From acoustic scattering layers to individuals - behaviour of a mesopelagic fish at different scales

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Preface

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Thank you for the good time, my past and present colleagues at AQUA, especially Lina, Bea, Jan and Mette.

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S. Christiansen

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Content

List of publications

I: Christiansen, S., Klevjer, T. A., Røstad, A., Aksnes, D. L., and Kaartvedt, S. 2021. Flexible behaviour in a mesopelagic fish (*Maurolicus muelleri*). ICES Journal of Marine Science: 1–13.

II: Christiansen, S., Titelman, J., and Kaartvedt, S. 2019. Nighttime Swimming Behavior of a Mesopelagic Fish. Frontiers in Marine Science, 6: 1–12.

III: Christiansen, S., Langangen, Ø., Vøllestad, L.A., and Kaartvedt, S. (Manuscript). Three-dimensional swimming behaviour and activity of a mesopelagic fish.

IV: Christiansen, S., Kaartvedt, S., and Sobradillo, B. (Manuscript). Influence of behaviour on target strength in a mesopelagic fish.

I will reference the four papers by their bold roman numerals in this synthesis.

Summary

This thesis describes the behaviour of *Maurolicus muelleri* at different temporal and spatial scales (Figure 1), ranging from vertical population distribution and diel vertical migrations to individual movement behaviour. The analysis is done based on acoustic datasets from three echosounders moored in Masfjorden between October 2010 and August 2011 (Prihartato *et al.*, 2015 Box 6). By focusing on small-scale patterns and individuals this thesis adds on previous acoustic research about *M. muelleri*'s diel vertical migration behaviour (Prihartato *et al.*, 2015; Staby *et al.*, 2011) and influence of night time light levels (Prihartato *et al.*, 2015).

Paper **I** highlights the diversity of behaviours found in *M. muelleri*, including social behaviour, bold behaviour and predator escape. We relate the observed behaviour to ambient light conditions. While variability in mesopelagic scattering layer distributions is often ascribed to environmental conditions and species composition, we show that considerable variability in behaviour exists within a largely monospecific population.

In paper **II**, we applied acoustic target tracking to explore the nighttime individual behaviour underlying twilight vertical migration in juvenile *M. muelleri* over four winter months. Twilight vertical migration is characterized by an ascent to surface waters at dusk followed by "midnight sinking" to ca. 40-90 m depth, another ascent to the surface in the morning and retreat to greater depths around sunrise. We found that step-wise swimming, during which the fish alternate between short periods of vertical swimming (steps) and periods without vertical movement (pauses), is the dominant mode of vertical relocation in juvenile *M. muelleri*. The step-wise behaviour during the dusk descent mirrored the dawn ascent. This suggests that predator avoidance is the main reason for the step-wise swimming pattern. The switch between midnight sinking and the slowly starting morning ascent seemed to be triggered by an internal clock, while changes in ambient light probably controlled the speed of the final ascent in the morning.

While the analysis in paper **II** was restricted to vertical behaviour, in paper **III** we augmented the dataset with the horizontal position information obtained from the split-beam echosounder. By combining vertical and horizontal velocities as well as turning behaviour we obtained a 3D representation of the individual movement. This analysis revealed some distinct individual movement features. Firstly, most juvenile

M. muelleri drifted with the currents at night, supporting the hypotheses of growth maximisation by low activity in the juvenile fish. Turning was relatively common throughout the night and activity levels increased during the migration periods. Finally, step-wise swimming was generally combined with turns in the horizontal plane, potentially helping in confusing predators.

In paper **IV**, we determined target strength (TS, representing individual backscatter) changes depending on the orientation of juvenile *M. muelleri*. Such an analysis is important for acoustic biomass assessments since uncertainties in target strength estimates lead to inaccurate density estimates. For physoclist fish, like the here analysed *M. muelleri*, the swim bladder creates 90% of the backscatter, but due to the elongated swim bladder shape the measured TS depends on the orientation of the fish in relation to the echosounder. We found that the measured TS was lower during ascent or descent than during pauses (**II**). However, high proportions of vertically moving fish during vertical migration did not affect the median TS or population backscatter, presumably due to the non-synchronised step-wise swimming behaviour.
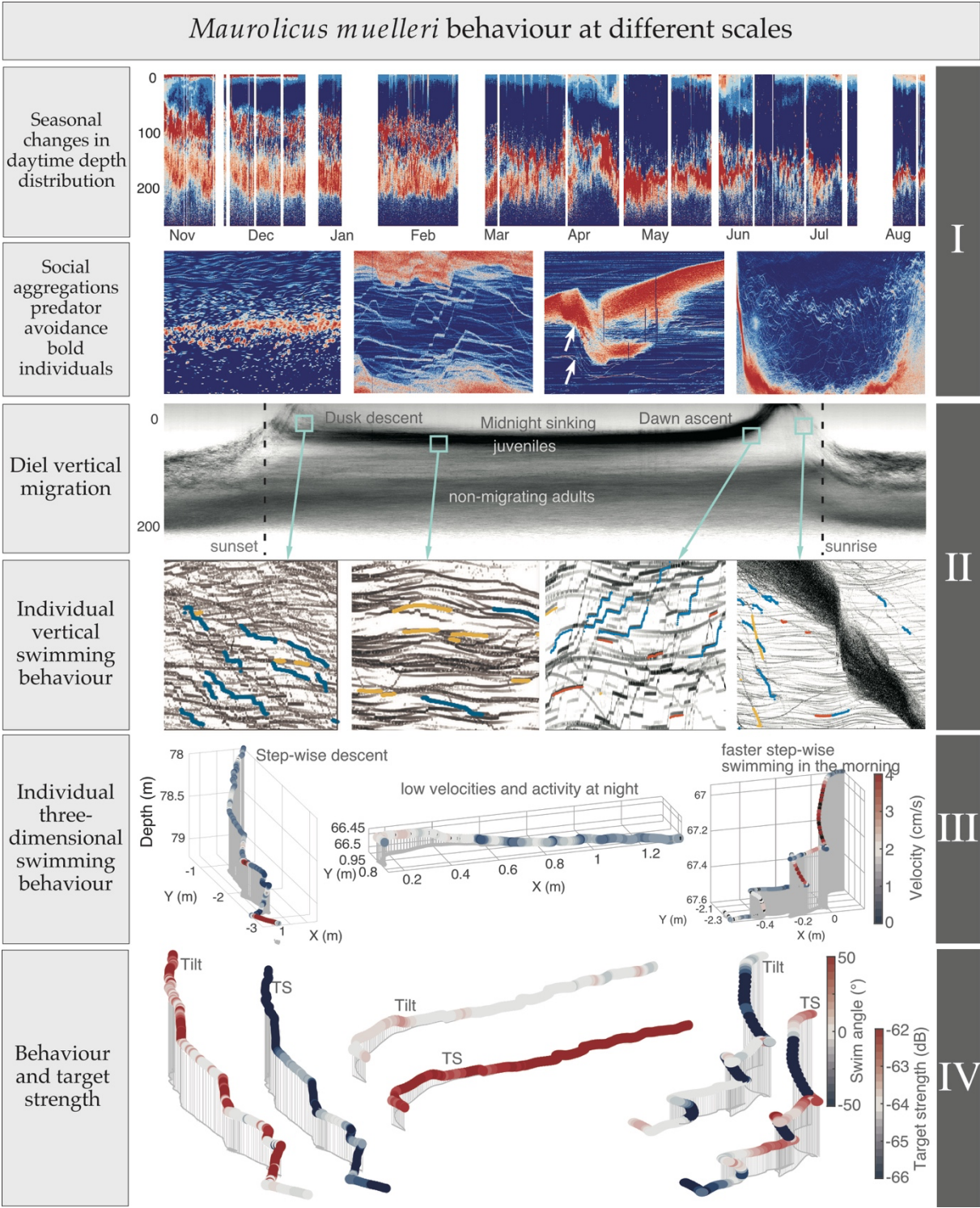
Figure 1: *Maurolicus muelleri* behaviour at different scales. Visualization of results from papers **I-IV**.
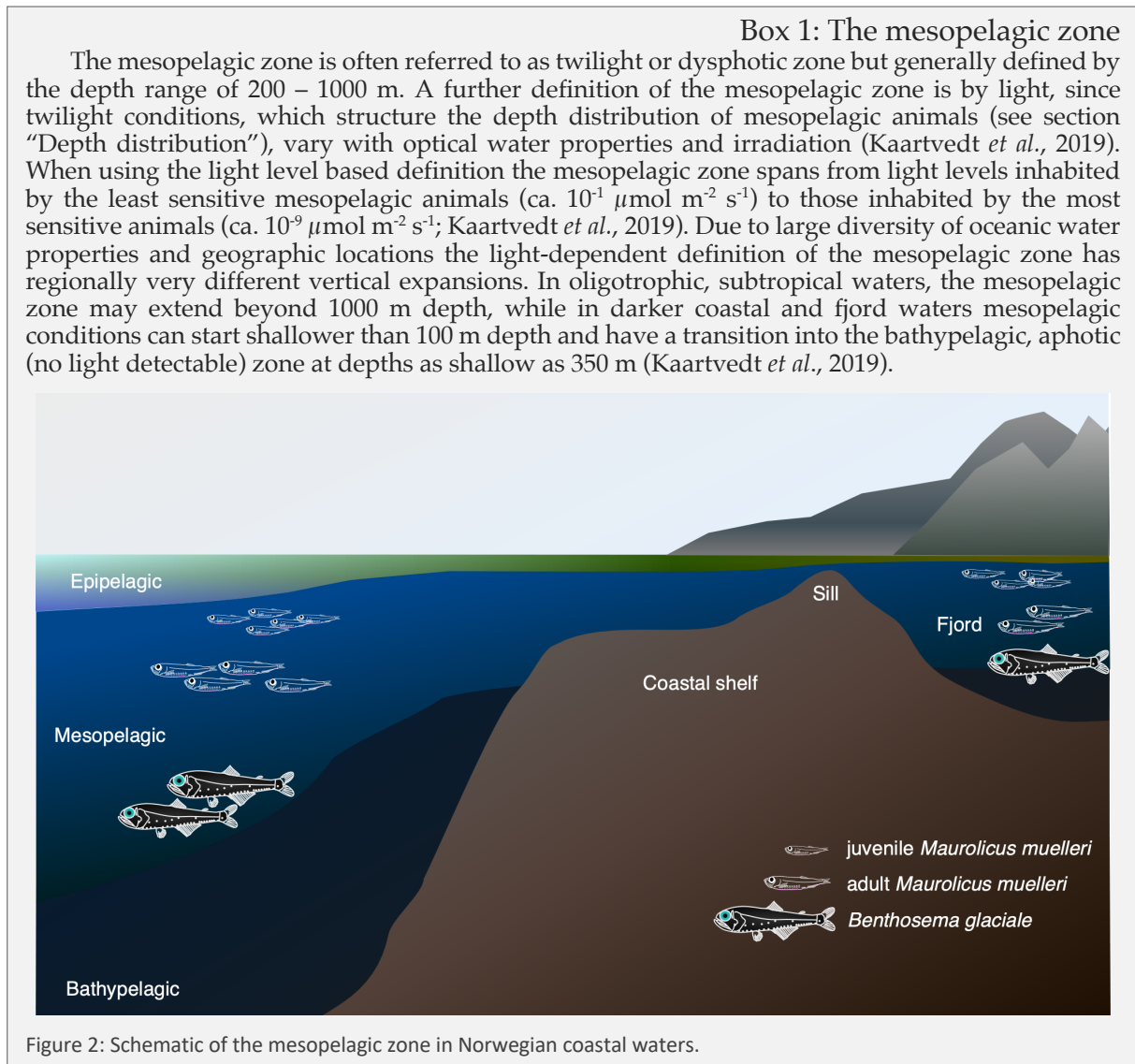
Introduction

Movement is an essential feature of animal behaviour. Motility patterns can indicate what kind of behaviour an animal engages with, how it interacts with its environment as well as its energetic requirements. Movement happens at very different scales. In the ocean, the largest and most prominent coordinated vertical movement behaviour is diel vertical migration, during which millions of animals rise to the surface layer at night to forage in the shelter of the dark, and retreat to depth before sunrise. Diel vertical migration is ubiquitous across ocean basins (Bianchi and Mislan, 2015; Dietz, 1948; Klevjer *et al.*, 2016) and animal taxa. Generally, diel vertical migration patterns reveal the daily trade-off of the need to feed and the need to avoid predation (Zaret and Suffern, 1976). However, the extent, timing, and mode of execution of diel vertical migration varies across time and space and between and within species.

Community behaviour results from the activities of its individuals. This individual behaviour is often highly variable - a basic requirement for life and evolution (Allen and McGlade, 1987). This variability can influence the overall footprint of a population (Shaw, 2020). Few individuals with deviating behaviour can have overrepresented impacts on species dispersal (Canestrelli *et al.*, 2016), distribution (**I**) and nutrient dynamics (Allen and McGlade, 1987; Allgeier *et al.*, 2020). Furthermore, details of individual behaviour can contribute to a higher level of understanding of the apparent large-scale patterns (Pearre, 2003, **II**, **III**). Consequently, analysing behaviour at different scales can be valuable for our overall understanding of ecological and biogeochemical processes.

While light attenuates quickly in the upper ocean layers, sound can penetrate the water and reach the **mesopelagic**[1] (Box 1) depths where diel vertical migrators hide during the day. Echosounders revealed that the animals of the mesopelagic zone are often organised in so-called sound scattering layers (Duvall and Christensen, 1946; Eyring *et al.*, 1948). Scattering layers exist in all oceans (Dietz, 1948; Klevjer *et al.*, 2016). They may host a large diversity of animals that sometimes inhabit several distinct layers (Barham, 1957; 1966; Dietz, 1948; Pearcy *et al.*, 1977). In open ocean scattering layers, scientific midwater trawls commonly catch more than 100 different mesopelagic fish species (Ariza *et al.*, 2016; Wang *et al.*, 2019). In addition to fish,

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[1] Terms emphasized by bold letters are explained in separate infoboxes.

invertebrates are represented in scattering layers, among them crustaceans and squid (Ariza *et al.*, 2016), but also gelatinous animals like medusae (Hosia *et al.*, 2008; Hoving *et al.*, 2020; Kaartvedt *et al.*, 2011), larvaceans (Hamner *et al.*, 1992), ctenophores (Hoving *et al.*, 2020; Robison, 2004) and siphonophores (Hoving *et al.*, 2020).

Box 1: The mesopelagic zone

The mesopelagic zone is often referred to as twilight or dysphotic zone but generally defined by the depth range of 200 – 1000 m. A further definition of the mesopelagic zone is by light, since twilight conditions, which structure the depth distribution of mesopelagic animals (see section "Depth distribution"), vary with optical water properties and irradiation (Kaartvedt *et al.*, 2019). When using the light level based definition the mesopelagic zone spans from light levels inhabited by the least sensitive mesopelagic animals (ca. 10^{-1} μmol m^{-2} s^{-1}) to those inhabited by the most sensitive animals (ca. 10^{-9} μmol m^{-2} s^{-1}; Kaartvedt *et al.*, 2019). Due to large diversity of oceanic water properties and geographic locations the light-dependent definition of the mesopelagic zone has regionally very different vertical expansions. In oligotrophic, subtropical waters, the mesopelagic zone may extend beyond 1000 m depth, while in darker coastal and fjord waters mesopelagic conditions can start shallower than 100 m depth and have a transition into the bathypelagic, aphotic (no light detectable) zone at depths as shallow as 350 m (Kaartvedt *et al.*, 2019).

Figure 2: Schematic of the mesopelagic zone in Norwegian coastal waters.

The mesopelagic animals that inhabit the scattering layers hold key positions in the oceanic food web. Most mesopelagic animals forage on lower trophic levels and are eaten by a whole range of high trophic level consumers, among them fish (Afonso *et al.*, 2014; Giske *et al.*, 1990; Howey *et al.*, 2016; Marchal, 1996), mammals (Doksæter *et al.*, 2009; Giménez *et al.*, 2018; Marçalo *et al.*, 2018; Naito *et al.*, 2013), sea turtles and sea birds (Watanuki and Thiebot, 2020). In addition to being important food for economically valuable fish species (Giske *et al.*, 1990; Howey *et al.*, 2016; Marchal, 1996; Mir-Arguimbau *et al.*, 2020), also the inhabitants of the mesopelagic themselves (e.g.

the mesopelagic fish *Maurolicus muelleri*) are increasingly seen as potential food and feed resource (Alvheim *et al.*, 2020; Grimaldo *et al.*, 2020; Olsen *et al.*, 2020; Standal and Grimaldo, 2020). The vastness of the oceans midwater and therefore expected very high biomass of mesopelagic fish (Irigoien *et al.*, 2014; Proud *et al.*, 2018) are regarded as a possible solution for increasing global food demands (Alvheim *et al.*, 2020; Grimaldo *et al.*, 2020; Olsen *et al.*, 2020; Standal and Grimaldo, 2020). However, biomass estimates still have a large uncertainty (Proud *et al.*, 2018) and the ecological and biogeochemical implications of a mesopelagic fishery are unclear (Martin *et al.*, 2020; St John *et al.*, 2016). Therefore, a better understanding of mesopelagic organisms and their role in the ocean is crucial (Martin *et al.*, 2020; St John *et al.*, 2016).

In addition to their role in the food web, mesopelagic organisms play an important part in biogeochemical cycling and carbon sequestration. The ocean takes up about 30% of the anthropogenically produced carbon dioxide (Friedlingstein *et al.*, 2020; Gruber *et al.*, 2019; Sabine, 2004) through physical, chemical and biological processes. Globally, the **biological carbon pump** (Box 2) is responsible for about 5.7 Pg C year^{-1} of the carbon export from the euphotic zone (Buesseler *et al.*, 2020). Migrating animals contribute to the active carbon transport into deeper layers by foraging in the productive surface layer and respiring, defecating and excreting at mesopelagic depths (Saba *et al.*, 2021). The active carbon transport may be crucial for the support of deep-sea and shelf ecosystems (Trueman *et al.*, 2014) and potentially plays a considerable role in nutrient cycles (Kiko *et al.*, 2020; Steinberg *et al.*, 2002), oxygen budgets (Bianchi *et al.*, 2013a; Kiko *et al.*, 2020) and carbon sequestration (Bianchi *et al.*, 2013b; Davison *et al.*, 2013; Saba *et al.*, 2021; Trueman *et al.*, 2014). Mesopelagic behaviour, particularly diel vertical migration but also predator-prey interactions (Trueman *et al.*, 2014) and activity levels at depth (Saba *et al.*, 2021), thus influence ocean biogeochemistry and on a larger scale the planets carbon budget.

Box 2: The biological carbon pump

The ocean can take up or outgas carbon dioxide by air-sea gas exchange at the surface. Phytoplankton transform the dissolved carbon into biomass during photosynthesis. Thereby the carbon enters the marine food web and particulate matter cycles. Passive sinking of organic material, mortality, repackaging of small particles into larger, faster sinking fecal pellets, but also active transport by diel vertical migration lead to the export of carbon and nutrients into deeper water layers (Archibald *et al.*, 2019; Davison *et al.*, 2013; Saba *et al.*, 2021).

Norwegian **fjord ecosystems** (Box 3) provide unique conditions for acoustic analyses of mesopelagic behaviour due to a stable hydrography and a comparably

simple mesopelagic community. The upper 200 m in Norwegian fjords are characterized by largely monospecific scattering layers formed by the mesopelagic fish *Maurolicus muelleri* (Giske *et al.*, 1990; Staby *et al.*, 2011). *M. muelleri* have been focus of mesopelagic research in Norwegian fjords for several decades. This research included ecosystem (Giske *et al.*, 1990; Kaartvedt *et al.*, 1988), life-history (Folkvord *et al.*, 2016; Gjøsæter, 1981; Goodson *et al.*, 1995; Kristoffersen and Salvanes, 1998; Rasmussen and Giske, 1994), distribution (Baliño and Aksnes, 1993; Giske *et al.*, 1990; Giske and Aksnes, 1992; Rosland and Giske, 1994; Staby and Aksnes, 2011) and diel vertical migration (Prihartato *et al.*, 2015; Staby *et al.*, 2011; 2013) analyses. As a result, there exists a broad knowledge background on the ecology of this mesopelagic species. Nevertheless, except for short-term observations (Kaartvedt *et al.*, 2008; Torgersen and Kaartvedt, 2001), little is known about *M. muelleri*'s individual behaviour.

Box 3: Fjords as study location for mesopelagic research

Fjords are remnants of glacier carvings from the last ice ages. Fjords are often several hundred meters deep and are comparatively dark due to strongly limited light penetration. Riverine runoff reduces fjord light levels at shallow depths in multiples ways ranging from suspended and dissolved organic materials to high nutrient supply and subsequently high productivity. The relative darkness in shallow water depths makes fjords suitable for mesopelagic communities comparable to those in greater depth in the adjoining ocean. In addition, sheltered conditions and proximity to land facilitate easy research access compared to open-ocean mesopelagic habitats. Fjords are separated from coastal waters by underwater sills. Below sill depth the physical conditions are quite stable due to water mass stratification, resulting in sluggish current speeds. This enables prolonged observations of individuals by stationary acoustics. The hydrographic conditions and the similarity of the ecosystem dynamics to the open ocean make fjords ideal for acoustic assessments of mesopelagic movement behaviour.

In this thesis, I build on, and extend, previous knowledge of *M. muelleri* behaviour with a particular focus on small-scale behavioural patterns and individual swimming behaviour. I use a high-resolution dataset obtained over ten months from three stationary echosounders in the Norwegian fjord **Masfjorden** (Box 4), to describe behaviour at different scales (Figure 1), from population and small-scale distribution patterns (**I, II**) to individual swimming patterns (**II, III**) and activity (**III**). I relate the observed individual behaviour to potential implications for biomass assessments (**IV**). In this synthesis, I first provide some background on *M. muelleri* and on applications of echosounders in mesopelagic research. I show up the opportunities, and explain sources of uncertainty in individual behaviour obtained from echosounders. Then, I embed the findings presented in papers **I-IV** into the context of general mesopelagic and specifically *M. muelleri* behaviour. Finally, I discuss potential consequences of the findings with regard to ecological, biogeochemical and methodological (**IV**) aspects.

Masfjorden is a sheltered fjord on the West coast of Norway. The fjord has a maximum depth of 494 m and a sill at 75 m depth, which is limiting the exchange with coastal waters (Kaartvedt et al., 1988). Masfjorden is about 20 km long and surrounded by mountainsides. The fjord experiences coastal water darkening (Aksnes et al., 2009) and periodically low oxygen conditions in deeper water layers (Aksnes et al., 2019). However, the dissolved oxygen concentrations were >3 ml l^{-1} throughout the period analyzed in this thesis (Aksnes et al., 2019) and thus not expected to limit movement behaviour in *M. muelleri*.

While the hydrographic conditions below sill depth are mostly constant over the year (Rosland and Giske, 1997), the light environment changes drastically in the course of the year due to the fjord's high-latitude location at 60°52' North 005°25' East. During winter, nights are long and days short and dusky, while in summer, the nights are short and light and the days long. Dusk and dawn periods are extended at this latitude and last throughout the night in summer. The weather in western Norway is often rainy and unsettled, with abrupt changes in incoming radiation.

The mesopelagic fish community in Masfjorden includes *Maurolicus muelleri*, which inhabit the upper 200 m and *Benthosema glaciale* at deeper depths. Furthermore, krill (mainly *Meganyctiphanes norvegica*) and pelagic shrimps (Giske *et al.*, 1990), mysids, jellyfish and siphonophores are common. The zooplankton biomass is highest in surface waters except during winter when Calanus hibernate at depths >150 m (Rosland and Giske, 1994). Predatory fish, particularly saithe and blue whiting, are the primary consumers of the mesopelagic fish (Giske *et al.*, 1990).

