

A comparison of the spatial ecology, trophic ecology, and hypoxia tolerance of Velvet belly lanternshark (*Etmopterus spinax*) and Blackmouth catshark (*Galeus melastomus*) in Norwegian fjords.



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Abstract

Climate change and ocean warming are major drivers of deoxygenation in the ocean, and the effects of oxygen loss are more pronounced in fjords due to the basic fjord topography. Velvet belly lanternshark (*Etmopterus spinax*) and Blackmouth catshark (*Galeus melastomus*) are common sharks in western Norwegian fjords, and though the ecology of these sharks has been more extensively studied elsewhere, studies from Norwegian fjords and in oxygen poor environments are lacking. This study uses survey data in combination with stomach content analysis and stable isotopes to explore and compare the spatial and trophic ecology, energetic physiology, and hypoxia tolerance of the two sharks. Abundance data include samples from 2020-2021 from Fensfjord and 2011-2021 from Masfjord where an extensive basin water oxygen loss occurred. While *E. spinax* presented a broad vertical distribution that extend from the seafloor and into the pelagic zone, *G. melastomus* was found to live and feed along the bottom. A clear difference was found in the species' diet, which was further demonstrated by their stable isotope signatures that presented *G. melastomus* to feed at one trophic level higher than *E. spinax*. Stomach content revealed a benthic associated diet of *G. melastomus* and a more pelagic diet of *E. spinax*. Furthermore, results show that *E. spinax* had a more efficient energy storage with a hepatosomatic index (HSI) of 20% and a water content of only 8%. In comparison, *G. melastomus* had an average HSI of 5% and a water content of ~30%. Most surprisingly our dataset revealed no clear effects of low oxygen levels on the ecology of either shark species. Our results increase the knowledge on these species and fill knowledge gaps on their ecology and hypoxia tolerance, especially in Norwegian fjords where information previously has been lacking. Increased knowledge on these species in hypoxic conditions is essential for future management purposes as the effects of climate change further accelerate.

1 Introduction

Human-induced climate change is a rising concern worldwide, and one major consequence is the deoxygenation of the world's ocean (Aksnes et al. 2017;Breitburg et al. 2018;Laffoley and Baxter 2019;Pitcher et al. 2021). Ocean warming and changes in circulation patterns due to warming are the largest drivers of deoxygenation in the ocean. According to Laffoley and Baxter (2019) this can be explained directly by the decrease in solubility of oxygen in water with increasing temperatures. Indirectly ocean warming can drive deoxygenation due to changes in circulation patterns, water mixing, and respiration (Oschlies et al. 2018). An expansion of oxygen-depleted areas has been detected in the open ocean as well as coastal regions (Pitcher et al. 2021), and marine species are affected by this (Laffoley and Baxter 2019). Deoxygenation appears to be more pronounced in coastal habitats compared to the open ocean (Pitcher et al. 2021). However, the effect of oxygen on these ecosystems and the species-specific consequences of oxygen loss are poorly known. This study focuses on the distribution and trophic interactions of two deep-water sharks from western Norwegian fjords and aims to compare their ecology and hypoxia tolerance.

In fjords, climate-driven deoxygenation may be further exacerbated by eutrophication which occurs due to runoffs from human waste and excess nutrients from aquaculture farms. Eutrophication can deplete oxygen in the deepest parts of the fjord due to increased bacterial metabolism (Breitburg et al. 2018;Laffoley and Baxter 2019). Norwegian fjords are characterized by three recognizable water layers (Stigebrandt 2012). A brackish layer on top is formed by water from outside the fjord coming into the fjord and mixing with less saline surface water. Below is an intermediate layer extending down to the depth of the sill, which is an elevation of the seafloor in the fjord entrance. The sill restricts water exchange and renewal of the basin water that covers the area below the sill (Stigebrandt 2012;Aksnes et al. 2019). Mixing only occurs once the surface water outside the fjord is heavier than the fjord basin water making mixing events rare (Aksnes et al. 2019;Darelius 2020), which further drives oxygen loss in the deep water. The basic fjord topography (i.e., deep basins separated by shallower sills) makes fjords especially vulnerable to climate-driven oxygen loss due to reductions in basin water renewal frequency with ocean warming (Darelius 2020).

Our study focuses on two fjords, Masfjord and Fensfjord, which have experienced contrasting oxygen regimes in recent years. While Masfjord experienced a period of rapid deoxygenation

between 2011-2018 and the basin water was hypoxic in 2017-2018, Fensfjord was well oxygenated during this period. Since the fjords are spatially very close and both host the two deep-water shark species, investigating the ecology of the sharks in these two fjords can provide information about their ecology and hypoxia tolerance. A reoxygenation event occurred in Masfjord during late spring of 2021, and oxygen levels were considerably lower in February than September of the same year. Fensfjord remained well oxygenated throughout this period, allowing the investigation of whether potential changes in the species' ecology could be related to seasonality or ambient oxygen levels. Observable changes in the species' distribution, diet, or abundance between February and September in Fensfjord would be related to seasonal changes. On the other hand, if there are changes in any of these aspects in Masfjord it may be related to changes in oxygen levels.

Hypoxia influences the biodiversity in marine ecosystems (Laffoley and Baxter 2019), and especially mesopelagic and benthic species are affected since they are associated with deep water where oxygen loss is more pronounced (Breitburg et al. 2018). The diversity and density of demersal fish communities are reduced under low oxygen conditions (Gallo et al. 2020), and an expansion of oxygen-depleted areas is thus expected to reduce biodiversity. Oxygen loss in certain areas may cause mobile organisms to migrate to more oxygenated water, causing habitat compression and thus reduced habitat volume (Gallo and Levin 2016; Pitcher et al. 2021). If oxygen loss and habitat compression causes diel vertically migrating organisms to visit deeper waters less frequently, it may reduce feeding opportunities for deep sea demersal organisms (Gallo 2018).

Using survey data and a combination of stomach content analysis (SCA), stable isotope analysis (SIA), and liver data, this study aims to examine and compare the distribution, diet, and energetic status of two sharks in western Norwegian fjords: Velvet belly lanternshark (*Etmopterus spinax*) and Blackmouth catshark (*Galeus melastomus*). Both species are marine sharks which are common in, but not limited to, Norwegian fjords. *E. spinax* is most commonly caught between 200-500 m depth and has a wide geographical distribution that extends across several climates, from the Eastern Atlantic to South Africa (Encyclopedia of Life Accessed 16. May 2022). *G. melastomus* is a demersal shark also common in Eastern Atlantic waters, and their distribution extends from the Faroe Islands to Senegal (Encyclopedia of Life Accessed 16. May 2022). According to Jac et al. (2021) the two species prefer different habitats, where *G. melastomus* prefers warmer, shallower waters, and *E. spinax* is attracted to deeper, colder

waters. Habitat segregation may lead to a different tolerance to anthropogenic activities (Jac et al. 2021) or hypoxia because they utilize different resources. According to the Encyclopedia of Life (<https://eol.org/>) *G. melastomus* has a higher hypoxia tolerance and have been found in habitats with oxygen levels as low as 1.8 ml l⁻¹, whereas *E. spinax* is rarely found at oxygen levels below 3.8 ml l⁻¹. Both sharks have a upper oxygen threshold of ~6 ml l⁻¹. Due to their late maturation, slow growth, and relatively low fecundity, *E. spinax* and *G. melastomus* may have more difficulties recovering from population declines than species with contrasting life history traits that mature early and have high fecundity (R-selected species) (e.g., Coelho and Erzini 2008;Dulvy et al. 2017;Delaval et al. 2022). Increasing knowledge about the distribution, diet, energetic status and hypoxia tolerance of chondrichthyans in Norwegian fjords is thus essential for predicting future ecological changes and for better conservation of the communities.

E. spinax, *G. melastomus*, and Spiny dogfish (*Squalus acanthias*) are frequently caught in Norwegian fjords. *E. spinax* and *G. melastomus* are the dominant catshark species in the fjord basins, while *S. acanthias* is present in lower numbers. Despite rare catches of *S. acanthias* in our dataset, they were included in the analysis when possible, to examine the spatial and trophic niche of this third catshark species. Even though all three species are similar in morphology, studies show that they hold a different ecological niche and coexist in many habitats (Fanelli et al. 2008;Bengil et al. 2018). Although previous studies have looked into the diet, trophic ecology, and distribution of *E. spinax* and *G. melastomus* in other regions (e.g., Carrasson et al. 1992;Valls et al. 2011;Anastasopoulou et al. 2013;Albo-Puigserver et al. 2015;D'Iglio et al. 2021), studies from Norwegian fjords are lacking and deserves more attention.

Previous studies from the Mediterranean and surrounding areas show that *E. spinax* and *G. melastomus* exploit different parts of the habitat, where *E. spinax* is attracted to colder waters and performs diel vertical migration (DVM) (Coelho and Erzini 2010;Jac et al. 2021), whereas *G. melastomus* prefers warmer waters and live along the seafloor (D'Iglio et al. 2021;Jac et al. 2021). Valls et al. (2011) however, concluded in their study on trophic interactions of common elasmobranchs in the Mediterranean that there is evidence of diet overlap and potential interspecific competition between *E. spinax* and *G. melastomus* in certain areas, which may explain the observed niche separation. Fanelli et al. (2008) and Bengil et al. (2018) also evidenced some dietary overlap between the two species. However, these studies were conducted in the Mediterranean and whether similar patterns hold in Norwegian fjords is

uncertain. Western Norwegian fjord and the Mediterranean are undoubtedly different ecosystems with distinct climates, and there are good reasons to believe that these two ecosystem types show different patterns regarding the ecology of *E. spinax* and *G. melastomus*.

E. spinax is a generalist, meaning that they feed on what is present and do not have strict requirements for habitat and prey. Euphausiids and decapods dominate their diet when young, while cephalopods and teleosts become a more significant part of their diet as size increases (Fanelli et al. 2008;Renwart and Mallefet 2013). This species is ovoviviparous, meaning that they birth live individuals. Producing eggs and carrying pups as they grow is costly, and females invests much energy into reproduction (Jac et al. 2021). Hickling (1963) concluded that the shark has a gestation period of under a year. Females tend to grow bigger than males, and sex- and/or length segregation has been observed in certain habitats where *E. spinax* and *G. melastomus* coexist (Fanelli et al. 2008;Coelho and Erzini 2010). The species also display a migratory behavior, using both benthic and pelagic habitats as foraging grounds (Coelho and Erzini 2010). In order to migrate vertically in the water column without increasing its susceptibility to predators, *E. spinax* camouflages its silhouette with bioluminescence by counterillumination (Claes et al. 2010). Counterillumination is a process where animals emit light ventrally to resemble the light coming from above and match the background (Claes et al. 2010). The emitted light has a wavelength like those found at 100-200 m depth (500 nm) and is stable around different intensities of ambient light. This suggests that *E. spinax* performs diel vertical migration in order to stay within a light comfort zone (Claes et al. 2010).

In contrast to *E. spinax*, *G. melastomus* is a demersal shark who lives and feed in the benthic habitat along the seabed. In the Mediterranean, *G. melastomus* shows a wide habitat range where it is present along the slopes but also in the deepest parts (D'Iglio et al. 2021). Their distribution in Norwegian fjords, however, is yet to be investigated. This species is oviparous, meaning that the females produce egg capsules that are laid and hatched outside the body (Porcu et al. 2020). Oviparous organisms generally have a shorter gestation period than ovoviviparous (Jac et al. 2021), and a tough egg capsule protects the embryo from predators and other threats outside the body. Even though not as costly as birthing live pups, producing big eggs is energetically demanding for females (Bet-Sayad 2008). Several studies on the foraging strategy of *G. melastomus* have contradicting results. While Fanelli et al. (2008) and Valls et al. (2011) describes the species as a specialist feeder which occupies a narrower niche, Anastasopoulou et al. (2013) and D'Iglio et al. (2021) concluded that the shark is a generalist at a population

level but holds a specialist niche at an individual level. As Fanelli et al. (2008) and Valls et al. (2011) conducted their studies in Western Mediterranean whereas Anastasopoulou et al. (2013) look at the species in the Ionian sea, it is possible that *G. melastomus* acts differently in various habitats. Whether *G. melastomus* acts as a specialist or generalist may depend on which other species are present or the availability of prey in the area, and its feeding ecology in Norwegian fjords may therefore differ from previous research. Teleost fishes have been identified as the most important prey type of *G. melastomus* in the Mediterranean, although crustaceans and mysids also contribute noticeably to their diet (Bengil et al. 2018).

Although several studies have investigated the spatial distribution of *E. spinax* and *G. melastomus*, and many compare their diet using a combination of stomach content analysis and stable isotopes, no such studies have been performed in western Norwegian fjords. Additionally, few studies aim to investigate these aspects in low oxygen environments. The objectives of this thesis were to (1) investigate the spatial and trophic ecology of *E. spinax* and *G. melastomus* in western Norwegian fjords using research survey data, stomach content analysis, and stable isotope analysis; (2) use liver data and hepatosomatic indices to explore and compare the energetic physiology of the two sharks; and (3) describe their sensitivity to changes in environmental oxygen conditions by examining how their distribution and trophic ecology changed during the deoxygenation period in Masfjord and in comparison to the nearby well-oxygenated Fensfjord.

