Dancing in the (moon) light: diel vertical migration and the behaviour of krill (*Meganyctiphanes norvegica*) during midwinter and midsummer nights

Sara Jegstad Thorsby

Master thesis in Marine Biology and Limnology

60 credits

Department of Biosciences

Faculty of Mathematics and Natural Sciences

UNIVERSITY OF OSLO

April 2023

2023

Dancing in the (moon) light: diel vertical migration and the behaviour of krill (*Meganyctiphanes norvegica*) during midwinter and midsummer nights

http://www.duo.uio.no/

Print: Reprosentralen, University of Oslo

Abstract

The euphausiid *Meganyctiphanes norvegica* performs diel vertical migrations (DVMs), staying in deeper waters during the day and ascending to the shallows at night. This behaviour is interpreted as a trade-off between food availability and visual predator avoidance.

Separation between day and night is a broad simplification, as nocturnal light may vary by orders of magnitude. The aim of this study was to research the behavioural differences in DVM by *M. norvegica* during the dark winter nights and brighter summer nights, along with the effect of moonlight during midwinter. Predator avoidance in these settings were assessed. An upwards facing 200 kHz echosounder was mounted at a 100 m deep location in the inner Oslofjord, Norway. Recordings were done during full and new moon periods from winter to summer in 2021. Trawls were used to identify and measure the organisms in the scattering layer. Hydrographical and light measurements were made to supplement the acoustic data.

The individuals caught were mainly *M. norvegica*, the glass shrimp *Pasiphaea sp*. accounting for ~10% of the catch at most. The length and weight of *M. norvegica* increased significantly with depth, suggesting that larger individuals stayed deeper to avoid visual predators. Hydrographical measurements did not seem to affect the distribution of *M. norvegica*.

M. norvegica performed DVM throughout the study period, ascending and descending in relation to the timing of sunset and sunrise. The population remained at ~40-100 m during the day, depending on season and weather. At night, *M. norvegica* were generally spread throughout the water column, possibly displaying asynchronous migrations. The nocturnal illumination seemed to influence the distribution of *M. norvegica*, causing a deeper distribution by midnight sinking when more light was available on a clear, moonlit night in winter compared to a cloudy night in spring. Yet, *M. norvegica* appeared to migrate to the upper waters during the brighter summer nights. These findings suggest that small fluctuations in light affect DVM in *M. norvegica* in the Oslofjord.

Fish were present in the upper waters (~0-30 m) at night, especially during the full moon period in winter and the brighter summer nights. *M. norvegica* appeared to avoid the surface layer to an extent. During spring and summer, schooling fish dispersed into the layer of *M. norvegica* at night, remerging into schools once *M. norvegica* descended. The predator-prey relationship between *M. norvegica* and fish was suggested to be influenced by nocturnal light.

Acknowledgements

These last couple of years have been a rollercoaster for many, with both good and bad moments and memories. I was fortunate enough to be able to carry out and write this thesis on a topic I have grown very passionate about, but not without the help of many wonderful people I would like to thank.

Firstly, thank you to my amazing supervisor, Stein Kaartvedt. I came to you in the middle of the world in shutdown, and you provided me with the greatest opportunity I could imagine. Thank you for always being available, for your patience, and for sharing your extensive knowledge with me. I have grown very fond of my little krill friends over the course of the thesis, and you introducing me to the pelagic world made me eager to continue exploring this strange place. I was able to carry out fieldwork with the help of Rita Amundsen, who taught me how to sample and how to process the samples in the lab. Thank you for your guidance, I would be lost without it. A big thank you to Svenja Christiansen, who taught me everything about using an echosounder, provided me with a lot of programming help, emotional support, and impressive knowledge on all things technical that was completely foreign to me in the beginning. Thank you to the crew on board R/V Trygve Braarud for the great cruise experiences and for your help with sampling.

I also want to thank my fellow study buddies that have been there for me through this entire process. Thank you for the encouraging words, the laughs, and the tears. Even if I could not see some of you much in person these last couple of years, I'm still immensely grateful to have you all.

Thank you to my family and close ones who have always cheered me on. To my mother and father, Per and Christine, who encouraged me to push on and kept me going through the hardest of times. Finally, I want to thank my wonderful partner, Giorgio. Thank you for your unconditional emotional support, your warmth and kindness. Not to mention helping me count krill in the lab and being a helpful proof-reader. I am very grateful to have shared this experience with all of you.

Table of Contents

1. Introduction

1.1 *Meganyctiphanes norvegica*

Meganyctiphanes norvegica (Sars, 1857) is the euphausiid with the most biomass in the North Atlantic and the Mediterranean, and occurs in abundance in fjord systems (Boysen & Buchholz, 1984; Saborowski et al., 2002; Tarling et al., 2010). In the North Atlantic, *M. norvegica* is a keystone species, linking primary and secondary production to higher predators in the food web (e.g. Båmstedt & Karlson, 1998; Lass et al., 2001). *M. norvegica* is an opportunistic feeder, mostly feeding on phytoplankton. However, the euphausiid can also portray as a selective carnivore, including preying on copepods of the genus *Calanus spp.* during winter in the North Atlantic (Abrahamsen et al., 2010; Kaartvedt et al., 2002). The preferred depth of *M. norvegica* is between 100 and 500 m during the day, depending on local conditions (Mauchline, 1967; Onsrud & Kaartvedt, 1998). This makes them adaptable to the changing environment along a depth gradient and to the changing conditions from the north to the south (Lass et al., 2001).

1.2 Diel vertical migration

Diel vertical migration (DVM) is recognised as one of the largest migrations of animals on Earth, normally involving ascent to near-surface waters at dusk and descent at dawn (Hays, 2003; Mauchline, 1980). This behaviour acts as a trade-off between feeding and avoiding visual predators in the upper waters at night (Kaartvedt, 2010). The organisms partaking in DVM play an important role with carbon flux in the vertical profile of the world's oceans, impacting the biological carbon pump (Archibald et al., 2019; Klevjer et al., 2016; Longhurst & Glen Harrison, 1989).

M. norvegica along the Norwegian coast carry out DVM (Figure 1.1) (e.g. Evans & Hopkins, 1981; Kaartvedt & Svendsen, 1990; Onsrud & Kaartvedt, 1998). In the inner Oslofjord, the population of *M. norvegica* normally resides below 70 m during the day (Kaartvedt et al., 2002; Onsrud & Kaartvedt, 1998; Vestheim et al., 2014).

Fluctuations in light, temperature, oxygen, and salinity are among the environmental parameters playing a role in DVM behavioural variations (Kaartvedt, 2010). To tolerate these changes in the environment, *M. norvegica* are flexible in their DVM patterns with variations between individuals and environments (Bandara et al., 2021; Cohen & Forward, 2016; Kaartvedt, 2010).

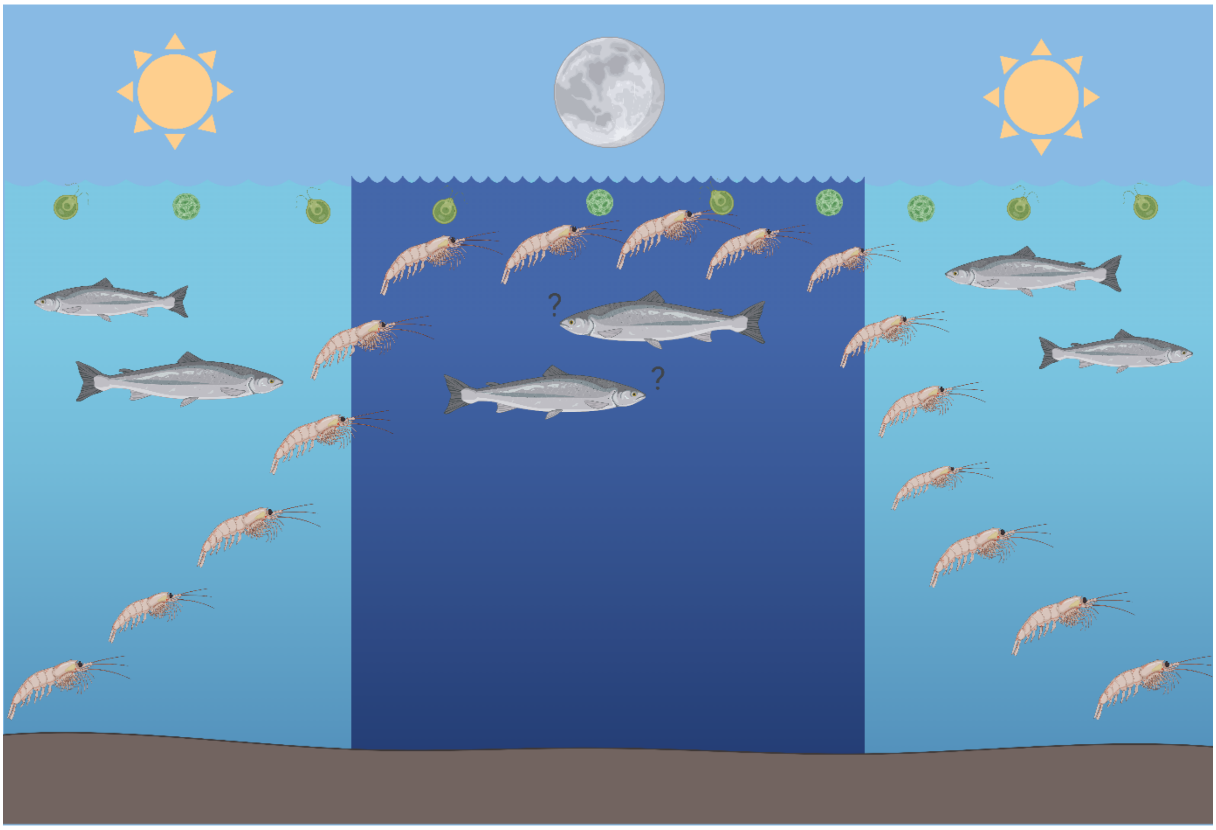

Figure 1.1. Simplified illustration of DVM by *M. norvegica*. The fish represent visual predators, and the green algae represent phytoplankton. Created with BioRender.com.

Temperature affects metabolic rates, energy consumption and growth in *M. norvegica* (Kaartvedt, 2010). It may also represent as a physical barrier for DVM to waters above ~15°C (Mauchline, 1980). However, *M. norvegica* have ascended to higher temperatures, for example in the Oslofjord (Kaartvedt et al., 2002). Therefore, this barrier is most likely not impenetrable (Kaartvedt, 2010), and migration can be halted due to other factors. For example, an adequate abundance of phytoplankton at the pycnocline slightly deeper in the water column (Andersen & Nival, 1991). Oxygen can also limit DVM, where low oxygen concentrations at depth can cause a “false bottom” (Kaartvedt, 2010). In the inner Oslofjord, low oxygen concentrations have been reported in certain, deep areas (Staalstrøm et al., 2021). Hypoxia affects the metabolism and feeding of *M. norvegica*, making them inclined to migrate to the upper waters to compensate for the lack of oxygen (Spicer et al., 1999; Torres & Childress, 1983).

The need to feed in the upper waters, risk of visual predation, hunger and satiation, and the individual's body condition such as state in the life cycle, moulting, and reproduction, all contribute to shaping migration behaviour in *M. norvegica* (Fiksen & Carlotti, 1998; Kaartvedt, 2010). Moulting *M. norvegica* do not feed, resulting in less motivation to undergo DVM. Besides, newly moulted individuals have reduced swimming capacity, making them vulnerable to predators (Kaartvedt, 2010; Thomasson et al., 2003). Asynchronous migration can occur where satiated individuals descend during the night. According to the hunger/satiation hypothesis (Pearre, 1979), the remaining hungry individuals near the surface continue feeding while satiated individuals sink towards the depths. Hungry individuals at depth can re-enter the surface during the night, which creates a wide nocturnal vertical distribution of *M. norvegica* (Sourisseau et al., 2008).

1.3 The effect of light on diel vertical migration

Light is known as the proximate cue for DVM, although which features of light that trigger migration are still being discussed (Cohen & Forward, 2016; Kaartvedt, 2010). Frank and Widder (1997) presented two potential cues that are more likely to affect DVM: a threshold of absolute light intensity, and/or a relative rate of change in light intensity. The first hypothesis describes how ascent at sunset and descent at sunrise is initiated when the light intensity decreases or increases above a threshold, respectively. For the second hypothesis, the cue for triggering DVM is the relative rate of change in light intensity near dusk and dawn (Cohen & Forward, 2016; Ringelberg, 1995). In the study by Frank and Widder (1997), the maximum rate of change in light intensity did not prompt DVM in *M. norvegica*, their results favouring the first hypothesis.

A study by Dickson (1972) found a correlation between ocean transparency and the depth of migrating organisms in the North Atlantic. With more light, the deeper the distribution of organisms. However, separating between day and night is a simplification, as both daylight and nocturnal light can vary by orders of magnitude (Kaartvedt, 2010; Mauchline, 1980). Cloud cover (Mauchline, 1969), turbidity (Frank & Widder, 2002; Kaartvedt et al., 1996), stratification (Pagés & Gili, 1991), seasonal changes (Bogorov, 1946), and urban light pollution (Moore et al., 2000) can all play a role in determining how deep light penetrates the water, affecting the depth of zooplankton distribution and visual predation (Onsrud & Kaartvedt, 1998).

Onsrud and Kaartvedt (1998) described how *M. norvegica* followed an isolume (preferred light level) during their ascent in the inner Oslofjord. According to the preferendum hypothesis, changes in the vertical distribution of isolumes are reflected in migration behaviour. This makes the organisms adapt to the increased or decreased light levels during their ascent at dusk. Light conditions can also affect the feeding behaviour of *M. norvegica*. Being a selective carnivore, *M. norvegica* can use visual predation to feed. Therefore, some light can be beneficial (Abrahamsen et al., 2010; Kaartvedt et al., 2002; Torgersen, 2001).

Seasonal changes in DVM for *M. norvegica* has been documented. Vestheim et al. (2014) observed a shallower daytime distribution of *M. norvegica* in an ice-covered Norwegian fjord. Contrasting the dark winters, bright summer nights could pose as a challenge for *M. norvegica* foraging near the surface, increasing the risk of visual predation, as seen in other migrating zooplankton (Dale & Kaartvedt, 2000; Norheim et al., 2016). However, there is a lack of studies describing the differences in migration patterns and behaviour of *M. norvegica* along with the predator-prey relationship during brighter summer nights at higher latitudes.

1.4 The effect of moonlight and moon phases on diel vertical migration

Light levels in the ocean at night can vary up to 5 orders of magnitude, compared to ~2 orders of magnitude for daylight (Kaartvedt et al., 2019). Moonlight increases exponentially with moon phases, meaning that the light from the full moon is ten times stronger than from a first or third quarter moon (Lane & Irvine, 1973; Palmer & Johnsen, 2015). Consequently, it can be assumed that moonlight affects DVM behaviour, at least to some extent.

For example, a study in the Gulf of Mexico by Ochoa et al. (2013) suggested that the ascent of zooplankton was delayed during the full moon. Last et al. (2016) found that zooplankton in the Arctic used the different moon phases to perform DVM during polar night, referred to as lunar vertical migration (LVM).

For *M. norvegica,* Tarling et al. (1999a) found a shift in vertical distribution in relation to a lunar eclipse in the Ligurian Sea. During the eclipse, *M. norvegica* reached the surface and remained there until the end of the eclipse. Before and after this occurrence, *M. norvegica* sank shortly after ascent when moonlight was present, suggesting an influence of moonlight on their nocturnal distribution (Tarling et al., 1999a).

Despite these discoveries in the Arctic and more southern parts of the world, little is known on how lunar illumination and moon phases affect *M. norvegica* in a temperate zone, such as the Oslofjord, Norway. The varying seasonal differences in moonlight intensity, especially during dark winter nights, is an interesting topic of research to further answer the questions about the uncertainty of light cues and their effects on DVM.

1.5 Predator-prey interactions

The predator-prey relationship between migrating *M. norvegica* and planktivorous fish is a fundamental aspect of DVM behaviour displayed by the species (Johnsen & Jakobsen, 1987; Onsrud & Kaartvedt, 1998). Increasing predation pressure has been documented to lead to a decrease of nocturnal ascent (Cohen & Forward, 2016; Kaartvedt, 2010). Onsrud and Kaartvedt (1998) found how *M. norvegica* had a deeper distribution at night when visual predators were abundant, some individuals even remaining at their daytime depth to hide. In such situations, it is possible that *M. norvegica* can utilise less nutritional food at depth, such as detritus, when predation pressure is high (e.g. Greene et al., 1988; Youngbluth et al., 1989).

Despite *M. norvegica* seeking shelter in the depths during the day, they are not deemed safe. Demersal fish adapted to low light conditions when hunting for prey may make *M. norvegica* vulnerable if migrating too close to the seafloor (Kaartvedt et al., 1996). A solution would be to remain in the midwaters where predation from demersal fish will be reduced, a compromise between avoiding fish from both near-surface and deeper waters (Kaartvedt, 2010; Kaartvedt et al., 2005).

Onsrud and Kaartvedt (1998) reported that schools of fish generally resided above the layer of *M. norvegica* during the day in the inner Oslofjord. Schools would appear near the surface just before dusk, then dispersing into the swarm of *M. norvegica* ascending from the depths. Once *M. norvegica* descended at dawn, they remerged into schools. The presence of demersal fish as well as pelagic fish may suggest that *M. norvegica* in shallower areas such as the inner Oslofjord are at risk of predation both from the upper waters and the depths.

1.6 Acoustic studies

Echosounders have been applied to study DVM and predator-prey interactions (e.g. Greene et al., 1992; Kaartvedt, 2010; Kaartvedt et al., 2009; Klevjer & Kaartvedt, 2003; Vestheim et al., 2014). Submerged, stationary echosounders can be programmed and left at sea, making them an unintrusive approach to *in situ* behavioural studies of pelagic organisms (Huse & Ona, 1996; Kaartvedt et al., 2009; Klevjer & Kaartvedt, 2003).

Migrating organisms may form sound scattering layers (SSLs) when detected by an echosounder (Iida et al., 1996; Sameoto, 1982). It is common to perform biological sampling along with acoustic studies to identify the acoustic targets in the SSL, for example by trawling. (Buchholz et al., 1995; Clarke & Tyler, 2008).

Many acoustic studies have been performed in fjord systems, since fjords can act as model systems for the open ocean (Christiansen, 1993; Kaartvedt, 2008; Kaartvedt et al., 2009). There are also advantages with accessibility and reduced transport costs when remaining relatively near the shore (Vestheim et al., 2014). For these reasons, various studies with echosounders have been performed on *M. norvegica* in deeper basins in the inner Oslofjord (e.g. Kaartvedt et al., 2002; Onsrud & Kaartvedt, 1998; Vestheim et al., 2014).

1.7 Aims

The main aim of this study is to increase knowledge about the effect of light on DVM by *M. norvegica*. This was done by describing behavioural differences in DVM during midwinter and midsummer nights, along with the effects of moonlight during winter. The distribution and behaviour of *M. norvegica* was studied with an upwards facing echosounder mounted at a 100 m deep research station in the inner Oslofjord. Measurements were taken during full and new moon periods from January to June in 2021. Biological and environmental sampling was performed. These methods were applied to address the following questions:

1. How does dark and bright nights affect DVM patterns and behaviour in *M. norvegica*?
2. Is there any difference in DVM behaviour during full moon and new moon/dark winter nights?
3. How is the interaction between *M. norvegica* and fish during dark and bright nights, spanning from midwinter to midsummer?

2. Materials and methods

2.1 Study area

The Oslofjord extends from the coastal waters of Skagerrak and northbound towards Oslo. It is separated by a bathymetric barrier into an inner and outer fjord (Thorsnæs, 2021). The division between these sections is defined by a 19 m deep sill near Drøbak, and along the 10 km long and 1 km wide Drøbak strait (Berge et al., 2014; Staalstrøm et al., 2021). The inside of the sill towards Oslo is known as the inner Oslofjord. Water exchange is limited in the sheltered inner fjord, especially within the deeper basins, where hypoxia can occur (Rosenberg et al., 1987).

Two main basins exist within the inner Oslofjord: The Vestfjord to the west and the Bunnefjord to the east. Both basins can reach depths of about 150 m (Askheim, 2021; Staalstrøm et al., 2021). This study was carried out in the Vestfjord, southwest of Steilene, at station Midtmeie (Figure 2.1). With a depth of 100 m and a high density of *M. norvegica* residing here (Staalstrøm et al., 2021), Midtmeie is an optimal site for acoustic and vertical migration studies.

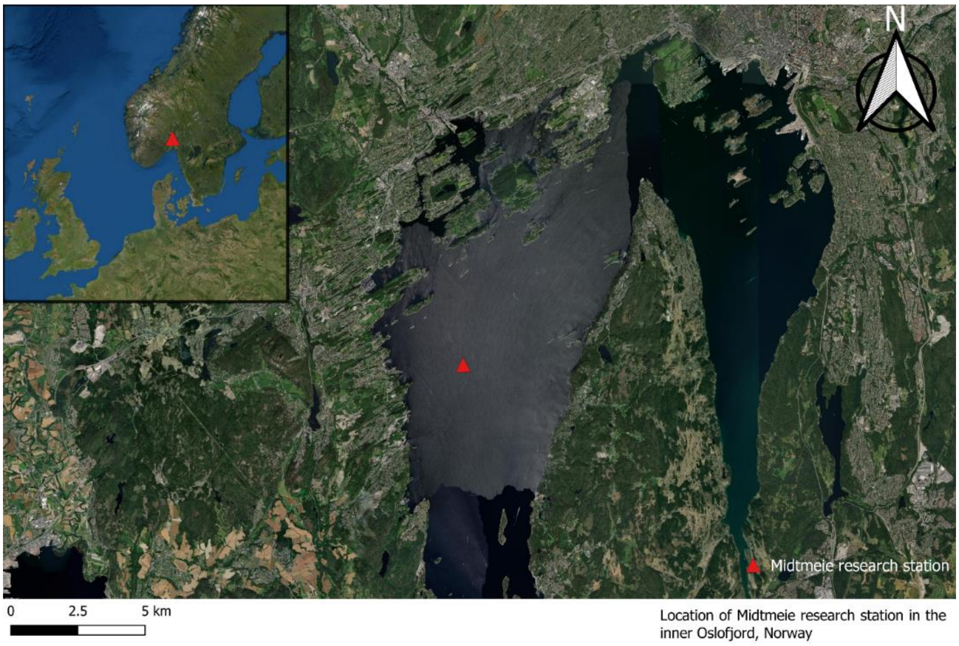

Figure 2.1. Map with satellite imaging illustrating the location of Midtmeie station in the inner Oslofjord (red triangle), with a reference map of Scandinavia attached. Created using the open-source mapping program QGIS (https://qgis.org/en/site/index.html).

2.2 Field sampling

Field sampling to supplement the acoustic data took place aboard R/V Trygve Braarud at Midtmeie station from January to June 2021. Field excursions usually lasted from the morning until the afternoon local time, with one excursion in February lasting a full day to collect samples of *M. norvegica* in the upper waters at night (Table 2.1).

Table 2.1. Overview of field sampling excursions, their duration (from arriving to leaving Midtmeie station, UTC), and the weather conditions (noted at arrival time). All dates are from 2021.

Date	Start time (UTC)	End time (UTC)	Weather conditions
19.01	08:15	13:00	Low clouds, frost, gentle winds. Air temperature: 0°C
17.02	09:00	20:00	Low clouds, snow. Some winds. Air temperature: -3°C
22.03	08:15	12:00	Sunny, passing clouds. No winds. Air temperature: 6°C
19.04	07:00	15:00	Clear and sunny, gentle winds. Air temperature: 12°C
20.05	07:15	11:45	Sunny, passing clouds. No winds. Air temperature: 13°C
15.06	07:20	12:00	Sunny, passing clouds. Some winds. Air temperature: 18°C

2.2.1 Hydrographical measurements

A Sea-Bird model SBE 9 Conductivity-Temperature-Depth (CTD) instrument (Figure 2.2) was used. The CTD instrument was also equipped with an oxygen saturation sensor and a fluorometer (Table 2.2). With a speed of 0.5 m/s, the CTD instrument collected continuous data both downwards and upwards in the water column from 0-100 m depth (Table 2.3). All recorded data were saved on an onboard computer. According to standard procedure, only the downcast profiles were used for analysing the environmental data.

The collected CTD data were uploaded to RStudio (Posit, 2022) for analysing. The data packages “oce” and “ocedata” (Kelley & Richards, 2022; Kelley et al., 2022) were used to process the files and create vertical profiles of the collected data.

Figure 2.2. Image of the Sea-Bird CTD probe (left) and Neil Brown CTD probe (right). The Neil Brown instrument was present as backup in case the Sea-Bird faulted, yet it was not used in this study.

Photo: Sara J. Thorsby (19.01. 2021)

Table 2.2. The various parameters measured along with their units and the serial numbers of the Sea-Bird CTD probes (where applicable).

Variable	Serial number probe	Unit
Conductivity	3840	psu
Temperature	5352	°C
Depth		m
Oxygen		% saturation
Fluorescence		Seapoint

Table 2.3. Date and time (UTC) of CTD measurements at Midtmeie station during the study period (2021) along with maximum depth reached.

Date	Time of measurement (UTC)	Max. depth reached (m)
19.01	08:30	100
17.02	10:24	96
22.03	08:34	99
19.04	07:26	97
20.05	07:27	98
15.06	07:30	97

2.2.2 Light measurements

Vertical light extinction was measured using a Li-Cor underwater quantum sensor (LI-COR, 2022) (Figure 2.3). The sensor measures PAR (Photosynthetically Active Radiation), with cosine corrected measurements expressed as PPFD (Photosynthetic Photon Flux Density, µmol photons m^{-2} s^{-1}). The sensor is sensitive to light from 400 to 700 nm.

Figure 2.3. Illustration of setup during light intensity measuring. Two light meters were used: one for the underwater quantum sensor (left) and the other for the quantum sensor on deck (right). Average measurements for each depth interval were recorded from each light meter.

Photo: Sara J. Thorsby (22.03 2021)

Average light measurements were taken from the surface (0 m) and recorded every meter until 12 m. Then, the interval between measurements changed to every other meter (12, 14, 16 m…) until 22-26 m, due to cable length limits (Table 2.4). Surface light was recorded with a sensor placed on deck. This was done to account for possible variations due to weather conditions. This measurement was not used during the field excursion in May due to constant readings from clear skies. Light measurements were not done during the night, as the instrument was not sensitive enough to record moonlight.

Measurements were processed in RStudio and analysed using base R functions (R Core Team, 2022). The light intensity data were adapted to a log-scale where a percentage of light attenuation was calculated (100% at surface).

Table 2.4. Date, time (UTC), start and end depth (m) of the Li-Cor underwater quantum sensor measurements, along with measurement intervals, for each field excursion at Midtmeie in 2021.

Date	Time of day (UTC)	Start depth (m)	End depth (m)	Interval 1 (0-12 m	Interval 2 (12-22 m)
19.01	09:20-09:40	0	24	1 m	2 m
17.02	09:50-10:10	0	22	1 m	2 m
22.03	09:35-09:43	0	22	1 m	2 m
19.04	09:15-09:35	0	26	1 m	2 m
20.05	08:23-08:39	0	22	1 m	2 m
15.06	08:24-08:36	0	22	1 m	2 m

2.2.3 Isaac-Kidd Midwater Trawl

R/V Trygve Braarud was equipped with a Simrad EK500 echosounder. This echosounder was used to determine the depth of the sound scattering layer (SSL) before and during sampling with the Isaac-Kidd Midwater Trawl (IKMT). The echosounder logged at two different frequencies: 38 kHz and 120 kHz. The first frequency was too low to effectively record smaller organisms such as *M. norvegica* and other plankton, yet it can record the presence of fish. 120 kHz was therefore the appropriate frequency to detect *M. norvegica*.

The 120 kHz frequency showed a clear SSL with somewhat varying depths during the day (extending from ~50-100 m depth). This layer was not visible on 38 kHz (Figure 2.4). The IKMT's were performed to identify the organisms in this layer, to confirm the presence of *M. norvegica*, and to detect other potential acoustic targets.

