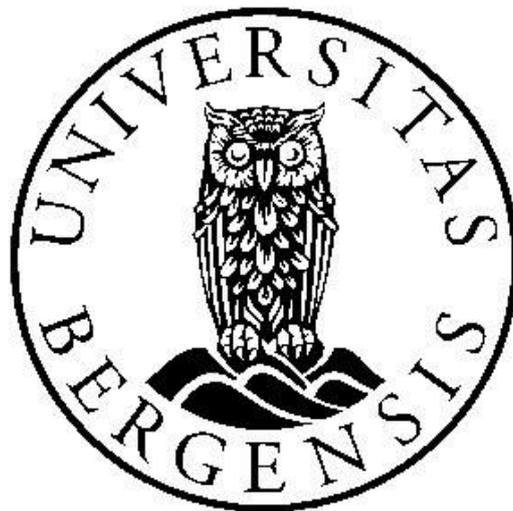


The role of bioluminescent prey in the diet of two hatchetfish species and four lanternfish species in the North Atlantic Ocean in relation to eye-size

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Master of Science in Biology – Biodiversity, Evolution and Ecology

Spring 2023

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Acknowledgement

This masters thesis is part of my education in biodiversity, evolution and ecology at the University of Bergen. The samples and datasets I have used were collected by The Institute for Marine Research (IMR) within the framework of the HARMES project (Research Council of Norway, project number 280546) and the MEESO project (EU H2020 research innovation programme, Grant Agreement No 817669). I would like to thank the employees at IMR for their collection of the samples and the help I have received while working in the lab.

Writing this thesis has been challenging, but also exciting and interesting. It has required a lot of work in the laboratory, doing analyses and writing. I feel like I have learnt a lot from the experience. My first memory of having a clear interest in biology is from an exhibition about the deep sea at the University Museum of Bergen many years ago. During my education in biology, I found a special interest in ecology, and during the first year of my master's programme, marine ecology. I have enjoyed circling back to what originally piqued my interest in biology for my thesis.

First, I would like to thank my supervisor from IMR, Eva Garcia-Seoane, who has supported me during all aspects of the work on my thesis. She has always made herself available and open to questions and discussions. I would also like to thank my supervisors from UiB, Tom Jasper Langbehn and Christian Jørgensen, who have also made themselves available whenever possible, even though we have been in different countries for large parts of the work on my thesis. I have received great help whenever needed.

Abstract

The mesopelagic zone, often referred to as “the twilight zone” can be defined as the area of the ocean at 200-1000 m depth. Here, light levels vary greatly and provides a varying visual scene. At shallow depths, down-welling daylight is the dominant light-source, but at greater depths, bioluminescent point-sources take over. Mesopelagic fish, therefore, have a variety of eye-sizes and other visual adaptations for better vision in the zones they inhabit. Several adaptations are designed to increase the eyes sensitivity to light because it is so sparse in the mesopelagic, and being able to take advantage of the light that is there is crucial. A larger eye provides extra sensitivity but is also costly. A smaller eye will have less sensitivity, but in a dark environment, it might be enough to distinguish a bioluminescent flash from the background. Therefore, I hypothesize that fish with relatively small eyes select bioluminescent prey because they are easier to see.

In this thesis, I compare the diets of mesopelagic fishes of different eye-sizes and other visual adaptations to see whether there is a link between the size or type of eye they possess and whether they have a selectivity for bioluminescent prey in the two hatchetfishes *Sternoptyx diaphana* and *Argyropelecus hemigymnus* and the four lanternfishes *Protoyctophum arcticum*, *Benthosea glaciale*, *Notoscopelus kroyeri* and *Lampanyctus macdonaldi*. I use samples and data from two separate cruises done by The Institute of Marine Research (IMR) on R.V G.O. Sars. I determine the eye-body-ratio, do stomach content and diet composition analyses, and use Ivlev’s electivity index to compare the diet of the studied fish with plankton data from the water column. My aim was to determine whether a pattern can be found of small-eyed fish selecting bioluminescent prey in larger proportions than their large-eyed counterpart.

I find that although there is a difference in selectivity especially between the hatchetfishes and the lanternfishes, the small-eyed lanternfish in this study do not have a higher selectivity towards bioluminescent prey than the lanternfish with larger eyes. However, the lanternfishes do have a much stronger selectivity against non-bioluminescent prey than the hatchetfishes. They also have a higher selectivity towards bioluminescent prey than *S. diaphana*, who had not eaten any bioluminescent prey.

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Introduction

The mesopelagic zone is a part of the ocean that can be defined as the region between 200-1000 meters (Sutton, 2013). Above it is the epipelagic from 0-200 m and below it is the bathypelagic zone from 1000-4000 m (Figure 1).

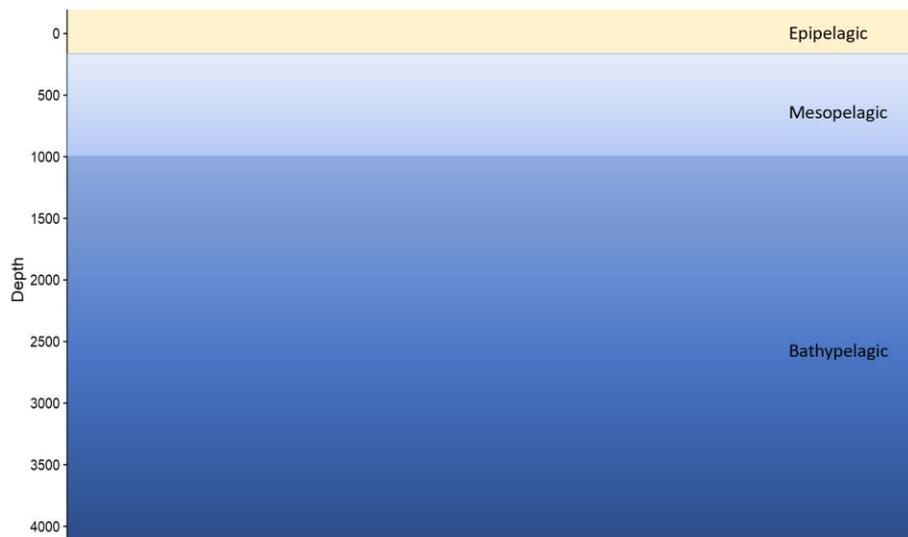


Figure 1: The different zones in the pelagic ocean

Often referred to as the twilight zone, it can also be defined by the levels of light present there: the top being where it meets the euphotic zone, where light still penetrates, but photosynthesis is no longer possible. The bottom is where irradiance is no longer sufficient for vision to be effective in capturing prey and the bathypelagic starts (Robinson *et al.*, 2010). This defines the mesopelagic by its light levels rather than a set depth interval. Another way to define it by the light levels is that it ranges from 10^9 to 10^{10} $\mu\text{mol quanta m}^{-2}\text{s}^{-1}$, where the lowest level corresponds with the visual threshold of lanternfishes and the highest corresponds to the upper light exposure of pearlsides (Kaatvedt, Langbehn and Aksnes, 2019). Above the twilight zone is the epipelagic zone, which is home to rich plankton communities, large predatory fishes and small fishes and invertebrates. The species of the mesopelagic and epipelagic are members of a complex and connected food web with phytoplankton at the base. The mesopelagic food web ultimately supports life in the entire ocean through a continuous rain of organic material and through being the only area in the pelagic where primary production takes place (Robinson *et al.*, 2010).

The mesopelagic itself holds the greatest vertebrate biomass (Irigoiien *et al.*, 2014) and diversity (Warrant and Locket, 2004) of animal life in the entire ocean, especially in the upper parts above about 650 m (Warrant and Locket, 2004). Because of this, it is also where 90 % of organic carbon

annually transported from surface waters is respired back to carbon dioxide (Robinson *et al.*, 2010). This is because the large and diverse community of animals contribute to the repackaging and reprocessing of sinking and suspended organic material (Robinson *et al.*, 2010). The massive marine biomass in the mesopelagic is also the origin of the Deep Scattering Layer (DSL), which is an acoustically dense layer that can be seen all across the ocean (Aksnes *et al.*, 2017). This layer has been observed to perform daily migrations (DVM) between zones in the pelagic, which is the movement between different depths performed by many mesopelagic organisms (Klevjer *et al.*, 2016). Many animals are said to seek refuge in the dark waters to avoid detection by visual predators during the day (Robinson *et al.*, 2010). However, many organisms actually stay within a narrow band of light intensities referred to as their light comfort zone (Langbehn *et al.*, 2019). Langbehn *et al.* (2019) find in their model that this light comfort zone for the mesopelagic fish *B. glaciale* is highly affected by the lower light sensitivity threshold of their predators. During the night, animals travel further up the water column to feed either in the epipelagic where photosynthesis happens or the upper mesopelagic zone (Opdal *et al.*, 2008; Robinson *et al.*, 2010). In this process, they contribute to the vertical carbon flux by respiring carbon dioxide, releasing faecal matters and dissolved organic carbon below the euphotic zone, and being preyed upon (Robinson *et al.*, 2010). This transportation of organic matter from the epipelagic to the meso- and bathypelagic layers is often referred to as the biological carbon pump (Sarmiento-Lezcano *et al.*, 2022). This biological carbon pump creates an important connection between the deep sea and the upper layers (Archibald, Siegel and Doney, 2019). The main mechanisms of the biological carbon pump are passive flux, active flux, and physical mixing of dissolved carbon. The active flux is the transport of carbon through zooplankton and micronekton performing DVM, and passive flux is related to sinking particulate carbon (Sarmiento-Lezcano *et al.*, 2022).

Despite its rich biodiversity and large biomass, not much is known about life in the mesopelagic because of the difficulty involved in studying it (Sutton, 2013). In the open oceans and at great depths, surveys are expensive and collecting intact samples has its challenges. Deep sea fishes that perform diel vertical migrations are also notoriously difficult to study in the lab because they are so light-sensitive. Fish in labs have been known to attempting to migrate downwards or battering themselves against the walls of aquaria until becoming lifeless (Salvanes and Kristoffersen, 2009). Therefore, most knowledge about their behaviour and ecology is based on field data like trawl- and acoustic data (Salvanes and Kristoffersen, 2009; Irigoien *et al.*, 2014). This does however also have limitations as mesopelagic fishes are known to present efficient net avoidance behaviour (Kartvedt, Staby and Aksnes, 2012).

The visual scene in the deep sea

Water absorbs light and therefore dramatically reduces its intensity, spectral composition, and degree of polarisation the further down the water column you go (Warrant and Locket, 2004). Some wavelengths are absorbed more easily by water than others, with red light of longer wavelengths being absorbed the earliest, and blue light of around 475 nm persisting further down the water column (Widder, 2010). These are also the wavelengths that lanternfishes use for bioluminescence, and their eyes are adapted to seeing (Turner *et al.*, 2009). Sexually dimorphic filters in the eyes of some of these fish indicate that they use bioluminescence for intraspecies communication (de Busserolles *et al.*, 2015). With increasing depth, the light in clear ocean water becomes nearly entirely blue, with red light being almost entirely absorbed at 100 m depth. Ultraviolet light and shorter wavelengths are also absorbed by the water, but not quite as effectively and may persist to about 200 m. Light that is scattered upwards from the depths, however, tends to be relatively rich in UV and shorter wavelengths (Warrant and Locket, 2004). The intensity of the light also decreases with depth. At 100 m below the surface of the water the number of photons available for vision in an eye with peak sensitivity is approximately $2.70 \times 10^{21} \text{ m}^{-2} \text{ s}^{-1} \text{ sr}^{-1}$, but only a 100 meters further down in completely clear ocean water, the number of photons decreases to $6.8 \times 10^{18} \text{ m}^{-2} \text{ s}^{-1} \text{ sr}^{-1}$ (Warrant and Locket, 2004). Below this depth the decrease in light intensity declines to about 1.5 orders of magnitude per 100 m in depth. At 600 – 700 meters during midday, it is similar to the light levels provided by starlight. Below 1000 meters in the bathypelagic, daylight is almost entirely absorbed, and the levels are not sufficient for visual predation (Warrant and Locket, 2004).

Because water has a higher refractive index than air, the entire 180° of the sky is compressed to a 97° cone of light underwater called Snell's window. This provides bright illumination when looking upwards in the water. Light scattered from particles present in the water column provides a wider visual scene than Snell's window (Warrant and Locket, 2004). This is called space light and aquatic animals can see it both from above and from the side. The intensity of light is however always brighter inside Snell's window and daylight is increasingly coming from above further down the water column (Warrant and Locket, 2004). Downwelling light provides an extended visual scene as a backdrop against which animals can both see other animals above and be spotted themselves by animals from below.

In deep water, the main light source is point-like bioluminescence (de Busserolles and Marshall, 2017). The threshold for where the main light source switches will depend on time of day and properties of the water, but Cronin *et al.* (2016) found that during the polar night in the high arctic, this change happens between 20- 40 m. Bioluminescence is especially prominent in the sea

compared to in freshwater- and terrestrial ecosystems. There are several possible explanations for this, including the ocean being more optically clear than freshwater, relatively stable conditions with long uninterrupted evolutionary histories where bioluminescence could have evolved, and the fact that large portions of the habitat receive little to no light (Haddock, Moline and Case, 2009). The production of bioluminescence is the result of a chemical reaction involving the light-emitting molecule luciferin and a catalysing enzyme, usually luciferase (Haddock, Moline and Case, 2009). Marine organisms use bioluminescence for several functions like defence or mate signalling (Haddock, Moline and Case, 2009). In the upper parts of the deep sea these bioluminescent point-sources are mainly seen when looking down. Further down than about 300 m where space light is no longer prominent, these can be seen from all directions. This change in the visual scene with depth has had a large influence on the evolution in the deep sea (de Busserolles *et al.*, 2020).

Bioluminescence of zooplankton in the deep sea

Many types of planktonic organisms are bioluminescent, including polychaetes, cnidarians and crustaceans. The luciferases they use for bioluminescence are species-specific with at least three different types of luciferins. Despite the taxonomic diversity of bioluminescence in the sea, the spectral properties are largely the same and constrained to the blue-green wavelengths (x-y nm) as these are the ones that can be seen the furthest down in the water column (Haddock, Moline and Case, 2009). Euphausiids, commonly called krill, have light organs along the lower surface of their body which they use for counterillumination. This is a common camouflage tactic where ventral photophores light up the underside of the belly to match the down-welling light and making an individual harder to spot from below (Haddock, Moline and Case, 2009). Copepods, who are one of the most abundant marine invertebrates, are also one of the most abundant bioluminescent groups in the sea, with common genera being *Pleuromamma*, *Metridia* and *Oncaea*. The widespread genus *Calanus*, however, is not bioluminescent. In this class, bioluminescence involves the luciferin coelenterazine and is either exhibited as intracellular flashes or emitted into the water as part of an escape response (Haddock, Moline and Case, 2009). Animals can turn their photophores on and off, but also control the intensity, colour and angular distribution of the light they emit (Haddock, Moline and Case, 2010).

Bioluminescence in copepods is primarily stimulated by interactions with predators. Buskey and Swift (1985) found that the bioluminescent copepod *Metridia longa* showed a photophobic response of sudden swimming bursts to flashes of imitated bioluminescence that the non-bioluminescent copepod did not. This suggests that these flashes can be used as a warning signal between individuals of the species and as a defence mechanism against predation (Buskey and Swift, 1985).

Pleuromamma xiphias have been shown to emit a bioluminescent discharge when exposed to prolonged stimuli that could be perceived as a threat (Hartline, Buskey and Lenz, 1999). This discharge was always coupled with a strong escape jump as part of an escape tactic (Hartline, Buskey and Lenz, 1999).

Fish eyes in the deep sea

Within the mesopelagic, vision is thought to be one of the dominant senses used in prey detection, although others like olfactory, hearing, electroreception and lateral lines also plays a part (de Busserolles and Marshall, 2017). All vertebrates have camera-type eyes, including those who live in the sea. Camera eyes have a lens, retina, and photoreceptors in the retina. Light goes through the pupil into the lens where an image is formed, and this image is received by the photoreceptors (Warrant and Locket, 2004). These photoreceptors generally come in two variants: rods and cones. Rods are the photoreceptors that are specialized for vision in dim light conditions, and most fish in the deep sea therefore have pure-rod retinas (de Busserolles *et al.*, 2020). An exception are the pearlsides, *Maurolicus* spp., who instead have rod-like cones specifically tuned to light conditions close to the surface at their most active periods: dusk and dawn (de Busserolles *et al.*, 2017). Camera eyes in the sea differ from terrestrial ones in that the cornea does not refract any light because it separates two media with an almost identical optical density (Warrant and Locket, 2004). Instead, eyes in aquatic vertebrates have a spherical lens which is very refractive. Animals with this type of eye have excellent sight. All mesopelagic fish except for the family Omosudidae and the genus *Maurolicus* (who have rod-like cones) have pure-rod retinas with a high density of the photosensitive pigment rhodopsin (Salvanes and Kristoffersen, 2009; de Busserolles *et al.*, 2017).

The visual range of an animal depends on the clarity of the water, the depth at which it resides and the sensitivity of its eyes, and it therefore varies greatly between species (Nilsson, Warrant and Johnsen, 2014). Because sight is such an important sense also in the dim environment of the deep sea, the amount of light captured by the eyes is crucial for survival. Depending on what it is an animal needs to see, there will be different strategies to increase the eyes' sensitivity (de Busserolles *et al.*, 2013). Eyes designed to be sensitive to point-like bioluminescence are quite different than those designed for sensitivity towards down-welling daylight. There is, however, one way of increasing the eye's sensitivity to light which is useful regardless of what type of light it is trying to capture: Increasing the size of the pupil (de Busserolles *et al.*, 2020). This can be done in two different ways: 1) increasing the overall size of the eye and thus the size of both the pupil and the lens and 2) increasing only the size of the pupil itself, for example with the help of an aphakic gap

between the lens and the iris (de Busserolles *et al.*, 2020). While a larger eye is more sensitive to light, it is also more costly (de Busserolles *et al.*, 2013). Fish that perform diel vertical migration often have a more general visual system which allows them to interpret different types of light signals compared to the ones confined to one specific light zone (de Busserolles *et al.*, 2020).

Many teleost fishes that rely heavily on sight have evolved large eyes because of the extra light-sensitivity they provide. Large eyes are also common in mesopelagic species, but the visual scene in the mesopelagic changes greatly with depth, and eye-sizes are also diverse in this environment (Warrant and Locket, 2004; de Busserolles *et al.*, 2020). Because a larger eye allows for higher sensitivity especially for down-welling daylight, it could logically be assumed that eye size would be inversely proportional to depth, but this is not always the case (de Busserolles *et al.*, 2013). If this was universally true for all mesopelagic fishes, one would find that all species higher up in the water column where daylight is sufficient as a light source had large eyes, and all species closer to the bathypelagic would have smaller eyes. While this pattern can be found in some species, it is not true for others (de Busserolles *et al.*, 2013). For example, *Lampanyctus crococilus*, who ventures down to the bathypelagic during the day has relatively small eyes, and *Myctophum nitidulum*, who is strictly mesopelagic and has relatively large eyes fit the pattern one would expect (de Busserolles *et al.*, 2013). *Lampanyctus omostigma*, on the other hand, has small eyes and are restricted to the mesopelagic, venturing no deeper than 400 m (de Busserolles *et al.*, 2013).

