Licence to Krill:

Diel Vertical Migration and the Pretador-Prey Interaction

between *Meganyctiphanes norvegica* and Fish in the Oslofjord

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Abstract

The pelagic zone is the largest ecosystem on Earth. The inhabitants of this ecosystem are not provided with any substances to hide behind. Diel vertical migration (DVM) is believed to be a trade-off between substantial feeding and minimal predation pressure. In the northern Atlantic, *Meganyctiphanes norvegica* is a key species in the marine food web, being important food for higher trophic levels such as fish, birds, and marine mammals. *M. norvegica* aggregations are common in Norwegian fjords, representing accessible ocean model systems in a sheltered environment.

This study's aim is to address M. norvegicas DVM in relation to the predator-prey interaction with fish in a shallow site, identifying when and where the fish will attack the krill and the krill's antipredator response. For this purpose, an upward-facing echosounder was placed at the seafloor in the Oslofjord, making continuous recordings of the krill and fish movements during this period. Hydrographical and light measurements were done, together with different types of net hauls performed to sample the target organisms. The organisms, including their stomach content, were analysed to investigate if they fed on krill.

The acoustic recordings showed DVM performance by the krill. During the daytime, the krill were attacked by fish schools from above, showing clear avoidance responses towards the fish. The krill layer concentrated near the seafloor during September and October, where they became vulnerable to predation by deep-living predators. The krill migrated towards the surface in the afternoon, followed by midnight sinking. At night, the fish interacted with the krill near the surface. Groups of fish were present throughout some nights and gathered as schools again in the morning. Single fish were also interacting with the krill both day and night as well. In the mornings, the fish descended after the krill.

The distribution of the krill seemed to be determined by the light intensities penetrating the water, both day and night. The daytime distribution was shallowest during the period with the highest light extinctions. During full moon events, the nocturnal distribution was deeper and vice versa. In lighter periods, the krill descend seemed to be blocked by the topography at the site. This is beneficial for the seafloor-related fish, which could visually forage more efficiently on the light-exposed krill. Krill is an important prey for fish in the Oslofjord.

Acknowledgements

I guess it is safe to say that the last two years with the COVID pandemic have been rough on many of us in regard of the restrictions, instability and uncertainties. I cannot express how grateful I am that my loved ones are all right and healthy.

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Thank you all for making this possible. I cannot wait for the next adventure!

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1. Introduction

1.1 The pelagic ecosystem

In Greek, pelagic means "open ocean" (Beaugrand, 2014). The pelagic realm covers 71% of our planet's surface (Beaugrand, 2014; Verity et al., 2002), with an overall volume of 1.33 trillion km^3 and an average depth of ~3.7 km, constituting the world's largest ecosystem (Beaugrand, 2014; Hylland & Vethaak, 2011). Pelagic organisms form the basis of several food webs within the ocean (Hylland & Vethaak, 2011). This ecosystem does not provide its inhabitants with anywhere to hide (Widder, 2002), apart from within plain sight (Johnsen, 2014). To be able to hide, the organisms have evolved adaptational mechanisms to become less noticeable to the predators (Vestheim & Kaartvedt, 2006). Such adaptations are physiological (e.g. transparency and crypsis) and behavioural, such as hiding within the darkness (Vestheim & Kaartvedt, 2006).

When the light hits and penetrates the surface, it is reflected, refracted, absorbed and scattered, leading to an exponential decrease of light intensities through the water (Widder, 2002). The primary producers are limited to the sunlit epipelagic zone (Angel, 1993), providing rich feeding grounds for planktonic species (Sato et al., 2013). Some planktonic species may leave the surface at day to reside at deeper depths (Sato et al., 2013). Limiting the surface visitations to nighttime are believed to be a trade-off between maximizing potential food intake and minimizing the predation risk (e.g. Burrows & Tarling, 2004; De Robertis, 2002; Kaartvedt, 2010; Pinti & Visser, 2019; Sato et al., 2013). Due to declining food availability and predation risk with depth (Burrows & Tarling, 2004). This behaviour is known as normal Diel Vertical Migration (DVM) and is part of the largest and most widespread animal migration on Earth (fig. 1) (Behrenfeld et al., 2019; Pinti & Visser, 2019). Cases of residency and reverse DVM (rDVM) (ascends at day and descends at night) exists as well (Pinti & Visser, 2019). However, DVM is usually limited to the upper 1000m of the water column, with some exceptions (Kaartvedt et al., 2020). The migrators face varieties of environmental conditions on their way through the water column, such as different light fields with optical variations, pressure, temperature (DeLeo & Bracken-Grissom, 2020), oxygen (Netburn & Koslow, 2015), and varying salinity (Lougee et al., 2002).
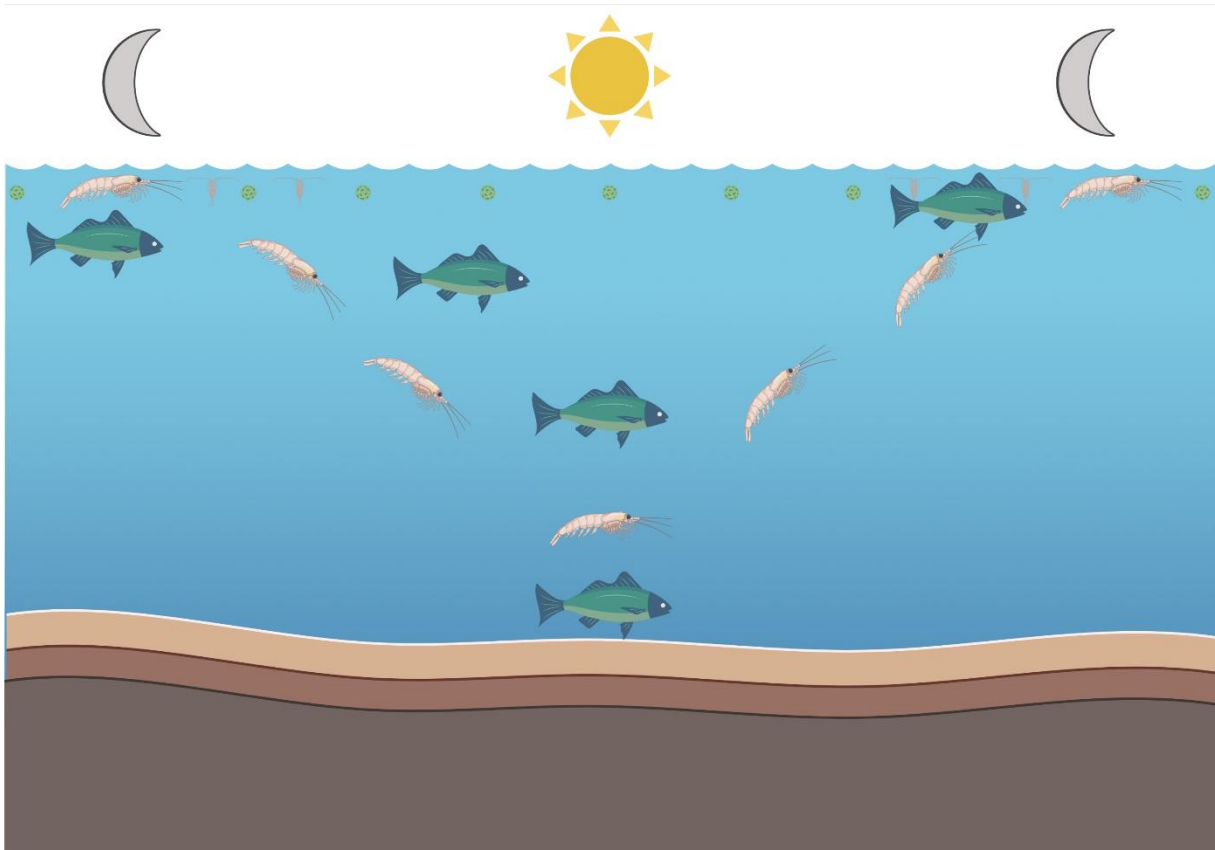
Figure 1: A simplified illustration of normal DVM by krill. Descending from the food-rich surface waters before dawn and residing within the depths during the day. Returning to the surface during the afternoon. The fish illustrates potential predators the krill are trying to avoid. Created with BioRender.com.

DVM has been a central topic to study for many years (Frank & Widder, 2002), where researchers have addressed both the proximate and ultimate explanations of the DVM behaviour (Berge et al., 2014a). DVM plays an important role in the contributions of biogeochemical processes in the biological pump (Berge et al., 2014a; Nocera et al., 2021) The biological pump is a process where the organic matter from the primary producers are exported from the surface waters to the depth by sinking, advection, vertical mixing and animal transport (Turner, 2015). The sinking speed of the matter depends on the size and the kind of primary producers, while ingestion and repacking of the matter can adjust the rate of export (Klevjer et al., 2016). When the DVM performers descend to several hundred meters, they actively transfer dissolved and particulate organic matter from the surface at night towards the seafloor at day (Darnis et al., 2017; Pinti & Visser, 2019). The migrators discharge the undigested carbon or nitrogen, while CO_2 and NH_4^+ are released through the organisms' respiration or excretion (Darnis et al., 2017).

On the return, the migraters transport energy and nutrients towards the surface again, enhancing the vertical coupling of our oceans (Klevjer et al., 2016).

1.2 Northern krill (*Meganyctiphanes norvegica*)

Zooplankton in the order Euphausiacea are important organisms in the pelagic zone, where they participate in diel vertical migration (DVM) (Boysen & Buchholz, 1984; Nicol, 1984). With their global distribution (Nocera et al., 2021), being especially important in the Antarctic seas, but also in the northern Atlantic (Klevjer & Kaartvedt, 2006), they play a central role as a keystone species (Cabrol et al., 2019; Klevjer & Kaartvedt, 2006). Here, they are a link allowing the transfer of energy and essential nutritional elements from the lower trophic levels in the marine food web to the consumers in the higher trophic levels (Cabrol et al., 2019; Greene et al., 1992), and therefore being a prominent prey in the diet of fish, birds and marine mammals (Kaartvedt et al., 2002). Three species dominate in the northern Atlantic krill communities: *Meganyctiphanes norvegica*, *Thysanoessa inermis* and *Thysanoessa raschii* (Cabrol et al., 2019). The focus of this thesis is *M. norvegica*, commonly known as Northern krill (fig. 2). This species is the largest and most widespread euphausiid in the northern hemisphere (Saborowski et al., 2002; Tarling et al., 1998), distributed from North America, over the shelf south of Greenland and Iceland, to the British Isles and the Norwegian Coast. The northernmost limits for this species are the Greenland Sea and the Barents Sea, while the southernmost limits are the Mediterranean Sea and Canary Islands (Schmidt, 2010). They usually inhabit depths between 100 and 500m during the daytime (Tarling et al., 2010), making them an adaptable species to a wide range of climatic conditions (Lass et al., 2001).
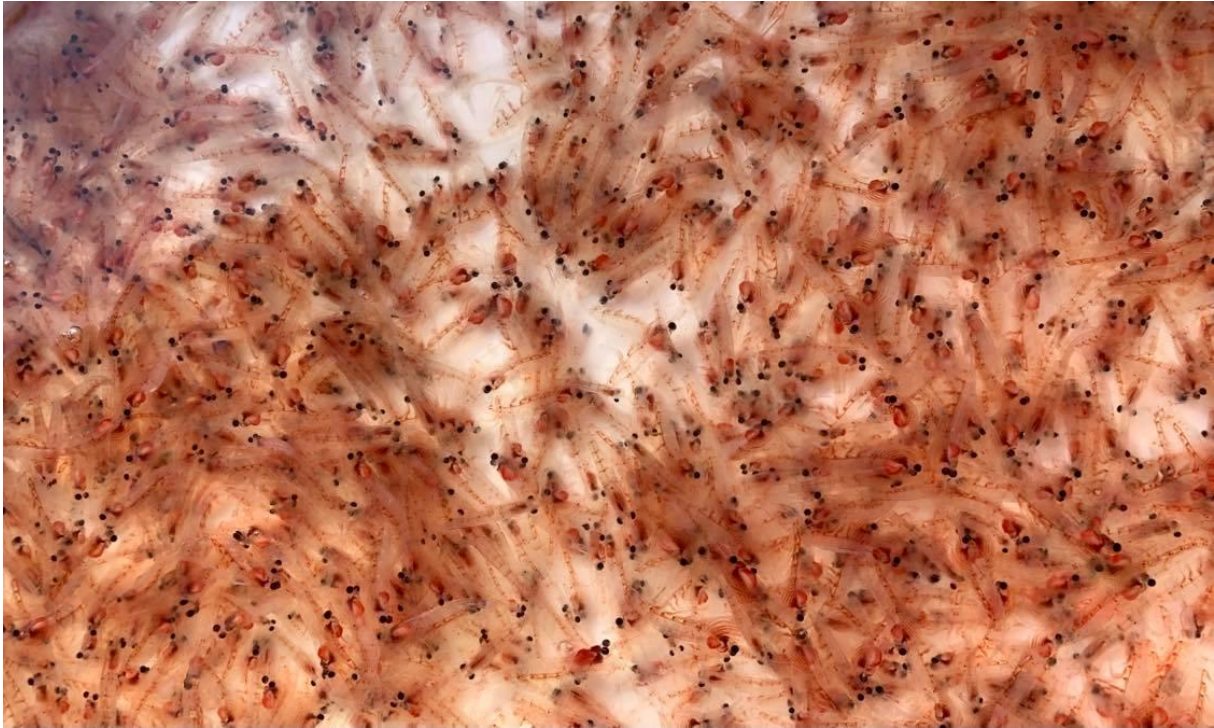
Figure 2: Meganyctiphanes norvegica from a trawl catch for this thesis.

When the night falls, the krill usually migrates in synchrony towards the rich surface waters in the shelter of the darkness (Onsrud & Kaartvedt, 1998; Vestheim et al., 2014). Through the night, they descend into dimer waters in a randomly matter, with a pulse of downward migration before dawn (Onsrud & Kaartvedt, 1998; Vestheim et al., 2014). *M. norvegica* is considered an omnivorous species, feeding on both zooplankton and phytoplankton (Kaartvedt et al., 2002), making up a versatile feeding biology (Schmidt, 2010). Their carnivorous behaviour can be linked to their eye physiology, where similar tubular eye shapes has been observed in other predatory zooplankton, suggesting that they search for prey in the silhouettes against the downwelling light (Torgersen, 2001). Being prey themselves, their aggregational behaviour may have positive effects on the krill's level of vigilance and decrease the probability of attack by potentially confusing the predators' senses (Burrows & Tarling, 2004).

1.3 Predator-prey interactions

Prey have evolved a wide variety of responses towards predation (Olivares et al., 2020). Such responses can be morphological, physiological or behavioural, acting alone or combined (Olivares et al., 2020). The meaning of these adaptions are to increase the preys' survival, but fitness costs can incur in regards of energy acquisition and food allocations (Olivares et al., 2020). The timing of migration are essential in the encounter of food and predators (Sato et al.,

2013). Fish typically depend on vision for foraging and feed more efficiently in shallower depths during daytime (Kaartvedt et al., 1996; Onsrud et al., 2004). The optical properties and light levels in the environment play essential roles in the predator-prey interaction between fish and krill (Kaartvedt et al., 1996). Several diel vertical migration (DVM) performing taxa have a phenotypic flexible behaviour to predator abundance and presence (Kaartvedt, 2010). Increasing predation pressure affect the portion of migrators and migration amplitudes (Kaartvedt, 2010). Even though the krill often stays below the fish during the day (Onsrud et al., 2004), demersal or benthopelagic fish can feed on the deeper part of the krill population distributed closer to the seafloor (Youngbluth et al., 1989).

The visual range of predators are influenced by the water clarity (Pinti & Visser, 2019). In areas with high turbidity, caused by suspended particles that scatters the light (Wing et al., 2021), organisms have shown to shallow their distribution, and vice versa (Frank & Widder, 2002). The turbidity influences the fishes' vision by altering the contrast between objects and the background (Wing et al., 2021). Predation pressure is also influenced by trophic interactions (Kaartvedt et al., 1996). Planktivorous fish are also predated on and might become more vulnerable in lighter parts of the water column (Kaartvedt et al., 2005). Their piscivorous predators needs higher light intensities to spot prey due to the preys lower numerical densities rather than the krill aggregations (Kaartvedt et al., 2005). At intermediate light intensity levels, the ratio of predation pressure and feeding rate can reach a minimum, and this scenario is called an 'anti-predator window' (Clark & Levy, 1988).

In Norwegian fjords, aggregations of krill and other organisms that normally appear offshore may be common (Baliño & Aksnes, 1993). Here, *Meganyctiphanes norvegica* generally perform DVM, with some variations (Onsrud & Kaartvedt, 1998). In the Oslofjord, these aggregations occur below 70m during the day, and starts ascending at dusk (Kaartvedt et al., 2002; Onsrud & Kaartvedt, 1998; Onsrud et al., 2004). Their predators have also been addressed through previous studies in this location, having unveiled Atlantic herring (*Clupea harengus*), withing (*Merlangius merlangus*) and Norway pout (*Trisopterus esmarkii*) (Onsrud et al., 2005; Røstad et al., 2006; Solberg & Kaartvedt, 2017).

1.4 Acoustical studies of behaviour

Several studies have used fjords for behavioural studies (e.g. De Robertis, 2002; Grenvald et al., 2016; Kaartvedt et al., 2008; Klevjer & Kaartvedt, 2011; Onsrud et al., 2004; Sato et al., 2013). The fjords provide sheltered calm waters that reduce the advection of potential acoustic targets (organisms) compared to open oceans (Kaartvedt et al., 2009; Kaartvedt et al., 2008). Fjords share similarities with open ocean communities (Meyer et al., 2020), where the deep fjord basins' fauna can resemble the fauna in the adjacent open ocean. Due to these similarities, fjords can be used as ocean models (Kaartvedt et al., 2008), where the logistics can be easier to arrange (Vestheim et al., 2014). Transport costs are reduced, and researchers will get easier access to the abiotic factors resembling the ecology within communities of the open ocean (Meyer et al., 2020).

Through the years, acoustic technology has advanced, evolving from hull-mounted transducers on ships, mainly used for fish stock assessments, into compact echosounders with pressurised housings, that can be left at sea for extended periods (Kaartvedt et al., 2009). The high resolution of these newer echosounders can reveal information about marine organisms' individual behaviour, and by being submerged, give information about the deep living organisms (Vestheim et al., 2014). Therefore, the submergible echosounders have been a significant contributor to behavioural studies of plankton, fish and in situ studies of predator-prey interactions (Kaartvedt et al., 2009).

Many diel vertical migration (DVM) performing zooplankton and fish form sound scattering layers (SSLs) (Baliño & Aksnes, 1993; Buchholz et al., 1995; Nocera et al., 2021). The sound waves reflected from the aggregations will produce a noticeable echo that can be recognised as a scattering layer above the background noise (Proud et al., 2015). Through these studies, echosounders have been, and still is, a significant contributor to exploring the DVM behaviour of different organisms (Liljebladh & Thomasson, 2001). Together with the echosounders, net hauls are usually performed to identify the acoustic target (Burrows & Tarling, 2004). By increasing our knowledge of DVM we can get a better understanding of the functions of pelagic food webs, predicting the ecosystem dynamics, and interpreting the mesoscale dispersion and organisation of the biomass in the ocean (Nocera et al., 2021).

1.5 Aims

The aim of this thesis is to increase our knowledge of the ecological aspect of diel vertical migration and the predator-prey interactions that occur within our oceans. To do this I will be describing and explaining the distribution and behaviour of fish and krill through day and night at a shallow site in the Oslofjord, where the krill may descend all the way to the seafloor. Thus, the krill are vulnerable to predation by pelagic fish from above and seafloor-related fish from below. With the help of an upward-facing echosounder deployed at the seafloor and net samples of the acoustic targets, I will try to address the following questions:

1) What is the driver/s of the krill's diel vertical migration behaviour?
2) Are there any constraints?
3) How is the fish distributed in relation to the krill?
4) Where and when does the fish attack the krill and how does the krill respond?

2. Materials and methods

2.1 Topography and study area

2.1.1 The topography of the Oslofjord

The Oslofjord is an extension of Skagerrak that penetrates the south-eastern part of Norway towards Oslo (Staalstrøm et al., 2020). The fjord has several deep basins separated by shallower sills (Thorsnæs, 2021). Usually, the fjord is referred to as an inner and outer part connected by the ~10km long Drøbak strait (Staalstrøm et al., 2020). Drøbak strait is the narrowest part of the Oslofjord between Hurum and Drøbak in Viken county (Askheim, 2021a), with an ~20m deep sill making the inner Oslofjord an enclosed system (Berge et al., 2014b). Passing the Drøbak sill, Håøya separates the fjord into two channels forming two smaller basins, before entering a larger fjord basin on the west side of Nesodden Peninsula (Staalstrøm et al., 2020). This basin is called the Vestfjord, and with the Bunnefjord basin on the eastern side of Nesodden, the inner Oslofjord forms a horseshoe of ~190 km^2 (Berge et al., 2014b; Staalstrøm et al., 2012).