2 Material and methods

2.1 Study area

Data used in this study were collected from several Western Norwegian fjords by research cruises supporting the HypOnFjordFish project and by BIO325 (Ocean Science) student field courses conducted at the Department of Biological Sciences (BIO) at the University of Bergen (UiB). Data material consists of annual trawl catches over 11-years from Masfjord from 2011-2021 and Fensfjord from 2020-2021 (Appendix A). Data were also collected from Førdefjord, Sørffjord, Lustrafjord, and Osterfjord, but except for two samples of *S. acanthias* from Sørffjord used in stable isotope analysis, these were excluded from further analysis due to low sample sizes (Appendix A).

Fensfjord (Figure 1) is located north of Bergen and is ~42 km long, with a maximum depth of the deep basin of 680 m. Masfjord (Figure 1) branches off Fensfjord over a 75 m shallow sill and has a maximum depth of 494 m (Aksnes et al. 1989), and the sill limits renewal of the deep basin water (Aksnes et al. 2019).

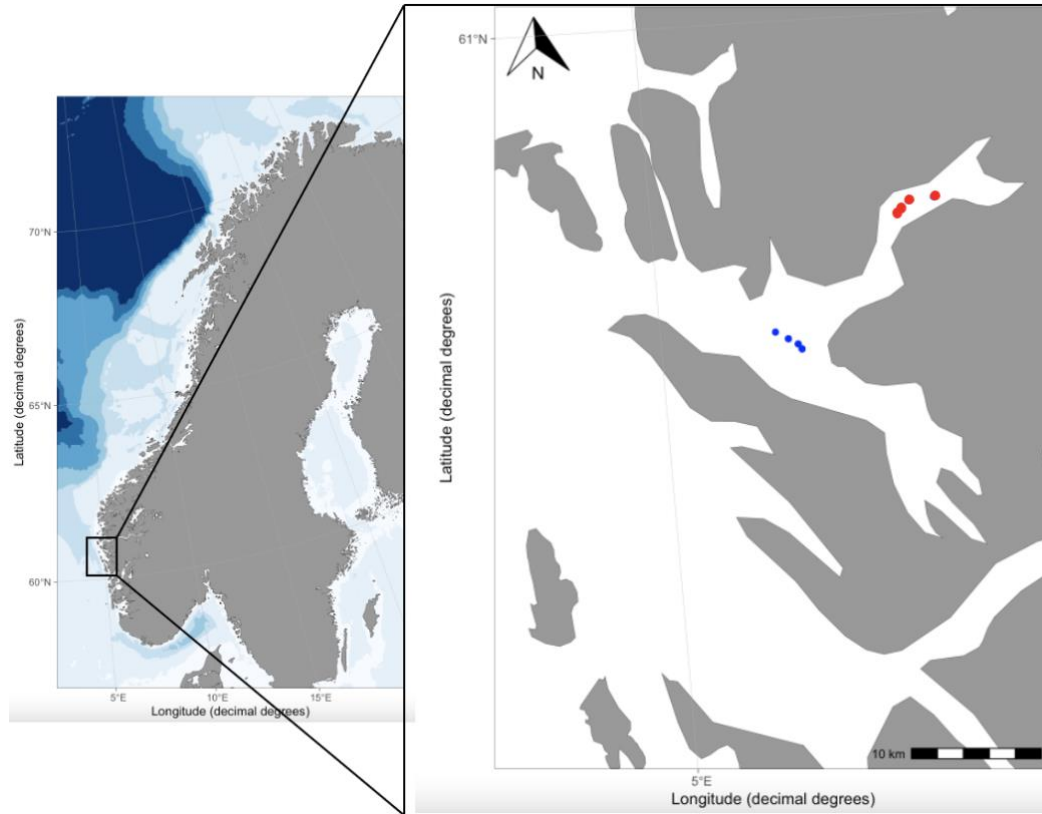


Figure 1: Location of the two fjords; Fensfjord (blue) and Masfjord (red) which are located along the western coast of Norway. Only a few sampling locations are showed on the map and additional sampling was performed in other locations in the fjords. The maps were made using RStudio with the package “ggOceanMaps” (Vihtakari 2022).

2.2 Sampling procedure

2.2.1 Environmental data collection

Environmental oxygen levels at different depths were measured using a CTD sensor equipped with an oximeter measuring oxygen concentration. The CTD provided information about the physical environment and measured conductivity, temperature, and depth from the surface to the seafloor at each station. CTD measures were taken in the deep basin of Masfjord every autumn between 2011-2021, which provided an important time series of oxygen trends in the fjord. CTD casts were conducted in close spatial and temporal proximity to all biological

samples to pair the environmental and biological data together. Typically, a CTD cast was conducted just prior to the net tow.

Oxygen was measured in both Fensfjord and Masfjord in February and September 2021. To examine if the vertical distribution of the two shark species is affected by differences in basin water oxygen conditions, we examined longline data from Masfjord, and Fensfjord collected before (February) and after (September) a rapid reoxygenation event in Masfjord. Fensfjord remained well oxygenated in both seasons, so any differences in the vertical distribution in Fensfjord would indicate a seasonal effect while differences in Masfjord would be related to changed oxygen conditions.

2.2.2 Sampling gear

Sampling was carried out using several gear types: pelagic trawls, bottom trawls, traps, and longlines. Bottom trawl and traps allowed sampling in the deepest parts closest to the seafloor, while pelagic trawls and longlines sampled throughout the water column. The Campelen 1800 bottom trawl with a cod-end of 22 mm mesh size was used in Masfjord only between 2011-2015 (Salvanes et al. 2018). Bottom trawls were used in the deep basin from 2011-2014, while in 2015 the bottom trawl sampled in the shallower basin (~350 m). The pelagic Harstad trawl was used with and without a Multisampler to sample in the pelagic zone. A Multisampler is a metal frame with three cod-ends of 20 mm mesh size that can be closed and opened remotely at chosen depth intervals, either at fixed depth intervals (300-200 m, 200-100 m, 100-0 m) or echo layers (acoustic scattering layers). Samples with a Multisampler were referred to as “T1”, “T2”, and “T3”, where T1 is the deepest cod-end, and T3 is the shallowest. Pelagic hauls without a Multisampler were referred to as “Periphylla hauls” or “Deep pelagic trawl”, and this gear sampled in the deep pelagic as close to the seafloor as possible without risk of damaging the trawl, approximately 50-150 m above the seabed. Pelagic trawls without Multisampler were open during the entire trawling period and therefore also sampled on the way up and down.

Traps and longlines are passive gears used to sample at the bottom and throughout the water column, respectively. Traps with a size of 95 x 60 x 70 cm containing bait were placed along the seabed. Two sets of traps, each set containing three individual traps, were placed at each location. The traps were baited and remained deployed for three days before retrieval. In February and September 2021, horizontal and vertical longlines were placed in Fensfjord and Masfjord. Horizontal longlines were placed along the bottom and were collected after only 4-7

hours due to hagfishes feeding on the bait. Vertical longlines had a length of 180 m with 2.3 m between each baited hook, enabling determination of capturing depth depending on hook number (1-75) since the sharks were labeled accordingly. All vertical longlines were equipped with a weight to avoid drifting and stayed out for 12 hours either during daytime or nighttime. Only data from vertical longlines were used in further analysis due to few samples from horizontal longlines.

2.2.3 Processing hauls

All individuals of *E. spinax* and *G. melastomus* caught were taken out of the total catch and measured, but due to time limitations onboard, only a restricted number of individuals were dissected. The remainder was frozen for later dissections. Total length (cm), weight (g), and sex were collected for all individuals of *E. spinax* and *G. melastomus*. The dissection procedure used for all individuals is explained in section 2.3: “Processing individuals”. To standardize catch across sampling types and trawls, Catch Per Unit Effort (CPUE) was used as a metric, and CPUE was measured as catch per hour (Salvanes et al. 2018).

2.3 Processing individuals

Frozen samples consisted primarily of individuals from 2021 February and September cruises. Total length (cm), total weight (g), liver weight (g), gonad weight (g), sex, and reproductive status were determined for each individual. Liver, stomach, and gonads were weighed using a fine laboratory scale (“BCE2202 – 1S”) with a precision of 0.01g, and livers and stomachs were put in individually labeled bags and frozen at -20 °C. Maturity stages were divided into four stages with distinct characteristics to use in further analysis (Table 1), and individuals lacking information about maturation stage were noted as NA. The gonads were used to determine maturation stage (Figure 2-3), after which they were discarded. Samples used for SIA were carefully selected to achieve a good representation of Fensfjord and Masfjord, sex, length, and reproductive status, and are shown in Appendix D; Table D. White tissue samples for SIA were extracted from the posterior side of the first dorsal fin, ensuring that the tissue was clean and not covered in blood (Valls et al. 2014; Carlisle et al. 2017). The tissue was frozen immediately at -20 °C after dissection until further analysis.

Table 1: Maturation stages identified for *E. spinax* and *G. melastomus* with the characteristics of each stage. Maturation stages of *E. spinax* follow Stehmann (2002), and maturation stages of *G. melastomus* follow Follesa and Carbonara (2019).

Maturation stage	<i>E. spinax</i> characteristics	<i>G. melastomus</i> characteristics
1	Immature. Gonads are small	Immature. Gonads are small
2	Maturing/developing. Gonads are starting to develop and getting bigger.	Maturing. Gonads are starting to develop. Claspers are relatively small in males.
3	Mature. Embryos are developing in females and gonads in males are growing.	Mature. Egg capsule is developing in the oviduct in females, and gonads are big in males. Claspers are big in males.
4	Developing pups/expecting (females only).	Egg capsule is laid (females only).
NA	No information was provided.	No information was provided.

Maturation stages of *E. spinax*

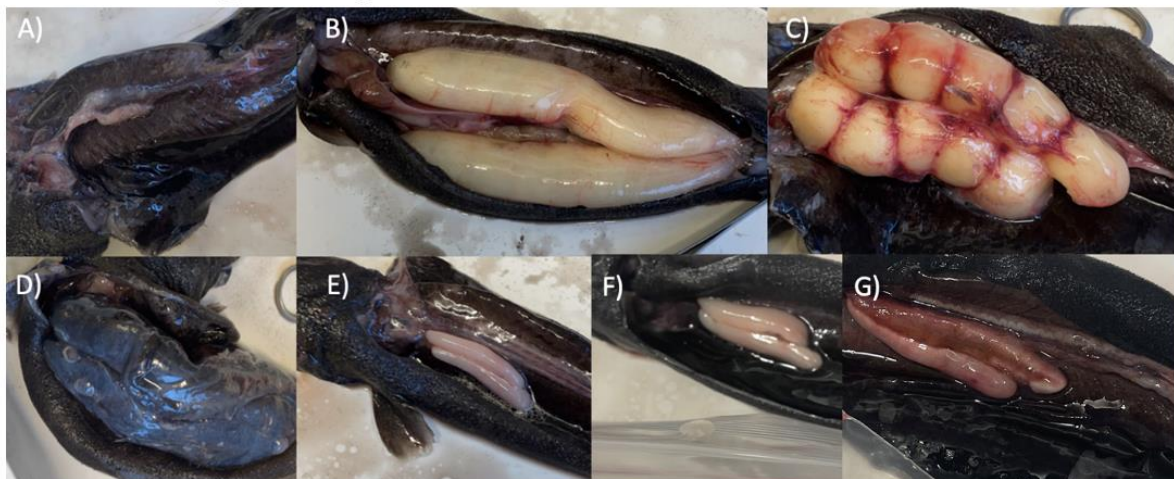


Figure 2: Maturation stages of *E. spinax*. A) immature female; B) maturing/developing female; C) mature female with developing embryos; D) mature female with pups; E) immature male; F) maturing male; and G) mature/active male.

Maturation stages of *G. melastomus*



Figure 3: Two maturation stages found in *G. melastomus*, as no immature individuals were documented; A) mature female; B) Developed egg capsule (from mature female); C) maturing male; and D) mature/active male

2.4 Stomach content analysis

Up to 30 individuals of both species from each fjord were dissected, but for *E. spinax* from Masfjord a larger sample number was available (N=75), and all were included in the analysis. In total, 132 individuals from Masfjord and Fensfjord were included in stomach content analysis (Appendix C). Empty stomachs were discharged after the fish-ID was noted to make sure that the data could be linked to other measures taken of the same individual. Stomachs with content were placed in Petri-dishes and left to thaw at room temperature. Thawed content was emptied into Petri-dishes and weighed before a squeeze bottle with water was used to rinse the insides of the stomach to completely empty it (Mulas et al. 2019). In accordance with Mulas et al. (2019), digestion level (0-3) of all stomachs containing prey was determined, where 0 represented empty stomachs, 1 represented non-digested, 2 represented partly digested, and 3 represented fully digested material (Table 2). Stomach repletion (0-1) was also estimated and referred to the degree of stomach fullness, where 0 referred to an empty stomach, and 1 referred to a full stomach (Table 3). Non-digested and/or identifiable (to either species or group) items were put on tissue paper to remove excess water and then weighed (g) and identified to the lowest possible taxonomic level. Material too digested to identify was weighed and categorized as “others”, although this was excluded in further analysis. For all stomachs examined, the

coloration was noted and used as an indicator of feeding pattern (Figure 4). Red coloration indicates a pelagic diet, mostly due to an increased contribution of mesopelagic crustaceans in a pelagic diet (Underwood et al. 2020). Brown coloration was an indication of feeding in the sediments. The coloration appears brown mostly due to an increased number of rocks, sediments, plant residues, and polychaetes in the stomachs (Figure 4). Manmade structures, plant residues, and non-organic material such as rocks and sand were noted but were excluded in further analysis. For content where coloration was indistinguishable, “none” was noted as the coloration.



