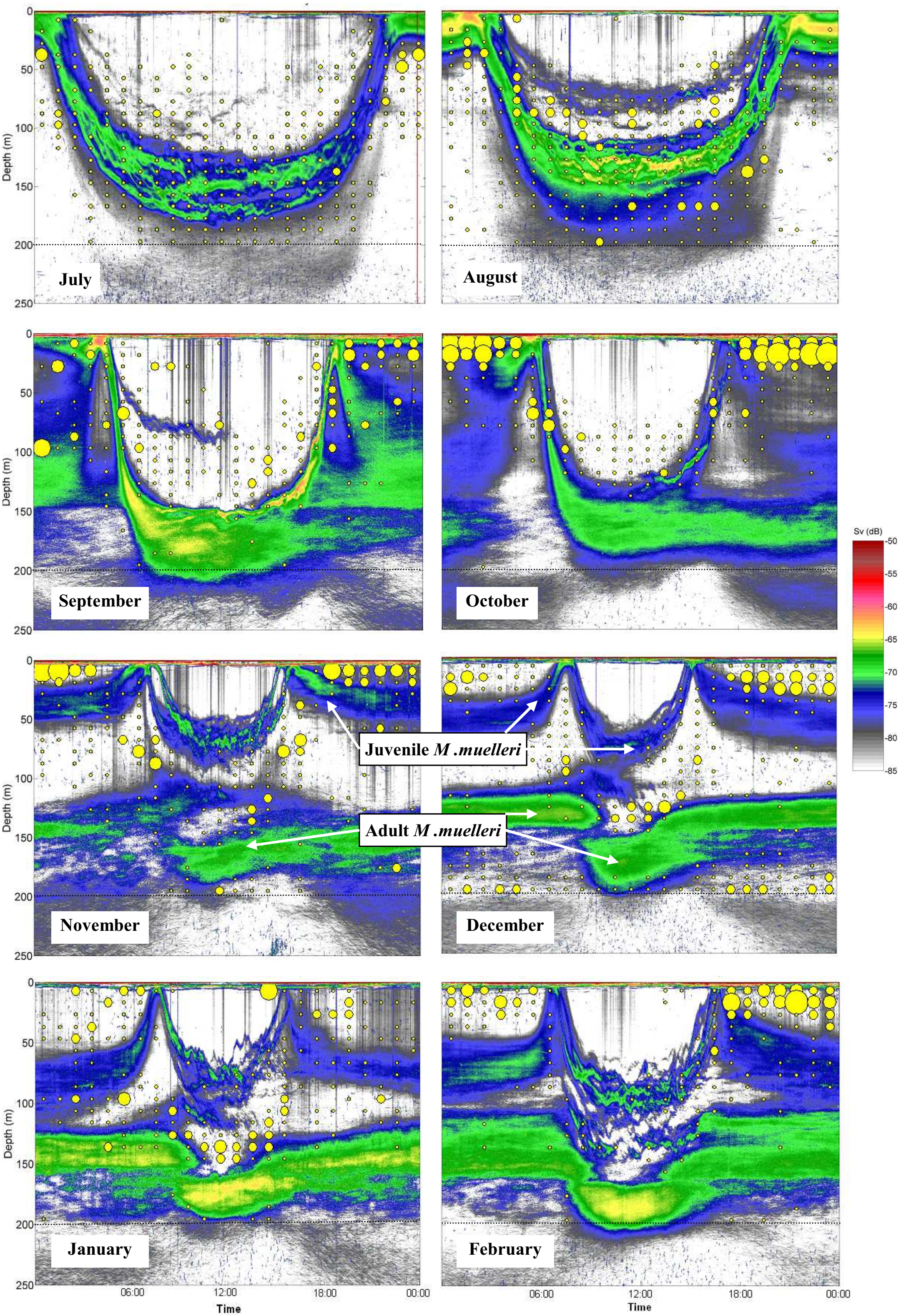