2.1.2 The sampling area in the Vestfjord basin

The Vestfjord's seafloor is undulating with several rocky ridges and deep valleys filled with clay and softer sediments (Askheim, 2021b; Ruud, 1968). The Vestfjord's average depth is approximately 50m (Ruud, 1968), where the deepest point in the fjord basin is 165m located east of Søndre Langåra (Staalstrøm et al., 2020). Situated in the southwest of the Steilene archipelago, lays the study area of this thesis, called Midtmeie (fig. 3) (Staalstrøm et al., 2021). This station is a fishing bank with a depth of ~100m, making it one of the more suitable places for trawling in the inner Oslofjord.
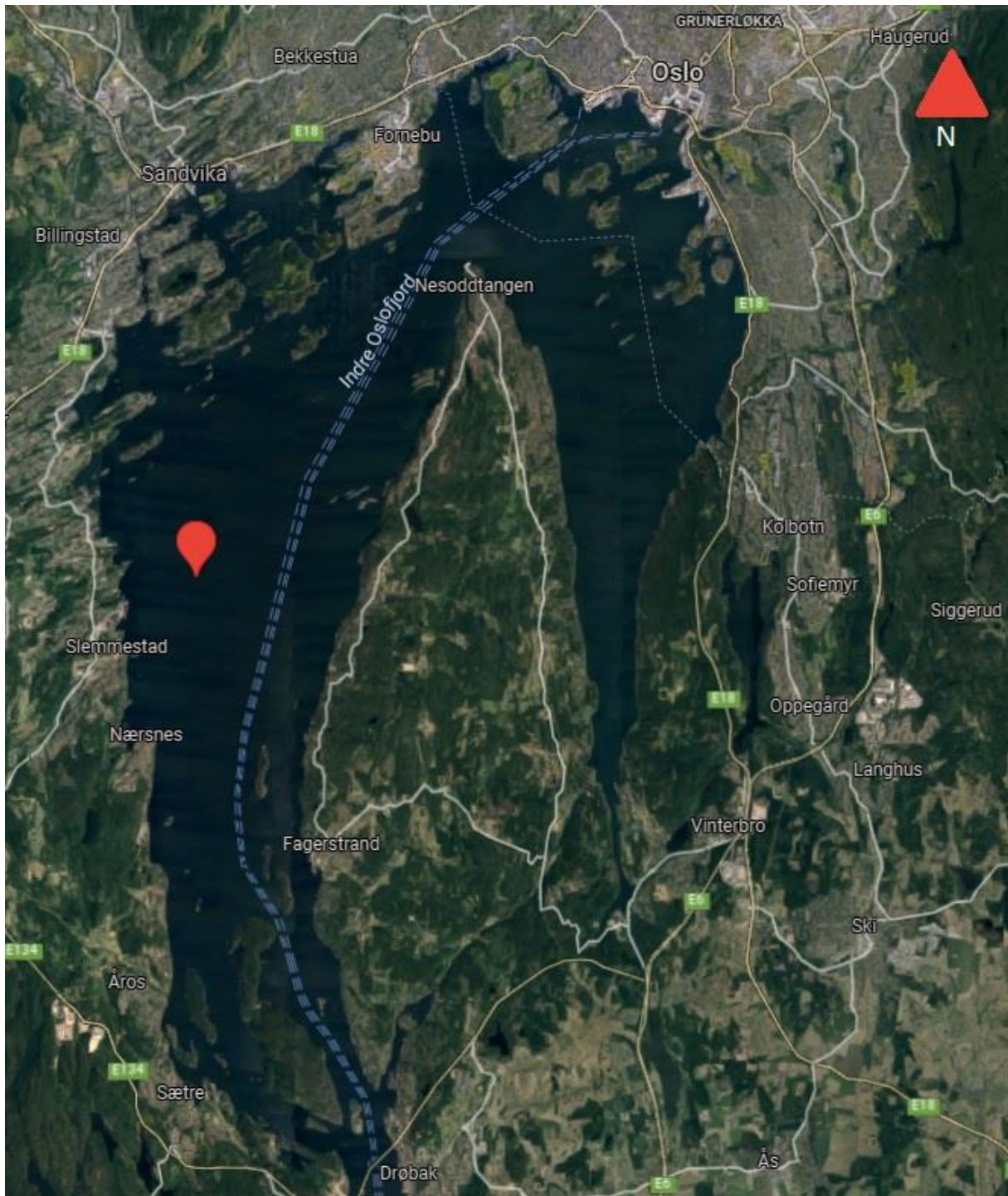
Figure 3: Map over the sampling station called Midtmeie in the Vestfjord in the inner Oslofjord. The main shipping lane is indicated in blue.

2.2 Field samplings

Several field campaigns were carried out throughout 2020. The field samplings took place in February, September and October onboard the University of Oslo's research vessel R/V Trygve Braarud.

2.2.1 Hydrographical measurements

To measure the hydrographical condition of the study area, a Neil Brown Conductivity-Temperature-Depth sonde (CTD) with attached oxygen sensors (fig. 4) was used in February 2020. The sonde was lowered to approximately two meters above the seafloor, recording the physical parameters continuously (tab. 1). Unfortunately, the CTD was sent for service and was not available for September and October. Instead, a STD sonde was used to measure temperature, salinity, and oxygen saturation (tab. 1). All hydrographical measurements from the cruises were saved on a computer onboard the vessel (tab.2).
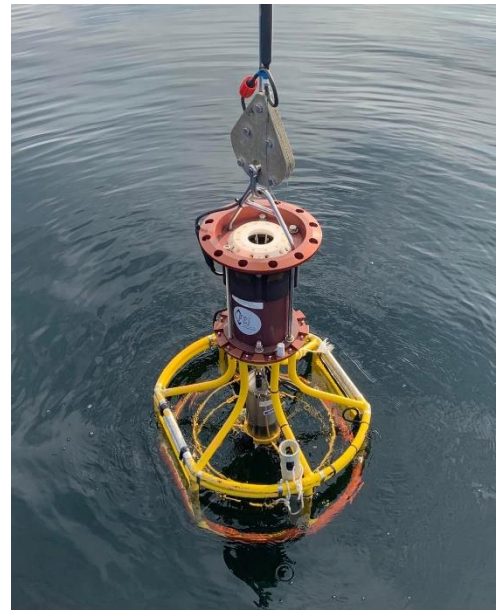
Figure 4: Descent of the Neil Brown CTD 21.09.2020 at Midtmeie.

Table 1: The hydrographical variables with units and the device that did the measurements.

Variable	Units	Device
Conductivity (salinity)	psu	CTD/STD
Temperature	°C	CTD/STD
Pressure (depth)	m	CTD/STD/Simrad EK500
Oxygen saturation	%	CTD/STD with oxygen sensors

Table 2: The measurements of hydrographical factors performed at Midtmeie 2020.

Station	Date	Time of the day
Midtmeie	07.02.20	Morning
Midtmeie	21.09.20	Morning
Midtmeie	12.10.20	Afternoon

2.2.2 Light measurements

A Li-Cor quantum sensor was used to measure the light intensities within the water column. The measurements started at the surface and every five meters were measured down to 25 or 30m (tab. 3). Surface light was stable during the records, except for September where the weather had varying cloudiness. Here, we used a deck cell, to compensate for any varying surface light during measurements, but due to a bad connection between the cell and the device, the measurements could not be used.

Table 3: The location, date, time, shallowest and deepest measurements with the length of each interval throughout the water column.

Station	Date	Time of day	Start depth (m)	Deepest depth (m)	Intervals (m)
Midtmeie	07.02.20	Morning	Surface	25	5
Midtmeie	22.09.20	Afternoon	Surface	30	5
Midtmeie	19.10.20	Afternoon	Surface	30	5

2.2.3. WP2 plankton net

Mesozooplankton (0.2-20mm), which could be potential prey for the krill, were sampled with a WP2 plankton net (fig. 5). We used a Nansen release mechanism that was activated by a drop messenger to separate the depth intervals. The opening of the plankton net was 56cm (r = 28cm), with a mesh size of 200μm, which was lowered and retrieved at a speed of 0.5 m/s. Three depth intervals were set to 95m – 70 m, 70 – 30 m and 30 – surface (0 m) (tab. 4). To preserve the samples for further plankton identification in the laboratory, the samples were put in small containers, marked, and placed in the freezer.

Figure 5: The WP2-net at Midtmeie.

To calculate the volume filtered for the intervals the areal of the WP2-nets opening were calculated (πr^2, r = 0.28m) and multiplicated with the depth intervals.

Table 4: The WP2 plankton net haul performed at Midtmeie 2020.

Date	Latitude	Longitude	Start UTC	Stop UTC	Intervals (m)
21.09.20	59°48.820N	10°33.063E	10:05	10:45	95-70
					70-30
					30-0
19.10.20	59°48.558N	10°32.409E	13:00	13:23	95-70
					70-30
					30-0

2.2.4 Isaac Kidd midwater trawl

The research vessel Trygve Braarud is equipped with Simrad EK500 echosounders operating at 38 and 120 kHz. The 38 kHz frequency is usually too low for plankton surveys (Simmonds & MacLennan, 2005), while a frequency of 120 kHz is more suitable to detect organisms such as krill (Simmonds & MacLennan, 2005). Fish are detectable on echograms with a 38 kHz frequency (Simmonds & MacLennan, 2005).

In all surveys, there was a marked acoustic layer at 120 kHz, which was much weaker at 38 kHz (fig. 6). To verify that the 120 kHz sound scattering layer (SSL) seen below 70m indeed are krill and to get samples for further measurements, an Isaac Kidd Midwater Trawl (IKMT) was used (coarse mesh, but with a 500μm rear section) (fig. 7A). In February, three trawl hauls were performed: 70m, 80m and 90m, while two trawl hauls were performed for September at 75m and 85m, and October at 75m and 90m (tab. 5). Trawl depths were monitored during sampling by a Scanmar depth sensor attached to the IKMT. Towing speed was between 2.8 knots to 3 knots. The tows lasted ~16min each (fig. 7B).
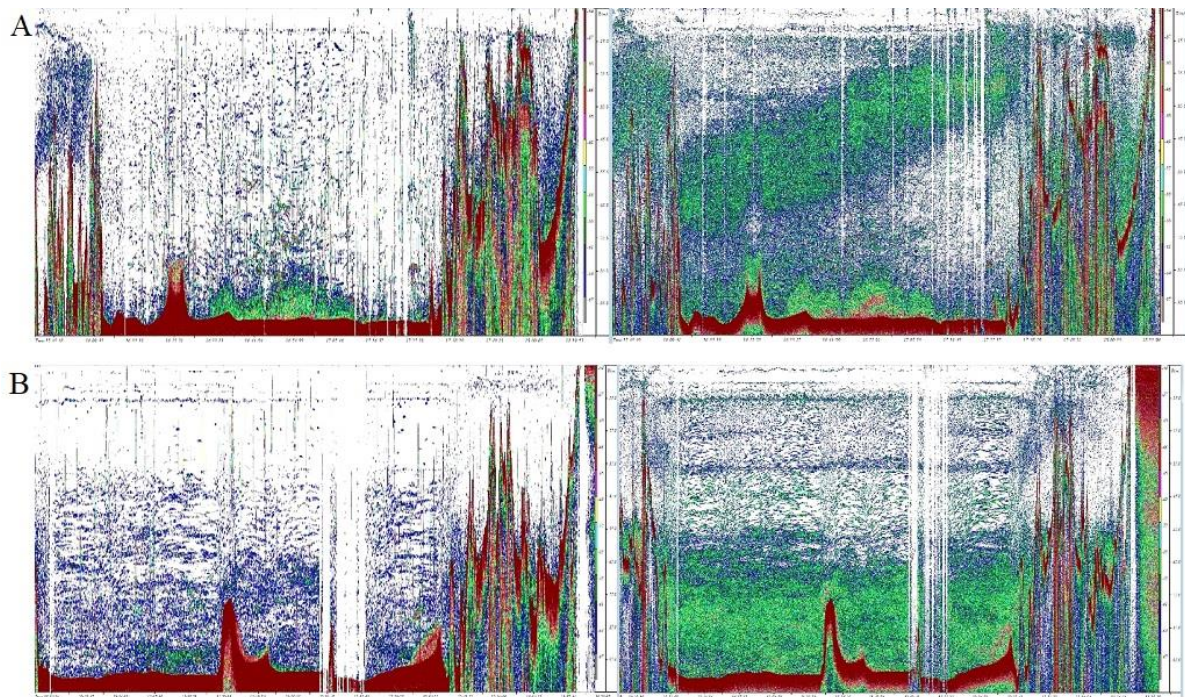
Figure 6: Echograms provided by the Simrad EK500 echosounder on Trygve Braarud. Left illustrating 38 kHz, right illustrating 120 kHz. (A) 05.02.2020, showing krill ascending in accordance with sunset shown at 120 kHz. (B) 07.02.2020, showing krill at daytime depth extending down to the seafloor.

The largest samples were divided into a subsample of 0.5L (fig. 7C). The organisms present in the samples were noted, and the gelatinous organisms removed. Samples were placed in thin layers of aluminium foil, marked, and put in plastic zip bags and placed in the freezer.

Figure 7: IKMT at Midtmeie (A) The IKMT on its way up after sampling (21.09.2020). (B) The net with catch (21.09.2020). (C) The krill catch (06.02.2020).

Table 5: The Isaac Kidd trawls for each expedition throughout 2020 with location, trawl depths, start and stop times and the duration of each haul.

Date	Trawl no.	Coordinates start	Coordinates stop	Depth (m)	Start UTC	Stop UTC	Duration (min)
06.02.20	1	59°48.256N, 10°32.169E	59°48.808N, 10°32.698E	70	11:30	11:48	18
	2	59°48.814N, 10°32.901E	59°48.065N, 10°32.953E	80	12:25	12:43	18
	3	59°48.230N, 10°32.157E	59°48.861N, 10°32.906E	90	12:50	13:06	16
21.09.20	1	59°48.700N, 10°32.800E	59°47.950N, 10°31.770E	70-75	12:43	13:00	17
	2	59°47.950N, 10°31.770E	59°48.700N, 10°32.800E	80-89	13:20	13:37	17
19.10.20	1	59°48.2930N, 10°32.100E	59°48.908N, 10°33.389E	75	11:20	11:35	15
	2	59°48.813N, 10°33.168E	59°48.091N, 10°32.020E	90	12:09	12:20	11

2.2.5 Pelagic trawl

A pelagic trawl was used for sampling fish (and krill) (fig. 8A). The pelagic trawl at Midtmeie was performed at 75 and 85m before noon on 21.09.2020. The trawl hauls lasted ~20min. The catch was put in a bucket where the small fish were put in marked zip bags and stored in the freezer, while there was taken a 0.5L subsample of the krill catches (fig. 8B). The subsamples were put in aluminium foil and placed in the freezer for further examination at the laboratory. The larger fish were either examined on the boat or preserved in the freezer for further examination in the laboratory as well (fig. 8C).

Figure 8: Pelagic trawling at Midtmeie 2020. (A) Deploying the trawl (22.09.2020). (B) Some of the krill catch (22.09.2020). (C) The fish catch (22.09.2020).

2.2.6 Bottom trawl

Fish from two bottom-trawls at Midtmeie on the 15th and 28th of October 2020 was made available for stomach investigations of more bottom-associated fish. The catch from 15.10.2020 was a subsample of 15% of the total catch and only contained one species. The whole catch from 28.10.2020 was available for investigations.

2.3 Acoustical recordings: Simrad WBAT Echosounder

To obtain behavioural observations, a stationary upward-facing echosounder was deployed at the seafloor. The echosounder employed in this study was a Simrad Wideband Autonomous Transceiver (WBAT), connected to a 200kHz split-beam transducer and fastened to a frame (Fig. 9C, D, E). The frame was attached to a plastic pallet and train tracks to ensure sufficient weight to stay stationary at the bottom (fig. 9A and B). A second bottom-weight was connected to the WBAT rig with a line and deployed on the seafloor in about 50-100m distance. An acoustic release was attached to the bottom-weight connected to a buoy with a ~30m line. The coordinates to the WBAT's and the buoy's location were noted. For retrieving the WBAT, the acoustic release was triggered, which let the buoy ascend to the surface, and the bottom-weight and the WBAT platform were retrieved. The WBAT contains a lithium battery with a capacity of 128 Ah. With this battery capacity, it is possible to leave the echosounder at the seafloor to do recordings over longer periods. At the communication end cap (fig. 9G), there is a USB-dedicated compartment for the flash drive that collects and saves the raw data recorded by the echosounder during the missions, as well as a serial line interface.

Before deployment, the echosounder is programmed to perform a predefined mission. The EK Mission Planner program runs on personal computers (PC), where the connection between the laptop and the transceiver is established with a serial line cable attached between the laptop's USB-port and the serial line interface. At the other end of the transceiver is the transducer end cap that is connected to the transducer with a cable.

Figure 9: The echosounder as deployed. The letters illustrate the different components assembled to construct Simrad WBAT echosounder rig: A) Plastic pallet B) Train tracks C) Steel frame D) Transceiver E) Transducer F) Transducer end cap G) Communication end cap.

The transducer transmits an acoustical pulse through the water column, referred to as a ping, which reflects after hitting a target (Simmonds & MacLennan, 2005). The ping interval was set to 0.5s between each ping with a pulse duration set to 256µs for all the recordings (tab. 4). Throughout the recordings, the data were continuously saved on the USB flash drive connected to the transceiver. Programming of the mission plan and downloading of data were done by PhD-student Svenja Christiansen.

Table 4: The recordings done for each mission with latitude, longitude, deployment/bottom depth, recording start and stop, and the duration of each recording.

Date	Latitude	Longitude	Depth (m)	Recording start UTC	Recording stop UTC	Event duration (h)
05.02.20 - 07.02.20	59°48.641N	010°32.541E	97	16:30	10:00	41,5
21.09.20 - 25.09.20	59°48.538N	010°32.270E	100	15:00	10:00	90
29.09.20 - 02.10.20	59°48.538N	010°32.270E	100	15:00	10:00	66
15.10.20 - 19.10.20	59°48.538N	010°32.270E	100	15:00	10:00	90

2.4 Laboratory work

2.4.1 Plankton counting and species identification

The WP2 plankton net samples were divided by a Folsom plankton sample splitter so it would be manageable to count the organisms within the samples (fig. 10A) (Motoda, 1959). The samples from the deepest depth interval (95-70m) were divided four times, while more numerous catches from the intermediate (70-30m) and shallowest (30-0m) intervals were divided eight times. The samples were placed in a counting tray (fig. 10B), where they were roughly identified and counted under a stereomicroscope. To figure out how many individuals that were present within per volume of water filtered (m^{-3}), the number of individuals were divided with the volume of water that had been filtered in the interval (m^3).
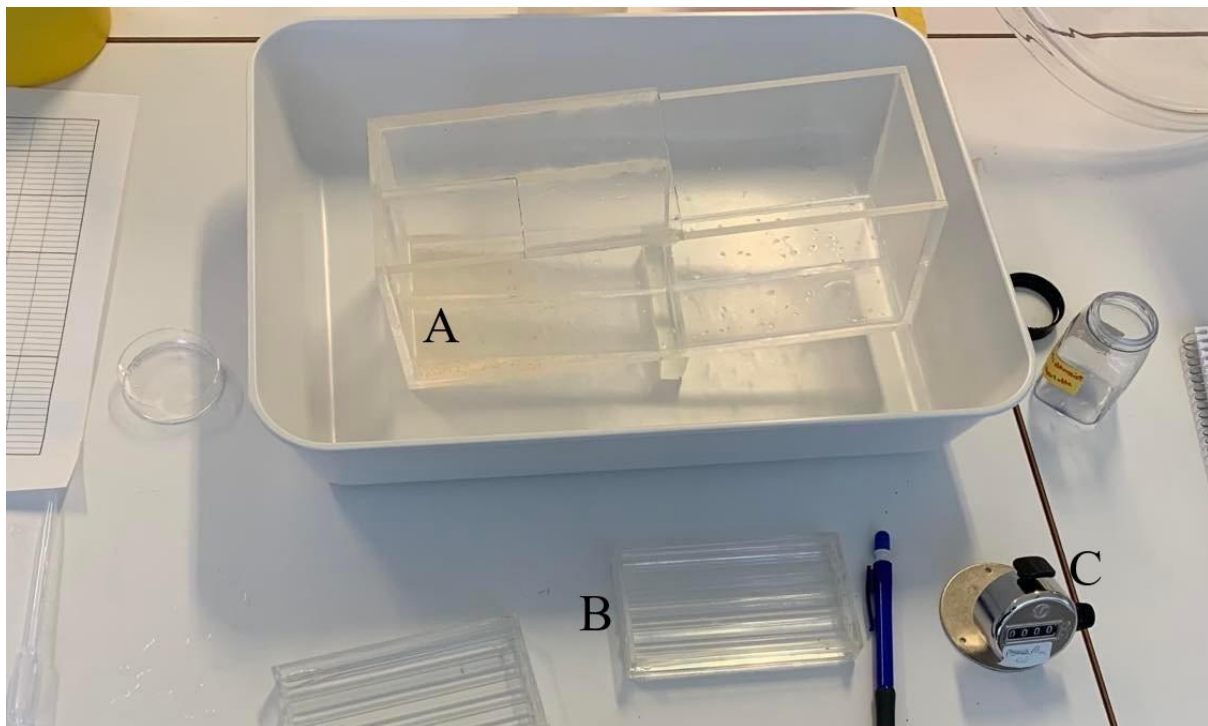
Figure 10: The equipment used for the plankton counting and species identification. (A) Folsom plankton sample splitter. (B) Counting tray. (C) Tally counter.

2.4.2 Krill measurement and stomach content analysis

In total, nine samples of krill were examined at the laboratory at the University of Oslo. From each sample, 50 krill were randomly picked and measured on graph paper with one millimetre between each square (fig. 11A), as advised by the Institute of Marine Research's handbook for sampling and pre-analysis of plankton (Hassel et al., 2013). The total length of the krill was

measured from the tip of the rostrum to the end of telson (Hassel et al., 2013). All the krill were counted in the smaller samples, while the larger samples were estimated like this:

$$\left(\frac{Total\ volume\ of\ krill}{Volume\ of\ 100\ krill}\right) * 100 = Total\ estimate\ of\ krill$$

After the measurements, 10 new krill from each sample were randomly collected. One at the time were put in a petri dish with water under a stereomicroscope. By using tweezers to get under the tip of the rostrum behind the eyes, the stomach could easily be accessed and pulled out of the body (fig.11B). The stomachs were placed on glass slides (fig. 11C), crushed with a scalpel blade and a few drops of water were added before the coverslips were added on top. Each preparation was searched carefully for copepods upper jaw, which is called mandibles (fig. 11D). The mandibles for each preparation were counted and noted. This was done to get an insight into the krill's feeding habits.
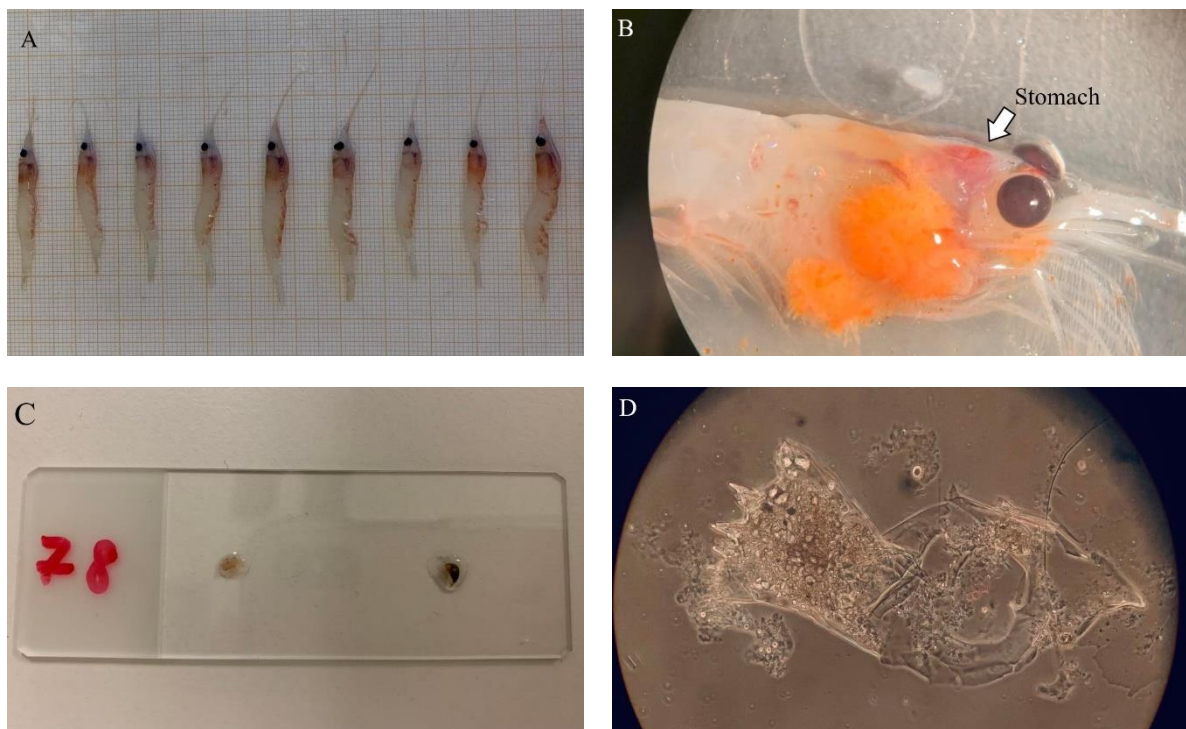
Figure 11: Size determination and stomach analyse of the krill. (A) Length measurements of the krill on millimetre paper. (B) The location of the stomach. (C) Stomachs from two krill, depicting the differences in stomach content between the individuals. (D) Picture of a mandible within a krill's stomach, magnifying at 10x. 4x were used to look for them.