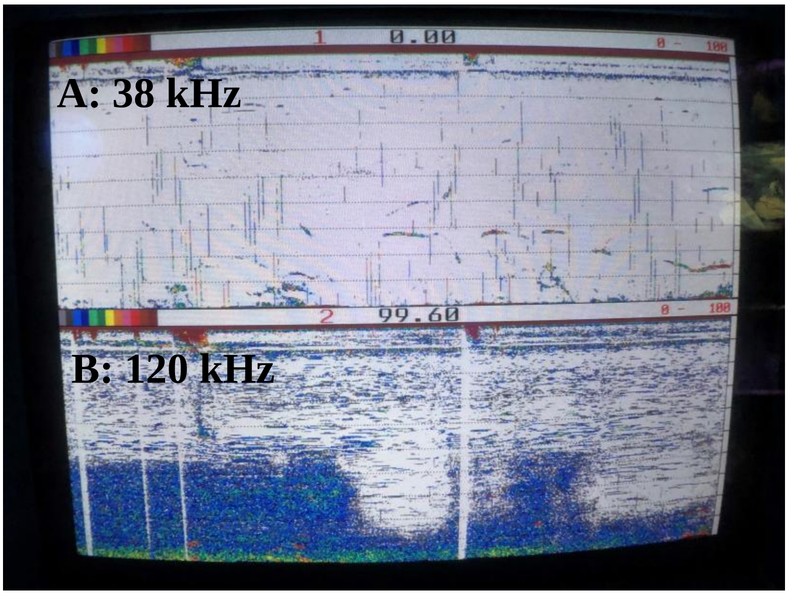

Figure 2.4. Echograms from Simrad EK500 aboard R/V Trygve Braarud during a field excursion. The echosounder ranged from 0-100 m. **A**: 38 kHz. The SSL is not visible. **B**: 120 kHz. The SSL is found from ~60 m on this day. The voids in the SSL were caused by avoidance from an approaching ROV with lights turned on.

Photo: Sara J. Thorsby (10.01 2022)

Three different depth intervals were planned for day sampling: 70, 80 and 90 m to sample the upper, middle, and lower part of the SSL. Adjusted sample depths were chosen based on the location of SSL in the water column on the EK500. Trawling took place along a specific transect (from north to south, then south to north, Table 2.5). The vessel travelled at a constant speed of 3 knots. Each sampling was planned to last ~15 minutes (Table 2.6). During the field excursion in February, IKMT sampling were performed at night in the upper waters in addition to day sampling.

During the night trawl, the lights from the research vessel could affect trawl catches since *M. norvegica* is sensitive to light. To avoid this possibility, the lights were turned off after the first haul and for the remainder of the excursion.

Table 2.5. General Midtmeie IKMT transect coordinates. The coordinates could vary slightly from each sample.

Midtmeie N	Midtmeie S
59°48.937'N, 10°32.986'E	59°47.966'N, 10°31.877'E

Table 2.6. Overview of IKMT trawl dates (2021), times (start and stop, UTC), durations (min), transects, depths (m), and speeds (knots). N = night trawl.

Date	Trawl no.	Start (UTC)	Stop (UTC)	Duration (min)	Transect	Depth start (m)	Depth stop (m)	Speed (knots)
19.01	1	10:20	10:35	15	Midtmeie N-S	72	72	3
	2	10:55	11:10	15	Midtmeie S-N	82	80	3
	3	11:32	11:47	15	Midtmeie N-S	92	90	3
	4	12:10	12:25	15	Midtmeie S-N	52	52	3
17.02	1	11:48	12:03	15	Midtmeie N-S	67	70	3
	2	12:28	12:43	15	Midtmeie S-N	87	90	3
	3	13:04	13:22	18	Midtmeie N-S	79	80	3
17.02N	1	17:57	18:11	14	Midtmeie N-S	17	14	3
	2	18:38	18:50	12	Midtmeie S-N	30	30	3
	3	19:18	19:38	20	Midtmeie N-S	50	50	3
22.03	1	10:07	10:22	15	Midtmeie N-S	71	69	3
	2	10:42	10:58	16	Midtmeie S-N	80	81	3
	3	11:21	11:36	15	Midtmeie N-S	87	90	3
20.05	1	09:39	09:54	15	Midtmeie N-S	68	72	3
	2	10:20	10:36	16	Midtmeie S-N	89	91	3
	3	11:02	11:17	15	Midtmeie N-S	79	81	3
15.06	1	09:15	09:30	15	Midtmeie N-S	61	63	3
	2	09:55	10:10	15	Midtmeie S-N	68	72	3
	3	10:27	10:44	17	Midtmeie N-S	82	84	3
	4	11:05	11:25	15	Midtmeie S-N	87	92	3

The IKMT consisted of a net with coarse mesh sizes in the front and 500 µm mesh size towards the end (Figure 2.5 A). A 500 mL bucket was attached to the end of the net to collect the biological samples (Figure 2.5 B). To monitor the depth, a Scanmar sensor was attached to the equipment. After retrieving the trawl, the sample was transferred to a container for sorting (Figure 2.5 C, D). The samples mostly contained *M. norvegica* and some *Pasiphaea* Savigny (1816) (glass shrimp). If the sample was large, a subsample of 200 mL was collected, and the volume of the total catch was noted. All *Pasiphaea sp.* from the sample were counted and collected before the subsample was measured. *M. norvegica* and *Pasiphaea sp.* were separated into plastic zip bags with information of quantity and/or volume noted and stored in a freezer aboard the research vessel. After the excursion, the samples were transported to the university for future analyses. Details of *M. norvegica* length and weight measurements from the IKMT trawls can be found in Appendix A.

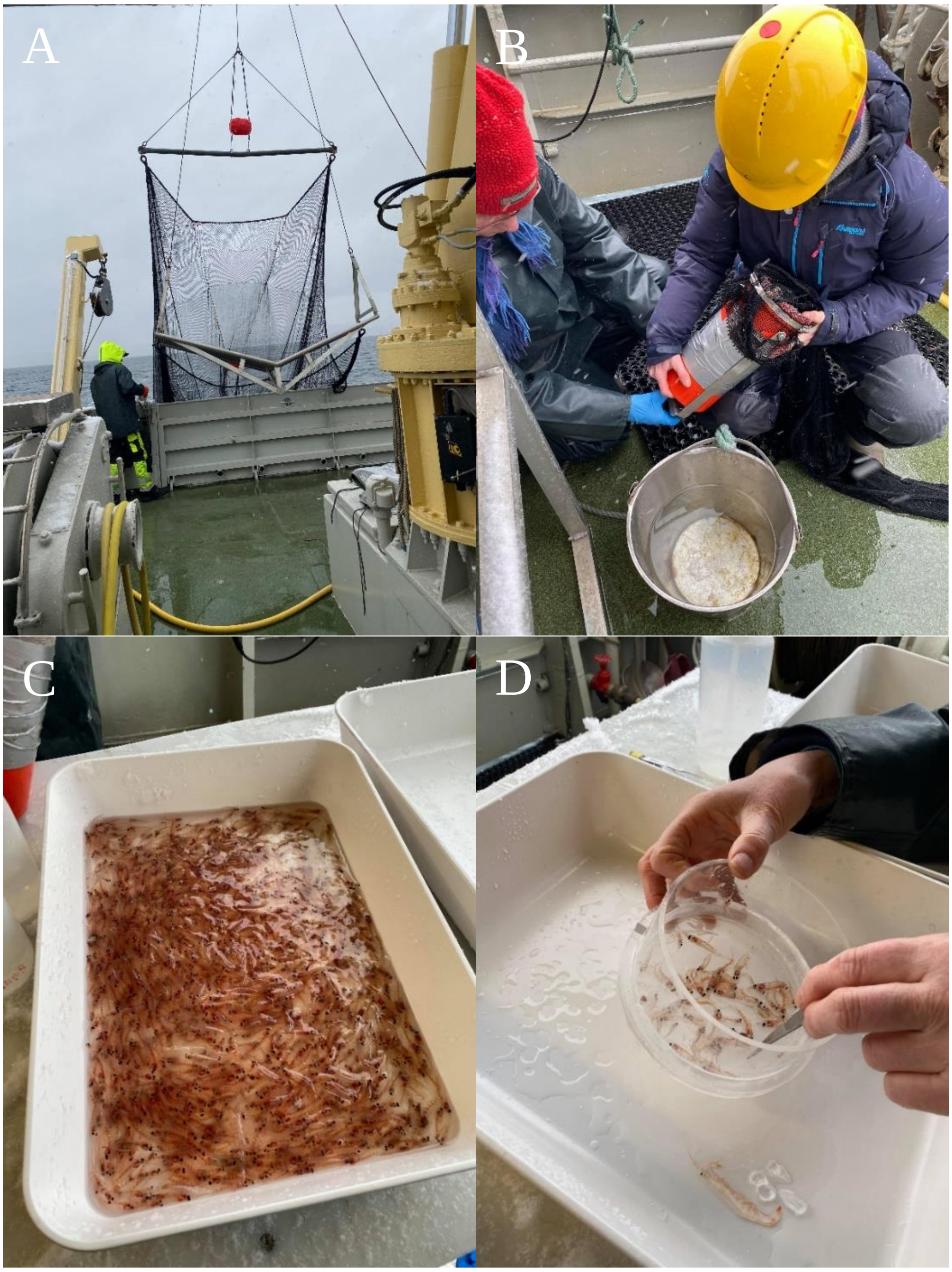

Figure 2.5. A: IKMT retrieved after sampling. Note the depth sensor attached (red brick). **B**: 500 mL bucket at the end of the IKMT with the biological sample. **C**: The catch after sampling with IKMT. Notice the dominance of *M. norvegica*. **D**: Sorting the biological sample. Note the jellyfish and the individual of *Pasiphaea sp*.

Photos: Sara J. Thorsby (17. 02 2021)

2.3 Acoustic data collection

A Simrad WBAT (Simrad Wideband Autonomous Transceiver) was used to obtain information on the acoustic layer at Midtmeie station. The WBAT had been calibrated at the surface using a 38.1 mm tungsten carbide standard sphere as described in Foote et al. (1987).

A 200kHz split-beam transducer (ES200-7CD, serial number 121) (Kongsberg maritime Simrad, (n.d.)) was attached to the WBAT mounted in a weighted rig (Figure 2.6). The rig was deployed and placed on the seafloor (~100 m depth) with a pre-programmed mission plan. The location of the rig was noted. (Table 2.7). The rig was retrieved after every mission using an acoustic release. The mission plans are summarized in Table 2.8.

Figure 2.6. Image of WBAT seafloor rig during deployment. Consists of a crate with weights attached, the transceiver (yellow tube) and transducer (orange cap).

Photo: Sara J. Thorsby (18.02 2021)

The ping interval of the transducer varied for this study (between 0.35 and 0.55 s), and the pulse duration was set to 128 µs with a Continuous Wave (CW) pulse form (Table 2.7).

Data was stored on a USB flash drive. Upon retrieval, the raw data was transferred to a computer or a hard drive for further storage before the flash drive was emptied and reattached to the WBAT for the next deployment. Data format was the standardised Simrad EK80 raw data format.

In certain logging periods (April and late June), the Simrad WBAT was mounted in a floating rig that was placed at 62 and 38 m depth, respectively. This was done to get better imagery of the upper waters due to the resolution of the acoustic data being reduced with distance from the transducer (Kaartvedt, 2010) (Figure 2.7).

The Simrad WBAT was set to log data from winter to summer, focusing on full and new moon periods. January and February will hereby also be referred to as winter, March and April as spring, and May and June as summer. The setup was biased toward more records at full (4) rather than new (2) moon phases to increase the chances of logging during the combination of full moon and clear nights.

To be able to research the effects of moonlight on DVM behaviour as well as predator-prey interactions, it was essential that the weather at night was clear. Table 2.9 summarises the weather conditions for the different full and new moon days in this study.

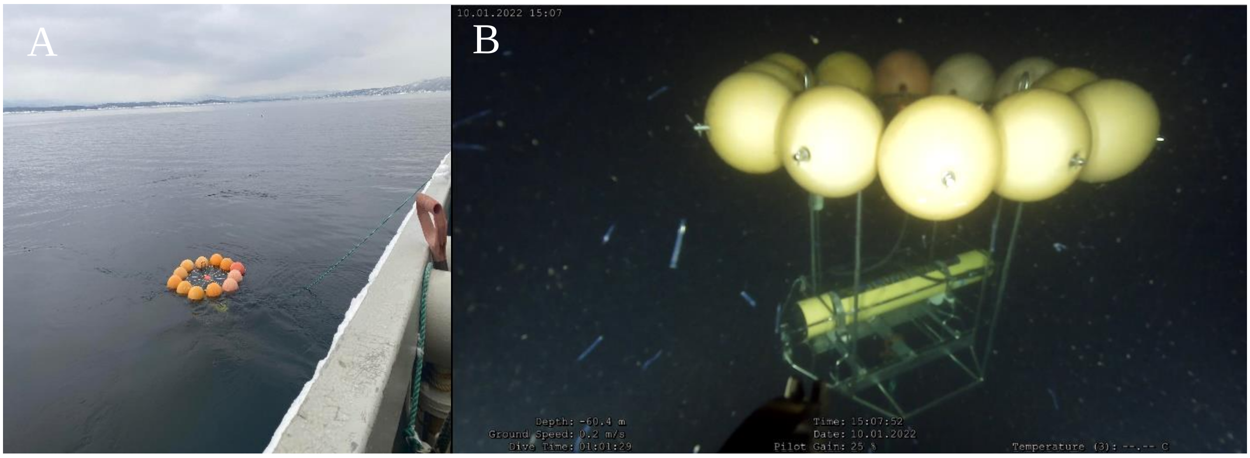

Figure 2.7. A: Image of WBAT midwater rig during deployment. The transducer was placed in the middle of the buoys. **B**: Image from ROV footage of the WBAT midwater rig. Chaetognaths were attracted to the light from the ROV.

Table 2.7. Position of deployment, depth of rig after deployment (m), pulse duration (μs), ping interval (s), range (m), and pulse form of WBAT for each deployment date (2021) in the study period.

Date	**Position WBAT rig**	**Depth (m)**	**Pulse duration (μs)**	**Ping interval (s)**	**Range (m)**	**Pulse form**
12.01	59°48.533’N 010°32.274’E	100	128	0.55	100	CW
18.02	59°48.533’N 010°32.274’E	100	128	0.55	100	CW
16.04	59°48.534’N 010°32.275’E	62	128	0.35	50	CW
19.05	59°48.541’N 010°32.305’E	100	128	0.55	105	CW
16.06	59°48.542’N 010°32.316’E	38	128	0.45	65	CW

Table 2.8. Overview of the WBAT mission plans (2021) with phases, start and stop date and times (UTC) for the different recordings, event duration (h), the amount of data logged (Gb) and battery used (Ah).

Date of deployment	Phase no.	Start (date, time)	Stop (date, time)	Event duration (h)	Data used (Gb)	Battery used (Ah)	Comments
21.01	0	21.01 17:00	23.01 11:00	42	300	86.4	
	1	26.01 00:00	30.01 11:00	107			
	2	09.02 00:00	12.02 11:00	83			
	3	16.02 00:00	18.02 08:00	56			
18.02	1	22.03 00:00	31.03 00:00	216	321	93.9	
16.04	0	16.04 14:00	20.04 07:00	88	66	26.4	In floating rig
20.05	0	23.05 11:00	28.05 11:00	120	239	72	
	1	08.06 11:00	13.06 11:00	120			
16.06	0	20.06 11:00	25.06 11:00	120	91	36	In floating rig

Table 2.9. Overview of full and new moon days, moonrise and moonset times (UTC), time of moon phase (UTC), and weather conditions during the study period (2021). The data is recorded from Oslo. All data is fetched from the website timeanddate.com (Time and Date, 2022).

Date	Moonrise	Moonset	Moonrise	Moon phase	Time of moon phase	Weather
28.01	-	08:16	14:24	Full	19:16	Passing clouds Wind: avg. 3 km/h Hi/lo temp: -10/-17°C
11.02	07:49	15:04	-	New	19:05	Clear Wind: avg. 10 km/h Hi/lo temp: -8/-18°C
28.03	-	05:30	17:18	Full	19:48	Partly clear, light rain Wind: avg. 17 km/h Hi/lo temp: 6/-3°C
26.05	-	02:24	20:39	Full	10:13	Passing clouds Wind: avg. 20 km/h Hi/lo temp: 15/4°C
10.06	01:50	21:04	-	New	10:52	Clear Wind: avg. 15 km/h Hi/lo temp: 24/12°C
24.06	-	01:07	21:10	Full	18:39	Passing clouds Wind: avg. 15 km/h Hi/lo temp: 22/11°

2.4 Laboratory procedures

All the collected samples and subsamples of *M. norvegica* and *Pasiphaea sp.* from field excursions were analysed in the laboratory. A total of 50 *M. norvegica* and 50 *Pasiphaea sp.* were randomly selected for length and wet weight measurements from each sample or subsample. If there were less individuals in the sample, all were processed. The length measurements were performed following the methods for processing zooplankton from Hassel et al. (2013). The selected specimens were fully stretched out on a piece of laminated millimetre paper (Figure 2.8 A1, B). The total length of each individual was noted, measured from the tip of the rostrum to the end of the telson on both species. Most rostrums were intact, but some individuals were missing their telson. An estimate of length was made for those individuals based on similar sized specimens. For further accuracy, a magnifying lamp with a ring light was used for closer inspection (Figure 2.8 A2). After the total length was measured and noted, each specimen was weighed on a scale with a 0.05 g accuracy (Figure 2.8 A3). The weight was noted.

In smaller, complete samples, all *M. norvegica* and *Pasiphaea sp.* were counted. The total number of individuals for each sample was noted. The weighted and measured *M. norvegica* and *Pasiphaea sp.* were added to the count (if the sample was larger than 50 individuals). In all subsamples, the total number of individuals per subsample was counted. An estimate of total individuals in the entire catch was calculated using the equation below:

$$\text{Estimate of total indivudials per catch} = \text{Total count subsample} * \frac{\text{Volume of entire sample}}{\text{Volume of subsample}}$$

Figure 2.8. **A**: Image of laboratory procedures during measurement of *M. norvegica*. (**1**) Millimetre paper for length measurements, (**2**) magnifying glass with ring light, (**3**) scale used to weigh specimens. **B**: laboratory procedures for measuring *Pasiphaea sp*. Same setup as used for *M. norvegica*.

2.5 Data analyses and processing

2.5.1 Acoustic data

The acoustic raw data from the Simrad WBAT was converted, a procedure required to analyse the data using the software Sonar5-Pro. During conversion, the calibration parameters from the WBAT were entered in the program (version 606.22). This program allows for reading of acoustic data, where both an Amp (Vertical Amplitude) echogram and a SED (Single Echo Detection) echogram can be analysed (Balk, 2019). For population studies in this study, only Amp echograms were used. A sound scattering layer (SSL) could be observed in the program which illustrated the behavioural patterns of migrating zooplankton. Since by far most organisms in this acoustic layer consisted of *M. norvegica* (see results), the SSL will hereby also be referred to as *M. norvegica*. For better visualisation, the files (each usually containing a few minutes of logged data) were merged into 24-hour echograms (from noon to noon). S_v

(volume backscattering strength) thresholds for analysing *M. norvegica* were usually set between -95 to -55 dB, whereas for fish the threshold was increased from -70 to -35 dB (with some variations for better visualisation). Ascent and descent times of *M. norvegica* were visually assessed, based on when the majority of the population appeared to begin and end the ascent/descent judging by the steeper slope of the SSL.

RStudio was used to create more visually appealing echograms, based on the raw data from the Simrad WBAT. The data was gridded and compressed to be processed in R through a script made by researcher Svenja Christiansen.

2.5.2 Weather and solar/lunar data

Information about moon phases, daylength and weather was retrieved from timeanddate.com (Time and Date, 2022) and compared to the respective echograms. The location was set to Oslo. Times were given in local time on the website, whereas the echo data was displayed in UTC. In this study, all times were converted from local time to UTC for simplification.

2.5.3 Laboratory measurements

Illustrations of catch sizes, individual length, and individual weight were created in RStudio using base R plot functions. Statistical analyses (ANOVA and Tukey HSD post hoc tests) were performed in R on the length and weight data.

3. Results

3.1 Environmental data

3.1.1 Hydrography and *in vivo* fluorescence

Temperature

Surface temperature varied throughout the study period. The first three months (January, February & March, Figure 3.1) had a cooler surface temperature than the deeper waters. In contrast, May and June had a higher surface temperature. April's surface temperature remained similar to the depths with a slight decrease in temperature at ~10 m. Temperatures were relatively stable by depth below ~20 m, hovering around ~8°C, except in January where it was ~10°C (Figure 3.1).

Salinity

In the upper waters, the salinity was generally lower than in the deeper waters. The salinity near the surface decreased from ~27 PSU in January to ~17 PSU in June (Figure 3.1), apart from February where the salinity remained above 30 PSU in the whole water column. From ~30-40 m, the salinity increased to ~33 PSU for all measurements and remained stable throughout the remainder of the water column (Figure 3.1).

Oxygen

In January and February, the oxygen saturation in the upper waters was similar to the stable saturation in the depths (Figure 3.1). A "dip" in saturation occurred between ~10 and 40 m depth. January had two peaks of low saturation: one at 10 m (~30%) and one at ~40 m (~40%). In March, April, May, and June, the saturation in the upper waters was higher than the saturation in the depths. The stable saturation in the lower water column was quite similar between all measurements, ranging from ~60-80%. Some oversaturation (over 100%) was observed in April, May, and June in the upper waters (Figure 3.1).

***In vivo* fluorescence**

The fluorescence profiles showed a decreasing trend by depth in the upper ~40 m. Some variations were detected in the upper water column, with the highest values in January and June. For all months except March, a smaller peak in Fluorescence occurred at ~20 m (Figure 3.1).

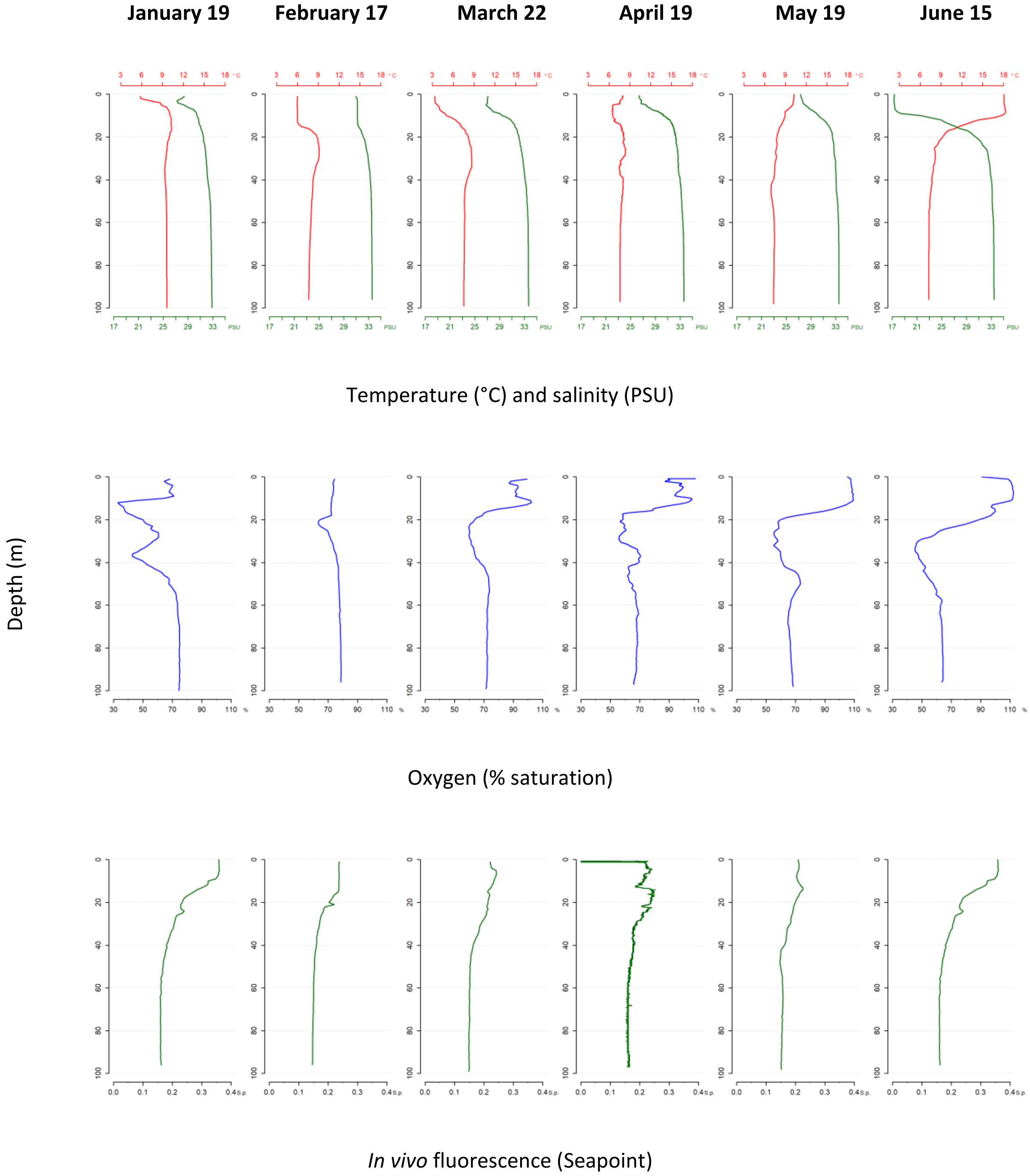

Figure 3.1. CTD profiles from Midtmeie station displaying temperature (°C, red axis) and salinity (PSU, green axis), oxygen saturation (%), and in vivo fluorescence (Seapoint) along a depth gradient (m) during the measurement period (January-June 2021).

3.1.2 Light attenuation

Throughout January to April, the light attenuation by depth remained fairly similar. For these measurements, the light gradually decreased with depth, reaching below 1% (the euphotic zone by rule of thumb) between 16 and 21 m, the deepest being in February. The attenuation was higher in May, while in June, the measurement reached 0% already at 9 m (Figure 3.2). Varying surface light or a methodological problem might have affected the June light attenuation. Therefore, the graph is capped at 10 m.

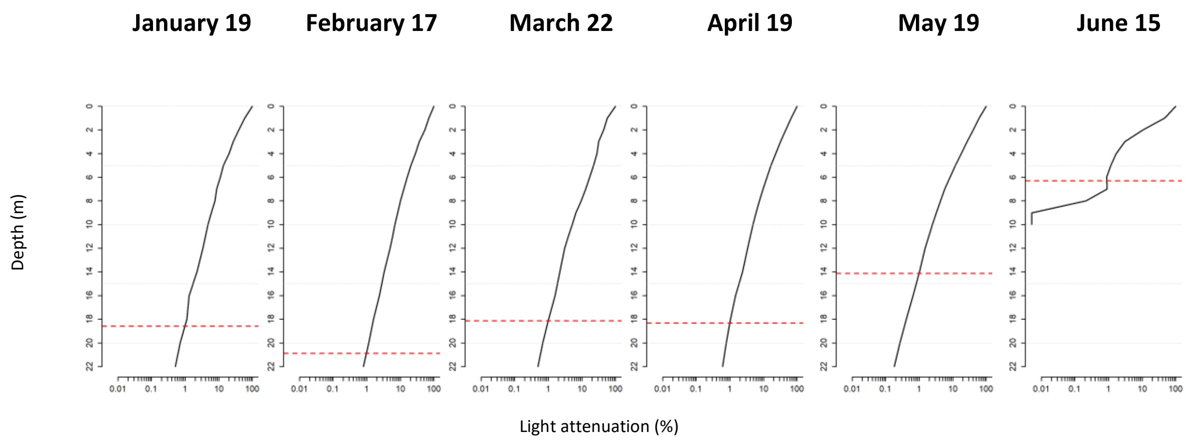

Figure 3.2. Light attenuation profiles from Midtmeie station displaying light attenuation (% of PPFD (Photosynthetic Photon Flux Density, µmol photons m^{-2} s^{-1}, 100% at surface) on a log-scale along a depth gradient (m) during the measurement period (January-June 2021). The red, dotted line represents the euphotic zone (1% light attenuation) calculated for each plot.

3.2 Biological studies

3.2.1 Total catch

Meganyctiphanes norvegica

The largest *M. norvegica* catch sizes from the daytime Isaac-Kidd Midwater Trawls (IKMTs) were at 90 m for all trawl hauls, except in February where the largest catch was at 80 m. February and March yielded the smallest catches, whereas June yielded the largest catch overall with almost 16000 individuals caught at 90 m. Few individuals were captured at 50-70 m, with the largest number in January of ~800 individuals caught (Figure 3.3).