Figure 4: *Stomachs contents with different coloration used to indicate feeding habitat. To the left is two examples of stomach content recognized as red, in the middle is brown and to the right is content identified as yellow.*

Table 2: *Assigned grading of digestion level (0-3) of the stomach content in SCA following Mulas et al. (2019).*

DIGESTION LEVEL	CHARACTERISTICS
0	Stomach is empty.
1	Digestion has started but it is still possible to identify to species.
2	Stomach content is partly digested. Eyes and other structures are visible but identification to species level is difficult.
3	Stomach content is fully digested, and identification is impossible.

Table 3: Assigned grading of stomach repletion (0-100%) of the stomach content in SCA following Mulas et al. (2019)

STOMACH REPLETION/FULLNESS	CHARACTERISTICS
0	Stomach is completely empty. No stomach fluid.
0.25	Very little stomach content. A mix of stomach fluid and small, often highly digested items.
0.50	Stomach is half-full. It is obvious that the stomach is not empty.
0.75	Stomach is full, but not stretched.
1	Stomach is completely full and stretched.

2.5 Stable isotope analysis

In total, 69 individuals were used in stable isotope analysis (Appendix D; Table D). Biological replicates of three individuals were performed for *E. spinax*, *G. melastomus*, and *S. acanthias* to estimate procedural error, and an average value of the triplicates was used in further analysis. Tin capsules were pre-weighed using a microscale (Sartorius-Micro-M3P) and put in a 96-well tray with a lid. Tissue samples were taken out from the freezer, four at a time, and put directly on ice. All samples were on ice for the entire preparation period to prevent tissue from thawing. A small piece (0.3-1.5 mg) of tissue was extracted and put in a petri dish. All tools in contact with tissue were cleaned in methanol between each sample to prevent cross contamination. Tools were dipped in methanol to remove excess tissue before being dipped in a separate container of methanol and air dried to ensure sterile tools. Both containers of methanol were replaced when dirty. Each tissue sample was soaked in 10 mL of deionized water (milli-Q) for five minutes, after which it was moved to a new petri dish and soaked again. The tissue was soaked three times in total to remove urea from the tissue (Carlisle et al. 2017). Urea is a waste product and is generally low in ^{15}N -values, and the presence of urea is therefore expected to lower the $\delta^{15}\text{N}$ value, providing biased results (Carlisle et al. 2017). Consequentially, urea had to be removed prior to analysis.

After rinsing, the tissue samples were put in the tin capsules and weighed using a microscale to obtain the wet weight of the tissue. Fish-ID was noted next to the respective well-ID. The tray was put in an oven at 60 °C for 48 h to dry (Valls et al. 2014; Espinoza et al. 2015). In the oven the lid was placed to cover all samples but still allow air flow. The lid was taped shut once

tissues were dry, and the tray was placed in a desiccator to cool to room temperature. The dry weight was calculated by subtracting the weight of the tin capsule from the total weight (after drying). We were targeting a dry weight of 0.2-0.4 mg. However, rinsing of the tissue made it challenging to predict dry mass based on wet mass since excess water made the wet masses highly variable. Final wet- and dry masses are listed in Appendix D; Table D. Due to variations in wet masses of the tissues, the samples were placed in two categories in the analysis; heavier and lighter samples, and these were run with different dilutions.

The tin capsules were then tightly folded into small cubes and sent to the FARLAB at the Department of Geosciences at UiB for analysis. Measurements of $\delta^{13}\text{C}$ and $\delta^{15}\text{N}$ were retrieved using a Thermo Scientific Flash 1112 Elemental Analyzer, connected to a Delta V+ Isotope Ratio Mass Spectrometer (IRMS). To calibrate N-measurements, IAEA-N1, IAEA-600, and IAEA-N2 were used as they are international standards. To calibrate C-measurements IAEA-CH6, USGS-24, and IAEA-600 were used. The analysis output was: $\delta^{13}\text{C}$ and $\delta^{15}\text{N}$ and the values are listed in Appendix D; Table D.

2.6 Liver analysis

To examine the energetic status of the individuals, the liver wet- and dry weight were collected for 256 individuals of *E. spinax* and *G. melastomus* (Appendix E; Table E). Liver wet weight was collected during dissections using a fine laboratory scale (BCE2202-1S) with a precision of 0.01 g. To obtain liver dry weight (g), the livers were placed in pre-weighed and labeled plastic containers and dried in an oven at 60-65 °C for 96 hours, or until dry. Livers were considered dry when there was less than 1% loss in mass in 24 hours. Liver dry weight was calculated by subtracting the weight of the plastic container from the total weight after drying. Hepatosomatic index (HSI) (Wootton et al. 1978) was calculated to provide an estimate of the energetic status of the individual.

$$\text{HSI} = \frac{W_{\text{liver}} (\text{g})}{W_{\text{total}} (\text{g})} * 100 \quad (1)$$

HSI was calculated as a percentage following Wootton et al. (1978) by dividing the wet weight of the liver (W_{liver}) by the total weight of the individual (W_{total}) and multiplying it by 100 (Equation 1).

The total proportion of water in the liver was calculated to examine differences in liver efficiency between the species.

$$\text{Water weight (g)} = \text{Liver wet mass (g)} - \text{liver dry mass (g)} \quad (2)$$

Water weight was calculated using Equation 2 by subtracting liver dry mass (g) from liver wet mass (g).

$$\text{Water proportion} = \frac{\text{Water weight (g)}}{\text{Liver wet mass (g)}} \quad (3)$$

The water weight (g) was then used in Equation 3 to calculate the proportion of water in the livers, and this was done by dividing the water weight (g) by the total mass of the liver (liver wet mass (g)).

2.7 Data analysis

2.7.1 Distribution

To standardize the abundance indices, Catch Per Unit Effort (CPUE) was calculated for each haul. This was done separately for *E. spinax* and *G. melastomus* in the various sampling methods. Since longlines and traps stay out for 12 hours and three days, respectively, CPUE could not be estimated for these gears.

$$CPUE = \frac{C_i}{t \text{ (min)}} * 60 \quad (4)$$

CPUE was calculated using sampling time in minutes (t) and total number of individuals caught in the respective haul (C_i) (Gremillet 1997). C_i was divided by the sampling time (min) and multiplied by 60 to get catch per hour (Equation 4).

2.7.2 Diet analysis

The contribution of each prey type to the diet of an individual shark can be calculated using the Prey-specific Index of Relative Importance (%PSIRI) following Brown et al. (2012). In this study, %PSIRI was calculated collectively for each species and each fjord and represents an average for all individuals in the respective population. To calculate the contribution of each

prey type to the average diet of the population, the frequency of occurrence (FO_i), percent prey number (%PN_i), and percent prey weight (%PW_i) were necessary.

$$\%FO_i = \frac{n_i}{n} \quad (5)$$

FO_i was calculated by dividing the number of stomachs containing prey type “i” (n_i) by the total number of stomachs examined (n) (Equation 5). Frequency of occurrence presents the proportion of sharks that have eaten at least one item of prey type “i” (Gaiotto et al. 2020).

$$\%PN_i = \frac{N_i}{N} \times 100 \quad (6)$$

The value N_i was obtained by counting the number of individuals of a prey category “i” within all the stomachs of the population (Equation 6). The percent prey number (%PN_i) was then calculated by taking N_i and dividing it by the total number of prey items of all prey categories found in the stomachs (N) and multiplying it with 100 (Brown et al. 2012;Gaiotto et al. 2020).

$$\%PW_i = \frac{W_i}{W} \times 100 \quad (7)$$

The prey percent weight (%PW_i) was calculated similarly as %PN_i, but the number of prey items was replaced with the weight of the prey items. Consequently, W_i refers to the weight of all prey items in a specific prey category “i”, and W refers to the total weight of the stomach content within the population (Equation 7). W_i (g) was divided by total weight (g), and this multiplied by 100 to get %PW_i (Brown et al. 2012;Gaiotto et al. 2020).

$$\%PSIRI = \frac{\%FO_i \times (\%PN_i + \%PW_i)}{2} \quad (8)$$

To get the relative importance of each prey category, as a percentage, Equations 5-7 were combined to form Equation 8. The output of this equation was the contribution of each prey category to the diet of a population and must be calculated individually for each prey category “i” (Equation 8).

2.7.3 Statistical analysis

All statistical analyses were performed using R statistical software version 1.4.1106 (R Development Core Team 2021), using the packages *tidyverse* (Wickham et al. 2019), *olsrr* (Hebbali 2020), *ggplot2* (Wickham 2016), *ggOceanMaps* (Vihtakari 2022), and *superheat* (Barter and Yu 2017). A p-value < 0.05 was considered significant in all analyses.

To compare differences in the vertical distribution of the species, mean distance from the seafloor was tested using a linear model. Distance from the bottom (m) was used as a continuous response variable, and species, fjord, and month was used as categorical predictor variables. The interaction term was removed from the final model if the interaction term was not statistically significant (p-value > 0.05).

To establish whether a sufficient sample size for stomach content analysis was met, a cumulative prey curve was plotted using Visual Studio Code version 1.62.3. According to Brown et al. (2012) sufficient sample size is reached when the slope of the regression line is < 0.05. However, due to smaller sample sizes this was not possible to calculate, and the graph was inspected visually. To compare the trophic ecology between and within species, two linear models with $\delta^{13}\text{C}$ and $\delta^{15}\text{N}$ as continuous response variables were tested separately. Forward selection was used to identify the most parsimonious model, and predictors found to be insignificant were removed from the model. Species, sex, and fjord were used as categorical predictor variables in both models.

A comparison of the energetic status was made by looking at both HSI and the water content of the livers. To test for differences in liver weight between species, a linear model with liver wet weight (g) as a continuous response variable was used. Forward selection was again used to identify the most parsimonious model, and predictors found to be insignificant were removed from the final model. Total weight (g), species, and fjord were used as continuous or categorical predictor variables. HSI (as a proportion) was tested using a generalized linear model to compare HSI between species and fjords. A generalized linear model was first performed with data solely from Masfjord to test for differences between species. Data from Fensfjord was removed due to missing samples of *G. melastomus* from Fensfjord in February. HSI was used as a continuous response variable, and species, month, sex, and length (cm) were used as predictor variables. HSI was also tested using a generalized linear model for *E. spinax* alone to

compare this species between fjords. HSI (as a proportion) was used as a response variable and fjord, month, and sex as categorical predictor variables. Maturation stage was removed as a predictor due to singularities (Appendix E; Figure E2). Quasibinomial distribution family was used in all generalized linear models.

Water content in the liver (as a proportion) was tested in the same manner as HSI, where the proportion of water in the liver was used as a continuous response variable. One test was performed with data from Masfjord alone to test for interspecific differences in water content. Species, sex, and month were used as categorical predictor variables in the final model. An additional test was performed using data of *E. spinax* only, where water content was used as a response variable, and fjord, month, sex, and length (cm) were used as predictor variables. Maturity stage was again removed due to singularities.

3 Results

3.1 Environmental data

A time series of oxygen measurements from Masfjord between 2011-2021 (Figure 5) show that in 2011-2014 the oxygen levels varied between 3-6 ml l⁻¹ throughout the water column, while in 2011-2018 a decline in oxygen levels was observed in the basin water. In 2021 a reoxygenation occurred and the oxygen level was 4 ml l⁻¹ at 400 m depth (Figure 5).

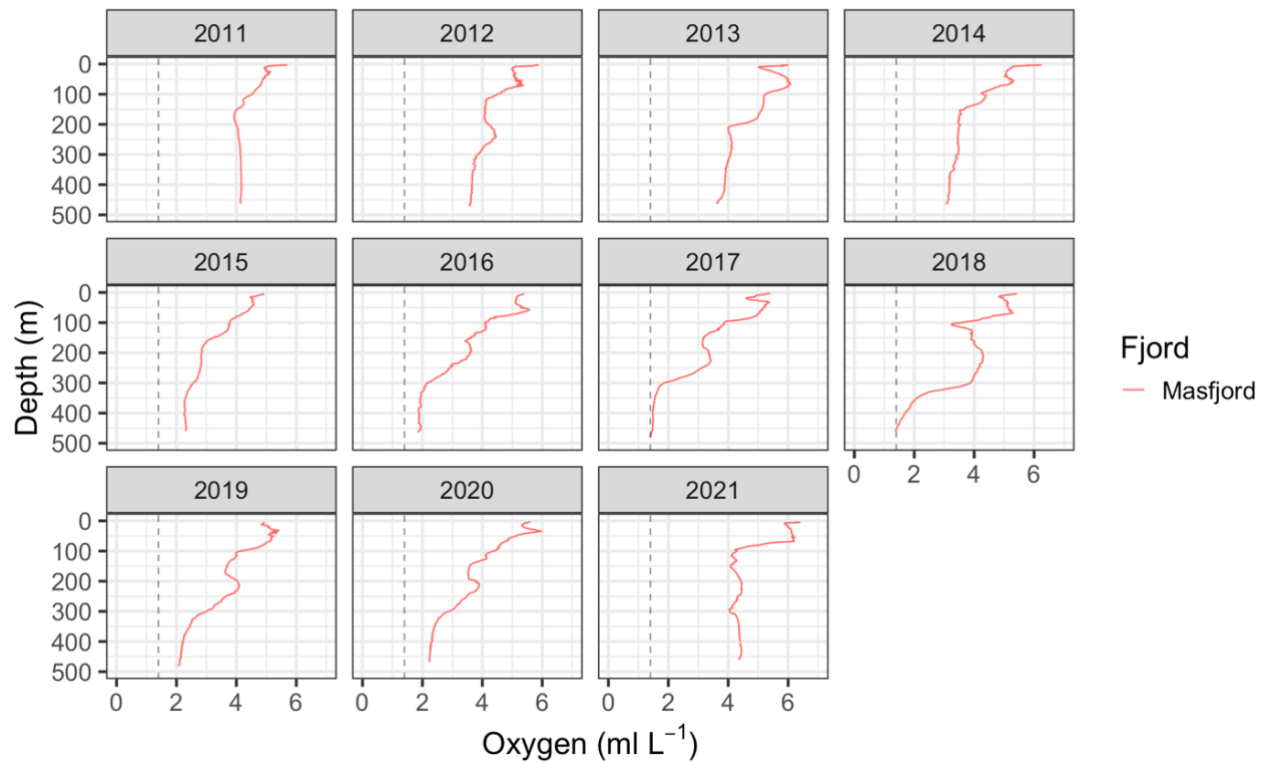


Figure 5: Depth profiles in Masfjord showing oxygen levels during autumn from 2011-2021. The dashed line represents the threshold of hypoxia in coastal systems (1.4 ml l^{-1}) defined by Hofmann et al. (2011).