2.4.3 Fish measurements and stomach content analysis

The fish from the different surveys were species determined, counted, measured with a ruler and weighted on a weight. The stomachs fillings were determined before they were opened (tab. 5), and the content and digestion level were determined by studying it under a stereomicroscope (tab. 6).

Table 5: Assessment of stomach fullness.

Stomach filling	Level (number)
Empty	1
Very little content	2
Some content	3
Full	4
Bulging	5
Inverted	6

Table 6: Level of digestion of stomach content.

Digestion state	Level (number)
Not started	1
Started	2
Advanced	3
More advanced	4
Almost finished	5

2. 5 Data processing: Echograms and programming

2.5.1 Acoustical data

The recordings from the Simrad WBAT Echosounder were processed in Sonar 5 pro version 6.0.6.16. The behavioural patterns were best seen in the Amp-echogram. Thresholds between -70 to -80 dB (S_v threshold) were used to investigate the krill behaviour and threshold between -50 to -65 dB (S_v threshold) were used to investigate the fish (Balk & Lindem, 2017).

2.5.2 Data programming and statistics

The graphs over catch sizes, lengths and stomach content analysis (SCA) of the biological samples were made in ggplots in rStudio. The statistical analysis to test if there was a significant size difference of krill between the different depth intervals were tested with a one-way-ANOVA and Tukey HSD post-hoc test.

3. Results

3.1 The Environment: Hydrography and light intensity

Temperature and salinity were relatively stable below ~25m throughout the year (fig 12). The temperature in the depths was ~9°C, while the surface temperatures varied between the seasons. Measuring the lowest temperature in February of 1.3°C, and the highest in September with 15.5°C. The salinity at the surface decreased from February with ~24.3 psu until October with 17.7 psu. The salinity stayed at ~32 psu near the seafloor. The water was more oxygenised in October compared to February (fig. 12A and C). In October, the water near the surface was over-saturated, decreasing towards the seafloor, reaching ~42% saturation. In February, the oxygen saturation had an increase at the surface and mid-water before it declined to 29% oxygen saturation near the seafloor.
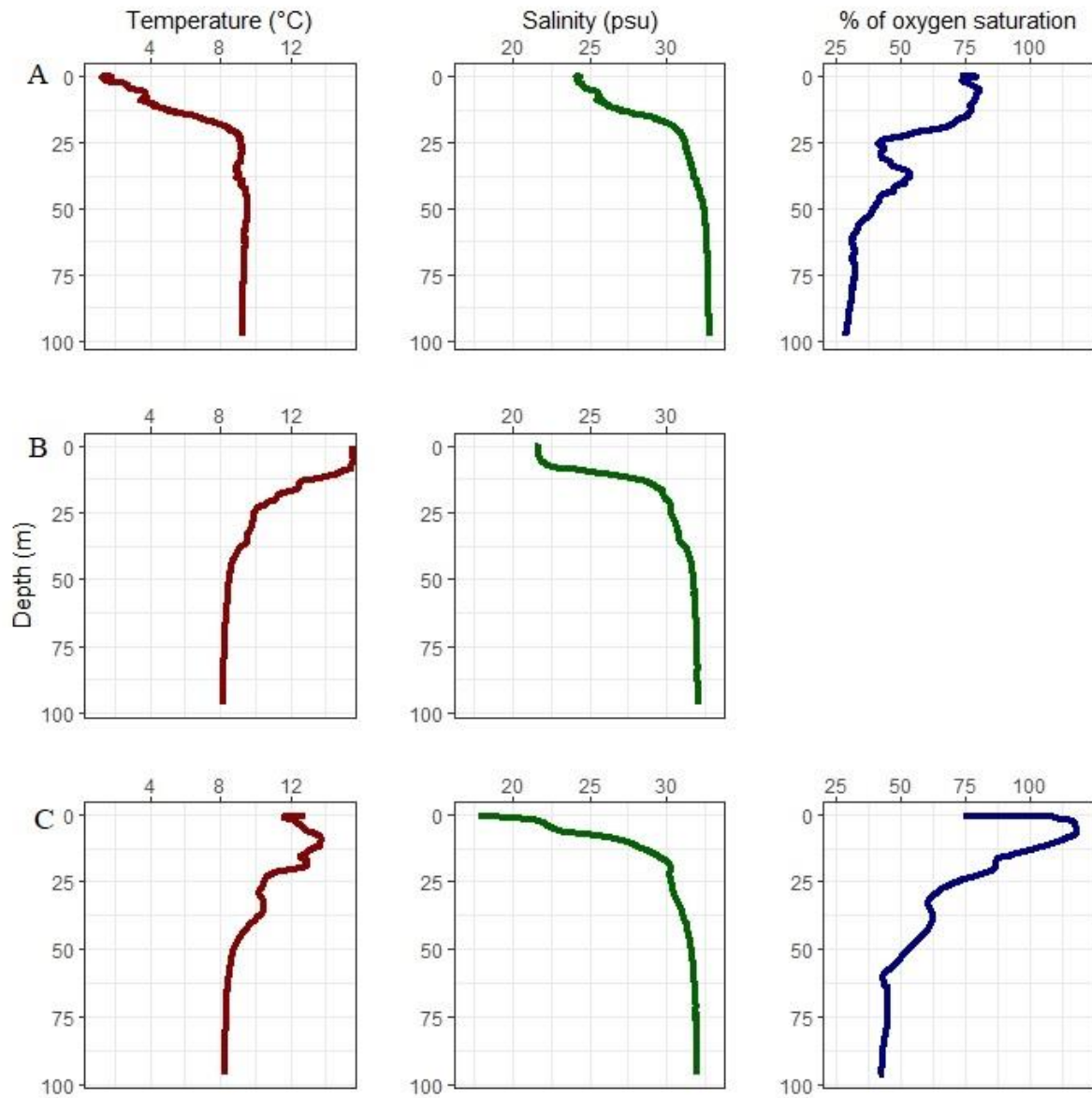
Figure 12: Vertical hydrographic profiles from Midtmeie in (A) February, (B) September and (C) October 2020. The oxygen saturation measurements are not included in September due to malfunction of the oxygen sensor.

The light intensity measurements showed that the light rapidly decreased in the upper 25-30m of the water column (fig 13). The light extinction was strongest in February, while being fairly similar in September and October.
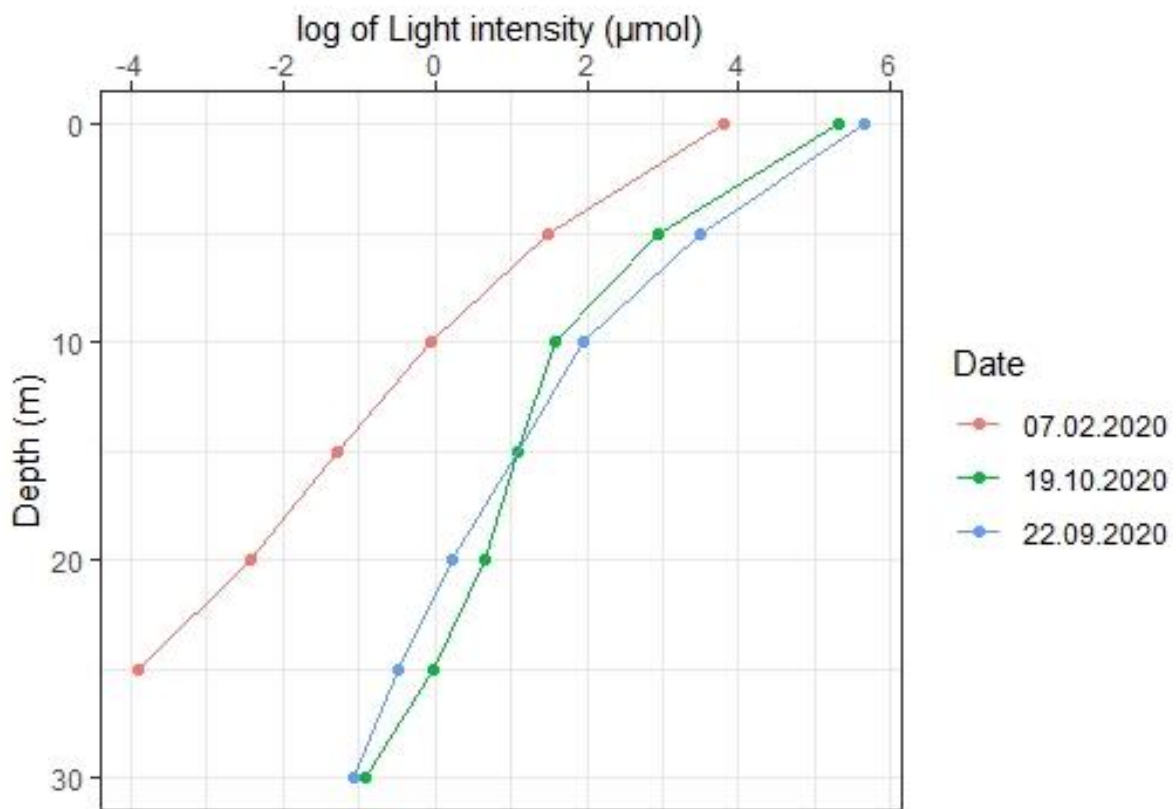
Figure 13: Light intensity (μmol) by depth, Midtmeie 2020.

3.2 Biological Studies

3.2.1 Plankton

WP2- net catches with species distribution

The plankton was most abundant in the shallowest depth interval (30-0m), with decreasing abundance towards the seafloor in September (fig. 14). This pattern had changed in the middle of October where the lowest plankton abundance was in the shallowest interval. The intermediate (70-30m) and the deepest depth interval (95-70m) had rather similar abundance in October. The shallowest and intermediate depth intervals were dominated by smaller copepods. At the deepest interval, a shift in the dominating species appeared and *Calanus spp.* became the dominating species. Other species were also present in the species analysis, but due to the small numbers, they are hard to see in the bar plots. The highest abundance of different taxa such as arrow worms, *Metrida* and *Temora* was in September at 70-30m. October had a rather low abundance of other species.
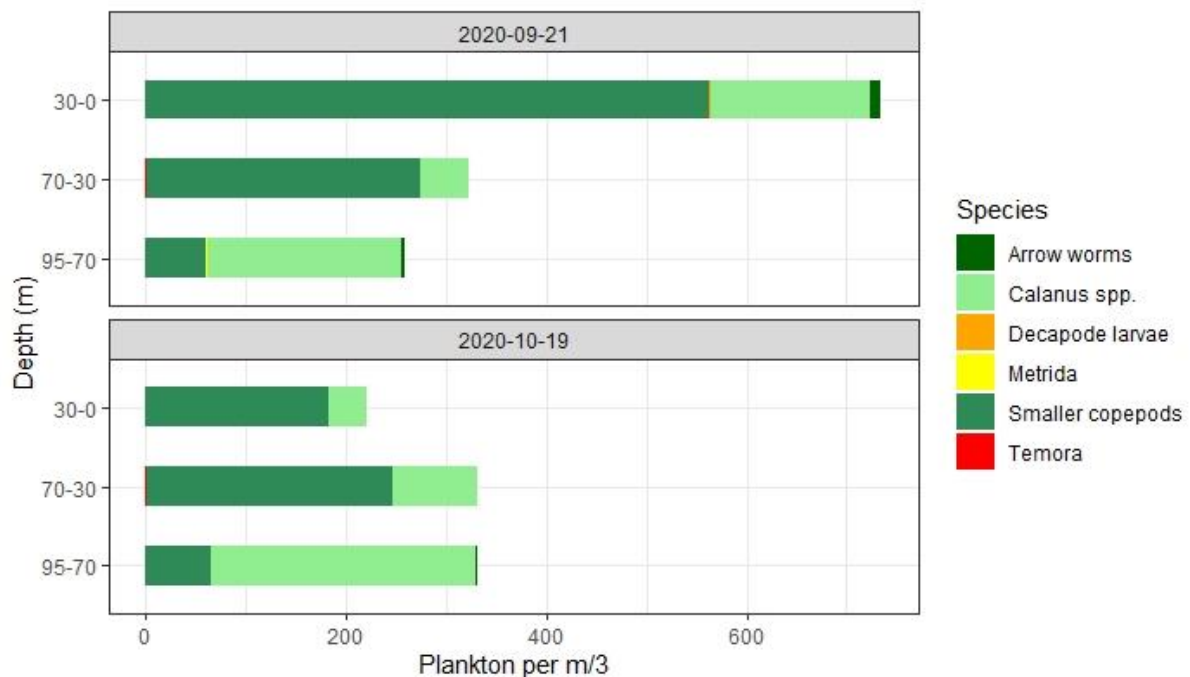
Figure 14: Catch from the WP2 plankton net at Midtmeie 2020. The abundance of arrow worms, decapod larvae, Metrida and Temora were low and can be hard to see in the plots.

3.2.2 Northern krill (*Meganyctiphanes norvegica*)

Total Catches

The krill catches from the Isaac Kidd midwater trawl (IKMT) increased from February until October, where the largest catches were caught below 80m depth (fig. 15). February had the overall smallest catch of all three, with the largest catch at 80m (~2 500 krill). The overall largest catches for both the shallowest (~800 krill) and deepest (~16 000 krill) intervals were caught in October. The pelagic trawl survey in September contained ~20 000 – 25 000 krill in the two depth intervals sampled (fig. 16).
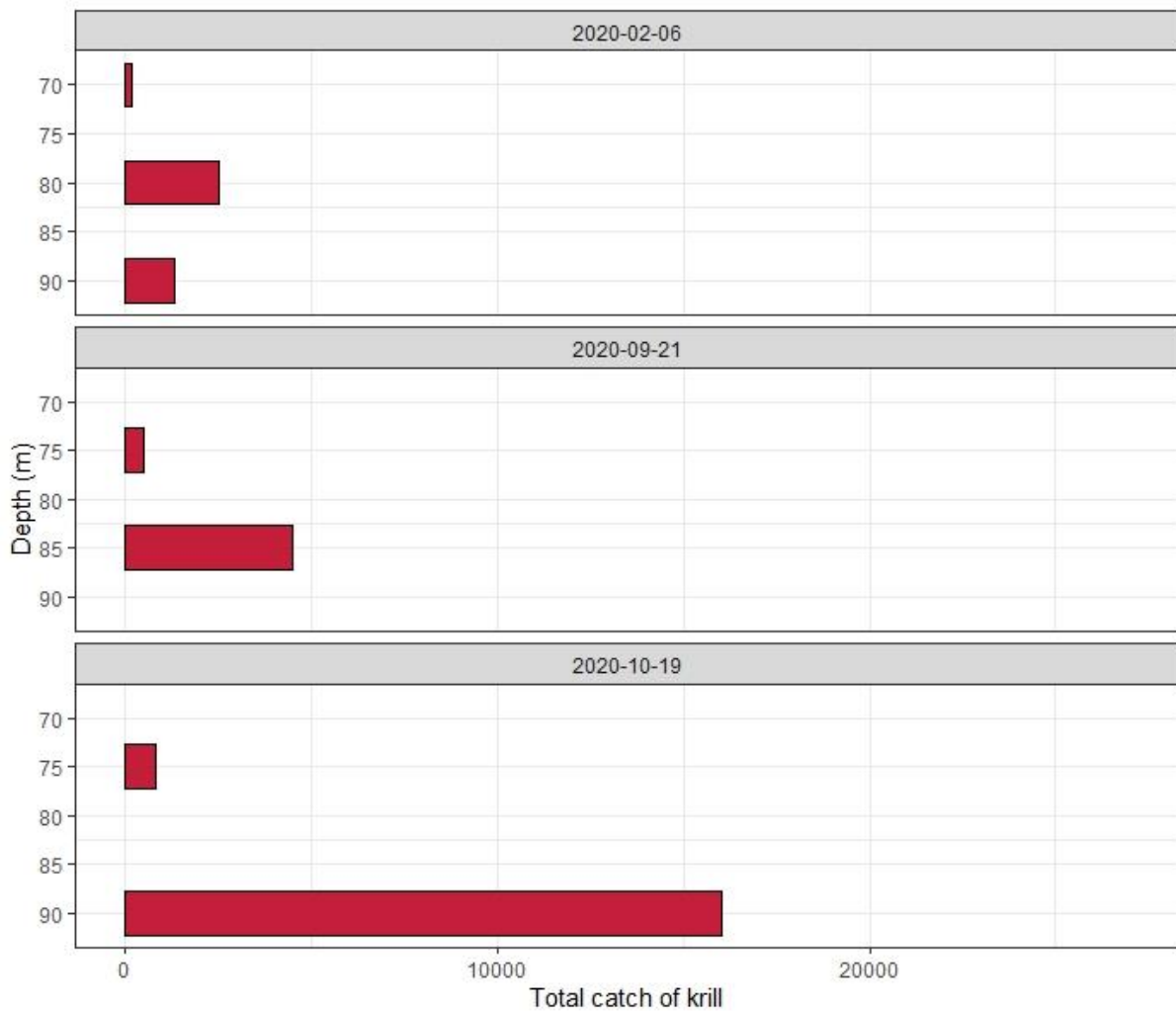
Figure 15: Total IKMT catches of M. norvegica at Midtmeie 2020.
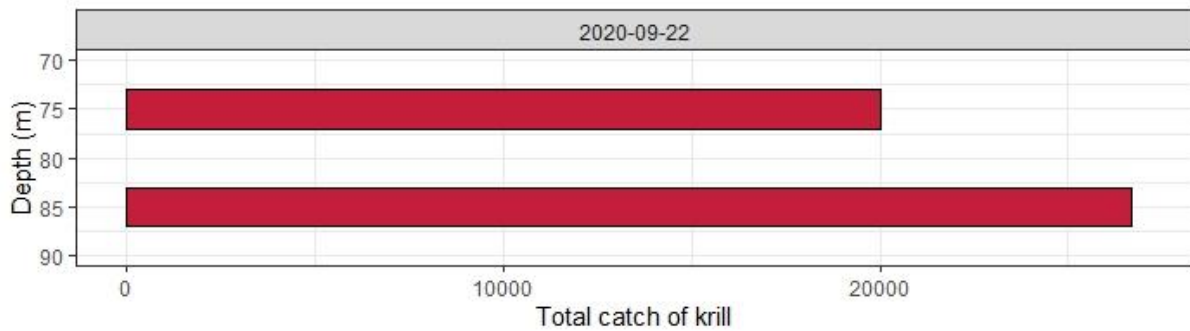
Figure 16: Total pelagic trawl catches of M. norvegica at Midtmeie 2020.

Size Distributions

Most of the samples had a dominance of individuals with sizes ranging from 32-36mm (fig. 17 and 18). The largest difference in size distribution between depths was in February, where the smallest individuals were found in the shallowest depth (70m) (Tukey HSD post hoc: $p < 0.001$). An opposite scenario was found in the September sampling (fig. 17), where a significant difference was found with the larger individuals in the shallowest interval (ANOVA: $p \leq 0.001$). This difference was not seen in the pelagic trawl sample (Fig. 18).
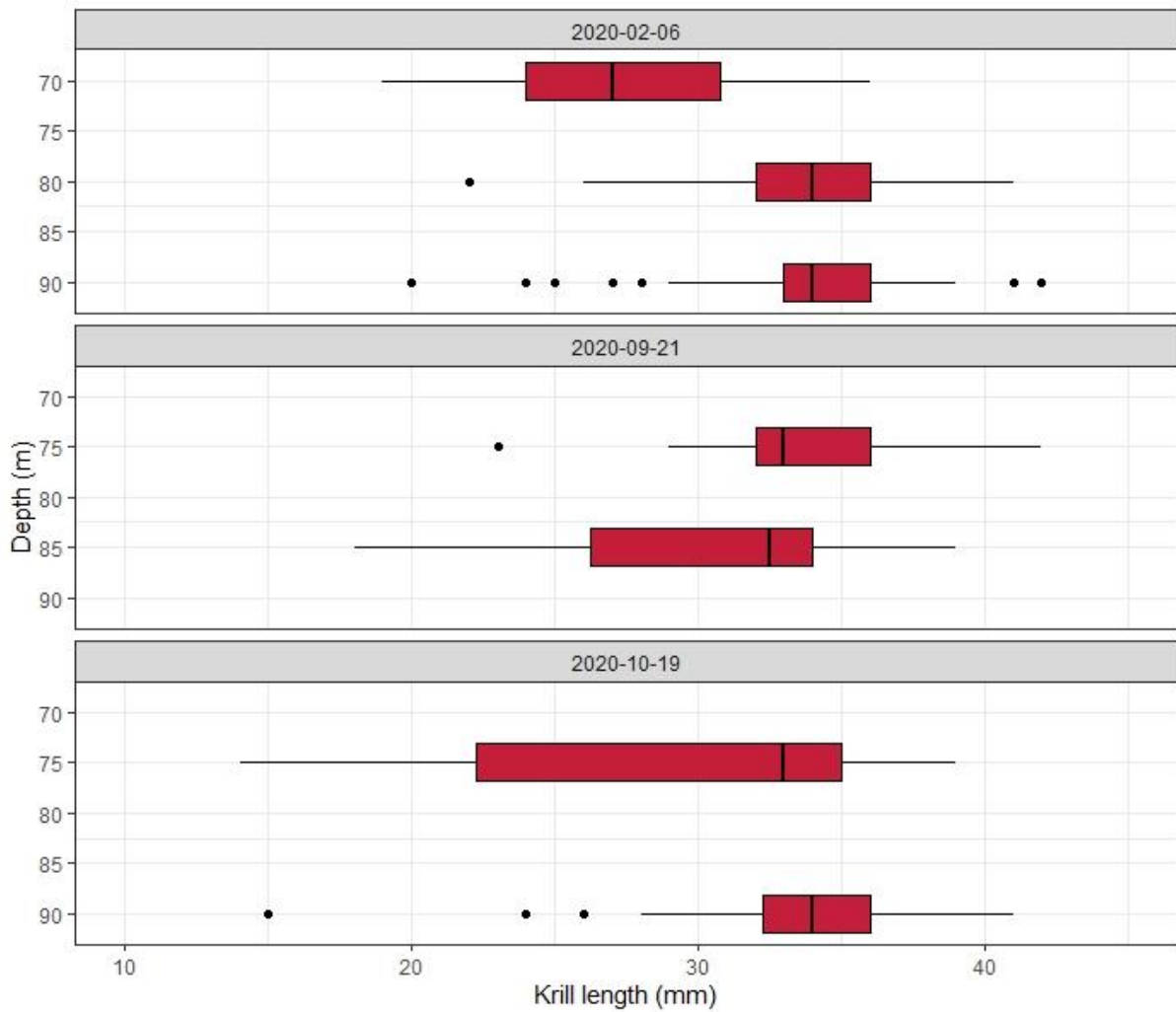
Figure 17: M. norvegicas size ditribution with depth from the IKMT at Midtmeie 2020. The outer points and whiskers of the boxplot shows the smallest and largest individuals, and the box shows 50% of the size range the individuals are found within.