Figure 3: Masfjorden on an overcast day in June.

The study species *Maurolicus muelleri*

The mesopelagic fish *Maurolicus muelleri* (GMELIN, Sternoptychidae, Figure 4) is the main species dealt with in this thesis. Fish of the genus *Maurolicus* occur worldwide (Rees *et al.*, 2020) in the shallow mesopelagic of shelf and coastal seas (Armstrong and Prosch, 1991; Clarke, 1982), around seamounts (Boehlert *et al.*, 2008; Campanella, 2021; Savinykh and Baytalyuk, 2010) and in fjords (Giske *et al.*, 1990; Valle-Levinson *et al.*, 2014). *M. muelleri* dominate the acoustic scattering layers <200 m depth in Norwegian fjords with younger age groups generally occupying shallower waters than the adults (Giske and Aksnes, 1992). *M. muelleri* are known for their **twilight migrations** (Box 5). They ascend to surface waters during two short periods around dusk and dawn, while spending the night at ~40-90 m depth ("**midnight sinking**"; Box 5) and retreating to ~100-200 m depth during the day (Staby *et al.*, 2011).

Figure 4: *Maurolicus muelleri*. The characteristic ventral photophores serve counter-illumination and explain *M. muelleri*'s common name "pearlside".

The fairly dense, monospecific scattering layers (Rasmussen and Giske, 1994) and shallow distribution make *M. muelleri* attractive for a potential mesopelagic fishery (Grimaldo *et al.*, 2020). However, the consequences of such a fishery for the ecosystem are unknown. *M. muelleri* presumably exert strong predation pressure on local zooplankton stocks (Bagøien *et al.*, 2001; Rasmussen and Giske, 1994) and are a preferred prey of commercially valuable fish species, particularly blue whiting and saithe (Giske *et al.*, 1990; Mir-Arguimbau *et al.*, 2020; Rasmussen and Giske, 1994).

M. muelleri reach up to 7 cm standard length, though only few exceed 5 cm (Gjøsæter, 1981; Rasmussen and Giske, 1994). The fish have a short life span of usually less than 3 years and a size-related fecundity (Gjøsæter, 1981; Rasmussen and Giske, 1994). The fish reach maturity after about one year, at ~2.5-4 cm standard length (Gjøsæter, 1981; Goodson *et al.*, 1995; Rasmussen and Giske, 1994). Batch spawning (Melo and Armstrong, 1991) occurs between March and October (Gjøsæter, 1981) and

balances high early life stage mortality in relation to environmental short-term fluctuations (Folkvord *et al.*, 2016).

M. muelleri are particularly adapted to life in the shallow mesopelagic. The fish have silver sides and ventral photophores (Figure 4) serving camouflage in comparatively light waters. In addition, *M. muelleri*'s eyes are specialised for twilight conditions with their retina having unique rod-like cones (de Busserolles *et al.*, 2017).

Box 5: Twilight migration and midnight sinking

Twilight migrations are a variant of "normal" diel vertical migrations, defined by occupation of near-surface waters at night and deep waters during the day. However, during twilight migrations, animals only use the periods around dusk and dawn for two short foraging periods at the surface (Giske et al., 1990; Prihartato et al., 2015; Staby et al., 2011; Valle-Levinson et al., 2014) while inhabiting slightly deeper waters at night, a behaviour termed midnight sinking (Cushing, 1951). A reason for midnight sinking could be that the benefits of residence in productive waters diminish when light levels are too low for foraging. In addition to satiation (Pearre, 2003; Tarling and Johnson, 2006), temperature benefits at larger depths (Giske et al., 1990) and predator avoidance (Prihartato *et al.*, 2015; Staby *et al.*, 2011; Tarling *et al.*, 2002, **II**) may cause the behaviour.
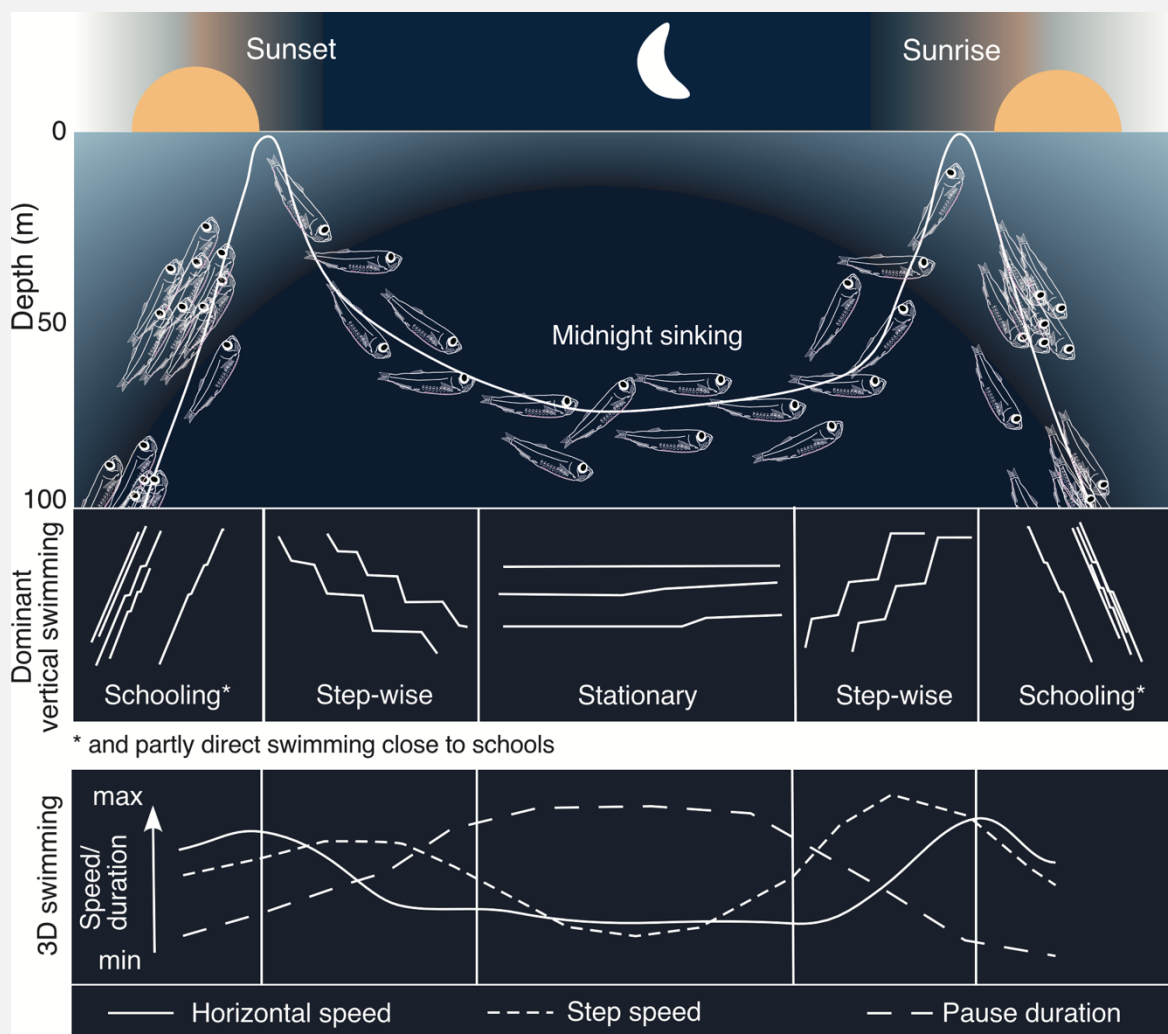
Figure 5: Twilight migration in juvenile *M. muelleri* during winter in Masfjorden with information on individual vertical swimming patterns and horizontal properties. Modified from paper **II** and supplemented with results from paper **III**.

Using echosounders to explore mesopelagic behaviour

Mesopelagic fish inhabit dark and usually deep water, are too small for tagging and often get damaged during capture. In-situ observations from manned submersibles provide insights into the fishes' behaviour (Barham, 1970; Robison, 2004) but are intrusive, costly and time-limited. Lights, e.g. from submersibles or remote and autonomous camera systems, influence fish behaviour (Kaartvedt *et al.*, 2019b; Underwood *et al.*, 2020). Acoustic methods provide the means to study mesopelagic fish over long periods without significantly affecting their behaviour. Echosounders monitor large volumes of water at mesopelagic depths and beyond (Kaartvedt *et al.*, 2020) for up to several months (Prihartato *et al.*, 2015; Staby *et al.*, 2011; Urmy *et al.*, 2012). When deployed stationary, close to the animals to be studied, the resolution of the acoustic signal allows the distinction of individuals, even when dealing with smaller taxa like krill (Kaartvedt *et al.*, 2008; Klevjer and Kaartvedt, 2003; 2006; Torgersen and Kaartvedt, 2001). In this section, I will provide an overview of the methods used to analyse the behaviour of mesopelagic organisms from echosounder data.

Sound in the sea and echosounders

Sound in water is about 5 times faster than in air (ca. 1450-1550 m s^{-1} in seawater, 330 m s^{-1} in air) and can penetrate deep into the water column. Sound generally spreads spherically from any sound source and is reflected, refracted or absorbed when the sound wave encounters an object with different density. Abrupt density changes like strong pycnoclines, the seafloor or animals, can refract and reflect a strong signal. This reflection, known as backscatter, can be recorded and has been used to investigate distributions of animals in the sea since the invention of echosounders (Duvall and Christensen, 1946; Eyring *et al.*, 1948; Sund, 1935). Echosounders are used in various applications which allow observations of distributions and behaviour of marine animals on various spatial and temporal scales and in multidisciplinary setups (Benoit-Bird *et al.*, 2018; Cotter *et al.*, 2021; Lavery *et al.*, 2007; Figure 5). While echosounders mounted on ships and autonomous vehicles provide spatial coverage, submerged stationary echosounders deliver low-noise data with high temporal and vertical resolutions and can be used in long term deployments (e.g. Box 6).

Three echosounders were deployed at 90, 270 and 390 m depth in Masfjorden between October 2010 and August 2011 (Prihartato et al., 2015).The echosounders recorded between 1-2 ping s⁻¹ at 200, 120 and 38 kHz to provide high-resolution data for the whole water column. The echosounders were cabled to a shore station which enabled continuous recording without power and data storage limitations. In addition, biological and hydrographical sampling was done at the beginning and end of the study period (**I**). The biological sampling included midwater trawls (**I**) and zooplankton net hauls (not shown). Surface light levels were measured continuously from December 2010 to August 2011 and complemented by water column light attenuation measurements (Prihartato et al., 2015).
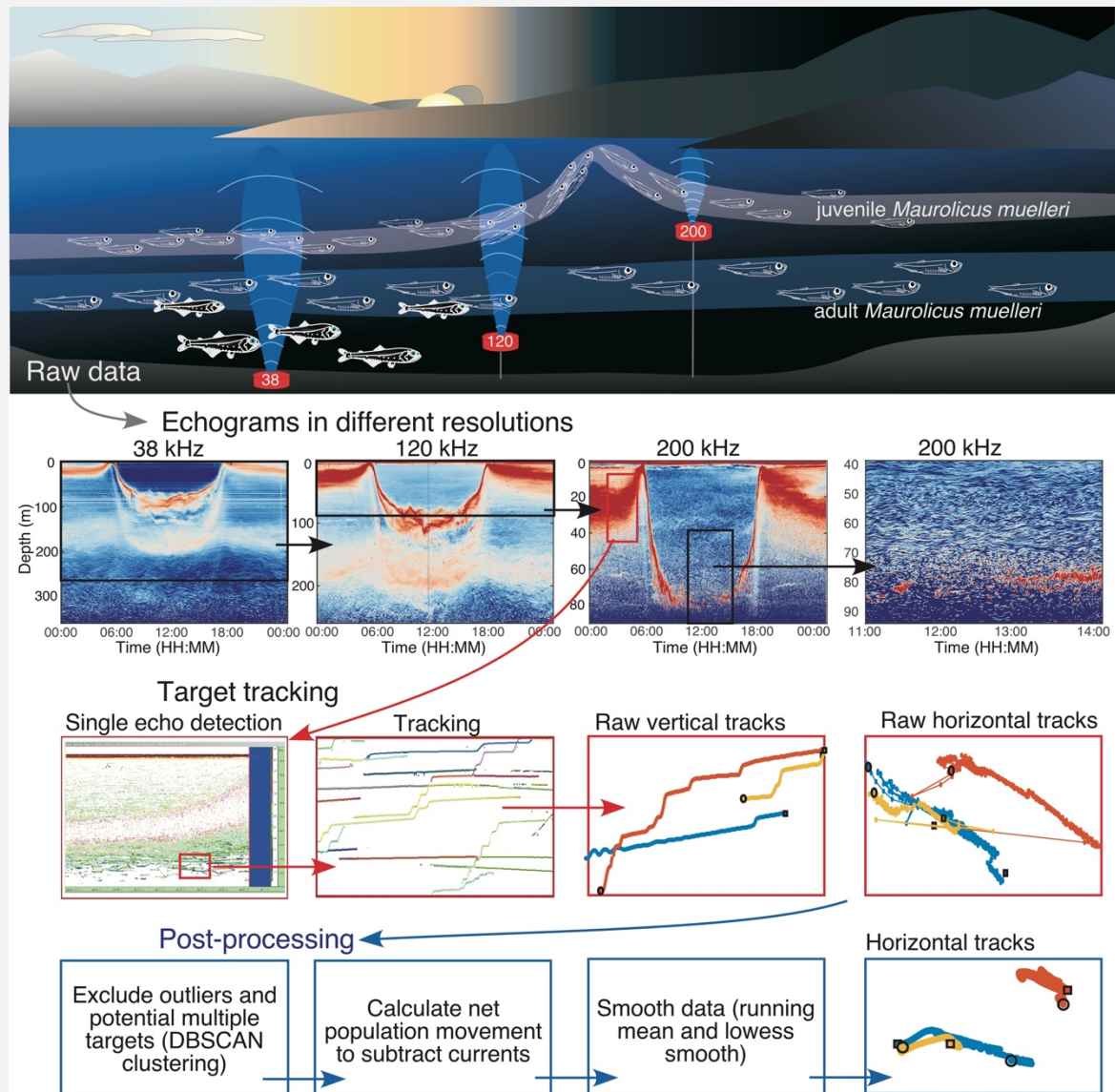

Figure 6: Setup of the three echosounders in Masfjorden and data flow.

Observing behaviour based on backscatter

Echograms - images of backscatter over time (or distance) and range (or depth) - provide a powerful tool for in-situ observations of mesopelagic animal behaviour at multiple scales simultaneously (e.g. Figure 1&5). By analysing echograms, one can gain insight into the behaviour of the organisms that produced the backscatter, which can lead to hypotheses and discoveries (e.g. Peña *et al.*, 2017). Echograms displaying

backscatter over days to months can reveal variations in vertical distributions from minutes to seasons (Figure 1).

For example, echograms allow the observation of diel vertical migration behaviour (Dypvik and Kaartvedt, 2013; Dypvik *et al.*, 2012; Prihartato *et al.*, 2015; Staby *et al.*, 2011, **II**) and short-term redistributions of scattering layers (Baliño and Aksnes, 1993; Kaartvedt *et al.*, 2017; Omand *et al.*, 2021). Furthermore, high-resolution echograms can display social behaviour (Benoit-Bird and Gilly, 2012; Benoit-Bird *et al.*, 2017; Escobar-Flores, 2019; Gauthier, 2002, **I**), trawl avoidance (Kaartvedt *et al.*, 2012b), as well as attraction (Røstad *et al.*, 2006) and repulsion (Peña, 2018) from vessels and light (Kaartvedt *et al.*, 2019b; Underwood *et al.*, 2020). Predator-prey interactions (Solberg and Kaartvedt, 2017) and escape behaviour (Kaartvedt *et al.*, 2012b, **I**) can be directly observed. Echo traces of individuals reflect swimming patterns (Handegard *et al.*, 2009; Kaartvedt *et al.*, 2011; 2020; Solberg *et al.*, 2012, **I**, **II**) and individual distributions and behaviours that deviate from the population (**I**). During further analysis, these observations can be related to physical conditions (Omand *et al.*, 2021; Prihartato *et al.*, 2015; Urmy and Horne, 2016, **I**). Multi-frequency and broadband echosounder data can be used to identify scattering layer compositions and behaviour of different animal groups (Ariza *et al.*, 2016; Bassett *et al.*, 2017; Blanluet *et al.*, 2019; Cotter *et al.*, 2021).

Individual behaviour based on target tracking

In addition to vertical distribution patterns and echo traces, echosounder data can provide quantitative information on individual movement. Split-beam echosounders record the backscatter in various parts, often quadrants, of the transducer separately. The recorded phase differences of any backscatter between the quadrants is used to estimate the angular location of a target relative to the vertical beam axis. Thus, in addition to recording range (distance from the transducer), time and backscatter, split-beam echosounders also provide horizontal position of sufficiently strong targets in the acoustic beam. Positions of echoes obtained from single targets (single echo detections, SED) can be traced over time in a process called target tracking (Brede *et al.*, 1990; Figure 6). Target tracking provided the basis for the analyses in papers **II-IV** and I will therefore give some background on the target tracking process and the related trade-offs, uncertainties and possibilities.

During target tracking, successive SED are manually or automatically assigned to

distinct targets. A main feature of automatic target tracking is the gating. The so-called gating process is divided into three steps: prediction, gating and association (Balk *et al.*, 2019; Handegard *et al.*, 2005). First, the position of the next echo in the current track is predicted. Then a gate, the spatial dimension around the predicted 3D location, is set. Finally, the new SED is associated by selecting the SED within the gate and closest to the predicted position. The three-dimensional extension of the gate is generally defined by the user and regional experience (Balk *et al.*, 2019; but see Handegard *et al.*, 2005). In cases that no SED is present within the gate dimensions, a ping gap is set.
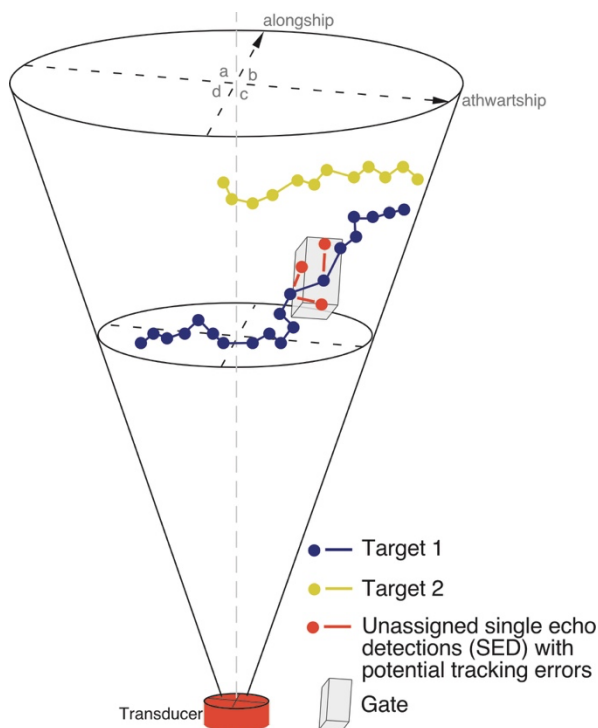

Figure 7: Target tracking with split-beam transducers. The gate is the 3D-region within which the tracking algorithm accepts new SED (see main text).

The gate size and other track criteria (e.g. maximum ping gap and minimum track length) can influence the tracking results significantly and represent a trade-off between connection and splitting errors (Handegard *et al.*, 2005). On the one hand, a small gate may result in ping gaps which will split a track into several fragments and on the other hand, a large gate may combine SED from multiple targets. Consequently, when working with tracking data, an important consideration is at which processing stage and how to ensure the quality of the tracks.

While manual target tracking reduces both splitting and connection errors, it drastically restricts the analysis of extensive datasets and may introduce subjective biases. When using automatic target tracking, the trade-off of splitting and connection

errors needs to be assessed with respect to the study goals.

For paper **II**, we developed a set of automatic target tracking parameters that allowed tracking *M. muelleri* at up to a range of ca. 85 m. This required a relatively large gate and ping gaps and thus increased the risk of connection errors. Paper **II** focused on individual vertical swimming behaviour. Connection errors can lead to artificial vertical swimming patterns when tracks at different ranges are connected. However, validation of subsets of tracks against echo traces in the echograms indicated that the vertical information obtained from the tracks represented the population behaviour. Therefore, we prioritised getting information from most parts of the population, and deemed the tracking appropriate for the purpose of the study.

In paper **III**, we aimed to append the horizontal movement to the vertical information to get a full three-dimensional representation which required more thorough handling of tracking errors. Connection errors have profound effects on horizontal tracks as they can lead to "jumps" in the horizontal positions and thus can substantially increase the risk of overestimating the horizontal speed (Handegard *et al.*, 2005). To account for this, we excluded data points that had a distinct likelihood of belonging to other targets by spatial clustering (**III**). A further uncertainty is that currents, internal waves and other water body or transducer movements may lead to motion that is related to the dynamic reference system instead of to fish behaviour (Handegard *et al.*, 2005; Klevjer and Kaartvedt, 2011). Therefore, we derived current speeds and directions by calculating the net movement of tracks within a certain time and depth interval and removed those from the individual tracks (Kaartvedt *et al.*, 2009). Finally, horizontal positions obtained from split-beam echosounders are based on the angular location in the beam and generally less reliable than vertical positions (Mulligan and Chen, 2000). Hence, horizontal tracks have to be smoothed to remove high-frequency course alterations from the track. To obtain information on velocities and turning patterns, spline (Handegard *et al.*, 2005), and lowess (**III**) smoothing can provide an estimate of the real track. In paper **IV**, we used the post-processed tracks as obtained from paper **III**, to ensure high quality of the analysed target strength and velocities.

We discuss the uncertainties of working with target tracking data in more detail in paper **III**. On the positive side, target tracking allows us to follow even individuals smaller than 5 cm in remote marine environments over long time periods. This

suggests that echosounders and target tracking are valuable in the further exploration of behaviour in the mesopelagic zone.

Mesopelagic behaviour at different scales

In the pelagic ocean, animals can increase fitness in several ways. An obvious survival strategy is to minimise encounters with predators. Animals can achieve this by hiding in places the predator cannot enter, shifting activity times to periods where the relative risk of predation is lowest (anti-predation window; Clark and Levy, 1988) and by disguising behaviour and appearance. Furthermore, social behaviour such as group formation can improve survival and foraging success (Magurran, 1990; Ritz *et al.*, 2011). Finally, an important point to keep in mind is that the needs of individuals differ over time and among individuals and that variability in movement behaviour can affect our perception of population impact (Allgeier *et al.*, 2020; Shaw, 2020). To gain an overall understanding of mesopelagic ecology, it is therefore essential to "observe processes at the scales on which they appear" (Godø *et al.*, 2014).

In the following section I will describe mesopelagic behaviour at different scales. I start this section with well-known large-scale behaviour and then move on to the more unknown fields of small-scale and individual mesopelagic behaviour. I will give an overview of general mesopelagic behaviour with particular focus on *M. muelleri* behaviour as found in papers **I-IV**.

Depth distribution

The pelagic ocean is characterized by strong vertical physical and biological gradients. Light gets attenuated quickly, restricting phytoplankton growth to the upper layer and leading to usually higher food availability in upper waters (Sutton, 2013; but e.g. see Bagøien *et al.*, 2001). Furthermore, temperature differences between surface waters and mesopelagic depths can be significant, and in regions with high productivity and limited ventilation, low oxygen concentrations may occur below the mixed layer.