In February, oxygen levels in Masfjord were close to the threshold of hypoxia described by Farrell and Richards (2009) in the deeper waters and varied between $2\text{-}3 \text{ ml l}^{-1}$ (Figure 6). In September however, the basin water had been renewed in Masfjord and the oxygen level had reached 4 ml l^{-1} . Fensfjord was well oxygenated from surface to seabed in both February and September of 2021 ($\sim 6 \text{ ml l}^{-1}$).

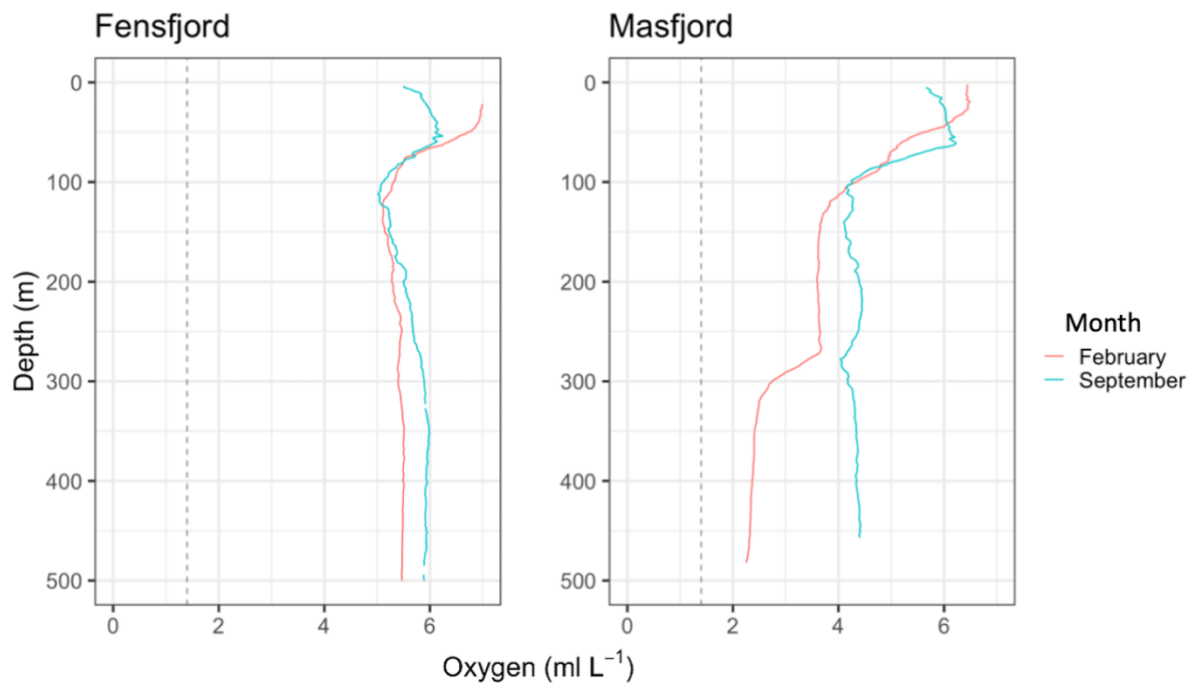


Figure 6: Depth profiles in Fensfjord and Masfjord showing oxygen levels (ml l^{-1}) in February (red) and September (blue) 2021.

3.2 Distribution

3.2.1 Catch per unit effort (per hour)

Bottom trawls were only conducted in Masfjord between 2011-2015 with a CPUE between 0-1000 individuals per species per hour. The catch per hour was similar between *E. spinax* and *G. melastomus*, however in 2012, 2013 and 2015 there was a slightly larger catch of *E. spinax* (Figure 7). Bottom trawls sampled in the deep basins from 2011-2014 while sampling in the deep basin in 2015.

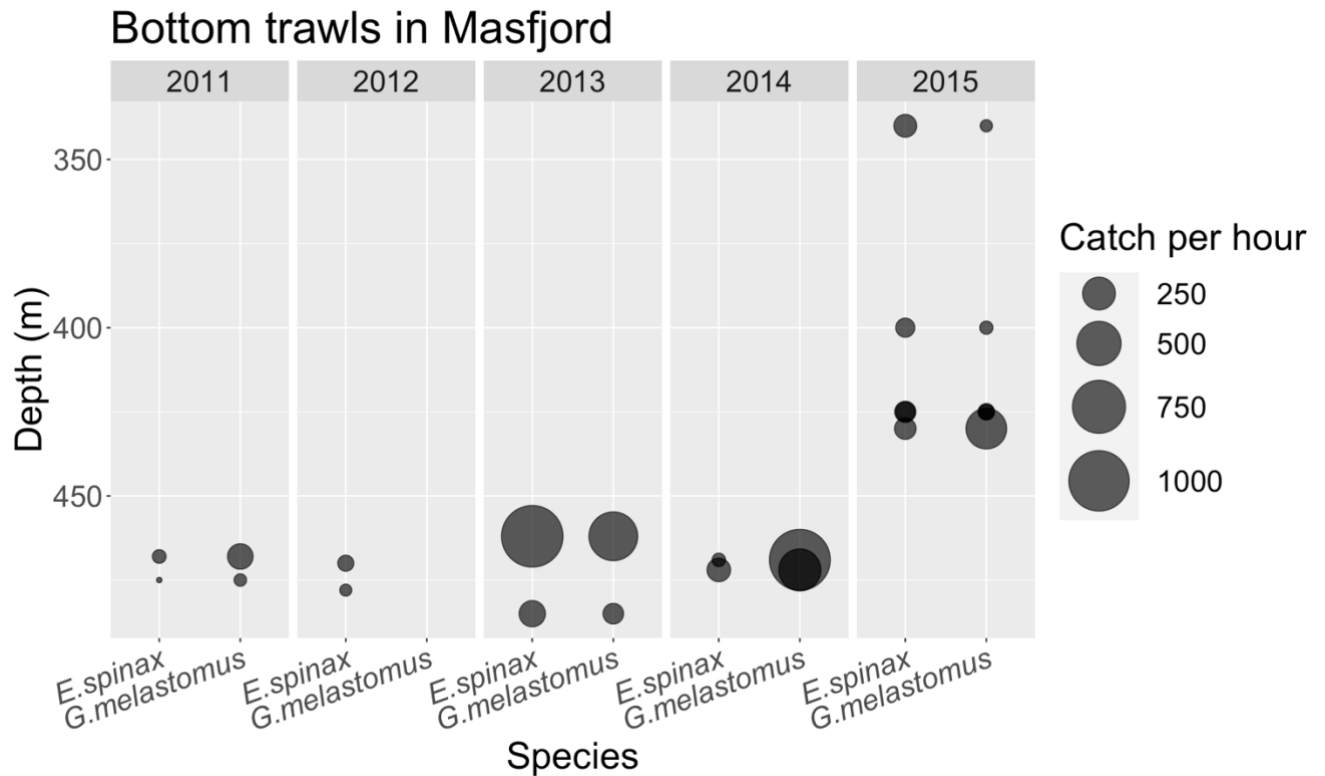


Figure 7: Calculated Catch Per Unit Effort (per hour) of *E. spinax* and *G. melastomus* from bottom trawls conducted in Masfjord between 2011-2015. Each bubble represents an individual trawl, and the size of the bubble reflects CPUE (catch per hour).

Pelagic trawls were conducted in Masfjord between 2014-2021 with a CPUE ranging between 0-60 individuals per hour for *E. spinax*, while catches of *G. melastomus* never exceeded ten individuals per hour (Figure 8). Pelagic trawls revealed a broader vertical distribution for *E. spinax* than *G. melastomus* in Masfjord. CPUE of *E. spinax* was higher than *G. melastomus* at nearly every haul from 2014-2021, although no individuals were caught in 2017. *G. melastomus* was never caught shallower than 300 m, while *E. spinax* was found at depths from 50-500 m, with the highest abundance between 200-300 m.

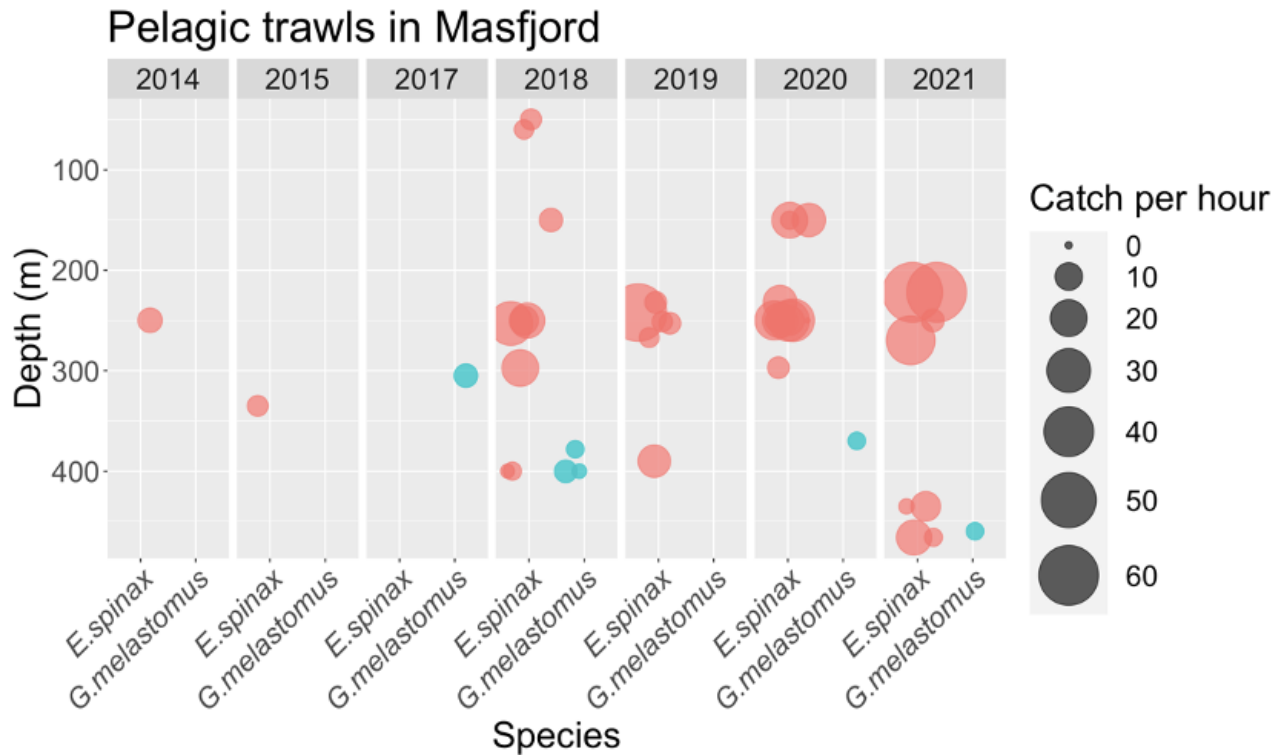


Figure 8: Estimated Catch Per Unit Effort (per hour) at different depths of *E. spinax* and *G. melastomus* from pelagic trawls in Masfjord between 2014-2021. Data consists of all pelagic trawls and includes Multisampler hauls (fixed depth intervals and follow echo layer) and deep pelagic hauls without Multisampler. Each bubble represents an individual haul, and the size of the bubble reflects the catch per hour.

Pelagic trawls were conducted in Fensfjord between 2020-2021 with a CPUE ranging between 0-20 individuals per hour for *E. spinax*. No individuals of *G. melastomus* were caught in pelagic trawls in these years (Figure 9). Pelagic data from Fensfjord reveals a wide vertical distribution of *E. spinax* where it was found between 100-450 m.