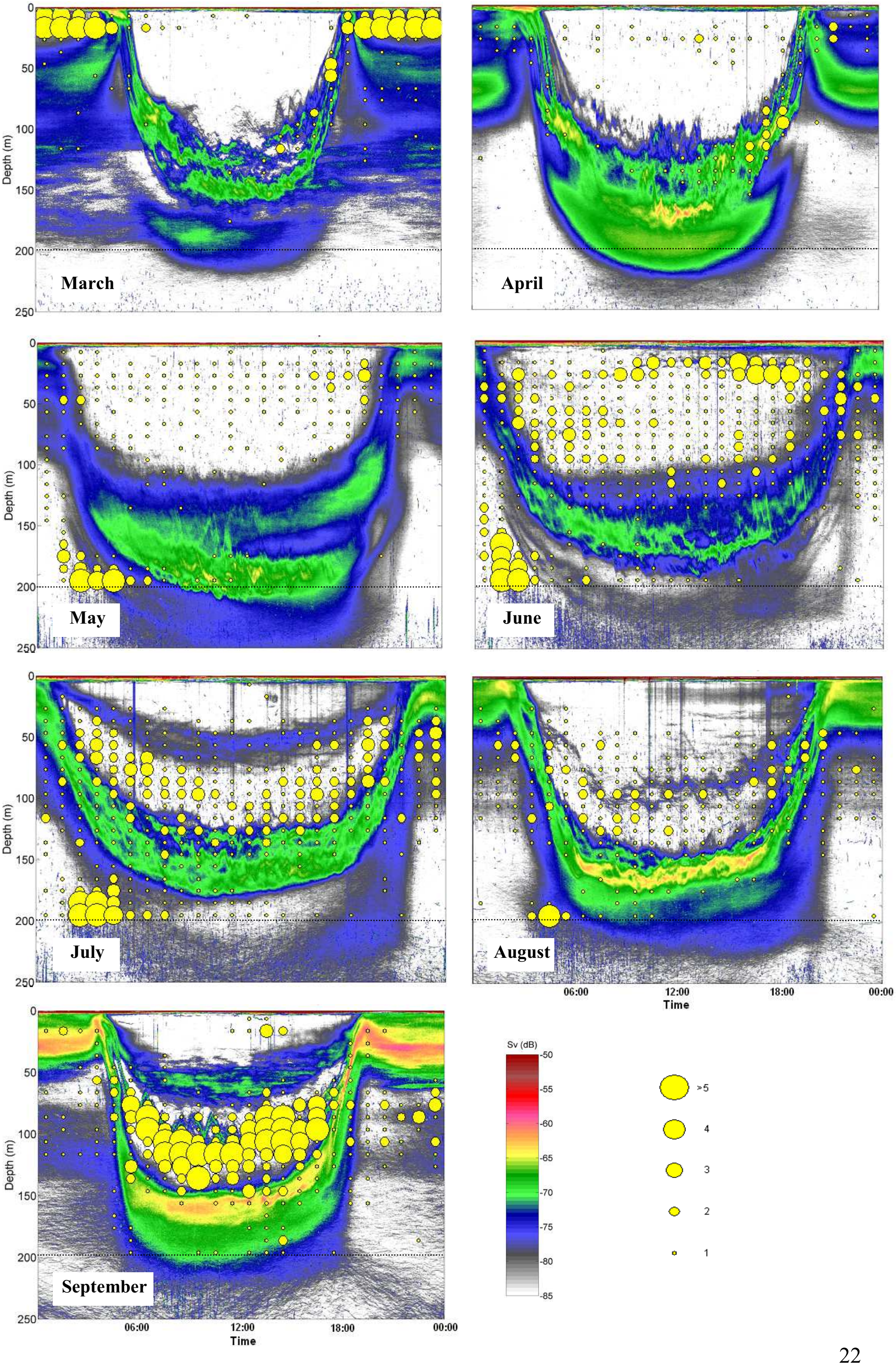