An aphakic cap is the region of the pupil that is not covered by the spherical lens (de Busserolles, Marshall and Collin, 2014). Aphakic gaps can either be crescent-shaped, which is a gap in a specific part of the pupil that enhances the relative retinal illumination in one zone of the eye, or circumlental, which is a gap all around the pupil that enhances the relative retinal illumination over the entire eye (de Busserolles, Marshall and Collin, 2014). Both can be found in the deep sea, but while crescent-shaped ones can also be found in shallow waters, circumlental ones are only found in deep sea species (de Busserolles *et al.*, 2020). Crescent-shaped gaps are common in lanternfishes and there are variations in where in the eye it is located, providing an increase in the visual field along different visual axes depending on its location (de Busserolles, Marshall and Collin, 2014).

Some species, like *Argyrolepecus hemigymnus*, have a unique eye structure called tubular eyes with large lenses and a larger field of binocular vision, improve the resolution and ability to judge distance. Coupled with short snouts, this is useful when scanning the water for prey in dim down-welling light and enables them to spot small planktonic organisms (Salvanes and Kristoffersen, 2009). These eyes, although they provide a good coverage of a small field, have a very restricted

field of vision, usually less than 50° wide because of their immobility (Warrant and Locket, 2004; de Busserolles *et al.*, 2020). This adaptation usually comes with the cost of less lateral vision, but many species have modified the eyes even further to mitigate this effect, for example by having a lens pads like in *Scopelarcus* (de Busserolles *et al.*, 2020). These tubular eyes can be placed either dorsally or frontally, depending on which direction they scan for prey in. Sit-and-wait predators that scan the water column above them for prey illuminated by the down-welling daylight have their tubular eyes placed dorsally, while predators that chase prey swimming directly ahead have them placed frontally (Warrant and Locket, 2004). The visual overlap that comes with both eyes viewing effectively the same space also provides extra sensitivity because it enables the eyes to capture double the amount of photons (Warrant and Locket, 2004). Because downwelling light is brighter than light from other directions, dorsally directed tubular eyes may be better at discriminating between downwelling light and bioluminescent point-sources, which then would cast a detectable shadow from below, making counterillumination less effective as camouflage (Johnsen, Widder and Mobley, 2004; Biagioni, Hunt and Collin, 2016). Another adaptation that has a similar use is that some fish have a yellow lens that work as a filter and enhances the spectral differences between the colour of ambient light and bioluminescence (Haddock, Moline and Case, 2010).

Diel vertical migration and fish feeding patterns

Many mesopelagic species perform diel vertical migration (DVM), or the travel between different water depths at different times of day. This is the largest animal migration in terms of biomass on the planet, and is performed both by fish and zooplankton (Irigoiien *et al.*, 2014). DVM has been found to take place globally, although the speed at which it happens and the distances travelled varies between locations (Bianchi and Mislán, 2016; Klevjer *et al.*, 2016). Fish in the mesopelagic often perform DVM to stay within their light-comfort zone, where they can both track their prey and avoid predation themselves (Aksnes *et al.*, 2017). Herbivorous zooplankton feed on the phytoplankton in the epipelagic where light is sufficient for photosynthesis. However, the water this close to the surface is well-lit during the day, making them easy prey for visual predators. Therefore, many herbivorous zooplankton stay in the deeper, darker waters during the day and only travel up to the surface during the night when light levels are closer to those in the deep sea (Hays, Warner and Proctor, 1995). This pattern of traveling up at dusk and down at dawn is called nocturnal vertical migration and is the most common pattern of DVM for zooplankton, and naturally, their predators often follow (Opdal *et al.*, 2008; Cisewski *et al.*, 2010; Catul, Gauns and Karuppasamy, 2011). Light is thought to be the main cue for migration because the timing largely corresponds with light levels

underwater (Cisewski *et al.*, 2010; Bianchi and Mislán, 2016). This also corresponds well with the Røstad, Kaartvedt and Aksnes (2016) light-comfort zone (Røstad, Kaartvedt and Aksnes, 2016).

The mesopelagic can be divided into an upper part above 600 meters and a lower part below that (Sutton, 2013). In the upper part, most fish that migrate have reflective sides and large vertical photophores as adaptations to avoid predators (Sutton, 2013). Characteristic fishes in the upper layer include Myctophidae, Gonostomidae and some Sternoptychidae. Fishes that inhabit the lower mesopelagic tend to be less reflective than the ones higher up, a trend that continues into the bathypelagic. There are representatives from several taxa in the deeper parts, like the families Myctophidae, Stomiidae, and Melamphidae and the genera *Sternoptyx* and *Cyclothone* (Sutton, 2013). Fish at these depths have also been found to have lower musculoskeletal robustness at lower depths. This has been linked to ambient light, and it is hypothesized that species with less available light have less need for movement associated with predator- and prey responses (Sutton, 2013). Moku *et al.* (2000) found a direct relationship between food consumption rate and migratory capacity in three myctophid species in the North Pacific Ocean, exemplifying the connection between metabolic demand and depth in deep sea fishes (Moku *et al.*, 2000). There is a clear pattern of fishes in the upper part of the mesopelagic performing extensive diel vertical migrations, while the ones further down performing little to no DVM (Sutton, 2013). The findings of epipelagic prey species in the stomachs of many myctophids show that they perform diel vertical migration and feed mainly at night (Catul, Gauns and Karuppasamy, 2011). For non-migrant species, such as *Cyclothone braueri*, no diel feeding patterns have been observed (Bernal *et al.*, 2015)

The aim of this thesis is to compare the diets of mesopelagic fishes of different eye-sizes and, where possible, other visual adaptations like tubular eyes and aphakic gaps to see whether there is a link between the size or type of eye they possess and whether or not they have a selectivity for bioluminescent prey. Six mesopelagic fish species has been selected for this study, two belonging to the family Sternoptychidae, or hatchetfishes: *Sternoptyx diaphana* and *Argyropelecus hemigymnus*, and four belonging to the family Myctophidae, or lanternfishes: *Benthosema glaciale*, *Notoscopelus kroyeri*, *Lampanyctus macdonaldi*, and *Protomyctophum arcticum*. There is a range of eye-sizes and visual adaptations in these species, both between and within the two families.

Materials and methods

Study area

The samples were taken on two different cruises: One from June 2018 and one from June 2021 within the framework of the HARMES project (Research Council of Norway, project number 280546) and the MEESO project (EU H2020 research and innovation programme, Grant Agreement No 817669). Both surveys were done in the North Atlantic Ocean on R.V. “G.O. Sars”. A total of 22 stations from the 2 cruises were selected for trophic analyses. Most of the selected stations from both cruises are located in the Iceland basin, but five stations from the 2018 cruise are located in the Rockall Basin and three stations from the 2021 cruise are located in the Norwegian Sea (Figure 1). Seven stations from 2021 are located at the Reykjanes Ridge, where the water is about 7°C at 400 meters depth, compared to the 8°C- 9°C in the rest of the Iceland Basin and in the Rockall Basin (Seidov *et al.*, 2018). When moving from these areas over the Greenland-Iceland-Faroe Ridge Complex and into the Norwegian sea, the temperature drops several degrees, to 2°C- 4°C (Hjartarson, Erlendsson and Blischke, 2017; Seidov *et al.*, 2018). Salinity also differs slightly between these three areas. The water is the saltiest in the Rockall Basin at about 35.4 g/kg at 400 m depth. At the Reykjanes Ridge, the salinity is slightly lower at about 35,2 g/kg. The water is freshest in the Norwegian Sea at 34.8 g/kg (Seidov *et al.*, 2018).

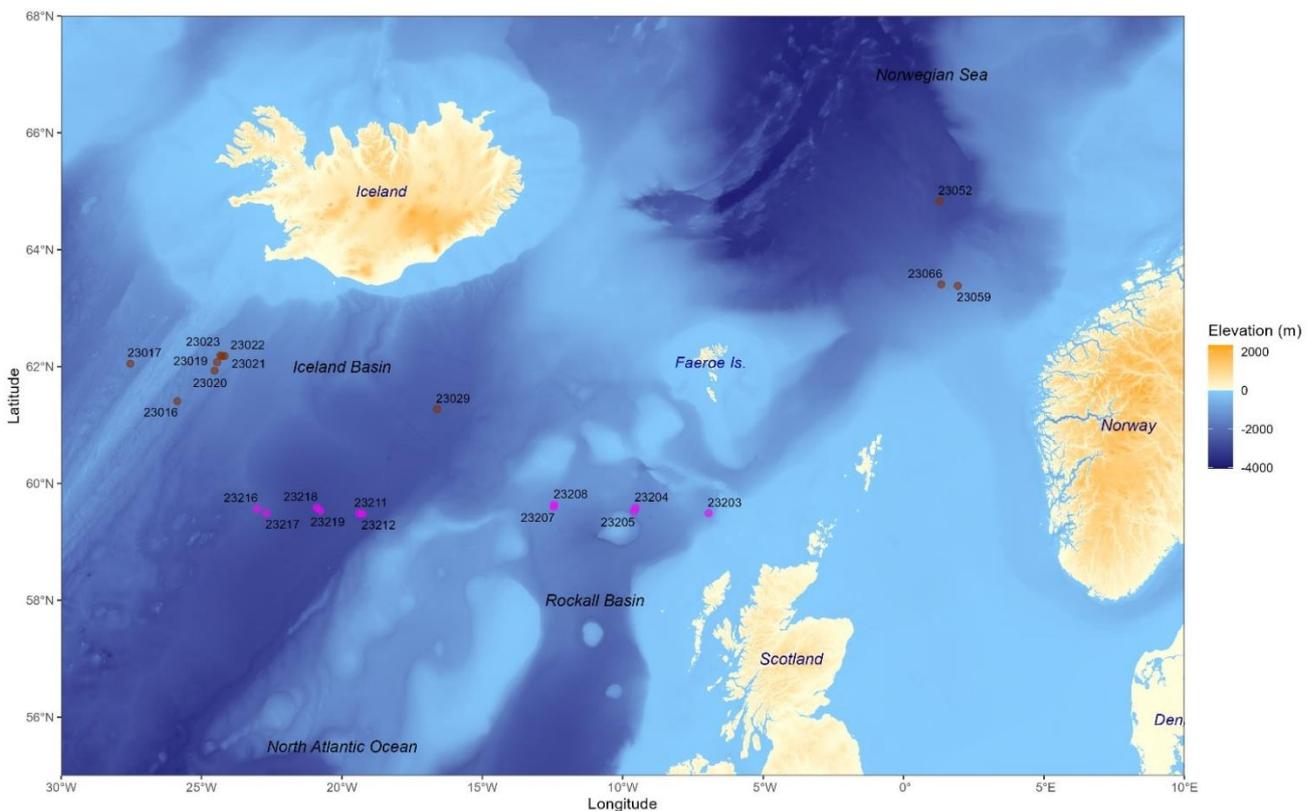


Figure 2: Map of the macrozooplankton trawls (Table 1, Table 2) done during the 2018 (magenta) and 2021 (amber) cruises.

2018 cruise

The samples from 2018 were collected from west of the Hebrides starting at 59.4°N, 23.0°W traveling along a transect and ending at 60.1°N, 5.6°E (Figure 1).

2021 cruise

The 2021 samples were collected by moving from the Icelandic Basin starting at 62.0 °N, 27.7°W to the south of Iceland and west of the Faroe Islands, and then into the Norwegian Sea ending at 63.6°N, 4.1°W (Figure 1).

Collecting the samples

Macrozooplankton trawls

Two different midwater trawls were used to collect the fish on the 2018 cruise, one small (6 x 6 m) with 8 mm liner mesh and one large (30 x 30 m) with 20 mm liner mesh. Hauls were deployed as V-hauls from the surface down to 1000 m depth and back up again with a constant towing speed of about 2 knots. Two different trawls were also used for the 2021 cruise, one small (66 m² average mouth opening) with 9 mm liner mesh and one large (300 m² average mouth opening) with 16 mm liner mesh.

MOCNESS and Mammoth

For the plankton samples, a 1 m MOCNESS (Multiple Opening/Closing Net and Environmental Sensing System) with 9 nets (N0-N8 for the MOCNESS and N1-N9 for the MAMMOTH) with a mesh size of 180 μ m was used on the 2018 cruise. On the 2021 cruise, a multinet MAMMOTH with the same specifications was used instead. The MOCNESS and MAMMOTH were deployed down to 1000 meters with N0 open from the beginning, and then hauled vertically to the surface with a towing speed of about 2 knots, maintaining a 45° angle. N0 MOCNESS and N1 MAMMOTH were not sampled and are therefore not part of the data. The rest of the nets were deployed at the same depth intervals for both the MOCNESS and MAMMOTH: 1000-800 m, 800-600 m, 600-400 m, 400-300 m, 300-200 m, 200-100 m, 100-50 m and 50-0 m,

The stations where the macrozooplankton trawls used to collect the fish were deployed and where the MOCNESS and MAMMOTH for the plankton samples were deployed are not exactly the same and have different names. Therefore, the stations for the microzooplankton trawl were matched with the closest stations for MOCNESS/MAMMOTH so they could be compared (Table 1, Table 2).

The earliest start time for any trawl done in 2018 was 05:47 GMT and the latest was 17:14 GMT. This means that all the trawls were done in daylight. Five of the trawls were done in the afternoon

(start time 12:45 – 17:14 GMT) and six were done in the morning (start time 05:57 – 10:56 GMT) (Table 2). All trawls lasted for between one and three hours.

Table 1: Trawls used to collect the fish on the 2018 cruise with corresponding plankton station.

Serial number	Start time (UTC)	Stop time (UTC)	Gear type	Corresponding plankton station
23203	16:14	18:29	Macrozooplankton trawl 6x6	275
23204	05:56	08:27	Macrozooplankton trawl 30x30	276
23205	14:43	16:51	Macrozooplankton trawl 6x6	276
23207	04:57	07:35	Macrozooplankton trawl 30x30	278
23208	11:45	14:17	Macrozooplankton trawl 6x6	278
23211	05:40	08:23	Macrozooplankton trawl 30x30	280
23212	13:44	16:05	Macrozooplankton trawl 6x6	280
23216	05:03	08:01	Macrozooplankton trawl 30x30	282
23217	14:21	16:47	Macrozooplankton trawl 6x6	282
23218	05:29	07:43	Macrozooplankton trawl 30x30	281
23219	09:56	11:22	Macrozooplankton trawl 6x6	281

The start times for the trawls on the 2021 cruise had a wider time span between start times for the trawls. Here, start times range from 01:45 – 21:29 GMT. All trawls lasted between under an hour and three hours (Table 2). Six have a starting time between 05:32 - 11:27 GMT, three between 13:22 - 21:29 GMT and two between 01:45 - 02:38 GMT (Table 3).

Table 2: Trawls used to collect the fish on the 2021 cruise with corresponding plankton station.

Serial number	Start time (UTC)	Stop time (UTC)	Gear type	Corresponding MOCNESS/MAMMOTH station
23016	10:27	12:29	Macrozooplankton trawl 66 m ² opening	171
23017	04:32	06:38	Macrozooplankton trawl 66 m ² opening	171
23019	05:23	06:30	Macrozooplankton trawl 300 m ² opening	171
23020	12:22	14:47	Macrozooplankton trawl 66 m ² opening	171
23021	00:45	01:07	Macrozooplankton trawl 66 m ² opening	171
23022	01:38	03:12	Macrozooplankton trawl 66 m ² opening	171
23023	05:01	06:57	Macrozooplankton trawl 66 m ² opening	171
23029	04:44	07:25	Macrozooplankton trawl 66 m ² opening	175
23052	09:36	11:39	Macrozooplankton trawl 300 m ² opening	178
23059	20:29	22:04	Macrozooplankton trawl 66 m ² opening	178
23066	17:15	18:53	Macrozooplankton trawl 66 m ² opening	179

Preparations on board for later laboratory work

Selection of fish species was done on board. For stomach analysis of the fishes from the 2018 cruise, a total of 14 species were chosen because of their range in eye-size and abundance in the samples: *Argyroleucus hemigymnus*, *A. olfersii*, *Benthoosema glaciale*, *Cyclothone braueri*, *C. microdon*, *C. pseudopadilla*, *Lampadena speculigera*, *Lampanyctus crocodillus*, *L. intricarius*, *L. macdonaldi*, *Myctophum punctatum*, *Notoscopelus kroyeri*, *Protomyctophum arcticum*, and *Sternophyx diaphana*. For the analysis of the fish from the 2021 cruise, *Benthoosema glaciale* was chosen to work with because they were abundant, which made it possible to compare the results from different areas. Samples from the larger trawl were used to complete length groups if there were not enough fish from the small trawl. The fish were frozen on board.

After the MOCNESS/MAMMOTH haul, the sample from one net was placed in a sorting tray where all large jellyfish (Scyphozoa) and comb jellies (Ctenophora) were removed from the sample and classified to the lowest taxonomic level possible. If the sample contained few large individuals, these were also removed. Then, the sample was placed in a Motoda plankton divider which was tilted back and forth several times until the sample was divided equally between the two chambers. When the

sample is divided, one chamber is opened and emptied onto a 180 μm sieve in a plastic container for fixation for later taxonomic analysis. Before tilting the Motoda back, the chamber was rinsed with seawater in case any individuals were stuck in the chamber. The Motoda was tilted back and then the other chamber was opened and emptied onto a 2000 μm sieve in a plastic container for biomass analysis.

After the splitting of the sample, superfluous water was removed with a fine-meshed sieve with a mesh-size that was the same as or smaller than the one of the nets in the MOCNESS/MAMMOTH. Very large samples were first placed back into the plankton divider and split further. The sample was transferred from the sieve into the sample bottle with a squirt bottle of seawater. Formalin was then added in with a 4% concentration in the final sample. If the volume of the sample would exceed half of the volume of formalin in the bottle it was split before placing it in the bottle. Lastly, 1mL borax for every 100mL of sample was added to the bottle. These were then stored until the taxonomic analysis.

Taxonomic analysis of the plankton samples in the laboratory

The fixated sample was placed on a 2000 μm sieve in a plastic container and sieved. The large organisms left on the sieve are then analysed as follows:

1. Chaetognath species were determined and counted, and the length of 25 individuals of each species was measured.
2. *Paraeuchaeta* spp. and *Calanus hyperboreus* were counted and stage was determined.
3. Other species were determined and counted.

Once the larger organisms had been counted the rest of the sample was examined. If the sample was small, it was counted separately. Otherwise, it was divided into subsamples with the Motoda in two steps:

1. **The sample was divided based on the most abundant/important species, usually *Calanus finmarchicus*.** This species is prioritised and at least 100 individuals should be counted. *C. finmarchicus* and *C. hyperboreus* are similar in appearance and are distinguished by looking at subtle morphological traits (Parent, Plourde and Turgeon, 2011). When doing the first rough estimate, there will therefore be a mix of the two species. Of the individuals initially identified as *C. finmarchicus*, the share of this that was *C. finmarchicus* vs. *C. hyperboreus* was determined. For this, 20 individuals each of the stages CV, CVI-female and CVI-male were identified.

2. **The rest of the sample was divided further for counting of less important species.** For this, the sample is divided so that the small, numerous species could be counted reasonably. The degree of division was determined based on the size of the sample and the number of individuals.

Stomach content analysis

The stomach analysis was done at IMR's zooplankton laboratory. First, the standard length of the fish, which is the length from the tip of the head to the fork in the base of the tail, was measured with calipers to the nearest millimetre (Figure 4). Fish were divided into 5 mm length groups from 10-14, 15-20 mm and so on, and only five fish from each length group were used for further analysis. The wet weight was measured on a scale with four decimals (Figure 4). Because the last decimal is not as accurate and susceptible to errors like inaccuracies in the scale itself, and so weight was rounded to the nearest 0.001 g.