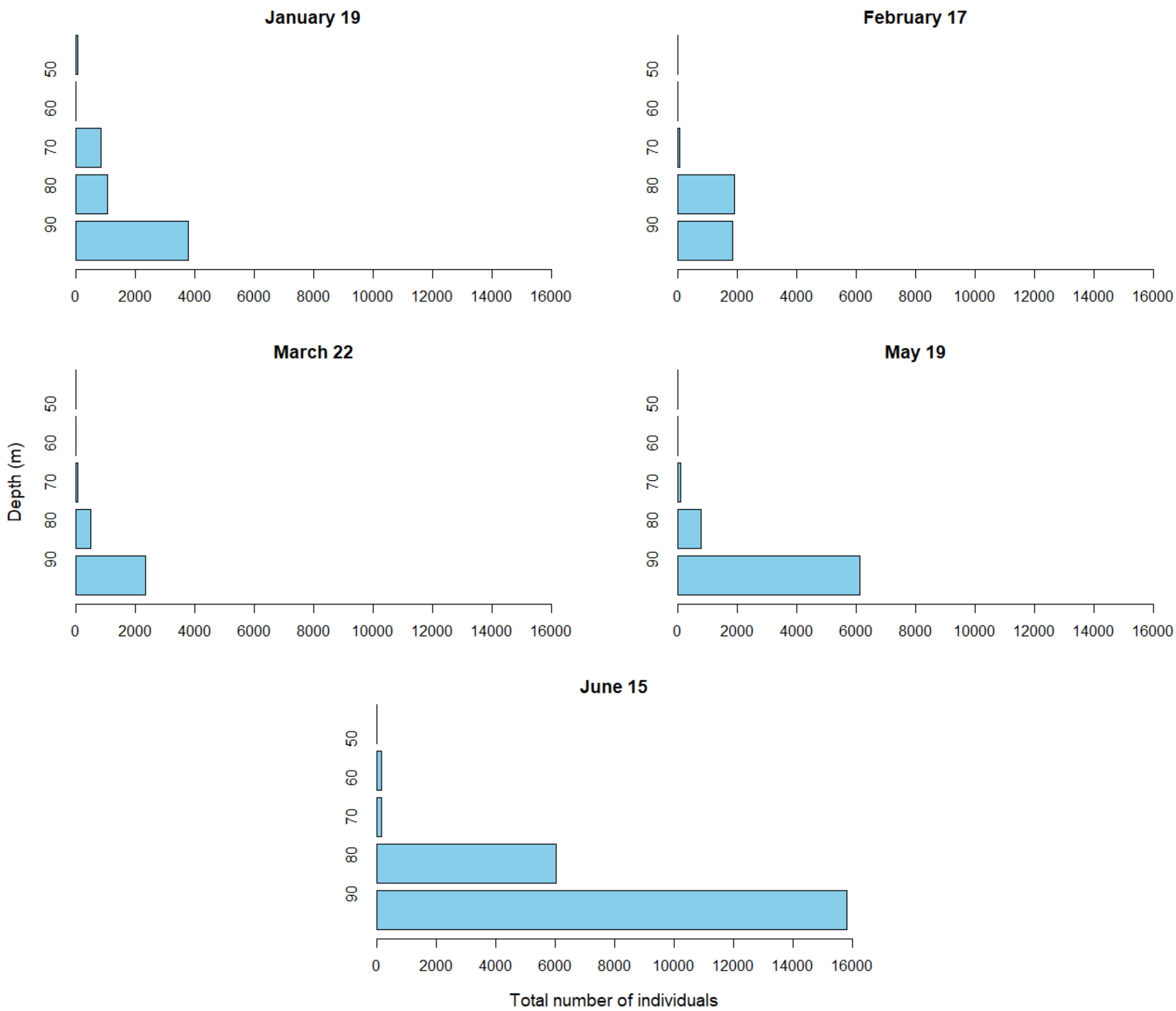

Figure 3.3. Total number of individuals of *M. norvegica* in relation to trawl depths (m) from IKMT hauls throughout the study period (2021). The data is based on counts from subsamples and total volume of each catch for each depth interval within the same month. Trawling was not performed in April.

Pasiphaea sp.

The IKMT catches also contained *Pasiphaea sp.* in addition to *M. norvegica*. The overall highest number of *Pasiphaea sp*. was in January with ~370 individuals caught at 90 m, which was ~10% of the total catch. The remainder of the catch consisted of *M. norvegica*, along with the occasional unidentified fish larvae or jellyfish. Other catches of *Pasiphaea sp.* were much smaller compared to the total number of *M. norvegica* caught. The catch sizes of *Pasiphaea sp*. decreased throughout the study period (Figure 3.4). In June, five individuals of *Pandalus borealis* were found at 90 m (data not shown).

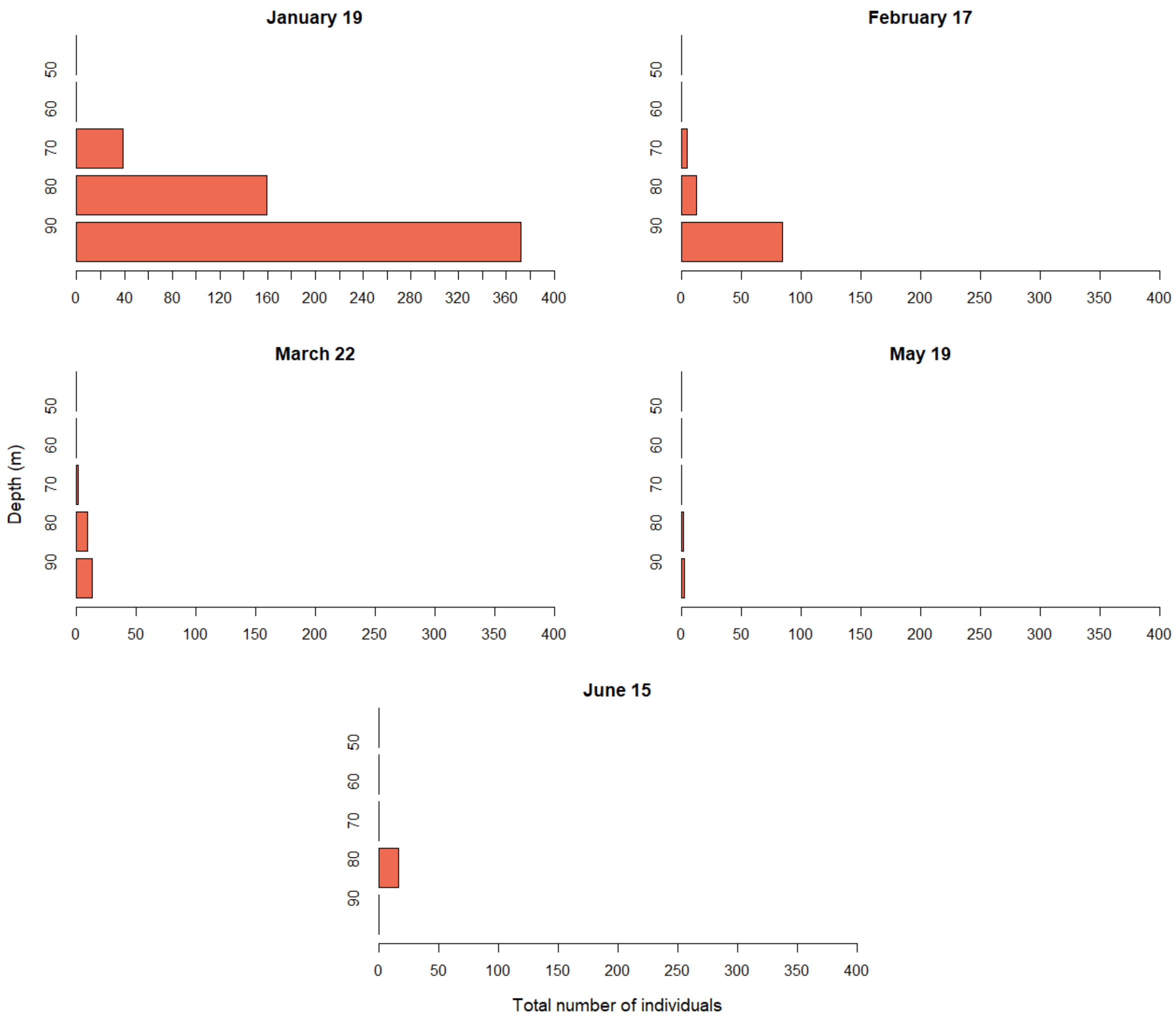

Figure 3.4. Total number of individuals of *Pasiphaea sp.* in relation to trawl depths (m) from IKMT hauls throughout the study period (2021). The data is based on counts from the total catch for each depth interval within the same month. Trawling was not performed in April. Five individuals of *P. borealis* were found in June at 90 m, data not shown.

Night trawl (17 February)

The number of *M. norvegica* caught was relatively similar from 30 m and below. Very few individuals (40) were caught at 15 m, whereas ~3500 individuals were caught at 50 m. The highest number of *Pasiphaea sp.* was caught at 50 m, about 1.6% of the total catch (Figure 3.5).

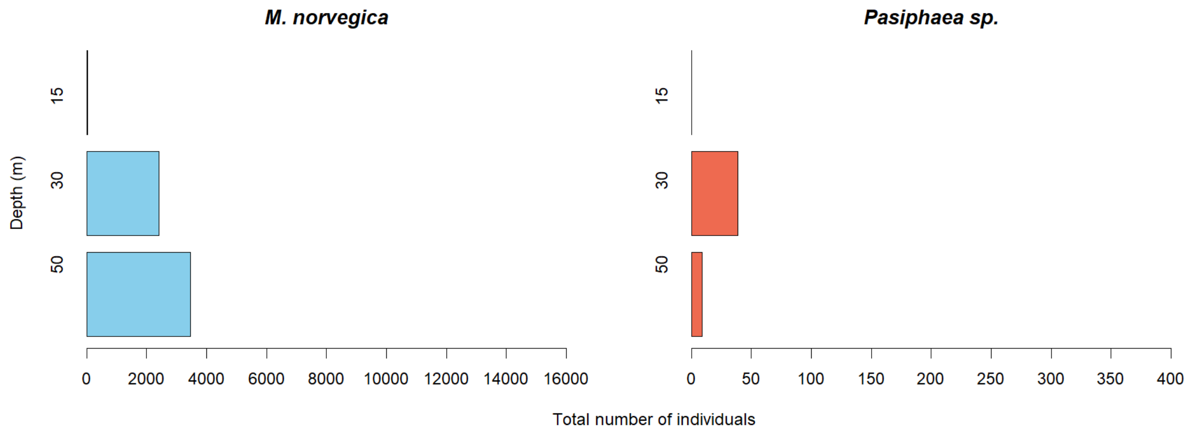

Figure 3.5. Total number of individuals of *M. norvegica* (blue) and *Pasiphaea sp.* (red) in relation to trawl depths (m) from IKMT night trawls 17 February 2021. The *M. norvegica* data is based on counts from subsamples and total volume of each catch for each depth interval. *Pasiphaea sp.* individuals were counted from the whole catch for each depth interval.

3.2.2 Length and weight distribution of *Meganyctiphanes norvegica*

The average length of *M. norvegica* during daytime ranged between 34 and 39 mm. The length increased with depth, and the largest individuals were mostly caught at 90 m. The largest variation in size range occurred at 70 m for most trawls, where individuals could span from 20-45 mm (Figure 3.6). The size distribution varied significantly by depth for all months (ANOVA: $p < 0.05$). However, there was no significant variation in length between 80 m and 90 m for all months (Tukey HSD post hoc: $p > 0.05$). There was no significant variation in length between all depth intervals in June (Tukey HSD post hoc: $p > 0.05$), except 80 m and 60 m (Tukey HSD post hoc: $p < 0.05$).

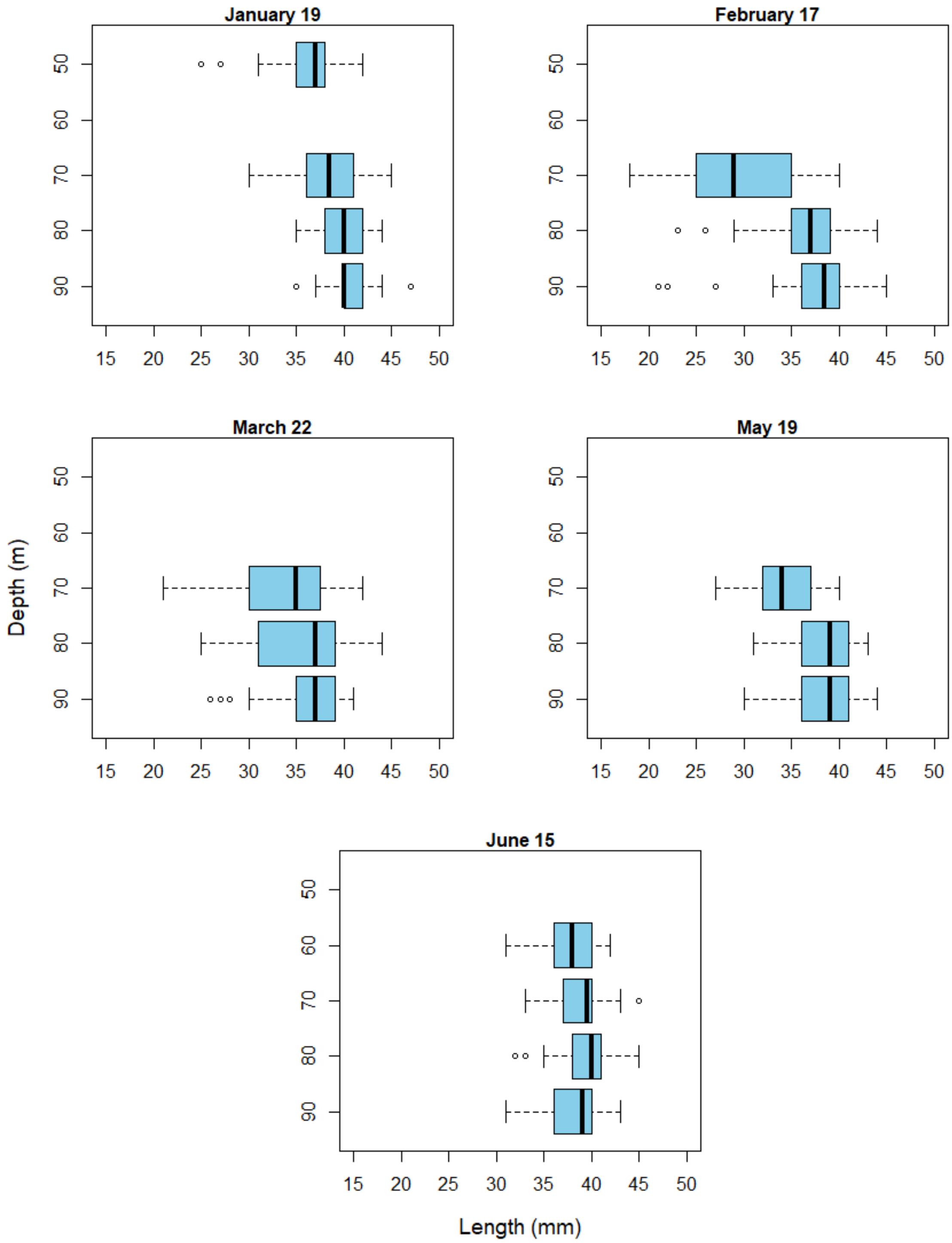

Figure 3.6. Length (mm) distributions by depth (m) of *M. norvegica*. The measurements were based on a subsample of 50 randomly selected individuals from the subsamples from each trawl. The boxes represent 50% of the size range of the individuals.

The lightest individuals of *M. norvegica* during daytime were mostly captured at the shallowest depth intervals, whereas the heaviest were found at 90 m. The average weight throughout the measurement period was between 0.25 and 0.35 g (Figure 3.7). There was significant difference between weight distribution and depth for all months (ANOVA: $p < 0.05$). There was no significant variation in weight between 90 m and 80 m (Tukey HSD post hoc: $p > 0.05$), except in March and June (Tukey HSD post hoc: $p < 0.05$).

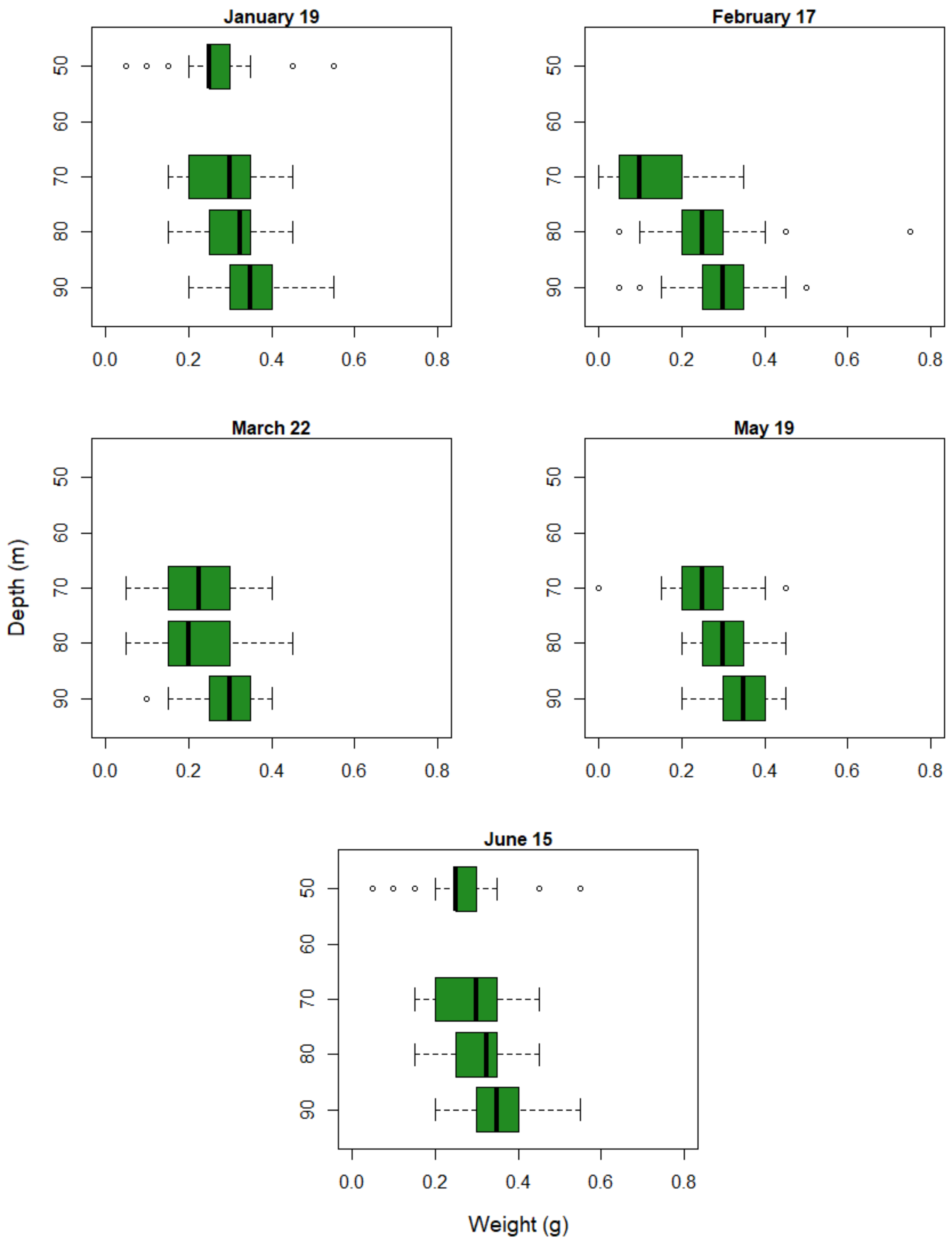

Figure 3.7. Weight (g) distributions by depth (m) of *M. norvegica*. The measurements were based on a subsample of 50 randomly selected individuals from the subsamples from each trawl. The boxes represent 50% of the weight range of the individuals.

Night trawl (17 February)

The smallest and lightest individuals were found at 15 m, whereas the largest and heaviest individuals were found at 50 m. There was a large range of length and weight for each depth interval with many outliers, especially for the weight distribution (Figure 3.8). A significant difference was found in the length measurements (ANOVA: $p < 0.05$), yet there was no significant variance in length between 50 m and 30 m (Tukey HSD post hoc: $p > 0.05$). There was no significant variation in weight distribution (ANOVA: $p > 0.05$).

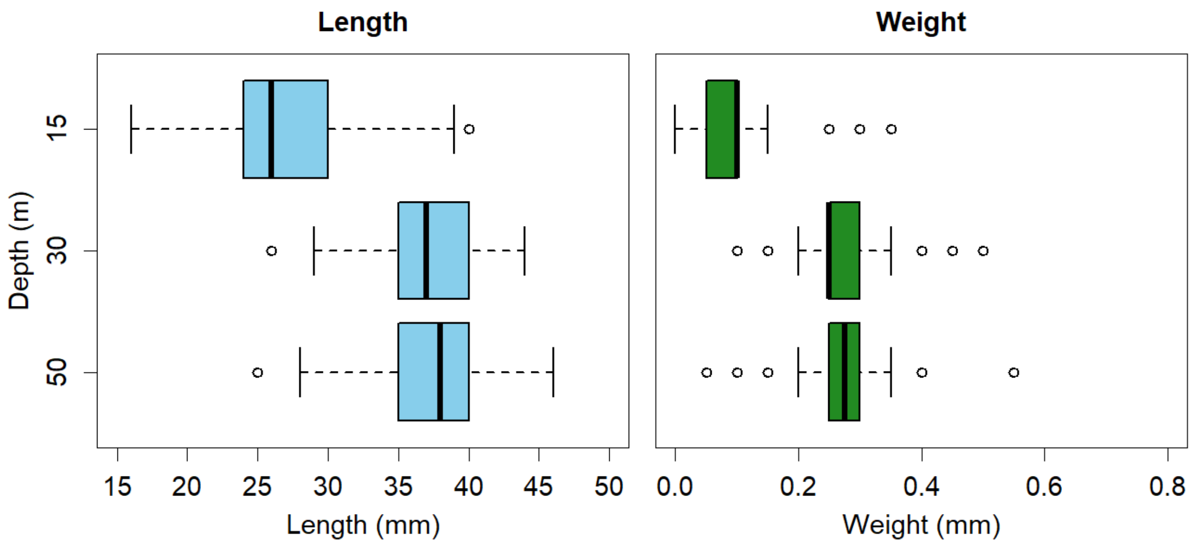

Figure 3.8. Length (mm, blue) and weight (g, green) distributions by depth (m) of *M. norvegica* from the night trawl 17 February. The boxes represent 50% of the size range of the individuals.

3.3 Acoustic data

M. norvegica performed diel vertical migration (DVM) during the entire recording period, here represented by one day from each month in Figure 3.9. Ascent and descent times, total migration times, and the distribution of *M. norvegica* and fish varied somewhat within the months due to weather conditions and changes in light availability.

Generally, *M. norvegica* migrated towards the surface in the evening and descended into the depths in the morning. This occurred regardless of season (Figure 3.9). *M. norvegica* remained from ~40-100 m depth during the day (from noon) depending on season and light availability. The acoustic layer was sometimes separated into several sublayers during the day. At night, individuals of *M. norvegica* were spread throughout the water column from ~0-90 m, exhibiting "midnight sinking" which occurred mainly in January and February.

However, many individuals would only sink down to ~20-30 m depth, causing a maximum density of individuals at this depth range. The presence of fish above or within the layer of *M. norvegica* was observed throughout the recording period, especially at night and in the brighter months. The acoustic records of fish were easily distinguishable on the echogram as stronger backscatter compared to *M. norvegica*, as will be further outlined below.

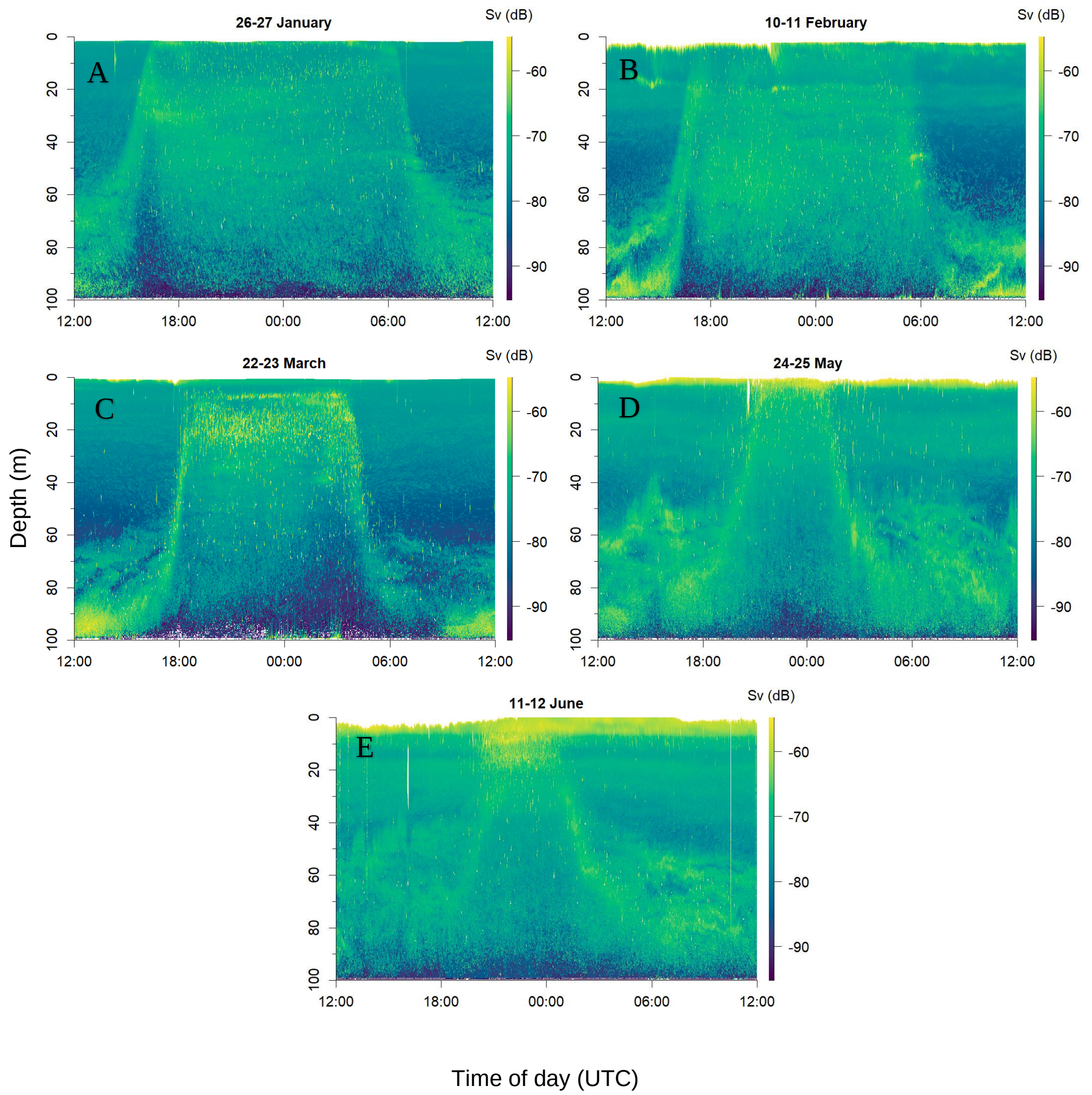

Figure 3.9. Excerpts of selected days from noon to noon from each month of the acoustic data collected throughout the study period using a 200 kHz echosounder mounted at the bottom of Midtmeie station. The horizontal axis displays the time of day (UTC), whereas the vertical axis displays depth (m). The colour bars display volume backscattering strength (Sv) with a threshold set from -95 to -55 dB. **A**: 26-27 January, **B**: 10-11 February, **C**: 22-23 March, **D**: 24-25 May, **E**: 11-12 June. The white colouring found near the surface on the echograms represents stronger echo than -55 dB.

3.3.1 January

The 5-day recording period in January (phase 1) was during a period of full moon (28 January). Weather conditions were overcast and windy during the first two days of recording (Appendix Table B.1), while it was clear with only a few passing clouds during the full moon. The moon was above the horizon at night throughout the period (Table 2.9).

A small separation in the echogram could be observed during the day and night at ~10 m depth. This layer was possibly related to the pycnocline of the Oslofjord and will hereby be referred to as the pycnocline in further analyses (Figure 3.9 A & Figure 3.17 A).

Scattering layer

M. norvegica performed DVM throughout the period with slight variation between days (Figure 3.9 A, Figure 3.10, Figure 3.11, Figure 3.16 A, Figure 3.17 A). The daytime distribution ranged from ~60-100 m depth with an apparent decreasing concentration of individuals towards the seafloor (Figure 3.9 A). However, due to the narrow echo-beam at this depth, it was difficult to visually deduce how many individuals resided there.

The median time for initiation of ascent was ~40 minutes before sunset, ranging from ~1 hour before sunset (22 January) to ~25 minutes before sunset (29 January; Appendix Table B.1). The median ascent duration was ~2 hours (Appendix Table B.1).

Midnight sinking of the scattering layer occurred throughout the recording period, creating an apparent, weak maximum at ~30 m. Otherwise, the number of individuals decreased with increasing depth, ranging from ~30-80 m (Figure 3.9 A, Figure 3.16 A, Figure 3.17 A). In the morning, the scattering layer descended synchronically from ~30 m depth to the daytime depth (Figure 3.9 A & Figure 3.16 A).