While temperature and oxygen may lead to physiological restrictions or preferences in the depth distribution of mesopelagic scattering layers (Klevjer *et al.*, 2016; Proud *et al.*, 2018a), mainly light and the optical properties of the water column drive mesopelagic depth distributions (Aksnes *et al.*, 2017; Kaartvedt *et al.*, 2019a; Kampa and Boden, 1954; Langbehn *et al.*, 2019; McFarland, 1986; Omand *et al.*, 2021;

Røstad *et al.*, 2016). Mesopelagic animals adjust their depth distribution on a diel and seasonal basis (e.g. Staby *et al.*, 2011; Urmy and Horne, 2016), and in response to short-term changes in incoming radiation. Rain showers (Baliño and Aksnes, 1993; Kaartvedt *et al.*, 2017), internal waves (Kaartvedt *et al.*, 2012a), and even slight changes in cloud cover (Omand *et al.*, 2021; Staby and Aksnes, 2011) lead to immediate vertical relocations of mesopelagic scattering layers.

Due to the direct relation of mesopelagic distributions to light intensity, the depth range inhabited by mesopelagic animals is often referred to as light comfort zone (Langbehn *et al.*, 2019; Røstad *et al.*, 2016). According to the light comfort zone concept, too high and too low light intensities limit a mesopelagic scattering layer's depth distribution and vertical extent, with resulting narrower distributions in murkier waters (Røstad *et al.*, 2016). A species' or individuals' light comfort zone depends on its visibility, i.e. its contrast to the surrounding water (Johnsen, 2014). Accordingly, the smaller juvenile *M. muelleri* generally inhabit shallower scattering layers than the larger adult conspecifics (Giske *et al.*, 1990; Goodson *et al.*, 1995; Staby *et al.*, 2011). Turbidity may likewise lower the relative mortality risk of prey due to stronger impairment of the predator's vision in turbid conditions (Giske *et al.*, 1994; Utne-Palm, 2002). Nonetheless, behaviour can also modify a mesopelagic species' depth distribution (Marchal, 1996, **I-III**).

Animals can extend their light comfort zone (and thus depth distribution) through social interactions. Dense aggregations, and in their ultimate form schools, provide shelter from visual predators (Magurran, 1990; Ritz *et al.*, 2011) and can allow the animals to stay at higher risk (e.g. ambient light) levels than when they are more dispersed (Feyten *et al.*, 2021). This is also the case for *M. muelleri* which form dense aggregations in the shallowest scattering layer in Masfjorden during daytime (**I**) and when leaving and approaching surface waters at dawn and dusk, respectively (**II**). Due to schooling *M. muelleri* can forage in surface waters during very light summer nights at high latitudes (Kaartvedt *et al.*, 1998; Prihartato *et al.*, 2015).

Finally, internal motivation, such as nutritional state or personality traits (Canestrelli *et al.*, 2016; Sih *et al.*, 2015), can lead to individuals leaving the species' apparent light comfort zone, extending the depth distribution of the population (**I**). Risky behaviour of individual fish is known, for example, from sprat, which "hold their breath" and dive into oxygen-depleted waters to forage on hibernating copepods

(Solberg and Kaartvedt, 2017). Similarly, bold individuals of *M. muelleri*, which leave the main scattering layers and swim into up to 1.5 orders of magnitude higher ambient light (**I**), potentially use the lighter conditions to forage during daytime (Bagøien *et al.*, 2001).

Such individual behaviour introduces variability into our expectations of size-related depth distributions. Within, and maybe also beyond, the light comfort zone, individuals may cross light gradients of several orders of magnitude, probably resulting in animals of different sizes co-occurring within different layers (**I**). The apparent need (Goodson *et al.*, 1995) and boldness of some individuals to swim at shallower and lighter depths potentially elicits more interactions with predators (**I**).

Predator-prey interactions

Predation risk depends on several factors: 1) the probability of encounter defined by densities, movement speeds and perception capacities of the predator, 2) The ability of the prey to detect and escape the predator before an attack and 3) the probability of surviving an attack. To reduce the probability of encounter, mesopelagic animals can hide in deeper, darker waters (see previous and following section) and reduce movement (see below; **III**). In addition, mesopelagic animals may sense approaching predators by visual, chemical and tactile stimuli (Dill, 1974; Dixson *et al.*, 2010; Stewart *et al.*, 2014), allowing them to escape (**I**). Also rapid information sharing between school members can be beneficial for predator-detection and escape (Herbert-Read *et al.*, 2015; Magurran, 1990; Rieucau *et al.*, 2014; Ritz *et al.*, 2011). The depth distributions of predators and prey may overlap, leading to frequent escape responses upon encounter (Kaartvedt *et al.*, 2012b; **I**).

Fish often react to stimuli by potential predators by sharply turning (Domenici and Blake, 1997; Eaton *et al.*, 1977; Meager *et al.*, 2006) and by burst swimming in a more or less unpredictable (protean) fashion (Humphries and Driver, 1967; Richardson *et al.*, 2018). The myctophid *Benthosema glaciale* shows fast diving behaviour upon encounter with predators (Kaartvedt *et al.*, 2012b), also at night at depth, suggesting very high sensitivity to approaching predators and resulting in efficient trawl avoidance (Kaartvedt *et al.*, 2012b). In paper **I**, we showed that *M. muelleri* apply the same type of diving escape reactions, but only at light levels $> 10^{-6}$ μmol m^{-2} s^{-1}; i.e. not in the darkness of night. *M. muelleri* hence seem to rely on detecting predators with their twilight-adapted eyes (de Busserolles *et al.*, 2017) during daytime (**I**). At night,

they apparently follow a different predator avoidance strategy. During darkness, midnight sinking and step-wise swimming (**II**), as well as slow swimming speeds and irregular turning (**III**), supposedly serve predator-avoidance by minimizing the probability of encounters and detection (Gerritsen and Strickler, 1977; Wright and O'Brien, 1982).

The echosounder data provided ample information on escape reactions though the success rates of these possible predator attacks are unknown. However, there seems to be a considerable overlap and interaction between *M. muelleri* and their predators in Masfjorden (**I**) suggesting that some of the attacks are successful. We particularly often observed dive reactions in bold *M. muelleri* (**I**), i.e. those individuals that chose substantially lighter depths than the main population. Bold behaviour could thus have implications on the importance of *M. muelleri* as prey species in Masfjorden.

Diel vertical migration

Diel vertical migration is broadly accepted as the trade-off between food acquisition and predation-risk in productive surface water (Robison, 2003; Zaret and Suffern, 1976), although physiological benefits may also play a role (Giske *et al.*, 1990; Rosland and Giske, 1994; Wurtsbaugh and Neverman, 1988). By limiting activity periods and residence in shallow waters to rather dark conditions, the animals make use of the anti-predation window (Clark and Levy, 1988). Also tactile predators consume mesopelagic animals (Robison *et al.*, 2020), but in the following, I will mainly focus on visual predation, as that is probably the main predation pressure on *M. muelleri* in Masfjorden (Giske *et al.*, 1990). Similarly, diel vertical migration exists in various forms, but I will mainly focus on the twilight migration patterns used by *M. muelleri* (Box 5).

M. muelleri's diel vertical migration behaviour varies with the seasons (Prihartato *et al.*, 2015; Staby *et al.*, 2011; Staby and Aksnes, 2011) and ontogeny (Giske and Aksnes, 1992; Staby *et al.*, 2013). The plasticity in *M. muelleri's* migration behaviour is a good example of how movement patterns can inform on a population or individuals' requirements. In winter, adult *M. muelleri* reside at depths of around 200 m throughout the day. In contrast, the juveniles (<1 year) live in shallower layers and perform active diel vertical migration in the form of twilight migrations. The adult and juveniles thus experience very different risk and food environments, which mirror different "fitness-to-feeding functions" (Giske and Aksnes, 1992). The adult *M.*

muelleri have low food requirements as they can benefit from fat reserves (Falk-Petersen *et al.*, 1986) and compensate weight loss by occasional daytime feeding (Bagøien *et al.*, 2001). The juveniles on the other hand need to prioritize growth over mortality risk since they gain massively in fitness by reaching maturity (Giske and Aksnes, 1992; Staby *et al.*, 2013).

Ontogenetic differences in diel vertical migration strategies diminish in spring. Then, increasing proportions of adults join the twilight migration (**IV**), and eventually, the adult and juvenile layers merge (Staby *et al.*, 2011). Between May and August, nocturnal light levels permit the fish to forage at the surface throughout the nights (i.e. no midnight sinking; Prihartato *et al.*, 2015). During the lightest nights around midsummer, the fish school at the surface (Kaartvedt *et al.*, 1998) as mentioned earlier.

Scattering layer movements only represent the average behaviour of the community. Within a seemingly homogenous and stable scattering layer, individuals may move actively – up and down e.g. during asynchronous DVM (Cottier *et al.*, 2006; Tarling and Johnson, 2006) or as small depth adjustments related to endogenous rhythms (**II**), as well as horizontally (**III**). Also, apparently steady ascents and descents of a scattering layer during migration do not necessarily reflect the individual behaviour within the layer (Torgersen and Kaartvedt, 2001). Resolving behaviour to the individual level is important to understand the mechanisms of diel vertical migration and related consequences for energy and carbon fluxes (Pearre, 2003).

Individual swimming behaviour

Individual swimming behaviour represents an animal's activity and its interactions with the environment (Andrews and Harvey, 2013; Kiørboe *et al.*, 2018). In general, motility is a trade-off between preserving energy for growth and maturation on the one hand, and moving to obtain food and avoid predation (and mate) on the other hand (Lima and Dill, 1990; Visser and Kiørboe, 2006). Swimming patterns can vary drastically between and within species (e.g. Titelman and Kiørboe, 2003). Variability at the individual level may seem obvious, but information on the timing and use of different movement patterns help us understand what mesopelagic animals do at depth and why (del Mar Delgado *et al.*, 2018; Pearre, 2003).

For example, the term midnight sinking implies a passive behaviour (Cushing, 1951; Tarling and Johnson, 2006). Suggested reasons for midnight sinking range from

passive sinking as a consequence of reduced activity (Cushing, 1951) and satiation sinking (Tarling and Johnson, 2006) to predator avoidance (Tarling *et al.*, 2002). However, without being able to observe the sinking itself, it is often difficult to deduce the underlying causes (Pearre, 2003; Tarling *et al.*, 2002). In paper **II**, we analysed the juvenile *M. muelleri*'s individual migration behaviour by acoustic target tracking. We showed that the fish actively swim towards deeper depths after foraging at the surface at dusk by descending in short bursts alternating with periods without vertical movement (step-wise swimming, Figures 1&8). Step-wise swimming likely serves predation-avoidance (see below). The step-wise descent, which mirrored the ascent in the morning, accordingly suggested that "midnight sinking" is an active, predator-avoidance behaviour in *M. muelleri* (**II**).

While we can probably regard step-wise swimming as *M. muelleri*'s main mode for vertical relocation, the fish also modify this behaviour (**II, III**). At night, steps are often short (median height 8 cm) at median vertical speeds of 1.7 cm s^{-1}, while pauses (i.e. vertical stationary swimming) dominate the apparent vertical behaviour (median 33 s). In contrast, during migration around dusk and dawn, the fish alter several components of their step-wise swimming to approach faster swimming towards or from the surface, including the shortening of pause durations (<25 s) and the increase of step speeds (~2.1 cm s^{-1}) and heights (~13 cm; **III**). The timing and resulting speed of migration, especially the descent at dusk, is highly variable within the scattering layer (**II**), which is visible on echograms as interrupted dusk migrations and a wide vertical spread of the scattering layer (Prihartato *et al.*, 2015; Staby *et al.*, 2011, **II**). Finally, individuals at the margins of schools and even within schools seemed to drop pauses altogether (**II**).

Step-wise swimming is a pattern of intermittent, which may provide energetic advantages, improve perception and reduce detectability (Kramer and McLaughlin, 2001). Our observation of step-wise swimming pattern modifications over time (**II, III, IV**) aided in narrowing down hypotheses for the reasons of this particular behaviour in *M. muelleri*. Mehner (2006) suggested that step-wise swimming could be physiologically necessary for swim bladder equilibration. However, mesopelagic fish also swim in a step-wise manner at greater depths (Kaartvedt *et al.*, 2008) with, according to Boyles' law, minor pressure-related volume changes of the swim bladder. Furthermore, the step-wise dusk descent mirrored the dawn ascent (**II**), although swim-bladder volume regulation should be faster during ascent than during

descent (Strand *et al.*, 2005). Finally, very short pauses during migration as well as occasional direct swimming in the proximity of schools (**II**) and the fast descent of schools themselves contradict the hypothesis.

Step-wise swimming could represent saltatory search behaviour (Kaartvedt *et al.*, 2008), during which animals use frequent relocations to increase their search volume during food searching (O'Brien *et al.*, 1989; 1990). Further research is needed to assess potential foraging behaviour in *M. muelleri* during the morning migration, but step-wise swimming persisted during midnight sinking and in the middle of the night (**II**), although light levels were probably too low for foraging. A further physiological reason for step-wise swimming could be energy saving. Fish can reduce energy expenditure by swimming in short bursts and gliding (Weihs, 1974). While steps can be regarded as bursts, the pauses usually did not resemble glide phases where speeds slowly decline. The most reasonable hypothesis for step-wise swimming is, therefore, predator avoidance.

M. muelleri have a characteristic set of ventral photophores (Figure 4) for counter-illumination (Cavallaro *et al.*, 2004; Clarke, 1963). The photophores' strictly downwards orientation (Cavallaro *et al.*, 2004) leads to reduced camouflage when tilting during vertical swimming (Janssen *et al.*, 1986). We documented such tilting by reduced target strength during steps compared to pauses in paper **IV**. Pauses during step-wise swimming can thus serve to reduce visibility during ascents and descents. This fits with our observations of step-wise swimming in bold individuals and individuals that switched between layers (**I**). These individuals were exposed to higher ambient light levels and excluded from the shelter of the scattering layer. When assuming important causes such as daytime feeding for their excursions, one might expect that the individuals would strive towards foraging conditions and back into shelter as directly as possible. However, many of the individuals used step-wise swimming, spending longer periods in supposedly high-risk environments (**I**).

Pelagic animals live in a three-dimensional habitat with generally free movement. Vertical swimming patterns such as step-wise swimming hence only represent part of the actual behaviour (Figure 8). The pauses during step-wise swimming do not necessarily mean complete inactivity of the fish, and vertical swimming speeds do not represent the animals' overall swimming capabilities. Looking at horizontal swimming speeds and turning can further improve our understanding of the animal's

behaviour and activity (**III**).

Observations from manned submersibles showed that some mesopelagic fish are torpid outside feeding and migration periods (Barham, 1970). Other studies reported extensive horizontal migrations of myctophids in shelf regions (Benoit-Bird and Au, 2006) and horizontal orientation and swimming against currents in relation to seamounts by *M. muelleri* (Wilson and Firing, 1992). In Masfjorden, the juvenile *M. muelleri* do not seem to swim against the currents or perform horizontal migration at night (**III**). In contrast, the fish apparently loiter and mostly drift with the currents. Median swimming speeds around 0.9 cm s^{-1} (**III**) suggest that the juvenile fish reduce their night-time swimming activity, possibly to maximise growth and maturation (Giske and Aksnes, 1992). Increasing target strength values over the winter (**IV**) indicated such growth. Low activity furthermore reduces encounter risk (Gerritsen and Strickler, 1977; Klevjer *et al.*, 2009; Robison *et al.*, 2020) and detection by predators (Janssen *et al.*, 1999; Wright and O'Brien, 1982). However, the fish were not entirely torpid - while the horizontal swimming speeds were usually below 0.5 body lengths s^{-1}, the fish did move and also frequently changed their swimming direction (**III**). About 23% of the tracked *M. muelleri* moved actively in the horizontal plane at night with horizontal swimming speeds >0.5 body lengths s^{-1} (up to ~4 cm s^{-1}) and frequent turning (**III**). Daytime and adult individual swimming patterns remain to be established.

- vertically relocate in fast steps
- alternated by periods without vertical swimming (pauses)
- usually more limited horizontal movement during pauses

- tilt strongly during steps
- orientate horizontally during pauses
- also turn horizontally between pauses and steps

- TS strongest during pauses
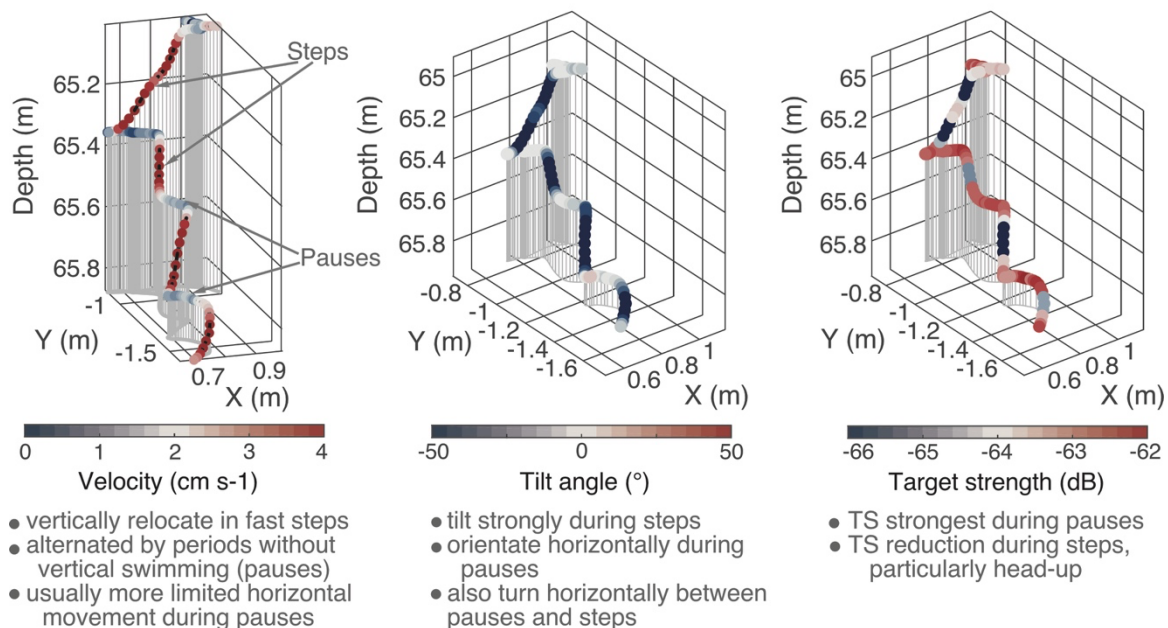- TS reduction during steps, particularly head-up

Figure 8: Example of a step-wise *M. muelleri* track displaying three-dimensional velocity, tilt angle and target strength and summarizing the most prominent features of *M. muelleri* individual swimming behaviour.

Changes in swimming direction can increase the search volume of an animal during food searching (O'Brien *et al.*, 1990), but *M. muelleri* do not forage at night in winter (Bagøien *et al.*, 2001; de Busserolles *et al.*, 2017). Turning can also represent protean behaviour, i.e. the use of unpredictable movement to confuse predators (Humphries and Driver, 1967). In addition to switching between vertical swimming modes, *M. muelleri* nearly always turned horizontally between steps and pauses of step-wise swimming (**III**). Turning angles were related to the pause duration with a median turning angle of 40° at a median pause duration of 10 s and a median turning angle of 65° at pause durations of 40 s (**III**). Overall, 95% of the step-wise swimming fish turned with more than 20° before or after every second pause (**III**). The turning limited horizontal displacement during vertical movement. During migration periods, with a higher risk of predation (Rosland and Giske, 1994), frequent turns may counterbalance the reduced duration of pauses (**III**).

Implications of small-scale and individual behaviour

Observations of individual fish behaviour in the mesopelagic and deep sea are still scarce. This thesis gives first insights into the behaviour on smaller temporal and spatial scales than normally focused on in mesopelagic research. The papers presented in the thesis focus on observations of behaviour. In this section, I provide a wider context and briefly discuss potential implications of the observed individual behaviour and variability on ecological, biogeochemical and methodological aspects, focusing on *M. muelleri*.

Ecological aspects

Small-scale and individual behaviour can represent ecological interactions between conspecifics and between predators and prey. Such interactions must be taken into account when evaluating the impacts of a potential new fishery (Alvheim *et al.*, 2020; Grimaldo *et al.*, 2020; Olsen *et al.*, 2020; Standal and Grimaldo, 2020). In papers **I-III**, we showed that *M. muelleri* use various strategies for predator avoidance and fitness gain.

The fish combine large-scale patterns like depth distribution and diel vertical migration with social behaviour (**I**). The formation of dense aggregations and the capability of sensing approaching predators (**I**) expectedly improves the chance of survival for the individual fish (Magurran, 1990; Ritz *et al.*, 2011). Nevertheless, a shallower depth distribution resulting from predator avoidance behaviour may lead to a larger overlap and increase the frequency of interactions with predators (**I**). Such overlaps can be crucial in sustaining predator populations (Marchal, 1996).

M. muelleri's individual swimming behaviour seems to represent one component of the arms race between predator and prey in Masfjorden. Individuals that leave the main scattering layer are likely subjected to higher predation pressure (**I**), which the individuals trade-off by swimming in a step-wise manner (**I**). Step-wise swimming reduces periods of tilted orientation (**IV**) during which the camouflage provided by the light organs is less effective. Similarly during migrations, which represent increased predation risk, step-wise swimming (**II**, **III**) and protean behaviour (**III**) are applied. At night, activity and resulting predator encounter probability is reduced when foraging and detection of predators is optically constrained (**III**). The flexible and multiple predator-avoidance strategies shown here, as well as co-adaptive behaviour of predator and prey (Pinti *et al.*, 2021) should be considered in fitness-

optimization models (De Robertis, 2002; e.g. Rosland and Giske, 1994) and can be useful in a trait-based approach to ecological modelling (Kiørboe *et al.*, 2018).

With regards to *M. muelleri*'s potential economic value (Alvheim *et al.*, 2020; Grimaldo *et al.*, 2020; Olsen *et al.*, 2020; Standal and Grimaldo, 2020), efficient predator avoidance could indicate a lesser role of the species for predatory fish with potentially lower impacts on those fish by a *M. muelleri* fishery. However, as mentioned earlier, the outcome of the frequent predator-prey interactions observed in this thesis (**I**) are unknown. Literature data on stomach contents of saithe and blue whiting in Masfjorden revealed a clear dominance (>70% of the prey items) of *M. muelleri* (Giske *et al.*, 1990) suggesting predation success despite the avoidance behaviour. Overall, we can assume that in the ecological game of predator and prey in Masfjorden, frequent interactions between *M. muelleri* and larger fish (as discussed above) lead to *M. muelleri* mortality. These findings underline the importance of small-scale behaviour in assessing a species role in the ecosystem.

Biogeochemical aspects

The scale of carbon removal from the euphotic zone (export) and eventually sequestration to deeper depths depends on the efficiency of passive and active carbon transport processes, defined e.g. by fecal pellet sinking speeds, migration depths and respiration rates (Aumont *et al.*, 2018; Belcher *et al.*, 2019; Davison *et al.*, 2013; Saba *et al.*, 2021; Saba and Steinberg, 2012; Steinberg and Landry, 2017) and by attenuation processes in the water column (Buesseler and Boyd, 2009; Steinberg and Landry, 2017). Recent estimates of migrating mesopelagic fish contributions to total vertical particulate organic carbon export out of the euphotic zone are on average 16% (Saba *et al.*, 2021). Large uncertainties in these estimates prevail, partly due to limited observations of respiration and activity in the mesopelagic zone (Saba *et al.*, 2021). Estimates of mesopelagic respiration and excretion are often based on constant activity rates (Belcher *et al.*, 2020). Nevertheless, mesopelagic animals rapidly move to adjust for changes in illumination (Baliño and Aksnes, 1993; Kaartvedt *et al.*, 2017; Omand *et al.*, 2021). Similarly, internal motivation may lead to increased activity in some individuals (**I**) at some stages. In general, mesopelagic populations might be more active than assumed (**II**, **III**) with potentially higher energy requirements.