Figure 18: *M. norvegicas size ditribution with depth from the pelagic trawl at Midtmeie 2020. The outer points and whiskers of the boxplot shows the smallest and largest individuals, and the box shows 50% of the size range the individuals are found within.*

Stomach Analysis for Mandibles

Copepode mandibles were found in the stomachs of krill from all the surveys. Most of the stomachs analysed were empty, only 16 out of 90 krill had mandibles in their stomachs (fig. 19 and 20). Of these 16 krill, 13 had only one mandible in their stomach and at the most, up to 5 mandibles were found in a single stomach.

Figure 19: Copepod mandibles found in 10 krill stomachs from each of the IKMT hauls. The lines within the bars represent krill with different amounts of mandibles in their stomachs.
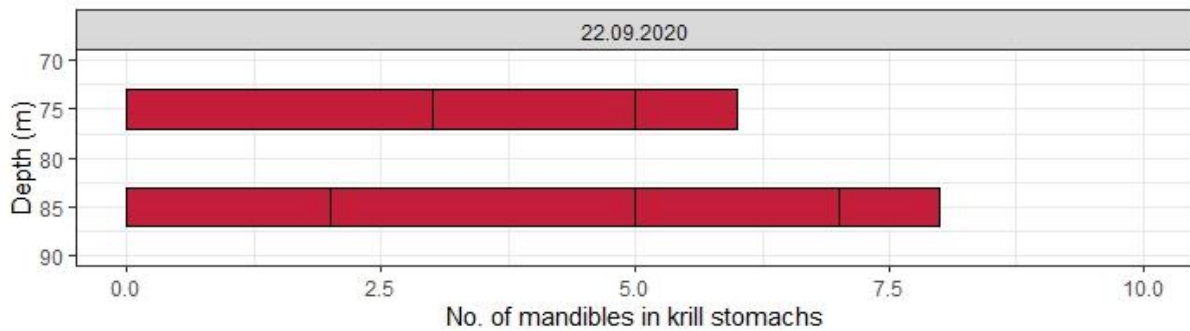
Figure 20: Copepod mandibles found in 10 krill stomachs from the pelagic trawl haul. The lines within the bars represent krill with different amounts of mandibles in their stomachs.

3.2.3 Glass shrimps (*Pasiphaea sivado*)

Total Catches

In addition to krill, the catches contained low numbers of glass shrimp. The overall largest catch of 84 glass shrimps accounted for ~6.4% of the total catch, the remainder being krill, caught in February at 90m depth (fig. 21 and 22). In the Isaac Kidd midwater trawl (IKMT) from September, glass shrimps were only counted in the subsample from the deepest trawl interval. Glass shrimps were observed in the shallowest interval upon initial sorting of the samples on board but were not represented in the subsample collected from the total catch, underlining their scarcity in the catches relative to krill. Likewise, glass shrimps were not registered in any of the subsamples in October but were observed in the total sample shortly after the trawl catch were measured. In the pelagic trawl survey from September, both trawl depths contained 48 glass shrimps each.
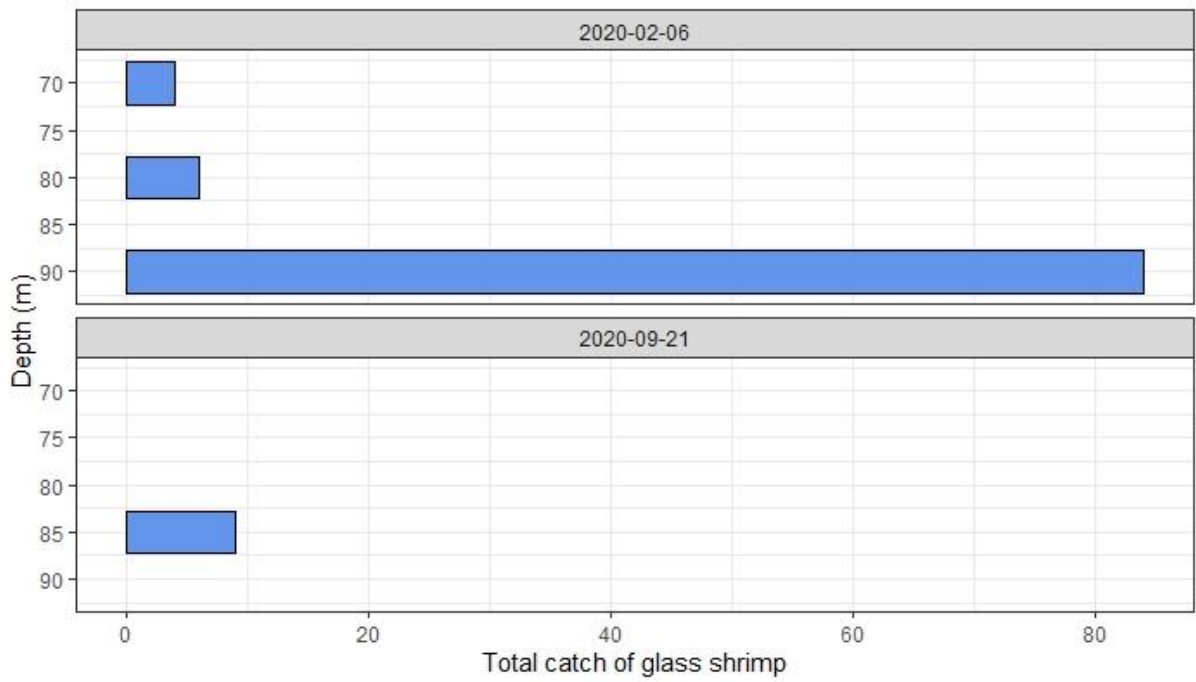
Figure 21: Total catches of glass shrimps caught at Midtmeie 2020 with the IKMT.
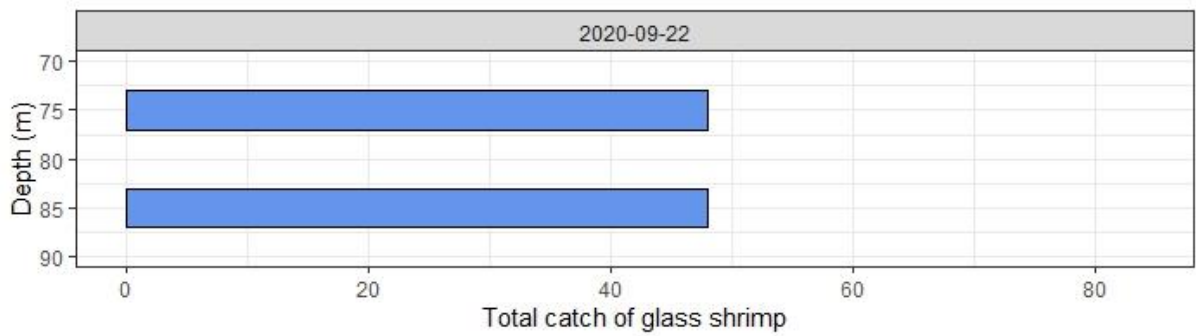
Figure 22: Total catches of glass shrimps caught at Midtmeie 2020 with the pelagic trawl.

Size distribution

The size ranges of glass shrimp varied between the surveys, where the sizes significantly increased with depth (ANOVA: $p < 0.05$) (fig 23 and 24).
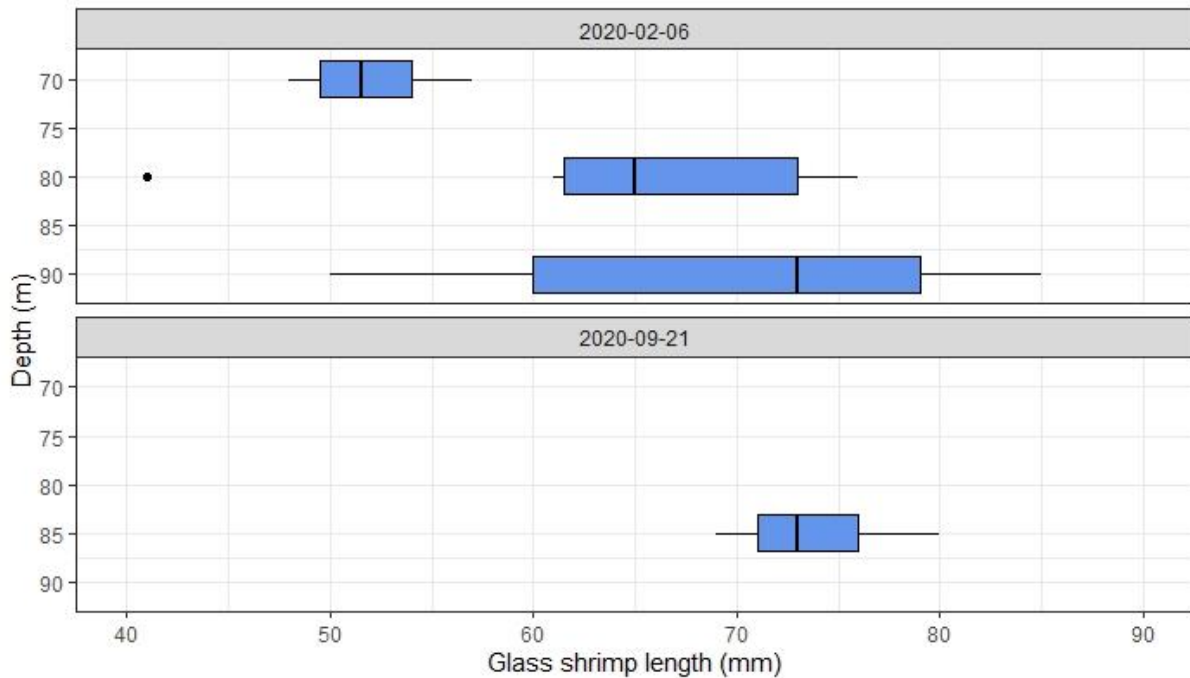
Figure 23: P. sivado from the IKMT at Midtmeie 2020. The outer points and whiskers of the boxplot shows the smallest and largest individuals, and the box shows 50% of the size range the individuals are found within.
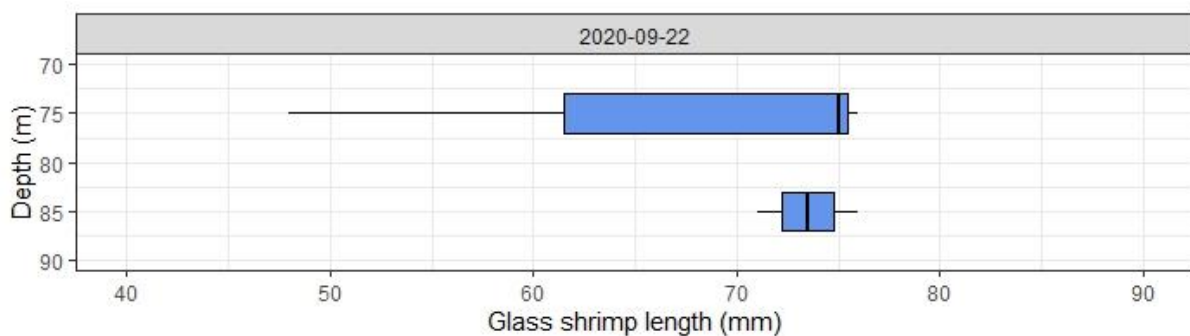
Figure 24: P. sivado from the pelagic trawl at Midtmeie 2020. The outer points and whiskers of the boxplot shows the smallest and largest individuals, and the box shows 50% of the size range the individuals are found within.

3.2.4 Fish

Pelagic Catch and Size Distribution

The deepest trawl haul at 85m contained saithe (*Pollachius virens*) and whiting (*Merlangius merlangus*) and more strictly pelagic fish such as anchovy (*Engraulis encrasicolus*), and sprat (*Sprattus sprattus*) (fig. 25). The shallowest trawl haul at 75m contained herring (*Clupea harengus*) and sprat. The largest fish species caught were saithe ranging from 34-37cm in size, with a mean size of 35.3cm (fig. 26). Whiting followed with a size range from 25-28cm and a mean of 26.5cm. The herrings size raged from 8.5-20cm, with a mean of 12.9cm, and the sprats ranging from 8.5-15cm in both depths. The sprat in the shallowest interval had a mean size of 12.25cm and the deepest had 11.5cm. The one anchovy measured 8.5cm.
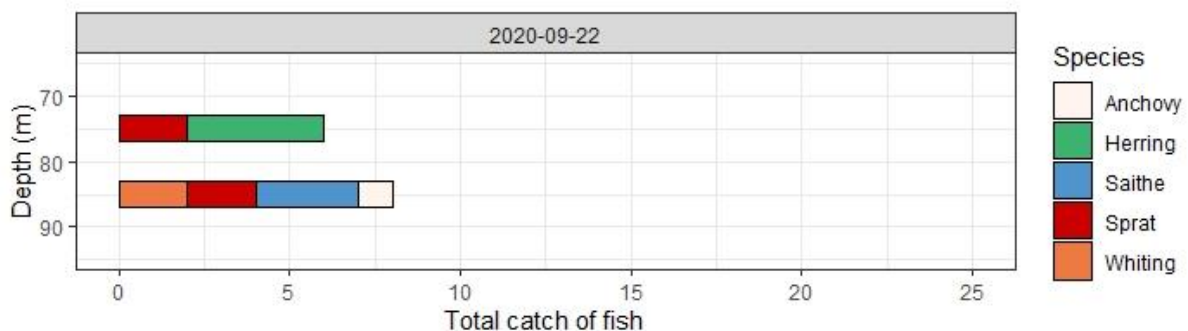
Figure 25: Total catch of fish from Midtmeie in September of 2020. The different colours illustrated the different species sampled.
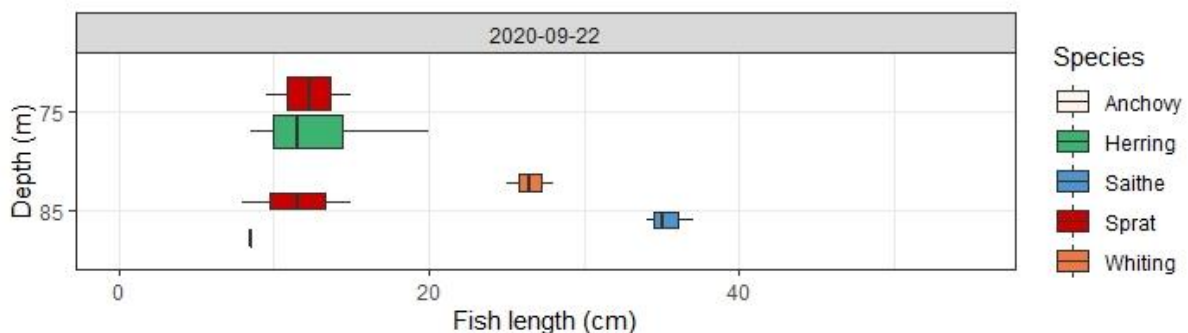
Figure 26: The size distribution of the different species with depth at Midtmeie 2020. The outer points and whiskers of the boxplot shows the smallest and largest individuals, and the box shows 50% of the si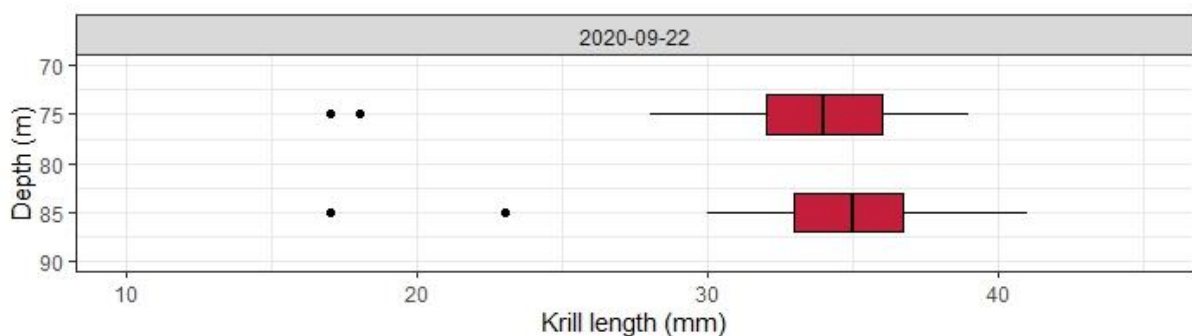ze range the individuals are found within. The lines occurring in both boxplots illustrates the measurements of one fish.

Bottom-Trawled Catch and Size Distribution

The subsample received from the catch on the 15.10.2020, only consisted of Norway pout (*Trisopterus esmarkii*). Other fish species were also caught in this trawl survey but were not available for this study. The sizes of the Norway pout ranged from 15-23cm. The mean size of these 24 Norway pouts were 18.1cm. Later in October, the sample from the bottom trawl contained 40 fish, poor cod (*Trisopterus minutus*), silvery pout (*Gadiculus thori*), Norway pout, saithe, whiting and even herring (fig. 27). Silvery pout ranged from 8.5cm to 13cm, with a mean size of 10.8cm, followed by poor cod ranging from 17cm to 25cm and a mean size of 19.5cm (fig. 28). The Norway pout in this survey ranged from 19cm to 23cm, with a mean size of 21.1cm. The largest species was the saithe where the smallest fish were 34cm and the largest 42cm, with a mean size of 38.1cm. Also, a single herring at (26cm) was caught with the bottom trawl.
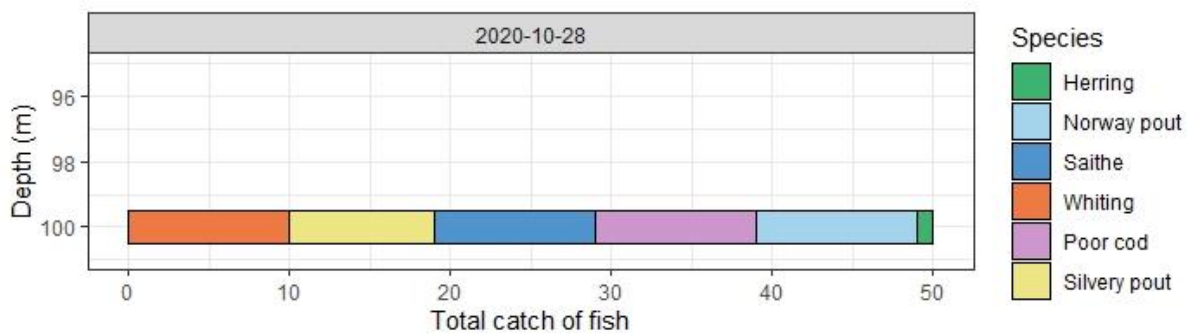
Figure 27: Bottom trawls performed at Midtmeie in October 2020.
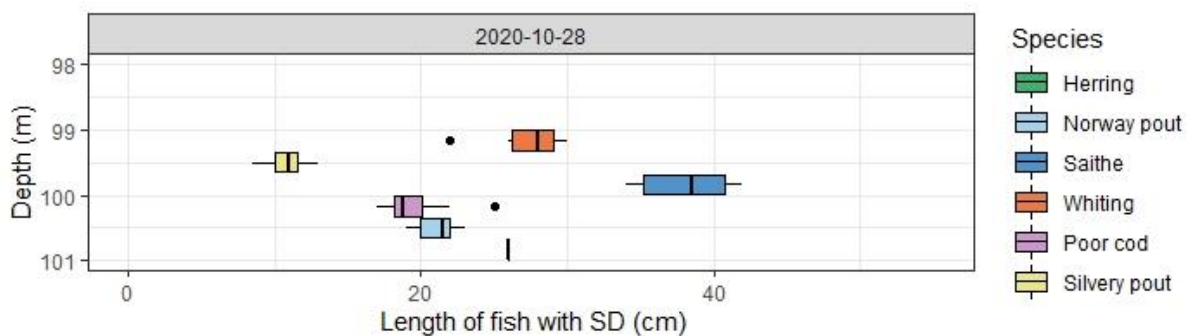
Figure 28: Length distribution including standard deviation of fish caught with the bottom trawl at Midtmeie in October 2020.