M. norvegica remained in the upper waters for approximately ~16 hours with slight variations between nights (Appendix Table B.1). The median time for initiation of descent was ~1 hour and 5 minutes before sunrise, ranging from ~50 minutes to ~1 hour and 10 minutes before sunrise. The approximate duration of descent to the daytime depth was ~1 hour and 30 minutes, which remained consistent throughout the recording period (Appendix Table B.1).

Fish

Rare occurrences of stronger backscatter, here representing fish, was scattered throughout the water column during the day. Fish were abundant in the upper waters at night with the highest density of individuals between ~0-30 m, especially during the night of the full moon (Figure 3.12 A & Figure 3.18 A). Few individuals were scattered throughout the water column and residing within the deeper backscatter ascribed to *M. norvegica*. As the descent took place, the fish seemed to follow *M. norvegica*, then separated from the scattering layer as *M. norvegica* reached beyond 50 m, some individuals of fish found residing at this depth in the morning (Figure 3.12 B).

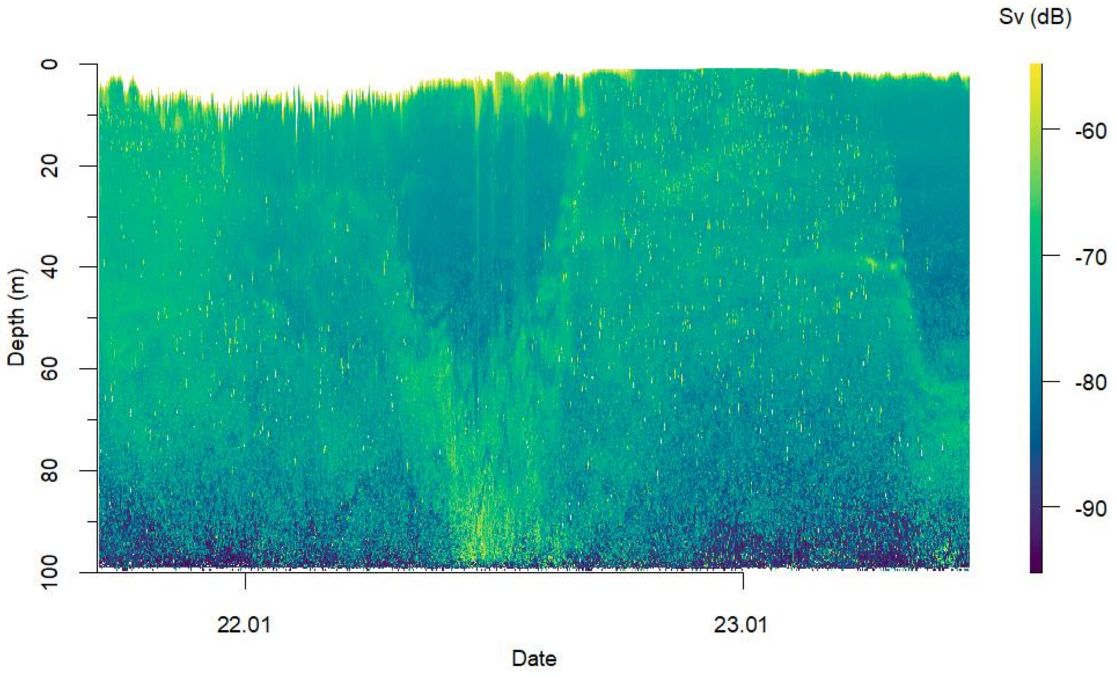

Figure 3.10. Acoustic data collected during January phase 0 (21-23 January) using a 200 kHz echosounder mounted at the bottom of Midtmeie station. The horizontal axis displays the date, whereas the vertical axis displays depth (m). The colour bar displays volume backscattering strength (Sv) with a threshold set from -95 to -55 dB. The white colouring found near the surface on the echogram represents stronger echo than -55 dB.

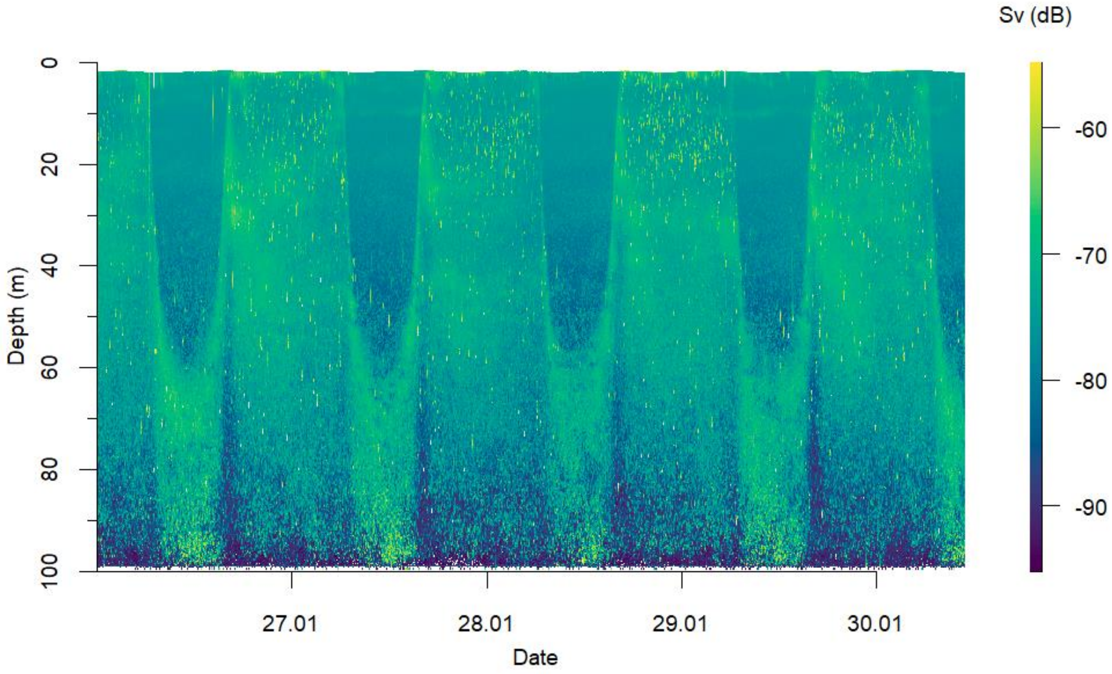

Figure 3.11. Acoustic data collected during January phase 1 (26-30 January) using a 200 kHz echosounder mounted at the bottom of Midtmeie station. The horizontal axis displays the date, whereas the vertical axis displays depth (m). The colour bar displays volume backscattering strength (Sv) with a threshold set from -95 to -55 dB.

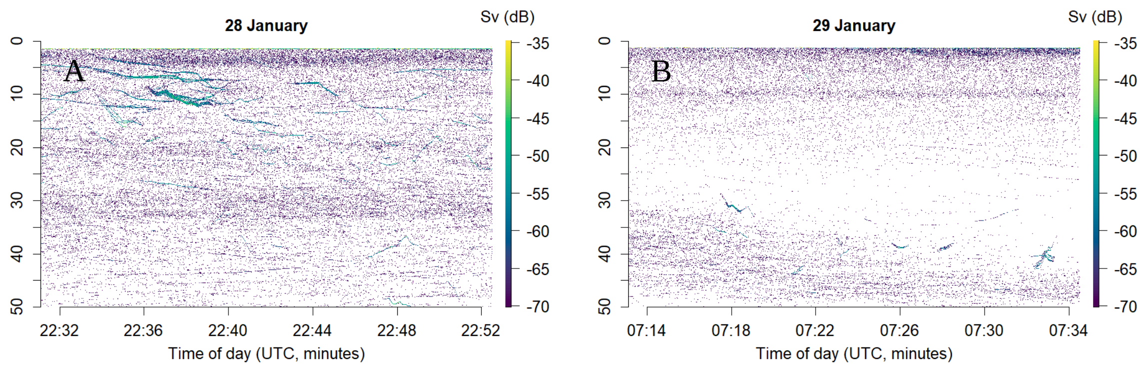

Figure 3.12. Echograms displaying fish activity in the upper waters during the January full moon night and morning (28-29 January). The horizontal axis displays hours and minutes (UTC), whereas the vertical axis displays depth (m). The colour bars display volume backscattering strength (Sv) with a threshold set from -70 to -35 dB. The echograms display a depth range of 0-50 m. **A**: fish observed during the January full moon night from ~0-20 m. **B**: fish following *M. norvegica* during the descent in the morning.

3.3.2 February

The February recording was during a new moon (11 February) period. The weather was clear except in the last two days (Appendix Table B.1). The moon was not above the horizon at night (Table 2.9). However, the small amount of illumination from the new moon could be compared to total darkness from a clear, starlit sky.

A distinct separation was found from ~20-30 m, possibly related to the pycnocline, and potentially limiting DVM above this "threshold" at night (Figure 3.9 B, Figure 3.16 B, Figure 3.17 B).

Scattering layer

DVM was performed by *M. norvegica* during this period (Figure 3.9 B, Figure 3.13, Figure 3.14, Figure 3.16 B, Figure 3.17 B). During the day, *M. norvegica* resided in two distinct layers: one at ~70-80 m and another at ~90-100 m. A space of little to no individuals separated the layers (Figure 3.9 B). The layers merged at ~70 m as the ascent begun (Figure 3.9 B). Patchiness was observed in the acoustic layer both during night and day which could be explained by wind (Appendix Table B.1).

The median time for initiation of ascent was ~25 minutes, ranging from ~15-30 minutes before sunset, which was shorter compared to January. The median ascent duration was ~1 hour and 30 minutes with a variation of ~1 hour and 20 minutes to ~2 hours (Appendix Table B.1).

During the night, *M. norvegica* was widely spread throughout the water column, ranging from ~0-90 m. Less prominent midnight sinking compared to January was displayed, creating a weak maximum at ~20 m (Figure 3.9 A & B, Figure 3.17 B). The layer of *M. norvegica* was somewhat patchy at night (Figure 3.9 B).

After remaining a median of ~12 hours in the upper waters, *M. norvegica* began descending approximately ~1 hour and 50 minutes before sunrise, ranging from ~1 hour to ~2 hours and 5 minutes before sunrise (Appendix Table B.1). Duration of descent increased by ~1 hour from January, lasting approximately ~2 hours and 40 minutes (Appendix Table B.1). During the descent, the acoustic layer was less prominent than the pattern seen during the ascent. Smaller patches of densely gathered individuals appeared during the decent at ~50 and ~60 m depth. After descending, *M. norvegica* split back into the two distinct layers as seen before the ascent, remaining separated throughout the day at their daytime depth (Figure 3.9 B).

Fish

During the day, little to no fish were found in the space between the two scattering layers, suggesting that the separation was not caused by visual predator avoidance (Figure 3.15 A). The presence of fish at night was less compared to January with individuals mostly detected above or just below the pycnocline (~20 m) (Figure 3.15 B, Figure 3.17 B, Figure 3.18 B). During the descent of the scattering layer, fish could be found near and in the patches observed, potentially hunting *M. norvegica* as more light was available (Figure 3.15 C).

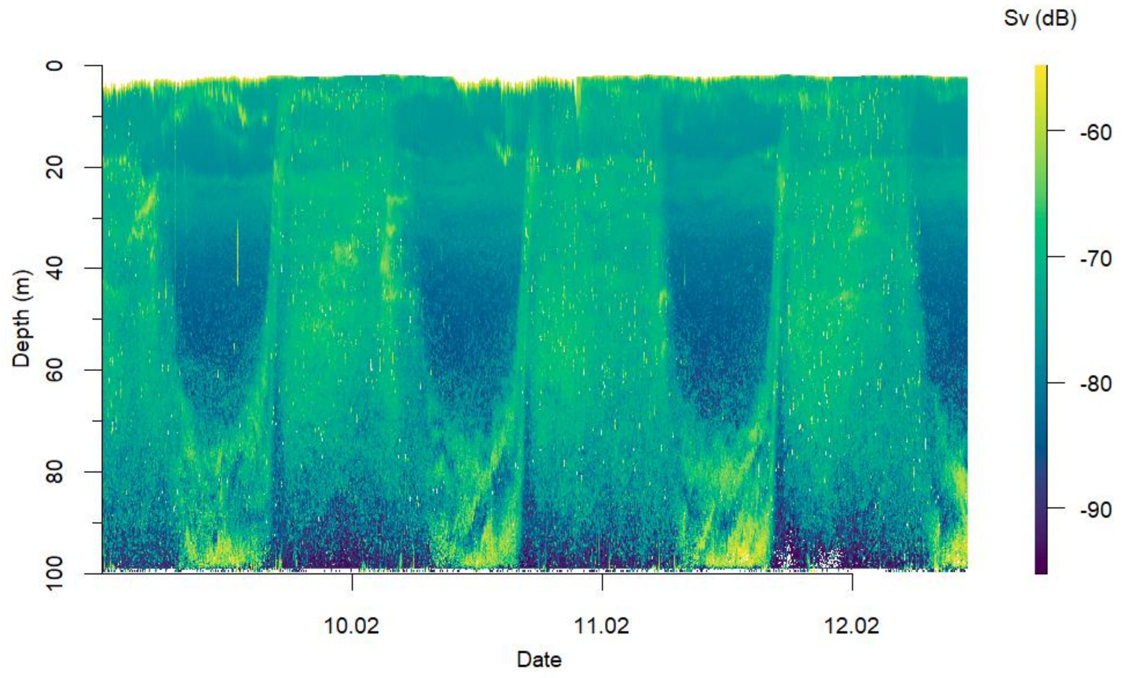

Figure 3.13. Acoustic data collected during January phase 2 (09-12 February) using a 200 kHz echosounder mounted at the bottom of Midtmeie station. The horizontal axis displays the date, whereas the vertical axis displays depth (m). The colour bar displays volume backscattering strength (Sv) with a threshold set from -95 to -55 dB. The white colouring found near the surface on the echogram represents stronger echo than -55 dB.

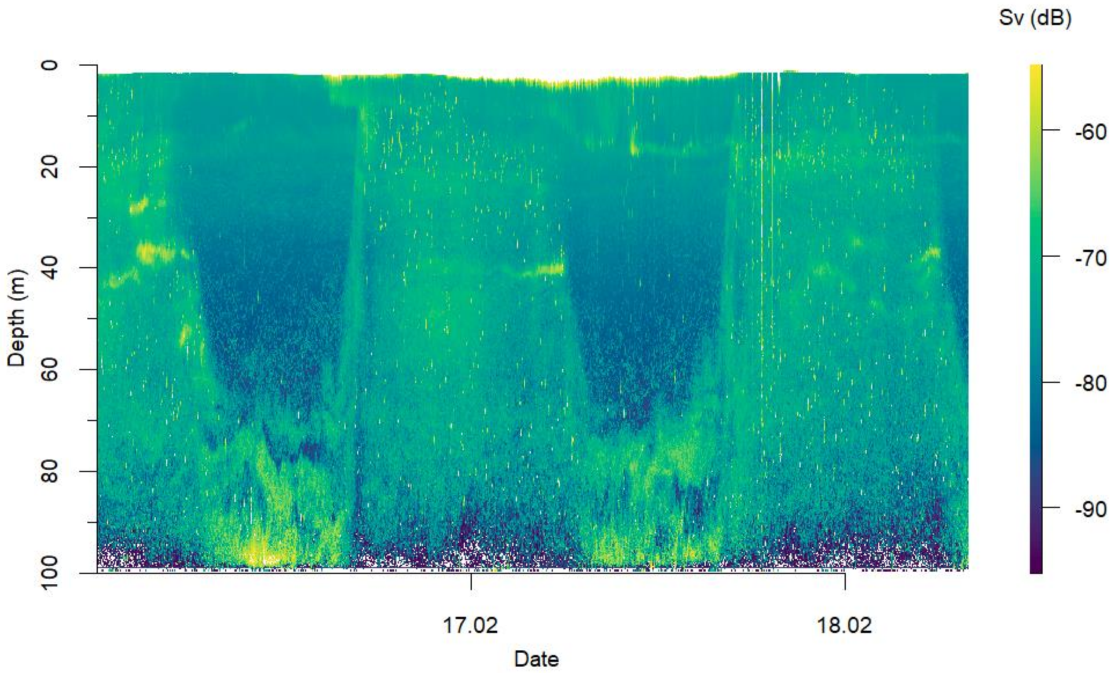

Figure 3.14. Acoustic data collected during January phase 3 (16-18 February) using a 200 kHz echosounder mounted at the bottom of Midtmeie station. The horizontal axis displays the date, whereas the vertical axis displays depth (m). The colour bar displays volume backscattering strength (Sv) with a threshold set from -95 to -55 dB. The white colouring found near the surface on the echogram represents stronger echo than -55 dB.

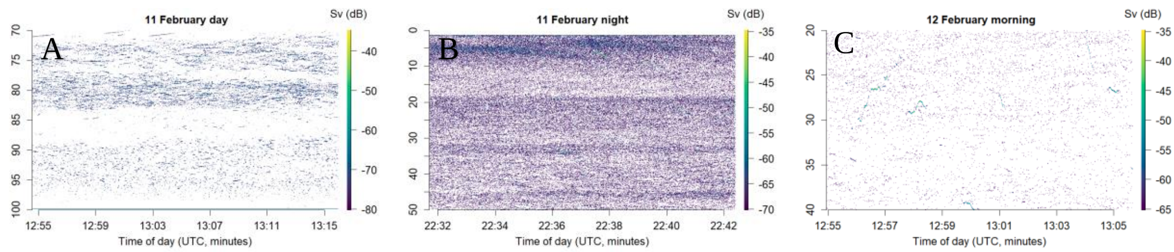

Figure 3.15. Echograms displaying fish activity during the February new moon (11-12 February). The horizontal axis displays hours and minutes (UTC), whereas the vertical axis displays depth (m). The colour bars display volume backscattering strength (Sv). Note the different depth scales and Sv thresholds for each figure. **A**: echogram ranging from 70-100 m with a Sv threshold set from -80 to -35 dB. Little to no fish observed during the day between the two layers of *M. norvegica*. **B**: echogram ranging from 0-50 m with a Sv threshold set from -70 to -35 dB. Little to no fish observed during the full moon night in the upper waters. **C**: echogram ranging from 20-40 m with a Sv threshold set from -65 to -35 dB. Some fish observed in a dense patch of *M. norvegica* during the descent in the morning.

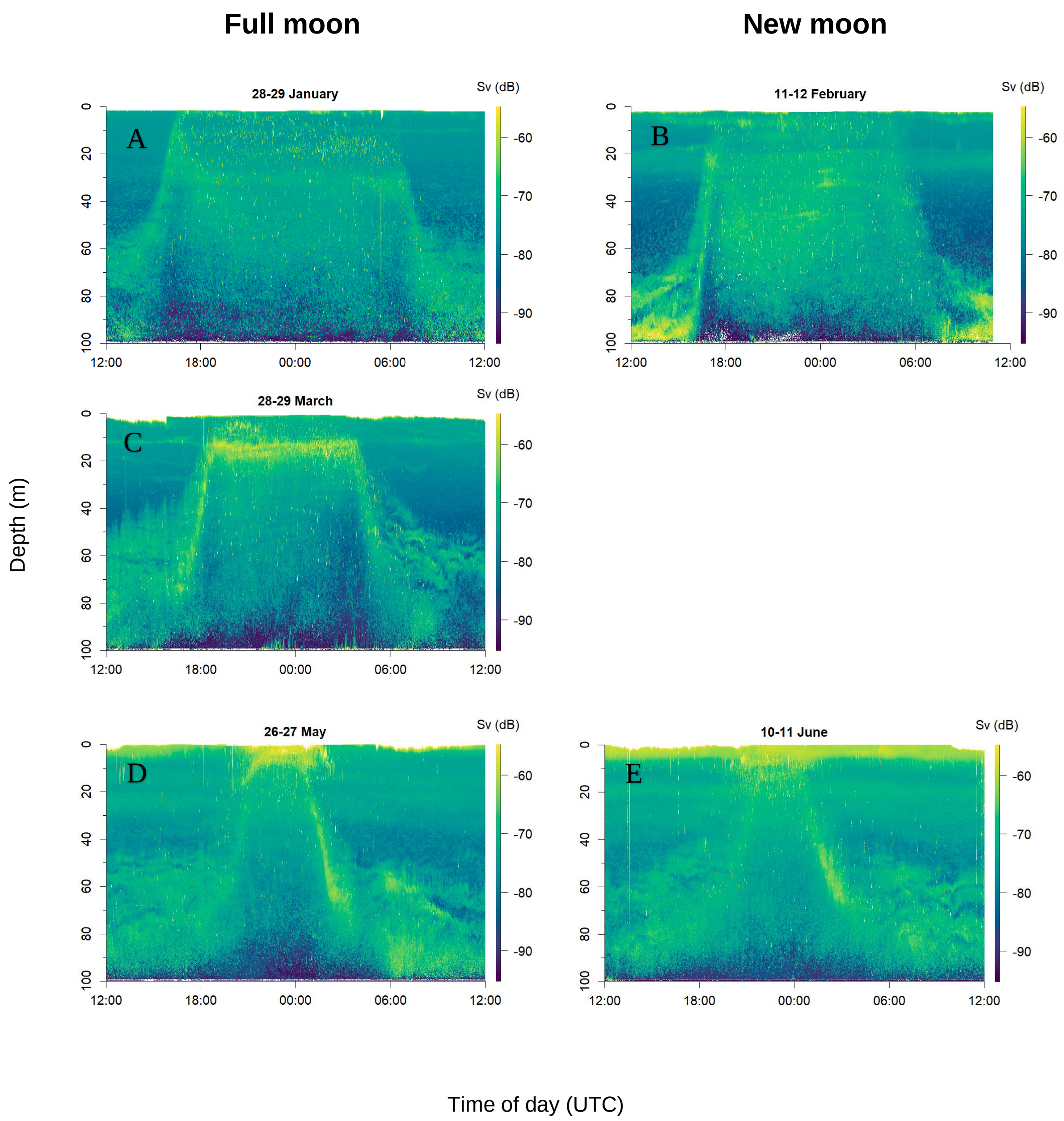

Figure 3.16. Acoustic data collected during full and new moon days throughout the study period using a 200 kHz echosounder mounted at the bottom of Midtmeie station. The horizontal axis displays the time of day (UTC), whereas the vertical axis displays depth (m). The colour bars display volume backscattering strength (Sv) with a threshold set from -95 to -55 dB. The white colouring found near the surface on the echograms represents stronger echo than -55 dB. **A**: 24-hour echogram (noon-noon) of the January full moon (28-29 January), **B**: 23-hour echogram (noon-11:00) of the February new moon (11-12 February) **C**: 24-hour echogram (noon-noon) of the March full moon (28-29 March), **D**: 24-hour echogram (noon-noon) of the May full moon (26-27 May). **E**: 24-hour echogram (noon-noon) of the June new moon (10-11 June).

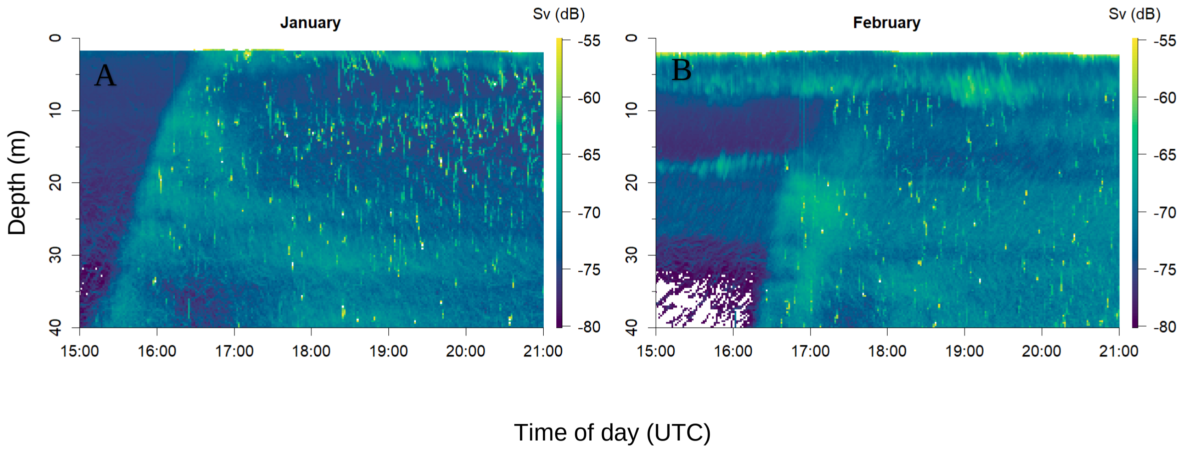

Figure 3.17. Acoustic data collected during the full moon in January (28 January) and new moon in February (11 February) during the study period using a 200 kHz echosounder mounted at the bottom of Midtmeie station. The horizontal axis displays the time of day (UTC), whereas the vertical axis displays depth (m). The colour bars display volume backscattering strength (Sv) with a threshold set from -80 to -55 dB. The white colouring on the echograms represents stronger echo than -55 dB. The echograms display a depth range of 0-40 m. **A**: echogram displaying the ascent and midnight sinking of *M. norvegica* along with the presence of fish in the upper wates during the January full moon. **B**: echogram displaying the ascent and midnight sinking of *M. norvegica* along with the presence of fish in the upper waters during the February new moon.

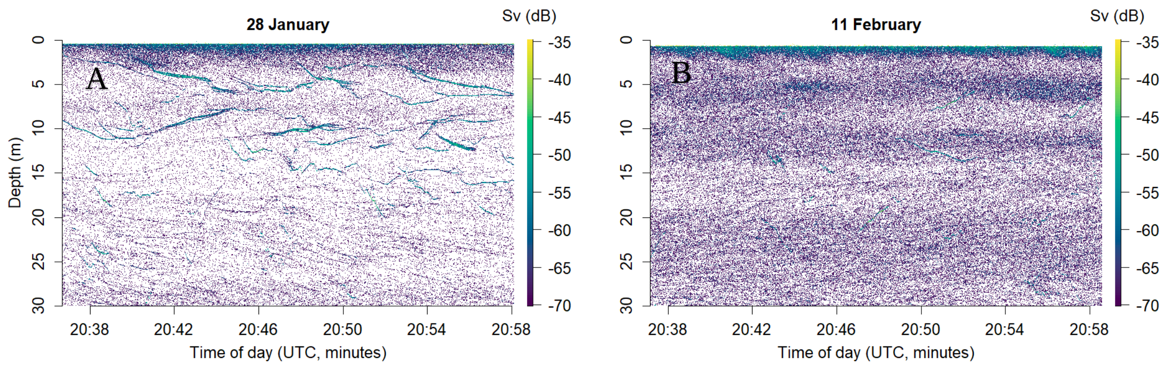

Figure 3.18. Echograms displaying fish activity in the upper waters during the January full moon night (28 January) and the February new moon night (11 February). The horizontal axis displays hours and minutes (UTC), whereas the vertical axis displays depth (m). The colour bars display volume backscattering strength (Sv) with a threshold set from -70 to -35 dB. The echograms display a depth range of 0-30 m. **A**: fish observed during the January full moon night from ~0-20 m. **B**: fewer fish observed during the February new moon night.

3.3.3 March

Recordings in March were done in relation to a period of full moon (28 March). The weather varied throughout the period (Appendix Table B.1). Overcast weather with light rain was present on the day of the full moon, potentially reducing the illumination from the moon reaching the study site. The moon was above the horizon during the night (Table 2.9).

The pycnocline was a distinct, visible line found on the echogram at ~11 m depth (Figure 3.16 C).

Scattering layer

M. norvegica performed DVM throughout the period (Figure 3.9 C, Figure 3.16 C, Figure 3.19). During the day, *M. norvegica* ranged between ~60-100 m in the first half of the recording period, whereas the distribution widened to ~50-100 m in the second half. Overcast weather could explain the wider range (Table 2.9 & Appendix Table B.1). The highest density of individuals was closest to the seafloor (~100 m) (Figure 3.9 C). However, the narrow echo-beam limited the certainty of this find, as explained in January. Between ~60-80 m during the day, the acoustic layer was patchy.

The initiation of ascent in the evening was similar to February with a median of ~37 minutes and 30 seconds before sunset, ranging from ~10 to 50 minutes before sunset. The median duration of ascent was ~1 hour and 30 minutes, varying between ~1 hour to ~1 hour and 30 minutes (Appendix Table B.1).

During the evening, *M. norvegica* did not migrate to the surface, instead ending the ascent near the pycnocline (~15 m) (Figure 3.9 C). Some individuals might have migrated closer to the surface, yet this was unclear. *M. norvegica* was widely spread throughout the water column between ~15-80 m depth. Some patchiness was observed at night from ~20-50 m.