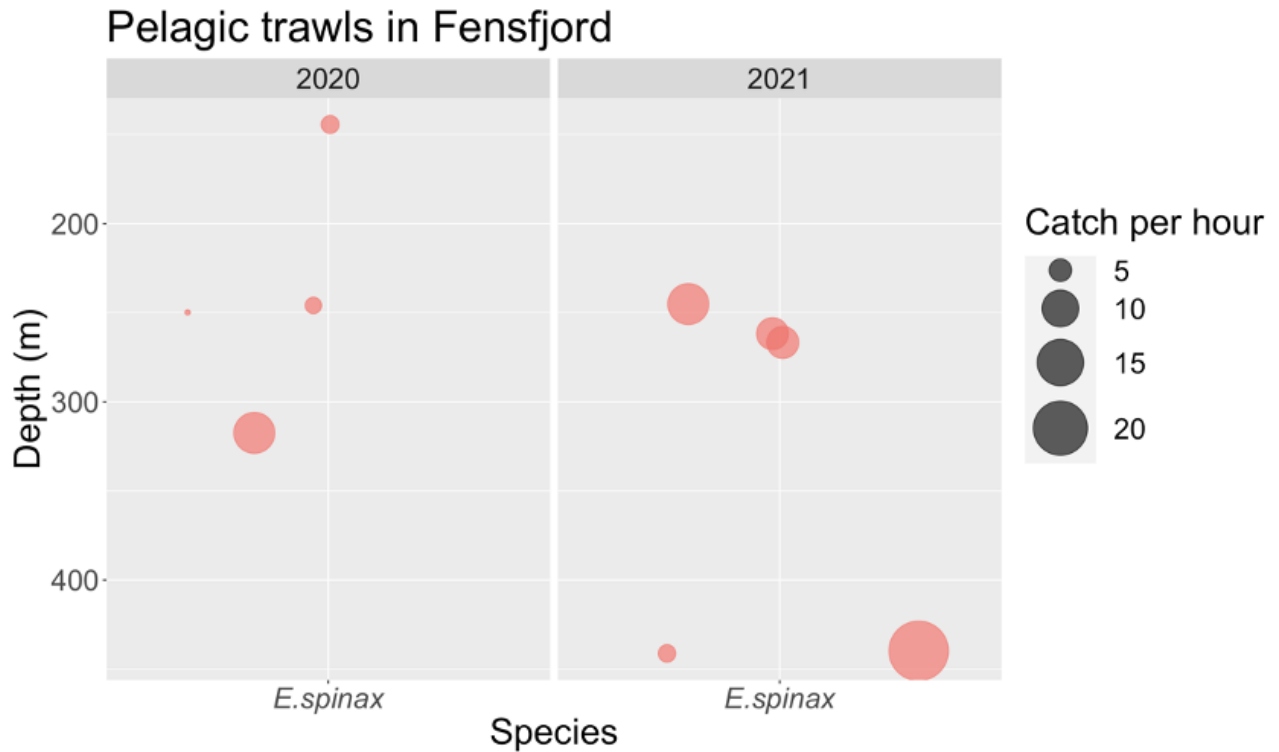


Figure 9: Estimated Catch Per Unit Effort (per hour) at different depths of *E. spinax* and *G. melastomus* from pelagic trawls in Fensfjord between 2020-2021. No individuals of *G. melastomus* were caught by pelagic trawls in Fensfjord in this period. Data consists of all pelagic trawls and includes Multisampler hauls (fixed depth intervals and follow echo layer) and deep pelagic hauls without Multisampler. Each bubble represents an individual haul, and the size of the bubble reflects the catch per hour.

3.2.2 Longline data

Species distribution from longlines presents similar results as pelagic trawl data: *E. spinax* has a broader vertical distribution than *G. melastomus* who shows a more restrained distribution limited to the bottommost 50 m (Figure 10). On average *G. melastomus* was caught deeper than *E. spinax* (lm; deviance = 49.83, $p \ll 0.05$; Figure 12; Model summary in Table 4). Both species had the same mean catch depth irrespective of month/season (lm; deviance = -0.95, $p = 0.45$; Figure 10). Additionally, no effects of oxygen conditions were observed in the distribution of either species, as both species had the same mean catch depth irrespective of fjord (lm; deviance = 2.65, $p = 0.75$; Figure 10).

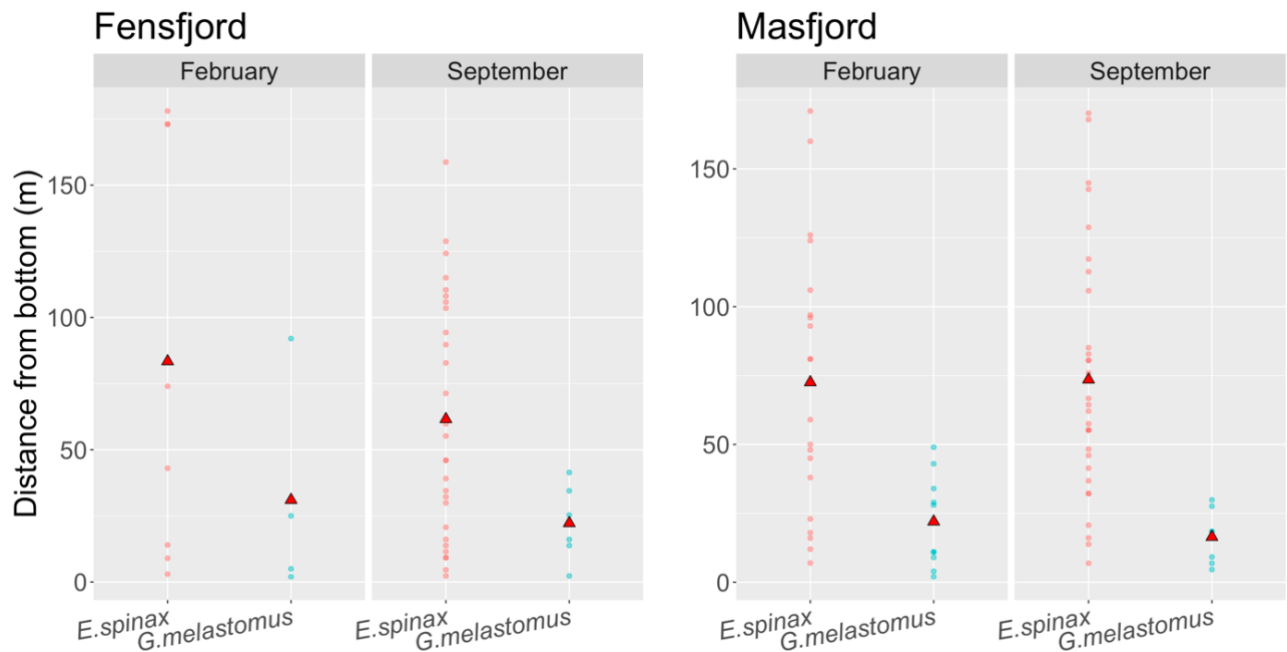


Figure 10: Vertical longline catch of *E. spinax* and *G. melastomus*, separated by fjord and month. Samples were collected in Fensfjord and Masfjord in February and September 2021. The red triangle represents mean distance from the bottom.

Table 4: Summary output of the best fitted linear model (*lm*) for distance from the bottom in vertical distribution (longline data). Species, fjord, and month were used as predictor variables.

Coefficients	Estimate	Std. Error	t-value	p-value
(Intercept)	75.2514	11.6983	6.433	3.35E-09***
speciesG.melastomus	-49.838	9.9138	-5.027	1.95E-06***
fjordMasfjord	2.6544	8.607	0.308	0.758
month	-0.9578	1.2689	-0.755	0.452

Signif.codes: 0 '***' 0.001 '**' 0.01 '*' 0.05 '.' 0.1 ' ' 1

R-sq (adj) = 0.1651

Longline data were merged due to no significant difference between season or fjord. The combined data demonstrate a clear difference in the vertical distribution of the two species. While *E. spinax* was caught in all depth intervals from 0-200 m above the seabed, the highest abundance was found at the deepest depth interval of 0-50 m above the seabed (Figure 11). *G. melastomus* was only caught in the deepest interval of 0-100 m above the seabed, and highest abundance was found in the deepest 50 m. Both species show a near-seafloor affinity although *E. spinax* comes further off the bottom than *G. melastomus*.

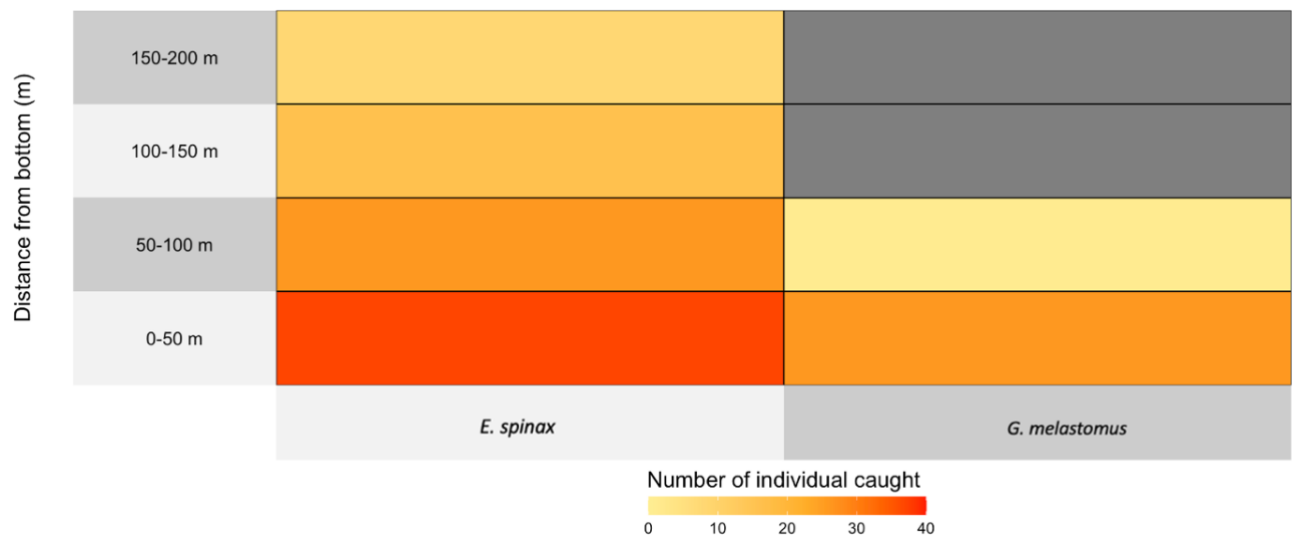


Figure 11: Total catch from vertical longlines from Fensfjord and Masfjord in February and September 2021, shown as total catch per 50 m depth interval measured as distance from the bottom. Different shades of yellow/red refer to the number of individuals caught in the respective depth interval, where red reflects the highest number. Grey areas reflect zero individuals were caught.

3.2.3 Length comparison

There was an observed interspecific difference in total length (cm) where *G. melastomus* were generally larger than *E. spinax*, but due to inconsistency in samples no further analysis were performed. Length distribution is shown in Appendix B; Figure B.

Bottom trawl data showed that only smaller individuals of both species inhabit the bottommost habitat (Figure 12). Larger individuals (>30 cm) emerged from the bottom and were caught by longlines and pelagic trawls. *G. melastomus* was not caught shallower than 250 m, and while *E. spinax* was caught at multiple depths ranging from 50-500 m, most individuals were caught between 200-500 m (Figure 12).

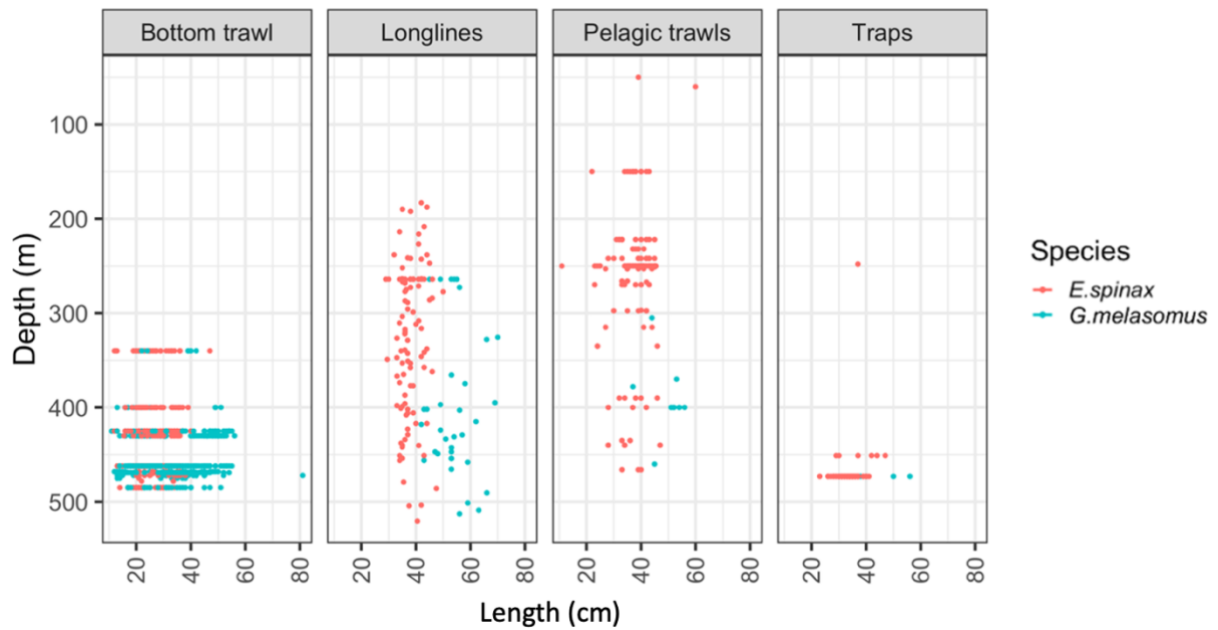


Figure 12: Length (cm) of *E. spinax* (red) and *G. melastomus* (blue) at different depths(m). Data consisted of research survey data from 2011-2021, separated by the different sampling gears.