Stomach Content Analysis

Stomach contents from the pelagic trawls

In September, 16.7% of the fish caught at 75m had eaten krill (fig. 29). Most of the fish at this depth had either empty stomachs (33.3%) or had eaten *Calanus spp.* (33.3%). The remaining 16.7% were fish with unidentifiable porridge in their stomachs. Herring was the only species that had eaten krill at 75m. At 85m, 50% of the fish had krill in their stomachs. The fish that had eaten krill at this depth was saithe and whiting. 25% of the fish had empty stomachs, while 12.5% respectively had *Calanus spp.* and unidentified porridge in their stomachs.
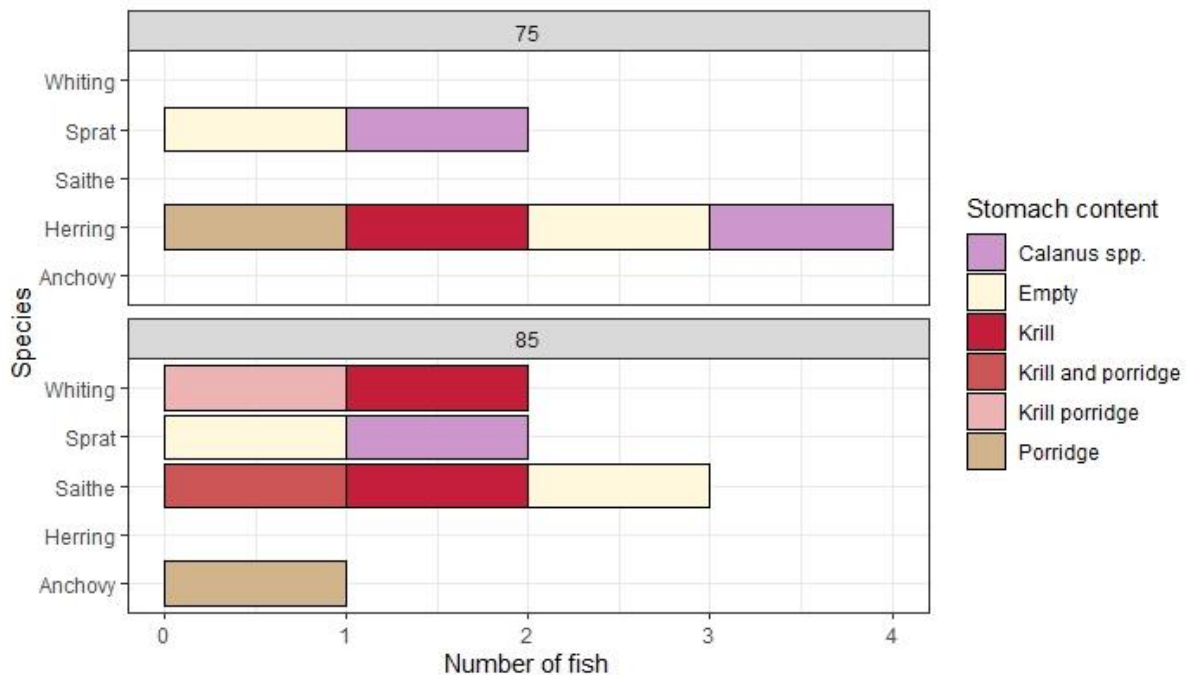
Figure 29: Stomach content from the fish trawled at Midtmeie in September 2020. Each section illustrates the trawl depth the fish were caught at.

Stomach content from the bottom trawls

50% of the Norway pouts stomach contained krill on the 15.10.2020. 33.3% of the fish had empty stomachs and 12.5% of the fish had porridge in their stomachs (fig. 30). One Norway pout had eaten a glass shrimp (4.1%).
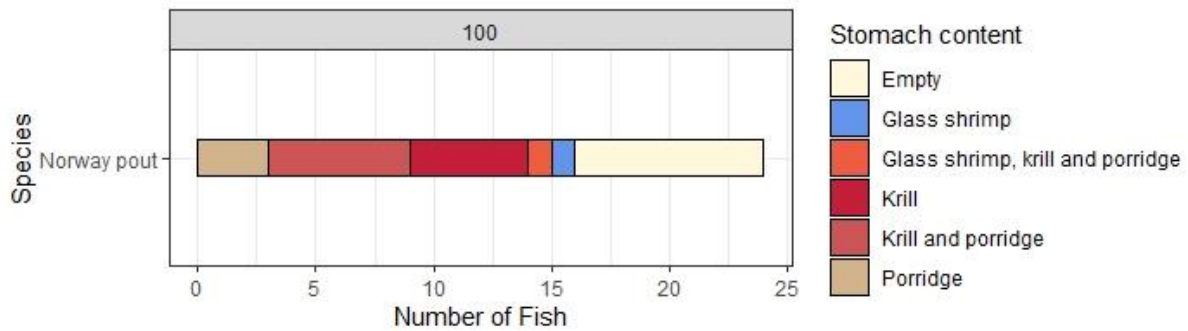
Figure 30: Stomach content on Norway pout from a subsample (15% of total catch) bottom trawled at Midtmeie 15.10.2020.

Later in October, 28% of the fish stomachs contained krill (fig. 31). The fish that had krill in their stomachs were Norway pout, poor cod, saithe, and silvery pout. Unfortunately, 28% of the fish had inverted stomach, preventing assessment of feeding. 16% of the fish had empty stomachs. One saithe and one whiting (4%) had porridge in their stomachs still impossible to identify to polychaetas. A poor cod (2%) had crab and fish juveniles in its stomach, another had mussel, ostracod and Aphrodita (2%) and a saithe had eaten a Spatangoida (2%).
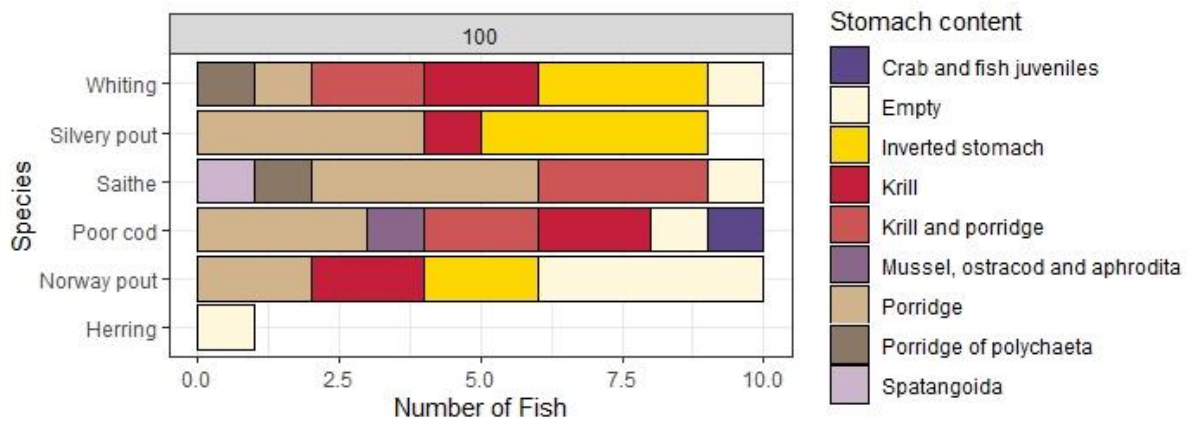
Figure 31: Stomach content from fish bottom trawled at Midtmeie 28.10.2020.

3.3 Acoustical studies: the behaviour of krill and fish

3.3.1 Krill diel vertical migration and behaviour

The krill performed diel vertical migration (DVM) at all times, distributed closer to the surface at night and residing closer to the seafloor at day. In February, the day distribution of krill, mainly restricted to a 25m wide sound scattering layer (SSL), extended from 55-80m with a decreasing concentration towards the seafloor (fig. 32). The SSL had a patchy pattern with a variety of higher and lower concentrations of krill, with spikes of backscatter at the uppermost part of the SSL. At mid-day, a gap occurred between 70-90m that can be ascribed to responses to sampling by the Isaac Kidd midwater trawl.

The whole population took part in DVM, ascending towards the surface in the afternoon. The krill reached the surface ~1h after sunset (timeanddate.no), followed by a subsequent descent below 15m ~1h after arrival. Not all the krill stayed in the shallower waters, descending towards the seafloor throughout the night. Despite of this, other krill stayed in the upper 5m throughout the night, dividing the nocturnal distribution into two krill layers, one in the upper 5m and the second between 15-50m (fig. 36). Closer to morning, krill from the deepest SSL ascended to the surface, where the two layers congregated. The congregation lasted for ~2h before the krill performed a coherent descent towards the seafloor. The krill reached the day distribution shortly after sunrise (timesanddate.no).
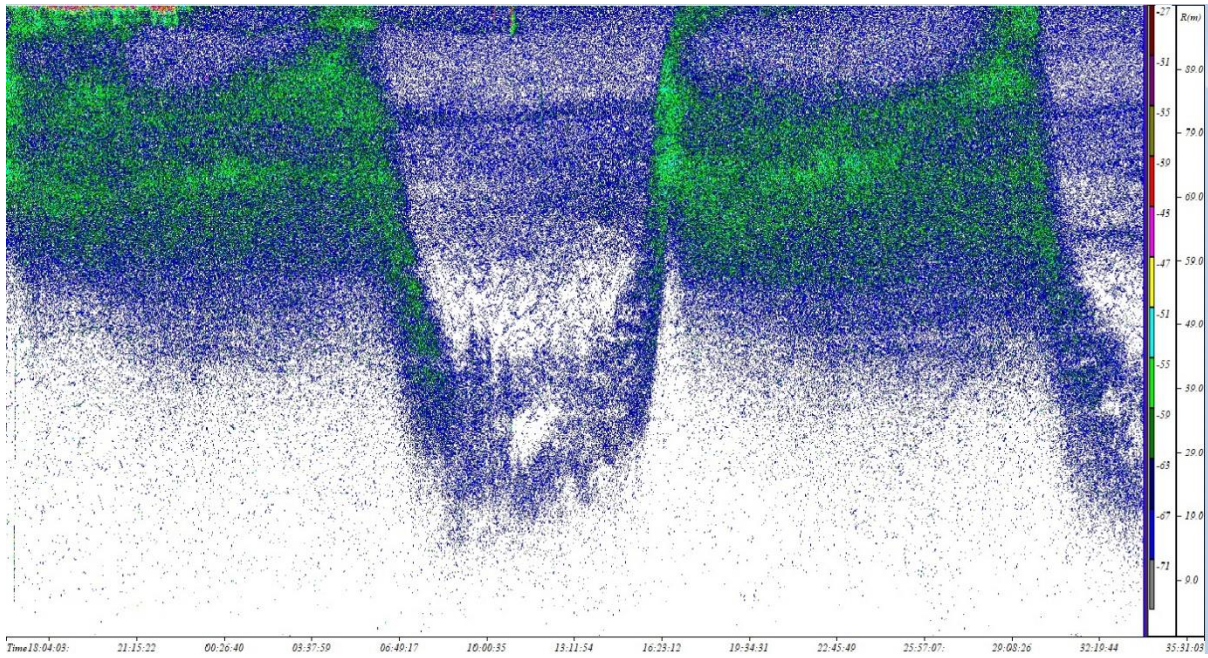
Figure 32: Acoustics records from a 200 kHz bottom-mounted echosounder at Midtmeie, 05.02.2020-07.02.2020. S$_v$ threshold of -75 dB. Depth scale shows range from echosounder.

The DVM during autumn corresponded with the recording from February. In September, the daytime distribution was relatively deeper, where the SSL occurred from 60m, with a strong distribution towards the seafloor (fig. 33). This SSL displayed a high degree of patchiness with prominent spikes at the uppermost part and records of low backscatter within the layer. Later in the afternoon, the whole population performed a coherent ascent before sunset, reaching the nocturnal distribution ~2h later – ~1h after sunset (timesanddate.no). Most of the krill stayed in the upper 20m of the water column throughout the night, with the highest concentrations at 10-15m. However, shortly after reaching the surface, part of the population descended to deeper water leaving a void in the krill registrations from the upper 10-15m throughout the night. The krill descended before sunrise, reaching back down to the day distribution ~1h after sunrise (timeanddate.no).

39
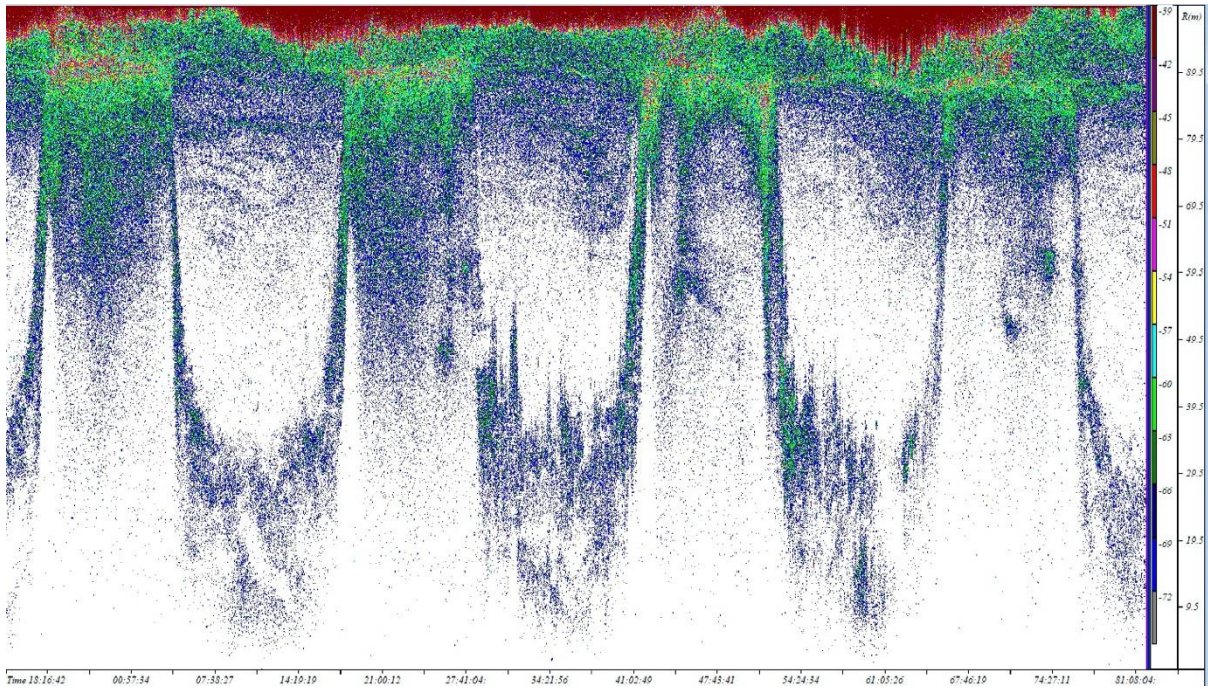
Echogram 33: Acoustics records from a 200kHz bottom-mounted transducer at Midtmeie, 21.09.2020-25.09.2020. S$_v$ threshold of -75 dB. Depth scale shows range from echosounder.

The distributions recorded in September corresponded with the recording performed later in the month and October (fig. 34). The day distribution from 60m down to the seafloor had a similar pattern of patchiness and spikiness, as earlier in September. Both the ascent in the afternoon and descent in the morning was in accordance with the sun setting or rising, where the whole krill population took part in the DVM. However, during the nocturnal distribution in October, the highest concentration of krill appeared closer to the surface, ranging from the surface to 15m (fig. 35). The krill performed mid-night sinking, like the earlier nocturnal descents recorded, where the krill concentration decreased from the surface to the seafloor.
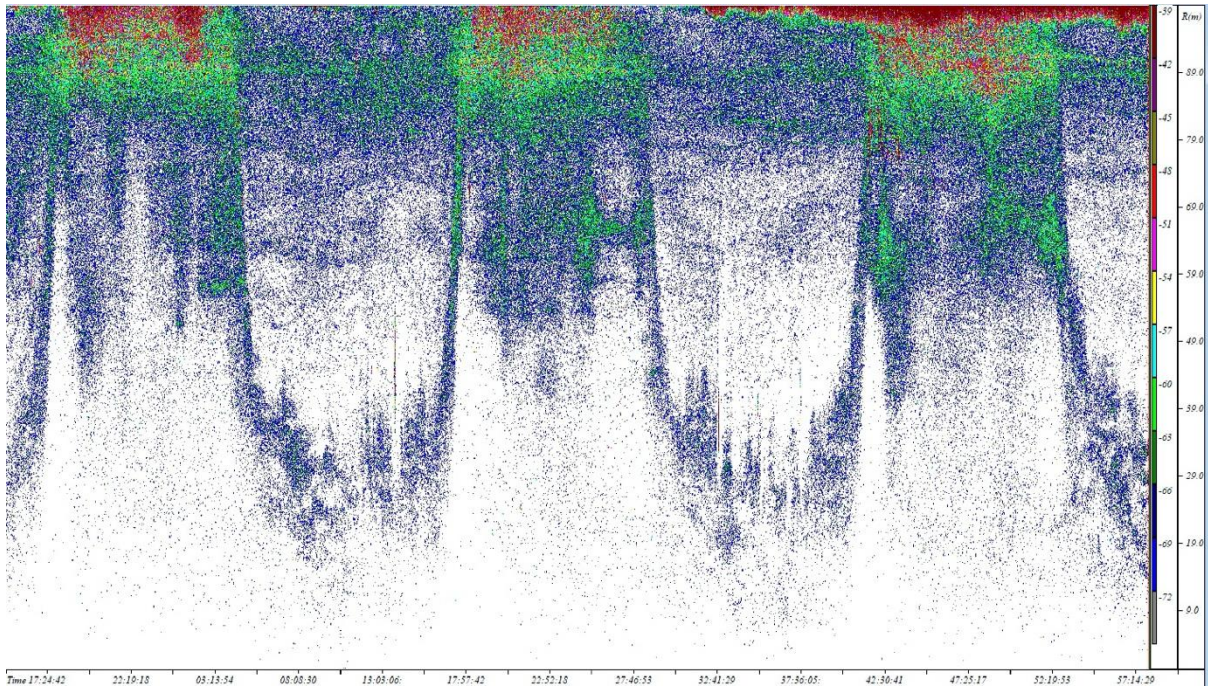
Figure 34: Acoustics records from a 200kHz bottom-mounted transducer at Midtmeie, 29.09.2020-02.10.2020. S$_v$ threshold of -75 dB. Depth scale shows range from echosounder.
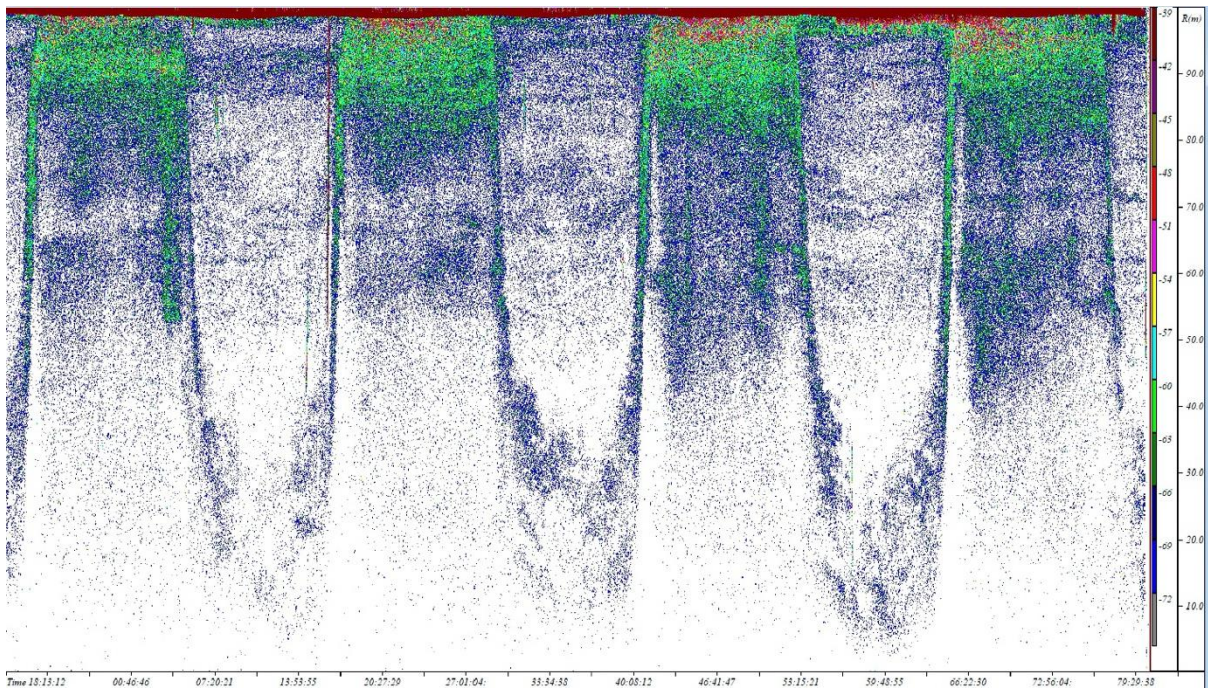
Figure 35: Acoustics records from a 200kHz bottom-mounted transducer at Midtmeie, 15.10.2020-19.10.2020. S$_v$ threshold of -75 dB. Depth scale shows range from echosounder.

3.3.2 Fish distribution and behaviour

Fish and krill often co-occurred within the same sound scattering layers (SSL) both day and night. During the day in February, fish were recorded through the whole water column, occurring as both single individuals and groups. Most of the fish recordings were at 40-80m depth, above and within the krill's day distribution at 55-80m, with fewer recordings of fish at the upper 20m and below 80m depth. Fish below the krill distribution could potentially be associated with the seafloor, entering from underneath the krill layer, while fish in shallower depths entered the layer from above.