The descent began after *M. norvegica* had resided in the upper waters a median of ~9 hours and 23 minutes, ~2 hours and 30 minutes shorter than in February. The median initiation of descent was ~1 hour and 30 minutes before sunrise, ranging from ~50 minutes to ~1 hour and 55 minutes before sunrise. The duration of descent was approximately ~2 hours, ~40 minutes shorter compared to February (Appendix Table B.1).

Fish

Only a few individuals of fish were found within the daytime distribution of *M. norvegica*, which likely did not explain the patchiness and the deeper distribution of the scattering layer. At night, a dense layer of fish was observed from ~0-20 m, which was not present in the previous months (Figure 3.20 A). Similar to January, the fish seemed to follow *M. norvegica* during the descent in the morning to some extent (Figure 3.20 B).

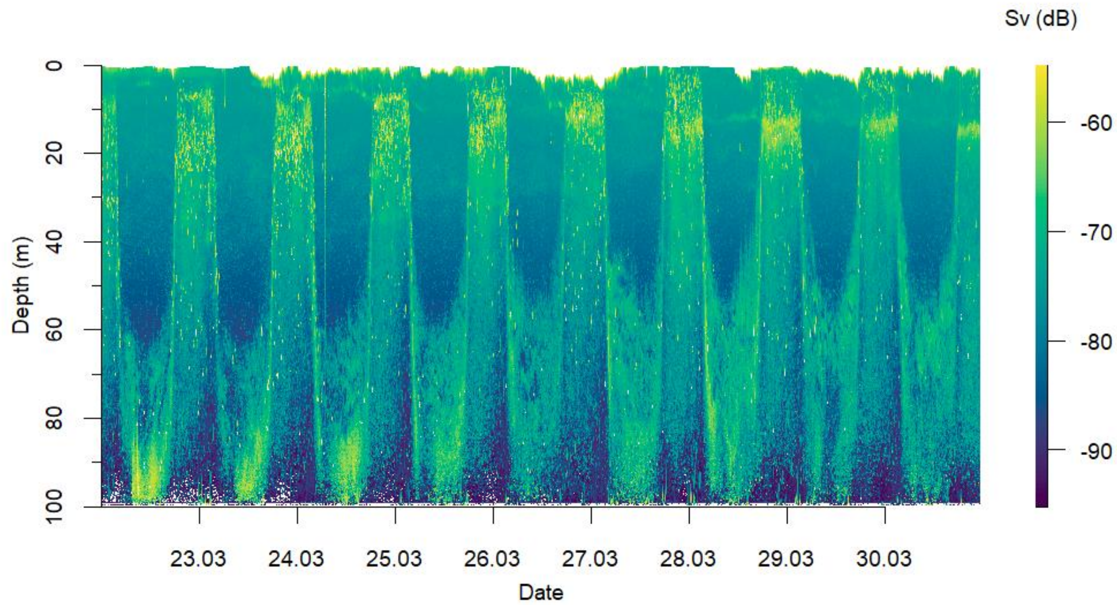

Figure 3.19. Acoustic data collected during February phase 1 (22-31 March) using a 200 kHz echosounder mounted at the bottom of Midtmeie station. The horizontal axis displays the date, whereas the vertical axis displays depth (m). The colour bar displays volume backscattering strength (Sv) with a threshold set from -95 to -55 dB. The white colouring found near the surface on the echogram represents stronger echo than -55 dB.

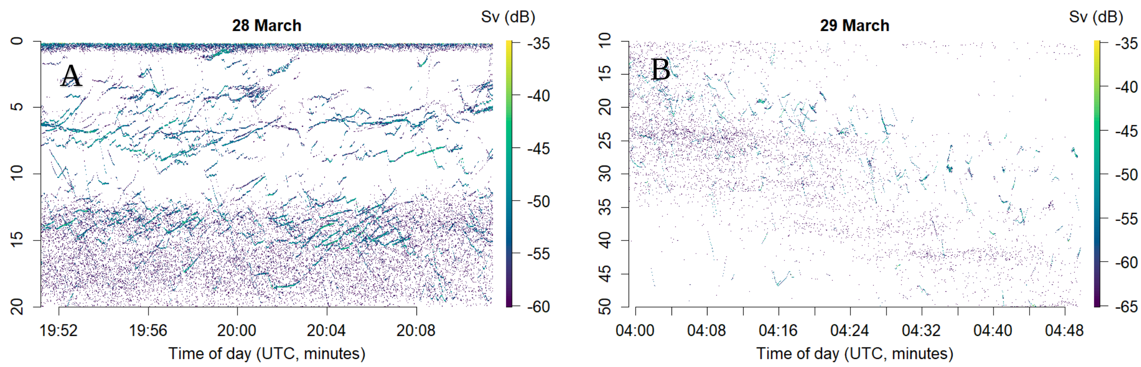

Figure 3.20. Echograms displaying fish activity in the upper waters during the March full moon night (28-29 March). The horizontal axis displays hours and minutes (UTC), whereas the vertical axis displays depth (m). The colour bars display volume backscattering strength (Sv). Note the different depth scales and Sv thresholds for each figure. **A**: echogram ranging from 0-20 m with a Sv threshold set from -60 to -35 dB. A high density of fish observed at night above and in the SSL ascribed to *M. norvegica*. **B**: echogram ranging from 10-50 m with a Sv threshold set from -65 to -35 dB. Fish following *M. norvegica* during the descent in the morning.

3.3.4 April

The recording in April occurred between the new and first quarter moon. The weather was clear throughout the period (Appendix Table B.1). The echosounder was planned to be in a floating rig at ~50 m. However, the echosounder was placed slightly deeper (62 m, Table 2.7), which resulted in lack of records in the upper 10 m. The analysis will be based on the depth range displayed in Figure 3.21. Daytime distribution and initiation of ascent and descent was not described for this period due to the placement of the echosounder (Appendix Table B.1).

Scattering layer

DVM was performed by *M. norvegica* in April (Figure 3.21). During the day, little to no individuals of *M. norvegica* were observed near the echosounder at ~40-50 m depth (Figure 3.21 A). *M. norvegica* reached the upper waters at ~19:30 UTC every recording day. Individuals were found throughout the entire range of the echosounder at night with the highest density near the surface to ~10 m.

The median duration of stay in the upper waters was ~7 hours and 18 minutes with small variations between days (Appendix Table B.1). The morning descent was less dense and patchier compared to the evening ascent.

Fish

Little to no fish were observed during the daytime. At night, some individuals of fish were observed in the scattering layer, sparsely scattered throughout the water column (Figure 3.22).

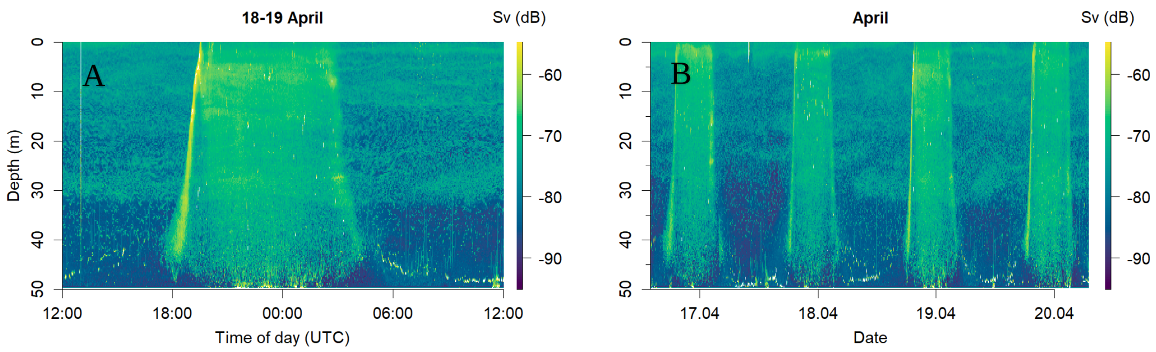

Figure 3.21. Acoustic data collected during April phase 0 (16-20 April) using a 200 kHz floating rig-mounted echosounder at 62 m depth. Note that the first 10 m of the water column is missing due to misplacement. The horizontal axis displays the time of day (UTC) and date, whereas the vertical axis displays depth (m). The colour bars display volume backscattering strength (Sv) with a threshold set from -95 to -55 dB. **A**: 24-hour excerpt (noon-noon) from the recording period in April (18-19 April). **B**: the entire recording period in April (16-20 April).

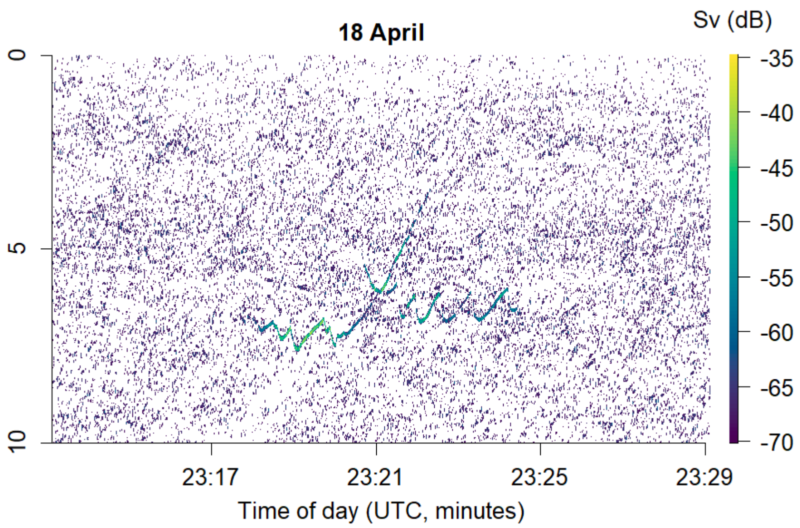

Figure 3.22. Echogram displaying fish activity in the upper waters on 18 April. The horizontal axis displays hours and minutes (UTC), whereas the vertical axis displays depth (m). The colour bar displays volume backscattering strength (Sv) with a threshold set from -70 to -35 dB. The echogram displays a depth range of 0-10 m.

3.3.5 May

Recording in May was done during a full moon (26 May) period. The weather varied between clear and light rain throughout the period. The moon was above the horizon at night (Table 2.9 & Appendix Table B.1). As the nights became brighter, the light from the moon was likely less influential on DVM behaviour.

Scattering layer

M. norvegica performed DVM in May with some variation between days (Figure 3.9 D, Figure 3.16 D, Figure 3.23, Figure 3.24, Figure 3.29 A). The acoustic layer was widely distributed and patchy during the day compared to other months, reaching from ~40-100 m (Figure 3.9 D). The weather during the first half of the recording was rainy, possibly reflecting on the range of *M. norvegica* (Appendix Table B.1).

Initiation of ascent began approximately ~1 hour and 15 minutes before sunset, varying from ~40 minutes to ~1 hour and 40 minutes before sunset. *M. norvegica* spent a median of ~2 hours and 15 minutes ascending, ranging between ~1 hour and 25 minutes and ~2 hours and 50 minutes (Appendix Table B.1). This finding was longer compared to earlier dates.

The acoustic layer reached ~4 m as the ascent ended on 24-25 May (Figure 3.24 A). *M. norvegica* could have migrated closer to the surface, yet due to strong, unidentified backscatter in the upper ~4 m, this was inconclusive. On 27-28 May, *M. norvegica* reached ~6 m after ascent (Figure 3.24 B). Again, it was uncertain whether parts of the scattering layer migrated closer to the surface. The weather was overcast and rainy on 24-25 May, whereas it was clear with passing clouds on 27-28 May, which could have affected these findings (Appendix Table B.1).

At night, *M. norvegica* generally ranged from ~4-50 m. Some individuals could be found below this range. The highest density of individuals was between ~4-10 m depth (Figure 3.16 D & Figure 3.29 A).

The median duration of stay in the upper waters was ~3 hours and 45 minutes with slight variations between days. The initiation of descent began approximately ~1 hour and 15 minutes before sunrise, ranging from ~50 minutes to ~2 hours before sunrise. The descent lasted approximately ~1 hour and 45 minutes, making the descent shorter than the ascent (Appendix Table B.1).

Fish

Smaller schools of fish and single individuals were observed in the scattering layer during the day, potentially causing some of the patchiness (Figure 3.25). Little to no individuals or schools were observed near the surface. During the evening, schools were found from ~0-7 m before *M. norvegica* reached the upper waters (Figure 3.26 A). These schools dispersed into the scattering layer as the ascent ended, displaying foraging behaviour, the fish ranging from ~0-20 m (Figure 3.26 B). As the descent of *M. norvegica* began, the fish remerged to schools (Figure 3.26 C). During the night of the full moon (26-27 May), a higher density of fish was observed. The fish were also more condensed compared to other recording days, ranging from ~0-10 m (Figure 3.29 A).

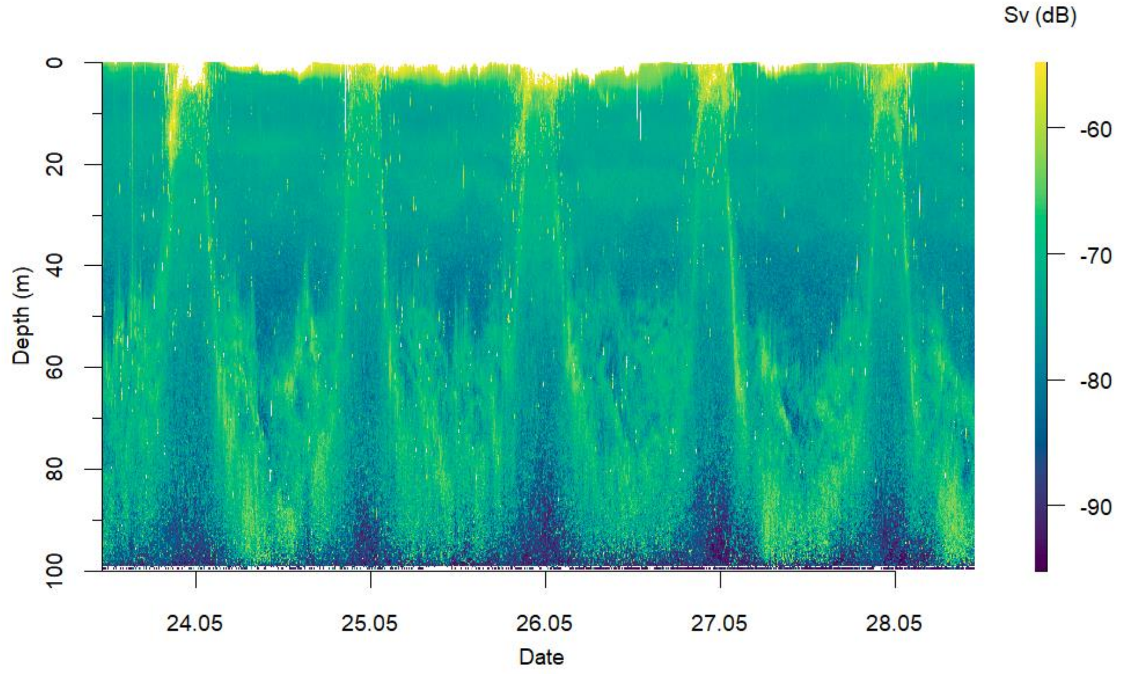

Figure 3.23. Acoustic data collected during May phase 0 (23-28 May) using a 200 kHz echosounder mounted at the bottom of Midtmeie station. The horizontal axis displays the date, whereas the vertical axis displays depth (m). The colour bar displays volume backscattering strength (Sv) with a threshold set from -95 to -55 dB. The white colouring found near the surface on the echogram represents stronger echo than -55 dB.

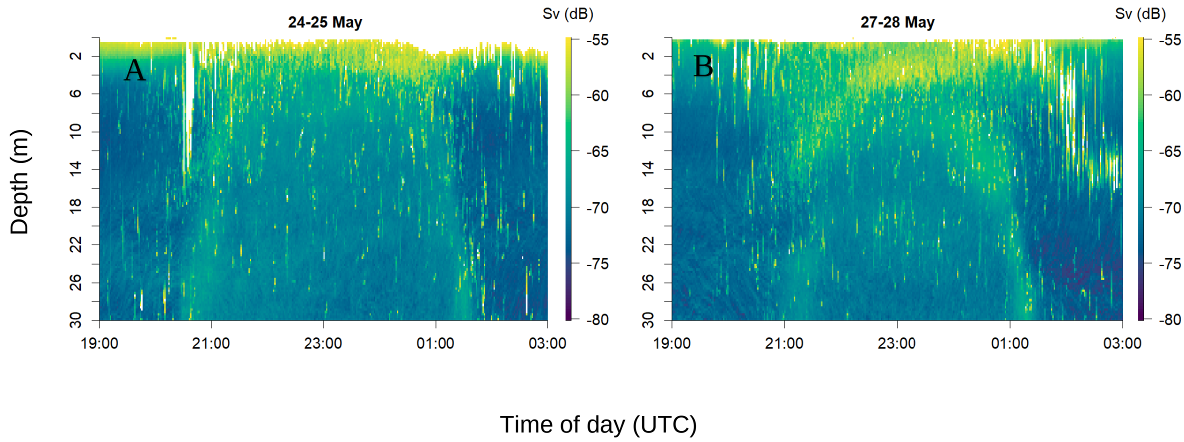

Figure 3.24. Echograms from 24-25 May (cloudy weather) (**A**) and 27-28 May (clear weather) (**B**) with focus on the upper 30 m at night. The horizontal axis displays the time of day (UTC), whereas the vertical axis displays depth (m). The colour bars display volume backscattering strength (Sv) with a threshold set from -80 to -55 dB. The white colouring found on the echograms represents stronger echo than -55 dB.

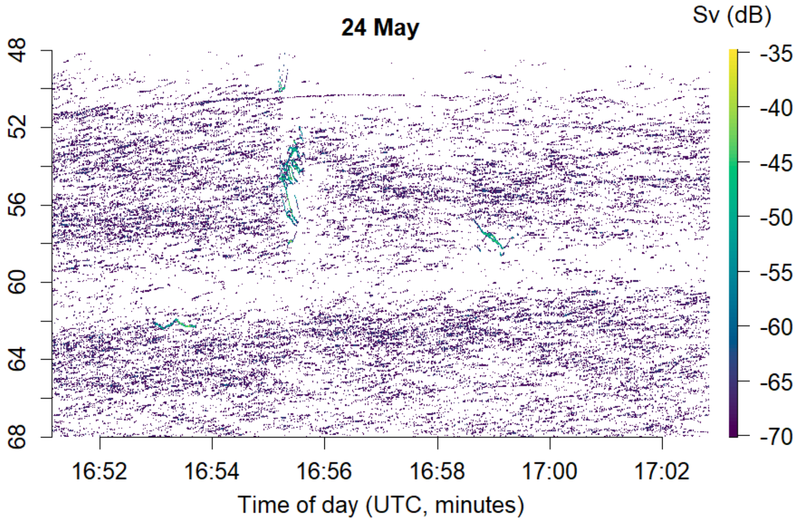

Figure 3.25. Echogram displaying fish activity and avoidance by *M. norvegica* in the deeper waters on 24 May. The horizontal axis displays hours and minutes (UTC), whereas the vertical axis displays depth (m). The colour bar displays volume backscattering strength (Sv) with a threshold set from -70 to -35 dB. The echogram displays a depth range of 48-68 m.

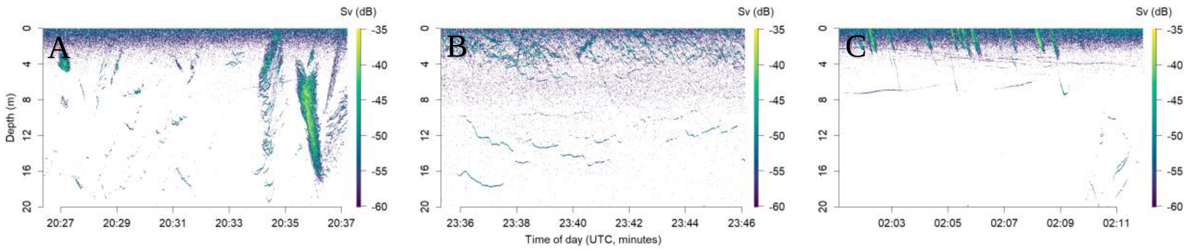

Figure 3.26. Echograms displaying fish activity in the upper waters during 24-25 May. The horizontal axis displays hours and minutes (UTC), whereas the vertical axis displays depth (m). The colour bars display volume backscattering strength (Sv) with a threshold set from -60 to -35 dB. The echograms display a depth range of 0-20 m. **A**: schooling fish during the evening before *M. norvegica* arrived. **B**: schools dispersing as *M. norvegica* arrived. **C**: fish re-emerging into schools after *M. norvegica* descended beyond 20 m. The stronger backscatter in the first ~4 m is unidentified echo.

3.3.6 June

Recordings in June were split into two phases: during the new moon (10 June) period with the echosounder in a bottom-mounted rig (100 m), and during the full moon (24 June) period using a floating rig placed at 38 m.

3.3.6.1 New moon period (08-13 June)

Weather throughout the new moon recording period was clear with some cloud cover. The moon was not above the horizon at night (Table 2.8 & Appendix Table B.1). Similar to May, the brighter nights caused moonlight to be less prominent. Therefore, no moon present likely had little to no effect on DVM behaviour.

Scattering layer

M. norvegica performed DVM with some variation between days throughout the recording period (Figure 3.9 E, Figure 3.16 E, Figure 3.27, Figure 3.29 B). During the day, the population ranged between ~50-90 m depth. The acoustic layer was patchy, similar to May findings (Figure 3.9 D & E, Figure 3.16 E).

The median time for initiation of ascent was ~1 hour and 45 minutes before sunset, ranging from ~1 hour and 25 minutes to ~2 hours and 5 minutes before sunset. The ascent lasted approximately ~45 minutes, varying between ~35 minutes and ~1 hour and 10 minutes (Appendix Table B.1).

M. norvegica reached ~10 m as the ascent ended. Due to strong unidentified echo in the upper ~10 m, it was difficult to determine how far *M. norvegica* migrated (Figure 3.29 B). *M. norvegica* ranged between ~10-80 m at night with the highest density of individuals from ~10-40 m (Figure 3.9 E).

After remaining in the upper waters for a median of ~3 hours, *M. norvegica* began descending approximately ~1 hour and 45 minutes before sunrise. The initiation of descent varied between ~1 hour and 25 minutes and ~1 hour and 50 minutes before sunrise. The median time of descent was ~2 hours (Appendix Table B.1).

Fish

Little to no fish were observed within the patches in the scattering layer during daytime compared to May (Figure 3.25). A higher density of fish with a wider distribution compared to May (~0-20 m) in the upper waters was observed during the night, infiltrating the scattering layer. The fish behaved similarly to May, arriving at the research station in schools during the evening and dispersing once *M. norvegica* arrived in the upper waters (Figure 3.28 A & B). After *M. norvegica* began descending, the fish returned to schooling behaviour (Figure 3.28 C).

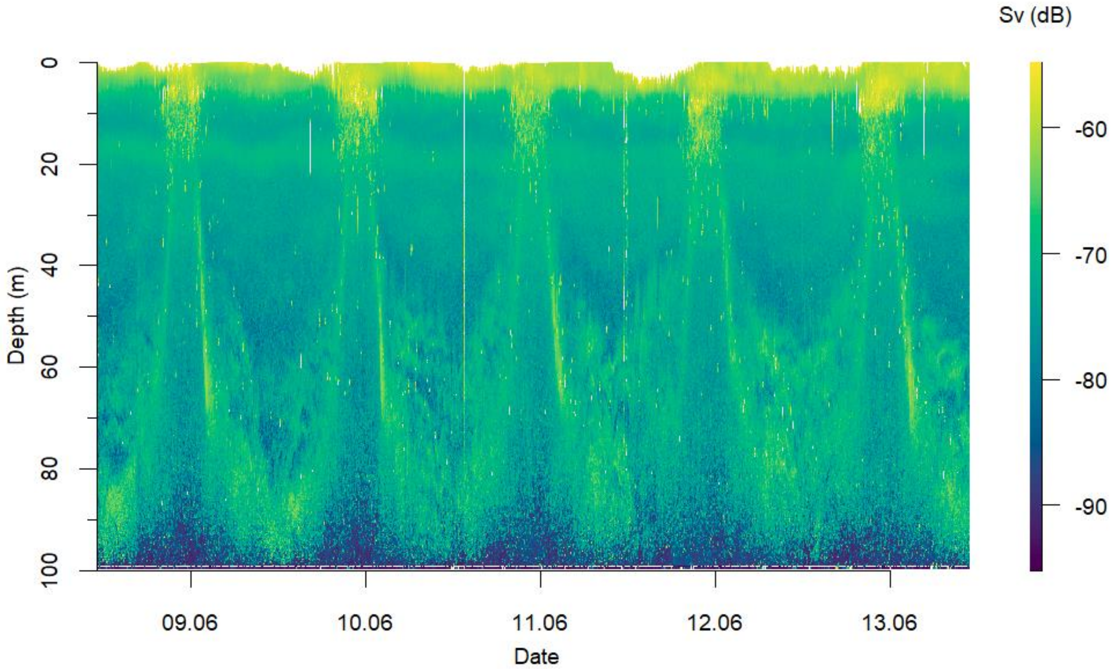

Figure 3.27. Acoustic data collected during May phase 1 (08-13 June) using a 200 kHz echosounder mounted at the bottom of Midtmeie station. The horizontal axis displays the date, whereas the vertical axis displays depth (m). The colour bar displays volume backscattering strength (Sv) with a threshold set from -95 to -55 dB. The white colouring found near the surface on the echogram represents stronger echo than -55 dB.

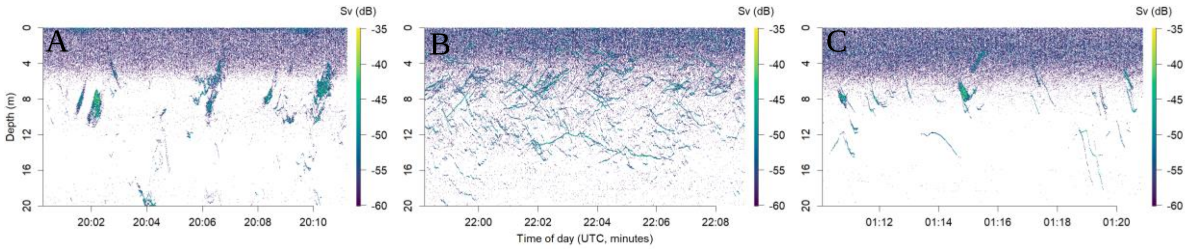

Figure 3.28. Echograms displaying fish activity in the upper waters during the June new moon night (10-11 June). The horizontal axis displays hours and minutes (UTC), whereas the vertical axis displays depth (m). The colour bars display volume backscattering strength (Sv) with a threshold set from -60 to -35 dB. The echograms display a depth range of 0-20 m. **A**: schooling fish during the evening before *M. norvegica* arrived. **B**: schools dispersing as *M. norvegica* arrived. **C**: fish re-emerging into schools after *M. norvegica* descended beyond 20 m. The stronger backscatter in the first ~6 m is unidentified echo.

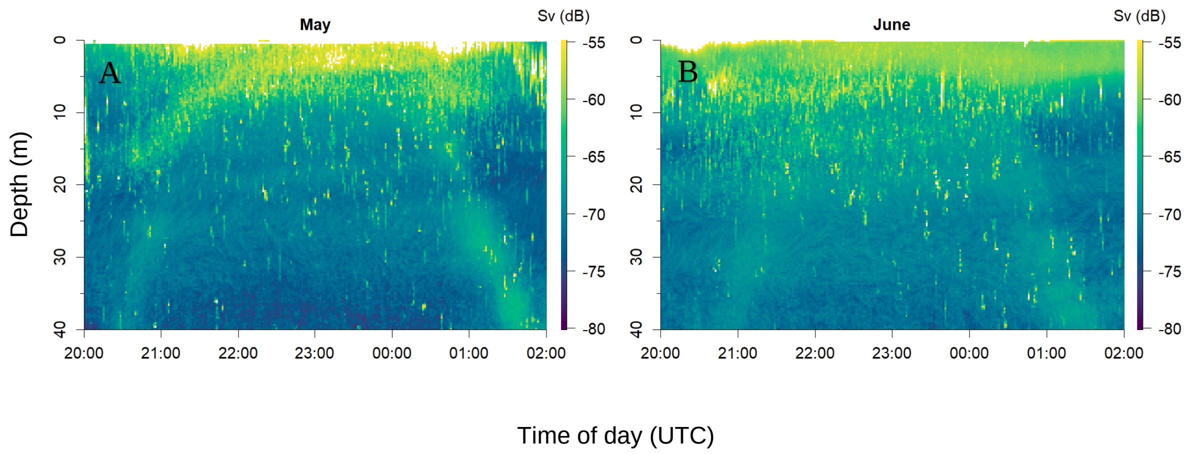

Figure 3.29. Acoustic data collected during the full moon in May (26-27 May) and new moon in June (10-11 June) during the study period using a 200 kHz echosounder mounted at the bottom of Midtmeie station. The horizontal axis displays the time of day (UTC), whereas the vertical axis displays depth (m). The colour bars display volume backscattering strength (Sv) with a threshold set from -80 to -55 dB. The white colouring found near the surface on the echograms represents stronger echo than -55 dB. The echograms display a depth range of 0-40 m. **A**: echogram displaying the ascent and descent of *M. norvegica* in the upper wates during the May full moon. **B**: echogram displaying the ascent and descent of *M. norvegica* in the upper waters during the June new moon.