Figure 1: Average number of daily occurrence of large fish (daily number of tracks) above 200 m depth, calculated for each month. Whiskers indicate the Standard deviation of the average, while upper and lower crossbars are maximum and minimum daily counts respectively. The number of valid days analysed is shown for each month.


July
August
September
October
November
December
January
February
Juvenile M .muelleri
Adult M .muelleri
Depth (m)
0
50
100
150
200
250
Time
06:00
12:00
18:00
00:00
Sv (dB)
-50
-55
-60
-65
-70
-75
-80
-85



March
April
May
June
July
August
September
Depth (m)
0
50
100
150
200
250
06:00
12:00
18:00
00:00
Time
Sv (dB)
-50
-55
-60
-65
-70
-75
-80
-85
>5
4
3
2
1

Figure 2: Composite monthly echograms generated from entire daily echograms (24 hours). Bubbles indicate average number of large fish, i.e. fish tracks (TS > -45dB) per 10 m (vertical) and one hour (horizontal) bin. Juvenile and adult scattering layers of *M. muelleri* are visible above 200 m depth (Staby et al. 2010)

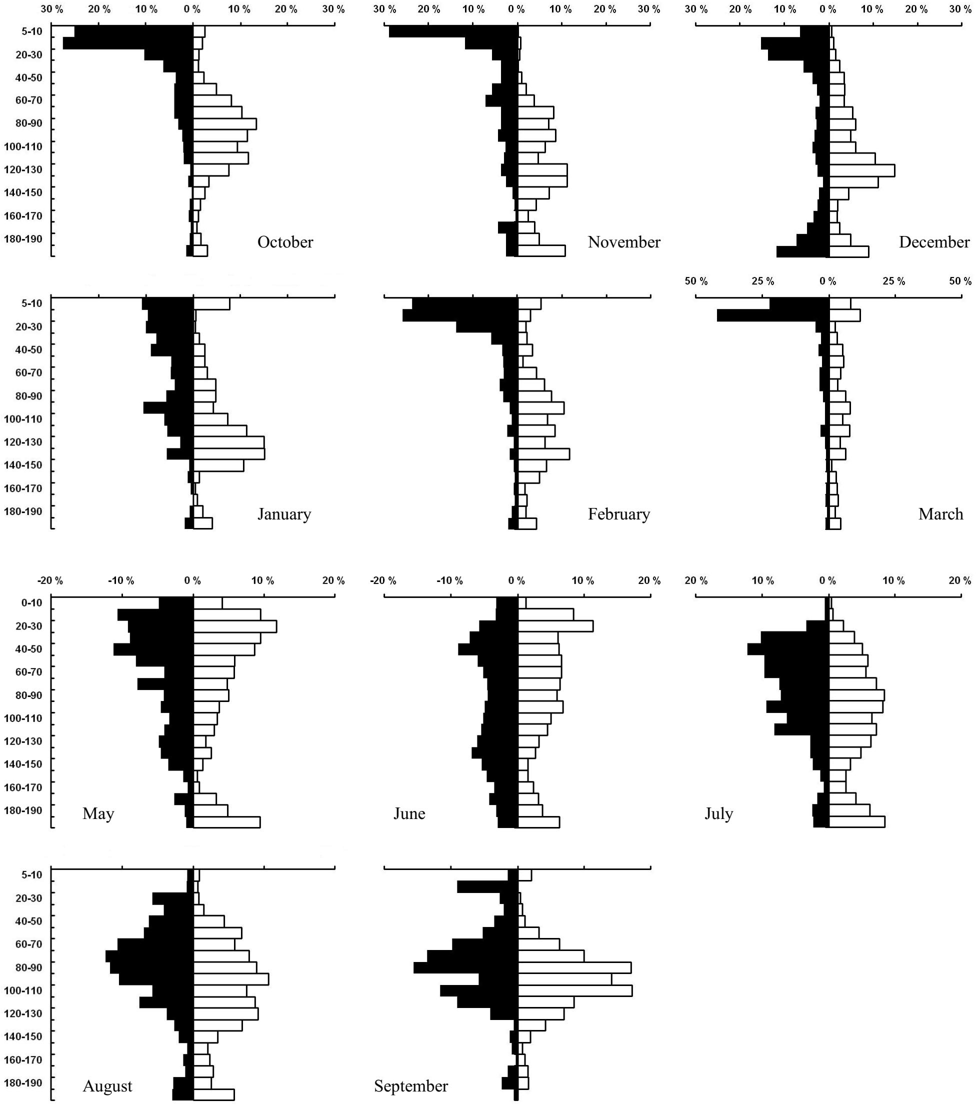


Figure 3: Vertical frequency distribution of large fish during night (dark bars) and day (open bars). Note different frequency scales.