In paper **III**, we estimated the order of impact of non-torpid nighttime behaviour of *M. muelleri* on community respiration. This estimate suggested that potentially

increased swimming cost due to slow swimming at night was negligible compared to an approximated standard metabolic rate. While this crude estimate supported hypotheses of growth maximization, it moreover highlighted the convenience of echosounders for future assessments of respiration rates at depth by supplying in-situ estimates of swimming speeds and turning behaviour.

Diel vertical migration is an energy-demanding process (Davison *et al.*, 2013; Strand *et al.*, 2005). Individual swimming patterns during migration, which ultimately define the energy consumption of the population, are not necessarily obvious from scattering layer movements (**II, III**). Seemingly continuous migration may include horizontal movement and turning behaviour (**I, III**).

Methodological aspects

Current mesopelagic research includes considerable efforts in stock assessments and biomass estimates of mesopelagic fish (Davison *et al.*, 2015; Grimaldo *et al.*, 2020; Irigoien *et al.*, 2014; Proud *et al.*, 2018). Numerical densities are determined acoustically by combining the population backscatter and the expected backscatter of the individual fish (target strength; TS; dB re 1 m^2). Despite each individual having a slightly different TS, a representative target strength estimate is required for reliable stock assessments.

TS is generally related to the size of the fish, with larger fish producing stronger TS. However, this relationship is disrupted due to resonance of small swim bladder-bearing fish at low acoustic frequencies (Simmonds and MacLennan, 2005). Measurements with higher frequencies on the other hand are susceptible to the orientation of the recorded animals (Blaxter and Batty, 1990; Fujino *et al.*, 2009). In swim bladder-bearing fish, the swim bladder is responsible for about 90% of the TS (Foote, 1980). Due to fish and swim bladder geometry the backscatter is at a maximum when the swim bladder is oriented horizontally (**IV**). Whenever the swim bladder is tilted as the fish swims up or down the TS is reduced due to smaller geometric extent perpendicular to the echosounder pulse (Frouzova *et al.*, 2005; Sameoto, 1980; Sawada *et al.*, 2011; **IV**).

M. muelleri are physoclist fish and thus expected to compensate pressure-related swim bladder volume changes to maintain neutral buoyancy. Their swim bladders are elongated with an average tilt of 24° relative to the fishes' lateral axis (Scoulding *et al.*, 2015; Sobradillo *et al.*, 2019). In paper **IV**, we investigated the effect of in-situ

swimming angles on measured target strength at 200 kHz. We found that the target strength was higher during pauses (-63.21 dB) than during steps. In accordance with the tilt of the swim bladder, the TS was higher in descending (-64 dB) than in ascending steps (-64.7 dB). However, we show that vertical swimming in large parts of the population did not notably influence the population TS. Due to unsynchronised step-wise swimming and short steps, periods of reduced TS were generally underrepresented during migration. Knowledge about individual behaviour can be used to estimate the influence of behaviour on TS and resulting numerical densities and biomass.

Closing remarks

The mesopelagic ocean is among the least explored habitats on our planet. The habitat is characterized by steep vertical gradients of light, temperature and food. The ecosystems that developed here are complex, interconnected and until now mostly poorly understood. Life and in particular evolution rely on diversity and inter-individual variation which must be measured and parameterised if we are to improve our understanding of how ocean ecosystems function.

This thesis describes new observations of the various behavioural patterns of a single species at scales from seasons (**I**) to seconds (**I-IV**) and from extensive scattering layers over smaller groups (**I**) to individual fish (**II-IV**). The emphasis is put on movement behaviour, which often reflects a trade-off between food acquisition, growth and reproduction, and survival. Much of the observed movement behaviour and variations in these behaviours can be seen in the context of this trade-off. *M. muelleri* hide in a light comfort zone during the day and perform midnight sinking at night, but ascend to surface waters for foraging around dusk and dawn (**II**) despite being more detectable at these depths. However, individual needs can deviate from that of the population. We observed this as variance in individual swimming speeds and patterns (**II, III**), and by the fact that some individuals left the daytime refuge of the scattering layer to forage in shallower and lighter waters (**I**). On the way to and from the surface, the fish either school or employ a step-wise swimming pattern (**II**) combined with frequent turning (**III**) to reduce vulnerability to predation. At night, the fish reduce their swimming activity to improve growth (**III, IV**) although they continuously slowly relocate (**II, IV**).

There is observational evidence for behavioural diversity at all scales. Whenever aiming to explain large-scale biological patterns, it is useful to have an understanding of processes operating at smaller scales. Research on individual behaviour does not only provide new insight on a particular species, it is moreover a key part of assessing the species' role in the ecosystem and in energetic cycles, since predator-prey interactions and metabolic demands happen at the individual level. Furthermore, as acoustic density estimates and stock assessments rely on correct target strength estimates, new knowledge on how behaviour influences these estimates can be of great value (**IV**). The findings highlight the potential of submerged, stationary echosounders for addressing current and future questions about mesopelagic life.

Acknowledgements

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I

Flexible behaviour in a mesopelagic fish (*Maurolicus muelleri*)

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Variability of mesopelagic scattering layers is often attributed to environmental conditions or multi-species layer composition. Yet, little is known about variation in behaviour among the individuals forming scattering layers. Based on a 10 months high-resolution dataset from stationary echosounders in a Norwegian fjord, we here assess short-term and long-term behaviour of a single mesopelagic fish species, the pearlside *Maurolicus muelleri*. The daytime vertical extension of the monospecific pearlside scattering layers spanned four orders of magnitude ambient light in the autumn and winter and less than one order of magnitude in summer. While the main layers tracked relatively stable light levels over daytime, some individuals actively crossed light gradients of up to 1.5 orders of magnitude. This included individuals that moved between scattering layers, and apparently bold individuals that made regular upward excursions beyond the main population distribution. During the daytime, *M. muelleri* mitigated the risk of predation by forming tight groups in the upper scattering layer and, at light levels $>10^{-6}\,\mu$mol m^{-2} s^{-1}, by instantly diving into deeper waters upon encounters with predators. Our observations suggest that individual, and probably state-dependent, decisions may extend the pearlsides' vertical distribution, with implications for predator–prey interactions.

Keywords: individual behaviour, light, predator avoidance, scattering layer variability, social aggregation, stationary echosounder

Introduction

The enormous mesopelagic, or twilight, zone lies below the sunlit euphotic ocean but still receives enough light to allow for visual predation by adapted animals. The complexity of mesopelagic vertical distribution became evident already soon after the discovery of deep scattering layers (Duvall and Christensen, 1946; Eyring *et al.*, 1948): often, multiple sound scattering layers are present, and net catches at mesopelagic depths revealed a high number of species present (Barham, 1957; 1966; Pearcy *et al.*, 1977). The most apparent behavioural pattern of deep scattering layers is their diel vertical migration (Welsh *et al.*, 1937) in tight synchrony with ambient light (Duvall and Christensen, 1946; Kampa and Boden, 1954; Dickson, 1972), although parts of layers may not migrate (Dietz, 1948). Contemporary mesopelagic

research focuses on quantifying biomass (Davison *et al.*, 2015; Proud *et al.*, 2019), harvest potential (Prellezo, 2019; Grimaldo *et al.*, 2020), food webs, and active vertical carbon transport (Hudson *et al.*, 2014; Belcher *et al.*, 2019), and would benefit from increased knowledge on the vertical behaviour of the animals of the scattering layers.

Animal behaviour and distribution are influenced by external and internal factors. Usually, the variability in the vertical distribution of scattering layers is correlated with environmental variability (Béhagle *et al.*, 2016; Urmy and Horne, 2016; Proud *et al.*, 2017; Boswell *et al.*, 2020) or attributed to differences in species composition (Gauthier *et al.*, 2014; Benoit-Bird *et al.*, 2017). Less knowledge exists about the variability in behaviour within species; High species diversity, often more than a hundred species

(Ariza *et al.*, 2016; Wang *et al.*, 2019), within oceanic scattering layers may prohibit unravelling such species-specific variability.

In contrast, scattering layers in Norwegian fjords resemble their oceanic counterparts in their dynamics but contain only a few species (Giske *et al.*, 1990). Fjord ecosystems therefore provide an opportunity to observe how variations in scattering layers are affected by individual behaviour within species. The pearlside *Maurolicus muelleri* forms nearly monospecific scattering layers in Norwegian fjords (Giske *et al.*, 1990; Staby *et al.*, 2011). Fish of the genus *Maurolicus* have a world-wide distribution (Rees *et al.*, 2020) and are known for their relatively high abundance in the upper mesopelagic (Gauthier *et al.*, 2014; Escobar-Flores, 2019). Pearlsides have a distinct vertical migration behaviour which is strongly influenced by season (Prihartato *et al.*, 2015; Staby *et al.*, 2011) and ontogeny (Giske *et al.*, 1990; Baliño and Aksnes, 1993; Staby *et al.*, 2013), and characterized by immediate reactions to changes in ambient light (Baliño and Aksnes, 1993; Staby and Aksnes, 2011), s.a. Supplementary Figure S1. This light-associated behaviour has been interpreted as a way to optimize vision-based food intake over vision-based predation risk (Clark and Levy, 1988; Giske *et al.*, 1990). As a result, the fish are expected to occupy a certain window of light intensities that has been referred to as "antipredation window" (Clark and Levy, 1988) and "light comfort zone" (Røstad *et al.*, 2016). Since individuals within a population will probably vary in hunger and energy reserves we hypothesize that deviating, "atypical" behaviour for some of the individuals exists.

Deviations from the average and thus individual variation ultimately drive evolution (Allen and McGlade, 1987). Processes with atypical outcomes may have large ecological consequences: For example, in studies of a reef fish population, Allgeier *et al.* (2020) showed that subsets of the population have a disproportional impact on nutrient production. Furthermore, "unusual" daytime schooling in the epipelagic by the mesopelagic fish *Vinciguerria nimbaria* contributes to sustaining tuna populations in the Atlantic Ocean (Marchal, 1996).

We analysed a 10-month long dataset of moored echosounders complemented with net sampling at the start and end of the registration period, for a fjord population of *Maurolicus*. The acoustic records provided continuous and high-resolution data throughout the water column, allowing for quantifying variability at various temporal and vertical scales for both populations and individuals. We relate these observations to light conditions, discuss possible implications, and suggest hypotheses to be tested in future studies of mesopelagic scattering layers.

Material and methods
Study site (Masfjorden)
Masfjorden is a sheltered fjord on the West coast of Norway. It is about 20 km long, 0.5–1.5 km wide and has a maximum depth of 494 m. The fjord is connected to the more open Fensfjorden via a sill at 75 m depth. Due to this sill, water masses are generally homogenous below ~80 m depth, with salinities > 34.9 and temperatures of ~8°C (Aksnes *et al.*, 2019). During the current study (2010/11), dissolved oxygen concentrations were >3 ml l^{-1} throughout the water column (Aksnes *et al.*, 2019).

Trawl catches
We used a pelagic trawl (100 m^2 net opening; square mesh size 20 cm × 20 cm declining to 3 mm × 3 mm in the cod-end), for assessing the mesopelagic community composition at the

beginning (8–11 October 2010) and end (14–18 August 2011) of the study period. The trawl was equipped with a Multisampler, holding three independent cod ends that could be opened and closed on command from the vessel (Engås *et al.*, 1997). We made 19 successful deployments in 2010 and 9 in 2011. Due to logistic constraints including very short summer nights in August, nocturnal sampling was limited. Each deployment was restricted to one depth layer, thus providing three consecutive "replicates", with the individual cod ends in most cases being opened for 10 min at ~2 knots tow speed. We allowed between 1 and 5 min for flushing of the trawl between closing the previous and opening the next cod end, thereby reducing contamination between nets. In total, 70 trawl samples were sorted, weighed, and counted upon retrieval. We here normalize the catch by dividing total numbers by the number of minutes trawled. Average individual weight was obtained by dividing the total number of individuals by the total weight, for each species.

Acoustic measurements
We deployed three upward-looking SIMRAD EK60 split-beam echo sounders (7.1° beam angle) in Masfjorden (~60° 50′N, ~5° 30′E), from 7 October 2010 to 15 August 2011 (s.a. Prihartato *et al.*, 2015). The submerged transceivers were kept in pressure-proof casings and cabled to a shore station for power supply and data storage. The echo sounders were mounted at the bottom (38 kHz; ~370 m; 512 µs; 1 ping s^{-1}) and in rigs floating at ~280 m (120 kHz; 256 µs; 1–2 pings s^{-1}) and ~90 m (200 kHz; 128 µs; 1–2 pings s^{-1}) in close vicinity to each other. The echo sounders were calibrated at the surface using standard methods (Foote *et al.*, 1987). We here mostly use data at 120 kHz, supplementing with records from the two other frequencies. We show representative echograms displaying mean volume backscattering strength (S$_v$; dB re 1 m^{-1}; MacLennan *et al.*, 2002) at selected days of the study period to exemplify different behaviours.

Scattering layer properties
We determined the vertical location and range, as well as backscatter properties of the noon (±15 min) *Maurolicus* scattering layers for each day of the study period. We prepared the 120 kHz S$_v$ data by binning (averaging in the linear domain) into 0.5 m and 1.44 min intervals. Then, we excluded parts of the echogram where the binned S$_v$ values were larger than the 95th percentile of the S$_v$ data to reduce the influence of strong echoes by larger fish (Supplementary Figure S2). For the remaining data, we calculated the backscatter anomaly by subtracting the running median (window size 5 datapoints, i.e. ~7.2 min) of the S$_v$ values in each depth bin. The backscatter anomaly represents the ratio of *Maurolicus* backscatter to background values (averaged over time) for each depth bin. Then, we defined the 5th, 25th, 75th, and 95th percentile of the backscatter anomaly such that we obtained depth profiles of backscatter anomaly percentiles. To be classified as a layer, more than 75% of the bins in one depth had to be stronger than the median over at least five consecutive depths (2.5 m). An additional condition was that the median of the S$_v$ at those depths was >−70 dB to exclude plankton layers. The detected layers were numbered and their minimum, maximum, and depth range, as well as their mean S$_v$ (calculated in the linear domain) determined.

We determined the upper edge of the shallowest scattering layer for selected days of the study period (dates where light

extinction was measured $\pm$ 3 days). For this purpose, the respective binned daytime data were smoothed (running median with window size 10 datapoints, i.e. 14.4 min and 5 m). Then, the upper edge of the daytime layer was defined as the shallowest point in the echogram which exceeded an empirically determined S_v threshold of -70 dB (January) or -65 dB (all other months) over at least 5 m depth, for each timepoint between sunrise and sunset.

Boldness

On some days, individuals of *Maurolicus* were located shallower than the main scattering layers. To get an impression of the extent of such apparently bold behaviour by individuals ascending into more illuminated waters, we quantified when and where such behaviour appeared by comparing it to the main population. We did this in conjunction with the layer detection (see previous section). To be detected as bold individuals the 5th percentile of the backscatter anomaly had to be >0. In addition, the respective depth bins also had to be defined as a non-layer and the 75th percentile of S_v had to be >-70 dB. The conditions for the layer and bold individual detection were tested empirically for several days within the study period. Adjoining depth bins labelled as bold individuals were combined as vertical sections, numbered, and their properties determined (same as for the layers). For an individual section to be defined as bold individuals, that section had to be shallower than the shallowest scattering layer. Only the bold individuals closest to the shallow layer were selected.

Velocity

We determined vertical swimming velocities of selected individuals using the acoustic post-processing program Sonar5-Pro (Balk, 2019). Individual fish could be identified by their echo traces and in some cases followed over several minutes. We marked and saved the range and time of the beginning and end of such echo traces with the mouse-tip logger. By dividing the range difference by the time difference, we obtained the vertical speed of that individual between the two points. Note that the speeds obtained by this method do not include information on horizontal swimming.

Potential predators and escape reactions

Maurolicus muelleri is preyed upon by gadoid fishes (Giske *et al.*, 1990) which can be identified as strong echo traces on the echograms. We often observed that pearlsides near such strong echo traces of potential predators dived suddenly. To get an overview of the times, depths, and light levels at which "dive reactions" occurred, we visually scanned the 120 kHz echograms from 21 days, evenly distributed between 15th December 2010 and 15th August 2011, in intervals of 30 min and 25 m depth, respectively. Each occurrence of a strong echo trace (usually > -45 dB) was classified depending on the apparent interaction with the pearlsides as (i) pearlsides absent, (ii) present but no reaction, or (iii) dive reaction. The respective time and depth were saved and used for obtaining estimates of light levels for each occurrence.

Light

Surface photosynthetically active radiation (PAR, 400–700 nm) was measured continuously with a calibrated LI-190 quantum sensor (lower sensitivity threshold of 1×10^{-4} µmol m^{-2} s^{-1}) from 10th December 2010 to the end of the study period

(see Prihartato *et al.*, 2015 for details). On five days in 2011 (26th January, 22nd February, 11th April, 16th June, and 16th August), water column PAR (400–700 nm, with a resolution of 3.3 nm) was measured around noon with a RAMSES ACC hyper-spectral radiometer (Trios-optical sensors, Oldenburg, Germany). Measurements were made at depths around 1, 5, and 10 m and then every 10 m down to around 90–95 m depth (Prihartato *et al.*, 2015). In August, three replicate measurements were recorded for every metre (<15 m depth) and then for every 5 m. In June, the 40 and 50 m measurements were unreliable and therefore treated as missing values. Simultaneous surface measurements enabled the calculation of light attenuation coefficients (K; m^{-1}; integrated for the full spectrum measured in the profiles, s.a.; Table 1), which we used to estimate PAR in the water column similar to Prihartato *et al.* (2015). Below the deepest available measurements, we assumed a constant attenuation coefficient of 0.0739 m^{-1} (K_d; m^{-1}) that was obtained by averaging all measured Ks from depths > 50 m. Thus, starting with the 90 m relative PAR estimate (i.e. given as a fraction of the surface light) obtained from the method used in Prihartato *et al.* (2015), we calculated the relative PAR at consecutive depths by extrapolation, using

$$E_z = E_{z-1} * \exp(-K_d) * \Delta z. \tag{1}$$

E_z is the relative PAR at depth z, E_{z-1} is the relative PAR at the previous (shallower) depth, K_d is the attenuation coefficient for depths > 90 m and Δz is the depth difference between the previous and current depth. The absolute ambient PAR was obtained by multiplying the surface PAR measurement with the relative PAR at the respective time and depth. Note that the extrapolated PAR values are very dependent on K_d and are prone to uncertainties since K_d might not be constant below 90 m. We estimated the light span (orders of magnitude) inhabited by *M. muelleri* from K_d and the respective depth range using:

$$\text{lightspan} = -\log10(\exp(-K_d * \text{depth range})). \tag{2}$$

Results
Community composition
The main taxa in the trawl catches were *Maurolicus muelleri*, *Benthosema glaciale*, krill (*Meganyctiphanes norvegica* and *Thysanoessa* sp.), and pelagic shrimps (*Pasiphaea* and *Sergestes*). *Maurolicus muelleri* was the prevailing fish captured in the daytime scattering layers of the upper 100–200 m and the only fish caught in the shallowest layer (<70 m) in October 2010 (Figure 1). At about 200 m, there then was a mixture of *M. muelleri* and *B. glaciale*. In August, the shallowest layer was located at ~200 m, and *M. muelleri* was the only abundant target, with catches of 10000–30000 individuals in the three replicates. In slightly deeper tows, just beneath the core of this layer, numbers decreased. *Maurolicus muelleri* was still prevailing, but also *B. glaciale* were caught in these tows. *Benthosema glaciale* by far became the prevailing fish in the deeper tows, where also pelagic shrimps were common. Nocturnal sampling was limited to October. *Benthosem glaciale* and *Sergestes* then made up a considerable proportion (~20%) of the catches by number at 70 m depth during the early night (Figure 1c; trawl number 14–16).

Mysids (*Boreomysis arctica*) were numerous at depth, but are not included because of their small size (ca. 2 cm) and expected

Table 1. Light attenuation coefficients (K; m^{-1}) between consecutive depths in Masfjorden in 2011.

Depth (m)	26 January 2011	22 February 2011	11 April 2011	16 June 2011	16 August 2011
0.5–5	0.283	0.176	0.299	0.491	0.275
5–10	0.116	0.174	0.143	0.272	0.195
10–20	0.096	0.131	0.177	0.203	0.141
20–30	0.081	0.109	0.079	0.209	0.122
30–40	0.076	0.089	0.141	NA	0.100
40–50	0.076	0.07	0.118	NA	0.086
50–60	0.079	0.059	0.067	0.088	0.078
60–70	0.083	0.06	0.068	0.085	0.072
70–80	0.072	0.034	0.078	0.061	NA
80–90	0.078	0.044	0.058	0.094	NA
>90			0.0739		

Below 90 m depth, we assumed a constant K that is the average of all Ks measured at depths > 50 m.
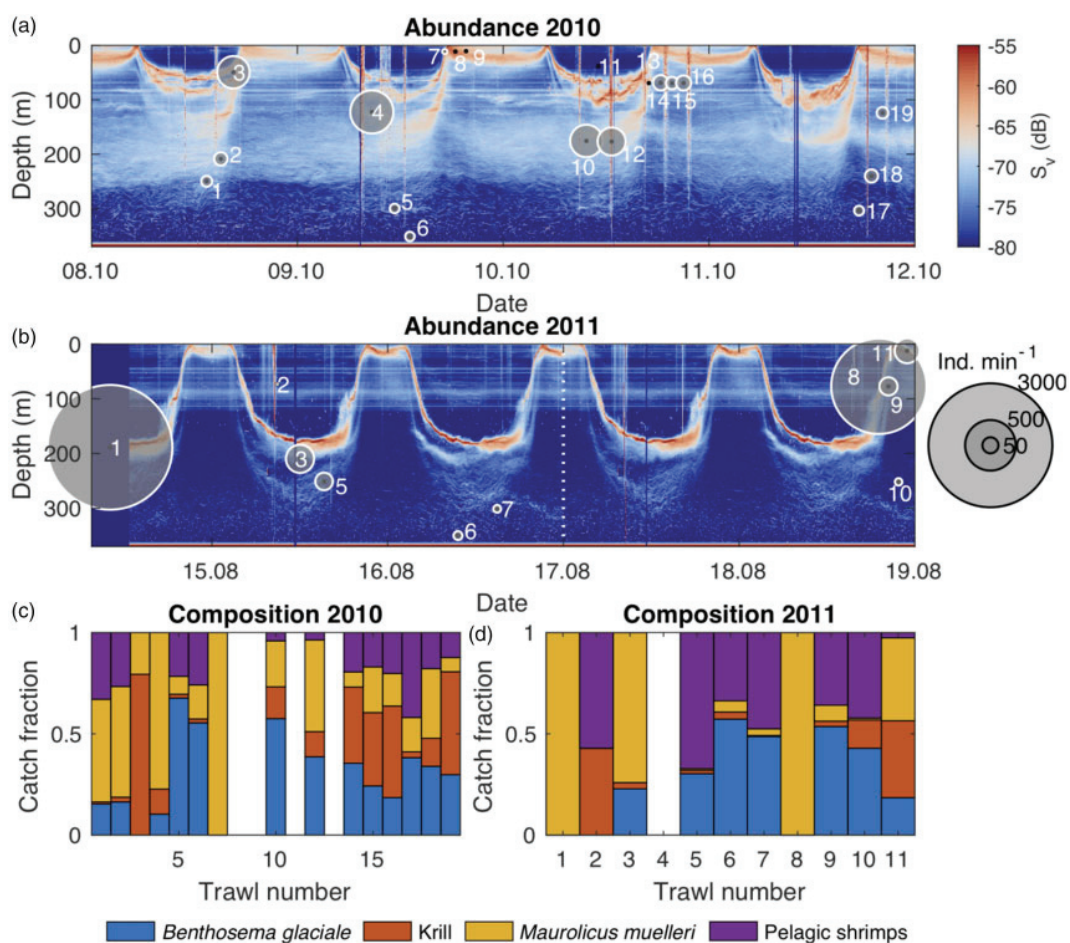

Figure 1. Location of trawl samples in October 2010 (a) and August 2011 (b), overlaid over the in-parallel obtained echogram from the submerged 38 kHz echosounder. Bubble sizes indicate the total number of individuals caught, normalized to sampling effort. As the 38 kHz echosounder was retrieved on the 17th August, the data from the two previous days are repeated on the 17th and 18th August (right of the vertical, dotted line). Panels (c) and (d) show the relative composition of the trawl catches with the numbers on the x-axis corresponding to the numbers in (a) and (b), respectively. Note that few krill were caught on the 14th August (trawl number 1 in 2011), but not quantified. Empty bars represent trawl catches that were not quantified.

negligible backscatter (Rudstam *et al.*, 2008). Gelatinous zoo-plankton including the siphonophore *Lensia* sp. (not pneumato-phore-bearing and thus not strongly scattering), and scyphozoan jellyfish were regularly caught, but in small numbers, and are therefore not included in the graphs. The in general small contributions to the acoustic backscatter from the invertebrates are sub-stantiated by the data at 38 kHz (Figure 1), which basically mirror those at 120 kHz (e.g. Figure 2).