The fish ascended at dusk, overlapping with the krill at the upper 15m of the water column. Followed by the krill subsequently splitting into two SSL after ascent, there were strong recordings of fish occupying the 10m between 5-15m, creating a gap within the krill's nocturnal distribution (fig. 36). Some of these fish released gas recognised by air bubbles ascending towards the surface, most likely being either herring or sprat. However, plenty of fish was distributed at the upper boundary of the krill layer, with fish diving into it and others residing within it throughout the night. Fish were also present below the krill layer and distributed towards the seafloor (50-100m), occasionally entering the krill layer from below.
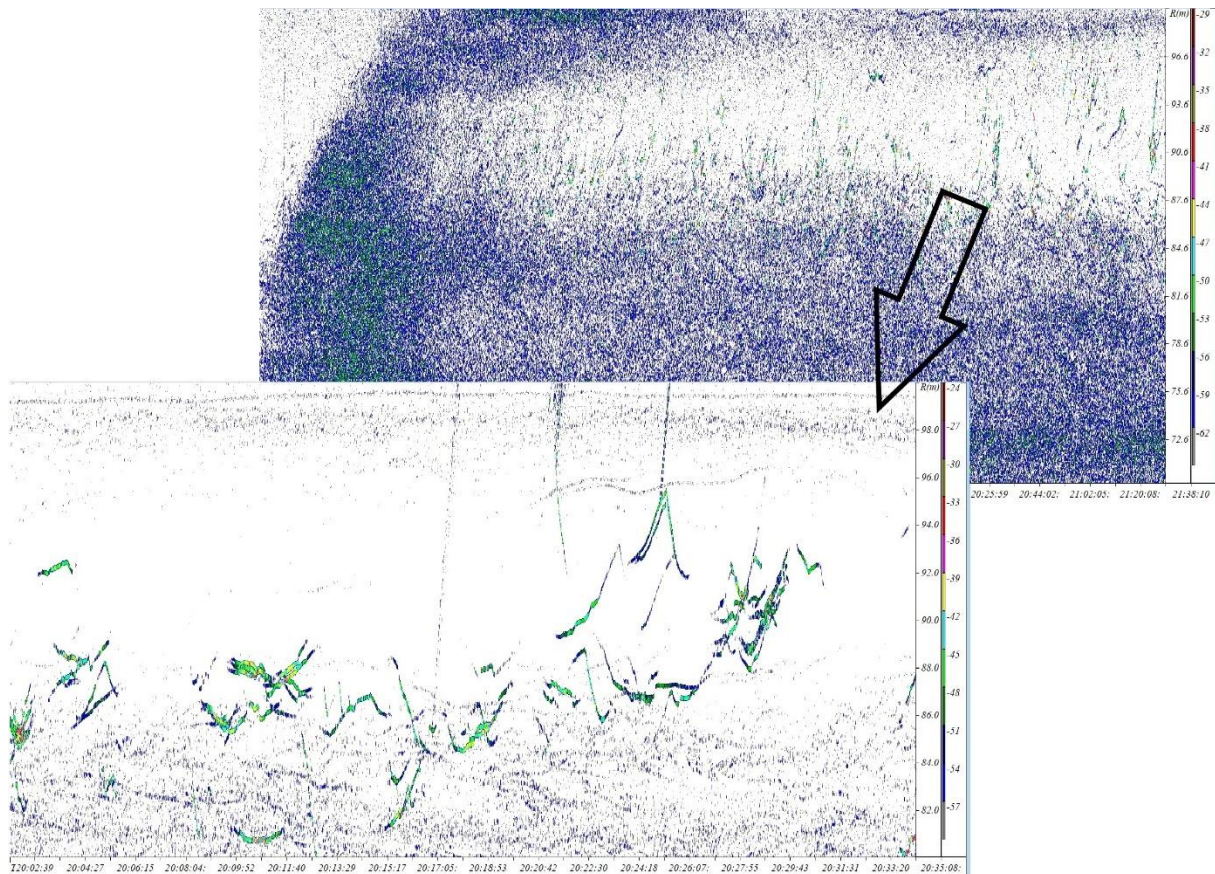
Figure 36: Midtmeie 06.02.2020. Threshold of the overall echogram is -65 dB, showing the nocturnal distribution of krill splitting into two layers, where the fish occupies the area in between 5-10m. Zooming in and changing the threshold to -60 dB, fish were distributed at the uppermost part of the krill's nocturnal distribution. Three of these fish are Clupeiformes recognised due to the gas release. Depth scale shows range from echosounder.

Close to the surface, at 6m depth, a thin unidentified layer was present, apparently attracting both single individuals and groups of fish (fig. 37). This layer does most likely not represent krill, as the fish left the upper 20m in the morning, trailing after the descending krill, while the unidentified layer remained.
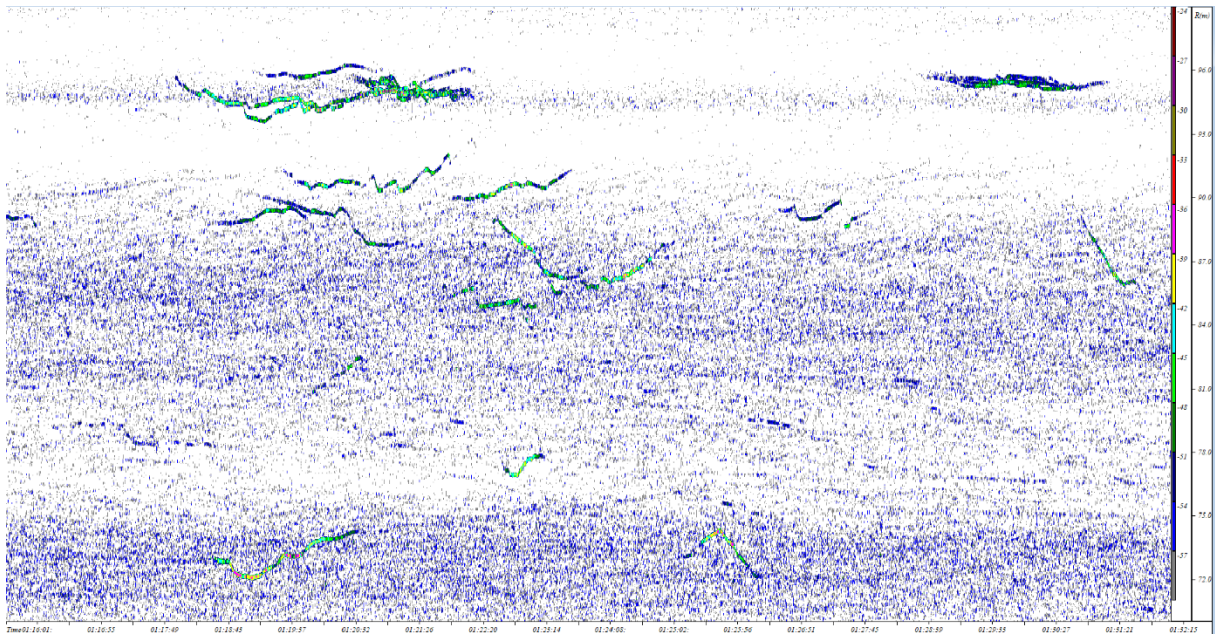
Figure 37: Midtmeie 06.02.2020. Unidentified layer at 6m attracting fish groups, even during night. Threshold of -60 dB. Depth scale shows range from the echosounder.

Also in September, strong recordings of fish were made close to, or overlapping with the krill's daytime distribution. Smaller fish schools, groups and single individuals occurred just above the krill layer at 50-60m, although smaller fish schools were recorded close to the surface. Fish were also present within the krill layer and near the seafloor (~60m-100m). In the following afternoons, fish schools, including Clupeiform schools, occurred near the surface during the krill ascent. They placed themselves below the krill layer at 20-30m depth during the night (fig. 38). Most of the groups present at the ascent released gas, and therefore could be identified as Clupeids. Single individuals not associated with groups could be other fish species. The trawl catches showed that numerous species were present during the daytime, but species could not be identified from the acoustic records.
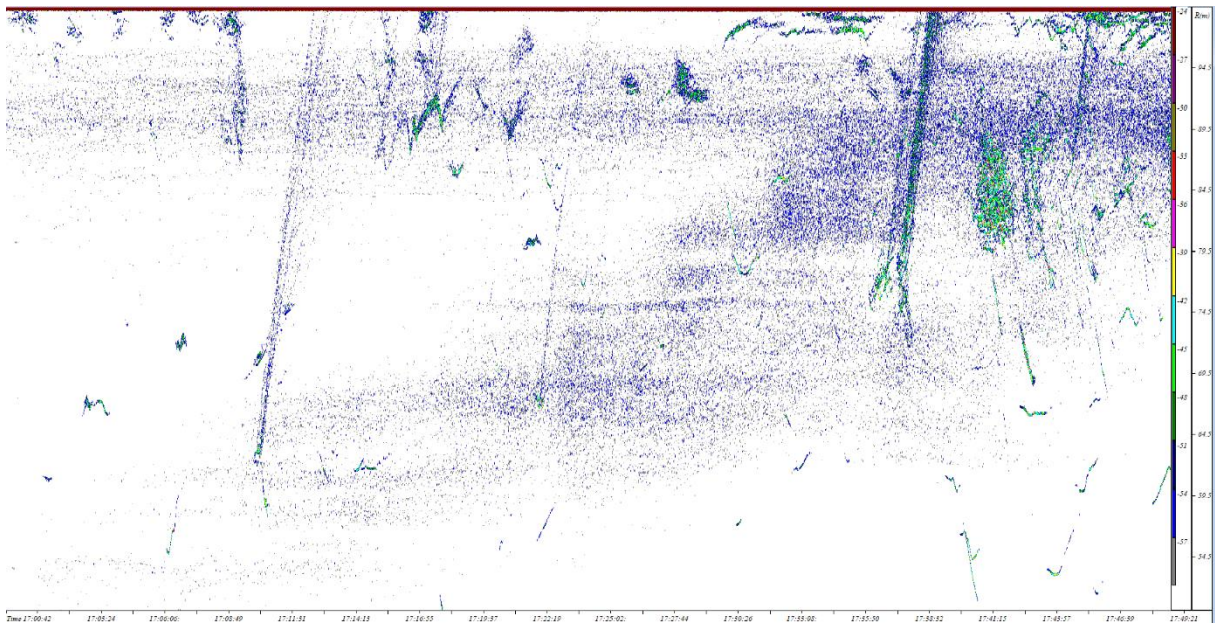
Figure 38: Midtmeie 30.09.2020. Threshold of -60 dB. Ascending fish schools, that are most likely sprat or herring due to the gas release, ascending together with the krill towards their nocturnal distribution. Depth scale shows range from echosounder.

After krill reached their nocturnal distribution in September, the krill layer did not split up as seen in the previous recordings from February. In these recordings, the fish and krill co-occurred in the upper 20m of the water column, with strong recordings of fish in the upper 10m. The fish subsequently separated into two layers, where the shallowest fish layer was distributed between the surface and 3m, and the deeper layer was distributed between 7-10m (fig. 39). These fish groups gathered and trailed after the krill when it descended before sunrise (fig. 40). Fish were also present at deeper depths during the krill's nocturnal distribution.
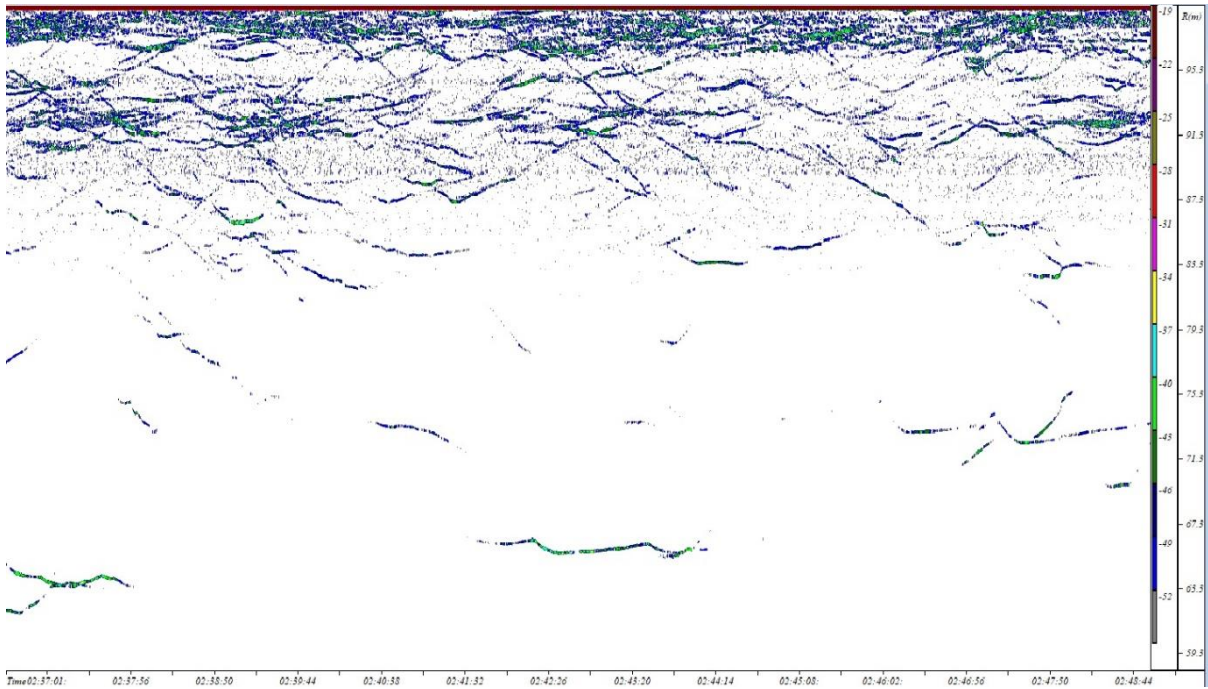
Figure 39: Midtmeie 30.09.2020. Fish splitting up into two layers – one at the upper 3m and another at from 10m (range). Threshold of -55 dB.
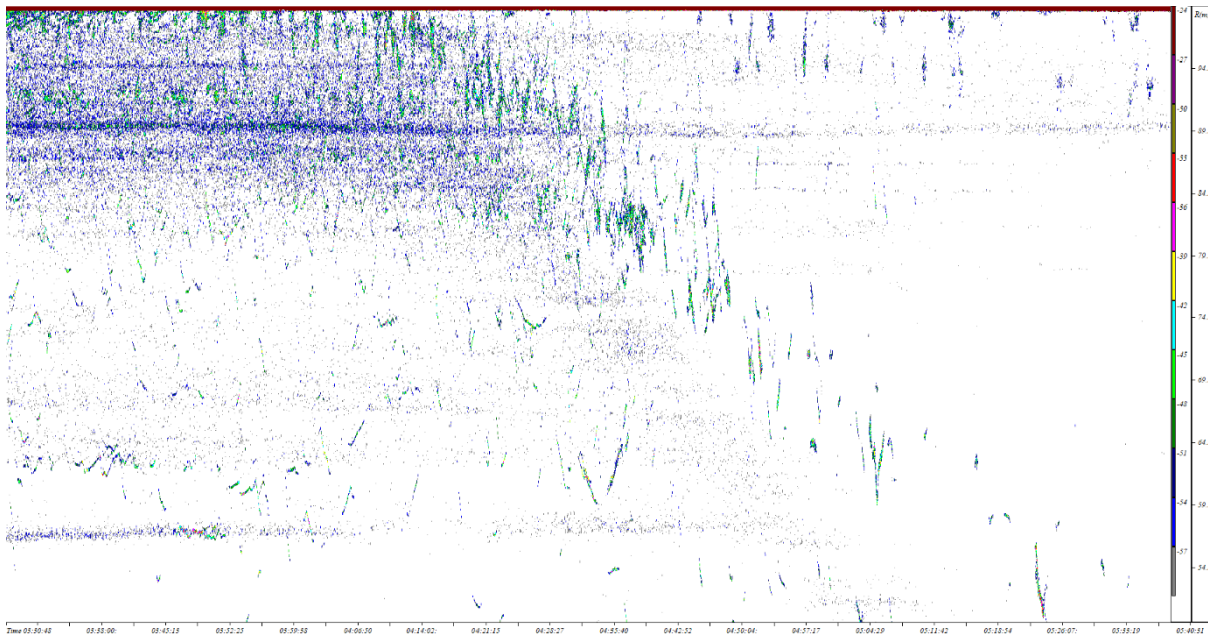
Figure 40: Midtmeie 30.09.2020. Threshold of -60 dB. Two fish groups gathering and trailing after the descending krill prior to sunrise. Depth scale shows range from echosounder.

In October, as in the previous recordings fish schools interacted with the krill's daytime SSL, at the uppermost part at 50-60m and deeper within the layer (60-80m) (fig. 41). The echograms showed that the krill performed apparent avoidance responses in the presence of the fish schools, leaving empty gaps in the backscatter. The fish interference with the krill layers created the spikes shooting up from the krill SSLs and the patchiness that occurred during the krill's daytime distribution in the recordings. Some of these fish schools showed gas release.
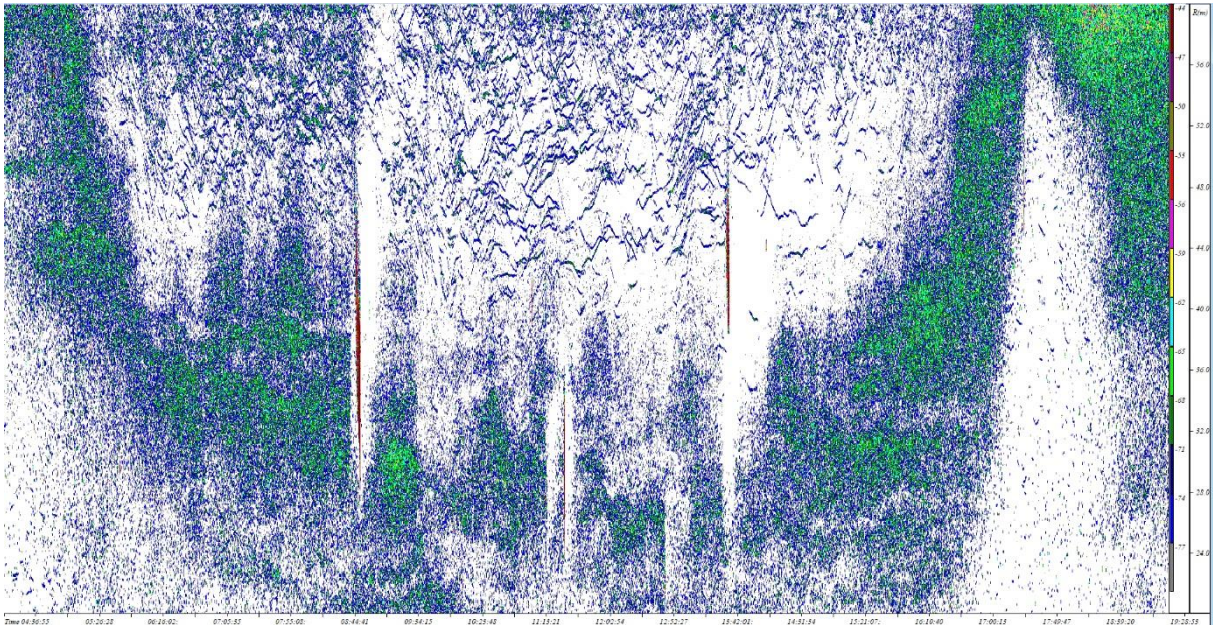
Figure 41: Midtmeie 01.10.2020. Fish schools interfering with the daytime layer of krill, resulting in avoidance by the krill. Threshold of -80 dB in this echogram. Depth scale shows range from echosounder.

Similar to the September recordings, the fish were already present near the surface when the krill ascended for their nocturnal distribution in the afternoon. The fish overlapped with the highest concentration of krill at the upper 10m of the water column. Other fish resided deeper, below the krill layer at 15m, and mainly occurred as single individuals near the seafloor. Early in October, the nocturnal distribution of fish was bimodal in relation to the krill's nocturnal distribution. The shallowest distribution was in the upper 10m, while the deeper was between 35-45m. Recordings of smaller fish schools decreased thought the night, even though they were present throughout some nights in the previous recordings. The fish schools reappeared again in the morning.

4. Discussion

The main aim of this thesis was to establish when and where the fish would attack the *Meganyctiphanes norvegica* and to describe and explain their behaviours in this predatory-prey interaction, respectively, through day and night. Through this study, the Oslofjord's environment has been studied with CTD/STDs- and light measurements, while different net hauls have given insight into who the fjords' inhabitants are. The echosounders have acted as our eyes under the water. Through this discussion, the measurements from the environment and the catches will be evaluated in accordance with the echograms from the recordings. The aim is that this thesis will contribute to a greater understanding of diel vertical migration (DVM) and the predatory-prey interaction between krill and fish.

Krill performed DVM, accompanied by migrating fish throughout the study period (February – October 2020). Differences in the depth distribution of krill occurred between the seasons. In February, the day distribution was shallower, and the nocturnal distribution deeper compared to the following recordings. At day, the krill stayed below 55-80m, with some individual exceptions. In the afternoon, the krill ascended to the surface. The majority of krill subsequently descended below 15m, while a thinner layer of krill stayed close to the surface through the night. The segregation of the layers occurred most likely due to high accumulations of fish that were visually foraging in the light of a nearly full moon. In autumn, the krill resided closer to the seafloor during their day distribution. Apparent interactions between the krill layer and fish occurred, and avoidance responses by the krill were observed. Fish and krill overlapped near the surface at night even though there was a full moon within this period. The weather during the full moon was overcast. Most of the fish caught had fed on krill at one point during the krill's DVM.

4.1 The hydrographical factors in the Oslofjord

There were no indications that the diel vertical migration (DVM) by *M. norvegica* was related to any of the hydrographical parameters measured in this study. The krill's vertical distribution and DVM extended throughout the entire water column regardless of the varying hydrography. At the day distribution, the krill's sound scattering layer (SSL) had a shallower distribution in February compared to September and October 2020, which had a deeper and more concentrated distribution towards the seafloor. Both temperature and salinity were relatively stable below

25m depth through 2020, indicating that neither temperature nor salinity most likely was the restricting factors of the day distributions depth.

Temperature is a fundamental factor controlling the metabolic processes in the ectothermic krill (Maps et al., 2014; Ollier et al., 2018), impacting their growth, survival, recruitment and can even affect the geographical distribution (Ollier et al., 2018). The warmer water at the nocturnal distribution in September and October could have been beneficial for the krill by accelerating metabolic rates that could contribute to increased growth rates (Ollier et al., 2018; Onsrud & Kaartvedt, 1998; Saborowski et al., 2002). Nonetheless, low temperatures did not seem to stop the krill from ascending to the cold surface in February, even though the nocturnal distribution segregated into two distinct layers subsequent after ascent. Salinity could neither explain the nocturnal distribution in the recordings. Krill seems to be adaptable to a variety of salinities (Tarling et al., 2010), considering its wide geographical distribution from the high salinity Mediterranean Sea to the low salinity Kattegat Channel (Tarling et al., 1998; Ventero et al., 2019).

The oxygen saturation near the seafloor was higher in October than in February 2020, likely related to a deep-water renewal that occurred between April and the summer of 2020 that brought new oxygen-rich water into the station (Staalstrøm et al., 2021). The oxygen saturation near the seafloor increased from 29% in February to 42% in October. Previous studies from the Bunnefjord has observed that krill inhabit the ranges of oxygen saturations encompassing the percentages found in this thesis, i.e. <30% oxygen saturation near the seafloor at the beginning of the measurements and >60% at the end (Klevjer & Kaartvedt, 2011; Solberg et al., 2012). Krill have even been observed at oxygen saturations as low as 15-20% during daytime (Klevjer & Kaartvedt, 2011). At such low saturations, the krill may switch over to anaerobic respiration (Klevjer & Kaartvedt, 2011). Low-oxygen-depths can act as a refuge for the krill from potential deep-living predators and entering oxygen-poor waters may be a behavioural strategy to avoid predators (Klevjer & Kaartvedt, 2011; Onsrud & Kaartvedt, 1998; Spicer & Saborowski, 2010). However, they may not be able to stay in low oxygen habitats for long periods due to build-ups of high L-lactate concentrations (Spicer & Saborowski, 2010). Therefore, reoxygenating in the shallower oxygen-richer waters at night might be crucial (Spicer & Saborowski, 2010).