Figure 3: Measuring the length of and weight of the fish.

Fishes were then opened from the anus to the head (Figure 5). The stomach including the oesophagus was removed and the eviscerated wet weight was measured (Figure 5). Sex of the fish was determined when possible. For *B. glaciale*, this was done by locating the luminous caudal glands. Males have a single supracaudal gland and females have a pair of smaller infracaudal glands (Halliday, Clark and Themelis, 2015). This was usually only determined for specimens larger than 30 mm standard length because in fish smaller than that these glands are normally not developed enough to be distinguishable.



Figure 4: Opening the fishing and removing the viscera.

For the stomach content analysis, the degree of fullness was first determined on a scale from 1 – 6 where 1 is empty, 5 is completely full, and 6 is when the stomach is eviscerated (Table 3, Figure 6). Then, the stomach was opened, and the contents were identified to the lowest taxonomic level possible and counted using binoculars. Life-stage from I-VI was determined for copepods by counting leg pairs and tail segments (Conway, 2012). If the copepod was stage VI, sex was also determined. Degree of degradation from 1 – 5 was also determined, with 1 being completely indigested and 5 being completely digested (Table 4, Figure 7). The length of each individual prey that was below digestion degree 3 was also measured. For copepods the prosome length was measured, while for amphipods and krill the entire length was measured. Whole chaetognaths are generally not found in the stomach of the fish because their body is very quickly digested, but the hooks can still be found and are quite easily recognisable. If hooks from chaetognaths were found, their presence was noted.

Table 3: Degree of stomach fullness according to IMR standards

Degree of fullness	Description
1	Empty
2	Almost empty and the stomach needs to be opened to determine whether it is empty or not
3	Some content and it is visible from the outside that the stomach is not empty
4	Full, but not fully expanded
5	Completely full, with the stomach being clearly expanded and slightly see-through
6	The stomach is turned inside out



Figure 5: Stomach after it has been removed from the fish. Left is an empty stomach (fullness degree 1) and right is a full stomach (fullness degree 5, slightly torn upon removal) seen under binoculars.

Table 4: Degree of prey degradation according to IMR standards

Degree of degradation	Description
1	Digestion has not been started
2	Digestion has started, but species can still be determined
3	Digestion is quite advanced and only systematic groups and not species can be determined
4	Digestion is so far advanced that only larger parts of the prey can be found
5	Digestion is almost complete, and the contents are mushy



Figure 6: Stomach contents. Left is completely digested material (digestion degree 5) and right is an undigested female *Paraeuchaeta norvegica* (digestion degree 1).

Individual prey of the same taxa, life-stage (and sex if stage VI) for copepods and degree of digestion were then placed in the same pre-dried and pre-weighted aluminium dish for drying. For example, all stage V *Calanus finmarchicus* with digestion degree 2 were placed in one aluminium dish. The bowls were then placed in an oven of 65 °C to dry for at least 12 hours. After the samples had been dried, they were weighted on a scale with five decimals. As with the previous scale, the last decimal is not as accurate and weight was therefore measured to the nearest 0.0001 g. The dry weight of the prey was determined by subtracting the weight of the dish without the prey from the weight of the dish with the prey.

Eye-size analyses

To determine whether the eyes of the fish species can be categorized as small, medium, or large, the ratio between eye-size and body-size was determined using ImageJ and pictures of each species, and then calculated:

Equation 1: Eye/body-ratio

$$Ratio = \frac{Size_{eye}}{Size_{body}}$$

Where body length = standard length of the body and eye-size = length of the eye from socket to socket across the middle of the pupil was used (Figure 8). When measuring in ImageJ, the scale was set by first measuring a known size in the image where possible and converting to mm, and on

pictures where there were no known sizes, the number of pixels were used for the ratios instead. Lastly, the ratios were calculated (Equation 1).

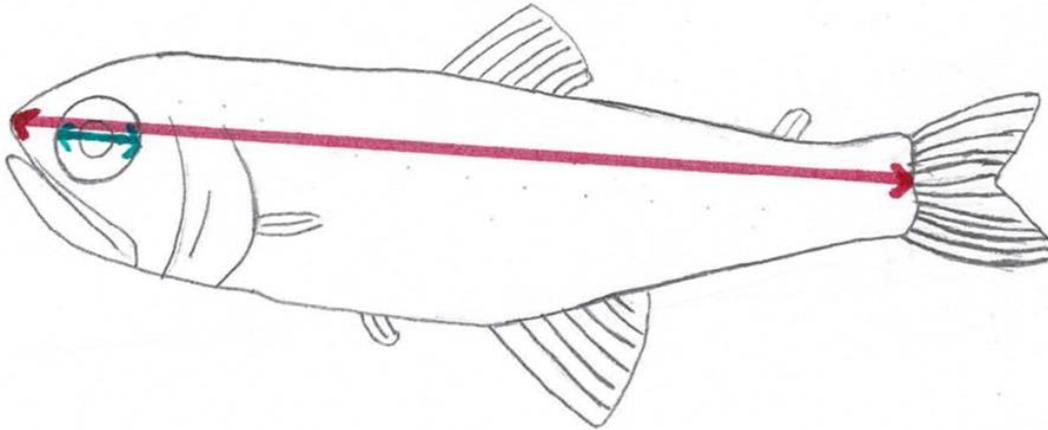


Figure 7: Measuring eye-size and body-length. The body length (red) is the standard length which is from the tip of the snout to the base of the tail. The eye-size (green) is from socket to socket across the middle of the pupil.

Fish species where the number of prey that was determined to at least the genus < 20 were excluded from the analyses so the results would be representative of the species and not an artifact of the low number of samples. This left six species for further analyses.

Three eye-size categories based on the eye-to-body ratio (Equation 1) were defined as follows: small = $0.01 - 0.05$, medium = $0.06 - 0.10$ and large = $0.11 - 0.15$. Other eye adaptations were researched in the literature for each species and so was their depth range and DVM behaviour.

Data analyses

To try to determine whether there is a difference in the selection of bioluminescent prey based on the eye-size of the fish, several different analyses were done in R (R Core Team, 2023): Different eye-sizes of the studied species, the percentages of bioluminescent, non-bioluminescent and potentially bioluminescent prey in the diet of the six chosen species of fish, proportions of different prey in the diet, the number of taxa in the diet of each fish species, zooplankton in the water column, the depth distribution of the plankton species, and a selectivity analysis. For the plot showing the proportions of the different higher taxa in the diet, if a taxon was also represented by a lower taxon, they higher taxon was removed. For example, Crustacea was removed because it was already represented by amphipods, copepods, krill, shrimps, and ostracods. For the plot showing the number of different

taxa, only the lowest taxa found in the diet of each fish was included. All graphs were plotted using the ggplot 2 package (Wickham, 2016).

The selectivity analysis was done to show to what degree the fish select certain prey species relative to their abundance in the water (Equation 2). Stations used for the fish trawls and the MOCNESS were not always the same, in these cases the fish stations were compared to the closest plankton station.

Only the plankton species that were found both in the water column and in the diet of the fish were used for selectivity analyses. This assumes that there are many other particles in the water column that are ignored, but that each species eaten by at least one of our predators are potential prey species for all of them. Some species in the water column had been identified to a lower taxonomic level than in the stomach, namely species level in the water column and genus level in the stomach. This is because the stomach contents are harder to identify than individuals caught during the plankton hauls due to digestion. In several of the genus used here the species present in either of the data sets are all in the same category of bioluminescence. For example, all species of *Pleuromamma* spp. are bioluminescent. In the stomach, *Pleuromamma* spp. had only been identified as *Pleuromamma* sp., while in the water column they had been identified as *Pleuromamma robusta*. However, because they are within the same genus and knowing that all *Pleuromamma* spp. are bioluminescent, the number of *P. robusta* in the water column can be compared to the number of *Pleuromamma* sp. in the diet. The same was done for *Paraechaeta norvegica*, *Thysanessa longicaudata* and *Calanus finmarchicus/hyperboreus*. During the stomach analysis the 2 species have variably been identified, *T. compressa*, *T. abyssorum* and *Themisto* sp. depending on degree of digestion. These were treated separately because of their different sizes, but because all *Themisto* spp. were identified to species level in the plankton data, these were lost in the selectivity analysis. *Calanus* sp. and *Metridia* sp. were removed from the stomach data because it is unlikely that they represent another species than the ones that had already been identified and are present in the data, and since it was rare that these were not identified in the zooplankton data, their selectivity would be skewed. An initial analysis showed that the selectivity was the same when they were grouped together.

For the selectivity analysis, Ivlev's electivity index was used:

Equation 2: Ivlev's electivity index

$$E = \frac{r_i - p_i}{r_i + p_i}$$

where E is the measure of electivity, r_i is the relative abundance (%) of a prey item i in the diet and p_i is the relative abundance (%) of a prey item in the environment (Strauss, 1979). This index ranges from positive 1 to negative 1. The selectivity was calculated per fish species per station, and then the mean selectivity and standard deviation for each fish species was calculated. Two different grouped plots for the bioluminescence categories were created: One where the ratio of each species within one category were summed and then treated as the species selectivity plot, and one where all species of each bioluminescence category were first grouped together, and then the ratio of each was calculated as a whole before being treated the same as the two others. Only prey that was found in the stomach of at least one of the fish was used to determine the ratios of each plankton species, and for the plots. Only the species that were found in the diet of the specific fish species was used in the plots. Often when doing selectivity analysis, prey that is rare in the water column are excluded from analysis because their selectivity can be skewed. However, because data on the species studied here are rare, they are included to get a glimpse of the bigger picture.

Results

Fish sampled

The eye-body-ratios of 14 different mesopelagic species were determined. *Cyclothone* sp. is the genus with the smallest eyes: *C. microdon* have an eye-body-ratio of 0.01, and *C. braueri* and *C. pseudopadilla* have one of 0.02 (Figure 9). *Lampanyctus* sp. is the genus with the second smallest eyes: *L. crocodilus* and *L. macdonaldi* both have an eye-body-ratio of 0.03, while *L. intricarius* has one of 0.05, which it shares with *N. kroyeri* (Figure 9). The rest of the fishes are not clumped together in genus of similar eye-sizes, but they are as follows: *L. speculigera*: 0.08, *B. glaciale*: 0.09, *A. olfersii*, *M. punctatum* and *P. arcticum*: 0.11, *A. hemigymnus*: 0.12 and lastly *S. diaphana* has an eye-body ratio of 0.15. The family with the biggest variation in eye-sizes in this study are the lanternfishes with eye-body ratios ranging from 0.03 (*L. macdonaldi*) to 0.11 (*M. punctatum* and *P. arcticum*) (Figure 9). The family with the smallest eyes were the bristlemouths, here represented by *Cyclothone* spp. The hatchetfishes had the biggest eyes, although *A. olfersii* had the same eye-body ratio as *M. punctatum* and *P. arcticum* (Figure 9).

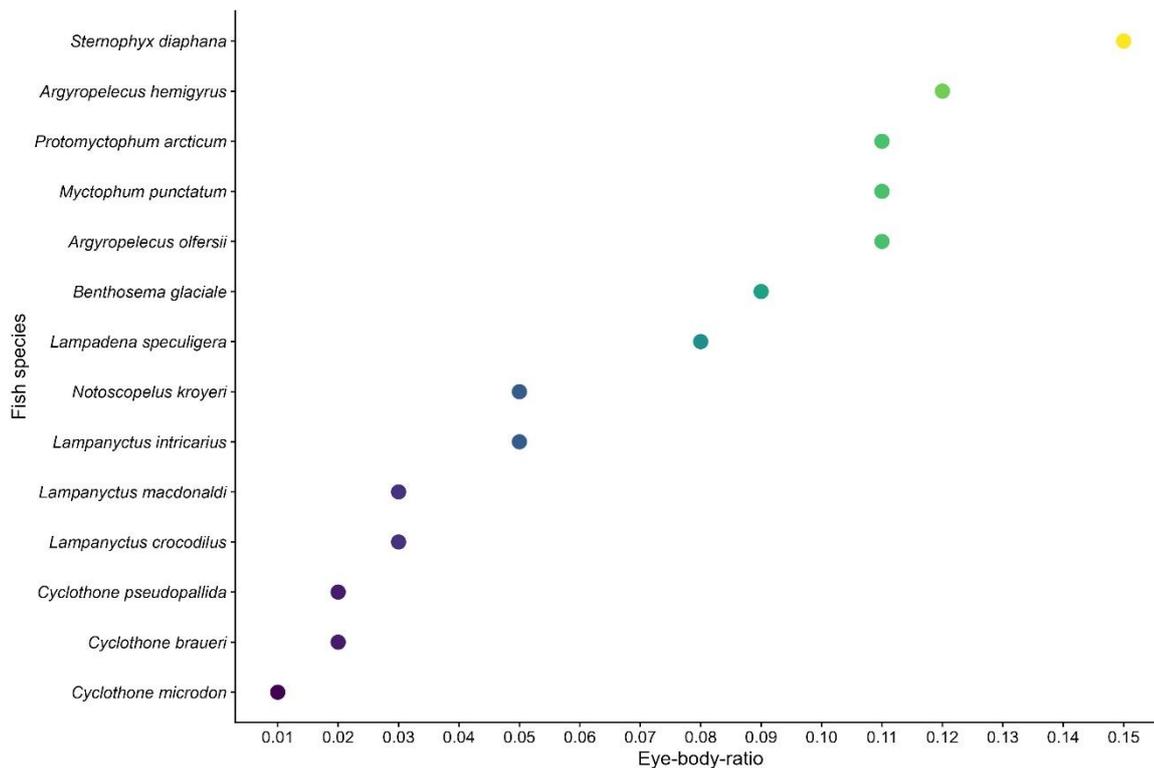


Figure 8: Eye-body-ratio of the sampled species. Each colour corresponds to one species of fish.

A total of 1160 stomachs of mesopelagic fish taken by different macrozooplankton trawls both on cruises in 2018 and 2021 were analysed. Standard length of the sampled individuals ranged from 14 mm (*A. hemigymnus*) to 147 mm (*L. macdonaldi*) with a mean length \pm standard deviation of 27 ± 6 mm for *A. hemigymnus* species, 26 ± 2 mm for *Argyropelecus olfersii*, 45 ± 12 mm for *B. glaciale* from 2018, 31 ± 4 mm for *C. braueri*, 42 ± 9 mm for *C. microdon*, 41 mm for *C. pseudopadilla*, 76 ± 13 mm for *L. speculigera*, 109 ± 10 mm for *L. crocodilus*, 115 ± 13 mm for *L. intricarius*, 63 ± 3 mm for *L. macdonaldi*, 54 ± 18 mm for *M. punctatum*, 102 ± 13 mm for *N. kroyeri*, 34 ± 6 mm for *P. arcticum*, 42 ± 4 mm for *S. diaphana* and 40 ± 14 mm for *B. glaciale* from 2021 (Table 5).

Six species had more than 20 prey in their stomach that could be identified to a taxonomic level where bioluminescence category could be determined and were therefore chosen for further quantitative analysis. These were two species of hatcETFishes (*Sternoptyx diaphana*, *Argyropelecus hemigymnus*) and four species of lanternfishes (*Protomyctophum arcticum*, *Benthosema glaciale*, *Notoscopelus kroyeri* and *Lampanyctus macdonaldi*)(Table 5). *M. punctatum* also had more than 20 prey, but most were too digested. The diets of these six species were then compared with nearby zooplankton community data to quantify prey selectivity.

Table 5: Number of individuals analyzed for diet composition. Highlighted species are the ones who were used for the analysis. Four lanternfish (purple) species and two hatchetfish (orange) species were selected.

Cruise 2018106																					
Fish Species	Individuals											Length (mm)			Weight (g)			Empty	Total prey		
	405	406	407	409	410	413	414	418	419	420	421	Total	Min	Max	Mean	Min	Max			Mean	
<i>Argyropspecus hemigyris</i>	14	25	3	19	9	19	6	14	-	39	2	150	14	42	27	0.03	1.45	0.47	3	54	
<i>Argyropspecus olfersii</i>	-	1	-	-	-	-	-	2	-	4	-	7	19	28	26	0.17	0.67	0.48	3	4	
<i>Benthoosema glaciale</i>	31	35	15	20	16	22	27	23	13	24	-	226	19	81	45	0.03	7.04	1.37	122	271	
<i>Cyclothone braueri</i>	-	-	-	11	-	-	12	-	11	-	-	34	20	38	31	0.03	0.20	0.10	8	5	
<i>Cyclothone microdon</i>	-	-	-	21	-	23	8	-	24	-	-	76	23	69	42	0.07	0.90	0.25	0	14	
<i>Cyclothone pseudopallida</i>	-	-	-	1	-	-	-	-	-	-	-	1	41	41	41	0.17	0.17	0.17	0	0	
<i>Lampadena speculigera</i>	-	-	-	-	-	1	1	1	-	-	-	3	64	94	76	4.03	10.15	6.44	0	13	
<i>Lampanyctus crocodilus</i>	-	-	-	-	-	1	1	-	-	-	-	2	107	110	109	10.98	12.58	12.05	0	5	
<i>Lampanyctus intricarius</i>	-	-	3	-	-	3	-	2	-	-	-	8	87	128	115	4.10	20.09	13.12	4	4	
<i>Lampanyctus macdonaldi</i>	4	25	21	36	5	32	26	19	16	-	-	184	23	147	63	0.06	27.68	3.47	87	50	
<i>Myctophum punctatum</i>	2	15	1	-	-	-	-	-	-	-	-	18	24	77	54	0.17	5.59	2.53	2	39	
<i>Notoscopelus kroyeri</i>	-	5	1	16	-	3	-	5	-	3	-	33	65	146	102	2.71	35.44	13.61	1	136	
<i>Protomyctophum arcticum</i>	-	-	8	15	4	3	14	11	13	17	-	85	17	45	34	0.07	1.47	0.58	2	484	
<i>Sternophyx diaphana</i>	-	-	-	-	-	3	-	3	-	-	-	6	35	47	42	1.43	3.29	2.50	0	26	

Cruise 2021105																					
Fish Species	Individuals											Length (mm)			Weight (g)			Empty	Total prey		
	68	69	71	72	73	74	75	81	104	111	118	Total	Min	Max	Mean	Min	Max			Mean	
<i>Benthoosema glaciale</i>	47	27	22	22	24	34	49	22	16	44	20	327	18	78	40	0.04	6.82	1.15	194	129	

Stomach content analysis

The prey most abundant in the diet of *S. diaphana* was *Themisto abyssorum*. Amphipods were the only type of prey found in the stomachs of these fish. *A. hemigyris* had eaten mostly *C. finmarchicus*, with some other prey in very low numbers. *P. arcticum* had eaten large numbers of *Pleuromamma* sp. and *Metridia lucens*, and only small numbers of other species in comparison. For *B. glaciale* the most abundant prey was *C. finmarchicus*. *Pleuromamma* sp. and *M. lucens* were also numerous. In the stomach of *N. kroyeri*, *Pleuromamma* sp. and *Paraeuchaeta norvegica* were the most abundant prey. *L. macdonaldi* had mostly eaten *P. norvegica* and *M. lucens*. In general, *M. lucens*, *P. norvegica* and *Pleuromamma* sp. were the prey eaten by most fishes, the only one not having eaten them being *S. diaphana* (Table 6).