3.3 Stomach content analysis

3.3.1 Sampling methods

Sharks analyzed for stomach contents were captured in 2020-2021 using pelagic trawls, traps, and vertical longlines. Since dietary results could be related to the method of capture, any notable differences in sampling are first presented. Samples of *E. spinax* came from all three sampling gears, while *G. melastomus* were mainly caught on the vertical longlines (Figure 13). In Fensfjord, no individuals of either species were caught using traps.

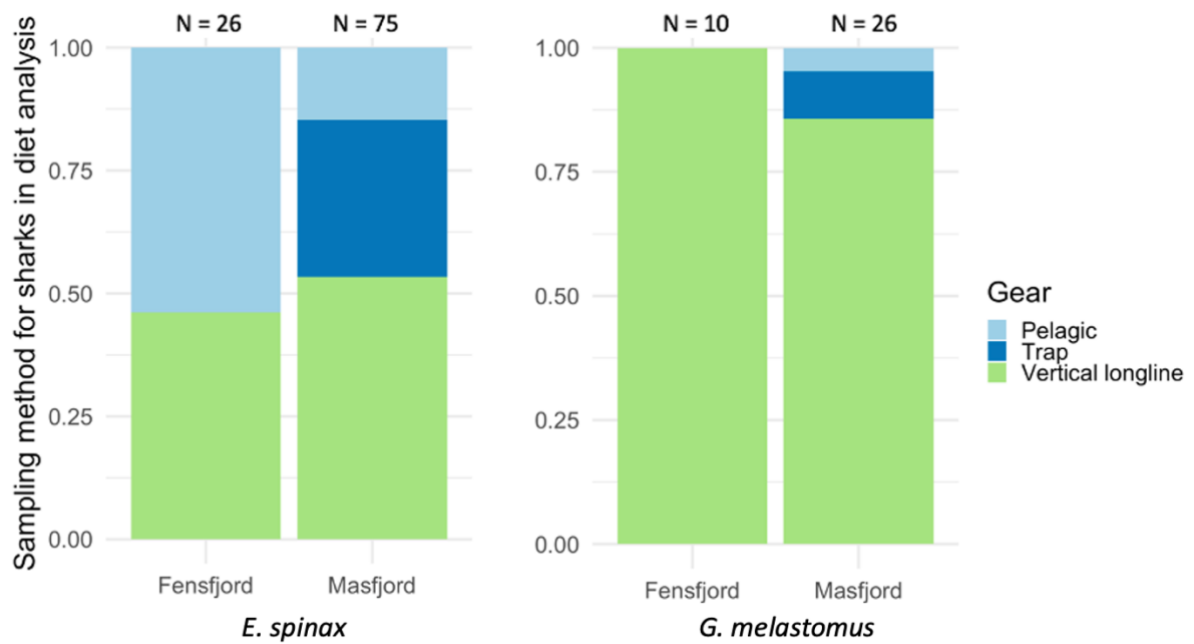


Figure 13: Sampling methods used to sample sharks used in diet analysis, where each sampling type is shown as a total proportion (0-1). “Pelagic” include all pelagic trawls performed with or without a Multisampler attached. Each bar represents all individuals of the species captured from the respective fjord. The sample number (N) is shown at the top of each bar.

3.3.2 Coloration of the stomach content

Both species had a higher number of empty stomachs in Masfjord. While the difference between fjords was not as pronounced for *G. melastomus*, *E. spinax* had over 50% empty stomachs in Masfjord while only having ~25% empty stomachs in Fensfjord (Figure 14). While red coloration contributed to over 50% of the coloration in *G. melastomus* in Fensfjord, brown coloration dominated in Masfjord. *G. melastomus* had a higher total contribution of brown coloration compared to *E. spinax*. Looking solely at stomachs containing prey, *E. spinax* was dominated by red coloration in both fjords.

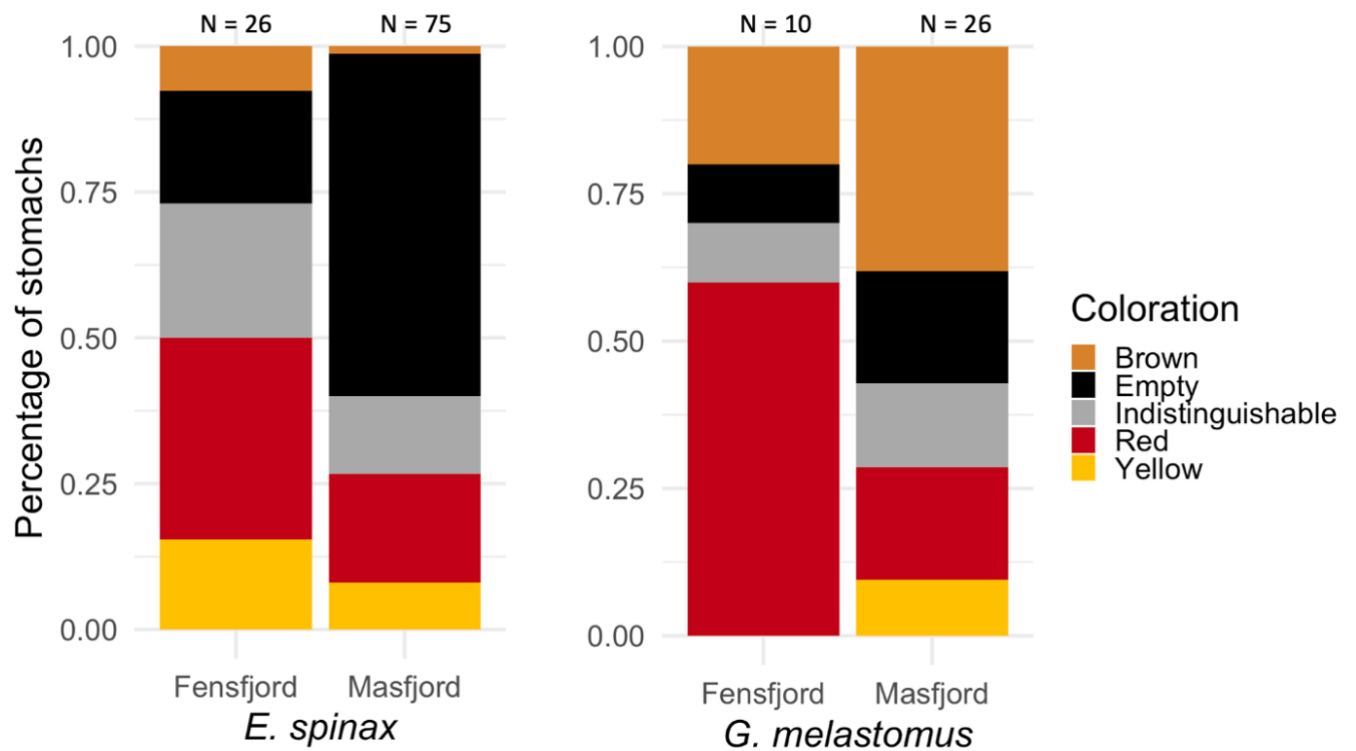


Figure 14: The proportion of different colorations (red, brown, yellow, and indistinguishable) as well as proportion of empty stomachs of *E. spinax* and *G. melastomus* in Fensfjord and Masfjord. The sample number (*N*) is written at the top of each bar and represents the number of stomachs analyzed for the respective population.

3.3.3 Cumulative prey curve

When comparing diet diversity between species, *G. melastomus* was found to consume almost twice as many prey types compared to *E. spinax* (Figure 15). While *G. melastomus* fed on 6 and 7 unique prey types in Fensfjord and Masfjord respectively, *E. spinax* fed on 3 and 6 unique prey in the same fjords. The cumulative prey curve shows a potential difference between fjord where both species seemed to have a more heterogenous diet in Fensfjord than in Masfjord, as indicated by the steeper rise in the cumulative prey curve in sharks captured in Fensfjord.

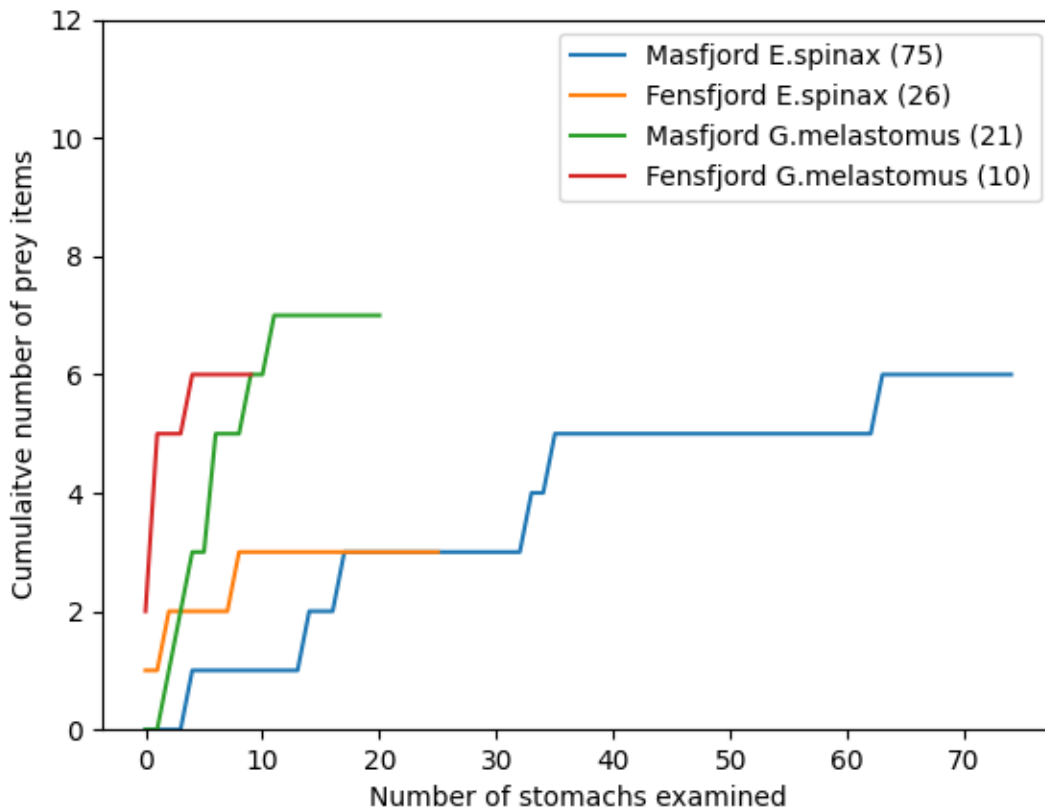


Figure 15: A cumulative prey curve showing the cumulative number of unique prey items in stomachs examined for; *E. spinax* in Masfjord (blue), *E. spinax* in Fensfjord (orange), *G. melastomus* in Masfjord (green) and *G. melastomus* in Fensfjord (red). The sample size for each group is shown in parentheses.

3.3.4 Prey-specific index of relative importance (PSIRI) curve

Stomach content analysis revealed clear differences in the diets of *E. spinax* and *G. melastomus* (Figure 16). Six unique prey items were found in the stomachs of *G. melastomus* in Fensfjord and eight in Masfjord. As for *E. spinax* four and seven unique prey items were found in the two fjords respectively. Bait was characterized as “indistinguishable” in Figure 14, and contributed considerably to the diet of *E. spinax*, especially in Masfjord where it accounted for ~75%. *Pasiphaea sp.*, *B. glaciale* and *M. muelleri* were limited to the diet of *E. spinax*, and besides those krill, *Sergestes sp.* and *Natantia* were also observed in the stomachs. *Natantia* is a collective designation of crustaceans that move by swimming and could not be identified to a lower taxonomic level. Some prey items limited to *G. melastomus* includes Mysida, Munididae, *D. bonnieri* and Reptantia. Reptantia represents crustaceans that walk on the seafloor and were not identified further. *G. melastomus* also had a fair contribution of *Natantia*, krill, *Sergestes sp.* and unidentified teleosts in their stomachs.