4.2 Light and krill behaviour

4.2.1 The krill size and distribution

The light measurements showed a rapid decrease by depth. Researchers argue that light is the proximate driver for migration (Aksnes et al., 2017; Cisewski et al., 2010; Norheim et al., 2016), but also one of the cues that determine the distribution depth (Kaartvedt, 2010; Widder & Frank, 2001). The highest light extinction in the upper 25m was recorded in February, with the krill's daytime distribution ranging from 55-80m depth. Vestheim et al. (2014) observed that the krill's day distribution became shallower with the lower light intensities during a snowfall after the surface had frozen. In comparison with the higher light intensities and deeper day distributions during autumn, it seems that light indeed determined the depth of the sound scattering layer (SSL) of krill. Therefore, providing the possibility to stay at shallower depths when lower light intensities penetrate the water and vice versa.

The krill migrated according to the sun rising in the morning and setting in the afternoon. The krill in this study could potentially be following isolumes, which is a layer of constant light (Tarling et al., 1998). The isolume hypothesis suggests that the migrators follow preferable light levels, not necessarily specific light levels, but it can appear when the migrators distribute in a variety of light intensities (Norheim et al., 2016). 'Light Comfort Zone' (LCZ), is a related concept, but encompass a range of light levels, i.e. a zone not too light or too dark (Norheim et al., 2016). It is anticipated that the preferred light levels are chosen based on factors like the organism's visual physiology and size, as well as other individualities such as sex and trade-offs related to feeding that is conspicuous for the predator (Hobbs et al., 2021; Kaartvedt, 2010). For example, LCZs can be controlled by the lowest light sensitivity threshold in the predator's eye (Langbehn et al., 2019). Nonetheless, behaviour related to particular light levels like isolumes is a quite disputed subject, with examples of organisms following or not following such constant light levels (Baliño & Aksnes, 1993; Benoit-Bird et al., 2009; Liljebladh & Thomasson, 2001; Onsrud & Kaartvedt, 1998).

The largest krill catches were caught below 80m in all the surveys. Krill from February and October had an increasing size distribution from the shallowest to the deepest trawl interval. Larger individuals are more optically conspicuous in higher light intensities and usually migrates into deeper and safer waters at daytime to avoid predation pressure (De Robertis, 2002; Giske et al., 1990; Langbehn et al., 2019), potentially selecting light intensities more preferable

to their size than the smaller individuals. With the lower light intensity in February, this corresponds with why the daytime distribution then were shallower than the autumn recordings – darker at shallower depths. However, krill does not only have predators in the upper part of the water column, SSLs of krill can become shallower if the predation pressure from below is high (Kaartvedt et al., 1996).

Although increasing size by depth was the most common pattern in this study, the size distribution in September showed cases of larger individuals in the shallower IKMT interval and no significant size difference between the krill caught with the pelagic trawl. This can be an example where the differences in selectiveness and efficiencies of the two trawls are reviled. Most of the krill had a length >30mm. The smallest captured krill was 14mm caught in September, while the largest krill were caught in February at 90m and in September at 75m depth. The krill sizes measured in this thesis correspond with the measurements of krill in another study in the Oslofjord, where the largest krill measured 44mm and the smallest 15mm (Onsrud & Kaartvedt, 1998). Usually, krill do not live through a second winter, and the small krill caught in September would be the young of the year (Boysen & Buchholz, 1984). Their growth rate correlates with the food availability from about April to October, and the food availability is scarce during the winter, reportedly leading to almost stagnant growth (Boysen & Buchholz, 1984). However, the krill at Midtmeie had reached sizes >30mm in February, potentially indicating that the feeding conditions in the Oslofjord had been good. The stomach content analysis (SCA) of the krill stomachs showed a carnivorous diet, indicating that the access of copepods may have been favourable through the winter and autumn.

4.2.2 Impacts of turbidity and topography

Midtmeie is a relative shallow site for krill that elsewhere can be found at 500m (Tarling et al., 2010). As mentioned in the introduction, turbidity can influence the predator's vision by altering the contrast between prey and the background (Wing et al., 2021). Based on this, turbidity can make it possible for krill to stay at shallower sites and not be as affected as the organisms at greater depths with optically clearer water (Ludvigsen et al., 2018). Norwegian Institute for Water Research (NIVA) reported that the visuality depth in all the stations from Steilene and inwards the Oslofjord was moderate to low in 2020 (Staalstrøm et al., 2021), which may explain why the krill thrive at a relatively shallow depth in the Oslofjord. This is supported by Onsrud & Kaartvedt (1998), that pointed out that the krill's shallow distribution in the Oslofjord compared to fjords in Western Norway could be due to the high water turbidity.

Nevertheless, the shallow topography at Midtmeie to some extent blocks the krill descent, as suggested by comparing with krill distribution in other parts of the fjord (Klevjer & Kaartvedt, 2011; Vestheim et al., 2014). The krill's close relation to the seafloor in the autumn recordings, could potentially be a scenario of entrapment outside their light intensity preferences (Aarflot et al., 2018). This phenomenon is called 'the topographic blockage mechanism' (Aarflot et al., 2018), and will be dealt with later in this thesis.

4.2.3 Impacts of moonlight

In the afternoons, the krill preformed a coherent synchronic migration towards their nocturnal distribution, reaching the surface shortly after sunset. The nocturnal distribution in February segregated into a layer above 5m and below 15m, while the nocturnal distributions in September and October were close to the surface. The February recording (05-07.02.2020) was in advance of a full moon (09.02.2020, timeanddate.no), where the moonlight is known to influence the nocturnal distribution of zooplankton (Tarling, 1999). Deeper nocturnal distributions are believed to be a result of visual predators such as fish that utilise the higher light intensity from the moon to hunt (Last et al., 2016). The weather was clear during this recording period, without any clouds blocking the light from the moon (timeanddate.no). This could be an explanation why most of the krill population had a deeper nocturnal distribution in February than September and October. The thinner layer above 5m could potentially be krill of smaller size or greater risktakers in demand for food, amongst other individualities (Hobbs et al., 2021; Kaartvedt, 2010). This is a question difficult to answer without any net catch from the specific depth interval at night.

In advance of the sound scattering layer (SSL) segregation, the krill stayed at the surface for ~1h before the majority descended below 15m. The krill ascended again before descent in the morning. This might suggest an antipredator window for the krill, which is described by Kaartvedt et al. (1996) as "the point where ratio of mortality risk to feeding rate is at a minimum at intermediate levels of light intensity" (Kaartvedt et al., 1996, p. 57). Christiansen et al. (2019) saw such dusk-and-dawn-ascent behaviour in mesopelagic fish in Masfjorden, Western Norway, and assumed that the fish were participating in foraging. This seems to be a reasonable explanation in this case, looking at the moon cycle for this period at timesanddate.no. The moon was hardly over the horizon and it could be possible that the light were at an intermediate level as Kaartvedt et al. (1996) stated, where the krill gets the chance to benefit from the food sources

at the surface. The dawn ascent could seem like some kind of "hitting the buffet one last time before closing time"-behaviour before they had to descend in advance of the sunrise.

Another full moon event occurred on the 01.10.2020 as well. However, in this case, krill seemed unaffected by the full moon. The nocturnal distribution in this period were relatively similar to the recording earlier in September and later in October, with a half-moon and new moon, respectively (timeanddate.no). Looking at the weather for this period, timeanddate.no showed that the weather was overcast. The cloud coverage most likely blocked the light from illuminating the water and decreased the pressure on krill by visual predators. These data may suggest that moonlight might be an exogenous cue for lunar rhythm in krill behaviour.

4.2.4 Feeding behaviour

It is well documented that krill and other zooplankton utilise the food resources in the shallower depths at night during their diel vertical migration (DVM) (e.g. Ichii et al., 2020; Kaartvedt, 2010; Onsrud & Kaartvedt, 1998; Tarling et al., 2002). Midnight sinking started subsequently after ascent in all the recordings and the krill distributed much of the water column. Such behaviour might reflect asynchronous migrations through the night. Such descent is in accordance with Pearre's (2003, p. 39) hunger/saturation hypothesis suggesting that: "once satiated, the animals would descend to deeper water". The stomach contents of krill have been observed to be fuller of chla pigment after nights at the surface (Onsrud & Kaartvedt, 1998). Onsrud & Kaartvedt (1998) stated that the migration behaviour between shallower food-rich waters and deeper darker depths could be an adaptive strategy to decrease the predation pressure. However, in contrast to the most common feeding pattern, krill have also been observed to feed within their daytime distribution, where the reason could be that they had fed on phytoplankton that had sunk from the surface (Kaartvedt et al., 2002; Onsrud & Kaartvedt, 1998).

Chlorophyll was not measured in this study. However, according to Norwegian Institute for Water Research (NIVA), the phytoplankton concentration at Steiliene, which is a station close to Midtmeie, were low until March of 2020 (Staalstrøm et al., 2021). The phytoplankton concentrations had a tiny increase in September before decreasing again, and lower concentrations continued throughout the year (Staalstrøm et al., 2021). Increased food supplies at the surface can be the driver leading to the overlap with the fish during the autumn recordings. In addition, to their phytoplankton diet, the krill are considered selective visual predators that

forage more efficiently in lighter conditions by spotting their prey in contrast to the down-welling light (Abrahamsen et al., 2010; Kaartvedt et al., 2002; Torgersen, 2001). Kaartvedt et al. (2002) recorded that during August, the krill were specifically focusing on *Temora longicornis* during their nocturnal ascent, while focusing on overwintering *Calanus spp.* within the daytime distribution in November. Similarly, Onsrud & Kaartvedt (1998) observed that krill preyed on copepods both day and night. Abrahamsen et al. (2010) suggested that they used mechanoreception through their antennules to catch prey when they were in their daytime distribution. Kaartvedt et al. (2002) suggested that visual foraging in the daytime habitat might be important. Through roughly identification of species from the WP2-net, a shift in the dominant species composition were observed. Smaller copepods dominated the two shallowest intervals while *Calanus spp.* dominated the deepest interval (95-70m), indicating that *Calanus spp.* and krill overlapped in their daytime distribution. The mandibles found in the krill stomach documented that the krill indeed was foraging carnivorously. When these mandibles were eaten is not known, but a more thorough species and digestion analysis of the stomach content might suggest where and when the krill had eaten them.

4.3 The fish predators of krill in the Oslofjord

4.3.1 Interactions and stomach content analysis

During the day in February, a tow with the Isaac Kidd midwater trawl (IKMT) was taken just above the echosounder. This recording shows that when the trawl entered the sound scattering layer (SSL), the krill performed rapid and apparent avoidance behaviour, swimming away from the trawl. The void in the krill records persisted for a few hours. The recordings from September and October showed that the krill had a similar response towards its fish predators – apparent avoidance behaviour. And the krill evidently was exposed to predators; by analysing the stomachs of all the fish, the stomach content analyses (SCA) showed that all the fish species, except for anchovy and sprat, had fed on krill. Undigested stomach content could indicate that the fish had fed on krill shortly before the fish were caught or even within the trawl, but krill in the stomachs were recorded in any digestive states. Most of these krill-feeding fish were caught in the deepest pelagic trawl depth or bottom trawled at daytime. Knowing that the krill stayed below 55m towards the seafloor, through trawling and acoustical methods, indicates that the krill and fish overlaps during the day.

4.3.2 Predatory/feeding behaviour of the fish

The echosounder recordings showed that the krill were influenced by fish schools at day and responded by fleeing from them. Most of the fish schools observed in these recordings had gas release, indicating that they could be either herring or sprat (Solberg & Kaartvedt, 2014). Onsrud et al. (2004) catches indicated that herring would form the deeper fish schools impacting the krill sound scattering layer (SSL) in their station. Even though the catches were small in my study, herring were present in trawl surveys from the shallowest interval to bottom trawls, while sprat were only caught in September. It is possible that the schools interfering with the krill SSL in the echograms most likely are herring. The stomach content analysis (SCA) of herring showed that they had eaten krill, verifying that the herring is a krill predator. The SCA of sprat showed that they most likely had another diet preference than krill in this period since their stomachs were either containing *Calanus spp.* or nothing.

In an earlier study on sprat from the Bunnefjord, Solberg et al. (2015) found that sprat dominantly fed on *Calanus spp.* and were a size-selective feeder, such as anchovies (Plounevez & Champalbert, 1999). Sprat only appears to choose prey such as krill when they are of a larger size (Falkenhaug & Dalpadado, 2013; Solberg et al., 2015). At Midtmeie, a thin layer was observed at ~6m through the recordings, raising the question if this layer could be of smaller plankton, which could be compatible with the results from the WP2-net where smaller copepods were most abundant at the shallowest depth interval. Several smaller fish schools and groups seemed to be attracted by this layer, especially at night.

Fish schools occurred above and within the daytime distribution of the krill. The fish schools seemed to attack the krill from above. The krill responded with avoidance behaviour, clearly swimming away from the fish. This attack pattern by the fish schools corresponds well with results by Onsrud et al. (2004) in the Oslofjord. Onsrud et al. (2004) suggested that the herring fed on krill during both daytime and nighttime at deeper depths based on their SCA. This agrees with the digestion state of some of the krill in the stomach of the herring. Onsrud et al. (2004) pointed out that the fish schools of herring fed on the shallowest fringe of the krill layer. This could be seen at Midtmeie during this study as well, although some fish schools went deeper into the krill layer. Onsrud et al. (2004) proposed that the depth was based on the herring's visual threshold to light intensities. Since Midtmeie is a shallower site, it could be possible that the herring could swim deeper into the krill SSL than in deeper locations, with the possibility of visual predation.

Single individuals of fish were also present in the krill SSL both day and night. Most of the pelagic trawls as well as the bottom trawl contained whiting. Being a non-schooling species (Røstad et al., 2006), whiting could potentially represent the single individuals in the upper part of the water column. Onsrud et al., (2004) connected the single individuals associated with the krill SSL day and night to be whiting, suggesting both diurnal and nocturnal foraging on the krill. This would correspond well with the SCA from this study, where the krill porridge could indicate night feeding and the not as digested krill could indicate newer feeding. Onsrud et al., (2004) expected the whiting to have a lower visual threshold than herring due to the whiting's larger eye size. The whiting is primarily considered to be a demersal fish (Baudron et al., 2019), and can be found in waters with low light penetration (Onsrud et al., 2004).

Norway pout, saithe, poor-cod and silvery pout occurred in the catches from the bottom trawl. The SCAs of Norway pout showed that they fed mainly on krill and glass shrimps, indicating that these crustaceans are important prey. This would suggest that the fish interacted with the krill from below. This also corresponds with Onsrud et al. (2004), concluding that the Norway pouts were feeding from the lower part of the krill SSL without any specific day or night feeding patterns found. They pointed out that Norway pout had large eyes making it possible for them to see prey in deeper darker waters at day. The sensitivity of the eyes increases with larger sizes since it yields larger lenses and pupils, by allowing more photons to reach the retina (de Busserolles et al., 2020). Yet, Onsrud et al. (2004) suggest that the Norway pout might switch to being an tactile ambush predator at night due to the morphology of its lateral-line. Albert (1994) found that Norway pouts performed diurnal vertical migration, ascend about 20m at dusk, and descend to 1.5m above seafloor at dawn.

The SCA of the saithe showed that they had fed on krill, glass shrimps and fish juveniles. The saithe around Norway have been reported to feed mainly on euphausiids and Norway pout (Homrum et al., 2012), while the larger saithe can predate on other larger fish (Homrum et al., 2012; Kaartvedt et al., 2005). The saithe is semi-pelagic (Homrum et al., 2012), and in the Barents Sea, considered more of a piscivore (Fall & Fiksen, 2019). Older saithe have been observed at deeper depths (Homrum et al., 2012). However, Kaartvedt et al., (2005) observed that large saithe located themselves below the krill swarms, where they instead of feeding on the krill, appeared to hunt for planktivores. This can result in a process called indirect trophic interaction and can be a antipredator strategy (Pinti et al., 2019), where the krill can get increased protection from these piscivores (Kaartvedt et al., 2005).

The benthopelagic poor-cod is regularly caught with bottom trawls (Magnussen & Magnussen, 2009). The diet of the poor-cod in the bottom trawl was diverse, but they had clearly fed on krill. Similarly, earlier observations from the Faroe Banks recorded feeding on euphausiids (Menon, 1950). The deep-living silvery pout that can inhabit both the mesopelagic and benthopelagic zone, have earlier shown to feed on different groups of crustaceans, and sometimes small fish (Gaemers & Poulsen, 2017). The SCA showed that one of these fish had evidently fed on krill some time prior to sampling, as the digestion had already started. It is unknown if it had fed on krill during the night or the early morning. It is possible that the porridge in the other silvery pouts are krill as well, but this cannot be determined.

The krill at Midtmeie, seems to be preyed upon both from pelagic and bottom associated fish, 'the topographic blockage mechanism' (Aarflot et al., 2018). Due to advection, new krill may descend towards the seafloor at Midtmeie in the morning, making them vulnerable to deep-living fish (c.f. Isaacs & Schwartzlose, 1965). Particularly, in the autumn recordings, the krill appeared to concentrate close to the seafloor. The shallow site limits the krill in migrating deeper, leading to the krill being exposed by the light, especially the larger individuals (Aarflot et al., 2018). This increases the deep-living fish such as Norway pout, saithe, poor-cod and silvery pout probabilities to detect the krill (Aarflot et al., 2018). Advection may provide continuous new supply of krill. The 'the topographic blockage mechanism' can be one of the reasons why Midtmeie is a suitable fish bank, facilitating foraging of both pelagic and bottom-associated fish.

4.4 Conclusion

Bottom-mounted echosounders are valuable for investigating the diel vertical migration (DVM) behaviour of krill and in revealing possible predator-prey-interaction. The krill showed clear DVM at Midtmeie, with their distribution being modified in accordance with the decreasing or increasing light intensities both day and night. High concentrations of krill near the seafloor appear as a result of topography blockage from further descent. The krill ascended in synchrony in afternoon, with a subsequent sinking towards deeper layers, which would be in accordance with the hunger-saturation hypothesis.

The trawl catches and the echograms indicated that fish and krill overlapped during daytime. This is beneficial for the deep-living seafloor-related fish that can visually forage more efficiently on the exposed krill. The fish schools were closely related to the upper fringe of the sound scattering layer (SSL) of krill. During the autumn recordings, fish schools, most likely herring, attacked the krill from above. The krill responded with an avoidance response, fleeing from the fish, contributing to the patchiness in the SSL. The stomach content analysis showed that the krill were prominent prey for most of the fish caught in this study and that krill were most likely fed on both day and night.

The recordings support earlier assumptions that krill are influenced by moonlight. During full moon in clear nights, majority of the krill descended into deeper depths, while the fish accumulated between krill layers, likely to predate on krill illuminated by the moonlight. In dark, overcast nights krill and fish overlapped in near-surface waters. The krill is never really safe, the predators are everywhere, and they are indeed licenced to krill.

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Appendix

Table C1: Measurements done on Meganyctiphanes norvegica from the Isaac Kidd midwater trawl catches at Midtmeie 2020. Table includes date of sampling, start and stop times of towing, the towing duration, haul number, depth (m), krill size (mm) and the total number of krill caught per depth interval.