B. glaciale had the highest percentage of empty stomachs (53.9 % in 2018 and 59.3 % in 2021), followed by *L. macdonaldi* (47.2 %), *A. hemigyris* (25.2 %), *N. kroyeri* (3.0), *P. arcticum* (2.3 %) and lastly *S. diaphana*, who had no empty stomachs.

Table 6: Diet composition of the studied fish from 2018. Bioluminescent prey is highlighted in green, non-bioluminescent in grey and potentially bioluminescent prey in white. Prey where bioluminescence could not be determined is in magenta.

“Occ.” is how many stomachs a prey item appeared in, “Weight” is biomass and “Abund.” Is the number of one prey item. All are percentages.

Plankton species	<i>Argyroleucus hemigymnus</i>			<i>Benthosema glaciale</i>			<i>Notoscolopelus kroyeri</i>			<i>Lamparyctus macdonaldi</i>			<i>Protomyctophum arcticum</i>			<i>Sternoptyx diaphana</i>		
	Occ.	Weight	Abund.	Occ.	Weight	Abund.	Occ.	Weight	Abund.	Occ.	Weight	Abund.	Occ.	Weight	Abund.	Occ.	Weight	Abund.
<i>Aetideus armatus</i>	1.4	1.1	1.9	0.9	0.3	0.4	-	-	-	-	-	-	12.1	8.6	2.5	-	-	-
<i>Calanus finmarchicus</i>	13.2	10.1	35.2	22.1	15.0	28.8	1.0	1.2	2	-	-	-	13.4	5.7	4.1	-	-	-
Digested	70.5	49.9	0.0	51.9	28.2	0.0	68.0	49.9	0	40.6	14.7	0.7	10.9	2.6	0.0	-	-	-
<i>Euaugaptilus magnus</i>	-	-	-	-	-	-	1.0	1.2	2	-	-	-	-	-	-	-	-	-
<i>Gaetanus brevispinus</i>	-	-	-	-	-	-	-	-	-	9.3	4.4	8.1	-	-	-	-	-	-
<i>Gaetanus tenuispinus</i>	-	-	-	0.9	0.6	0.4	-	-	-	-	-	-	-	-	-	-	-	-
<i>Heterorhabdus</i> sp.	1.4	1.1	1.9	-	-	-	2.0	2.3	0	-	-	-	-	-	-	-	-	-
<i>Hymenodora</i> sp.	-	-	-	-	-	-	1.0	1.1	2	-	-	-	-	-	-	-	-	-
<i>Mauroliticus muelleri</i>	-	-	-	-	-	-	-	-	-	3.1	1.4	0.7	-	-	-	-	-	-
<i>Meganyctiphanes norvegica</i>	-	-	-	-	-	-	-	-	-	6.2	3.1	2.2	1.2	0.7	0.2	-	-	-
<i>Metridia lucens</i>	1.4	1.1	1.9	9.6	3.6	15.1	3.0	2.3	12	6.2	1.2	5.1	48.7	26.9	44.6	-	-	-
<i>Oithona</i> sp.	-	-	-	-	-	-	-	-	-	-	-	-	1.2	0.2	0.2	-	-	-
<i>Oncaea</i> sp.	-	-	-	-	-	-	-	-	-	-	-	-	1.2	0.8	0.4	-	-	-
Other	35.2	32.8	51.9	45.1	26.2	25.8	22.6	21.1	42	68.7	39.0	36.8	29.2	13.6	6.0	50	20.0	11.5
<i>Paraeuchaeta norvegica</i>	2.9	1.9	3.7	10.5	5.6	6.6	8.2	7.3	20	28.1	11.0	12.5	12.1	6.2	3.9	-	-	-
<i>Paraeuchaeta</i> sp.	-	-	-	2.8	0.9	1.1	2.0	2.3	4	6.2	1.1	0.7	1.2	0.3	0.2	-	-	-
<i>Pleuromamma</i> sp.	2.9	2.0	3.7	28.8	17.8	21.0	4.1	4.6	6	15.6	8.1	15.4	54.8	30.3	36.0	-	-	-
<i>Pseudocalanus glaciale</i>	-	-	-	0.9	0.6	0.0	-	-	-	-	-	-	-	-	-	-	-	-
<i>Pseudocalanus</i> sp.	-	-	-	-	-	-	-	-	-	-	-	-	1.2	0.8	0.2	-	-	-
<i>Pseudochirella pustulifera</i>	-	-	-	-	-	-	1.0	1.1	0	-	-	-	-	-	-	25	10.0	3.8
<i>Scottocalanus</i> sp.	-	-	-	-	-	-	1.0	1.2	2	-	-	-	-	-	-	-	-	-
<i>Sergestes</i> sp.	-	-	-	-	-	-	-	-	-	3.1	0.8	0.7	-	-	-	-	-	-
<i>Themisto abyssorum</i>	-	-	-	-	-	-	1.0	1.2	2	6.2	1.3	3.7	-	-	-	50	20.0	46.2
<i>Themisto compressa</i>	-	-	-	0.9	0.3	0.4	2.0	2.2	4	6.2	1.3	5.9	-	-	-	50	20.0	15.4
<i>Themisto</i> sp.	-	-	-	2.8	1.0	0.4	1.0	1.2	2	15.6	6.2	2.9	8.5	3.3	1.7	75	29.9	23.1
<i>Thysanoessa</i> sp.	-	-	-	-	-	-	-	-	-	6.2	2.2	1.5	-	-	-	-	-	-
<i>Thysanoessa tenera</i>	-	-	-	-	-	-	-	-	-	9.3	4.3	2.9	-	-	-	-	-	-

Table 7: Diet composition of the studied *B. glaciale* from 2021. Bioluminescent prey is highlighted in green, non-bioluminescent in grey and potentially bioluminescent prey in white. Prey where bioluminescence could not be

determined is in magenta. “Occ.” is how many stomachs a prey item appeared in, “Weight” is biomass and “Abund.” Is the number of one prey item. All are percentages.

<i>Benthosema glaciale</i>			
Plankton species	Occ.	Weight	Abund.
<i>Calanus finmarchicus</i>	6.7	3.6	21.7
<i>Calanus hyperboreus</i>	0.7	0.7	0.8
<i>Calanus sp.</i>	3.7	0.7	3.9
Digested	55.6	35.5	-
<i>Gaetanus tenuispinus</i>	0.7	0.2	0.8
<i>Metridia longa</i>	3.0	0.7	3.1
<i>Metridia sp.</i>	0.7	0.3	2.3
Other	38.3	40.5	45.7
<i>Paraeuchaeta norvegica</i>	3.0	5.0	3.1
<i>Paraeuchaeta sp.</i>	7.5	7.7	10.1
<i>Pleuromamma robusta</i>	0.7	0.1	0.8
<i>Pleuromamma sp.</i>	3.0	0.4	3.9
<i>Themisto abyssorum</i>	1.5	1.6	1.6
<i>Themisto sp.</i>	0.7	1.2	0.8
<i>Thysanoessa longicaudata (head)</i>	0.7	0.8	0.8
<i>Thysanoessa sp.</i>	0.7	1.0	0.8

The diet of *S. diaphana* consisted of more than 75 % amphipods, and the remainder was chaetognaths and one copepod (Figure 10). *A. hemigymnus* had a diet consisting mainly of copepods and gastropods, with small amounts of chaetognaths, krill and ostracods. *P. arcticum* had eaten almost exclusively copepods (over 90 %), with only a few amphipods, krill and ostracods. *B. glaciale* from the 2018 cruise had eaten mainly copepods, with small numbers of amphipods, chaetognaths, fish, krill and ostracods. *B. glaciale* from the 2021 cruise had eaten mainly copepods, and a few krill, eggs, chaetognaths, appendicularians, and amphipods. *N. kroyeri* had eaten about 50 % copepods, a little under 25 % amphipods, about 10 % fish and krill, and small amounts of cephalopods, chaetognaths, ostracods and shrimp. *L. macdonaldi* had eaten mainly copepods and some amphipods, krill and shrimp (Figure 10).

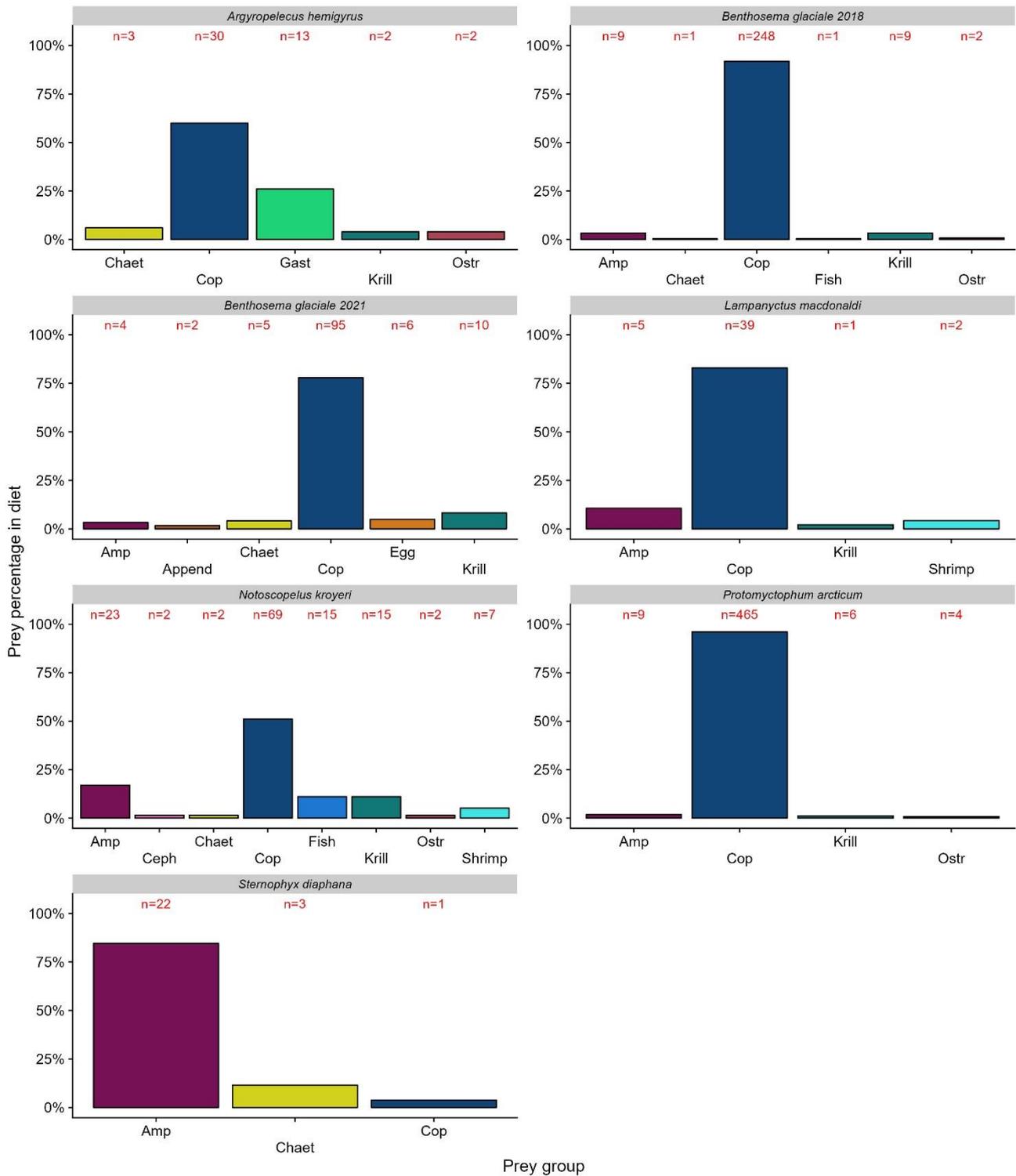


Figure 9: Different groups of prey in the diet of the studied species. Amp = amphipods, Ceph = cephalopods, Chaet = chaetognats, Cop = copepods, Ostr = ostracods, Gast = gastropods.

N. kroyeri was the species with the most varied diet, with prey from 14 different taxa, and *S. diaphana* was the species with the least varied diet, with prey from only five different taxa. The rest

of the fish species had prey from the following number of taxa in their diet: *B. glaciale* (2018): 13, *B. glaciale* (2021): 12, *L. macdonaldi*: 12, *P. arcticum*: 11, and *A. hemigymnus*: 10 (Figure 11).

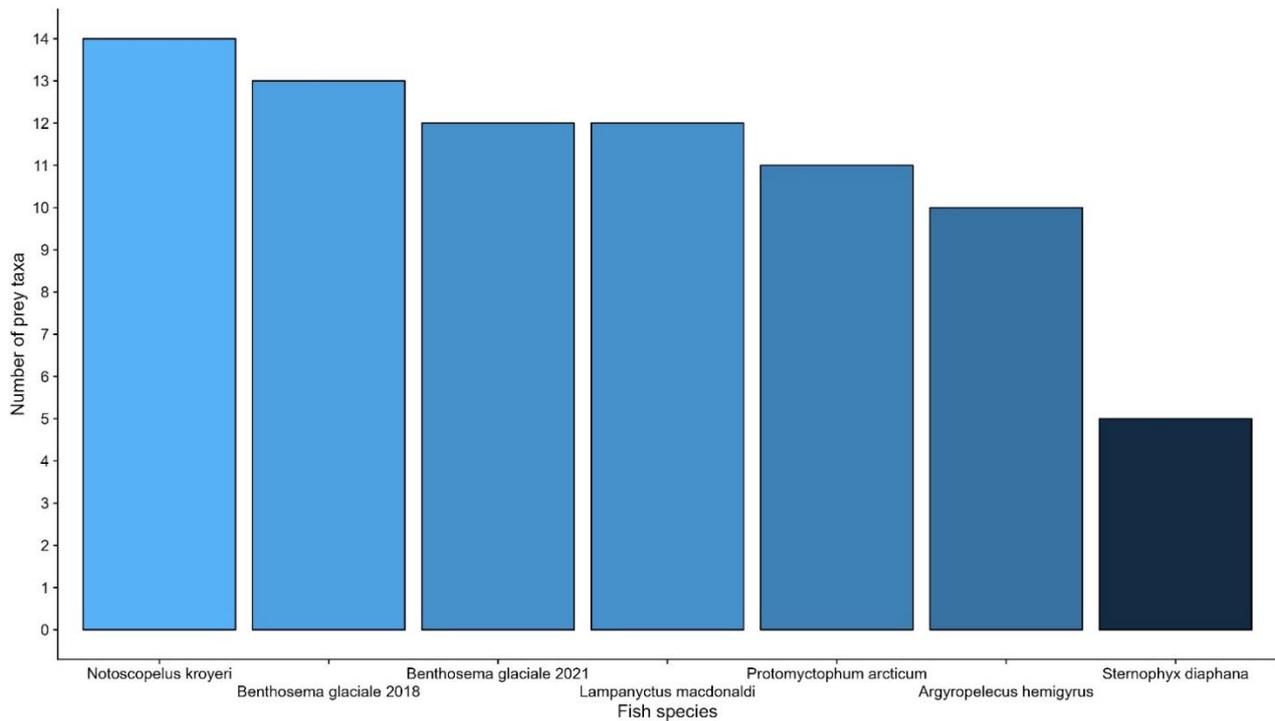


Figure 10: Prey taxa in the diet of the studied species. Only lowest possible taxon is represented.

From the 2018 cruise, it is clear that hatchetfishes had eaten mainly or only non-bioluminescent prey, while lanternfishes had eaten a larger proportion of bioluminescent prey. *Argyropelecus hemigymnus*, *Lampanyctus macdonaldi* and *Notoscopelus kroyeri* had all clearly eaten more non-bioluminescent prey than bioluminescent prey (Figure 12). *Benthosema glaciale* had also eaten more non-bioluminescent prey, but the difference was not as big. *Protomyctophum arcticum* had clearly eaten both ore bioluminescent than non-bioluminescent prey and the most bioluminescent prey of all the species of fish. It had also been eating the most total prey of all the fish species. *Sternophyx diaphana* had only eaten non-bioluminescent prey (Figure 12).

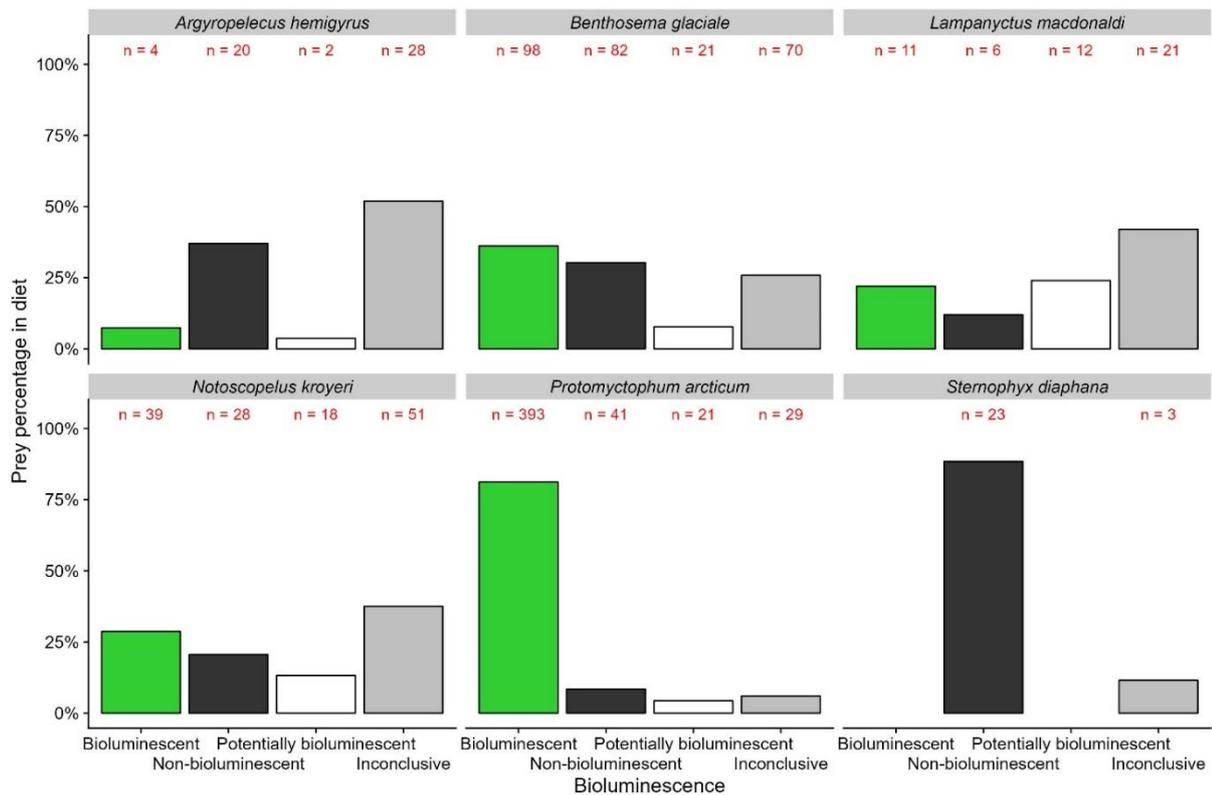


Figure 11: Diet composition of the different bioluminescent categories of the studied species collected during the 2018 cruise. Inconclusive are the prey that could not be determined to a taxonomic level where bioluminescence could be determined.