Maurolicus muelleri had average individual weights between about 0.2 and 1.25 g while *B. glaciale*'s weights ranged between 0.25 and 3.4 g (Supplementary Figure S3). Both species had a larger average weight at greater depths, with *B. glaciale* getting three times as heavy (about 2.5–3 g fish^{-1}) as *M. muelleri* (about 0.8 g fish^{-1}).

Population behaviour

The vertical extension of the pearlside distribution varied by a factor of ∼6 throughout the sampling period, spanning 4 orders of magnitude ambient light in the autumn and <1 order of magnitude in summer (Table 2, Figures 2 and 3). Changes of the population distribution patterns happened over different time scales, from days (fusion of layers in April) to months (e.g. proportion of migrating adults in winter). In autumn, the *M. muelleri* population (defined as the scattering layers in the upper ∼200 m based on the trawl catches) separated into two main scattering layers, ranging over ∼120 m of the water column (Figure 1). The shallower layer performed diel vertical migration and usually separated into several sublayers in the upper 150 m during the day. The deeper main layer largely remained at mesopelagic depth

>150 m throughout the diel cycle (Figure 1). Between January and April, an increasing proportion of the deeper layer resumed diel vertical migration (e.g. Figure 2). After the fusion of the shallow and deep part of the population in mid-April, the vertical range of the population got narrower (Figures 2 and 3). Around midsummer usually only one, very narrow (less than 20 m), scattering layer existed (Figures 2 and 3, Supplementary Figure S4).

The daytime light exposure of the scattering layers changed over the season. During winter, the upper edge of the shallow layer moved along with the ∼10^{-2} µmol m^{-2} s^{-1} isolume (e.g. Figure 2, Table 2). The deeper layer during that season followed approximately the ∼10^{-4} µmol m^{-2} s^{-1} isolume (Table 2). In spring and summer, the deeper layer moved into darker conditions, until the upper part of the layer followed the ∼5×10^{-5} µmol m^{-2} s^{-1} isolume in August. In the afternoon, the upper edge of the shallowest scattering layer crossed the 10^{-4} µmol m^{-2} s^{-1} and sometimes even the 10^{-2} µmol m^{-2} s^{-1} isolume (Figure 2). This result may in part be an artefact due to our assumption that light attenuation is independent of time of day (i.e. independent of the angular distribution of incoming sunlight). Therefore, we mainly restrict our discussion to the light conditions outside the migration periods.

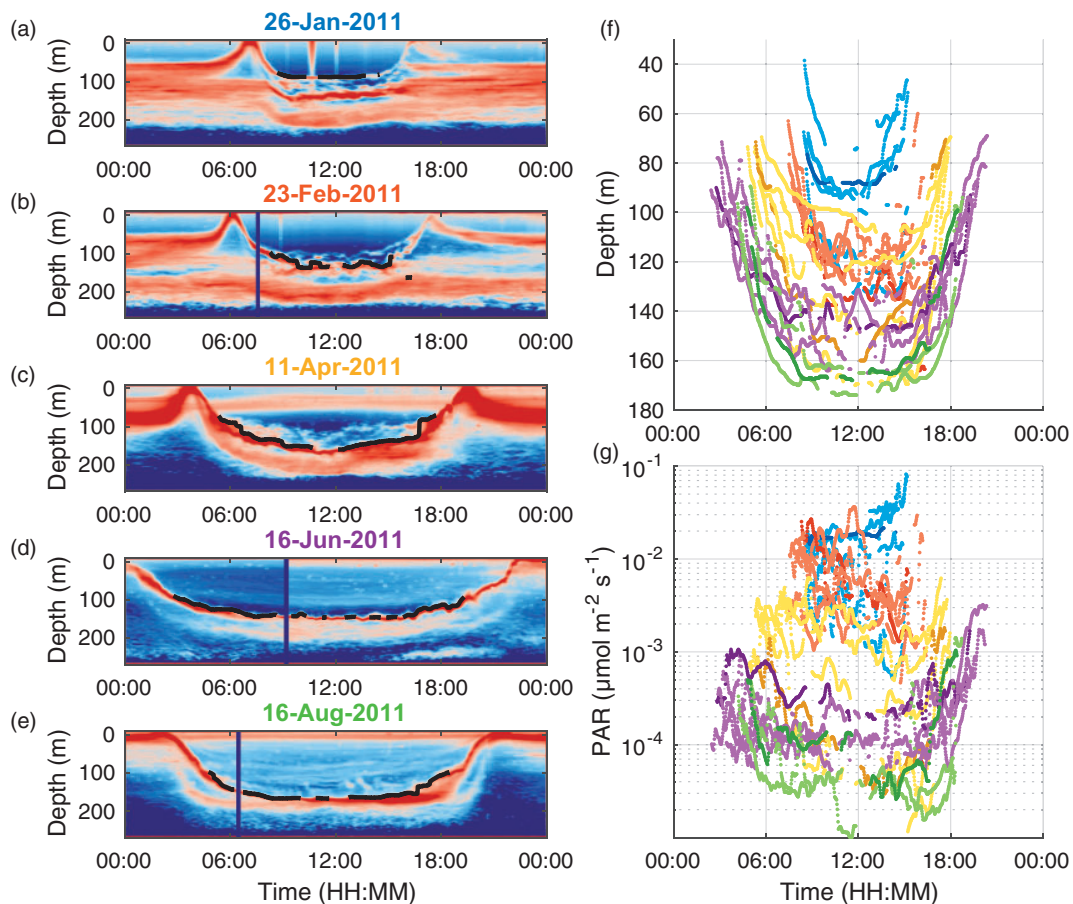**Figure 2.** Echograms from the 120 kHz echosounder on the five dates where light attenuation was measured (a–e). The black lines indicate the upper edge of the shallowest scattering layer. Depth (f) and light (PAR) (g) at the upper edge of the shallowest scattering layer on the same dates (colours as in the titles in the left). In addition, we have included three days just before and after the measurement day (lighter colours).

Table 2. Scattering layer properties around noon on the days where light attenuation was measured.

	Layer	26 January 2011	22 February 2011	11 April 2011	16 June 2011	16 August 2011
Min depth (m)	Shallow	99	134	/	/	/
	Deep	187	193	169	157	177
Weighted mean	Shallow	128	148	/	/	/
depth (m)	Deep	208	218	203	160	189
Max depth (m)	Shallow	160	161	/	/	/
	Deep	230	243	236	164	201
Depth range (m)	Shallow	61	27	/	/	/
	Deep	44	50	67	7	24
PAR max	Shallow	9×10^{-3}	4×10^{-3}	/	/	/
(μmol m^{-2} s^{-1})	Deep	1×10^{-5}	5×10^{-5}	3×10^{-5}	1×10^{-4}	4×10^{-5}
PAR min	Shallow	1×10^{-4}	6×10^{-4}	/	/	/
(μmol m^{-2} s^{-1})	Deep	5×10^{-7}	1×10^{-6}	2×10^{-7}	6×10^{-5}	7×10^{-6}
PAR span (orders of	Shallow	2	0.9	/	/	/
magnitude)	Deep	1.4	1.6	2.2	0.2	0.8

Layers are defined as median backscatter > -68 dB, where shallow layers reside in the upper 150 m and deep layers below.

Aggregations

Maurolicus formed aggregations which varied strongly in vertical extent, size, and apparent behaviour, depending also on the frequency and distance from the observing echosounder (Figure S5). The deeper winter layer (>150 m) usually had low density (mean S_v values < -65 dB; Figure 2), although, on about 50% of the winter days, dense aggregations ($S_v > -63$ dB) formed at depths beyond 125 m (Figures 3 and 4a). In contrast, dense aggregations (mean $S_v > -63$ dB) regularly formed in the shallowest (<100 m) layers during daytime (Figure 4b). In winter, such group formation occurred mainly at PAR levels $>5 \times 10^{-3}\mu$mol m^{-2} s^{-1} (Figure 2). From about mid-April though, the deeper and shallow layers fused and formed tight aggregations at light levels of about $5 \times 10^{-5}\mu$mol m^{-2} s^{-1} (Figure 2).

Bold individuals and individuals moving between main layers

Particularly in February/March and April/May, individuals and small groups of *M. muelleri* were located shallower, sometimes more than 40 m, than the upper-most daytime scattering layer (e.g. Figure 5; more examples in Supplementary Figure S6). The association of these "bold individuals" with the shallow main layer was evident from observations of individuals returning to or ascending from the main layer (Figures 5 and 6, Supplementary Figure S6). Both the main layer and the bold individuals responded upon sudden increases or decreases in surface light by downward or upward swimming, respectively (Supplementary Figure S6). Yet, the bold individuals were exposed to light levels up to ~1.5 orders of magnitude higher than the light intensity of the shallowest part of the main layer.

Individuals also switched between the main layers (Figure 6a, Supplementary Figure S7), solitarily or in small groups. The distance between the main scattering layers was on average around 25 m between November and December, around 20 m in January and decreased strongly thereafter (Figure 2). Thus, individuals switching between the main layers crossed on average 0.8 orders of magnitude of ambient light in late December, and about 0.6 orders of magnitude in January with $K_d = 0.0739$ (Figure 2). Individuals swam between layers at vertical velocities between 0.5

and 2.5 cm s^{-1}. Some of the individuals moved in a step-wise pattern (Figure 6).

Encounter with predators

Potential predators of *M. muelleri* appeared as strong echo traces in the echograms. During the daytime, *M. muelleri* often suddenly dived into deeper waters upon encounter with such strong fish echoes (Figure 7). This type of response occurred in the upper scattering layer, in small groups, and in individually swimming fish. Sometimes, the diving led to a cascading effect with vertical relocations manifesting out to a range of more than 50 m from the triggering echo (Figure 7a). Vertical velocities during diving were between 5 and 20 cm s^{-1} over a short time period (usually <1 min). We observed dive reactions at ambient light levels between 10^{-6} and $10^{-1}\mu$mol m^{-2} s^{-1} (Figure 8a). Most dives happened at light levels between 10^{-4} and $10^{-2}\mu$mol m^{-2} s^{-1}. Both predator presence and the proportion of dive reactions upon predator encounter increased with increasing light (Figure 8c).

Discussion

We demonstrate that the flexible behaviour of *Maurolicus muelleri* strongly modulates the appearance of acoustic scattering layers. Ten months of recordings provided continuous high-resolution data throughout the water column and resolved novel individual behavioural patterns, reflecting variation in risk taking, and adding to seasonal and short-term population patterns. In addition to individuals swimming within the main scattering layers, we discerned three individual behavioural patterns; as (i) bold individuals that apparently took a higher risk by swimming into more illuminated waters above the main population, (ii), individuals that switched between the main scattering layers, and (iii) individuals that apparently reduced predation risk by swimming away from predators.

Both the environment, other animals and individual state modulate behaviour including vertical distribution. Light appears to be the primary environmental factor modulating the vertical distribution of mesopelagic scattering layers (Kampa and Boden, 1954; Dickson, 1972; Aksnes *et al.*, 2017), although temperature and oxygen may also play a role (Netburn and Koslow, 2015). In addition, fish size and ontogeny, with associated variation in visibility and physiology determine the vertical distributions of
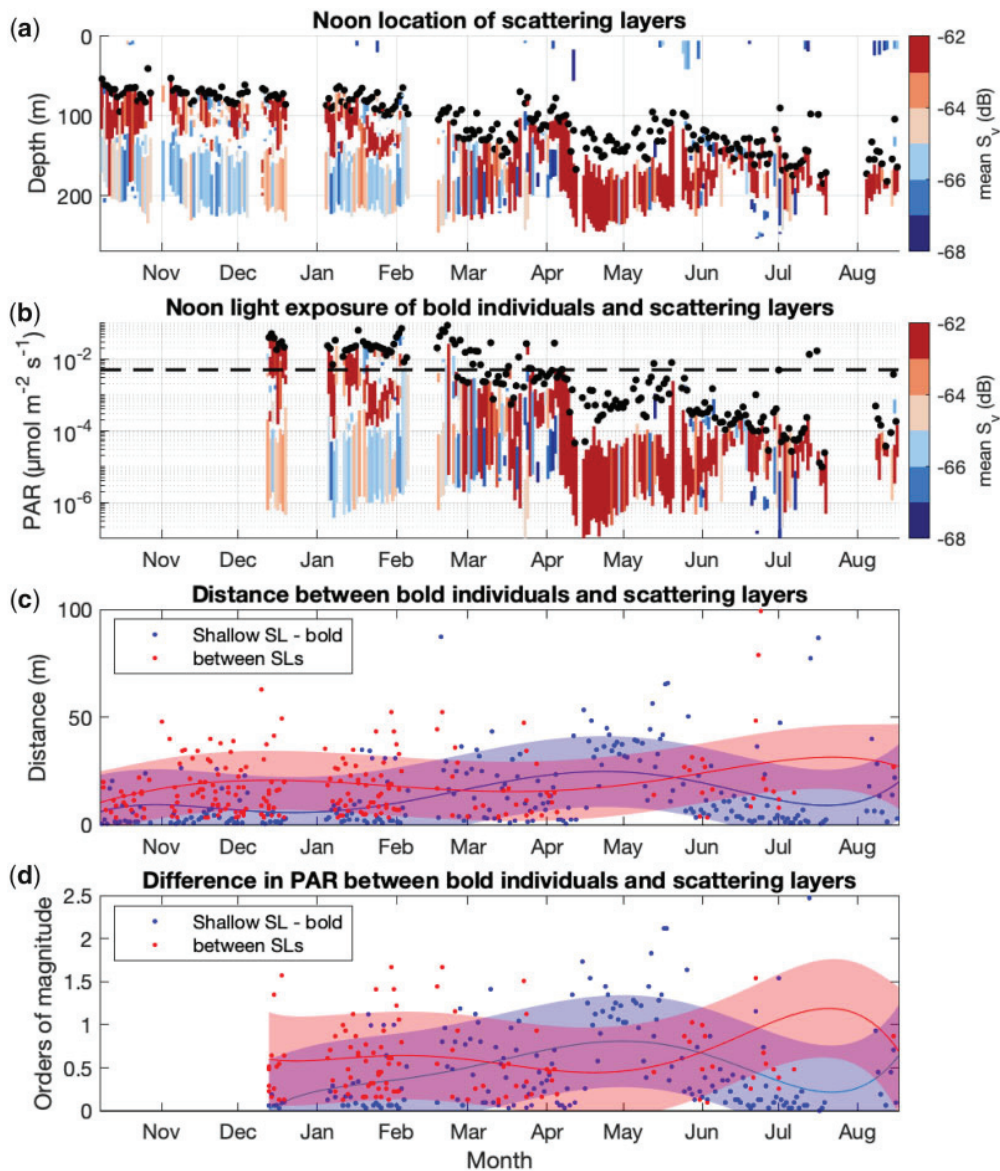
Figure 3. Noon location (a) and light exposure (b) of scattering layers (SL; coloured bars and dots) and bold individuals (black dots). The colours represent the average volume backscatter (S_v) of the respective layer. The vertical distance between bold individuals and the uppermost scattering layer (blue dots) as well as between the scattering layers (red dots) is indicated in metres (c) and orders of magnitude in PAR (d).

pearlsides (Giske *et al.*, 1990; Baliño and Aksnes, 1993; Staby *et al.*, 2013). The ambient light conditions for the main pearlside layers (Figure 3, Table 2) are consistent with previous observations (Rasmussen and Giske, 1994; Staby and Aksnes, 2011; Røstad *et al.*, 2016) and confirm that most pearlsides within a particular scattering layer are exposed to a similar range of light conditions throughout the day.

The fact that the light intensity of the upper and lower edges of the scattering layers differ substantially, supports the concept of a light comfort zone (Røstad *et al.*, 2016) where individual fish avoid both too high and too low illumination (Dupont *et al.*, 2009). Our data thus contrast the traditional "isolume hypothesis" (Clarke and Backus, 1957; Frank and Widder, 2002), where individuals are assumed to be attracted by a specific light

intensity. Our results suggest strong seasonal variation in the pearlside's light comfort zone as indicated by the thickness of their scattering layers (very narrow in summer). Increased light attenuation is expected to narrow a specific light comfort zone (Røstad *et al.*, 2016) but is unable to account for the variation in thickness seen here. Our observations rather suggest that the light comfort zone of *M. muelleri* is dynamic and emerges from the individual state in addition to size-related differences in vertical distribution (Giske *et al.*, 1990; Baliño and Aksnes, 1993; Staby *et al.*, 2013). Also, bolder fish which explored depths that are out of the comfort zone of most of the population likely add to the variation in comfort zones.

The variation in light comfort zones is supported by our observations of individuals which in a short time crossed light

gradients both within and between layers (individuals between layers) as well as appearing outside, and shallower than, the main layers (bold individuals). The data do not allow for assessing if the bold individuals repeatedly and consistently acted "atypically", thus being specialized individuals (Bolnick *et al.*, 2003; Sih *et al.*, 2015), or if deviating behaviour was state-related
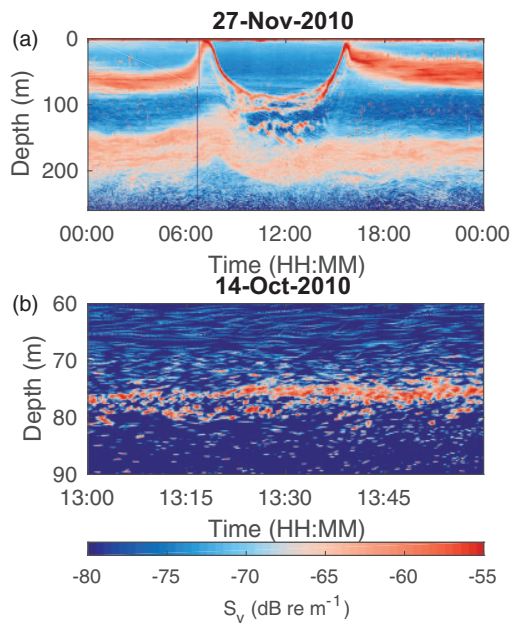

Figure 4. Aggregations formed during daytime by *Maurolicus muelleri* as seen from the 120 kHz (a) and 200 kHz (b) echosounder.

(e.g. hunger) and could occur in any individual (Sih *et al.*, 2015). Nevertheless, in addition to the established importance of light and fish size, the switching between layers reported here likely unveils the impact of some internal motivation. Internal state or individuals more willing to take risks (Sih *et al.*, 2015) may thus lead to deviations from the assumed size-dependent depth distribution. Larger individuals, which are most frequent at depth, may move to a shallower layer consisting of mostly smaller individuals, and vice versa. Future research with high-resolution target sampling could test this hypothesis. Furthermore, net sampling on bold individuals could elucidate if certain groups (age, size, sex, maturity, and stomach fullness) prevailed among these individuals, to provide further indications of reasons for their apparently different risk assessment.