Date	Start	Stop	Event_duration	Haul	Depth	Size	Total_Catch
06.02.2020	11:30	11:48	18	1	70	22	147
06.02.2020	11:30	11:48	18	1	70	33	147
06.02.2020	11:30	11:48	18	1	70	28	147
06.02.2020	11:30	11:48	18	1	70	30	147
06.02.2020	11:30	11:48	18	1	70	29	147
06.02.2020	11:30	11:48	18	1	70	32	147
06.02.2020	11:30	11:48	18	1	70	32	147
06.02.2020	11:30	11:48	18	1	70	26	147
06.02.2020	11:30	11:48	18	1	70	33	147
06.02.2020	11:30	11:48	18	1	70	34	147
06.02.2020	11:30	11:48	18	1	70	32	147
06.02.2020	11:30	11:48	18	1	70	30	147
06.02.2020	11:30	11:48	18	1	70	27	147
06.02.2020	11:30	11:48	18	1	70	28	147
06.02.2020	11:30	11:48	18	1	70	31	147
06.02.2020	11:30	11:48	18	1	70	33	147
06.02.2020	11:30	11:48	18	1	70	21	147
06.02.2020	11:30	11:48	18	1	70	29	147
06.02.2020	11:30	11:48	18	1	70	25	147
06.02.2020	11:30	11:48	18	1	70	22	147
06.02.2020	11:30	11:48	18	1	70	24	147
06.02.2020	11:30	11:48	18	1	70	19	147
06.02.2020	11:30	11:48	18	1	70	25	147
06.02.2020	11:30	11:48	18	1	70	28	147
06.02.2020	11:30	11:48	18	1	70	28	147
06.02.2020	11:30	11:48	18	1	70	23	147
06.02.2020	11:30	11:48	18	1	70	24	147
06.02.2020	11:30	11:48	18	1	70	26	147
06.02.2020	11:30	11:48	18	1	70	35	147
06.02.2020	11:30	11:48	18	1	70	25	147
06.02.2020	11:30	11:48	18	1	70	20	147
06.02.2020	11:30	11:48	18	1	70	34	147
06.02.2020	11:30	11:48	18	1	70	36	147
06.02.2020	11:30	11:48	18	1	70	25	147
06.02.2020	11:30	11:48	18	1	70	35	147
06.02.2020	11:30	11:48	18	1	70	24	147

06.02.2020	11:30	11:48	18	1	70	27	147
06.02.2020	11:30	11:48	18	1	70	24	147
06.02.2020	11:30	11:48	18	1	70	28	147
06.02.2020	11:30	11:48	18	1	70	21	147
06.02.2020	11:30	11:48	18	1	70	20	147
06.02.2020	11:30	11:48	18	1	70	27	147
06.02.2020	11:30	11:48	18	1	70	25	147
06.02.2020	11:30	11:48	18	1	70	24	147
06.02.2020	11:30	11:48	18	1	70	20	147
06.02.2020	11:30	11:48	18	1	70	31	147
06.02.2020	11:30	11:48	18	1	70	25	147
06.02.2020	11:30	11:48	18	1	70	25	147
06.02.2020	11:30	11:48	18	1	70	23	147
06.02.2020	11:30	11:48	18	1	70	28	147
06.02.2020	12:25	12:43	18	2	80	32	2500
06.02.2020	12:25	12:43	18	2	80	31	2500
06.02.2020	12:25	12:43	18	2	80	32	2500
06.02.2020	12:25	12:43	18	2	80	32	2500
06.02.2020	12:25	12:43	18	2	80	36	2500
06.02.2020	12:25	12:43	18	2	80	34	2500
06.02.2020	12:25	12:43	18	2	80	37	2500
06.02.2020	12:25	12:43	18	2	80	33	2500
06.02.2020	12:25	12:43	18	2	80	33	2500
06.02.2020	12:25	12:43	18	2	80	36	2500
06.02.2020	12:25	12:43	18	2	80	35	2500
06.02.2020	12:25	12:43	18	2	80	34	2500
06.02.2020	12:25	12:43	18	2	80	37	2500
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06.02.2020	12:25	12:43	18	2	80	37	2500
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06.02.2020	12:25	12:43	18	2	80	33	2500
06.02.2020	12:25	12:43	18	2	80	33	2500
06.02.2020	12:25	12:43	18	2	80	36	2500
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06.02.2020	12:25	12:43	18	2	80	37	2500
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06.02.2020	12:25	12:43	18	2	80	34	2500
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06.02.2020	12:25	12:43	18	2	80	39	2500

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06.02.2020	12:25	12:43	18	2	80	35	2500
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06.02.2020	12:25	12:43	18	2	80	32	2500
06.02.2020	12:25	12:43	18	2	80	31	2500
06.02.2020	12:25	12:43	18	2	80	35	2500
06.02.2020	12:25	12:43	18	2	80	34	2500
06.02.2020	12:25	12:43	18	2	80	29	2500
06.02.2020	12:25	12:43	18	2	80	34	2500
06.02.2020	12:25	12:43	18	2	80	34	2500
06.02.2020	12:25	12:43	18	2	80	38	2500
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06.02.2020	12:25	12:43	18	2	80	29	2500
06.02.2020	12:25	12:43	18	2	80	32	2500
06.02.2020	12:25	12:43	18	2	80	35	2500
06.02.2020	12:25	12:43	18	2	80	35	2500
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06.02.2020	12:50	13:06	16	3	90	35	1320
06.02.2020	12:50	13:06	16	3	90	34	1320
06.02.2020	12:50	13:06	16	3	90	32	1320
06.02.2020	12:50	13:06	16	3	90	37	1320
06.02.2020	12:50	13:06	16	3	90	37	1320
06.02.2020	12:50	13:06	16	3	90	35	1320
06.02.2020	12:50	13:06	16	3	90	37	1320
06.02.2020	12:50	13:06	16	3	90	42	1320
06.02.2020	12:50	13:06	16	3	90	36	1320
06.02.2020	12:50	13:06	16	3	90	34	1320
06.02.2020	12:50	13:06	16	3	90	42	1320
06.02.2020	12:50	13:06	16	3	90	35	1320
06.02.2020	12:50	13:06	16	3	90	32	1320
06.02.2020	12:50	13:06	16	3	90	33	1320
06.02.2020	12:50	13:06	16	3	90	29	1320
06.02.2020	12:50	13:06	16	3	90	33	1320
06.02.2020	12:50	13:06	16	3	90	32	1320
06.02.2020	12:50	13:06	16	3	90	34	1320
06.02.2020	12:50	13:06	16	3	90	34	1320
06.02.2020	12:50	13:06	16	3	90	36	1320
06.02.2020	12:50	13:06	16	3	90	36	1320
06.02.2020	12:50	13:06	16	3	90	34	1320
06.02.2020	12:50	13:06	16	3	90	32	1320

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06.02.2020	12:50	13:06	16	3	90	35	1320
06.02.2020	12:50	13:06	16	3	90	35	1320
06.02.2020	12:50	13:06	16	3	90	34	1320
06.02.2020	12:50	13:06	16	3	90	33	1320
06.02.2020	12:50	13:06	16	3	90	35	1320
06.02.2020	12:50	13:06	16	3	90	35	1320
06.02.2020	12:50	13:06	16	3	90	36	1320
06.02.2020	12:50	13:06	16	3	90	34	1320
06.02.2020	12:50	13:06	16	3	90	38	1320
06.02.2020	12:50	13:06	16	3	90	25	1320
06.02.2020	12:50	13:06	16	3	90	20	1320
06.02.2020	12:50	13:06	16	3	90	28	1320
06.02.2020	12:50	13:06	16	3	90	38	1320
06.02.2020	12:50	13:06	16	3	90	42	1320
06.02.2020	12:50	13:06	16	3	90	35	1320
06.02.2020	12:50	13:06	16	3	90	34	1320
06.02.2020	12:50	13:06	16	3	90	36	1320
06.02.2020	12:50	13:06	16	3	90	25	1320
06.02.2020	12:50	13:06	16	3	90	34	1320
06.02.2020	12:50	13:06	16	3	90	39	1320
06.02.2020	12:50	13:06	16	3	90	33	1320
06.02.2020	12:50	13:06	16	3	90	27	1320
06.02.2020	12:50	13:06	16	3	90	31	1320
06.02.2020	12:50	13:06	16	3	90	35	1320
06.02.2020	12:50	13:06	16	3	90	34	1320
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21.09.2020	12:43	13:00	17	1	75	31	486
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21.09.2020	12:43	13:00	17	1	75	32	486
21.09.2020	12:43	13:00	17	1	75	33	486
21.09.2020	12:43	13:00	17	1	75	30	486
21.09.2020	12:43	13:00	17	1	75	31	486
21.09.2020	12:43	13:00	17	1	75	33	486
21.09.2020	12:43	13:00	17	1	75	37	486
21.09.2020	12:43	13:00	17	1	75	36	486
21.09.2020	12:43	13:00	17	1	75	31	486
21.09.2020	12:43	13:00	17	1	75	33	486
21.09.2020	12:43	13:00	17	1	75	36	486
21.09.2020	12:43	13:00	17	1	75	39	486
21.09.2020	12:43	13:00	17	1	75	32	486
21.09.2020	12:43	13:00	17	1	75	31	486
21.09.2020	12:43	13:00	17	1	75	33	486

21.09.2020	12:43	13:00	17	1	75	36	486
21.09.2020	12:43	13:00	17	1	75	35	486
21.09.2020	12:43	13:00	17	1	75	33	486
21.09.2020	12:43	13:00	17	1	75	33	486
21.09.2020	12:43	13:00	17	1	75	29	486
21.09.2020	12:43	13:00	17	1	75	35	486
21.09.2020	12:43	13:00	17	1	75	32	486
21.09.2020	12:43	13:00	17	1	75	33	486
21.09.2020	12:43	13:00	17	1	75	36	486
21.09.2020	12:43	13:00	17	1	75	30	486
21.09.2020	12:43	13:00	17	1	75	33	486
21.09.2020	12:43	13:00	17	1	75	37	486
21.09.2020	12:43	13:00	17	1	75	34	486
21.09.2020	12:43	13:00	17	1	75	33	486
21.09.2020	12:43	13:00	17	1	75	23	486
21.09.2020	12:43	13:00	17	1	75	33	486
21.09.2020	12:43	13:00	17	1	75	34	486
21.09.2020	12:43	13:00	17	1	75	32	486
21.09.2020	12:43	13:00	17	1	75	42	486
21.09.2020	12:43	13:00	17	1	75	36	486
21.09.2020	12:43	13:00	17	1	75	34	486
21.09.2020	12:43	13:00	17	1	75	35	486
21.09.2020	12:43	13:00	17	1	75	36	486
21.09.2020	12:43	13:00	17	1	75	31	486
21.09.2020	12:43	13:00	17	1	75	32	486
21.09.2020	12:43	13:00	17	1	75	34	486
21.09.2020	12:43	13:00	17	1	75	37	486
21.09.2020	12:43	13:00	17	1	75	34	486
21.09.2020	12:43	13:00	17	1	75	37	486
21.09.2020	12:43	13:00	17	1	75	34	486
21.09.2020	12:43	13:00	17	1	75	33	486
21.09.2020	12:43	13:00	17	1	75	37	486
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21.09.2020	13:20	13:37	17	2	85	35	4500
21.09.2020	13:20	13:37	17	2	85	19	4500
21.09.2020	13:20	13:37	17	2	85	32	4500
21.09.2020	13:20	13:37	17	2	85	33	4500
21.09.2020	13:20	13:37	17	2	85	26	4500
21.09.2020	13:20	13:37	17	2	85	37	4500
21.09.2020	13:20	13:37	17	2	85	21	4500
21.09.2020	13:20	13:37	17	2	85	33	4500
21.09.2020	13:20	13:37	17	2	85	21	4500
21.09.2020	13:20	13:37	17	2	85	32	4500
21.09.2020	13:20	13:37	17	2	85	19	4500

21.09.2020	13:20	13:37	17	2	85	32	4500
21.09.2020	13:20	13:37	17	2	85	36	4500
21.09.2020	13:20	13:37	17	2	85	22	4500
21.09.2020	13:20	13:37	17	2	85	33	4500
21.09.2020	13:20	13:37	17	2	85	21	4500
21.09.2020	13:20	13:37	17	2	85	33	4500
21.09.2020	13:20	13:37	17	2	85	31	4500
21.09.2020	13:20	13:37	17	2	85	33	4500
21.09.2020	13:20	13:37	17	2	85	20	4500
21.09.2020	13:20	13:37	17	2	85	28	4500
21.09.2020	13:20	13:37	17	2	85	33	4500
21.09.2020	13:20	13:37	17	2	85	35	4500
21.09.2020	13:20	13:37	17	2	85	31	4500
21.09.2020	13:20	13:37	17	2	85	27	4500
21.09.2020	13:20	13:37	17	2	85	33	4500
21.09.2020	13:20	13:37	17	2	85	31	4500
21.09.2020	13:20	13:37	17	2	85	36	4500
21.09.2020	13:20	13:37	17	2	85	32	4500
21.09.2020	13:20	13:37	17	2	85	32	4500
21.09.2020	13:20	13:37	17	2	85	36	4500
21.09.2020	13:20	13:37	17	2	85	19	4500
21.09.2020	13:20	13:37	17	2	85	33	4500
21.09.2020	13:20	13:37	17	2	85	31	4500
21.09.2020	13:20	13:37	17	2	85	18	4500
21.09.2020	13:20	13:37	17	2	85	35	4500
21.09.2020	13:20	13:37	17	2	85	34	4500
21.09.2020	13:20	13:37	17	2	85	25	4500
21.09.2020	13:20	13:37	17	2	85	32	4500
21.09.2020	13:20	13:37	17	2	85	33	4500
21.09.2020	13:20	13:37	17	2	85	33	4500
21.09.2020	13:20	13:37	17	2	85	37	4500
21.09.2020	13:20	13:37	17	2	85	21	4500
21.09.2020	13:20	13:37	17	2	85	20	4500
21.09.2020	13:20	13:37	17	2	85	38	4500
21.09.2020	13:20	13:37	17	2	85	38	4500
21.09.2020	13:20	13:37	17	2	85	33	4500
21.09.2020	13:20	13:37	17	2	85	34	4500
21.09.2020	13:20	13:37	17	2	85	39	4500
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19.10.2020	11:20	11:35	15	1	75	35	809
19.10.2020	11:20	11:35	15	1	75	34	809
19.10.2020	11:20	11:35	15	1	75	34	809
19.10.2020	11:20	11:35	15	1	75	20	809
19.10.2020	11:20	11:35	15	1	75	35	809

19.10.2020	11:20	11:35	15	1	75	38	809
19.10.2020	11:20	11:35	15	1	75	34	809
19.10.2020	11:20	11:35	15	1	75	37	809
19.10.2020	11:20	11:35	15	1	75	38	809
19.10.2020	11:20	11:35	15	1	75	21	809
19.10.2020	11:20	11:35	15	1	75	17	809
19.10.2020	11:20	11:35	15	1	75	37	809
19.10.2020	11:20	11:35	15	1	75	19	809
19.10.2020	11:20	11:35	15	1	75	39	809
19.10.2020	11:20	11:35	15	1	75	32	809
19.10.2020	11:20	11:35	15	1	75	33	809
19.10.2020	11:20	11:35	15	1	75	34	809
19.10.2020	11:20	11:35	15	1	75	25	809
19.10.2020	11:20	11:35	15	1	75	33	809
19.10.2020	11:20	11:35	15	1	75	30	809
19.10.2020	11:20	11:35	15	1	75	35	809
19.10.2020	11:20	11:35	15	1	75	37	809
19.10.2020	11:20	11:35	15	1	75	35	809
19.10.2020	11:20	11:35	15	1	75	35	809
19.10.2020	11:20	11:35	15	1	75	22	809
19.10.2020	11:20	11:35	15	1	75	14	809
19.10.2020	11:20	11:35	15	1	75	20	809
19.10.2020	11:20	11:35	15	1	75	33	809
19.10.2020	11:20	11:35	15	1	75	34	809
19.10.2020	11:20	11:35	15	1	75	34	809
19.10.2020	11:20	11:35	15	1	75	27	809
19.10.2020	11:20	11:35	15	1	75	33	809
19.10.2020	11:20	11:35	15	1	75	31	809
19.10.2020	11:20	11:35	15	1	75	24	809
19.10.2020	11:20	11:35	15	1	75	18	809
19.10.2020	11:20	11:35	15	1	75	37	809
19.10.2020	11:20	11:35	15	1	75	36	809
19.10.2020	11:20	11:35	15	1	75	22	809
19.10.2020	11:20	11:35	15	1	75	23	809
19.10.2020	11:20	11:35	15	1	75	19	809
19.10.2020	11:20	11:35	15	1	75	35	809
19.10.2020	11:20	11:35	15	1	75	33	809
19.10.2020	11:20	11:35	15	1	75	34	809
19.10.2020	11:20	11:35	15	1	75	37	809
19.10.2020	11:20	11:35	15	1	75	39	809
19.10.2020	11:20	11:35	15	1	75	15	809
19.10.2020	11:20	11:35	15	1	75	30	809
19.10.2020	11:20	11:35	15	1	75	35	809
19.10.2020	11:20	11:35	15	1	75	22	809

19.10.2020	12:09	12:20	11	2	90	33	16000
19.10.2020	12:09	12:20	11	2	90	33	16000
19.10.2020	12:09	12:20	11	2	90	40	16000
19.10.2020	12:09	12:20	11	2	90	35	16000
19.10.2020	12:09	12:20	11	2	90	39	16000
19.10.2020	12:09	12:20	11	2	90	35	16000
19.10.2020	12:09	12:20	11	2	90	36	16000
19.10.2020	12:09	12:20	11	2	90	38	16000
19.10.2020	12:09	12:20	11	2	90	39	16000
19.10.2020	12:09	12:20	11	2	90	26	16000
19.10.2020	12:09	12:20	11	2	90	35	16000
19.10.2020	12:09	12:20	11	2	90	28	16000
19.10.2020	12:09	12:20	11	2	90	15	16000
19.10.2020	12:09	12:20	11	2	90	32	16000
19.10.2020	12:09	12:20	11	2	90	35	16000
19.10.2020	12:09	12:20	11	2	90	40	16000
19.10.2020	12:09	12:20	11	2	90	36	16000
19.10.2020	12:09	12:20	11	2	90	34	16000
19.10.2020	12:09	12:20	11	2	90	30	16000
19.10.2020	12:09	12:20	11	2	90	34	16000
19.10.2020	12:09	12:20	11	2	90	33	16000
19.10.2020	12:09	12:20	11	2	90	33	16000
19.10.2020	12:09	12:20	11	2	90	36	16000
19.10.2020	12:09	12:20	11	2	90	36	16000
19.10.2020	12:09	12:20	11	2	90	31	16000
19.10.2020	12:09	12:20	11	2	90	34	16000
19.10.2020	12:09	12:20	11	2	90	39	16000
19.10.2020	12:09	12:20	11	2	90	28	16000
19.10.2020	12:09	12:20	11	2	90	33	16000
19.10.2020	12:09	12:20	11	2	90	35	16000
19.10.2020	12:09	12:20	11	2	90	24	16000
19.10.2020	12:09	12:20	11	2	90	26	16000
19.10.2020	12:09	12:20	11	2	90	33	16000
19.10.2020	12:09	12:20	11	2	90	36	16000
19.10.2020	12:09	12:20	11	2	90	37	16000
19.10.2020	12:09	12:20	11	2	90	35	16000
19.10.2020	12:09	12:20	11	2	90	34	16000
19.10.2020	12:09	12:20	11	2	90	38	16000
19.10.2020	12:09	12:20	11	2	90	37	16000
19.10.2020	12:09	12:20	11	2	90	31	16000
19.10.2020	12:09	12:20	11	2	90	29	16000
19.10.2020	12:09	12:20	11	2	90	36	16000
19.10.2020	12:09	12:20	11	2	90	34	16000
19.10.2020	12:09	12:20	11	2	90	33	16000

19.10.2020	12:09	12:20	11	2	90	31	16000
19.10.2020	12:09	12:20	11	2	90	41	16000
19.10.2020	12:09	12:20	11	2	90	37	16000
19.10.2020	12:09	12:20	11	2	90	34	16000
19.10.2020	12:09	12:20	11	2	90	32	16000
19.10.2020	12:09	12:20	11	2	90	36	16000

Table C2: Measurements done on Meganyctiphanes norvegica from pelagic trawl at Midtmeie 2020. Table includes date of sampling, start and stop times of towing, the towing duration, haul number, depth (m), krill size (mm) and the total number of krill caught per depth interval.

Date	Start	Stop	Event_duration	Haul	Depth	Size	Total_Catch
22.09.2020	10:45	11:05	20	1	75	34	20000
22.09.2020	10:45	11:05	20	1	75	35	20000
22.09.2020	10:45	11:05	20	1	75	33	20000
22.09.2020	10:45	11:05	20	1	75	32	20000
22.09.2020	10:45	11:05	20	1	75	36	20000
22.09.2020	10:45	11:05	20	1	75	36	20000
22.09.2020	10:45	11:05	20	1	75	37	20000
22.09.2020	10:45	11:05	20	1	75	35	20000
22.09.2020	10:45	11:05	20	1	75	36	20000
22.09.2020	10:45	11:05	20	1	75	38	20000
22.09.2020	10:45	11:05	20	1	75	17	20000
22.09.2020	10:45	11:05	20	1	75	34	20000
22.09.2020	10:45	11:05	20	1	75	32	20000
22.09.2020	10:45	11:05	20	1	75	33	20000
22.09.2020	10:45	11:05	20	1	75	32	20000
22.09.2020	10:45	11:05	20	1	75	32	20000
22.09.2020	10:45	11:05	20	1	75	35	20000
22.09.2020	10:45	11:05	20	1	75	34	20000
22.09.2020	10:45	11:05	20	1	75	36	20000
22.09.2020	10:45	11:05	20	1	75	34	20000
22.09.2020	10:45	11:05	20	1	75	37	20000
22.09.2020	10:45	11:05	20	1	75	35	20000
22.09.2020	10:45	11:05	20	1	75	37	20000
22.09.2020	10:45	11:05	20	1	75	18	20000
22.09.2020	10:45	11:05	20	1	75	32	20000
22.09.2020	10:45	11:05	20	1	75	39	20000
22.09.2020	10:45	11:05	20	1	75	32	20000
22.09.2020	10:45	11:05	20	1	75	34	20000
22.09.2020	10:45	11:05	20	1	75	33	20000
22.09.2020	10:45	11:05	20	1	75	38	20000
22.09.2020	10:45	11:05	20	1	75	36	20000
22.09.2020	10:45	11:05	20	1	75	33	20000
22.09.2020	10:45	11:05	20	1	75	37	20000
22.09.2020	10:45	11:05	20	1	75	36	20000
22.09.2020	10:45	11:05	20	1	75	38	20000
22.09.2020	10:45	11:05	20	1	75	36	20000
22.09.2020	10:45	11:05	20	1	75	30	20000
22.09.2020	10:45	11:05	20	1	75	32	20000
22.09.2020	10:45	11:05	20	1	75	32	20000
22.09.2020	10:45	11:05	20	1	75	37	20000
22.09.2020	10:45	11:05	20	1	75	36	20000

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22.09.2020	10:45	11:05	20	1	75	34	20000
22.09.2020	10:45	11:05	20	1	75	35	20000
22.09.2020	10:45	11:05	20	1	75	31	20000
22.09.2020	10:45	11:05	20	1	75	36	20000
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22.09.2020	10:45	11:05	20	1	75	34	20000
22.09.2020	10:45	11:05	20	1	75	35	20000
22.09.2020	10:45	11:05	20	1	75	32	20000
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22.09.2020	11:47	12:05	18	2	85	33	26667
22.09.2020	11:47	12:05	18	2	85	36	26667
22.09.2020	11:47	12:05	18	2	85	32	26667
22.09.2020	11:47	12:05	18	2	85	37	26667
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22.09.2020	11:47	12:05	18	2	85	37	26667
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22.09.2020	11:47	12:05	18	2	85	36	26667
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22.09.2020	11:47	12:05	18	2	85	37	26667
22.09.2020	11:47	12:05	18	2	85	31	26667
22.09.2020	11:47	12:05	18	2	85	35	26667
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22.09.2020	11:47	12:05	18	2	85	35	26667
22.09.2020	11:47	12:05	18	2	85	35	26667
22.09.2020	11:47	12:05	18	2	85	36	26667
22.09.2020	11:47	12:05	18	2	85	35	26667
22.09.2020	11:47	12:05	18	2	85	37	26667
22.09.2020	11:47	12:05	18	2	85	34	26667
22.09.2020	11:47	12:05	18	2	85	35	26667

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22.09.2020	11:47	12:05	18	2	85	32	26667
22.09.2020	11:47	12:05	18	2	85	37	26667
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22.09.2020	11:47	12:05	18	2	85	31	26667
22.09.2020	11:47	12:05	18	2	85	32	26667
22.09.2020	11:47	12:05	18	2	85	36	26667
22.09.2020	11:47	12:05	18	2	85	40	26667
22.09.2020	11:47	12:05	18	2	85	36	26667
22.09.2020	11:47	12:05	18	2	85	35	26667
22.09.2020	11:47	12:05	18	2	85	40	26667
22.09.2020	11:47	12:05	18	2	85	32	26667
22.09.2020	11:47	12:05	18	2	85	41	26667
22.09.2020	11:47	12:05	18	2	85	35	26667
22.09.2020	11:47	12:05	18	2	85	37	26667