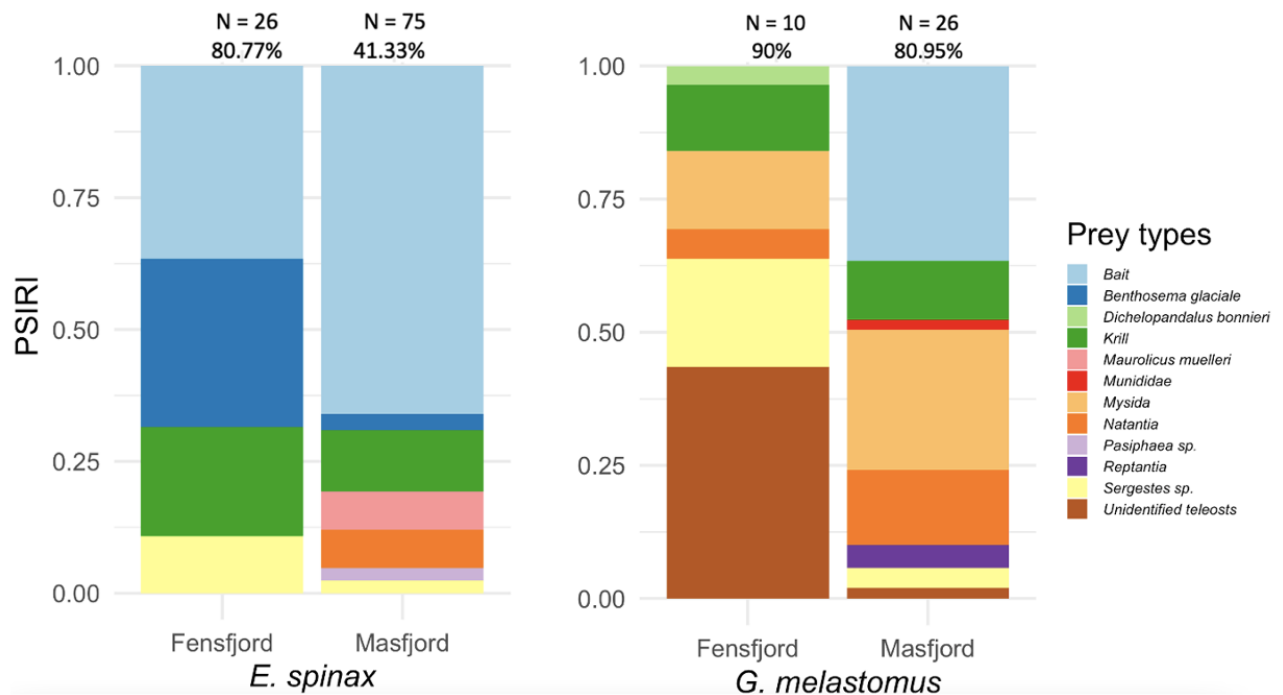


Figure 16: The contribution (as a proportion) of each prey type to the diet of *E. spinax* and *G. melastomus* in Fensfjord and Masfjord, shown as a mean for the total population. PSIRI was calculated using equation 8 (Brown et al. 2012). The sample number (N) of the respective population is written at the top of each bar, and the percentage of stomachs containing prey is written just underneath.

3.4 Stable isotope analysis

While stomach content provided a synoptic view, stable isotopes allowed us to observe differences in diet integrated over several months, and a clear difference in the trophic niches of the two sharks was identified. *G. melastomus* had a higher $\delta^{13}\text{C}$ -signature than *E. spinax* (lm; deviance = 1.54, $p \ll 0.05$; Figure 17-18; Model summary in Appendix F; Table F1). *G. melastomus* also had a $\delta^{15}\text{N}$ -signature on average 2-2.5 per mil higher than *E. spinax* (lm; deviance = 2.17, $p \ll 0.05$; Figure 17-18; Model summary in Appendix F; Table F2). The enriched $\delta^{13}\text{C}$ and $\delta^{15}\text{N}$ signatures of *G. melastomus* point to it having a more benthic-associated diet or feeding on a higher trophic level than *E. spinax*. Both species had lower signatures in Masfjord compared to Fensfjord. Though both species had a higher isotopic signature in Fensfjord compared to Masfjord, this was restricted to the $\delta^{15}\text{N}$ -signature. The stable isotope signatures of *G. melastomus* and *E. spinax* were also compared to a third shark species, *S. acanthias*. Samples of *S. acanthias* were constrained to two individuals and originated solely from Sørfjord. Based on these samples, *S. acanthias* feeds at the lowest trophic level or has the most pelagic diet of the three shark species, and our results showed a trophic

niche separation of *S. acanthias* from both *E. spinax* and *G. melastomus* (Figure 17). Exact values of $\delta^{15}\text{N}$ and $\delta^{13}\text{C}$ are shown in Appendix D; Table D.

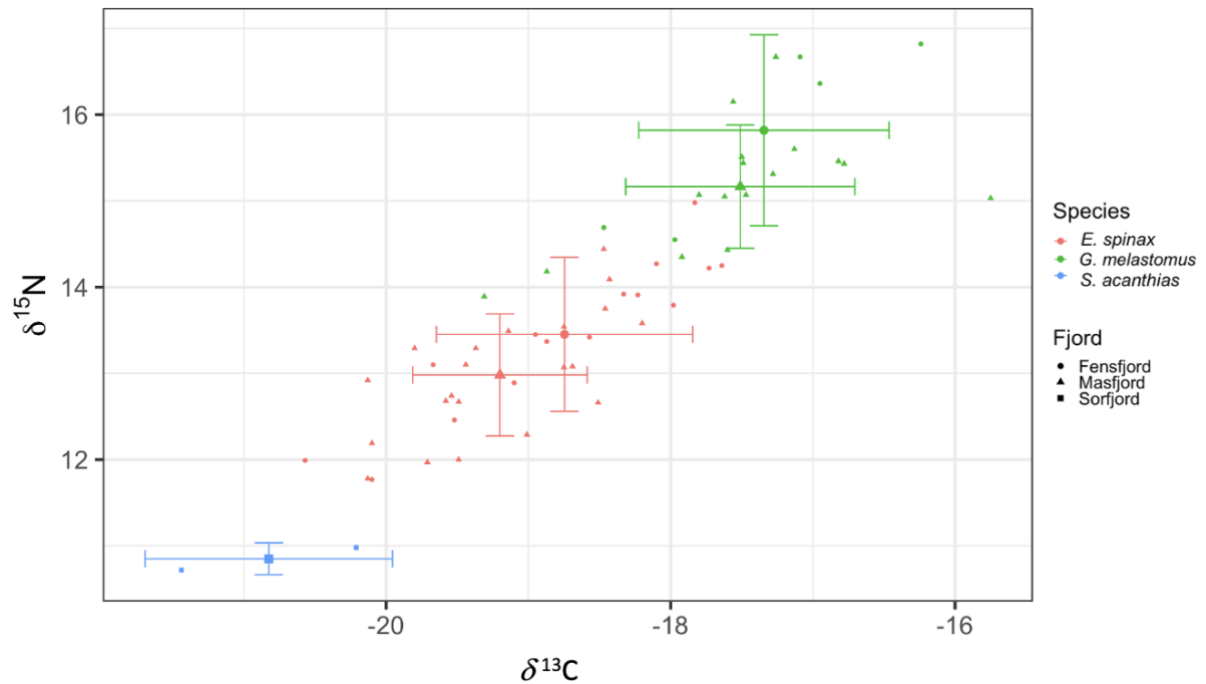


Figure 1: The isotope signature of $\delta^{15}\text{N}$ and $\delta^{13}\text{C}$ of *E. spinax* (red), *G. melastomus* (green), and *S. acanthias* (blue) separated by fjord, plotted as a stable isotope biplot of means \pm standard error.

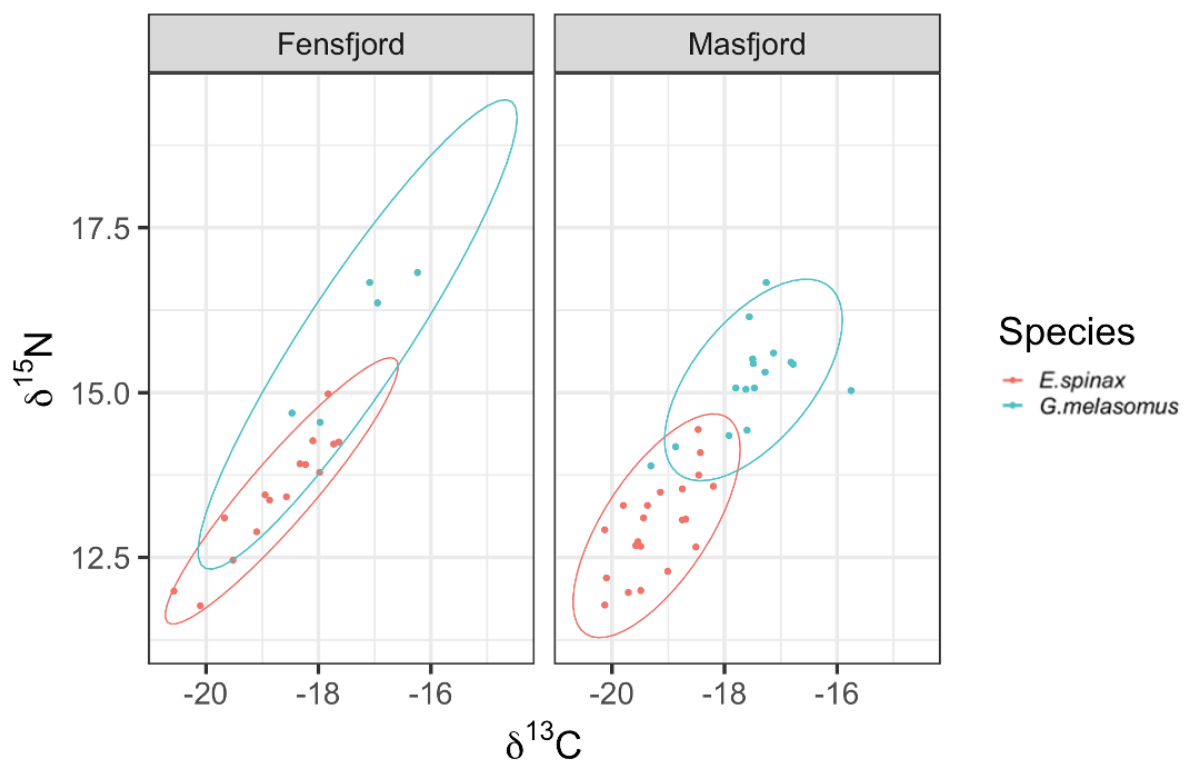


Figure 18: The isotope signature of $\delta^{15}\text{N}$ and $\delta^{13}\text{C}$ of *E. spinax* (red), *G. melastomus* (green) and *S. acanthias* (blue) plotted with 95% confidence interval ellipse, separated by fjord.

Since diet and food assimilation could be sensitive to different stages of maturity and reproductive status, we tested for differences in stable isotope signatures across sex and maturity stage for *E. spinax* and *G. melastomus* (Figure 19). There was no difference in *E. spinax* regarding maturation stage in either their $\delta^{13}\text{C}$ -signature (lm; deviance = 0.04, $p = 0.77$; Figure 19) or $\delta^{15}\text{N}$ -signature (lm; deviance = 0.139, $p = 0.42$; Figure 19). Sample size was not sufficient to compare maturation stage in *G. melastomus*, and only one ellipse (NA) was provided for this species (Figure 19). The diet did not change in response to seasonality or changes in oxygen conditions in either species, as no difference in isotopic signature was observed between months (lm; $p > 0.05$; Appendix D; Figure D2). A difference was observed between sex in the $\delta^{13}\text{C}$ -signature, and in both species males had a higher $\delta^{13}\text{C}$ -signature than females (lm; deviance = 0.41, $p = 0.04$; Appendix D; Figure D1; Model summary in Appendix F; Table F2).

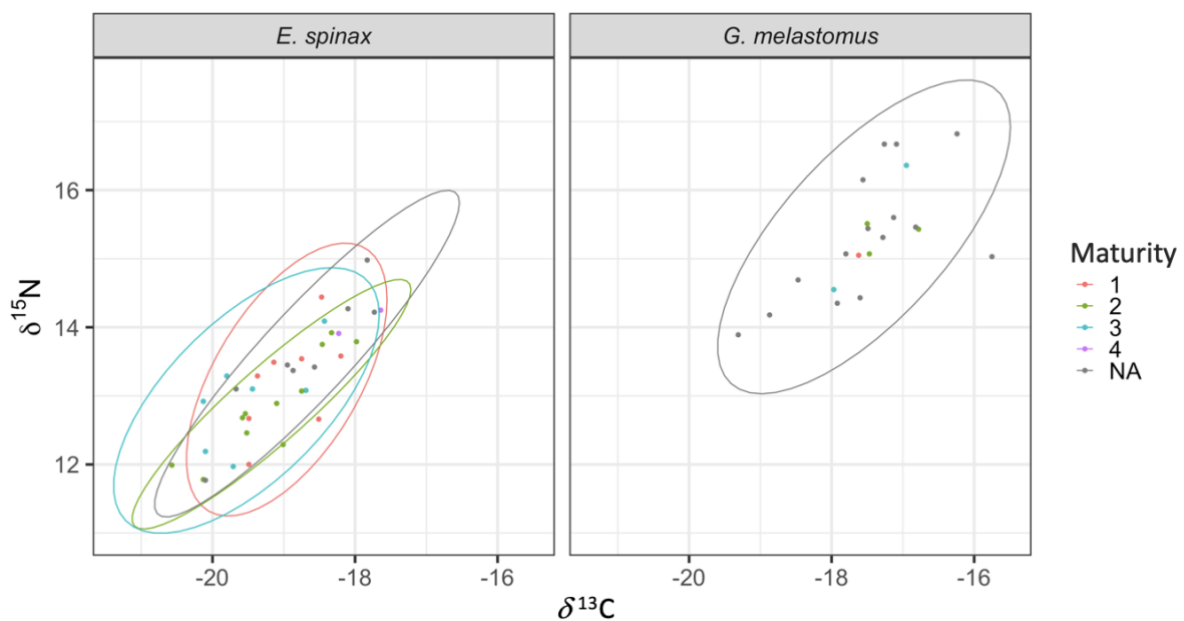


Figure 19: Isotope biplot showing the $\delta^{13}\text{C}$ and $\delta^{15}\text{N}$ values of *E. spinax* and *G. melastomus*, separated by maturity stage, and plotted with a 95% confidence interval ellipse. Only one ellipse is provided for *G. melastomus* due to insufficient sample size in maturity stages 1-4. Maturation stages (1-4 + NA) are described in Table 1.