From the 2021 cruise, *B. glaciale* had eaten more than twice as much non-bioluminescent prey as both bioluminescent and potentially bioluminescent prey. They had eaten the most potentially bioluminescent prey relative to other prey types of all the samples (Figure 13).

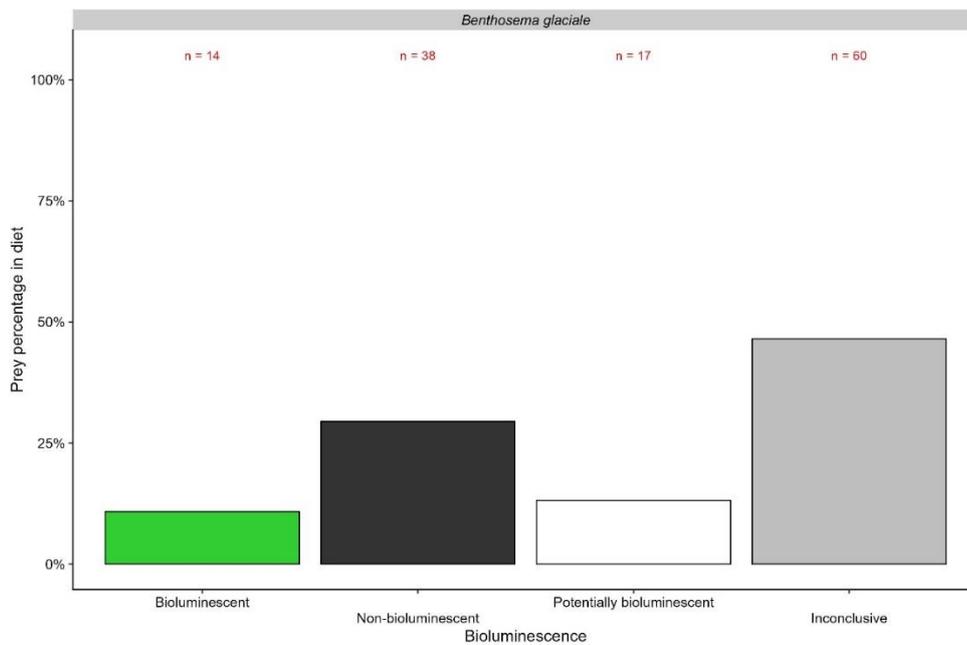


Figure 12: Diet composition of the different bioluminescent categories of *B. glaciale* collected during the 2021 cruise. Inconclusive are the prey that could not be determined to a taxonomic level where bioluminescence could be determined.

Zooplankton distribution

In the MOCNESS from the 2018 cruise, the most abundant group at all stations was copepods, followed by foraminifers. *Oithona* spp. was the most abundant taxa. *Acartia* spp, *Metridia* sp. and *Calanus finmarchicus/hyperboreus* were also abundant (Figure 14). Station 278 had the highest total plankton numbers, and station 282 had the lowest (Figure 14). Although *Oithona* spp. was the dominant taxa in all the stations, its relative abundance varies greatly between them. The highest relative abundance of *Oithona* spp. was found in station 276 (77 %) located in the Rockall Basin (Figure 14). The lowest relative abundance of *Oithona* spp. was found at station 282 located in the Iceland Basin (Figure 14). *Acartia* spp., which was the second most abundant at station 278, had a relative abundance of under 1% at stations 276, 280 and 281 and was not found at all at station 282. *Metridia* sp. only had a relative abundance over 1 % at stations 278 and 275, but was found at all stations. It was most abundant at station 275 (8 %) *Calanus finmarchicus/helgolandicus* had a relative abundance over 1 % at all stations, with the highest being at station 282 and the lowest at station 275. There were relatively high numbers of Foraminifera at stations 282 (13 %), 280 (9 %), 281 (19 %) and 278 (6 %), and a lower abundance at station 275 (2 %). It was also present at station 276, but with a relative abundance under 1 %. *Pseudocalanus* spp. had a high relative abundance at

station 278 (10 %) and 276 (7 %) and a relative abundance of 1 % at station 280, but a relative abundance below 1 % at all other stations.

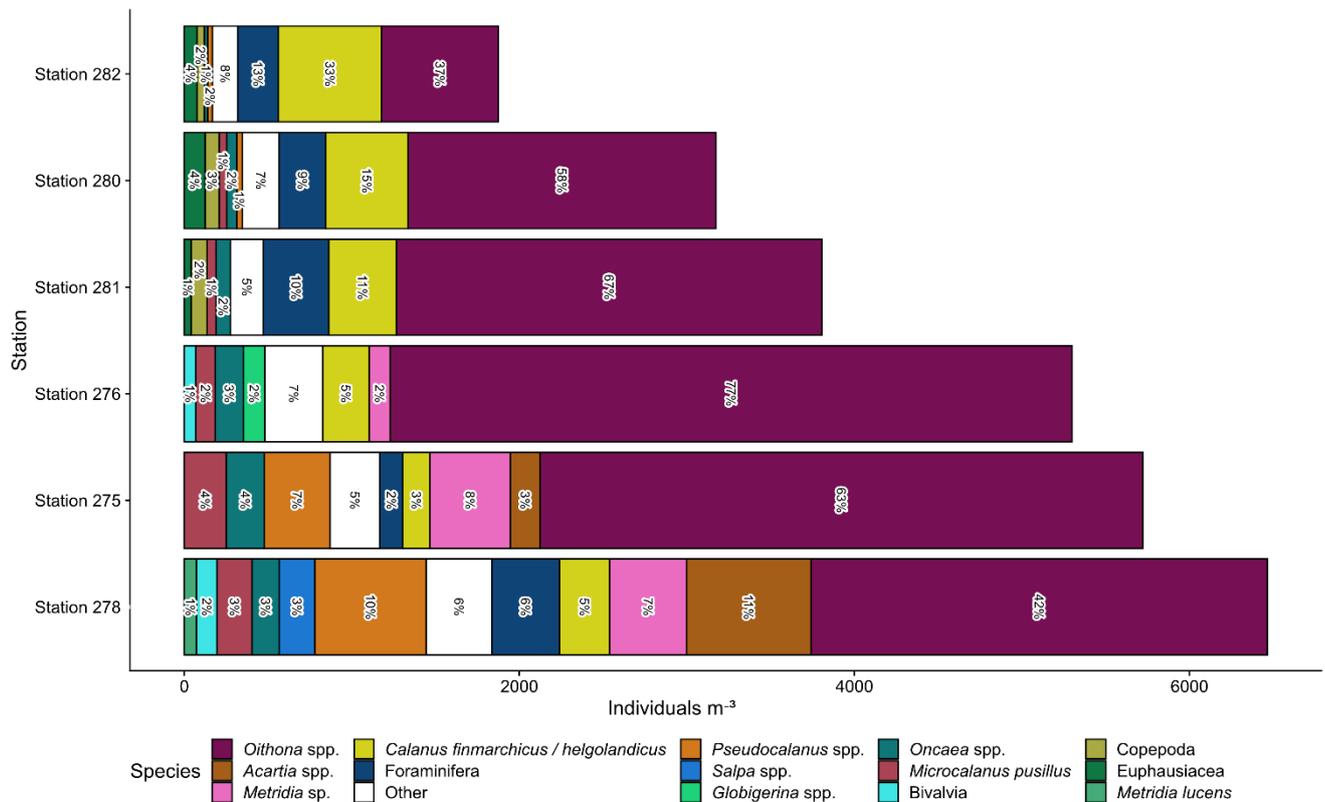


Figure 13: Zooplankton distribution in the Iceland and Rockall Basin. Plankton with abundance < 1% were grouped together as “Other”.

In the MAMMOTH from the 2021 cruise, copepods were the most dominant group. Other prominent groups were bivalves, gastropods, foraminifers (*Globigerina* spp.) and *Oithona* spp. was also the most abundant at most of the stations in this cruise, with the exception of station 178, where *Calanus finmarchicus/helgolandicus* was the most abundant. *Calanus finmarchicus/hyperboreus* were also abundant (Figure 15). Station 178 in the Norwegian Sea had the lowest total number of plankton, but the highest amount of species making up more than 1 % of the total abundance. Station 171 in the Iceland Basin, where the total number of individuals was the highest and the dominating taxa *Oithona* spp., had the highest relative abundance and was also the one with the least species making up more than 1 % of the total abundance (Figure 15). This trend was true also for the two remaining stations: Station 179 in the Norwegian Sea had a lower plankton abundance and *Oithona* spp. had a lower relative abundance, but there was one more species with a relative abundance over 1 % than at

station 175 in the Iceland Basin where the total number of plankton and *Oithona* spp. had a higher relative abundance.

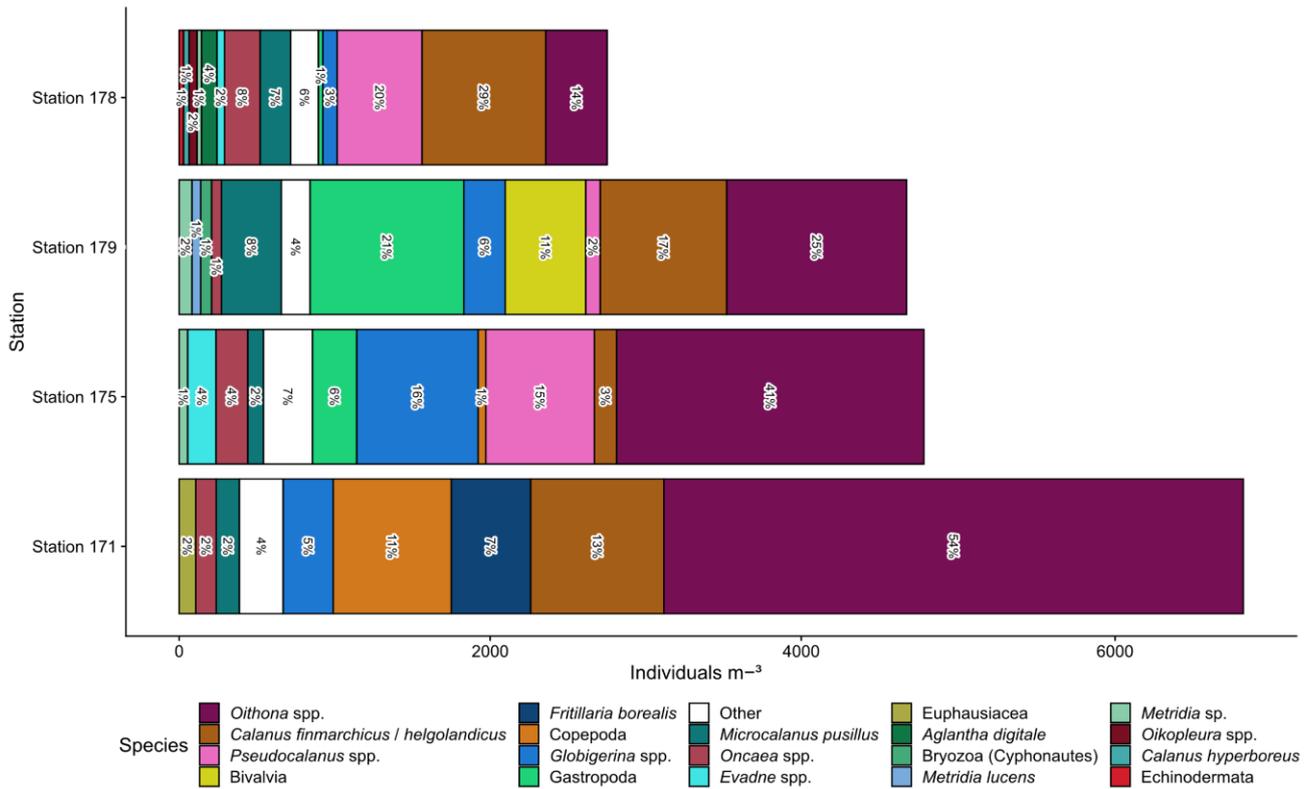


Figure 14: Zooplankton distribution from the 2021 cruise. Plankton with abundance < 1% were grouped together as “Other”.

All plankton species from the 2018 cruise were present to some degree in the lower depth layers, but four were absent from the upper 400 meters: *Euaugaptilus magnus*, *Gaetanus brevispinus*, *Pseudochirella pustulifera* and *Scottocalanus* sp. (Figure 16)

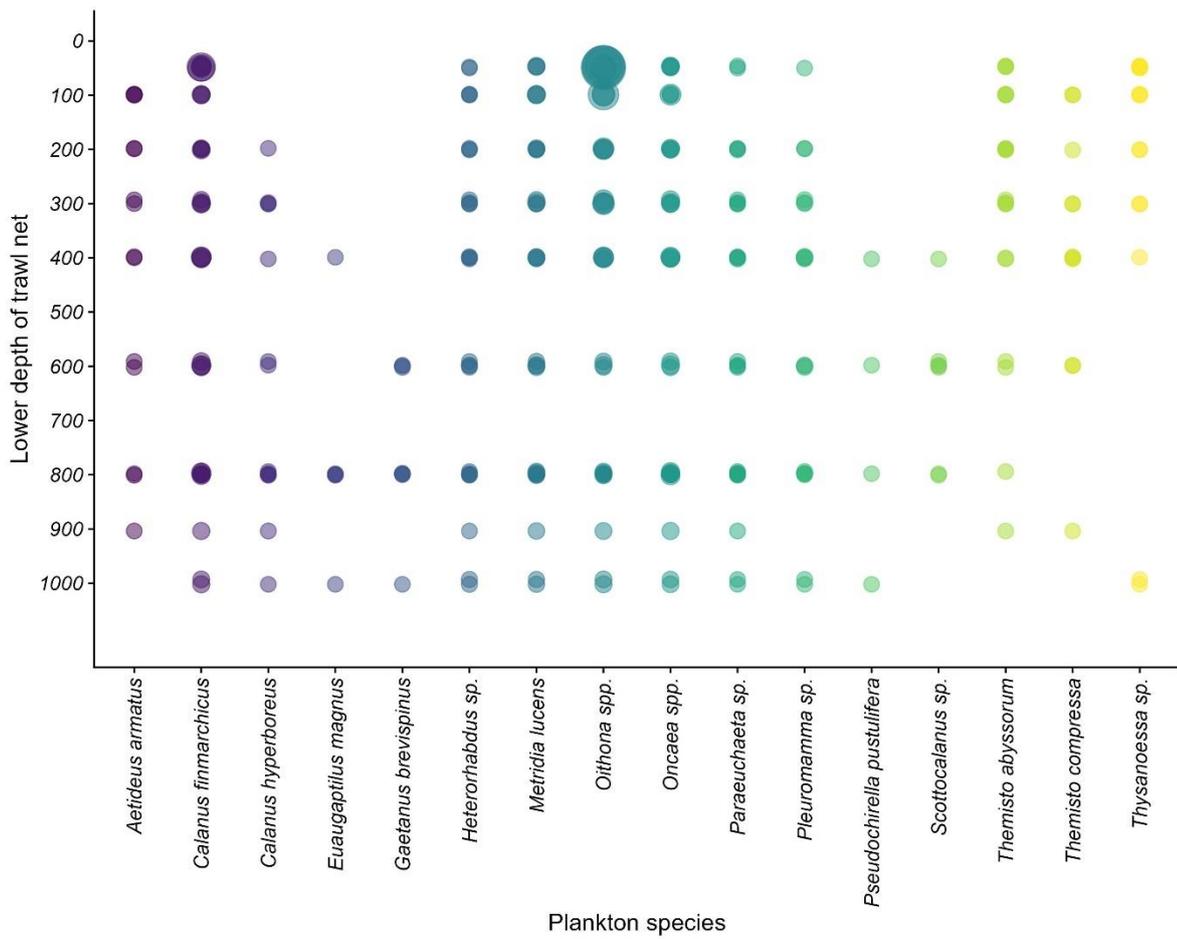


Figure 15: Depth distribution of plankton species at each station from the 2018 cruise based on the lower depths of the nets of the MOCNESS. Each colour corresponds to a different species. Sizes of the dots corresponds to the density of the plankton.

All plankton species were present in most strata in at least one station from the 2021 cruise. *Metridia longa* was not present in the upper 100 meters and *Pleuromamma sp.* was not present in the lower 900 meters (Figure 17).

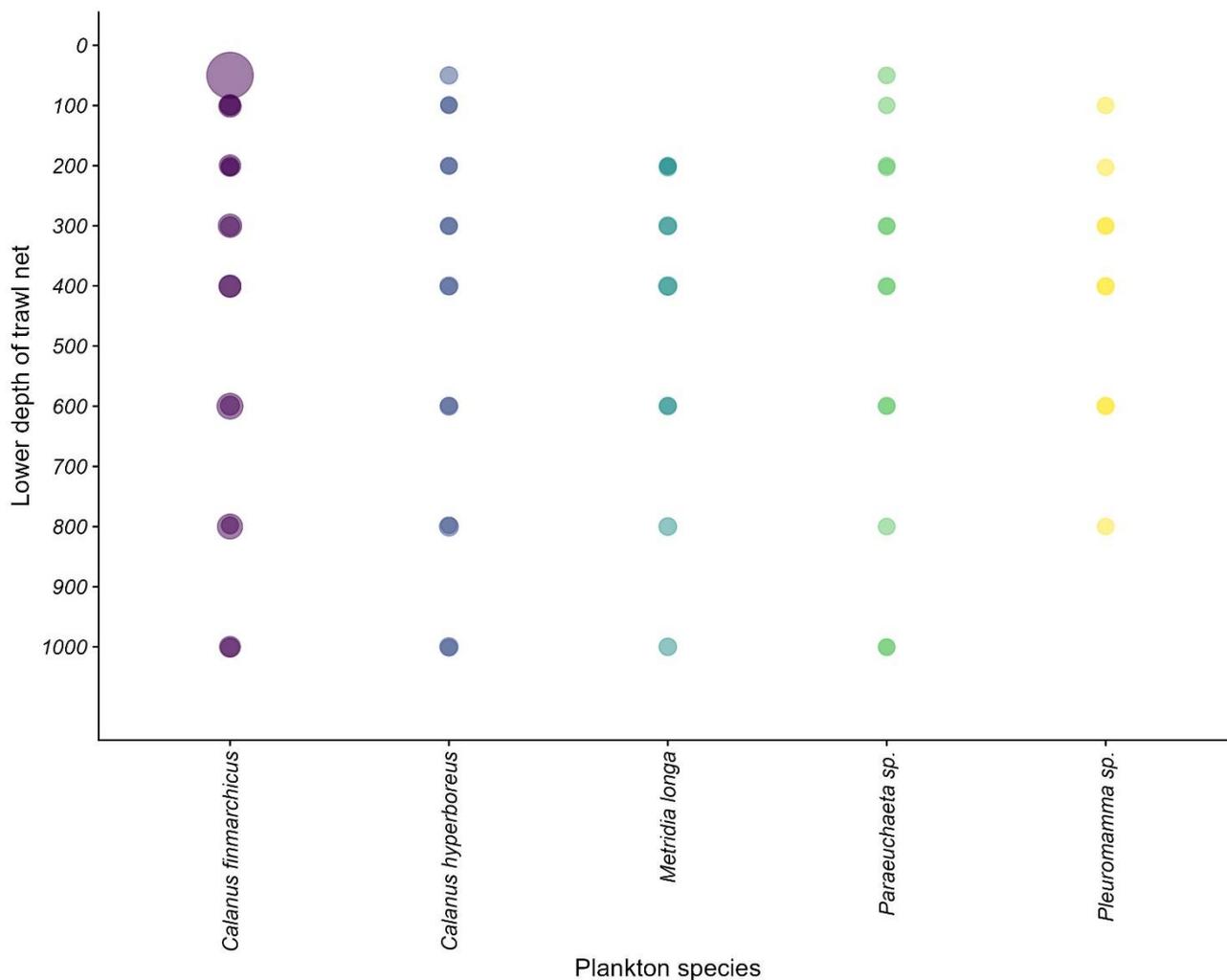


Figure 16: Figure 8: Depth distribution of plankton species from the 2021 cruise based on the lower depths of the nets of the MAMMOTH. Each colour corresponds to a different species. Sizes of the dots corresponds to the density of the plankton.