Animals have sophisticated behavioural repertoires to avoid predation and the actual risk of being eaten is affected by the probability to be detected by a predator and the probability of a successful escape (Lima and Dill, 1990). In the pelagic environment, prey may adopt several strategies to mitigate the risk of visual predation. The most apparent anti-predator behaviour of animals in mesopelagic scattering layers is continuously hiding in relatively dark waters, such as in diel vertical migration (Clarke and Backus, 1957; Clark and Levy, 1988). In addition, reports of schooling mesopelagic fish exist (Barham, 1970; Saunders *et al.*, 2013). Recent research has also highlighted social interactions in response to predators in the mesopelagic zone (Benoit-Bird *et al.*, 2017). Daytime schooling of myctophids (Saunders *et al.*, 2013), other mesopelagic fish (Marchal, 1996), and also pearlsides (Gauthier *et al.*, 2014), in the epipelagic zone has been reported. Our close-range, highly resolved data show both flexibility in vertical migration and group dynamics on different time scales. In addition to their vertical migration, the pearlsides formed tight
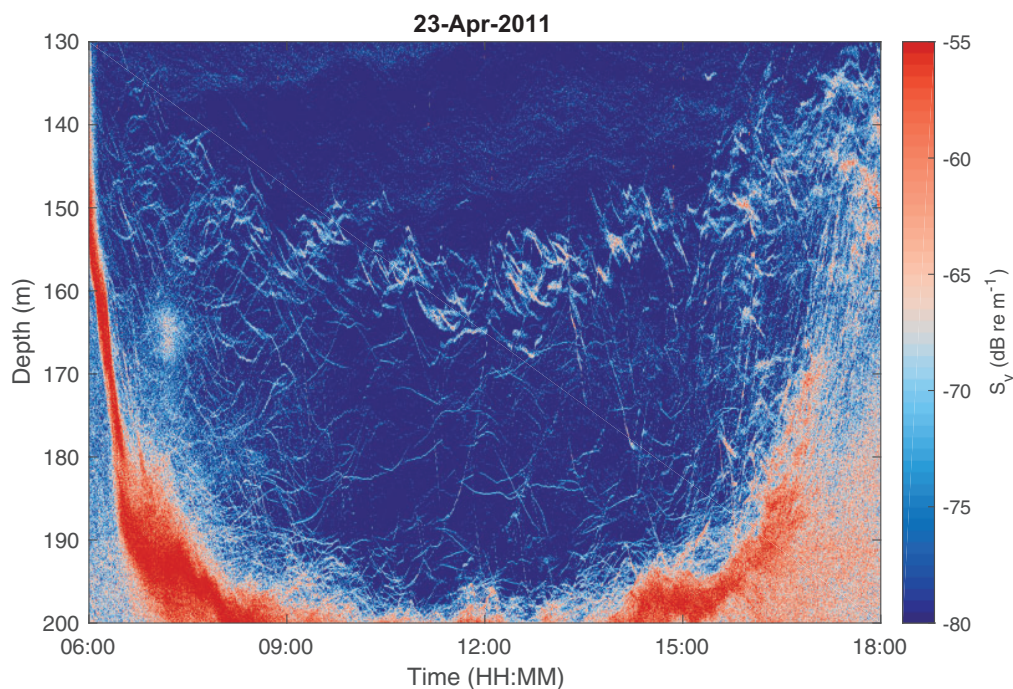

Figure 5. Example of bold individuals, which stayed at shallower depths than the main layers during the day, as observed from the 120 kHz echosounder.
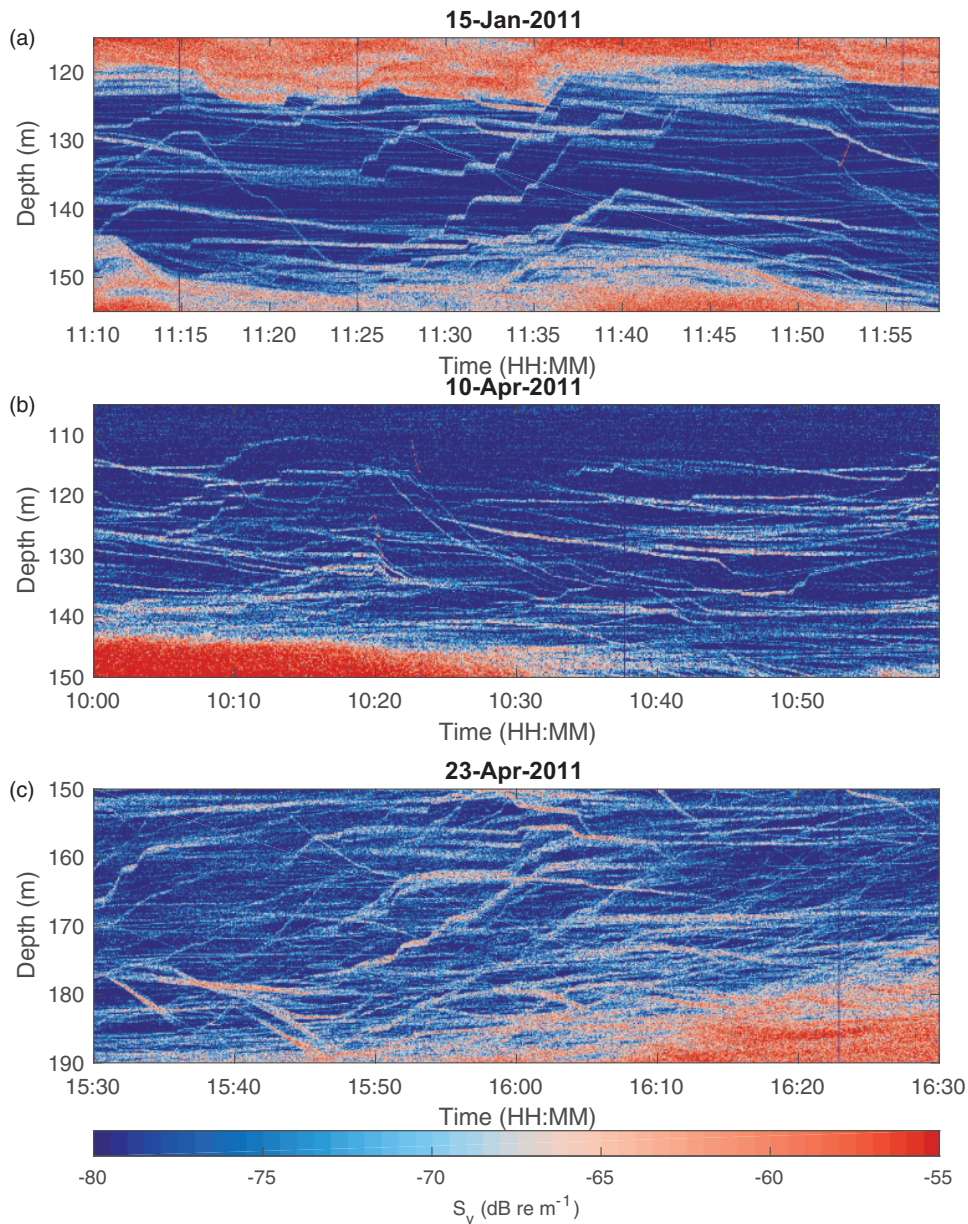
Figure 6. Echo traces of individuals moving between scattering layers and above the upper scattering layer as observed with the 120 kHz echosounder. (a) Relocations between a deep and shallow layer, (b) and (c) bold individuals relocating above the shallowest layer. Some of the fish use a step-wise swimming behaviour during relocation.

groups in the upper scattering layer during daytime. Pearlsides thus appear capable of optimizing their response to a dynamically changing environment using a combination of vertical distribution and social interactions. Probably, the social interactions allow for behaviours that would be sub-optimal for single individuals (Ritz *et al.*, 2011). Social interactions and aggregations may thereby modify the species' realized niche, in this case, their light comfort zone.

While schools may be beneficial under certain (light) conditions, large aggregations are likely more conspicuous than smaller groups (Ritz *et al.*, 2011). Additionally, a main drawback of grouping is intraspecific competition for resources

(Parrish and Edelstein-Keshet, 1999). Optimal group size therefore varies dynamically "as a function of resources, physiology, predominant activity, and limitations of the sensing abilities of the members" (Parrish and Edelstein-Keshet, 1999). The bold individuals regularly formed small groups which occupied depths with light levels up to 1.5 orders of magnitude higher than at the upper edge of "their" layer. They thus seemed to take more risk than the majority of the population, yet also with enhanced chances of reward in their visual search for prey (see below). Bold individuals returned to or ascended from the main layer at different times of the day. This suggests that a decision to leave the main layer could be
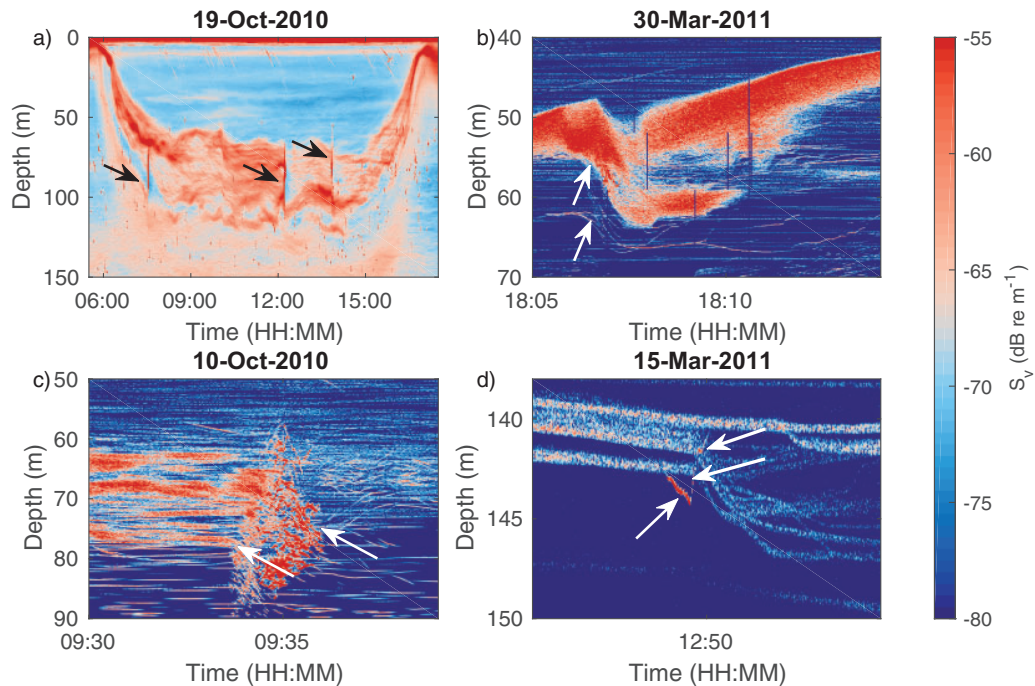
Figure 7. Reactions of *Maurolicus muelleri* interpreted as encounter with predators (highlighted by arrows). (a) Sudden displacements of the scattering layer (by more than 50 m) interpreted as cascading dive responses. (b) *M. muelleri* dive and split into two vertical layers during the dusk ascent, the vertical lines are noise, (c) The scattering layer dives and partly splits at daytime, (d) a potential predator first swims down but then ascends quickly, possibly attacking a group of *M. muelleri* from below. The pearlsides start diving only upon direct encounter. The echograms in (a) and (d) are reproduced from the 120 kHz data, (b) and (c) from the 200 kHz data.
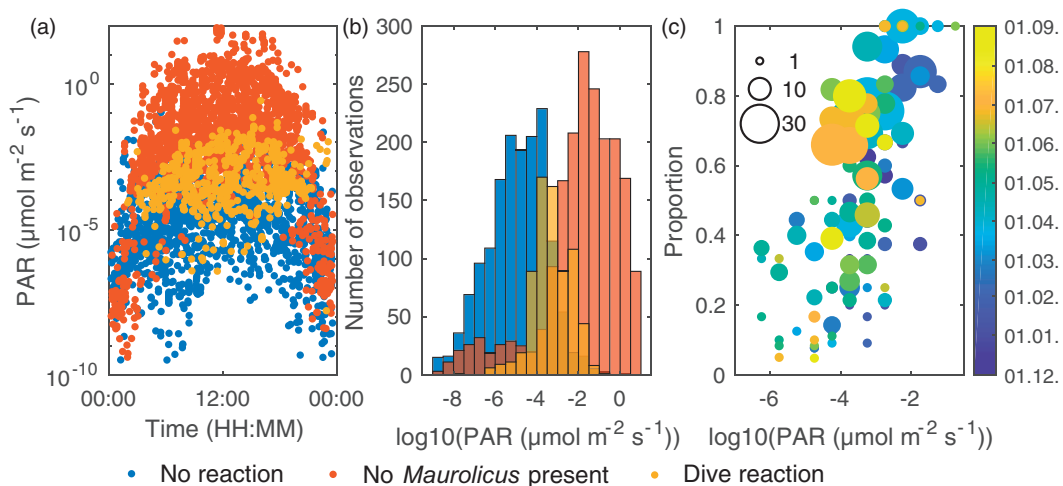

Figure 8. Light intensity at depths where potential predators (strong echo traces on the echogram) were observed as a function of the time of day (a). The histogram (b) shows the corresponding frequency distribution. The colours in (a) and (b) show the type of reaction by *Maurolicus muelleri*. Panel (c) shows the proportion of encounters between potential predators and *M. muelleri* that resulted in a dive reaction. The size of the circles indicates how many dive reactions were observed at the respective light level and day.

state-dependent, as suggested for other mesopelagic species (Dypvik *et al.*, 2012).

Animals constantly have to manage the benefits and risks of what they do, and reasons for observed behaviour may be manifold. One possible and plausible reason for leaving the main layer could be hunger. In winter in Masfjorden, zooplankton biomass

is highest at depths deeper than ~70 m (Rosland and Giske, 1997), and some pearlsides feed during the daytime in winter (Bagøien *et al.*, 2001). The light exposure of the bold groups was in the same order of magnitude as that in surface waters at dusk and dawn, and would thus likely be sufficient for visual feeding with the pearlside's twilight-adapted retina

(de Busserolles *et al.*, 2017). Bold behaviour could thus reflect hungry pearlsides making brief feeding trips to shallower waters and returning to safer depths when satiated. Similarly, behaviour could be related to differential spawning status during spring (Melo and Armstrong, 1991).

Vertical swimming speeds of individuals switching between layers were usually $1–2\,cm\,s^{-1}$, which correspond to <1 body length s^{-1}. Animals move at a range of velocities, depending on their requirements for energy conservation, migration, foraging, and predator avoidance (Beamish, 1978; Nathan *et al.*, 2008; Fernö *et al.*, 2011). The values reported here are comparable to those of nocturnal swimming velocities in juvenile pearlsides (Christiansen *et al.*, 2019) and other mesopelagic fish (Torgersen and Kaartvedt, 2001). The step-wise migration pattern may represent a way of reducing the risk of predation when outside of larger groups, as the fish tilt angle may affect the benefit of counter illumination by their prominent ventral light organs (cf. Christiansen *et al.*, 2019). In contrast, vertical escape reactions were rapid. The pearlsides reacted to encounter with potential predators, likely larger gadoid fishes, by diving at speeds up to $15–20\,cm\,s^{-1}$.

The pearlside's escape reactions indicated that the mesopelagic fish sense predators at several metres distance. Fish may detect predators visually (Kelley and Magurran, 2003), by olfactory cues (Dixson *et al.*, 2010), by sensing pressure waves emitted by the predator (Stewart *et al.*, 2014) or by a combination of senses. Escape diving was recorded both among bold individuals (Figures 6b and 7d) and scattering layers and sometimes led to cascading reactions, similar to the "escape waves" described by Herbert-Read *et al.* (2015). Escape reactions only appeared between light levels of 10^{-6} and $10^{-1}\,\mu mol\,m^{-2}\,s^{-1}$. This indicates a visual response, with a threshold level of ca. $10^{-6}\,\mu mol\,m^{-2}\,s^{-1}$. The lack of dive reactions at light levels below this suggests that bioluminescence did not matter for avoidance.

Conclusion

The pearlside *Maurolicus muelleri* has a rich repertoire of behaviours and various distribution patterns. Although the fish mainly seem to react upon changes in the environment (especially light, but also predators), we could also clearly observe individuals deviating from the main population behaviour. These individuals actively sought higher or lower risk areas, potentially due to difference in satiation state and risk aversion, and thus showed some level of decision making (Lima and Dill, 1990). Furthermore, social interactions seem to play an important role in defining the fishes light comfort zone. The variability in behaviour of the single species analysed here can only be a small representation of the true variability found in the open ocean, where mesopelagic scattering layers may consist not of one or two, but more than 100 fish species (Ariza *et al.*, 2016; Wang *et al.*, 2019). Nevertheless, we show that high-resolution and long-term observations can reveal diverse aspects of life in one of the most unexplored regions on our planet and broaden our knowledge about this vast ecosystem.

Supplementary data

Supplementary material is available at the *ICESJMS* online version of the manuscript.

Author contributions

This study was conceptualized by S.K. S.C. analysed and visualized the data. T.A.K., A.R. and D.L.A. collected the data. S.C. and S.K. wrote the first version of the manuscript. All authors contributed to the further writing of the article.

Data availability

The echosounder data underlying this article are available at the Norwegian Marine Data Centre and can be accessed with http://metadata.nmdc.no/metadata-api/landingpage/73073a8b13dad043 44dc9ecfa4280453. The light data will be shared on reasonable request to the corresponding author.

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Nighttime Swimming Behavior of a Mesopelagic Fish

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Nocturnal migration of mesopelagic fish into surface waters is well-documented. Yet, although there is increasing evidence of individual-based deviations from average population migrations and of the importance of small-scale individual behavior for predator-prey interactions and energetic cycling, little is known about what mesopelagic animals do when in upper waters. Using high-resolution data from an upward-facing, moored, split-beam echosounder we analyzed the night-time individual vertical swimming behavior of pearlsides (*Maurolicus muelleri*) over one winter. The population behavior is characterized by migration to the surface after sunset, "midnight-sinking" and another migration to the surface in the morning, followed by return to the daytime habitat. Focusing on individuals unveiled diverse behavioral patterns during different phases of the migration. After ascending to upper layers at dusk, *M. muelleri* leaves the surface waters, not by sinking, but by actively swimming in a step-wise pattern characterized by relocations alternated by pauses. Following the descent, vertical swimming is sustained at lower levels. Around midnight, the vertical swimming direction changes from predominantly downward to upward. Several hours before dawn, the fish start ascending toward the surface in a step-wise pattern. During population ascent in the afternoon and descent in the morning, some individuals at the fringes of schools migrate without intermittent pauses. This study documents the feasibility of using submerged, stationary echosounders in unveiling the individual behavior of mesopelagic fish.

Keywords: individual behavior, nocturnal, target tracking, diel vertical migration, *Maurolicus muelleri*

INTRODUCTION

Large scale phenomena, such as diel vertical migration, are normally studied at the population and community level, and *in situ* studies of individual behavior are still scarce among plankton and micronekton (Pearre, 2003). Yet, populations consist of individuals of different states doing different things, many of which may or may not deviate from the average (Torgersen, 2001; Solberg and Kaartvedt, 2017). Understanding the behavior of individuals may improve our understanding of metabolic demands (Treberg et al., 2016), predator-prey interactions (O'Brien et al., 1990), and ultimately carbon flux (Pearre, 2003).

Animals engage in a range of behaviors related to foraging, mating, migrations, or resting. To date, especially the night time behavior of marine animals, such as fish, remains largely elusive, mostly due to methodological restrictions (Hammerschlag et al., 2017). Mesopelagic fish

and other diel vertical migrants are usually expected to feed near the surface at night. How the organisms actually spend the night, though, varies between species (Simard et al., 1985; Giske et al., 1990; Balino and Aksnes, 1993; Pearre, 2003), seasons (Staby and Aksnes, 2011; Prihartato et al., 2015), and states (Simard et al., 1985; Pearre, 2003; Staby et al., 2012). Despite studies indicating this variability among mesopelagic fish (Torgersen, 2001; Kaartvedt et al., 2008; Olivar et al., 2017; Solberg and Kaartvedt, 2017), quantitative data of their individual behavior is largely lacking. We know next to nothing about what these fish do at night.

Twilight migrations, where animals ascend to the ocean surface around dusk and dawn, but return to intermediate depths during night (midnight sinking) are common among pelagic taxa and repeatedly documented for acoustic scattering layers (Tarling et al., 2002; Staby et al., 2011; Valle-Levinson et al., 2014). Potential reasons for such behavior are manifold, but include reduced activity after satiation (Cushing, 1951; Rudjakov, 1970), temperature selection for energy optimization (Giske and Aksnes, 1992), prey distribution (Torgersen et al., 1997; Valle-Levinson et al., 2014) and predator avoidance (Torgersen et al., 1997; Staby, 2010; Staby and Aksnes, 2011; Prihartato et al., 2015). Still, we know very little about the individual behavior and activities resulting in such commonly observed population distribution patterns.

One mesopelagic fish that is known for its twilight migrations is the small (<6 cm standard length; (Rasmussen and Giske, 1994; Goodson et al., 1995) Mueller's pearlside (*Maurolicus muelleri*, Sternoptychidae). It forms the shallow-most mesopelagic scattering layers in Norwegian fjords (e.g., Giske et al., 1990; Staby and Aksnes, 2011). In winter, adult *M. muelleri* reside in a scattering layer at around 150–200 m depth throughout the diel cycle (Staby et al., 2011). The adult fish may rely on lipids built up over the summer and autumn (Falk-Petersen et al., 1986), but may also forage on overwintering *Calanus* during daytime (Bagøien et al., 2001). Juveniles (<1 year) instead maximize growth by feeding on plankton in shallower waters during twilight (Giske et al., 1990; Bagøien et al., 2001). The juveniles form a shallow scattering layer with a strong diel migration pattern with ascent to the surface in the afternoon, subsequent midnight-sinking during a non-feeding period at night (Giske and Aksnes, 1992; Bagøien et al., 2001) and a dawn ascent in the morning before returning to daytime depth (Staby and Aksnes, 2011; Prihartato et al., 2015). Juveniles are a main prey for e.g., blue whiting and saithe (Giske et al., 1990).

Here we explore the night-time behavior of juvenile Mueller's pearlside throughout the winter (December 2010–March 2011) in a well-studied fjord system (e.g., Kaartvedt et al., 1988; Giske et al., 1990; Staby et al., 2011). We applied an upward-looking echosounder floating in an anchored rig enabling studies of individuals with a temporal resolution of 2 records s^{-1} throughout the study period. Based on their population averages (e.g., Staby et al., 2012; Prihartato et al., 2015), we hypothesized that activity of juveniles changes during the night, yet with higher variability in individual behavior than that predicted from average diel vertical migration patterns.

MATERIALS AND METHODS
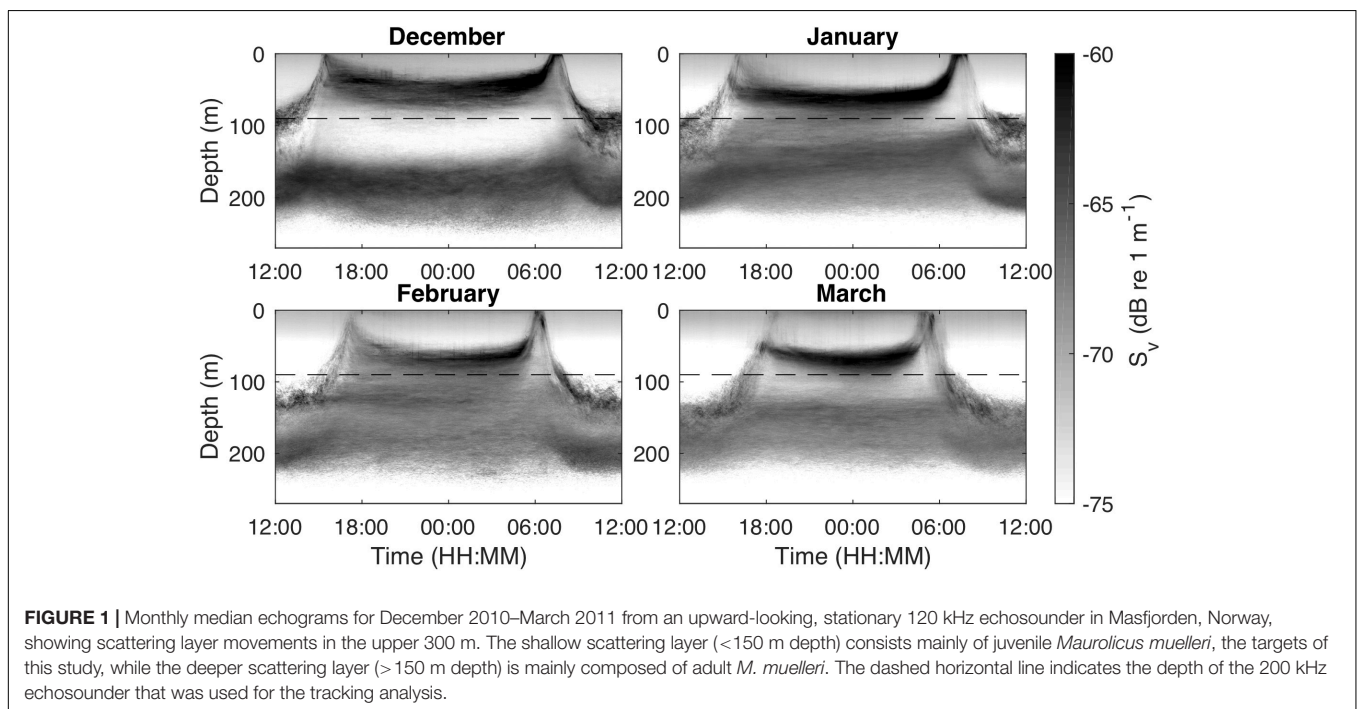
Location and Target Species

Masfjorden is a 20 km long fjord at the west coast of Norway (∼60°50' N, ∼005°30' E). It has a maximum depth of 494 m and a sill depth of 75 m bordering to Fensfjorden, which is connected to the coastal ocean (details in Kaartvedt et al., 1988). In Masfjorden, scattering layers shallower than 200 m are almost entirely formed by *M. muelleri* with juvenile fish in a shallow scattering layer (<100 m at night and ∼100 m during the day) and the adults in a deeper scattering layer (around 200 m) during autumn and winter (Giske et al., 1990; Staby et al., 2011). The two layers merge in spring (Staby et al., 2011). The glacier lanternfish *Benthosema glaciale* prevails below ∼200 m, with limited diel vertical migration in winter (Giske et al., 1990; Kaartvedt et al., 2009).