3.3.6.2 Full moon period (20-25 June)

The weather changed from precipitation in the beginning of the recording period to light cloud cover towards the end (Table 2.9 & Appendix Table B.1). The moon was above the horizon during the period. As mentioned for May and the June new moon period, the bright summer nights made moonlight less apparent and reduced the potential effect on DVM behaviour of *M. norvegica*.

Scattering layer

Due to the position of the echosounder, the daytime distribution of *M. norvegica* could not be described. At ~10 m, there was a clear distinction between the waters above and below (Figure 3.30, Figure 3.31, Figure 3.32). This observation could be related to the freshwater input to the fjord creating a density difference. However, the reason for this echo was unclear, and will be referred to as unidentified.

At night, the scattering layer was observed below ~10 m. The highest density of *M. norvegica* was found around ~11-12 m (Figure 3.30 A).

M. norvegica remained in the upper waters for a median of ~4 hours, which was consistent throughout the recording period (except for 24-25 June, ~3 hours and 30 minutes). This observation differed from earlier in the month, where duration of stay was generally shorter (Appendix Table B.1).

Fish

Little to no fish were observed during the day. Similar to May and the June new moon period, a high density of schooling fish appeared in the evening, dispersing as *M. norvegica* arrived in the upper waters. This caused a clear avoidance in the scattering layer at night (Figure 3.31 A & B). The fish remained just above the scattering layer at ~8-10 m depth (Figure 3.30 A). Less fish were present in the morning as *M. norvegica* descended (Figure 3.31 C).

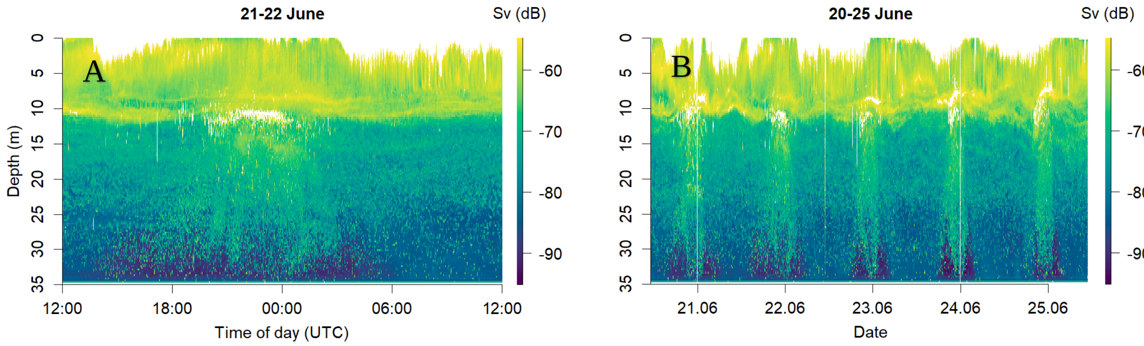

Figure 3.30. Acoustic data collected during the June full moon period using a 200 kHz floating rig-mounted echosounder at 38 m depth. The horizontal axis displays the time of day (UTC) and date, whereas the vertical axis displays depth (m). The colour bars display volume backscattering strength (Sv) with a threshold set from -95 to -55 dB. The white colouring found on the echograms represents stronger echo than -55 dB. **A**: 24-hour excerpt (noon-noon) from the recording period during the summer solstice (21 June). **B**: the entire recording from the June full moon period (20-25 June).

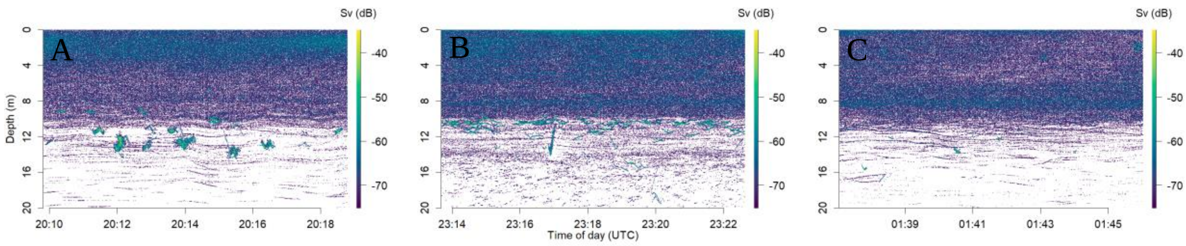

Figure 3.31. Echograms displaying fish activity in the upper waters during 21-22 June. The horizontal axis displays hours and minutes (UTC), whereas the vertical axis displays depth (m). The colour bars display volume backscattering strength (Sv) with a threshold set from -75 to -35 dB. The echograms display a depth range of 0-20 m. **A**: schooling fish during the evening before *M. norvegica* arrived. **B**: schools dispersing as *M. norvegica*

arrived. **C**: fish re-emerging into schools after *M. norvegica* descended beyond 20 m. The stronger backscatter in the first ~10 m is unidentified echo.

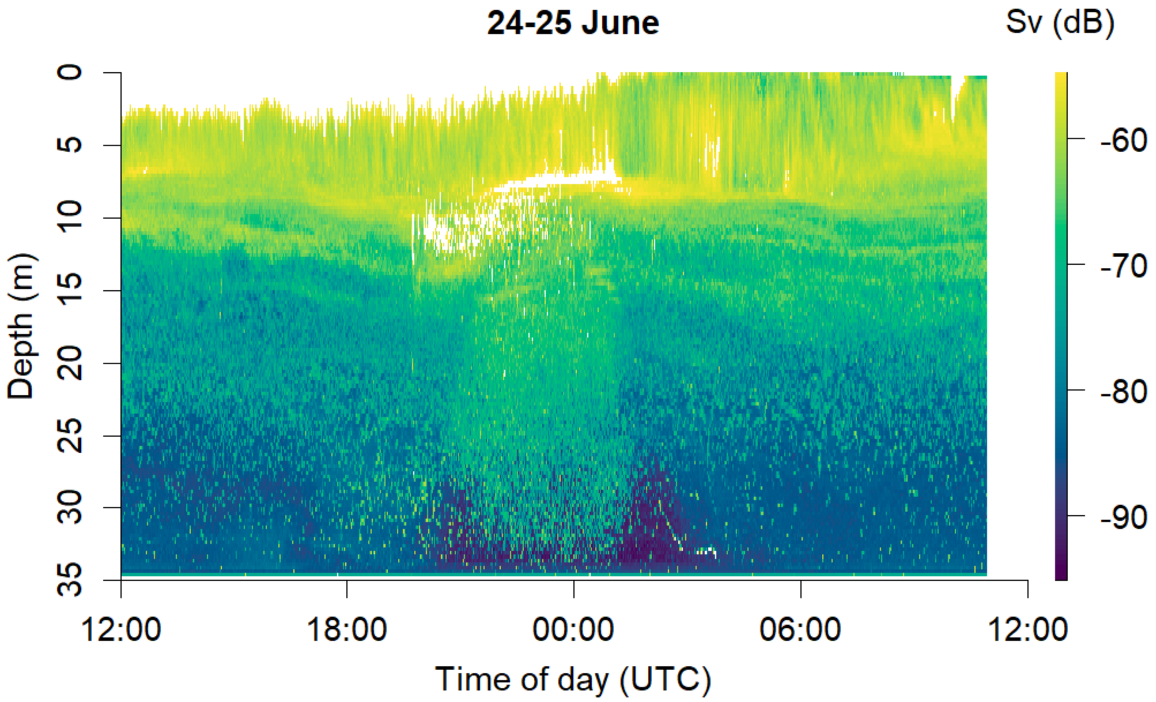

Figure 3.32. Acoustic data collected during the June full moon (24-25 June) using a 200 kHz floating rig-mounted echosounder at 38 m depth. The horizontal axis displays the time of day (UTC), whereas the vertical axis displays depth (m). The colour bar displays volume backscattering strength (Sv) with a threshold set from -95 to -55 dB. The white colouring found on the echogram represents stronger echo than -55 dB.

4. Discussion

The main aim of this study was to further understand the effects of light on diel vertical migration (DVM) of *Meganyctiphanes norvegica*, especially the differences between midsummer and midwinter nights in a higher latitude. Another question raised was how different moon phases at night during the dark winter could affect the nocturnal vertical distribution of the euphausiids. Overlap between potential predators and prey was also assessed relative to nocturnal light. These questions were studied by using an echosounder to obtain acoustic data throughout the entire water column at the study site in the inner Oslofjord. Environmental parameters were recorded with CTD, oxygen, fluorescence, and light extinction measurements, and trawls were performed to confirm the presence of *M. norvegica* in the sound scattering layer (SSL).

M. norvegica performed DVM with variations in behaviour throughout the study period, as seen in the acoustic data. During the day, the SSL ascribed to *M. norvegica* resided from ~40-100 m, depending on the month and season. At dusk, the scattering layer ascended to near-surface waters. At night, *M. norvegica* was widely distributed throughout most of the water column, which might be related to asynchronous migrations (Pearre, 2003). At dawn, the scattering layer descended to the daytime depth. Fish were present in the upper waters at night, being particularly abundant during summer. The echo data suggest that *M. norvegica* displayed antipredator behaviour by avoiding the upper layers during the night. In winter, this often resulted in *M. norvegica* sinking down to ~30 m depth. Moonlight from the full moon during winter seemed to have an impact on the nocturnal distribution of *M. norvegica* and the abundance of predators in the upper waters.

4.1 Hydrographical parameters and *in vivo* fluorescence

DVM was performed by *M. norvegica* regardless of season and varying hydrography, suggesting that there was little to no relation between DVM and the hydrographical parameters measured. The daytime distribution of *M. norvegica* varied somewhat throughout the study period, being shallower during spring and summer. Yet, the stable temperature and salinity below ~40 m for all months indicated that these parameters likely did not influence the daytime depth of *M. norvegica.* The night-time distribution in June may have been restricted by the density difference in the first ~10 m, as seen on Figure 3.30, Figure 3.31, and

Figure 3.32. The maximum value of *in vivo* fluorescence could have been an indicator of how shallow *M. norvegica* would need to migrate to find adequate amounts of food.

4.1.1 Temperature and salinity

Temperature is known to affect metabolic rates in the ectothermic *M. norvegica* (Fry, 1971). Ectothermic animals tend to conserve energy in colder waters to remain satiated during periods of less food availability (McLaren, 1963). In warmer waters, the growth rate and metabolic rate increases, increasing the need for energy (Fry, 1971). Despite of this, *M. norvegica* was seen ascending to the colder waters near the surface in the winter, migrating regardless of the vertical temperature profiles in the current study (Figure 3.1). This suggested that temperature did not affect their distribution nor migration pattern.

Brackish water at the surface is a typical characteristic of a fjord system due to freshwater input from land (Farmer & Freeland, 1983). *M. norvegica* has been reported by Buchholz and Boysen-Ennen (1988) to tolerate low salinity (~24 PSU), with larva capable of tolerating even lower levels. *M. norvegica* has been found to migrate through pycnoclines (Mauchline, 1969), while other findings resulted in the pycnocline being a barrier for vertical migration (Kaartvedt & Svendsen, 1990). In the current study, the salinity was as low as 17 PSU in June in the first 10 m (Figure 3.1), suggesting that it could potentially be avoided by *M. norvegica* during migration. Even so, it is difficult to distinguish between any hydrographical effects and nocturnal light in summer. Regardless, the noise in the acoustic records made it impossible to assess if *M. norvegica* migrated above 10 m in June (Figure 3.29 B).

4.1.2 Oxygen

There was little to no indication that neither the vertical migration nor daytime distribution of *M. norvegica* was limited by oxygen availability in the current study. Kaartvedt (2010) reported that the lower tolerable level of oxygen saturation at ~7 °C for *M. norvegica* was ~7% in the inner Oslofjord, creating a “false bottom” that constrained daytime distribution. Correspondingly, Onsrud and Kaartvedt (1998) found that an oxygen concentration of 1.3 ml L^{-1} did not limit DVM in *M. norvegica* in the inner Oslofjord. In the current study, the oxygen saturation remained relatively high in the deeper waters, and the scattering layer could be found residing down to ~100 m during certain recording periods (Figure 3.1 & Figure 3.9). This indicated that there were no limitations in the daytime distribution of *M. norvegica* regarding oxygen availability.

4.1.3 *In vivo* fluorescence

The *in vivo* fluorescence in the upper waters did not change much from winter to summer, with the highest level of fluorescence found in June (Figure 3.1). *M. norvegica* is known to feed on phytoplankton near the surface at night. Therefore, increased levels of fluorescence indicates improved feeding conditions and motivation to undergo DVM (Mauchline, 1969). Phytoplankton concentrations drastically diminish during winter (e.g. Eilertsen & Degerlund, 2010; Vestheim et al., 2014). However, *M. norvegica* continuously migrated throughout winter during the current study. The fluorescence in the upper waters indicated a presence of phytoplankton, despite the short and weakly illuminated winter days. Randelhoff et al. (2020) found that phytoplankton were still present in winter and growing despite sea ice hindering light infiltrating the water. Thus, the possible presence of phytoplankton in the current study, even if it was less than in the spring and summer, indicated that *M. norvegica* had access to food in the upper waters.

4.2 The impact of light

Light had an impact on DVM behaviour and the daytime distribution of *M. norvegica*. Overcast weather likely caused a wider distribution of the scattering layer during the day compared to a clear day. Larger individuals were generally found deeper during the day, possibly relating to them being at higher predation risk. Asynchronous migrations likely occurred during winter at night, causing a wide nocturnal distribution. Urban light pollution could have affected the nocturnal distribution of *M. norvegica*, causing a deepening effect during winter. Moonlight from the full moon in winter appeared to cause a deepening of the scattering layer at night, with many individuals staying beneath the upper layers that had an abundant presence of visual predators. The scattering layer migrated to near-surface waters, despite the nights becoming brighter towards summer. The findings suggested avoidance behaviour in *M. norvegica,* both during the full moon in winter and during the brighter summer nights when more visual predators were present.

4.2.1 Daytime distribution

The Euphotic zone (1% light attenuation) ranged between ~21 m in February and ~6 m in June, reflecting the varying light penetration to deeper waters throughout the study period (Figure 3.2). It was previously reported that the daytime depth of *M. norvegica* in the inner Oslofjord was generally below 70 m (Kaartvedt et al., 2002; Onsrud & Kaartvedt, 1998). In the current study, the distribution was shallower, reaching up to ~40-50 m in May and June

(Figure 3.9 D & E). In the winter and early spring (January, February, and March) the distribution was deeper, generally ranging from ~60 m (Figure 3.9 A, B, C).

Vestheim et al. (2014) found how the distribution of *M. norvegica* in the Oslofjord became shallower as the study site froze with snow covering the ice. Turbidity could also affect the daytime distribution, making *M. norvegica* reside deeper in clear waters with less turbidity and higher light penetration in the inner Oslofjord (Onsrud & Kaartvedt, 1998). In comparison to the current study, *M. norvegica* had a deeper distribution when the euphotic zone was lower and vice versa (Figure 3.2 & Figure 3.9), indicating that light extinction did influence the daytime distribution of *M. norvegica*.

Weather conditions also affect light at depth, and thus the daytime distribution of *M. norvegica* (Appendix Table B.1). An example of this was in March where the weather was mostly clear for the first three days of recording (Figure 3.19). Fog appeared for the next two days (Appendix Table B.1). This was reflected in the echo data as a lesser accumulation of *M. norvegica* was seen in the depths when the weather as overcast (Figure 3.19). Therefore, weather conditions likely had an impact on the daytime distribution of *M. norvegica* in the current study. Since light attenuation measurements were only performed during field excursions, there is a lack of data for the remainder of the days recorded with the echosounder.

4.2.2 Size distribution

The length and weight of *M. norvegica* individuals increased significantly with depth during daytime, while there was no significant variation in weight distribution for the night catches (Figure 3.6, Figure 3.7, Figure 3.8). Larger zooplankton are conspicuous and known to be selected first by for example the Atlantic herring (*Clupea harengus*) in low light conditions (Batty et al., 1990). Therefore, hiding in the deeper, darker waters would be advantageous for the larger individuals to avoid increased predation risk. Giske et al. (1990) found how zooplankton size across species increased with depth during daytime, which fits the trawl results from the current study. The individuals from the night trawl at 15 m depth had a wider range of length compared to other trawls, ranging from 15-40 mm (Figure 3.8). This size range corresponds with another study in the inner Oslofjord, where individuals of *M. norvegica* were measured from 15 mm to >30 mm (Onsrud & Kaartvedt, 1998). The wider size distribution could be related to reduced light levels from the new moon period in

February, which led to larger individuals migrating closer to the surface due to reduced predation risk.

4.2.3 Diel vertical migration and winter nights

M. norvegica performed DVM during winter throughout the study period, ascending and descending before sunset and sunrise (Appendix Table B.1). Further light measurements would be needed to confirm whether *M. norvegica* followed isolumes (cf. Onsrud & Kaartvedt, 1998), responded to rate of change (Ringelberg, 1995) or if ascent and descent was cued by a threshold of absolute light intensity at dusk and dawn (Frank & Widder, 1997).

After the ascent, *M. norvegica* was spread throughout the water column at night with individuals distributed from near-surface waters to the daytime depth (Figure 3.9 A & B). Correspondingly, Vestheim et al. (2014) found that *M. norvegica* ranged from the surface to ~75 m depth at night in a 150 m deep basin in the inner Oslofjord. Midnight sinking occurred during the winter in the current study, where a weak maximum of the scattering layer would sink down to ~20-30 m after the ascent, the remainder of the population spreading out in the water column below (Figure 3.9 A & B). This behaviour was in accordance with the hunger/satiation hypothesis, where satiated individuals would return to deeper waters, whereas hungry individuals would ascend to feed (Pearre, 1979). This pattern likely caused asynchronous feeding migrations over the course of the night and could explain the wide nocturnal distribution of *M. norvegica*.

Some individuals might not undergo DVM and will remain at their daytime depth throughout the night. In the current study, very few individuals appeared to remain at their daytime depth, but many returned shortly after the evening ascent in January and February (Figure 3.9 A & B). These could be individuals at high risk for predation, for example due to their larger size or individuals undergoing moulting, thus not feeding (De Robertis, 2002; Thomasson et al., 2003).

Light pollution from land affects nocturnal light levels in the Oslofjord, as demonstrated in Figure 4.1, a photo taken during the sampling in February. Snow-covered ground and clouds reflecting the urban lights made the skies appear much brighter than what would be expected on a winter night. Moore et al. (2000) reported that the depth distribution of *Daphnia* was greatly reduced from light pollution in a suburban lake. This phenomenon could affect the nocturnal distribution of *M. norvegica* as well.

To compensate for the lack of phytoplankton during winter, *M. norvegica* can act as a selectively feeding carnivore during this season (Abrahamsen et al., 2010; Kaartvedt et al., 2002). The stomach content of *M. norvegica* was not analysed in this study. Yet, it can be speculated that they fed on both phytoplankton and other zooplankton during the winter, based on previous findings. An experimental study by Torgersen (2001) described evidence for visual predation in *M. norvegica* feeding on zooplankton, which may allow daytime predation in deep waters (Kaartvedt et al., 2002; Torgersen, 2001). Therefore, some access to light at night during winter could be beneficial for *M. norvegica* hunting for prey in upper waters.

Figure 4.1. Image of urban light pollution from Midtmeie research station during winter (picture taken around 19:00 UTC).

Photo: Sara J. Thorsby (17.02 2021)

4.2.4 Diel vertical migration and summer nights

The short summer nights caused *M. norvegica* to remain in the upper waters for much shorter than in winter. Ascent and descent times seemed to follow the sun as during the winter and spring. Interestingly, while the nocturnal distribution of *M. norvegica* ranged widely throughout the water column, they still appeared to migrate to near-surface waters despite the brighter summer nights in the inner Oslofjord (Figure 3.9 D & E).

The light level at the top of the scattering layer (~70 m depth) of *M. norvegica* during the day was estimated at 1.2 x 10^{-4} µmol m^{-2} s^{-1} in June in the study by Onsrud and Kaartvedt (1998), the isolume during the ascent having the same value. Prihartato et al. (2016) measured the nocturnal surface irradiance in early summer (May & June) to be between 10^{-1}-10^{-3} µmol m^{-2} s^{-1} in Masfjorden, Norway, at ~60°N. In the current study, the euphotic zone (1% light attenuation, i.e. a light level of 10^{-3} µmol m^{-2} s^{-1} with surface light of 10^{-1} m^{-2} s^{-1}) was found between 6-14 m at the same time of year. This suggests higher nocturnal near-surface light levels than experienced by *M. norvegica* at their daytime depth. Noise in the upper 10 m in June made it difficult to see how far *M. norvegica* migrated, while results from late May showed that the euphausiid did indeed migrate into the euphotic zone. It could be reasoned that the motivation to undergo DVM to feed on nutritious phytoplankton was greater than the possible elevated predation risk in the brighter months. Yet, *M. norvegica* migrated to shallower depths during a night in May when clouds were present compared to a cloud-free night (Figure 3.24).

Trawl catches in the Kattegat documented that *M. norvegica* ascended to 30-5 m during summer (Tarling et al., 1999b). Tarling (2003) found that female *M. norvegica* spent 4 hours in the upper waters (15-0 m) at night during midsummer in the Clyde Sea. Therefore, there is evidence that *M. norvegica* do migrate to the upper waters during bright summer nights at higher latitudes (though slightly lower than the Oslofjord), which coincides with the findings in the current study.

A comparison can be drawn between the full moon during winter and a cloudy night in May. According to Kaartvedt et al. (2019), surface light during the full moon is about one order of magnitude higher than light levels at the lower end of the daytime scattering layer of mesopelagic fish during an overcast night. Early midnight sinking occurred during the rising of the full moon in January in the current study (Figure 3.17 A), whereas the distribution of *M. norvegica* was shallower on the cloudy night in May (Figure 3.24 A). This strongly suggested a potential effect of moonlight intensity on DVM behaviour of *M. norvegica*.

4.2.5 The impact of moonlight and moon phases in winter

The results show a deepening effect on the scattering layer ascribed to *M. norvegica* during the full moon periods compared to the new moon periods in winter (Figure 3.17). Moonlight intensity during a bright or full moon has been reported by Denton (1990) to be 3 x 10^{-6} that of sunlight (i.e. 3 x 10^{-3} µmol quanta m^{-2} s^{-1}). Onsrud and Kaartvedt (1998) reported that the light level at noon in accordance with the upper boundary of *M. norvegica* in the inner Oslofjord in November varied between 1.3-2.3 x 10^{-4} µmol m^{-2} s^{-1} (at ~70 m) in two different years. Comparing these findings with the moonlight intensity at the surface from Denton (1990), the surface light during a full moon is ~1-2 order of magnitude higher than where *M. norvegica* resided during daytime in the study by Onsrud and Kaartvedt (1998). This means that more light is available in the upper waters during a full moon compared to the daytime depth of *M. norvegica*, which can put them at risk for increased visual predation at night, should they migrate (Onsrud et al., 2004). Therefore, the midnight sinking by *M. norvegica* during the January full moon period in the current study could act as predator avoidance behaviour. This was done to avoid the brighter near-surface waters with an increased presence of visual predators under the moonlight.

Various studies have reported that migrating deep scattering layers (generally mesopelagic fish) resided deeper in the water column during a full moon night compared to a new moon night or a night with lower light intensity (Clarke, 1973; Dietz, 1962). The migration patterns changed gradually with moon phases, where deeper distributions were seen when the illumination of the moon was past 50% (first or third quarter) (Dodson, 1990). Prihartato et al. (2016) concluded that the full moon had a significant deepening effect on the nocturnal distribution of the scattering layer (defined as mostly mesopelagic fish by Irigoien et al. (2014)) in their study. In the current study, the deeper distribution of *M. norvegica* during the full moon period corresponded with previous findings. While this result explains general patterns in nocturnal distributions of scattering layers, it appears to be valid even with varying taxonomic compositions. It can be discussed whether the observed nocturnal distribution was a result of increased presence of visual predators, an increase in light intensity, or a combination of both variables, which the results suggest is the most likely.

4.3 Predator-prey interactions

Throughout the study period, fish mostly stayed in the upper 20 m at night, yet were found sporadically throughout the entire water column (Figure 3.12, Figure 3.15, Figure 3.18, Figure 3.20, Figure 3.22, Figure 3.25, Figure 3.26, Figure 3.28, Figure 3.31). Fish such as Norway pout (*Trisopterus esmarkii*), Whiting (*Merlangius merlangus*), Atlantic herring (*Clupea harengus*), and Atlantic cod (*Gadhus morhua*) are typical predators of *M. norvegica* at the location of the current study (e.g. Onsrud et al., 2004; Solberg & Kaartvedt, 2017). The Norway pout resides deeper than whiting and herring, largely being associated with the bottom during the day, attacking *M. norvegica* from below (Onsrud et al., 2004). In the current study, a higher abundance of fish was seen above the scattering layer of *M. norvegica*. Some of the fish attacking *M. norvegica* here were shown to release gas bubbles on the echo readings (not shown), suggesting that these might be Atlantic herring (Solberg & Kaartvedt, 2014). The abundance of fish in the upper waters likely had a higher impact on the distribution of *M. norvegica* than single individuals of Norway pout in the deeper waters.

During the January full moon period, the increased presence of fish in the upper ~20 m (Figure 3.18 A) suggested high mortality risk imposed by both the abundance of fish and their likely more effective visual search for prey. As a response, *M. norvegica* seemed to avoid the surface by midnight sinking to lessen the risk of predation (Kaartvedt et al., 2019). This behaviour could explain the distribution of *M. norvegica* at night. During the February new moon period, less fish were observed in the upper waters (Figure 3.18 B), and the lesser light intensity would reduce their visual range. Thus, *M. norvegica* had the opportunity to migrate shallower due to reduced predation pressure. Even so, some fish were still present in the upper waters, suggesting that there was sufficient nocturnal light available for them to feed (Kaartvedt et al., 2009). Individuals of fish were also seen spread throughout the range of *M. norvegica* at night. The reason for this is uncertain, although bioluminescence from *M. norvegica* could make them detectable by planktivorous fish even in darker environments (Warrant & Adam Locket, 2004). Fish may also detect prey by mechanosensory in low light conditions, using the lateral-line system (e.g. Janssen, 1997; Janssen et al., 1995).

Schools of fish appeared in the evening during May and June recording periods in the upper ~20 m before *M. norvegica* ascended (Figure 3.26 A, Figure 3.28 A, Figure 3.31 A). Schools were generally not detected during daytime. It is possible that the observed schools in the evening migrated from other parts of the fjord to the research station, the fish being aware of the ascent of the scattering layer at this location being rich in *M. norvegica*. As *M. norvegica* arrived in the upper waters, the schools dispersed, individuals of fish displaying feeding behaviour, then remerging into schools at dawn once *M. norvegica* descended (Figure 3.26 B & C, Figure 3.28 B & C, Figure 3.31 B & C). Onsrud and Kaartvedt (1998) reported the same behaviour for schooling fish in their study in the inner Oslofjord.

During the recording periods in June at night, an increased number of fish were seen in the upper waters compared to May (Figure 3.26, Figure 3.28, Figure 3.31). During the June full moon period, antipredator responses from *M. norvegica* were seen during the night, the scattering layer swimming away from foraging fish (Figure 3.31 B). This response has been described as typical for *M. norvegica*, along with using darker waters as shelter (Simard & Harvey, 2010). The noise in the first 10 m during the June full moon period made it difficult to determine the nocturnal distribution of *M. norvegica* compared to fish (Figure 3.31). However, it appeared that *M. norvegica* remained a short distance from the surface. This could be a potential result of the presence of visual predators, forcing them to remain deeper due to increased light availability (Kaartvedt et al., 2019; Onsrud & Kaartvedt, 1998; Zaret & Suffern, 1976).

Conclusion

Using a bottom-mounted echosounder allowed for detailed, *in situ* assessment of the DVM pattern of *M. norvegica* in the inner Oslofjord. The population performed DVM throughout the study period with some variations, mainly relating to changes in light intensity both seasonally and within individual days and nights.