Selectivity analyses

Only the prey species found in at least one stomach is part of the ratios, and only the species in the diet of a particular fish species are shown in each plot.

Sternoptyx diaphana

S. diaphana had mainly eaten *T. compressa* and *T. abyssorum* and showed a strong positive selectivity towards it (Figure 18). There was however found one copepod in the diet of *S. diaphana* (*P. pustulifera*). There was a positive selectivity for all the species in its diet (0.99).

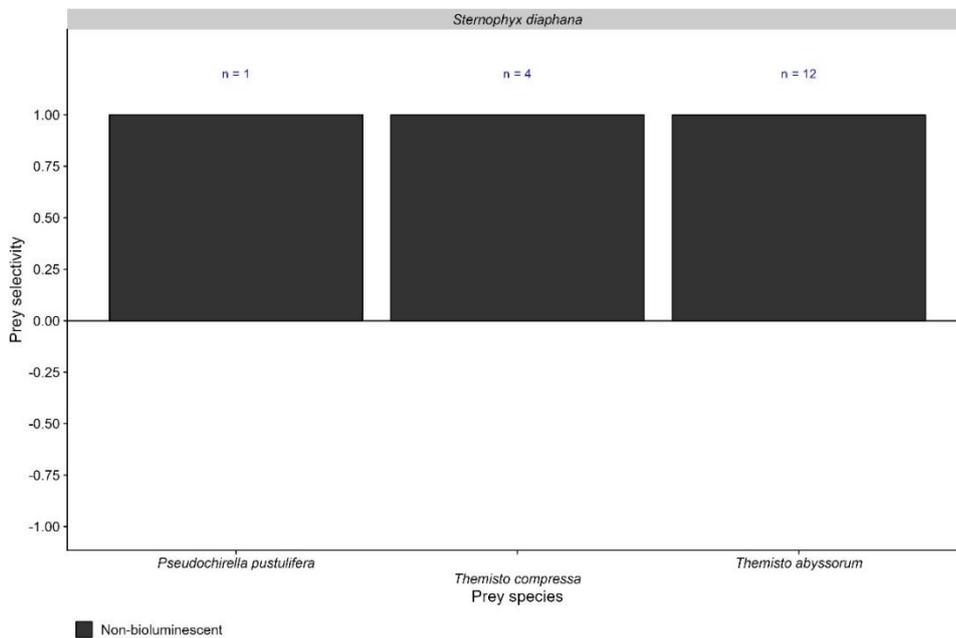


Figure 17: Average Ivlev's selectivity index calculated for *S. diaphana* according to the available zooplankton taxa in the water column. The whiskers represent the standard deviation.

Argyropelecus hemigymnus

A. hemigymnus showed a strong positive selectivity towards *Aetideus armatus* (0.99), *Paraeuchaeta* sp. (0.99), *Heterorhabdus* sp. (0.99) and *Pleuromamma* sp. (0.97) It showed a weaker positive selectivity towards *M. lucens* (0.79) and *C. finmarchicus* (0.55) but had eaten mostly *C. finmarchicus* (Figure 19).

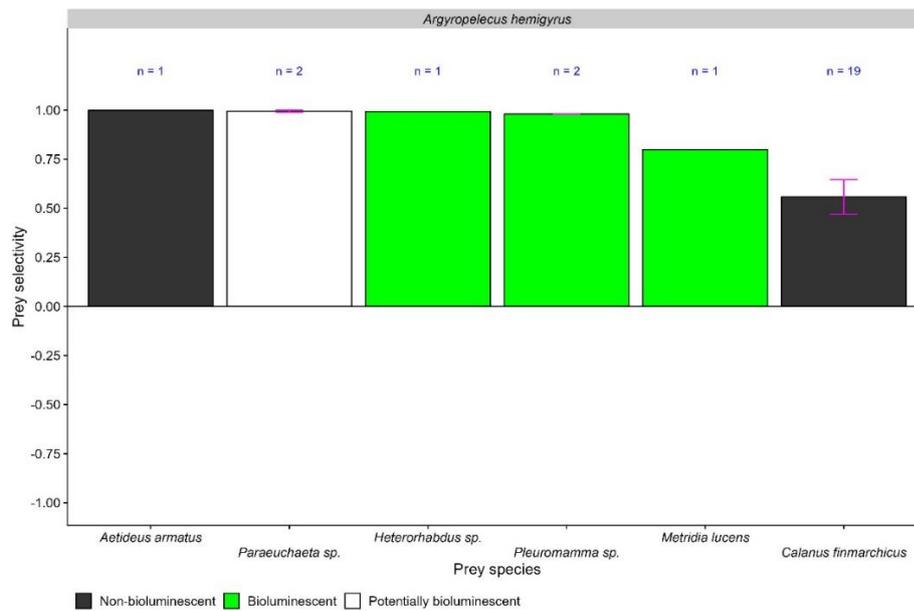


Figure 18: Average Ivlev's electivity index calculated for *A. hemigyrus* according to the available zooplankton taxa in the water column. The whiskers represent the standard deviation.

Protomyctophum arcticum

P. arcticum showed an especially strong positive selectivity towards *Paraeuchaeta* sp. (0.98), and *Pleuromamma* sp. (0.98). There was a weaker but still strong positive selectivity towards *A. armatus* (0.93), *M. lucens* (0.85) and *Oncaea* sp. (0.38), and a negative selectivity towards *Oithona* sp. (-0.31) and *Calanus finmarchicus* (-0.42) (Figure 20).

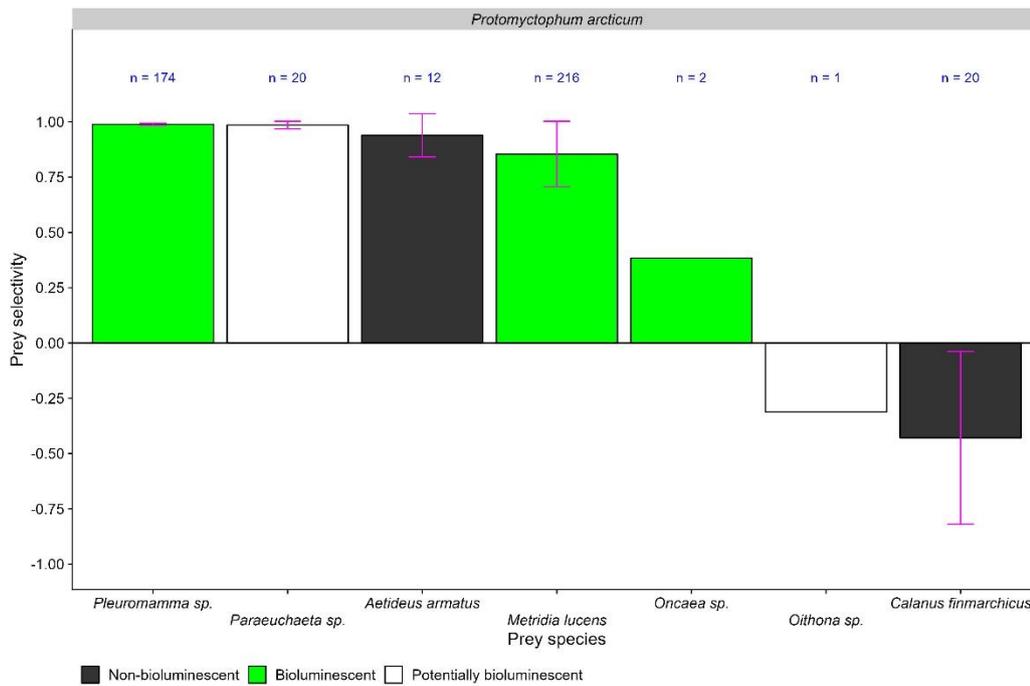


Figure 19: Average Ivlev's electivity index calculated for *P. arcticum* according to the available zooplankton taxa in the water column. The whiskers represent the standard deviation.

Benthosema glaciale

B. glaciale from 2018 showed a strong positive selectivity for *Paraeuchaeta sp.* (0.99), *Pleuromamma sp.* (0.97), *T. compressa* (0.95), and *A. armatus* (0.98). There were high numbers of *Paraeuchaeta sp.* and *Pleuromamma sp.*, but small numbers of *Themisto sp.* and *A. armatus* in the stomachs. It also showed a weaker positive selectivity for *M. lucens* (0.53) and *C. finmarchicus* (0.14) (Figure 21). From the 2021 cruise, *B. glaciale* showed similar trends for prey type with regard to bioluminescence, although overall lower selectivity. The main difference in prey species from 2021 is that the selectivity for *Metridia sp.* (0.76) in 2021 than for *M. lucens* (0.53) in 2018 and a lower selectivity for *Pleuromamma sp.* in 2021 (0.66) as well as the presence of *C. hyperboreus*, *M. longa* and some individuals that could only be identified to *Calanus sp.* (Figure 21).

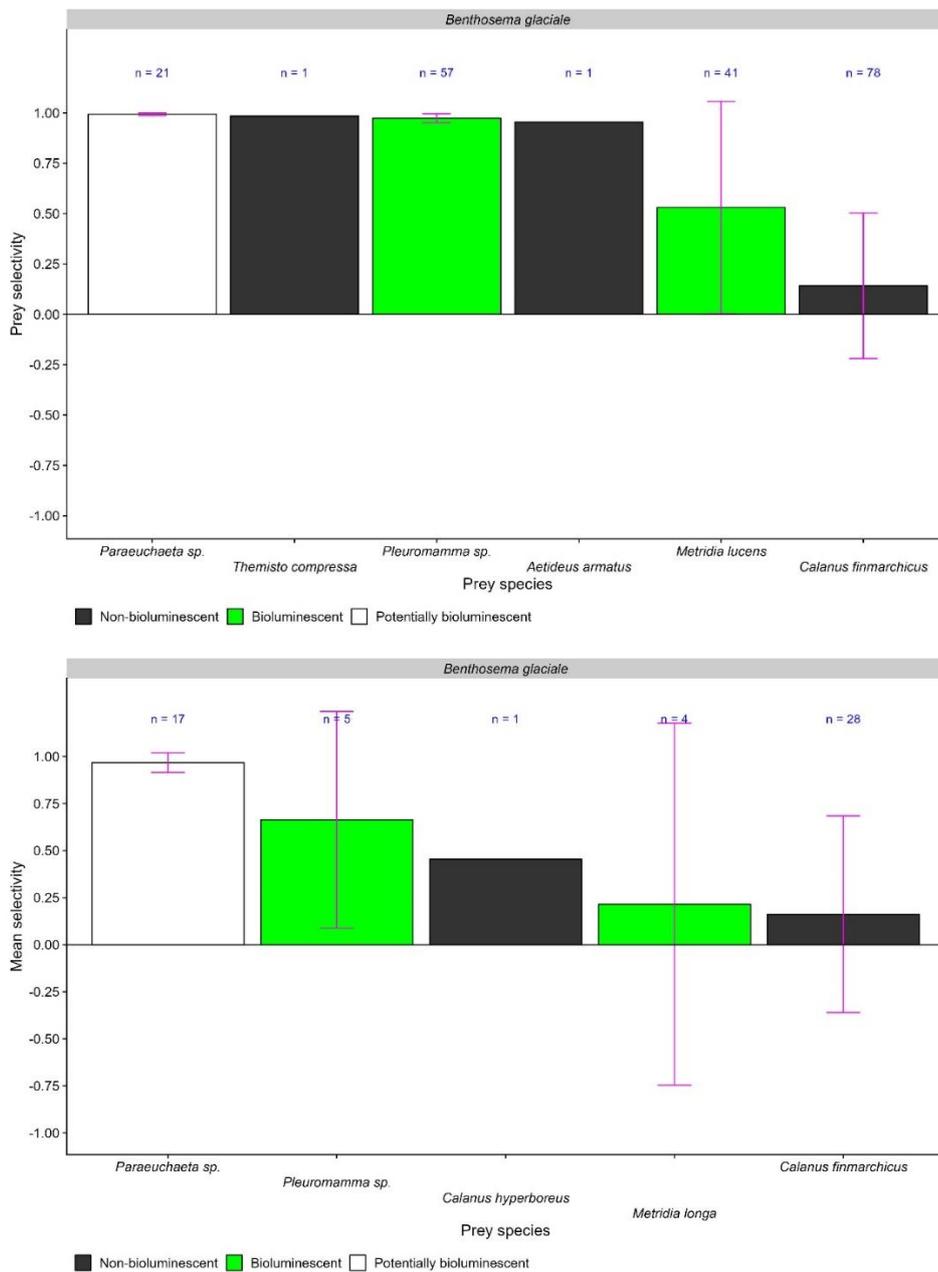


Figure 20: Average Ivlev's electivity index calculated for *B. glaciale* from the 2018 cruise (upper) and 2021 cruise (lower) according to the available zooplankton taxa in the water column. The whiskers represent the standard deviation.

Notoscopelus kroyeri

N. kroyeri showed a strong positive selectivity for all the prey found in its diet, with the strongest being *G. brevispinus* (0.99), *T. abyssorum* (0.99), *T. compressa* (0.99), and *Paraeuchaeta sp.* (0.99), *Thysanoessa sp.* (0.99) and *Pleuromamma sp.* (0.98) and a weaker one for *M. lucens* (0.86) (Figure 22).

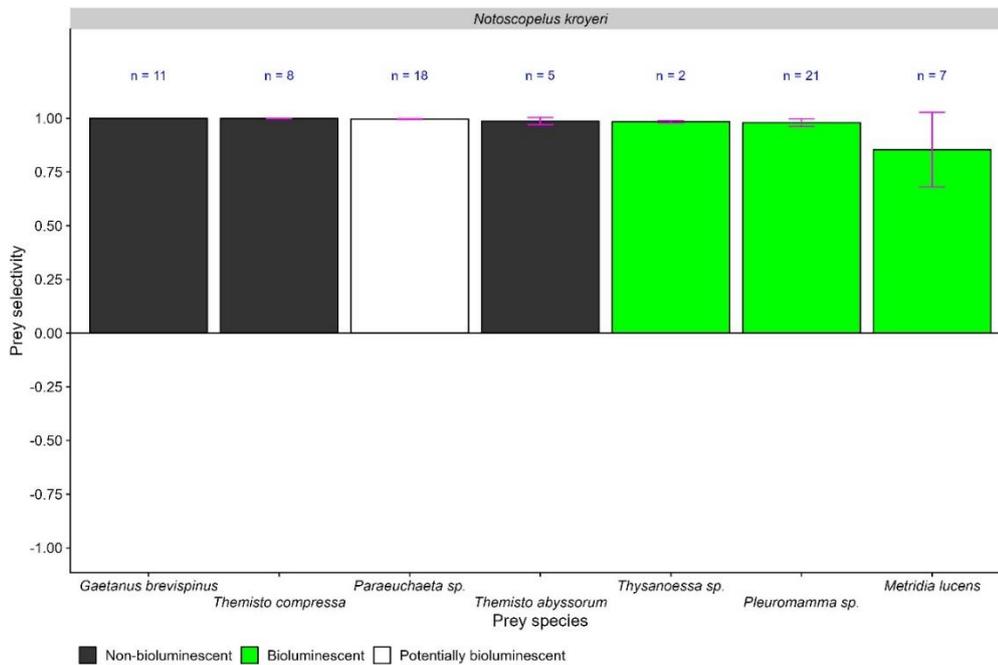


Figure 21: Average Ivlev's electivity index calculated for *N.kroyeri* according to the available zooplankton taxa in the water column. The whiskers represent the standard deviation.

Lampanyctus macdonaldi

L. macdonaldi showed positive selectivities for all prey found in its diet except for *C. finmarchicus*, which it showed a negative selectivity for (-0.29). It showed particularly strong selectivities for *E. magnus* (0.99), *Scottocalanus* sp. (0.99), *T. compressa* (0.99), *T. abyssorum* (0.99) and *Paraeuchaeta* sp. (0.99). It also showed a strong selectivity towards *Pleuromamma* sp. (0.92) and *M. lucens* (0.73) (Figure 23).

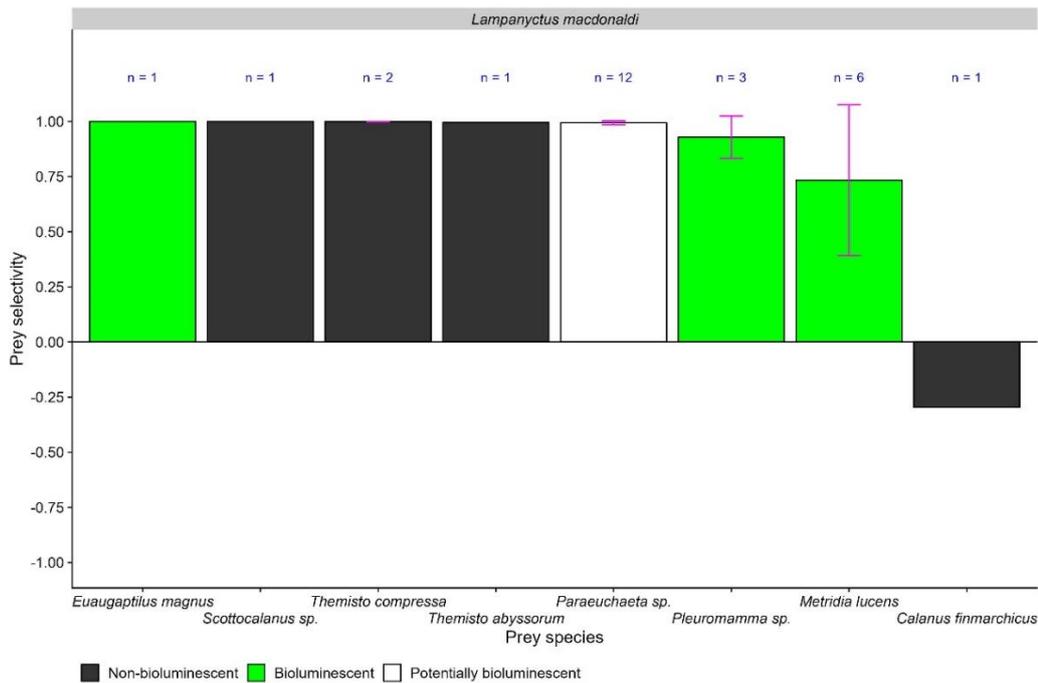


Figure 22: Average Ivlev's electivity index calculated for *L. macdonaldi* according to the available zooplankton taxa in the water column. The whiskers represent the standard deviation.