Dataset

Three upward facing stationary split-beam echosounders (EK60, Simrad) were deployed in Masfjorden between October 5–7, 2010 and recovered on August 17, 2011. Echosounders were moored at ∼370 m (38 kHz), ∼250 m (120 kHz), and ∼90 m depth (200 kHz) to enable high resolution of acoustic signals throughout the water column. The deepest echosounder was located at the bottom, the two shallower mounted in floating, anchored rigs in the same part of the fjord. The echosounders were cabled to shore and, with the exception of short periods of power failures, continuous recordings are available from all three frequencies for the entire study period. For further details about the setup of the echosounders see Prihartato et al. (2015). Here, we use data from the 200 kHz echosounder for the analysis of scattering layer depth and individual behavior. In addition, we consulted data from the deeper located 120 kHz echosounder for an overall assessment of the population behavior. This allowed to monitor the full diel migrating cycle including when juveniles migrated to below the 200 kHz echosounder (**Figure 1**), and also the largely non-migrating adults.

We analyzed data from December 2010 to March 2011, which enabled detailed analysis of individual swimming behavior of juvenile *M. muelleri* without the inclusion of deeper-living targets that only to a limited degree migrated vertically during this period (see e.g., Prihartato et al., 2015). Echosounder data with a temporal resolution of ∼2 s^{-1} were available from 98 days. Surface light levels (2 m above water) were measured continuously after the end of December 2010, yet the sensitivity of the light meter was too low for winter night-time measurements (see Prihartato et al., 2015).

For information on approximate nocturnal light levels during the study period, we obtained cloud cover and precipitation data from the nearby (∼20 km) weather station Takle from https://seklima.met.no/observations/ (download on November 12, 2019) and moon phases from https://www.timeanddate.com/moon/phases/ (accessed on November 12, 2019). Night time cloud cover and precipitation were calculated by averaging data collected within 0.3 days around midnight on each day. Time of sunrise and sunset were calculated for each day using the function

FIGURE 1 | Monthly median echograms for December 2010–March 2011 from an upward-looking, stationary 120 kHz echosounder in Masfjorden, Norway, showing scattering layer movements in the upper 300 m. The shallow scattering layer (<150 m depth) consists mainly of juvenile *Maurolicus muelleri*, the targets of this study, while the deeper scattering layer (>150 m depth) is mainly composed of adult *M. muelleri*. The dashed horizontal line indicates the depth of the 200 kHz echosounder that was used for the tracking analysis.

sunRiseSet[1]. All dates and times are presented in UTC (local time -1 h; maximum deviation from apparent solar time about 33 min on December 1, 2010).

Population Analysis

One aim of the study was to relate individual behavior to that of the *M. muelleri* population. Therefore, the location and migration velocity of the scattering layer formed by juvenile *M. muelleri* were determined. The raw EK60 data were reorganized into a three-dimensional grid, with a daytime (resolution of 90 s), depth (resolution of 0.3 m) and date dimension, in order to improve computation times and data accessibility. Each grid cell contained the average (calculated in the linear domain) volume backscattering strength (S_v, dB re 1 m^{-1} (MacLennan, 2002), in the following referred to as backscatter), calculated from the raw data of the given depth and time interval. The gridded backscatter data were used in all of the following population analyses. We calculated monthly median backscatter from the 120 kHz data by computing the median backscatter for each depth and daytime interval over all dates in the respective month.

Properties of Scattering Layers

The depth of the scattering layer was determined for each day of the study period using night time data (between sunset and sunrise) between 2 and 84 m depth. Data closer to the transducer could not be used due to noise (ping interference) at about 86 m depth. Between 0.1 day (144 min) after sunset and before sunrise, all values with depths < 19 m were excluded to reduce the inclusion of night time surface signals (**Supplementary**

Figure S1). Backscatter values > −53 dB re 1 m^{-1} usually occurred due to extended surface signals or strong individual targets (potentially larger fish). These high backscatter values were thus not representative for the *M. muelleri* population and therefore excluded from the analysis. The thresholds for these data exclusions were determined empirically from the echograms. The remaining backscatter data were linearized to s_v (m^{-1}), the volume backscattering coefficient (MacLennan, 2002). For each time point, the cumulative s_v over depth was calculated and the depth where the cumulative s_v reached 50% of its maximum value was defined as the midpoint of the scattering layer. In some cases, the *M. muelleri* scattering layer could not be clearly identified due to low fish densities, which we defined as a cumulative $s_v < 5 \times 10^{-6}$ m^{-1}. Periods where the cumulative s_v fell below this threshold were excluded from the scattering layer analysis. We calculated the vertical velocity of the scattering layer by applying a moving slope approach[2] with a time window of 0.05 decimal days (72 min) on the scattering layer depth.

Delineating Dusk Descent and Dawn Ascent

Individual targets could not be resolved when in surface waters at dusk and dawn, and we here focus on the nocturnal behavior in-between these timepoints. The midnight sinking period was marked by the population starting to descend from the surface to deeper layers in the evening (from now on referred to as dusk descent) and the ascent to the surface in the morning (from now on dawn ascent). We used the location of the scattering layer to determine the start of the dusk descent and the end of the dawn

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[1]https://se.mathworks.com/matlabcentral/fileexchange/62180-sunriseset-lat-lng-utcoff-date-plot; downloaded on January 15, 2019.

[2]https://se.mathworks.com/matlabcentral/fileexchange/16997-movingslope; downloaded on April 5, 2018.

ascent of the population (**Figure 2**). We chose the first time-point when the center of the scattering layer was at its shallowest depth in the afternoon and morning, respectively, as criteria. We also calculated the time spent in near-surface waters < 20 m depth at dusk and dawn for each day.

## Identification of *Maurolicus muelleri* and Description of Swimming Behavior

The proximity of the *M. muelleri* scattering layer to the 200 kHz transducer at night enabled the identification of night-time individual swimming behavior. Densities of fish in the core of the scattering layer were too high for separating individuals during some parts of the night and at long distance from the transducer (i.e., shallow depth), while individuals outside the core and during periods of lower density could be distinguished successfully. Types of swimming patterns were first visually identified from echograms in the Sonar5-Pro software (Balk and Lindem, 2017) on separate days and thereafter quantified using target tracking.

Target Tracking

Successive echoes of individual targets can be combined and thus the path of individuals over depth, time and in along and athwart direction can be followed (target tracking; Brede et al., 1990). We used target tracking to assess the individual vertical swimming of *M. muelleri* over the entire study period. Target tracking was performed in the software Sonar5-Pro (Version 6.0.4, Balk and Lindem, 2000, 2017). Prior to the tracking, the files were pre-processed by cross-filter detection (Balk and Lindem, 2001, 2017), a procedure which improves the detection of individual tracks in single echo detection mode. Default settings were selected for the cross-filter detection. The thus modified single echo detection echograms were then analyzed by

automatic target tracking. We optimized the parameters for the target tracking (**Table 1**) beforehand by comparing manual and automatic tracking at different time points of the study period. We adjusted the tracking parameters depending on distance from the transducer (range), which reduces the uncertainties at longer ranges compared to when using a single set of parameters. Individuals were tracked between 5 and 85 m range (i.e., ∼9–89 m depth). The use of cross-filter detection introduces uncertainties. While enabling tracking at increased ranges and at higher densities (Balk and Lindem, 2002), it also increases the risk of multiple detections, increases ping gaps and introduces noise into the target strength (MacLennan, 2002) of tracks. Yet, we decided to accept these uncertainties to be able to analyze individual movements throughout most of the water column and with longer track durations that enabled the differentiation between behaviors. Only few individuals (∼3%) were tracked at ranges > 60 m (shallower than 34 m depth; **Supplementary Figure S2**). While these few individuals have limited influence on the overall results, they contribute information about processes and behavior in the upper water column.

High population densities hamper individual tracking detection (Handegard, 2007). Correspondingly, individuals close to the transducer are tracked more effectively due to the higher resolution of targets. Differences in population densities over time, e.g., lower densities during the dusk descent, and distances to the transducer, e.g., shorter distances in the morning when many individuals already started descending, thus led to a higher number of descending tracks. Nevertheless, a visual comparison of the tracks and echograms indicated that the tracks' position information and thus behavior of the individuals were represented well. This also makes us confident that we are not assessing the behavior of outliers with deviating behavior and that the large-scale picture of the behavioral repertoire observed here is representative.
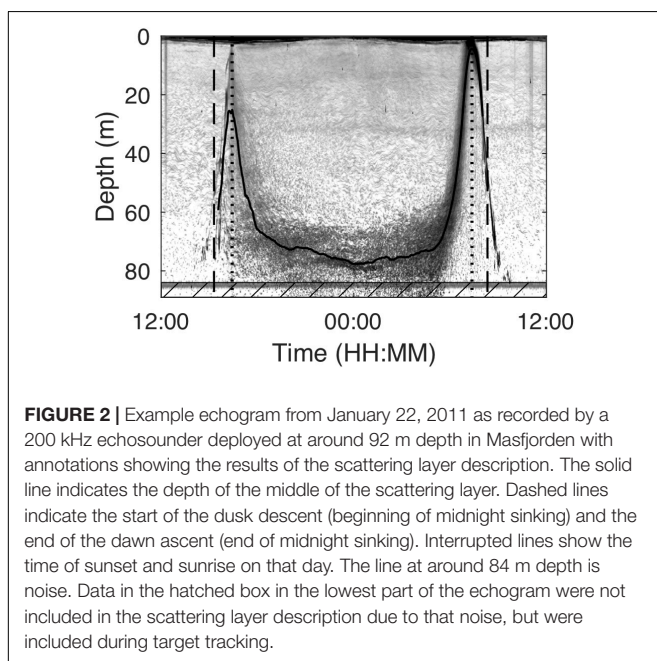
Quantification of Tracks and Behavior

The workflow during track processing and filter criteria as outlined below are summarized in the **Supplementary Figure S3**. The data were processed and analyzed in Matlab (Mathworks; R2017b). We first applied a filter to exclude potential other targets than *M. muelleri*. This identity filter included a threshold in mean TS (**Figure 3**) and excluded daytime tracks from after sunrise and before sunset. We determined the TS thresholds by manually tracking *M. muelleri* individuals on one randomly selected day of each of the 4 months (about 800 tracks per day) and then identifying the TS range that included about 90% of the tracked individuals on these 4 days. Tracks with a mean TS outside the defined range were excluded from further analysis. This procedure allowed identification of *M. muelleri* with a reduced influence of tilt angles (Miyashita et al., 1996) as fish in all different angles were included during the manual tracking. A minimum track duration of 30 s was used. The first time-point of each track determined whether the tracks were within the defined night-time hours.

After applying the identity filter, 613003 tracks remained and were further processed. Depth outliers of each individual track

FIGURE 2 | Example echogram from January 22, 2011 as recorded by a 200 kHz echosounder deployed at around 92 m depth in Masfjorden with annotations showing the results of the scattering layer description. The solid line indicates the depth of the middle of the scattering layer. Dashed lines indicate the start of the dusk descent (beginning of midnight sinking) and the end of the dawn ascent (end of midnight sinking). Interrupted lines show the time of sunset and sunrise on that day. The line at around 84 m depth is noise. Data in the hatched box in the lowest part of the echogram were not included in the scattering layer description due to that noise, but were included during target tracking.

TABLE 1 | Settings used in the automatic target tracking analysis in Sonar5-Pro (Balk and Lindem, 2017).

	Range (m)								
Track properties	**10**	**20**	**30**	**40**	**50**	**60**	**70**	**80**	**90**
Minimum track length (Nr. of echoes)	10	20	20	30	40	30	30	30	30
Maximum ping gap (Nr. of echoes)	3	5	5	5	10	10	5	5	0
Gating	**Ping**		**Range (m)**		**Ath (°)**		**Alo (°)**		
Initial size	1		0.1		5		5		
Increase with missing ping			0.01		0.1		0.1		
Association	**Ping**		**Range (m)**		**Ath (°)**		**Alo (°)**		**TS (dB)**
Distance weights	50		10		1		1		1
Prediction	**A**		**B**						
Alpha Beta	0.5		0.5						

Note that names in the table reflect those in the program. Range (m) represents distance from the transducer, where a range of 10 m is at about 84 m depth and a range of 90 m is at ~4 m depth. Gating describes the process where the location of the next echo of a track is estimated. The association unit evaluates different track predictions based on user-defined weights. Gating and weights for association are defined for ping distance, range (m), along (Alo (°)), and athwart (Ath (°)) angles. Association also includes a weight on TS (target strength, dB). Alpha Beta is a prediction method. See Balk and Lindem (2017) for further information.

FIGURE 3 | Comparison of target strengths of manually (blue bars) and automatically (orange bars) tracked individuals on four randomly selected dates (one from each month; December 10, 2010, January 8, 2011, February 24, 2011, and March 1, 2011). The red vertical line indicates the median target strength and the black lines the limits of the 90% distribution of target strengths which were used to filter automatically tracked *M. muelleri* tracks.

were removed by first calculating a running median as well as a running median absolute deviation (MAD) (each with a window of 10 echoes) of the track's depths and then replacing depth values that deviated from the running median by more than the MAD × 10 by the running median. In the next step, a running mean (window size of 10 echoes) was applied to the depth values of each such treated track. We calculated net vertical displacement (m), track duration (s) and vertical velocity (vertical displacement divided by track duration; cm s^{-1}) of each track. Each track was also examined for patterns of alternations between segments of active vertical ascent or descent, and pauses in which fish maintained a constant depth,

although they might have been active in the horizontal plane (**Supplementary Figure S4**). We determined and subsequently counted the pauses in each track using thresholds. We defined parts of the tracks with depth changes < 0.01 m between at least four subsequent echoes, as pauses and those with larger depth changes as active phases. Single values of pauses or active phases were filled by the surrounding values. For example, when in the vector $x = [0,0,0,1,0,0,1,1,1,1,0,0]$, the digit 1 stands for "pause" and 0 for "active phase," then the resulting index vector of which echoes should be regarded as pause would look like this: $y = [0,0,0,0,0,0,0,1,1,1,1,0,0]$. The first and last segments (i.e., the first and last ascent, descent or pause) of each accepted track with more than two pauses were excluded in order to reduce errors from the target tracking, stemming from potentially overlapping tracks. Tracks with < 60 echoes were considered fragments and were therefore excluded from further analysis. The remaining 272290 tracks were used for behavioral analysis.

Based on net vertical displacement, number of pauses and track duration, the tracks were assigned to either of three main swimming patterns (**Supplementary Figure S3**):

1. Step-wise swimming: targets change depth by alternating active upward/downward swimming and pauses (**Supplementary Figure S4**).
2. Stationary: targets maintain a constant depth throughout the track.
3. Direct swimming: targets change depth without pauses.

We then calculated the average active swimming speed (swimming speed, cm s^{-1}), i.e., the vertical velocity during active segments of each step-wise track. In stationary and direct tracks, the swimming speed equals the vertical velocity. Furthermore, we determined the proportion of the three different swimming patterns in relation to time from the start of the dusk descent and time to the end of the dawn ascent, in order to account for seasonal changes. We also calculated the proportion of ascending
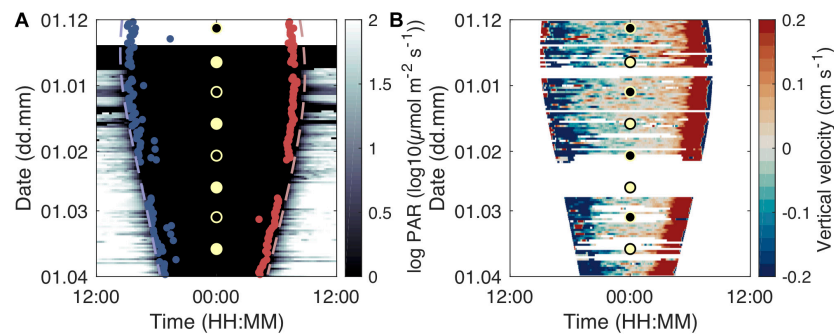
FIGURE 4 | Development of migration timing and velocity over daytime and season. Light intensity and start of dusk descent (beginning of midnight sinking; blue dots) and end of morning ascent (end of midnight sinking; red dots) over the study period and daytime **(A)**. The dashed lines indicate sunset (blue) and sunrise (red). Development of scattering layer vertical velocity over daytime and the study period **(B)**. Warm colors denote upward movement of the scattering layer while cold colors show a downward movement. The circles indicate full moon (yellow fill) and new moon (black fill).

and descending step-wise tracks, as well as their average vertical velocities in relation to daytime and depth using data binned by depth (3 m intervals) and time (72 min). The proportion of ascending tracks for each bin was determined when more than five tracks were found in the respective bin.

RESULTS

Population Migration

The vertical distribution of the scattering layer ascribed to juvenile *M. muelleri* differed distinctly between day and night and was characterized by short-term migrations to the surface at dusk and dawn (**Figure 1**). After the dusk ascent, the population returned to intermediate depths, deepening from an average of 60 m in December to 70 to 75 m in February and March. From mid-January, the vertical distribution changed continuously throughout the night, with the scattering layer moving deeper before midnight and reversing direction after midnight (**Figure 4**). The daytime distribution was generally deeper and below 100 m. The deeper scattering layer ascribed to the adults mostly stayed below 120 m depth throughout the diel cycle, but a small proportion of this adult population sometimes migrated to shallower depths at night (**Figure 1**).

The timing of the dusk descent and dawn ascent of the juveniles changed over the study period in accordance with seasonal changes in sunrise and sunset (**Figure 4A**). The dusk descent from near-surface waters started about 20–70 min after sunset after the fish had spent around 20–40 min in waters shallower than 20 m. The dawn ascent ended around 40–70 min before sunrise on most days and the fish stayed in near-surface waters (<20 m) for about 40–60 min. The duration between these migrations and sunset/sunrise shortened over the study period (**Figure 4A**). On darker, foul weather days (e.g., March 20–25, 2011; **Figure 4A**), dusk descent started earlier and dawn ascent ended later. We did not find a clear relationship of population movement with moon phases (see **Supplementary Figure S5** for a combination of **Figure 4** with cloud cover and moon phase data). Interrupted upward migrations in the afternoon,

where the majority of the population started descending again before reaching the surface, were observed on 39 out of 98 analyzed diel echograms.

Population descent velocities were highest ∼30 min after the start of the dusk descent, while ascent velocities were highest 30–40 min before reaching the surface layers in the morning (**Figure 4B**). The maximum velocity of the scattering layer during the dusk descent increased from ∼0.5 cm s^{-1} in December to ∼0.8 cm s^{-1} in March. The maximum velocity during the dawn ascent increased from ∼1 cm s^{-1} in December to ∼1.5 cm s^{-1} in March. On most days, the dawn ascent was faster than the dusk descent.

Individual Swimming Behavior

Of the 272290 tracks, 142547 were classified as step-wise swimming, with 56744 tracks ascending and 85803 descending (**Table 2**). In total 127221 tracks displayed no or little vertical movement and were classified as stationary. An additional 2522 tracks were directly ascending/descending without steps. Duration and net vertical displacement of individuals depended on the respective swimming pattern (**Table 2** and **Figure 5**).
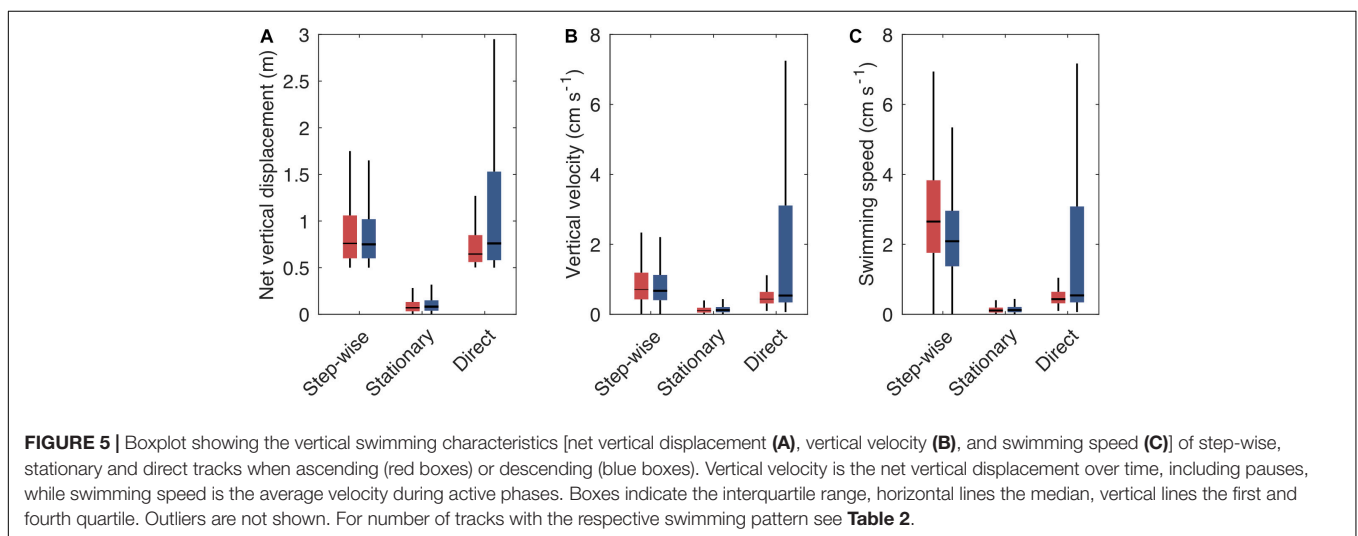
Step-wise swimming was especially prominent during the dusk and dawn migrations (**Figures 6, 7**). Around 75% of the fish swam step-wise around the start of the dusk descent. Although descending step-wise tracks dominated throughout this period of population descent, some ascending individuals were also recorded. During the latter part of the night, the proportion of step-wise swimming behavior increased (**Figure 7**), reaching a maximum of 87% at the end of the dawn ascent, but then also with a high proportion (>25%) of step-wise descending individuals. The net vertical relocation speed was ∼0.9 cm s^{-1}, while the actual swimming speed during the vertical steps was ∼2–3 cm s^{-1} (**Table 2**).

Vertically stationary tracks dominated (>50%) the nocturnal records throughout most of the night. These tracks usually lasted for > 1 min, with the track duration being restricted by the number of co-occurring tracks (**Figure 6C**). In most of the cases where *M. muelleri* relocated vertically, they moved step-wise (**Figures 6, 7**). Additional vertical displacement was caused by

TABLE 2 | Major track parameters obtained by automatic target tracking for the whole study period from December 1, 2010 to March 31, 2011 (92 days with tracking data).

	Number	Duration (s)	Net vertical displacement (m)	Vertical velocity (cm s^{-1})	Swimming speed (cm s^{-1})
Step-wise	142547	150 ± 220	0.91 ± 0.5	0.89 ± 0.7	2.54 ± 1.6
Ascending	56744	145 ± 237	0.94 ± 0.56	0.94 ± 0.8	2.93 ± 1.7
Descending	85803	152 ± 208	0.9 ± 0.46	0.86 ± 0.7	2.28 ± 1.4
Stationary	127221	79 ± 46	0.1 ± 0.09	0.14 ± 0.1	0.14 ± 0.1
Direct	2522	149 ± 103	1.1 ± 0.93	1.57 ± 2.0	1.58 ± 2.1
Ascending	770	162 ± 95	0.88 ± 0.7	1.03 ± 1.6	1.04 ± 1.6
Descending	1752	143 ± 106	1.22 ± 1	1.81 ± 2.2	1.81 ± 2.2
Total	272290	117 ± 166	0.54 ± 0.56	0.55 ± 0.7	1.41 ± 1.7

Data are mean ± standard deviation. Vertical velocity is the net vertical displacement over time, including pauses, while swimming speed is the average velocity during active phases.