The hydrographical measurements likely did not affect neither the daytime nor nocturnal distribution of *M. norvegica*. The individual size and weight increased significantly with depth both from day and night trawls, suggesting that the larger, more conspicuous individuals hid in the depths to avoid visual predators.

The daytime distribution was likely affected by weather conditions. After the ascent, *M. norvegica* deepened their distribution in the upper waters during full moon nights compared to new moon nights in winter. This supported previous findings regarding the effects on moonlight on the nocturnal distribution of scattering layers. The abundance of visual predators in near-surface waters during full moon nights likely led to avoidance behaviour by *M. norvegica* performing midnight sinking.

Despite the brightness of the summer nights, *M. norvegica* migrated to the upper waters where visual predators were abundant, yet the scattering layer seemed to avoid the surface by some extent. Individuals of *M. norvegica* were seen swimming away from foraging fish. Based on these findings, it can be concluded that even small fluctuations in light affect DVM in *M. norvegica* in the Oslofjord.

Further studies could involve continuous measurements of light both during the day and night at the surface and in the water along with the echo recordings of the scattering layer. High resolution echo data in the upper waters for longer periods of time and across seasons could further display the nocturnal distribution of *M. norvegica* along with predator-prey relationships under varying light conditions. These implementations may reveal further detail in DVM behaviour of *M. norvegica* and the relationship with visual predators during the full moon to see if *M. norvegica* indeed are dancing in the moonlight.

References

Abrahamsen, M. B., Browman, H. I., Fields, D. M., & Skiftesvik, A. B. (2010). The three-dimensional prey field of the northern krill, *Meganyctiphanes norvegica*, and the escape responses of their copepod prey. *Marine Biology*, *157*(6), 1251-1258. https://doi.org/10.1007/s00227-010-1405-9

Andersen, V., & Nival, P. (1991). A model of the diel vertical migration of zooplankton based on euphausiids. *Journal of marine research*, *49*(1), 153-175.

Archibald, K. M., Siegel, D. A., & Doney, S. C. (2019). Modeling the Impact of Zooplankton Diel Vertical Migration on the Carbon Export Flux of the Biological Pump. *Global Biogeochemical Cycles*, *33*(2), 181-199. https://doi.org/https://doi.org/10.1029/2018GB005983

Askheim, S. (2021). *Indre Oslofjord*. Store norske leksikon. https://snl.no/Indre_Oslofjord

Balk, H. (2019). *Sonar4 and Sonar5-Pro post processing systems, operator manual version 606.16*.

Båmstedt, U., & Karlson, K. (1998). Euphausiid predation on copepods in coastal waters of the Northeast Atlantic. *Marine Ecology Progress Series*, *172*, 149-168.

Bandara, K., Varpe, Ø., Wijewardene, L., Tverberg, V., & Eiane, K. (2021). Two hundred years of zooplankton vertical migration research. *Biological Reviews*, *96*(4), 1547-1589. https://doi.org/https://doi.org/10.1111/brv.12715

Batty, R. S., Blaxter, J. H. S., & Richard, J. M. (1990). Light intensity and the feeding behaviour of herring, *Clupea harengus*. *Marine Biology*, *107*(3), 383-388. https://doi.org/10.1007/BF01313419

Berge, J. A., Amundsen, R., Gitmark, J. K., Gundersen, H., Haande, S., Johnsen, T. M., Kroglund, T., Ledang, A. B., Lømsland, E. R., & Staalstrøm, A. (2014). Overvåking av Indre Oslofjord i 2013.

Bogorov, B. (1946). Peculiarities of diurnal vertical migrations of zooplankton in polar seas. *Journal of marine research*, *6*(1), 25-32.

Boysen, E., & Buchholz, F. (1984). *Meganyctiphanes norvegica* in the Kattegat. *Marine Biology*, *79*(2), 195-207. https://doi.org/10.1007/BF00951828

Buchholz, F., & Boysen-Ennen, E. (1988). *Meganyctiphanes norvegica* (Crustacea: Euphausiacea) In the Kattegat: Studies on the horizontal distribution in relation to hydrography and zooplankton. *Ophelia*, *29*(1), 71-82. https://doi.org/10.1080/00785326.1988.10430820

Buchholz, F., Buchholz, C., Reppin, J., & Fischer, J. (1995). Diel vertical migrations of *Meganyctiphanes norvegica* in the Kattegat: Comparison of net catches and measurements with Acoustic Doppler Current Profilers. *Helgoländer wissenschaftliche Meeresuntersuchungen*, *49*(1), 849-866. https://doi.org/10.1007/BF02368407

Christiansen, B. (1993). A television and photographic survey of megafaunal abundance in Central Sognefjorden, Western Norway. *Sarsia*, *78*(1), 1-8. https://doi.org/10.1080/00364827.1993.10413515

Clarke, A., & Tyler, P. A. (2008). Adult Antarctic Krill Feeding at Abyssal Depths. *Current Biology*, *18*(4), 282-285. https://doi.org/https://doi.org/10.1016/j.cub.2008.01.059

Clarke, T. A. (1973). Some aspects of the ecology of lanternfishes (Myctophidae) in the Pacific Ocean near Hawaii. *Fishery Bulletin US*, *71*, 401-434.

Cohen, J. H., & Forward, R. B. (2016). Zooplankton diel vertical migration—a review of proximate control. *Oceanography and marine biology*, 89-122.

Dale, T., & Kaartvedt, S. (2000). Diel patterns in stage-specific vertical migration of *Calanus finmarchicus* in habitats with midnight sun. *ICES Journal of Marine Science*, *57*(6), 1800-1818. https://doi.org/10.1006/jmsc.2000.0961

De Robertis, A. (2002). Size-dependent visual predation risk and the timing of vertical migration: An optimization model. *Limnology and Oceanography*, *47*(4), 925-933. https://doi.org/https://doi.org/10.4319/lo.2002.47.4.0925

Denton, E. J. (1990). Light and vision at depths greater than 200 metres. *Light and life in the sea*, 127-148.

Dickson, R. R. (1972). On the Relationship Between Ocean Transparency and the Depth of Sonic Scattering Layers in the North Atlantic. *ICES Journal of Marine Science*, *34*(3), 416-422. https://doi.org/10.1093/icesjms/34.3.416

Dietz, R. S. (1962). The Sea's Deep Scattering Layers. *Scientific American*, *207*(2), 44-51. http://www.jstor.org.ezproxy.uio.no/stable/24936635

Dodson, S. (1990). Predicting diel vertical migration of zooplankton. *Limnology and Oceanography*, *35*(5), 1195-1200. https://doi.org/https://doi.org/10.4319/lo.1990.35.5.1195

Eilertsen, H. C., & Degerlund, M. (2010). Phytoplankton and light during the northern high-latitude winter. *Journal of Plankton Research*, *32*(6), 899-912. https://doi.org/10.1093/plankt/fbq017

Evans, R. A., & Hopkins, C. C. E. (1981). Distribution and standing stock of zooplankton sound-scattering layers along the north Norwegian coast in February—March, 1978. *Sarsia*, *66*(2), 147-160. https://doi.org/10.1080/00364827.1981.10414532

Farmer, D. M., & Freeland, H. J. (1983). The physical oceanography of Fjords. *Progress in Oceanography*, *12*(2), 147-219. https://doi.org/https://doi.org/10.1016/0079-6611(83)90004-6

Fiksen, Ø., & Carlotti, F. (1998). A model of optimal life history and diel vertical migration in *Calanus finmarchicus*. *Sarsia*, *83*(2), 129-147. https://doi.org/10.1080/00364827.1998.10413678

Foote, K. G., Knudsen, H. P., & Vestnes, G. (1987). *Calibration of acoustic instruments FDR fish density estimation: a practical guide* (8774827537).

Frank, T., & Widder, E. (2002). Effects of a decrease in downwelling irradiance on the daytime vertical distribution patterns of zooplankton and micronekton. *Marine Biology*, *140*(6), 1181-1193. https://doi.org/10.1007/s00227-002-0788-7

Frank, T. M., & Widder, E. A. (1997). The correlation of downwelling irradiance and staggered vertical igration patterns of zooplankton in Wilkinson Basin, Gulf of Maine. *Journal of Plankton Research*, *19*(12), 1975-1991. https://doi.org/10.1093/plankt/19.12.1975

Fry, F. E. J. (1971). The effect of environmental factors on the physiology of fish. In *Fish Physiology* (Vol. 6, pp. 1-98). Elsevier.

Giske, J., Aksnes, D. L., Baliño, B. M., Kaartvedt, S., Lie, U., Nordeide, J. T., Salvanes, A. G. V., Wakili, S. M., & Aadnesen, A. (1990). Vertical distribution and trophic interactions of zooplankton and fish in Masfjorden, Norway. *Sarsia*, *75*(1), 65-81.

Greene, C. H., Widder, E. A., Youngbluth, M. J., Tamse, A., & Johnson, G. E. (1992). The migration behavior, fine structure, and bioluminescent activity of krill sound-scattering layers. *Limnology and Oceanography*, *37*(3), 650-658. https://doi.org/https://doi.org/10.4319/lo.1992.37.3.0650

Greene, C. H., Wiebe, P. H., Burczynski, J., & Youngbluth, M. J. (1988). Acoustical Detection of High-Density Krill Demersal Layers in the Submarine Canyons off Georges Bank. *Science*, *241*(4863), 359-361. https://doi.org/doi:10.1126/science.241.4863.359

Hassel, A., Endresen, B., Martinussen, M., Knutsen, T., & Johannessen, M. E. (2013). *Håndbok for prøvetaking og pre-analyse av plankton*.

Hays, G. C. (2003). *A review of the adaptive significance and ecosystem consequences of zooplankton diel vertical migrations* Dordrecht.

Huse, I., & Ona, E. (1996). Tilt angle distribution and swimming speed of overwintering Norwegian spring spawning herring. *ICES Journal of Marine Science*, *53*(5), 863-873. https://doi.org/10.1006/jmsc.1996.9999

Iida, K., Mukai, T., & Hwang, D. (1996). Relationship between acoustic backscattering strength and density of zooplankton in the sound-scattering layer. *ICES Journal of Marine Science*, *53*(2), 507-512. https://doi.org/10.1006/jmsc.1996.0073

Irigoien, X., Klevjer, T. A., Røstad, A., Martinez, U., Boyra, G., Acuña, J. L., Bode, A., Echevarria, F., Gonzalez-Gordillo, J. I., Hernandez-Leon, S., Agusti, S., Aksnes, D. L., Duarte, C. M., & Kaartvedt, S. (2014). Large mesopelagic fishes biomass and trophic efficiency in the open ocean. *Nature Communications*, *5*(1), 3271. https://doi.org/10.1038/ncomms4271

Janssen, J. (1997). Comparison of response distance to prey via the lateral line in the ruffe and yellow perch. *Journal of Fish Biology*, *51*(5), 921-930. https://doi.org/https://doi.org/10.1111/j.1095-8649.1997.tb01531.x

Janssen, J., Jones, W. R., Whang, A., & Oshel, P. E. (1995). Use of the lateral line in particulate feeding in the dark by juvenile alewife (*Alosa pseudoharengus*). *Canadian Journal of Fisheries and Aquatic Sciences*, *52*(2), 358-363. https://doi.org/10.1139/f95-037

Johnsen, G. H., & Jakobsen, P. J. (1987). The effect of food limitation on vertical migration in *Daphnia longispina*. *Limnology and Oceanography*, *32*(4), 873-880. https://doi.org/https://doi.org/10.4319/lo.1987.32.4.0873

Kaartvedt, S. (2008). Photoperiod may constrain the effect of global warming in arctic marine systems. *Journal of Plankton Research*, *30*(11), 1203-1206. https://doi.org/10.1093/plankt/fbn075

Kaartvedt, S. (2010). Chapter Nine - Diel Vertical Migration Behaviour of the Northern Krill (*Meganyctiphanes norvegica* Sars). In G. A. Tarling (Ed.), *Advances in Marine Biology* (Vol. 57, pp. 255-275). Academic Press. https://doi.org/https://doi.org/10.1016/B978-0-12-381308-4.00009-1

Kaartvedt, S., Langbehn, T. J., & Aksnes, D. L. (2019). Enlightening the ocean's twilight zone. *ICES Journal of Marine Science*, *76*(4), 803-812. https://doi.org/10.1093/icesjms/fsz010

Kaartvedt, S., Larsen, T., Hjelmseth, K., & Onsrud, M. S. (2002). Is the omnivorous krill *Meganyctiphanes norvegica* primarily a selectively feeding carnivore? *Marine Ecology Progress Series*, *228*, 193-204.

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

Kaartvedt, S., Røstad, A., Fiksen, Ø., Melle, W., Torgersen, T., Breien, M. T., & Klevjer, T. A. (2005). Piscivorous fish patrol krill swarms. *Marine Ecology Progress Series*, *299*, 1-5.

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

Kaartvedt, S., & Svendsen, H. (1990). Advection of euphausiids in a Norwegian fjord system subject to altered freshwater input by hydro-electric power production. *Journal of Plankton Research*, *12*(6), 1263-1277. https://doi.org/10.1093/plankt/12.6.1263

Kelley, D., & Richards, C. (2022). *ocedata: Oceanographic Data Sets for 'oce' Package*. Dan Kelley. https://CRAN.R-project.org/package=ocedata

Kelley, D., Richards, C., Layton, C., & British Geological Survey. (2022). *oce: Analysis of Oceanographic Data*. Dan Kelley. https://CRAN.R-project.org/package=oce

Klevjer, T. A., Irigoien, X., Røstad, A., Fraile-Nuez, E., Benítez-Barrios, V. M., & Kaartvedt, S. (2016). Large scale patterns in vertical distribution and behaviour of mesopelagic scattering layers. *Scientific Reports*, *6*(1), 19873. https://doi.org/10.1038/srep19873

Klevjer, T. A., & Kaartvedt, S. (2003). Split-beam target tracking can be used to study the swimming behaviour of deep-living plankton in situ. *Aquatic Living Resources*, *16*(3), 293-298. https://doi.org/10.1016/S0990-7440(03)00013-5

Kongsberg maritime Simrad. ((n.d.)). *Simrad ES200-7C split-beam transducer* [Brochure]. https://www.simrad.online/td_200/es200_7c/sales/es200_7c_ds_en_a4.pdf

Lane, A. P., & Irvine, W. M. (1973). Monochromatic phase curves and albedos for the lunar disk. *The Astronomical Journal*, *78*, 267.

Lass, S., Tarling, G. A., Virtue, P., Matthews, J. B., Mayzaud, P., & Buchholz, F. (2001). On the food of northern krill *Meganyctiphanes norvegica* in relation to its vertical distribution. *Marine Ecology Progress Series*, *214*, 177-200.

Last, Kim S., Hobbs, L., Berge, J., Brierley, Andrew S., & Cottier, F. (2016). Moonlight Drives Ocean-Scale Mass Vertical Migration of Zooplankton during the Arctic Winter. *Current Biology*, *26*(2), 244-251. https://doi.org/https://doi.org/10.1016/j.cub.2015.11.038

LI-COR. (2022). *Light measurement - the standard for over 50 years* [Brochure]. https://licor.app.boxenterprise.net/s/3bjwy50xsb49jqof0wz4

Longhurst, A. R., & Glen Harrison, W. (1989). The biological pump: Profiles of plankton production and consumption in the upper ocean. *Progress in Oceanography*, *22*(1), 47-123. https://doi.org/https://doi.org/10.1016/0079-6611(89)90010-4

Mauchline, J. (1967). The distribution of the euphausiid crustacean *Meganyctiphanes norvegica*. *Serial Atlas of The Marine Environment*, *13*, 2.

Mauchline, J. (1969). The biology of the euphausiids. *Advances in Marine Biology*, *7*, 1-454.

Mauchline, J. (1980). The biology of mysids and euphausiids. Part 2. The biology of euphausids. *Advances in Marine Biology*, *18*, 372-623.

McLaren, I. A. (1963). Effects of Temperature on Growth of Zooplankton, and the Adaptive Value of Vertical Migration. *Journal of the Fisheries Research Board of Canada*, *20*(3), 685-727. https://doi.org/10.1139/f63-046

Moore, M. V., Pierce, S. M., Walsh, H. M., Kvalvik, S. K., & Lim, J. D. (2000). Urban light pollution alters the diel vertical migration of *Daphnia*. *Internationale Vereinigung für theoretische und angewandte Limnologie: Verhandlungen*, *27*(2), 779-782.

Norheim, E., Klevjer, T. A., & Aksnes, D. L. (2016). Evidence for light-controlled migration amplitude of a sound scattering layer in the Norwegian Sea. *Marine Ecology Progress Series*, *551*, 45-52.

Ochoa, J., Maske, H., Sheinbaumc, J., & Candela, J. (2013). Diel and lunar cycles of vertical migration extending to below 1000 m in the ocean and the vertical connectivity of depth-tiered populations. *Limnology and Oceanography*, *58*(4), 1207-1214. https://doi.org/https://doi.org/10.4319/lo.2013.58.4.1207

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

Onsrud, M. S. R., Kaartvedt, S., Røstad, A., & Klevjer, T. A. (2004). Vertical distribution and feeding patterns in fish foraging on the krill *Meganyctiphanes norvegica*. *ICES*

Journal of Marine Science, *61*(8), 1278-1290. https://doi.org/10.1016/j.icesjms.2004.09.005

Pagés, F., & Gili, J.-M. (1991). *Vertical distribution of epipelagic siphonophores at the confluence between Benguela waters and the Angola Current over 48 hours* Dordrecht.

Palmer, G., & Johnsen, S. (2015). Downwelling spectral irradiance during evening twilight as a function of the lunar phase. *Applied Optics*, *54*(4), B85-B92. https://doi.org/10.1364/AO.54.000B85

Pearre, S. (2003). Eat and run? The hunger/satiation hypothesis in vertical migration: history, evidence and consequences. *Biological Reviews*, *78*(1), 1-79. https://doi.org/10.1017/S146479310200595X

Pearre, S., Jr. (1979). Problems of detection and interpretation of vertical migration. *Journal of Plankton Research*, *1*(1), 29-44. https://doi.org/10.1093/plankt/1.1.29

Posit. (2022). *RStudio is now Posit, our mission continues*. Posit. https://posit.co/

Prihartato, P. K., Irigoien, X., Genton, M. G., & Kaartvedt, S. (2016). Global effects of moon phase on nocturnal acoustic scattering layers. *Marine Ecology Progress Series*, *544*, 65-75.

R Core Team. (2022). *R-4.2.2 for Windows*. R Foundation for Statistical Computing. https://cran.r-project.org/bin/windows/base/

Randelhoff, A., Lacour, L., Marec, C., Leymarie, E., Lagunas, J., Xing, X., Darnis, G., Penkerc'h, C., Sampei, M., Fortier, L., D'Ortenzio, F., Claustre, H., & Babin, M. (2020). Arctic mid-winter phytoplankton growth revealed by autonomous profilers. *Science Advances*, *6*(39). https://doi.org/10.1126/sciadv.abc2678

Ringelberg, J. (1995). Changes in Light Intensity and Diel Vertical Migration: a Comparison of Marine and Freshwater Environments. *Journal of the Marine Biological Association of the United Kingdom*, *75*(1), 15-25. https://doi.org/10.1017/S0025315400015162

Rosenberg, R., Gray, J. S., Josefson, A. B., & Pearson, T. H. (1987). Petersen's benthic stations revisited. II. Is the Oslofjord and eastern Skagerrak enriched? *Journal of Experimental Marine Biology and Ecology*, *105*(2), 219-251. https://doi.org/https://doi.org/10.1016/0022-0981(87)90174-2

Saborowski, R., Bröhl, S., Tarling, G., & Buchholz, F. (2002). Metabolic properties of Northern krill, *Meganyctiphanes norvegica*, from different climatic zones. I.

Respiration and excretion. *Marine Biology*, *140*(3), 547-556. https://doi.org/10.1007/s00227-001-0730-4

Sameoto, D. D. (1982). Zooplankton and Micronekton Abundance in Acoustic Scattering Layers on the Nova Scotian Slope. *Canadian Journal of Fisheries and Aquatic Sciences*, *39*(5), 760-777. https://doi.org/10.1139/f82-104

Sars, M. (1857). Om 3 nye norske Krebsdyr. *Förhandlimgar vid det Skandinaviska Naturforskaremötet*, *7*, 160-175.

Savigny, J. (1816). *Mémoires sur les animaux sans vertèbres*. G. Dufour.

Simard, Y., & Harvey, M. (2010). Chapter Ten - Predation on Northern Krill (*Meganyctiphanes norvegica* Sars). In G. A. Tarling (Ed.), *Advances in Marine Biology* (Vol. 57, pp. 277-306). Academic Press. https://doi.org/https://doi.org/10.1016/B978-0-12-381308-4.00010-8

Solberg, I., & Kaartvedt, S. (2014). Surfacing behavior and gas release of the physostome sprat (*Sprattus sprattus*) in ice-free and ice-covered waters. *Marine Biology*, *161*(2), 285-296. https://doi.org/10.1007/s00227-013-2334-1

Solberg, I., & Kaartvedt, S. (2017). The diel vertical migration patterns and individual swimming behavior of overwintering sprat *Sprattus sprattus*. *Progress in Oceanography*, *151*, 49-61. https://doi.org/https://doi.org/10.1016/j.pocean.2016.11.003

Sourisseau, M., Simard, Y., & Saucier, F. J. (2008). Krill diel vertical migration fine dynamics, nocturnal overturns, and their roles for aggregation in stratified flows. *Canadian Journal of Fisheries and Aquatic Sciences*, *65*(4), 574-587. https://doi.org/10.1139/f07-179

Spicer, J. I., Thomasson, M. A., & Strömberg, J.-O. (1999). Possessing a poor anaerobic capacity does not prevent the diel vertical migration of Nordic krill *Meganyctiphanes norvegica* into hypoxic waters. *Marine Ecology Progress Series*, *185*, 181-187.

Staalstrøm, A., Engesmo, A., Andersen, G. S., Gran, S., Borgersen, G., Moy, S. R., Valestrand, L., Brooks, S., Hylland, K., & Holth, T. F. (2021). Undersøkelse av hydrografiske og biologiske forhold i Indre Oslofjord Årsrapport 2020. *NIVA-rapport*.

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

Tarling, G. A., Buchholz, F., & Matthews, J. B. L. (1999a). The effect of lunar eclipse on the vertical migration behaviour of *Meganyctiphanes norvegica* (Crustacea: Euphausiacea) in the Ligurian Sea. *Journal of Plankton Research*, *21*(8), 1475-1488. https://doi.org/10.1093/plankt/21.8.1475

Tarling, G. A., Cuzin-Roudy, J., & Buchholz, F. (1999b). Vertical migration behaviour in the northern krill *Meganyctiphanes norvegica* is influenced by moult and reproductive processes. *Marine Ecology Progress Series*, *190*, 253-262. https://www.int-res.com/abstracts/meps/v190/p253-262/

Tarling, G. A., Ensor, N. S., Fregin, T., Goodall-Copestake, W. P., & Fretwell, P. (2010). Chapter One - An Introduction to the Biology of Northern Krill (*Meganyctiphanes norvegica* Sars). In G. A. Tarling (Ed.), *Advances in Marine Biology* (Vol. 57, pp. 1-40). Academic Press. https://doi.org/https://doi.org/10.1016/B978-0-12-381308-4.00001-7

Thomasson, M., Johnson, M., Strömberg, J.-O., & Gaten, E. (2003). Swimming capacity and pleopod beat rate as a function of sex, size and moult stage in Northern krill *Meganyctiphanes norvegica*. *Marine Ecology Progress Series*, *250*, 205-213.

Thorsnæs, G. (2021). *Oslofjorden*. Store norske leksikon. https://snl.no/Oslofjorden

Time and Date. (2022). *timeanddate*. https://www.timeanddate.com/

Torgersen, T. (2001). Visual predation by the euphausiid *Meganyctiphanes norvegica*. *Marine Ecology Progress Series*, *209*, 295-299.

Torres, J. J., & Childress, J. J. (1983). Relationship of oxygen consumption to swimming speed in *Euphausia pacifica*. *Marine Biology*, *74*(1), 79-86. https://doi.org/10.1007/BF00394278

Vestheim, H., Røstad, A., Klevjer, T. A., Solberg, I., & Kaartvedt, S. (2014). Vertical distribution and diel vertical migration of krill beneath snow-covered ice and in ice-free waters. *Journal of Plankton Research*, *36*(2), 503-512. https://doi.org/10.1093/plankt/fbt112

Warrant, E. J., & Adam Locket, N. (2004). Vision in the deep sea. *Biological Reviews*, *79*(3), 671-712. https://doi.org/10.1017/S1464793103006420

Youngbluth, M. J., Bailey, T. G., Davoll, P. J., Jacoby, C. A., Blades-Eckelbarger, P. I., & Griswold, C. A. (1989). Fecal pellet production and diel migratory behavior by the euphausiid *Meganyctiphanes norvegica* effect benthic-pelagic coupling. *Deep Sea*

Research Part A. Oceanographic Research Papers, *36*(10), 1491-1501. https://doi.org/https://doi.org/10.1016/0198-0149(89)90053-8

Zaret, T. M., & Suffern, J. S. (1976). Vertical migration in zooplankton as a predator avoidance mechanism. *Limnology and Oceanography*, *21*(6), 804-813. https://doi.org/https://doi.org/10.4319/lo.1976.21.6.0804

Appendix

Appendix A. *M. norvegica* length and weight measurements from IKMT trawls throughout the study period

Appendix Table A.1. Length (mm) and weight (g) measurements of subsamples of *M. norvegica* from IKMT trawling in January 2021. Depth intervals where length and weight are marked with NA were not performed this month. Individuals measuring 0 g were too light for the scale to measure.

Number of individual	Length (mm)	Weight (g)	Depth (m)
1	36	0.25	50
2	40	0.30	50
3	36	0.25	50
4	37	0.25	50
5	37	0.45	50
6	40	0.30	50
7	34	0.30	50
8	37	0.25	50
9	38	0.25	50
10	31	0.15	50
11	35	0.25	50
12	38	0.30	50
13	27	0.10	50
14	39	0.25	50
15	38	0.25	50
16	37	0.25	50
17	37	0.35	50
18	25	0.05	50
19	38	0.25	50
20	40	0.30	50
21	37	0.30	50
22	37	0.20	50
23	40	0.35	50
24	38	0.25	50
25	42	0.55	50
26	35	0.25	50
27	37	0.30	50
28	38	0.35	50
29	35	0.20	50
30	41	0.35	50
31	32	0.20	50
32	34	0.20	50
33	39	0.30	50

34	37	0.15	50
NA	NA	NA	60
1	43	0.40	70
2	36	0.20	70
3	33	0.20	70
4	37	0.25	70
5	40	0.30	70
6	40	0.35	70
7	38	0.30	70
8	38	0.25	70
9	37	0.30	70
10	43	0.40	70
11	42	0.40	70
12	44	0.45	70
13	44	0.40	70
14	42	0.35	70
15	37	0.25	70
16	40	0.35	70
17	31	0.15	70
18	43	0.35	70
19	36	0.25	70
20	45	0.40	70
21	42	0.45	70
22	41	0.35	70
23	36	0.20	70
24	39	0.35	70
25	38	0.30	70
26	38	0.25	70
27	38	0.20	70
28	30	0.15	70
29	34	0.20	70
30	40	0.30	70
31	41	0.25	70
32	37	0.25	70
33	32	0.15	70
34	37	0.30	70
35	36	0.20	70
36	40	0.30	70
37	39	0.25	70
38	42	0.30	70
39	44	0.40	70
40	35	0.20	70
41	37	0.30	70

42	40	0.35	70
43	38	0.25	70
44	43	0.40	70
45	40	0.25	70
46	33	0.15	70
47	33	0.15	70
48	36	0.20	70
49	40	0.35	70
50	40	0.30	70
1	44	0.45	80
2	40	0.35	80
3	42	0.35	80
4	44	0.45	80
5	42	0.40	80
6	37	0.25	80
7	43	0.40	80
8	41	0.35	80
9	36	0.15	80
10	42	0.35	80
11	38	0.25	80
12	43	0.40	80
13	39	0.35	80
14	36	0.25	80
15	39	0.30	80
16	41	0.35	80
17	38	0.25	80
18	39	0.30	80
19	38	0.25	80
20	44	0.40	80
21	40	0.30	80
22	41	0.40	80
23	40	0.30	80
24	40	0.30	80
25	40	0.35	80
26	42	0.40	80
27	40	0.35	80
28	38	0.30	80
29	41	0.30	80
30	39	0.25	80
31	37	0.30	80
32	40	0.30	80
33	38	0.35	80
34	42	0.40	80

35	42	0.45	80
36	36	0.25	80
37	40	0.20	80
38	35	0.20	80
39	38	0.35	80
40	40	0.35	80
41	40	0.25	80
42	42	0.40	80
43	37	0.25	80
44	40	0.30	80
45	43	0.45	80
46	37	0.25	80
47	37	0.30	80
48	38	0.35	80
49	38	0.35	80
50	38	0.30	80
1	37	0.30	90
2	40	0.35	90
3	38	0.35	90
4	41	0.35	90
5	38	0.25	90
6	44	0.40	90
7	47	0.50	90
8	43	0.35	90
9	41	0.35	90
10	40	0.30	90
11	40	0.30	90
12	41	0.40	90
13	43	0.50	90
14	41	0.35	90
15	42	0.40	90
16	43	0.40	90
17	35	0.20	90
18	40	0.35	90
19	42	0.35	90
20	40	0.30	90
21	41	0.35	90
22	40	0.35	90
23	40	0.30	90
24	42	0.30	90
25	40	0.25	90
26	43	0.50	90
27	39	0.25	90

28	40	0.30	90
29	43	0.45	90
30	40	0.30	90
31	40	0.35	90
32	40	0.35	90
33	40	0.40	90
34	41	0.40	90
35	42	0.35	90
36	35	0.25	90
37	40	0.30	90
38	37	0.25	90
39	38	0.40	90
40	40	0.30	90
41	40	0.35	90
42	42	0.45	90
43	38	0.30	90
44	43	0.55	90
45	37	0.30	90
46	40	0.40	90
47	40	0.35	90
48	42	0.40	90
49	38	0.35	90
50	40	0.35	90

Appendix table A.2. Length (mm) and weight (g) measurements of subsamples of *M. norvegica* from IKMT trawling in February 2021. Depth intervals where length and weight are marked with NA were not performed this month. Individuals measuring 0 g were too light for the scale to measure.