Considering non-bioluminescent prey grouped before determining the ratio, there is a strong positive selectivity for non-bioluminescent prey in *S. diaphana* (0.99). *A. hemigygnus* showed a strong positive selectivity for potentially bioluminescent (0.99) and bioluminescent (0.93) a weaker positive selectivity for non-bioluminescent prey (0.64) (Figure 24). *P. arcticum* have a positive selectivity for all the prey types, with the strongest positive selectivity for bioluminescent (0.87) and weaker for potentially bioluminescent sp. (0.76) the weakest towards non-bioluminescent (0.19). *B. glaciale* from the 2018 cruise shows the strongest selectivity for potentially bioluminescent prey (0.99), a weaker but still strong positive selectivity for bioluminescent prey (0.81), and a weak positive selectivity for non-bioluminescent prey (0.32) (Figure 24). *N. kroyeri* shows strong positive selectivity for potentially bioluminescent (0.99) and non-bioluminescent (0.99) and a weaker, but still strong selectivity towards non-bioluminescent (0.94). *L. macdonaldi* showed the strongest positive selectivity for potentially bioluminescent prey (0.99), and a weaker but still strong positive selectivity for bioluminescent prey (0.87). The weakest, but still positive selectivity was for non-bioluminescent prey (0.67) (Figure 24).

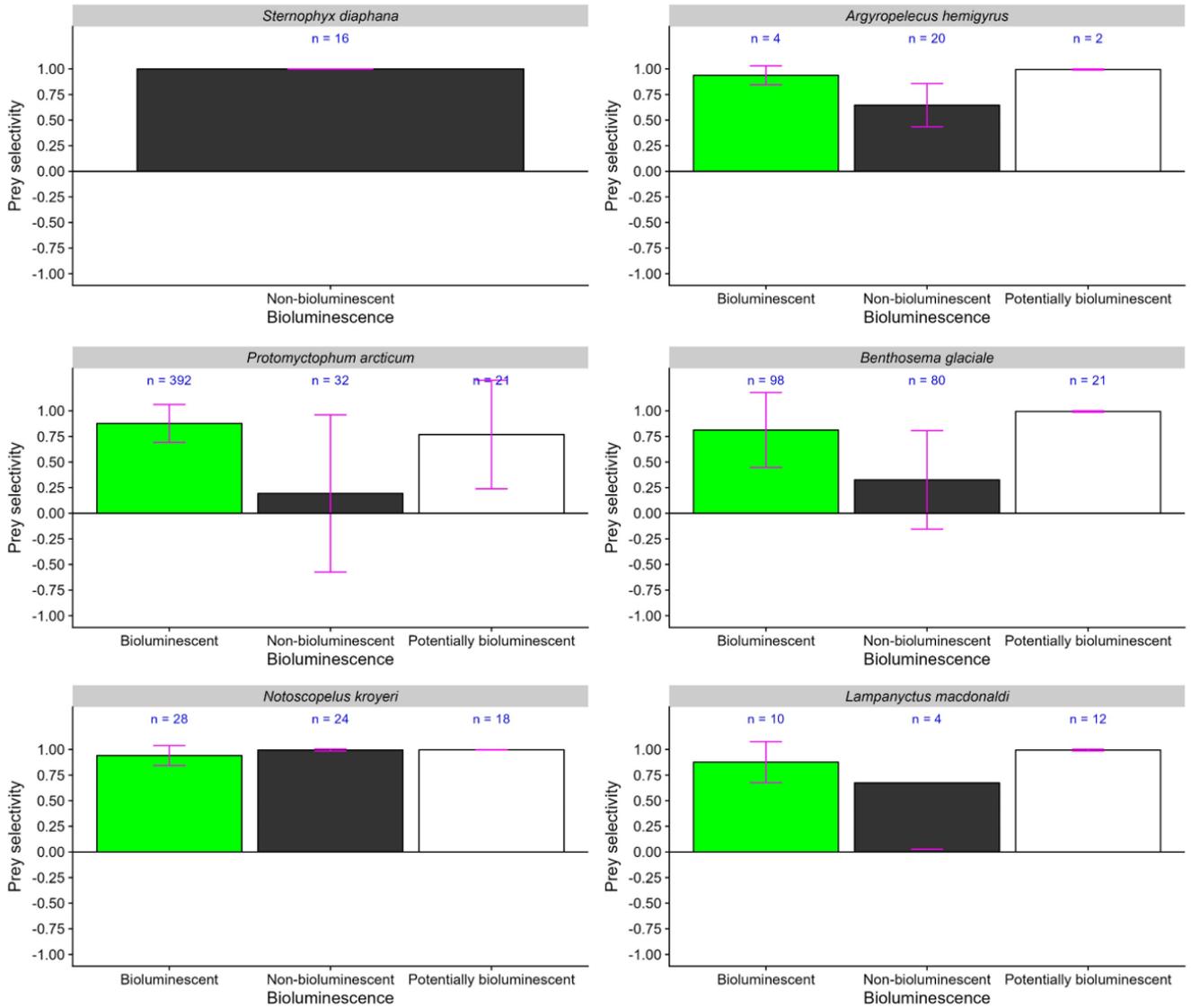


Figure 23: The studied species collected on the 2018 cruises' selectivity for bioluminescence grouped after species ratios were calculated with error bars (magenta).

B. glaciale from the 2021 cruise had a positive selectivity for all bioluminescence categories, but it showed the strongest selectivity towards potentially bioluminescent prey (0.96), a weaker for bioluminescent (0.48) and the weakest for non-bioluminescent prey (0.22) (Figure 25).

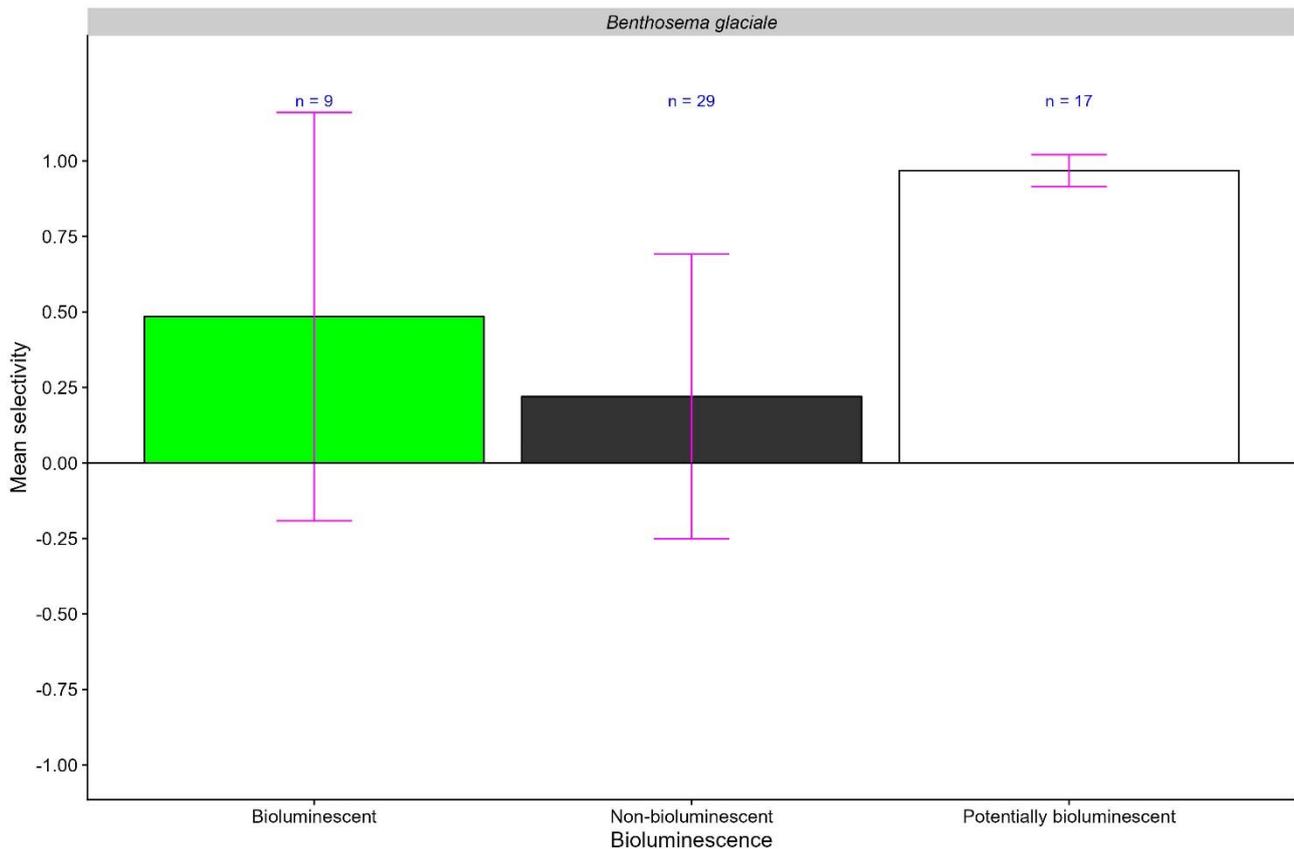


Figure 24: *B. glaciale* collected on 2021 cruises Selectivity for bioluminescence grouped after species ratios were calculated with error bars (magenta).

Looking at bioluminescence categories groups before determining ratios, *S. diaphana* shows a weak selectivity for non- bioluminescent prey (0.09). *A. hemigymnus* shows the strongest selectivity for potentially bioluminescent prey (0.58), then bioluminescent prey (0.42) and a weak negative selectivity for non-bioluminescent prey (-0.03) (Figure 26). *P. arcticum* showed a very strong selectivity for bioluminescent prey (0.81), a weaker one for potentially bioluminescent prey (0.36) and a strong negative one for non-bioluminescent prey (-0.81) (Figure 26). *B. glaciale* showed a strong positive selection for potentially bioluminescent prey (0.86), a weaker one for bioluminescent prey (0.59) and a negative one for non-bioluminescent prey (-0.39). *N. kroyeri* showed a strong selectivity towards potentially bioluminescent prey (0.80), a weaker but still strong one for bioluminescent prey (0.62) and a negative selectivity towards non-bioluminescent prey (-0.31) (Figure 26). *L. macdonaldi* showed a strong selectivity towards potentially bioluminescent prey (0.85), a weaker one for bioluminescent (0.56) and a negative one for non-bioluminescent prey (-0.5) (Figure 26).

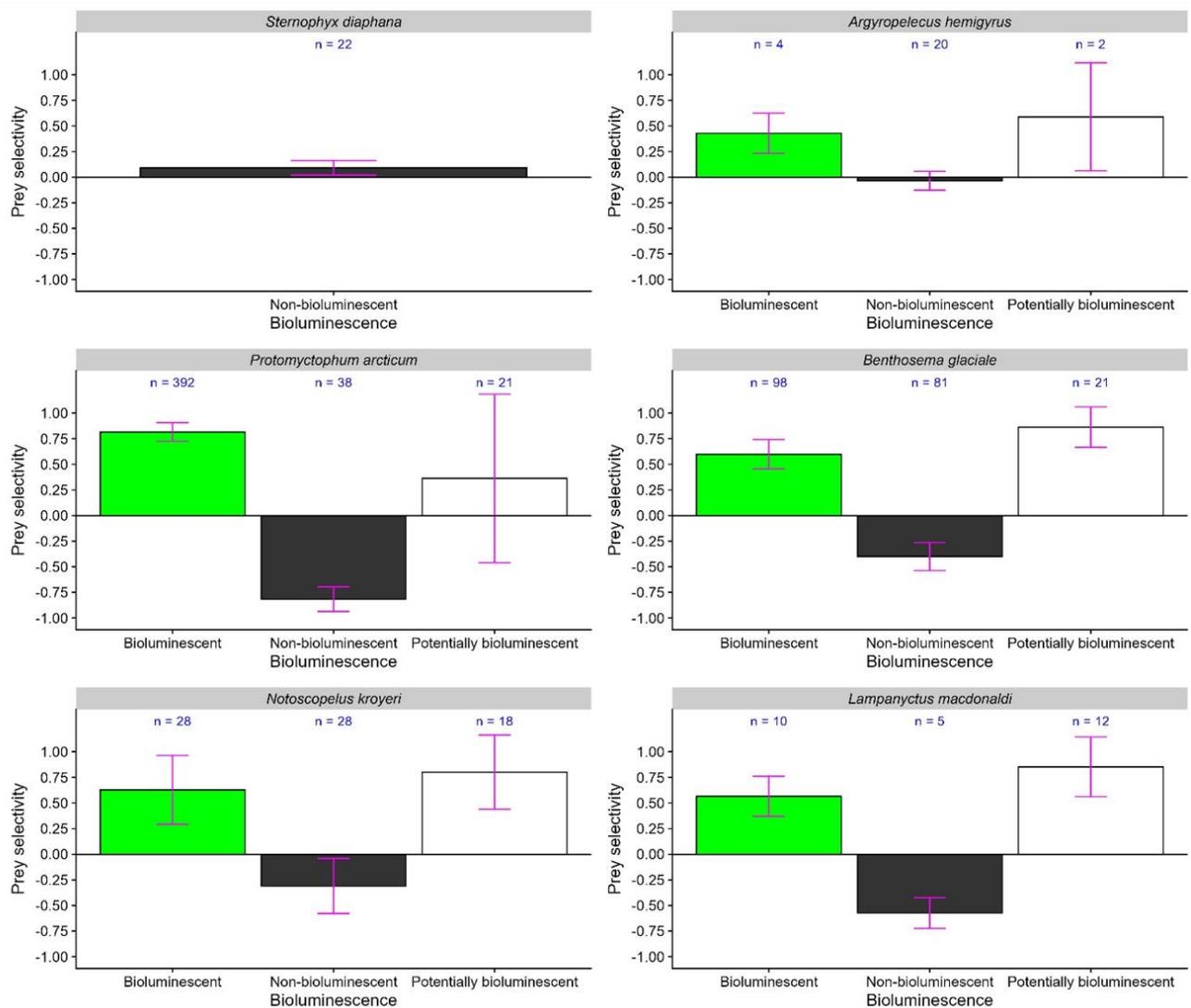


Figure 25: The studied species collected on the 2018 cruises selectivity for bioluminescence when grouped before determining ratios with error bars (magenta).

B. glaciale from 2021 showed a strong selectivity towards potentially bioluminescent prey (0.93), a weak selectivity towards bioluminescent prey (0.26) and a negative selectivity towards non-bioluminescent prey (-0.28) (Figure 27).

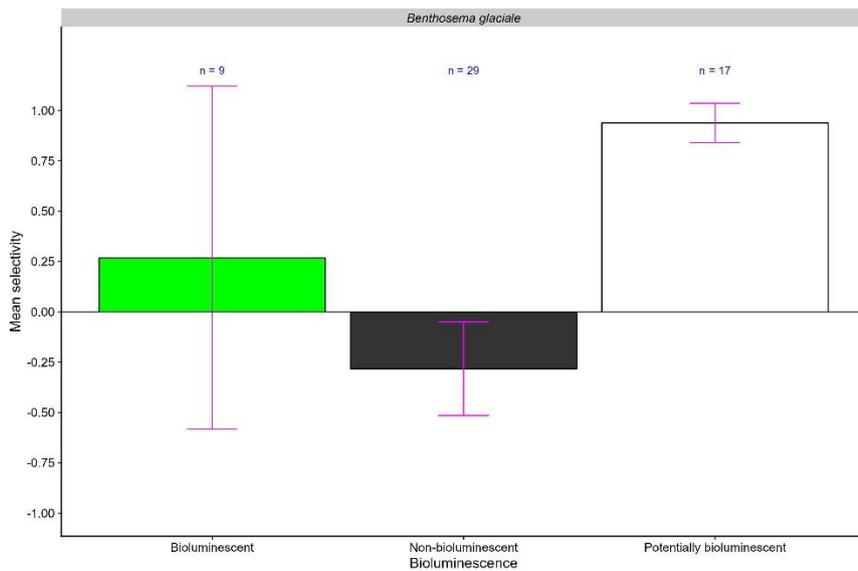


Figure 26: *B. glaciale* collected on the 2021 cruises species selectivity for bioluminescence when grouped before determining ratios with error bars (magenta).

Discussion

Despite the fact that the mesopelagic holds the greatest vertebrate biomass (Irigoien *et al.*, 2014) and its organisms contribute greatly to the transport and later storage of atmospheric carbon (Sarmiento-Lezcano *et al.*, 2022), not much is known about the organisms that reside there. Mesopelagic fishes have a wide variety of eye-sizes, and although it has earlier been hypothesized that the size of a species eye is an inverse relationship with its depth distribution, study shows that this is not always the case (de Busserolles *et al.*, 2013). Fishes with overlapping depth distribution have a variety of both eye-sizes and eye adaptations (de Busserolles *et al.*, 2013). For example, the species studied in this thesis all have overlapping depth distributions to some degree but have differing eye-sizes and show different foraging behaviours (Table 8, Figure 27).

The ecology of mesopelagic species is generally not well known, so to familiarize the reader with the mesopelagic ecosystem and the different roles and adaptations of the species in this study I begin with a brief review with a focus on vision and foraging (see also Table 8 and Figure 26 for structured summaries) before I discuss insights from the stomach content analysis and its relation to the observed zooplankton communities, and particularly the role bioluminescence of the prey may play.

Vision, vertical migration, and foraging in the mesopelagic

There is a variety of eye-sizes and ecological features in the fish species studied in this work. *A. hemigymnus* is not known to migrate, while all the other species have been found to migrate (Table

8). *S. diaphana* migrates the furthest, from 700-900 m at day to 100-200 m at night (Table 8, Figure 27). *P. arcticum* migrates to the epipelagic near the surface, *B. glaciale* migrates from mesopelagic depths up to the epipelagic between 200-0 m, *N. kroyeri* migrates from the mesopelagic to the bottom of the mesopelagic, and *L. macdonaldi* migrates within the mesopelagic (Table 8, Figure 27). *P. arcticum* has a wide depth range (250-1000 m), while *A. hemigymnus* has two very narrow ones in comparison (300-400 m and 700-800 m). Adult *L. macdonaldi* has a total depth range of 250- 1000 m, and only migrates within the mesopelagic (Klimpel *et al.*, 2006; Opdal *et al.*, 2008). Sigurðsson, Jónsson and Pálsson (2002) found *L. macdonaldi* to be the most abundant at below 500 m, which may indicate that being their main distribution, and 250-500 m being their migratory distribution.