FIGURE 5 | Boxplot showing the vertical swimming characteristics [net vertical displacement **(A)**, vertical velocity **(B)**, and swimming speed **(C)**] of step-wise, stationary and direct tracks when ascending (red boxes) or descending (blue boxes). Vertical velocity is the net vertical displacement over time, including pauses, while swimming speed is the average velocity during active phases. Boxes indicate the interquartile range, horizontal lines the median, vertical lines the first and fourth quartile. Outliers are not shown. For number of tracks with the respective swimming pattern see **Table 2**.
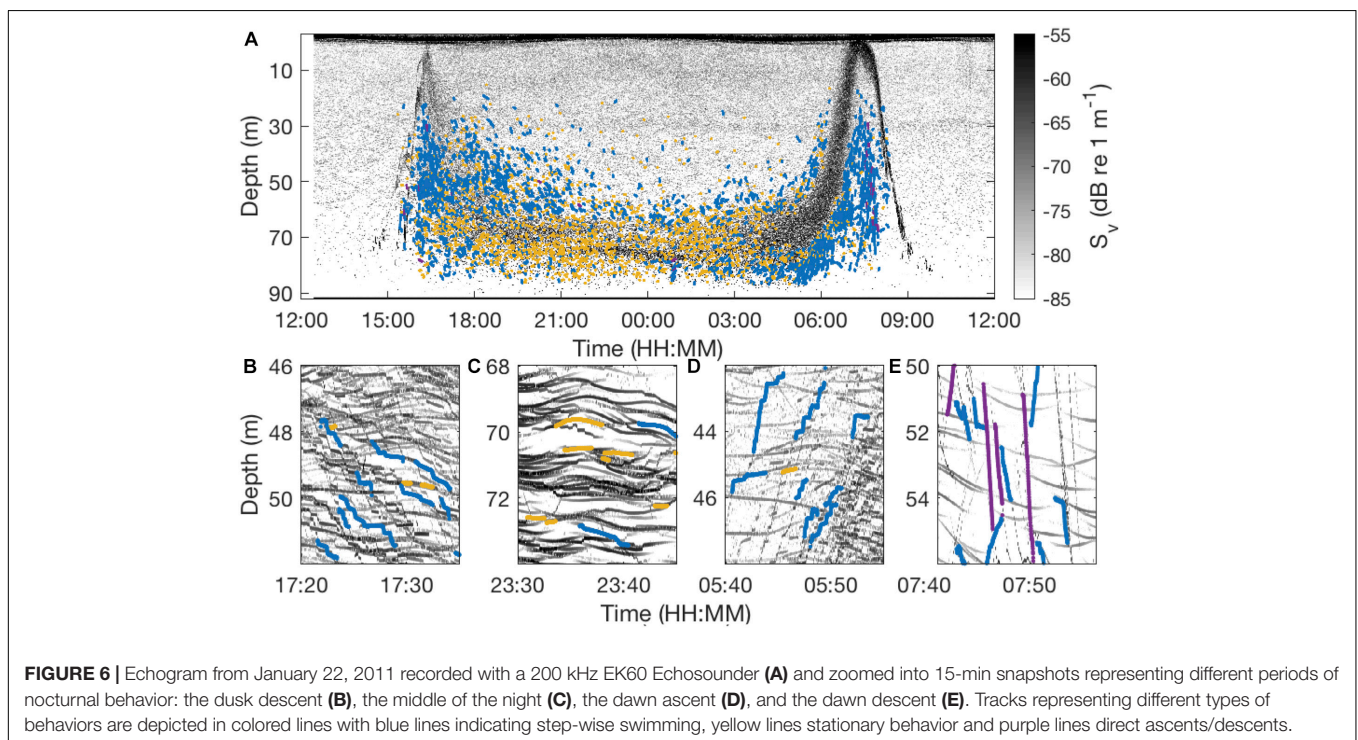
apparent internal waves. In a subsample of randomly selected days, internal wave amplitudes were around 0.7 m (range 0–1.8 m) and periods about 10 min (range 0–30 min). Internal waves led to vertical transitions of up to 0.6 cm s^{-1}, but usually around 0.2 cm s^{-1}, in otherwise stationary animals.

Even though there were main migration periods at dusk and dawn and dominance of stationary tracks at night, there was a clear pattern of the majority of step-wise relocating individuals descending before midnight and ascending after midnight (**Figure 8**). This pattern was accentuated toward the end of the study period (**Figure 8A**). The proportion of descending and ascending tracks depended on depth (**Figure 8B**). During the first half of the night, descending tracks dominated at all depths, nevertheless we observed the highest proportion of descending tracks in shallow layers of 20–40 m depth. In layers between 70 and 80 m, there always was a strong majority of ascending tracks subsequent to midnight. Correspondingly, the average displacement was downward before midnight and upward after midnight. Individual velocities reached > 1 cm s^{-1} during the dusk and dawn migrations, while velocities in the middle of the night were mostly lower. Maximum velocities increased over winter.

The individual behavior during the overall population's upward migration in the afternoon and descent in the morning, differed from that observed at night. During these main migration periods, most pearlsides schooled and individuals could not be resolved. However, individuals could occasionally be detected close to these schools. The pause duration in these individuals was short and some of these individuals refrained from pausing altogether and either ascended or descended directly (**Figure 8**). The highest vertical velocities were achieved in such direct tracks, with means of 1.0 and 1.8 cm s^{-1} in ascending and descending tracks, respectively (**Table 2**).
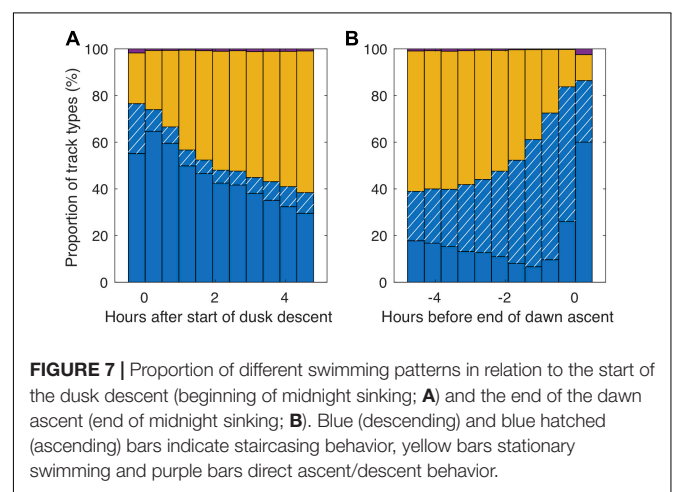
DISCUSSION

Our approach allowed for unique observations of the individual behavior of a mesopelagic fish. The long-term records, combined with high temporal resolution generated representative data for a whole winter period. We are confident in allocating the observed behavior to juvenile *M. muelleri* due to their well established and distinct vertical distribution pattern in this location (Giske et al., 1990; Staby and Aksnes, 2011;

FIGURE 6 | Echogram from January 22, 2011 recorded with a 200 kHz EK60 Echosounder **(A)** and zoomed into 15-min snapshots representing different periods of nocturnal behavior: the dusk descent **(B)**, the middle of the night **(C)**, the dawn ascent **(D)**, and the dawn descent **(E)**. Tracks representing different types of behaviors are depicted in colored lines with blue lines indicating step-wise swimming, yellow lines stationary behavior and purple lines direct ascents/descents.
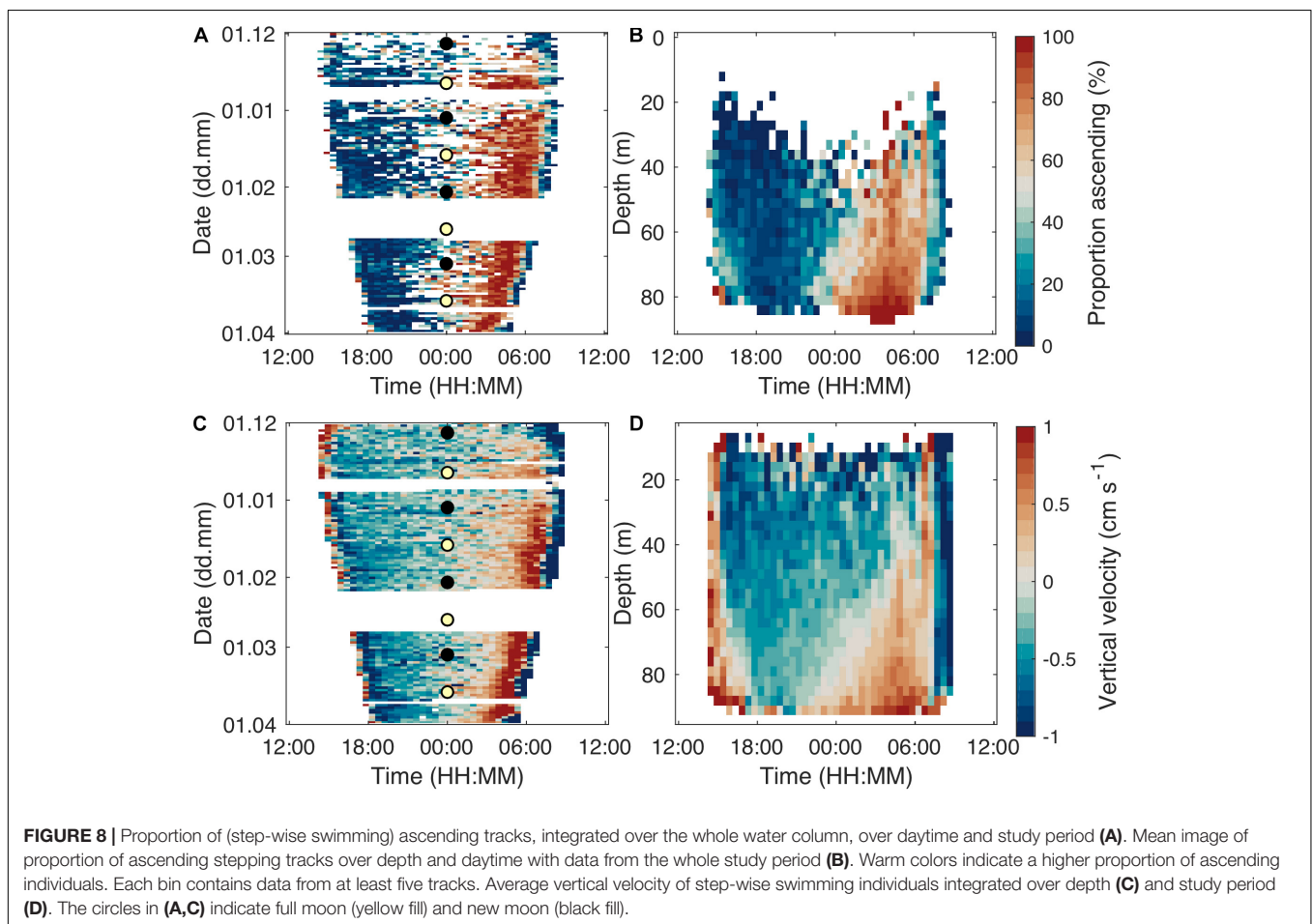
Staby et al., 2012; Prihartato et al., 2015) that was also confirmed by trawling at the initiation and termination of our campaign (own unpublished results). **Figure 9** summarizes the typical population movement and the dominant individual swimming patterns of the juvenile *M. muelleri* population in Masfjorden during the winter of 2010/2011.

Also earlier short-term acoustic studies have revealed step-wise swimming in individual mesopelagic fish and preliminarily assigned the behavior to *M. muelleri* and *B. glaciale* (Torgersen, 2001; Kaartvedt et al., 2008). Our study using hundreds of thousands of tracks from a period of 4 months shows that *M. muelleri* juveniles consistently swim step-wise when changing depth at night. The dominance of step-wise swimming during the dusk descent – roughly mirroring the dawn ascent – indicates that midnight sinking is not "sinking," but rather encompasses active behavior in *M. muelleri*. The fishes may have been slightly negatively buoyant during the descent as secretion of gas into the swim bladder takes time (Strand et al., 2005), and juveniles often seemed to slowly sink during pauses of their step-wise descent (average 0.25 cm s^{-1}; preliminary results). Nevertheless, swimming speeds during active relocation were almost 10-fold higher.

To what extent midnight sinking represents sinking or an active behavior is often unknown (Pearre, 2003). The consistent active choice of deeper night-time distribution by *M. muelleri* underscores the biological significance of such behavior. Some visual predators are capable of nocturnal feeding also in low light levels (Ryer and Olla, 1999; Kaartvedt et al., 2019). This includes gadoids, which are main predators of *M. muelleri* in Masfjorden (Giske et al., 1990; Staby, 2010), and which indeed migrate to surface waters during winter nights (Staby, 2010).

FIGURE 7 | Proportion of different swimming patterns in relation to the start of the dusk descent (beginning of midnight sinking; **A**) and the end of the dawn ascent (end of midnight sinking; **B**). Blue (descending) and blue hatched (ascending) bars indicate staircasing behavior, yellow bars stationary swimming and purple bars direct ascent/descent behavior.

The predator distribution indicates that deeper would be safer. It also suggests that descending in a step-wise pattern may reflect some anti-predatory behavior (see below). Although the increase of the population's night-time depth over winter could agree with a deepening of the temperature maximum in Masfjorden (c.f. Prihartato et al., 2015), the continuous relocation of individuals throughout the night indicates no particular temperature preference. This suggests that other factors than growth optimization in warmer temperatures (Wurtsbaugh and Neverman, 1988; Giske and Aksnes, 1992; Staby et al., 2011; Prihartato et al., 2015), play a role for nocturnal descent in *M. muelleri*.
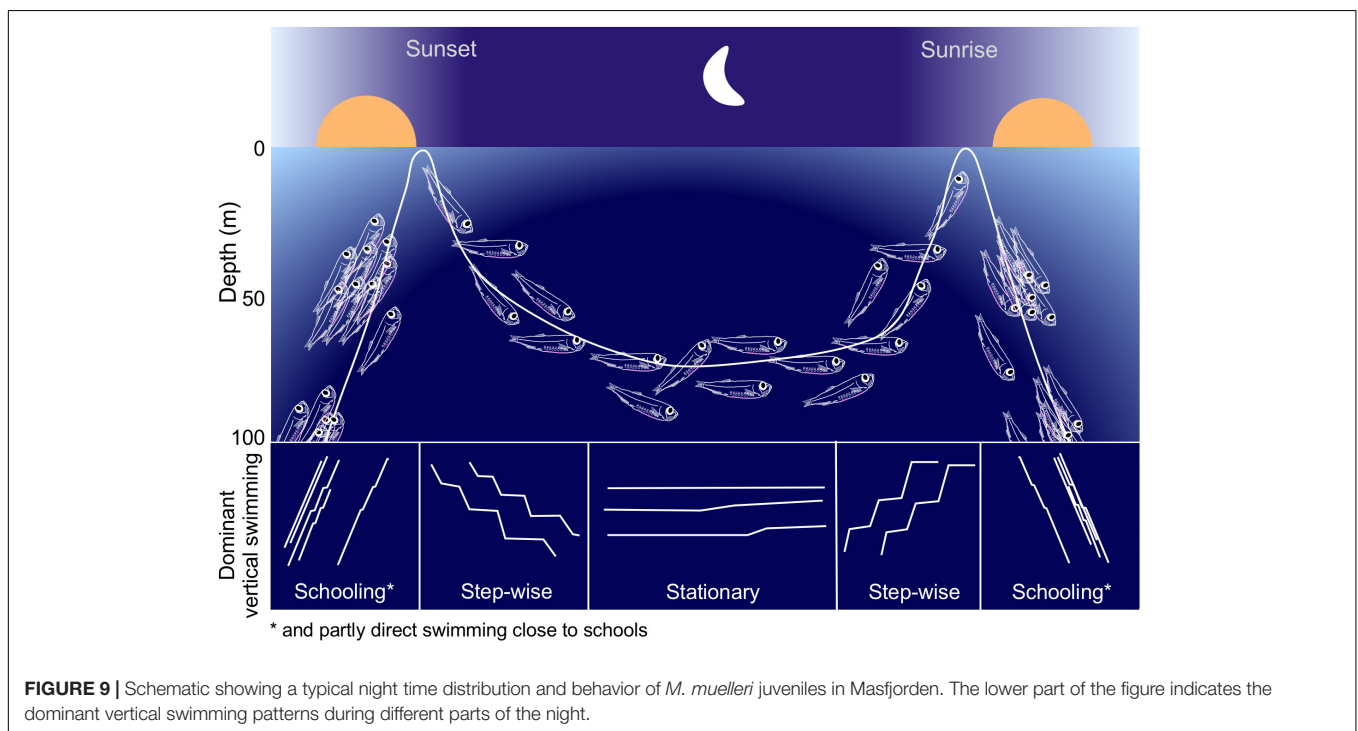
FIGURE 8 | Proportion of (step-wise swimming) ascending tracks, integrated over the whole water column, over daytime and study period **(A)**. Mean image of proportion of ascending stepping tracks over depth and daytime with data from the whole study period **(B)**. Warm colors indicate a higher proportion of ascending individuals. Each bin contains data from at least five tracks. Average vertical velocity of step-wise swimming individuals integrated over depth **(C)** and study period **(D)**. The circles in **(A,C)** indicate full moon (yellow fill) and new moon (black fill).

After the dusk descent and through most of the night, the majority of the fish appeared to be neutrally buoyant, remaining relatively stationary, with short vertical relocations intermitted by long pauses. Such behavior may both save energy (Videler and Weihs, 1982; Torgersen, 2001) and reduce conspicuousness (O'Brien et al., 1990). Nevertheless, there was a small percentage of relocating individuals at all times, which is also reflected in the scattering layer not reaching a constant depth at night. It is intriguing that the shift from predominantly downward to upward swimming on most days took place many hours before dawn during the long winter nights (cf. **Figures 4**, **8**; Staby et al., 2011). This suggests that internal processes, e.g., an internal clock determine the start of the ascent (Cohen and Forward, 2005; Sloman et al., 2005; Tosches et al., 2014; Häfker et al., 2017), while only the speed of the ascent is regulated by the change in light hours later.

The dawn ascent was usually faster than the dusk descent, both on population and individual levels. Although reflecting apparently similar behavior, dusk descent and dawn ascent occur under vitally different environmental conditions. During the dusk descent, the fish swim into darkening water after light levels at the surface have become too low for foraging (de Busserolles et al., 2017), so that the fish merely retreat to more favorable conditions to spend the hours of darkness. In contrast, the

step-wise swimming toward increasing light during the dawn ascent initiates a foraging period.

The step-wise behavior observed for both situations, i.e., with and without foraging, contrasts suggestions that stepwise relocation in mesopelagic fish represents saltatory search for prey (Kaartvedt et al., 2008). The similar behavior at descent and ascent is probably also unrelated to swim-bladder adjustment (Mehner, 2006; Fujino et al., 2009), as filling the swim-bladder during descent is a considerably slower process than emptying it during ascent (ascent; Strand et al., 2005). Also, some individuals at the fringes of the schools swam without stepping, i.e., without apparent need for swim-bladder adjustment. Being relatively safe in the vicinity of a school of conspecifics may elicit a different swimming behavior than when swimming solitary, in concordance with a hypothesis of predator-avoidance by step-wise swimming (O'Brien et al., 1990).

Motility represents a balance between maximizing encounter with prey and mates and minimizing encounter with predators. The probability of detection by a predator is higher when moving (O'Brien et al., 1990), and the pauses during step-wise swimming can reduce detection by both visual (De Robertis, 2003; Kaartvedt et al., 2008) and tactile predators (Sørnes and Aksnes, 2004). Moreover, for *M. muelleri,* the intermittent stepping behavior may minimize periods of reduced protection associated with

FIGURE 9 | Schematic showing a typical night time distribution and behavior of *M. muelleri* juveniles in Masfjorden. The lower part of the figure indicates the dominant vertical swimming patterns during different parts of the night.

change in tilt. The pearlside is particularly well equipped with ventral photophores for counter illumination (Cavallaro et al., 2004), which are less effective at tilted angles, i.e., when moving vertically (Janssen and Harbison, 1986).

Individual behavior generally, but not always, concurred with the behavior of the scattering layer. For example, at times of fast, continuous scattering layer movements, we also recorded a high proportion of step-wise swimming. Similarly, mostly stationary fish made up the very slow population movements in the middle of the night. On the other hand, we demonstrate that actual swimming speeds during relocations cannot be inferred from the average population movement. Active swimming speeds reached about 1 body length s^{-1} (assuming a body length of about 2.6 cm; Goodson et al., 1995), while scattering layer and individual net velocities always remained well below this value. This may have implications for understanding the energetics of these fish (Giske and Aksnes, 1992; Staby et al., 2012), as energetic costs typically assume a non-linear dependency on speed (e.g., McKenzie, 2011), and energetic models often assume a speed of 1 body length s^{-1} (Staby et al., 2012). Furthermore, there were always individuals swimming in opposite direction to that of the main population, documenting a more diverse behavioral repertoire than that expressed by the main population results.

While the population behavior by necessity results from the cumulative of the individual behaviors, we document that it is not possible to infer individual behavior from the behavior of the average population. We observed intraspecific variability in swimming behavior, both on population level, e.g., in migration timing, and on individual level, e.g., vertical directionality and swimming pattern. Probably, variability in population behavior

may best be explained by external factors generating reliable large-scale interpretable signals, as for example light conditions (Prihartato et al., 2015). Water column light levels depend strongly on weather and mesopelagic fish react directly to e.g., darkening caused by rainfall (Kaartvedt et al., 2017) or to moon light (Last et al., 2016; Prihartato et al., 2016). Moon light may deepen night time scattering layer depths (Prihartato et al., 2016) and delay vertical migrations. However, in the typically cloudy and rainy Western Norway and Masfjorden, clear full moon nights are rare, suggesting limited if any influence of moonlight on the behavioral variability in our study (s.a. **Supplementary Figure S5**).

The behavioral options of each individual are manifold, and reflect responses to a whole suite of more local sensory cues, e.g., from predators, prey and conspecifics, and behavior obviously also depends on individual state (Pearre, 2003; Sih et al., 2015). The observed variability in individual behavior suggests that although the vertical migration in *M. muelleri* is generally synchronized, the fishes may behave independent of the group. Whether these differently behaving individuals differ in size, metabolic demands or are otherwise distinguishable from the rest of the population remains unknown for now.

While we can still only speculate about why mesopelagic fish behave as they do, our study documents the feasibility of using a submerged, stationary echosounder in unveiling the individual behavior responsible for the large scale, more easily observed, scattering layer movements of mesopelagic fish. We demonstrate that midnight sinking is not sinking, but an active behavior. The behavioral repertoire of these fish changes not only during the crepuscular migrations, but also during the night at large, with consistent patterns throughout the winter, and

with variations between the individuals within the population. Only with an increased understanding of what these fish actually do can we begin to estimate the ecological interactions involving the enormous amounts of small mesopelagic fish in the world's oceans.

DATA AVAILABILITY STATEMENT

All data supporting the conclusion of this manuscript will be made available upon request, to any qualified researcher.

ETHICS STATEMENT

The acoustic studies did not involve any animal treatment, handling, or experiments. Data and results were only obtained by remote, unobtrusive observation.

AUTHOR CONTRIBUTIONS

SK designed the study and obtained the field data. SC organized and analyzed the data and wrote the manuscript. JT and SK contributed to the improvement of the analysis and writing of the manuscript. All authors contributed to manuscript revision.

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SUPPLEMENTARY MATERIAL

The Supplementary Material for this article can be found online at: https://www.frontiersin.org/articles/10.3389/fmars.2019.00787/full#supplementary-material

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