Number of individual	Length (mm)	Weight (g)	Depth (m)
NA	NA	NA	50
NA	NA	NA	60
1	20	0.05	70
2	25	0.05	70
3	27	0.10	70
4	37	0.30	70
5	35	0.25	70
6	35	0.25	70
7	27	0.15	70
8	21	0.05	70
9	37	0.30	70
10	24	0.05	70
11	24	0.05	70
12	35	0.20	70

13	30	0.15	70
14	35	0.25	70
15	37	0.25	70
16	27	0.10	70
17	39	0.25	70
18	37	0.25	70
19	29	0.10	70
20	23	0.05	70
21	28	0.10	70
22	39	0.35	70
23	30	0.10	70
24	25	0.05	70
25	35	0.20	70
26	34	0.20	70
27	26	0.05	70
28	27	0.10	70
29	34	0.15	70
30	35	0.20	70
31	35	0.25	70
32	25	0.10	70
33	30	0.10	70
34	40	0.25	70
35	27	0.10	70
36	33	0.15	70
37	34	0.15	70
38	28	0.10	70
39	35	0.20	70
40	39	0.30	70
41	34	0.15	70
42	23	0.05	70
43	29	0.10	70
44	28	0.10	70
45	33	0.20	70
46	25	0.10	70
47	18	0.05	70
48	28	0.10	70
49	23	0.05	70
50	24	0.05	70
51	25	0.05	70
52	18	0.00	70
1	39	0.40	80
2	41	0.40	80
3	32	0.20	80
4	37	0.75	80
5	35	0.25	80
6	38	0.30	80

7	37	0.30	80
8	35	0.25	80
9	34	0.20	80
10	29	0.10	80
11	39	0.25	80
12	37	0.25	80
13	40	0.30	80
14	39	0.35	80
15	38	0.30	80
16	35	0.20	80
17	33	0.15	80
18	38	0.25	80
19	33	0.15	80
20	38	0.30	80
21	37	0.20	80
22	26	0.05	80
23	32	0.15	80
24	44	0.45	80
25	44	0.25	80
26	23	0.05	80
27	36	0.20	80
28	38	0.25	80
29	36	0.25	80
30	38	0.25	80
31	44	0.40	80
32	36	0.25	80
33	40	0.35	80
34	37	0.20	80
35	36	0.25	80
36	40	0.30	80
37	40	0.35	80
38	36	0.25	80
39	36	0.20	80
40	39	0.35	80
41	43	0.45	80
42	39	0.30	80
43	30	0.15	80
44	39	0.35	80
45	35	0.25	80
46	37	0.25	80
47	39	0.25	80
48	40	0.25	80
49	35	0.30	80
50	39	0.35	80
1	40	0.30	90
2	39	0.30	90

3	37	0.25	90
4	43	0.40	90
5	42	0.35	90
6	41	0.30	90
7	40	0.30	90
8	38	0.30	90
9	38	0.35	90
10	39	0.25	90
11	43	0.35	90
12	37	0.25	90
13	40	0.35	90
14	40	0.30	90
15	39	0.30	90
16	33	0.15	90
17	37	0.30	90
18	40	0.35	90
19	22	0.05	90
20	39	0.40	90
21	40	0.35	90
22	40	0.30	90
23	33	0.15	90
24	40	0.40	90
25	43	0.40	90
26	37	0.25	90
27	39	0.25	90
28	38	0.25	90
29	43	0.35	90
30	40	0.30	90
31	38	0.30	90
32	37	0.35	90
33	37	0.30	90
34	36	0.30	90
35	41	0.35	90
36	38	0.25	90
37	40	0.40	90
38	34	0.20	90
39	34	0.20	90
40	43	0.45	90
41	35	0.25	90
42	36	0.30	90
43	35	0.25	90
44	37	0.35	90
45	36	0.20	90
46	45	0.50	90
47	27	0.10	90
48	21	0.05	90

49	36	0.20	90
50	42	0.40	90

Appendix Table A.3. Length (mm) and weight (g) measurements of subsamples of M. norvegica from IKMT trawling in March 2021. Depth intervals where length and weight are marked with NA were not performed this month. Individuals measuring 0 g were too light for the scale to measure.

Number of individual	Length (mm)	Weight (g)	Depth (m)
NA	NA	NA	50
NA	NA	NA	60
1	26	0.10	70
2	37	0.25	70
3	40	0.35	70
4	30	0.15	70
5	37	0.25	70
6	38	0.30	70
7	35	0.20	70
8	40	0.35	70
9	36	0.25	70
10	41	0.35	70
11	42	0.35	70
12	40	0.30	70
13	40	0.30	70
14	40	0.35	70
15	31	0.15	70
16	36	0.30	70
17	37	0.30	70
18	40	0.30	70
19	25	0.10	70
20	31	0.15	70
21	41	0.30	70
22	33	0.15	70
23	39	0.30	70
24	30	0.15	70
25	28	0.10	70
26	36	0.30	70
27	25	0.10	70
28	34	0.20	70
29	42	0.35	70
30	35	0.25	70
31	28	0.10	70
32	35	0.25	70
33	32	0.15	70
34	31	0.15	70
35	31	0.15	70

36	25	0.05	70
37	35	0.20	70
38	37	0.30	70
39	36	0.25	70
40	36	0.25	70
41	41	0.40	70
42	30	0.15	70
43	30	0.15	70
44	25	0.05	70
45	35	0.25	70
46	32	0.15	70
47	37	0.25	70
48	34	0.20	70
49	23	0.05	70
50	27	0.05	70
51	22	0.05	70
52	21	0.05	70
53	30	0.15	70
54	30	0.10	70
55	40	0.25	70
56	35	0.30	70
1	27	0.10	80
2	44	0.45	80
3	41	0.30	80
4	34	0.20	80
5	34	0.20	80
6	33	0.20	80
7	39	0.35	80
8	40	0.35	80
9	39	0.30	80
10	40	0.40	80
11	32	0.20	80
12	28	0.05	80
13	29	0.05	80
14	31	0.15	80
15	30	0.05	80
16	37	0.30	80
17	40	0.25	80
18	40	0.20	80
19	41	0.35	80
20	31	0.10	80
21	30	0.15	80
22	37	0.35	80
23	37	0.30	80
24	37	0.30	80
25	32	0.15	80

26	39	0.30	80
27	39	0.25	80
28	25	0.05	80
29	32	0.10	80
30	31	0.15	80
31	38	0.30	80
32	33	0.10	80
33	31	0.10	80
34	42	0.30	80
35	33	0.15	80
36	37	0.20	80
37	25	0.05	80
38	38	0.25	80
39	42	0.30	80
40	37	0.20	80
41	28	0.10	80
42	35	0.20	80
43	37	0.25	80
44	38	0.30	80
45	40	0.30	80
46	33	0.15	80
47	42	0.30	80
48	39	0.30	80
49	27	0.05	80
50	36	0.20	80
1	40	0.25	90
2	38	0.25	90
3	41	0.30	90
4	41	0.40	90
5	40	0.30	90
6	37	0.30	90
7	36	0.25	90
8	30	0.10	90
9	37	0.25	90
10	36	0.25	90
11	40	0.30	90
12	33	0.20	90
13	35	0.20	90
14	36	0.25	90
15	40	0.40	90
16	36	0.30	90
17	37	0.25	90
18	37	0.35	90
19	39	0.35	90
20	38	0.30	90
21	40	0.30	90

22	40	0.30	90
23	39	0.40	90
24	38	0.30	90
25	36	0.25	90
26	40	0.35	90
27	40	0.35	90
28	38	0.35	90
29	37	0.30	90
30	40	0.35	90
31	37	0.25	90
32	27	0.15	90
33	33	0.15	90
34	30	0.15	90
35	35	0.30	90
36	38	0.35	90
37	38	0.35	90
38	40	0.35	90
39	34	0.20	90
40	34	0.30	90
41	31	0.20	90
42	38	0.30	90
43	37	0.30	90
44	30	0.15	90
45	26	0.10	90
46	38	0.30	90
47	39	0.30	90
48	28	0.10	90
49	27	0.10	90
50	39	0.35	90

Appendix Table A.4. Length (mm) and weight (g) measurements of subsamples of M. norvegica from IKMT trawling in May 2021. Depth intervals where length and weight are marked with NA were not performed this month. Individuals measuring 0 g were too light for the scale to measure.

Number of individual	Length (mm)	Weight (g)	Depth (m)
NA	NA	NA	50
NA	NA	NA	60
1	38	0.40	70
2	38	0.40	70
3	40	0.45	70
4	39	0.30	70
5	39	0.30	70
6	40	0.45	70
7	40	0.40	70
8	38	0.40	70

9	36	0.00	70
10	35	0.25	70
11	27	0.15	70
12	33	0.25	70
13	32	0.20	70
14	32	0.20	70
15	33	0.25	70
16	33	0.25	70
17	35	0.25	70
18	38	0.40	70
19	37	0.35	70
20	35	0.25	70
21	31	0.20	70
22	35	0.25	70
23	33	0.25	70
24	33	0.20	70
25	32	0.20	70
26	33	0.25	70
27	32	0.20	70
28	35	0.25	70
29	35	0.25	70
30	30	0.15	70
31	37	0.35	70
32	28	0.15	70
33	35	0.25	70
34	33	0.20	70
35	35	0.25	70
36	33	0.20	70
37	30	0.15	70
38	28	0.15	70
39	30	0.20	70
40	30	0.20	70
41	33	0.25	70
42	36	0.30	70
43	36	0.30	70
44	38	0.40	70
45	36	0.30	70
46	37	0.35	70
47	31	0.20	70
48	33	0.25	70
49	30	0.15	70
50	32	0.20	70
1	40	0.30	80
2	39	0.35	80
3	38	0.30	80
4	39	0.25	80

5	39	0.30	80
6	41	0.40	80
7	33	0.20	80
8	36	0.20	80
9	40	0.35	80
10	37	0.40	80
11	41	0.30	80
12	38	0.35	80
13	42	0.40	80
14	42	0.30	80
15	40	0.35	80
16	39	0.35	80
17	31	0.25	80
18	36	0.30	80
19	42	0.40	80
20	42	0.40	80
21	42	0.40	80
22	36	0.30	80
23	42	0.45	80
24	41	0.40	80
25	35	0.20	80
26	35	0.20	80
27	43	0.40	80
28	42	0.45	80
29	40	0.35	80
30	35	0.25	80
31	37	0.30	80
32	32	0.20	80
33	41	0.35	80
34	43	0.35	80
35	37	0.30	80
36	33	0.25	80
37	40	0.40	80
38	40	0.35	80
39	37	0.25	80
40	33	0.25	80
41	43	0.40	80
42	37	0.35	80
43	40	0.35	80
44	36	0.30	80
45	37	0.30	80
46	33	0.20	80
47	40	0.30	80
48	39	0.25	80
49	38	0.30	80
50	39	0.30	80

1	39	0.30	90
2	39	0.35	90
3	35	0.35	90
4	38	0.40	90
5	43	0.45	90
6	42	0.40	90
7	40	0.30	90
8	43	0.35	90
9	40	0.35	90
10	36	0.30	90
11	33	0.25	90
12	36	0.40	90
13	35	0.35	90
14	35	0.30	90
15	36	0.35	90
16	30	0.20	90
17	37	0.25	90
18	41	0.30	90
19	35	0.20	90
20	37	0.35	90
21	42	0.40	90
22	34	0.20	90
23	40	0.35	90
24	42	0.40	90
25	40	0.40	90
26	40	0.30	90
27	38	0.30	90
28	38	0.30	90
29	40	0.35	90
30	41	0.35	90
31	38	0.25	90
32	40	0.45	90
33	42	0.45	90
34	33	0.25	90
35	41	0.35	90
36	37	0.30	90
37	42	0.40	90
38	30	0.20	90
39	44	0.45	90
40	37	0.30	90
41	41	0.45	90
42	40	0.35	90
43	38	0.45	90
44	39	0.40	90
45	40	0.40	90
46	36	0.30	90

47	36	0.25	90
48	43	0.40	90
49	40	0.30	90
50	35	0.25	90

Appendix Table A.5. Length (mm) and weight (g) measurements of subsamples of *M. norvegica* from IKMT trawling in June 2021. Depth intervals where length and weight are marked with NA were not performed this month. Individuals measuring 0 g were too light for the scale to measure.

Number of individual	Length (mm)	Weight (g)	Depth (m)
NA	NA	NA	50
1	41	0.40	60
2	36	0.30	60
3	38	0.35	60
4	42	0.45	60
5	34	0.25	60
6	42	0.40	60
7	42	0.45	60
8	40	0.35	60
9	40	0.40	60
10	42	0.50	60
11	40	0.35	60
12	42	0.50	60
13	38	0.40	60
14	40	0.40	60
15	39	0.35	60
16	37	0.30	60
17	39	0.35	60
18	38	0.35	60
19	40	0.35	60
20	33	0.20	60
21	41	0.35	60
22	37	0.25	60
23	34	0.25	60
24	38	0.30	60
25	40	0.30	60
26	39	0.35	60
27	34	0.25	60
28	37	0.25	60
29	41	0.35	60
30	41	0.40	60
31	40	0.40	60
32	40	0.45	60
33	38	0.30	60
34	37	0.30	60

35	36	0.30	60
36	38	0.30	60
37	33	0.25	60
38	35	0.30	60
39	33	0.25	60
40	36	0.35	60
41	37	0.30	60
42	40	0.40	60
43	36	0.35	60
44	42	0.35	60
45	37	0.30	60
46	37	0.35	60
47	32	0.25	60
48	31	0.25	60
49	31	0.20	60
50	33	0.20	60
1	43	0.50	70
2	40	0.30	70
3	42	0.40	70
4	38	0.35	70
5	40	0.35	70
6	40	0.30	70
7	40	0.40	70
8	40	0.35	70
9	41	0.40	70
10	33	0.25	70
11	40	0.50	70
12	36	0.20	70
13	37	0.25	70
14	39	0.35	70
15	40	0.35	70
16	39	0.35	70
17	39	0.35	70
18	38	0.25	70
19	42	0.35	70
20	34	0.25	70
21	40	0.40	70
22	36	0.30	70
23	39	0.30	70
24	42	0.35	70
25	40	0.40	70
26	40	0.40	70
27	42	0.35	70
28	45	0.40	70
29	43	0.30	70
30	37	0.30	70

31	40	0.35	70
32	38	0.35	70
33	35	0.30	70
34	33	0.20	70
35	37	0.20	70
36	35	0.30	70
37	39	0.25	70
38	36	0.35	70
39	38	0.25	70
40	39	0.45	70
41	41	0.40	70
42	41	0.40	70
43	38	0.45	70
44	39	0.30	70
45	41	0.45	70
46	40	0.40	70
47	33	0.40	70
48	41	0.40	70
49	40	0.40	70
50	37	0.30	70
1	40	0.45	80
2	37	0.30	80
3	40	0.35	80
4	42	0.45	80
5	36	0.30	80
6	42	0.45	80
7	37	0.35	80
8	40	0.40	80
9	40	0.45	80
10	35	0.30	80
11	42	0.50	80
12	35	0.35	80
13	42	0.45	80
14	39	0.40	80
15	40	0.45	80
16	38	0.40	80
17	37	0.35	80
18	39	0.35	80
19	35	0.45	80
20	32	0.25	80
21	41	0.40	80
22	40	0.40	80
23	42	0.45	80
24	42	0.40	80
25	42	0.50	80
26	41	0.40	80

27	40	0.35	80
28	38	0.40	80
29	39	0.40	80
30	41	0.45	80
31	38	0.40	80
32	33	0.25	80
33	42	0.40	80
34	45	0.50	80
35	41	0.40	80
36	42	0.50	80
37	38	0.35	80
38	39	0.35	80
39	43	0.40	80
40	42	0.45	80
41	41	0.40	80
42	40	0.35	80
43	40	0.40	80
44	38	0.35	80
45	39	0.30	80
46	40	0.35	80
47	41	0.40	80
48	40	0.50	80
49	41	0.40	80
50	40	0.35	80
1	36	0.30	90
2	43	0.45	90
3	35	0.20	90
4	39	0.35	90
5	40	0.35	90
6	43	0.40	90
7	39	0.35	90
8	42	0.45	90
9	36	0.30	90
10	40	0.30	90
11	33	0.20	90
12	37	0.25	90
13	40	0.40	90
14	36	0.25	90
15	38	0.30	90
16	33	0.20	90
17	40	0.30	90
18	33	0.20	90
19	40	0.35	90
20	40	0.35	90
21	32	0.20	90
22	41	0.45	90

23	40	0.40	90
24	40	0.40	90
25	41	0.35	90
26	36	0.35	90
27	39	0.35	90
28	34	0.15	90
29	40	0.35	90
30	36	0.30	90
31	40	0.40	90
32	36	0.25	90
33	37	0.25	90
34	31	0.20	90
35	36	0.25	90
36	37	0.30	90
37	36	0.25	90
38	40	0.40	90
39	42	0.40	90
40	39	0.35	90
41	35	0.25	90
42	42	0.45	90
43	36	0.35	90
44	40	0.35	90
45	37	0.25	90
46	41	0.35	90
47	40	0.35	90
48	38	0.30	90
49	42	0.40	90
50	38	0.30	90

Appendix Table A.6. Length (mm) and weight (g) measurements of subsamples of *M. norvegica* from IKMT night trawling in February 2021. Depth intervals where length and weight are marked with NA were not performed this month. Individuals measuring 0 g were too light for the scale to measure.

Number of individual	Length (mm)	Weight (g)	Depth (m)
1	17	0.00	15
2	28	0.10	15
3	28	0.10	15
4	33	0.15	15
5	24	0.05	15
6	22	0.05	15
7	27	0.10	15
8	30	0.15	15
9	25	0.10	15
10	25	0.10	15
11	30	0.10	15

12	25	0.05	15
13	22	0.05	15
14	37	0.30	15
15	25	0.10	15
16	23	0.05	15
17	28	0.10	15
18	26	0.10	15
19	25	0.10	15
20	30	0.10	15
21	29	0.10	15
22	40	0.35	15
23	30	0.10	15
24	35	0.25	15
25	21	0.05	15
26	26	0.05	15
27	20	0.05	15
28	39	0.30	15
29	40	0.30	15
30	16	0.05	15
31	21	0.05	15
32	24	0.05	15
33	24	0.05	15
34	39	0.30	15
35	30	0.15	15
36	25	0.05	15
37	30	0.10	15
38	29	0.05	15
39	25	0.05	15
1	40	0.30	30
2	37	0.25	30
3	41	0.35	30
4	36	0.25	30
5	40	0.40	30
6	37	0.30	30
7	41	0.35	30
8	40	0.40	30
9	40	0.30	30
10	41	0.35	30
11	40	0.30	30
12	37	0.30	30
13	36	0.20	30
14	31	0.15	30
15	26	0.15	30
16	36	0.30	30
17	38	0.35	30
18	35	0.30	30

19	29	0.15	30
20	39	0.35	30
21	42	0.40	30
22	33	0.25	30
23	35	0.25	30
24	43	0.50	30
25	30	0.25	30
26	35	0.20	30
27	30	0.15	30
28	38	0.30	30
29	37	0.25	30
30	35	0.25	30
31	38	0.25	30
32	42	0.30	30
33	37	0.25	30
34	44	0.40	30
35	31	0.20	30
36	37	0.25	30
37	35	0.25	30
38	39	0.25	30
39	40	0.25	30
40	36	0.20	30
41	39	0.30	30
42	38	0.25	30
43	38	0.25	30
44	40	0.30	30
45	35	0.25	30
46	36	0.25	30
47	39	0.25	30
48	29	0.10	30
49	32	0.25	30
50	44	0.45	30
1	40	0.30	50
2	35	9.30	50
3	38	0.30	50
4	42	0.35	50
5	28	0.10	50
6	41	0.40	50
7	30	0.10	50
8	32	0.20	50
9	38	0.30	50
10	30	0.15	50
11	36	0.25	50
12	36	0.25	50
13	40	0.40	50
14	38	0.25	50

15	40	0.35	50
16	40	0.30	50
17	25	0.05	50
18	29	0.10	50
19	41	0.35	50
20	42	0.35	50
21	37	0.25	50
22	38	0.25	50
23	39	0.30	50
24	31	0.15	50
25	40	0.25	50
26	40	0.30	50
27	37	0.30	50
28	40	0.35	50
29	39	0.30	50
30	31	0.15	50
31	38	0.30	50
32	33	0.20	50
33	36	0.25	50
34	38	0.25	50
35	40	0.30	50
36	40	0.30	50
37	33	0.15	50
38	42	0.40	50
39	35	0.20	50
40	36	0.25	50
41	36	0.25	50
42	30	0.10	50
43	40	0.35	50
44	40	0.40	50
45	36	0.25	50
46	46	0.55	50
47	39	0.30	50
48	36	0.25	50
49	37	0.25	50
50	41	0.30	50

Appendix B. Solar data, DVM ascent/descent times and weather conditions during the study period

Appendix Table B.1. Overview of sunset and sunrise times throughout the study period, along with approximate ascent and descent start and stop times of the acoustic layer, and a summary of weather conditions. Ascent and descent times are not applicable for data from rig measurements. The information displayed below is from 12:00 UTC on the first date until 12:00 UTC on the second date. All times are displayed in UTC.

Date	Sunset	Sunrise	Ascent	Descent	Weather
22-23 Jan	15:06	07:49	14:00-16:00	07:00-08:30	Light rain, cloudy Wind: avg. 20 km/h Hi/lo temp: 3/-2°C
26-27 Jan	15:16	07:41	14:30-16:30	06:40-08:10	Passing clouds, light snow Wind: avg. 2 km/h Hi/lo temp: -8/-17°C
27-28 Jan	15:19	07:39	14:45-16:45	06:30-08:00	Passing clouds Wind: avg. 4 km/h Hi/lo temp: -8/-16°C
28-29 Jan	15:21	07:36	14:40-16:40	06:30-08:00	Passing clouds Wind: avg. 3 km/h Hi/lo temp: -11/-17°C
29-30 Jan	15:24	07:34	15:00-16:30	06:30-08:00	Cloudy, sleet Wind: avg. 2 km/h Hi/lo temp: -11/-15°C
09-10 Feb	15:53	07:07	15:30-17:00	05:00-07:30	Clear, partly cloudy Wind: avg. 10 km/h Hi/lo temp: -6/-19°C
10-11 Feb	15:55	07:05	15:40-17:10	05:00-07:40	Clear Wind: avg. 10 km/h Hi/lo temp: -6/-16°C
11-12 Feb	15:58	07:02	15:30-17:30	05:20-08:30	Clear Wind: avg. 10 km/h Hi/lo temp: -6/-18°C
16-17 Feb	16:11	06:48	15:40-17:00	05:00-07:45	Light snow Wind: avg. 10 km/h Hi/lo temp: -3/-5°C
17-18 Feb	16:14	06:46	15:50-17:10	05:45-08:00	Light snow Wind: avg. 7 km/h Hi/lo temp: -3/-5°C
22-23 Mar	17:36	05:09	17:00-18:30	03:30-05:30	Clear, passing clouds

					Wind: avg. 6 km/h Hi/lo temp: 11/-1°C
23-24 Mar	17:39	05:06	17:00-18:30	03:45-05:15	Clear, passing clouds Wind: avg. 20 km/h Hi/lo temp: 10/2°C
24-25 Mar	17:41	05:03	17:30-18:30	04:00-06:00	Clear, passing clouds Wind: avg. 15 km/h Hi/lo temp: 10/0°C
25-26 Mar	17:44	05:00	17:00-18:30	03:30-05:30	Clear, fog Wind: avg. 10 km/h Hi/lo temp: 8/-1°C
26-27 Mar	17:46	04:57	17:00-18:30	04:00-05:30	Light rain, fog Wind: avg. 22 km/h Hi/lo temp: 5/3°C
27-28 Mar	17:48	04:54	17:30-18:30	04:00-06:00	Clear, passing clouds Wind: avg. 15 km/h Hi/lo temp: 6/-3°C
28-29 Mar	17:51	04:51	17:00-18:30	04:00-06:00	Partly clear, light rain Wind: avg. 17 km/h Hi/lo temp: 11/3°C
29-30 Mar	17:53	04:48	17:30-19:00	04:00-06:00	Passing clouds Wind: avg. 15 km/h Hi/lo temp: 16/3°C
16-17 Apr	18:37	03:54	-	-	Clear, passing clouds Wind: avg. 15 km/h Hi/lo temp: 14/0°C
17-18 Apr	18:40	03:51	-	-	Clear, passing clouds Wind: avg. 10 km/h Hi/lo temp: 17/-1°C
18-19 Apr	18:42	03:48	-	-	Clear Wind: avg. 8 km/h Hi/lo temp: 17/-1°C
19-20 Apr	18:45	03:45	-	-	Clear Wind: avg. 10 km/h Hi/lo temp: 17/-1°C
23-24 May	20:06	02:20	18:30-21:15	01:30-03:00	Light rain, cloudy Wind: avg. 10 km/h Hi/lo temp: 14/7°C
24-25 May	20:08	02:18	18:20-21:30	01:15-03:00	Clear, light rain Wind: avg. 15 km/h

					Hi/lo temp: 14/7°C
25-26 May	20:10	02:16	19:45-21:10	01:00-02:45	Clear, light rain Wind: avg. 20 km/h Hi/lo temp: 13/8°C
26-27 May	20:12	02:15	19:30-21:00	00:15-02:15	Clear, partly cloudy Wind: avg. 15 km/h Hi/lo temp: 15/4°C
27-28 May	20:14	02:13	19:00-21:15	00:15-02:30	Passing clouds Wind: avg. 15 km/h Hi/lo temp: 22/3°C
08-09 Jun	20:34	01:57	20:00-21:45	00:15-02:15	Partly clear Wind: avg. 5 km/h Hi/lo temp: 24/11°C
09-10 Jun	20:35	01:57	19:50-21:15	00:20-02:15	Passing clouds Wind: avg. 15 km/h Hi/lo temp: 24/12°C
10-11 Jun	20:36	01:56	19:45-21:50	00:30-02:30	Partly clear Wind: avg. 20 km/h Hi/lo temp: 24/14°C
11-12 Jun	20:37	01:55	19:30-21:00	00:30-03:00	Passing clouds Wind: avg. 20 km/h Hi/lo temp: 22/11°C
12-13 Jun	20:38	01:55	20:00-22:00	01:00-03:00	Passing clouds Wind: avg. 10 km/h Hi/lo temp: 20/9°C
20-21 Jun	20:43	01:53	-	-	Broken clouds, light rain Wind: avg. 15 km/h Hi/lo temp: 17/12°C
21-22 Jun	20:43	01:54	-	-	Light rain, cloudy Wind: avg. 15 km/h Hi/lo temp: 17/11°C
22-23 Jun	20:23	01:54	-	-	Partly clear Wind: avg. 10 km/h Hi/lo temp: 22/12°C
23-24 Jun	20:43	01:54	-	-	Passing clouds Wind: avg. 10 km/h Hi/lo temp: 22/11°C
24-25 Jun	20:43	01:55	-	-	Passing clouds Wind: avg. 15 km/h Hi/lo temp: 22/10°C