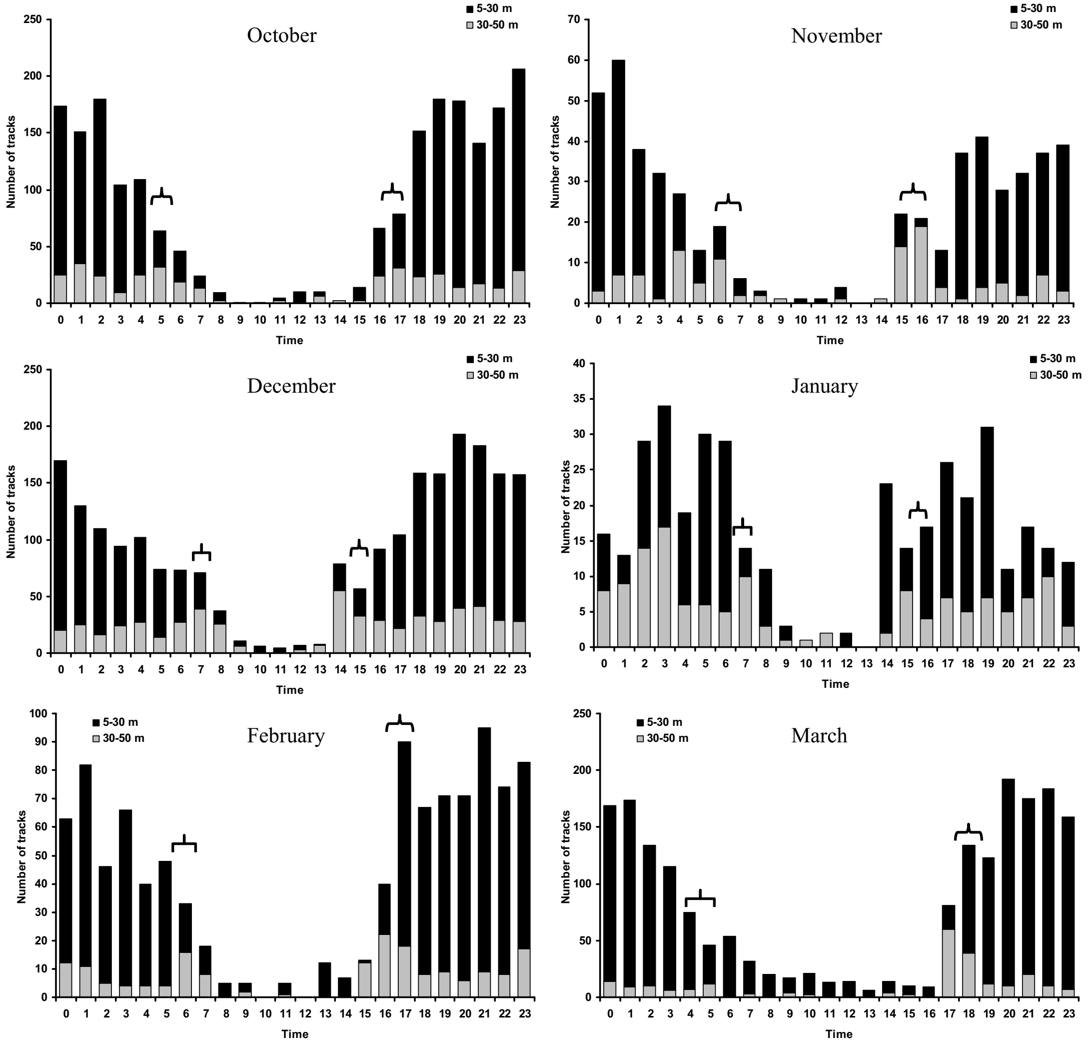


Figure 4: Total number of large fish tracks counted in the upper 30 and 50 m at different times of the day during the period October 2007 and March 2008. Brackets indicate the approximate time period when *M. muelleri* were observed at the surface. Note different y-axis scales.

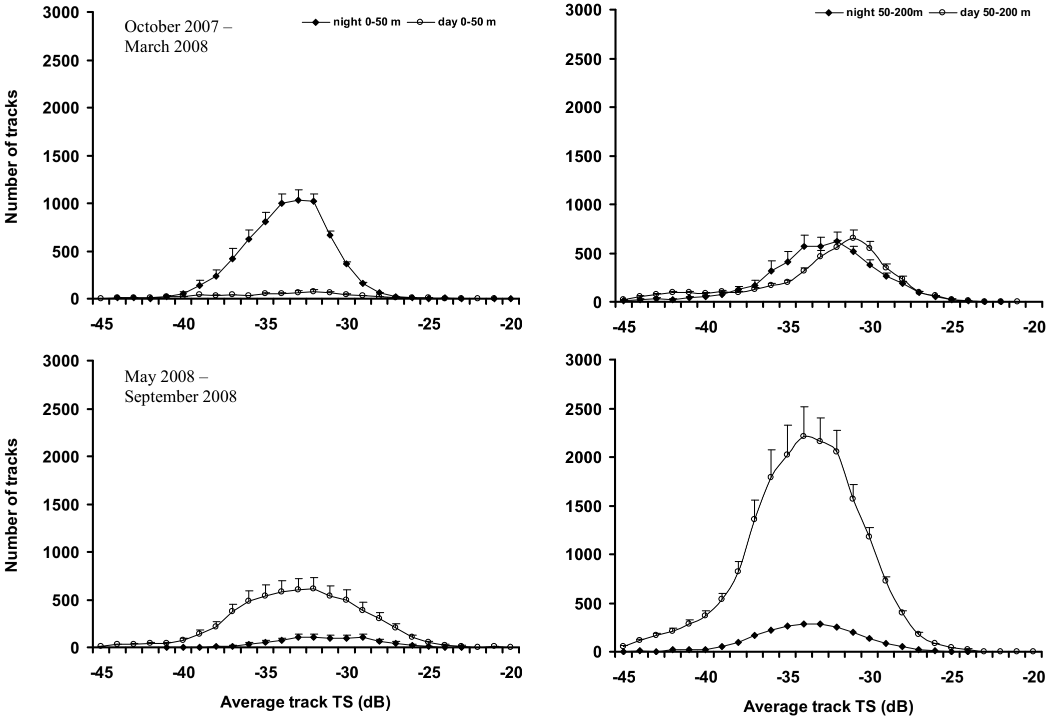


Figure 5: Frequency distributions of average track target strengths (TS) in the upper 50 m (left) and 50 – 200 m (right) from October 2007 to March 2008 (upper panel) and from May to September 2008 (lower panel). Error bars indicate Standard deviation. Fish tracks recognised in the hour bin corresponding with the start and end time of civil twilight were not included.