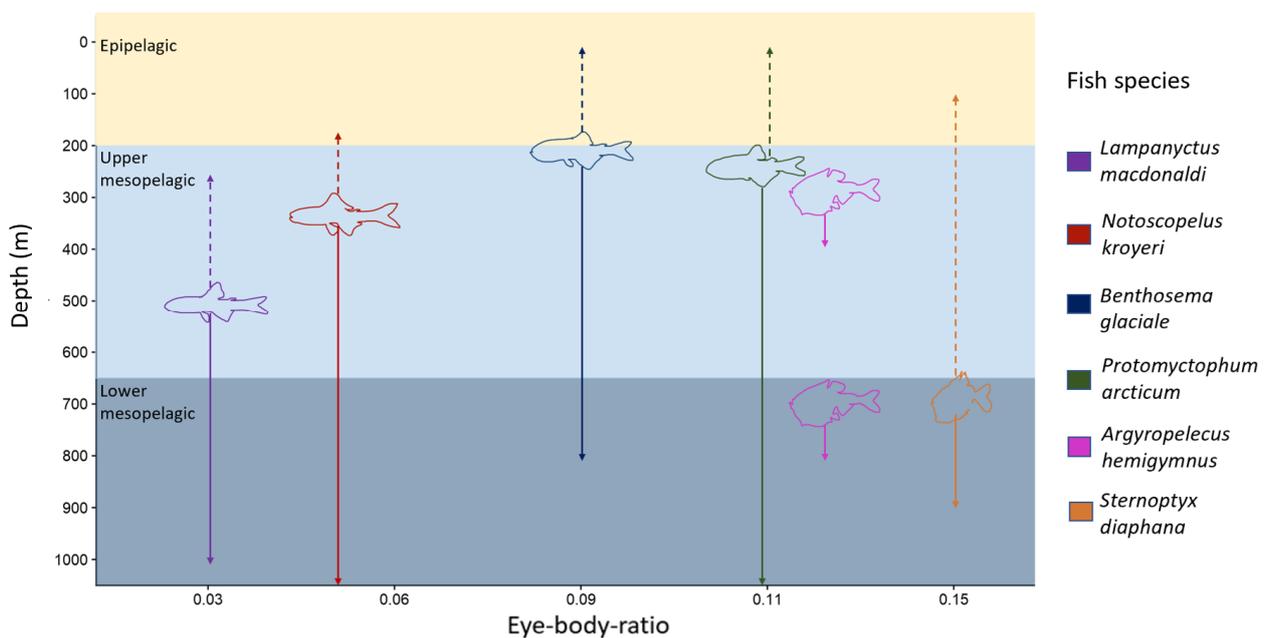


Figure 27: Daytime (whole lines) and night time (dashed lines) distributions and eye-size of the studied species.

A. hemigymnus is the only of the studied species with tubular eyes and in addition has very large eyes. All the other studied species have an aphakic gap. *S. diaphana* and *P. arcticum* have large eyes, *B. glaciale* has medium sized eyes, *N. kroyeri* and *L. macdonaldi* have small eyes. *S. diaphana* also has a ventral area retinae, a (Table 8).

Table 8: Visual characteristics and DVM behaviour of the studied species from the 2018 and 2021 cruises in the North Atlantic.

Fish species	Eye-body-ratio	Eye-size category	Additional eye adaptations	Daytime depth range (m)	DVM
<i>S. diaphana</i>	0.015	large	Ventral area retinae, aphakic gap (Locket, 1970; Wagner <i>et al.</i> , 1998; Davis <i>et al.</i> , 2020)	700 – 900 (Justino <i>et al.</i> , 2022)	Up to 100-200 m (Eduardo <i>et al.</i> , 2020)
<i>A. hemigymnus</i>	0.012	large	Tubular eyes (Biagioni, Hunt and Collin, 2016)	300 - 400 and 700- 800 (Eduardo <i>et al.</i> , 2020)	No (Eduardo <i>et al.</i> , 2020)
<i>P. arcticum</i>	0.11	large	Aphakic gap (de Busserolles, Marshall and Collin, 2014)	250 - 1000 < (Cook <i>et al.</i> , 2013)	To the surface/epipelagic (Cook <i>et al.</i> , 2013)
<i>B. glaciale</i>	0.09	medium	Aphakic gap (Douglas, Partridge and Marshall, 1998)	200 – 800 (Sameoto, 1988)	To the surface/epipelagic (Opdal <i>et al.</i> , 2008)
<i>N. kroyeri</i>	0.05	small	Aphakic gap (de Busserolles, Marshall and Collin, 2014)	325 – 1000 < (Keskin and Eryilmaz, 2010)	Mesopelagic - bottom of epipelagic (Opdal <i>et al.</i> , 2008)
<i>L. macdonaldi</i>	0.03	small	Aphakic gap (de Busserolles, Marshall and Collin, 2014)	500 – 1000 (Sigurðsson, Jónsson and Pálsson, 2002; Klimpel <i>et al.</i> , 2006)	Within the mesopelagic (Klimpel <i>et al.</i> , 2006; Opdal <i>et al.</i> , 2008)

Different sizes and other eye features like a tubular shape and an aphakic gap are eye adaptations to different light sources, conditions and foraging behaviours (de Busserolles *et al.*, 2020).

Bioluminescence is an important ecological trait in the mesopelagic and has been widely discussed, both in plankton and fishes (Haddock, Moline and Case, 2009). It is both a source of light where down-welling daylight is too dim and a mechanism for intraspecies communication and, in some cases, predator evasion (Haddock, Moline and Case, 2009; de Busserolles *et al.*, 2020). Larger eyes are an adaptation to increase the eyes sensitivity, and smaller eyes with relatively large pupils are an

adaptation to vision in dimmer scenes with bioluminescent point-sources (Warrant and Locket, 2004). Although there have been several papers on stomach analysis of mesopelagic fishes (Hopkins and Baird, 1985; García-Seoane, Dalpadado and Vázquez, 2013; Eduardo *et al.*, 2020; Knutsen *et al.*, 2023), there is not much research on whether there is a connection between fishes eye-sizes and a tendency to select bioluminescent prey. This is what I have tried to illuminate in my thesis.

I have determined the eye-to-body ratio of 14 mesopelagic fish species and used stomach content analysis data from IMR on a total of 833 individuals from an IMR cruise done in 2018 in the Rockall and Iceland Basins. I have also done stomach analysis on 327 *Benthoosema glaciale* from a separate IMR cruise done in 2021 in the Iceland Basin and Norwegian Sea. With these data, I have performed further diet composition and selectivity analysis on two species of hatchetfishes: *Sternoptyx diaphana*, *Argyropelecus hemigymnus*, and four species of lanternfishes: *Protomyctophum arcticum*, *Benthoosema glaciale*, *Notoscopelus kroyeri* and *Lampanyctus macdonaldi*.

Insights from diet and selectivity analyses

S. diaphana was the only species where none of the individuals had empty stomachs or digested materials in the stomach. Carmo *et al.* (2015) found *S. diaphana* to have a high percentage of fresh prey in its stomach and although they found empty stomachs, the percentage was low. This could be in part because the prey they had eaten were large and therefore take longer to digest, but also because of a slow metabolism since respiratory rates decrease rapidly with increasing habitat depth in mesopelagic fishes (Panov *et al.*, 2019). It was also the species that had the least variety in the prey items eaten. It was also, however, the species with the fewest individuals with only six individuals examined, which may be part of the reason for this. My findings of mainly *Themisto* spp. in its diet corresponds well with Hopkins and Beard (1985), who found *S. diaphana* to eat mainly amphipods, ostracods and copepods and Carmo *et al.* (2015), who also found mainly amphipods in its diet. Carmo *et al.* (2015) found the stomach fullness to be highest at 10:00, 14:00 and 17:00, but fresh prey (digestion degree 1) were also found at several other times during the day and one at night. Hopkins and Baird (1973) hypothesized based on their findings that *S. diaphana* eats prey from varying taxa and size classes that it is an opportunistic predator with limited pursuit capabilities, whose feeding strategy consists mainly of taking the nearest prey (Hopkins and Baird, 1973). Although the diet in my analysis does not contain a lot of individuals, the trend of *S. diaphana* feeding mainly on copepods fits well with other findings, and is therefore somewhat representative.

From the stomach content analysis of *A. hemigymnus*, we find that all the prey that could be identified to the genus level were copepods, and copepods were the main group in the diet. This fits well with other studies of *A. hemigymnus* diet, who have also found that *A. hemigymnus* eat mainly copepods (Hopkins and Baird, 1985; Carmo *et al.*, 2015).

There was a clear difference between the two hatchetfishes and the four lanternfishes in diet composition when it came to bioluminescence: the lanternfishes had eaten a much larger proportion of bioluminescent prey than the hatchetfishes. *S. diaphana* had not eaten any bioluminescent prey at all. De Busseroles *et al.* (2017) found that lanternfishes are more sensitive to downwelling light compared to some bathypelagic fishes, but not as sensitive as other mesopelagic representatives. This could be because they are more sensitive to bioluminescent sources (de Busseroles and Marshall, 2017). Turner *et al.* (2009) found in their study of lanternfishes visual pigments that their eyes are especially sensitive to bioluminescence. The lanternfishes also had a wider variety of prey taxa than the hatchetfishes, which could point to them being more generalist. There were also some variations within the lanternfishes, with *P. arcticum* having eaten a lot more bioluminescent prey than the others. This contradicts the hypothesis that the studied species with smaller eyes are adapted to seeing mainly bioluminescent point-sources. When it came to prey species selectivity, there were varying patterns, but *S. diaphana* stood out again with high selectivities for non-bioluminescent plankton species. When looking at selectivity for bioluminescence as a trait, there was again a difference between the hatchetfishes and the lanternfishes, but not as clear as the difference in diet composition.

The selectivity for non-bioluminescent prey was strongly negative for all the studied species except for *S. diaphana*, but not nearly as negative for *A. hemigymnus* as for the lanternfishes.

Selectivity in light of fish ecology of the sampled species

In general, large eyes are an adaptation that provide higher light sensitivity, which is useful for vision in dim down-welling daylight and to spot bioluminescence point-sources. While providing higher sensitivity, large eyes are also costly. Smaller eyes with a relatively large pupil could be sufficient for spotting bioluminescent point-sources against a darker background with less down-welling daylight, as seen in both some mesopelagic and bathypelagic species (Hays, Warner and Proctor, 1995). Consequently, I hypothesized that fish with small eyes select bioluminescent prey because they would be easier to see with small eyes, less sensitive eyes. Fish with larger eyes, on the other hand, would perhaps not specifically select bioluminescent prey as their point-sources would be more difficult to spot in the extended visual scene these fish are adapted to, and they would have to see the prey by other means, like being able to spot them in a larger visual angle. Therefore, if mesopelagic

fish select their prey based on their bioluminescence status, one would expect an inverse proportional relationship between a fish species eye-size and their selectivity towards bioluminescent prey. This means that fish with small eyes would select mainly bioluminescent prey and fish with large eyes would select mainly non-bioluminescent prey. Because some of these fish feed at different depths, the depth distributions of the plankton species could affect the fishes selectivity for them. However, most of the plankton species could be found at most depths in at least one station. Therefore, their depth distribution is not thought to be a large constraint on their availability to the fish in this study.

The hatchetfish *S. diaphana* have the largest eyes out of all the fishes in this study. In addition to the large eye-size, they have aphakic gaps to increase the size of the pupil so even more light can be absorbed. They also have a ventral area retinae, which is an adaptation where ganglion cell densities are higher in the ventral part of the retina that facilitates sight upwards (Wagner *et al.*, 1998; de Busserolles and Marshall, 2017). Based on the extensive adaptations to be able to utilize down-welling light as a light source, it would not be expected that *S. diaphana* relies on bioluminescence in their prey to be able to see them. This is supported by the results in this study where *S. diaphana* was not found to have eaten any bioluminescent prey. They are also the species that migrate the furthest in this study, from the lower depths of the mesopelagic zone all the way up to the upper 100-200 m of the epipelagic.

The hatchetfish *A. hemigymnus* has large, tubular eyes located rostrally that are adapted to looking upwards in the water column when searching for prey (Figure). This grants them a very high sensitivity, but also a limited visual angle. They are only able to see in the direction their eyes are pointed. It follows then that they are mainly able to see prey directly above them, but their visual range is long. These eyes are well suited for lie-in-wait predators that attack their prey from below (Warrant and Locket, 2004). Tubular eyes are an adaption for vision upwards in the water column, where down-welling light is a good light source. Considering this, one would not expect that *A. hemigymnus* would specifically select bioluminescent prey because they can see them better. This is supported by the fact that they have eaten about 80% non-bioluminescent prey, but not by the selectivity results. *A. hemigymnus* have a stronger selectivity for both potentially bioluminescent and bioluminescent prey than for non-bioluminescent prey. In contrast, the species it has the strongest selectivity for is the copepod *A. armatus*, which is non-bioluminescent and rare in the water column, which can skew the selectivity. All species except *C. finmarchicus* (another non-bioluminescent species) are present in very small numbers in the diet (i.e., one or two individuals identified in the stomachs), which means these results have to be interpreted with caution. However, it does have the

highest positive selectivity for *C. finmarchicus* out of all the studied fish species, which is interesting to note.

On the other hand, lanternfish species showed a different pattern from the hatchetfishes. In particular, *P. arcticum* has the largest eyes of the lanternfish in this study and an aphakic gap that allows for even higher sensitivity to light. Because of its large eye, it could be expected to rely mainly on downwelling light for vision. However, the large amount of bioluminescent prey could indicate that it seeks out point-sources of bioluminescence when searching for prey.

B. glaciale has medium sized eyes and an aphakic gap, which allows for extra light sensitivity. Its daytime depth range is wide (200-800 m) (Sameoto, 1988), and it migrates a relatively short distance up to the upper epipelagic (Opdal *et al.*, 2008) compared to other species in this study. It has a relatively varied diet consisting of species from different taxa (Sameoto, 1988; Hudson *et al.*, 2014; Knutsen *et al.*, 2023). It has also been shown that *B. glaciale* mainly eats in the epipelagic, but occasionally feeds at other times of the day (Sameoto, 1988). As a vertical migrator, *B. glaciale* would be expected to have more generalised visual system, enabling them to visualise different light signals (de Busserolles *et al.*, 2020). Based on the fact that *B. glaciale* is a migrator (Dypvik, Røstad and Kaartvedt, 2012), the composition of its diet and the selectivity for prey of different bioluminescence categories, it seems that *B. glaciale* is adapted to vision with both down-welling light and bioluminescent light as their light source. It also seems possible that they specifically select bioluminescent prey.

N. kroyeri has small eyes but shares the adaptation of an aphakic gap with most of the species in this study (de Busserolles, Marshall and Collin, 2014). It has a wide and relatively deep daytime depth distribution and migrates relatively short distances to the bottom of the epipelagic (Opdal *et al.*, 2008; Keskin and Eryilmaz, 2010). One would expect that if small eyes is specifically linked to a selectivity for bioluminescence prey, this species would have a high selectivity towards bioluminescent prey. On the species/genus level of the prey, this is not the case. *N. kroyeri* appears to be selecting both bioluminescent and non-bioluminescent prey species. However, when looking at biodiversity as a trait, this does seem to be the case. So, *N. kroyeri* does perhaps select prey based on their bioluminescence to some degree. But, this selection is not stronger than the one of the larger eyed *P. arcticum* and *B. glaciale*. The bioluminescence of its prey is possibly a factor in its selection, but it does not seem to be the main driver.

L. macdonaldi has the smallest eyes out of the studied species but has an aphakic gap like all lanternfishes, which allows for a higher light sensitivity. It has a deep daytime distribution and only

migrates within the mesopelagic (Klimpel *et al.*, 2006). It therefore also is one of the species that inhabits one of the dimmest environments in this study. Out of the migrating species, it is the only one that stays within the mesopelagic also when migrating. This all points to their eyes being adapted to bioluminescence as their main light source rather than down-welling light. However, this does not have to mean that they selectively eat the plankton that are the sources of the bioluminescence. They could simply be using the point-source as their light source to seek out other prey. However, the fact that the selectivity for the trait bioluminescence shows *L. macdonaldi* a strong negative selectivity towards non-bioluminescent prey could indicate that they do to some degree select their prey based on bioluminescence.

A clear inverse proportionality of eye-size and selectivity towards bioluminescent could not be universally found for all species in this study. However, the hatchetfishes with the largest eyes do have higher selectivities for non-bioluminescent prey than the myctophids that all have comparatively smaller eyes, although they fall within varying categories (Table 8). This is especially true for *S. diaphana*, which has the largest eyes of all the studied species. It had not eaten any bioluminescent or potentially bioluminescent prey, and had a strong positive selectivity for non-bioluminescent prey. This species does however have extra adaptations to sight upwards in the water column, where down-welling light is the main light source (Wagner *et al.*, 1998; de Busserolles and Marshall, 2017). There was a variety in the selectivity for the different bioluminescence categories in the lanternfishes, and there was not a clear pattern of higher selectivity for bioluminescent prey in the species with small eyes than the ones with larger eyes.

Something that is worth noting here however is that the species with the relatively larger eyes (*P. arcticum* and *B. glaciale*) are also quite a bit smaller in body size than the ones with smaller eyes (*N. kroyeri* and *L. macdonaldi*). Most of the bioluminescent copepods in this study are relatively small compared to the non-bioluminescent prey consumed by these fish, with the exception of *E. magnus*, which the large *L. macdonaldi* had a strong positive selectivity for. The smallest of the lanternfish, *P. arcticum* was also the only one found to have eaten the smaller copepods *Oithona* sp. and *Oncaea* sp. Garcia-Seoane, Dalpadado and Vazquez (2013) found that in the diet of *B. glaciale*, the contribution of larger sized prey increased with increasing fish length. Hopkins and Baird (1985) found similar patterns for hatchetfishes. Extending this pattern to interspecies variation in sizes, one could assume that bigger species will eat bigger prey. It is possible therefore that bioluminescence does play a role in prey selectivity of mesopelagic fishes, but the size of the prey might be just as important. Another reason for this pattern could be that the species use vision differently. If the fish search for prey by scanning the environment a relatively larger eye compared to those of fish who use vision mainly for

pursuit or recognition tasks (Nilsson, Warrant and Johnsen, 2014). Not enough is known about all the features of the eyes and exactly how all these species use vision in their search for prey to draw conclusions on this, but it could be an interesting topic for further studies. The selectivity of bioluminescent prey cannot be tied directly to eye-size in the lanternfishes in this study, but the contrast between these and the larger eyed hatchetfishes, especially *S. diaphana*, indicate that the family in general has a selectivity towards bioluminescent prey. The hatchetfish *A. hemigymnus* also seem to select bioluminescent prey, while *S. diaphana* does not.

Limitations in the methods

Stomach content analysis is a commonly used method to analyse the diet of fishes, but there are some limitations to it. There is a wide variety of plankton groups available for the fishes to eat, but because of the difference in their biology, they have different digestion times in the stomach. For example, a gelatinous jellyfish will be digested a lot faster than crustaceans with a hard exoskeleton (Clarke *et al.*, 2020). Jellyfish are seldom found in stomach analysis, but because of this the absence of jellyfish in the stomach content analysis does not necessarily mean that the fishes have not eaten any jellyfish. DNA-analyses of fish diets have found that myctophids in the mesopelagic do indeed eat jellyfish (Clarke *et al.*, 2020). However, they are not present in the stomach content analysis because they are already digested. This is further evidenced by the presence of chaetognath hooks in the stomachs: The fishes clearly eat them, but because of their soft bodies, only their hooks remain in the stomach. Stomach content analysis does however provide information that cannot be derived from DNA-analyses, like more precise prey weight, abundance and size rather than approximations or only frequency of occurrence (Clarke *et al.*, 2020). Selectivity analyses like the one performed here have the weakness that they are vulnerable to rare plankton in the water column possibly having skewed selectivities (Strauss, 1979).

Ideas for future research

The visual capabilities of a species cannot be determined solely by its eye-size, as there are other adaptations to vision in the deep sea. It is therefore hard to know if small-eyed fishes are as limited in their sight as is often assumed, or if their other adaptations compensate for the small eyes. Very few studies have examined the visual systems of lanternfishes and hatchetfishes in detail. This is needed to fully understand how the size of the eye and other adaptations is linked to ecological factors like feeding preference, depth distribution and migratory behaviour. In the case of selectivity towards bioluminescence because it might make a prey easier to spot, more research is needed on how mesopelagic fish react to bioluminescent flashes: Do they immediately seek out the source of the

flash as a potential prey, or do the flashes function more as a light source in which they can spot other prey?

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