3.5 Liver analysis

3.5.1 Liver size

G. melastomus both had a higher total body weight and a smaller liver size compared to *E. spinax* (lm; deviance = 4.60, $p \ll 0.05$; Figure 20; Model summary in Appendix F; Table F3). *E. spinax* had a larger liver on average, however this difference is more pronounced in the larger individuals (Figure 20).

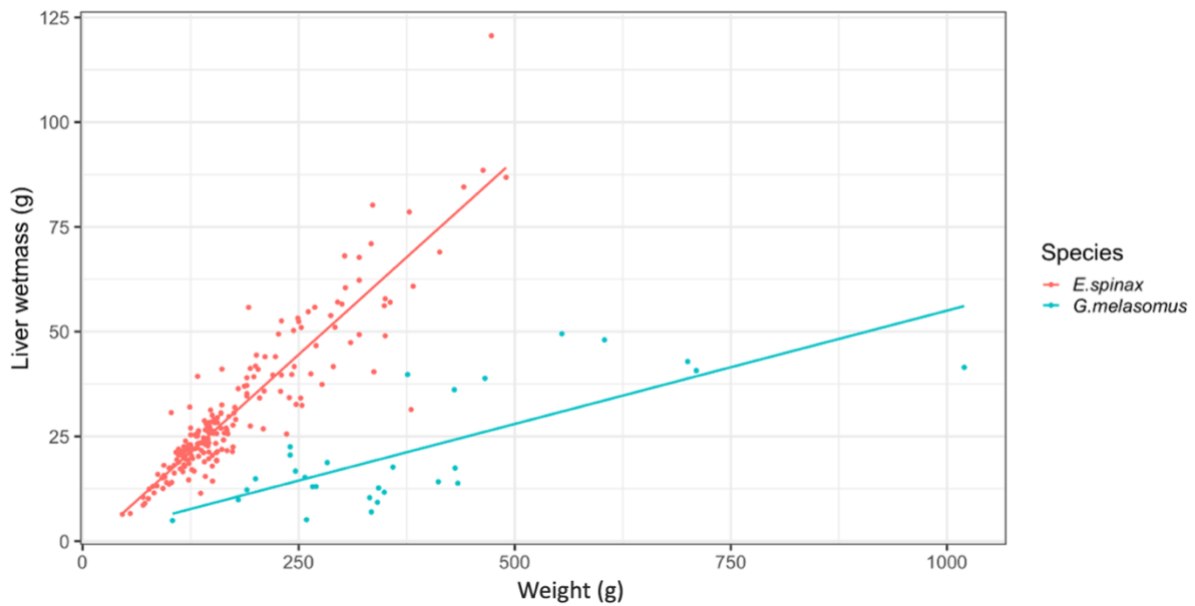


Figure 20: Liver wet mass (g) plotted against total weight (g) for *E. spinax* (red) and *G. melastomus* (blue). Data from both fjords are pooled together.

The livers of both species were typically smaller in Masfjord compared to Fensfjord (lm; deviance = -4.81, $p \ll 0.05$; Figure 21A; Model summary in Appendix F; Table F3), however individuals of *G. melastomus* were also bigger in Fensfjord. Additionally, no visible effect of sex was observed in either species (Figure 21B).

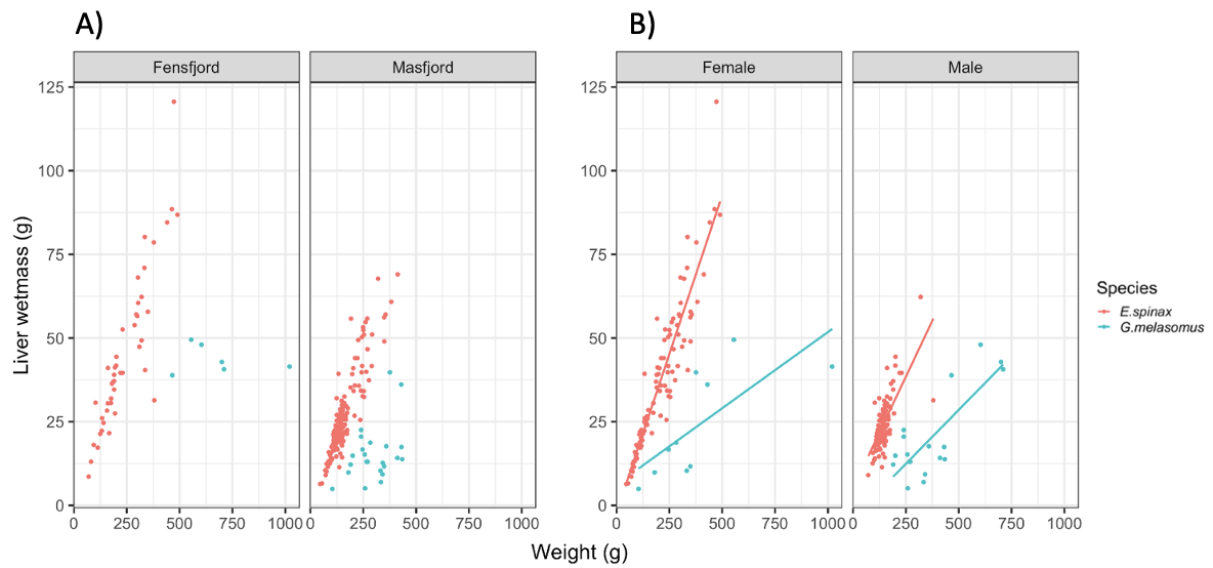


Figure 21: Liver wet mass (g) plotted against total weight (g) for *E. spinax* (red) and *G. melastomus* (blue) and separated by A) fjord and B) sex.

3.5.2 Hepatosomatic Index

The liver of *E. spinax* typically grew to ~20% of the total body mass, whereas *G. melastomus* had a liver that was ~5% of the total body mass (Figure 22). *G. melastomus* had a lower HSI than *E. spinax* in both seasons (glm; deviance = -1.19, $p \ll 0.05$; Figure 22; Model summary in Appendix F; Table F4).

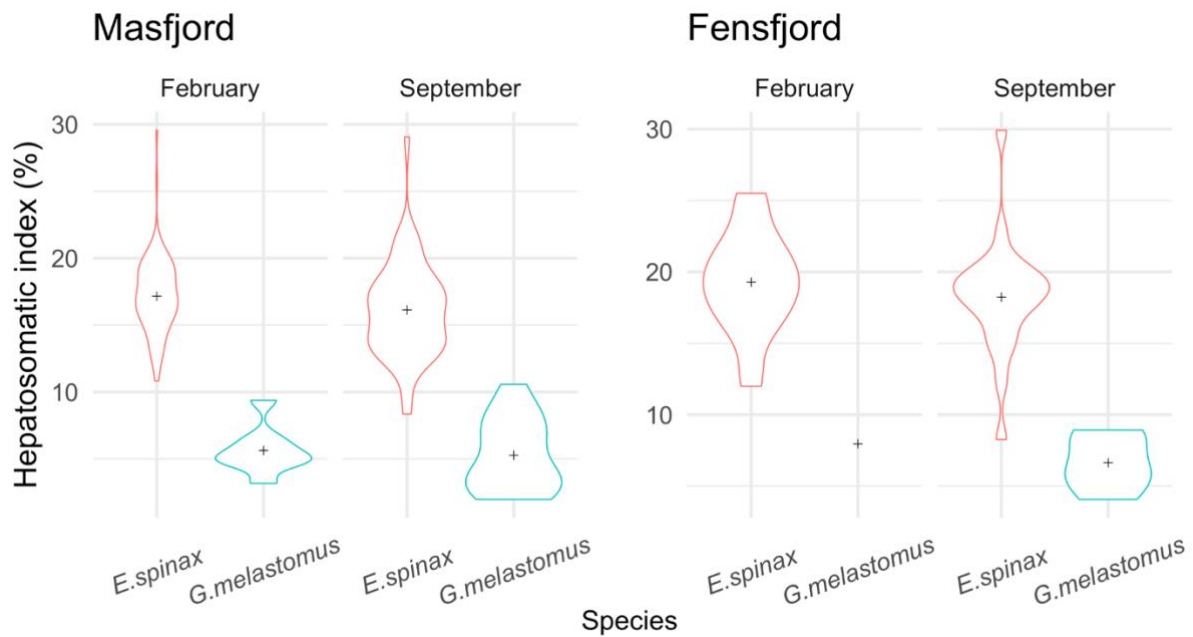


Figure 22: The hepatosomatic index (HSI) from equation 1 plotted for *E. spinax* (red) and *G. melastomus* (blue) and separated by month and fjord. The black symbol “+” shows the mean value.

The HSI of *E. spinax* was somewhat lower in Masfjord than Fensfjord (glm; deviance = -0.11, $p < 0.05$; Figure 23; Model summary in Table 5), and HSI slightly decreased from February to September (glm; deviance = -0.008, $p < 0.05$; Figure 23). Difference in HSI between fjord was not possible to investigate for *G. melastomus* due to low sample size There was no difference in HSI related to sex in *E. spinax* (glm; $p = 0.91$; Appendix E; Figure E1).

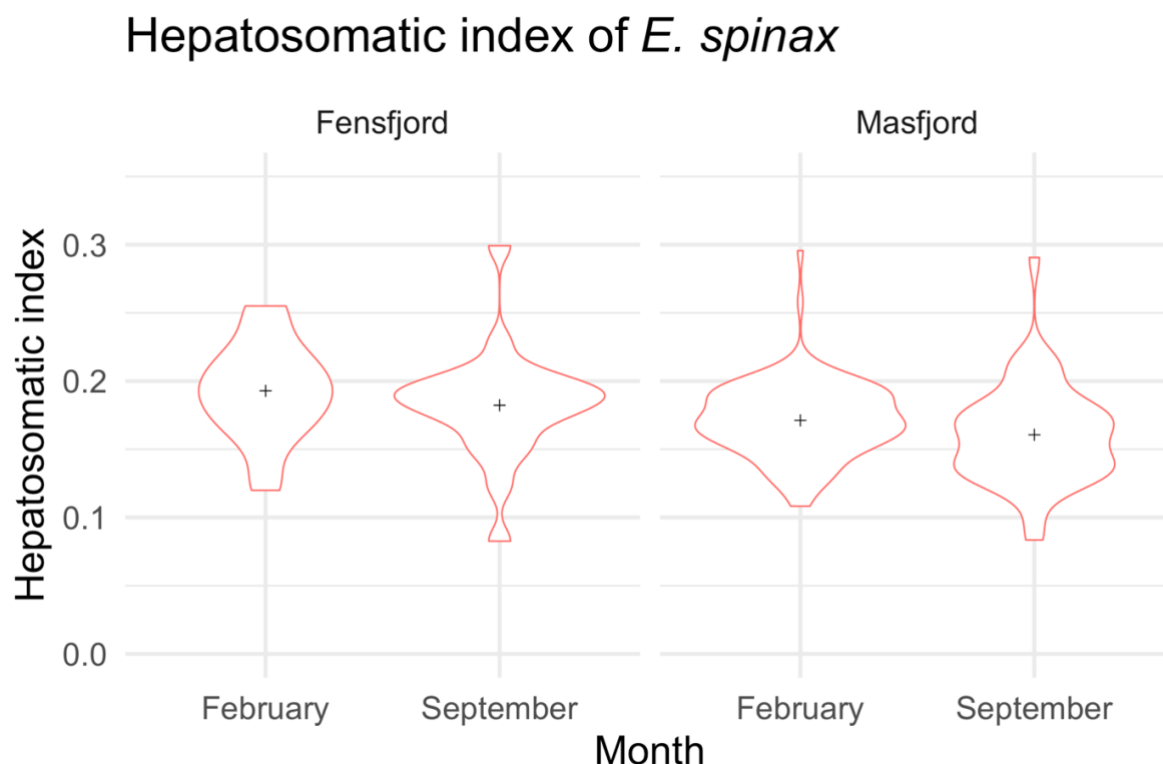


Figure 23: The hepatosomatic index (HSI) from equation 1 plotted for *E. spinax*, separated by fjord and month. The black symbol “+” shows the mean value.

Table 5: Summary output from the best fitted generalized linear model (glm) for HSI from *E. spinax* only. Fjord, month, and sex were used as predictor variables.

Coefficients	Estimate	Std. Error	t-value	p-value
(Intercept)	-1.618512	0.035586	-45.482	2.00E-16***
fjordMasfjord	-0.116741	0.031754	-3.676	0.000303***
month	-0.008755	0.004048	-2.163	0.031721*
sexm	-0.021404	0.026523	-8.07E-01	0.420627

Signif.codes: 0 ‘*’ 0.001 ‘**’ 0.01 ‘*’ 0.05 ‘.’ 0.1 ‘ ’ 1**

3.5.3 Liver water content

To examine the energetic quality of the livers of *E. spinax* and *G. melastomus*, we assessed differences in water content in the livers. *E. spinax* had a mean liver weight of 30 g, and only 8% water loss (Table 6). *G. melastomus* which had a lower mean liver weight of 21 g had a water loss of 27% (Table 6).

Table 6: Mean liver wet- and dry weight of *E. spinax* and *G. melastomus* and estimated water loss (%). Includes samples from both Fensfjord and Masfjord combined.

Species	Mean liver wet weight (g)	Mean liver dry weight (g)	Mean water loss (%)
<i>E. spinax</i>	30.37	27.89	8.16
<i>G. melastomus</i>	21.29	15.58	26.82

The differences in water loss between species was visible after drying in many cases, and the livers of *E. spinax* contained a higher amount of oily residue (Figure 24).

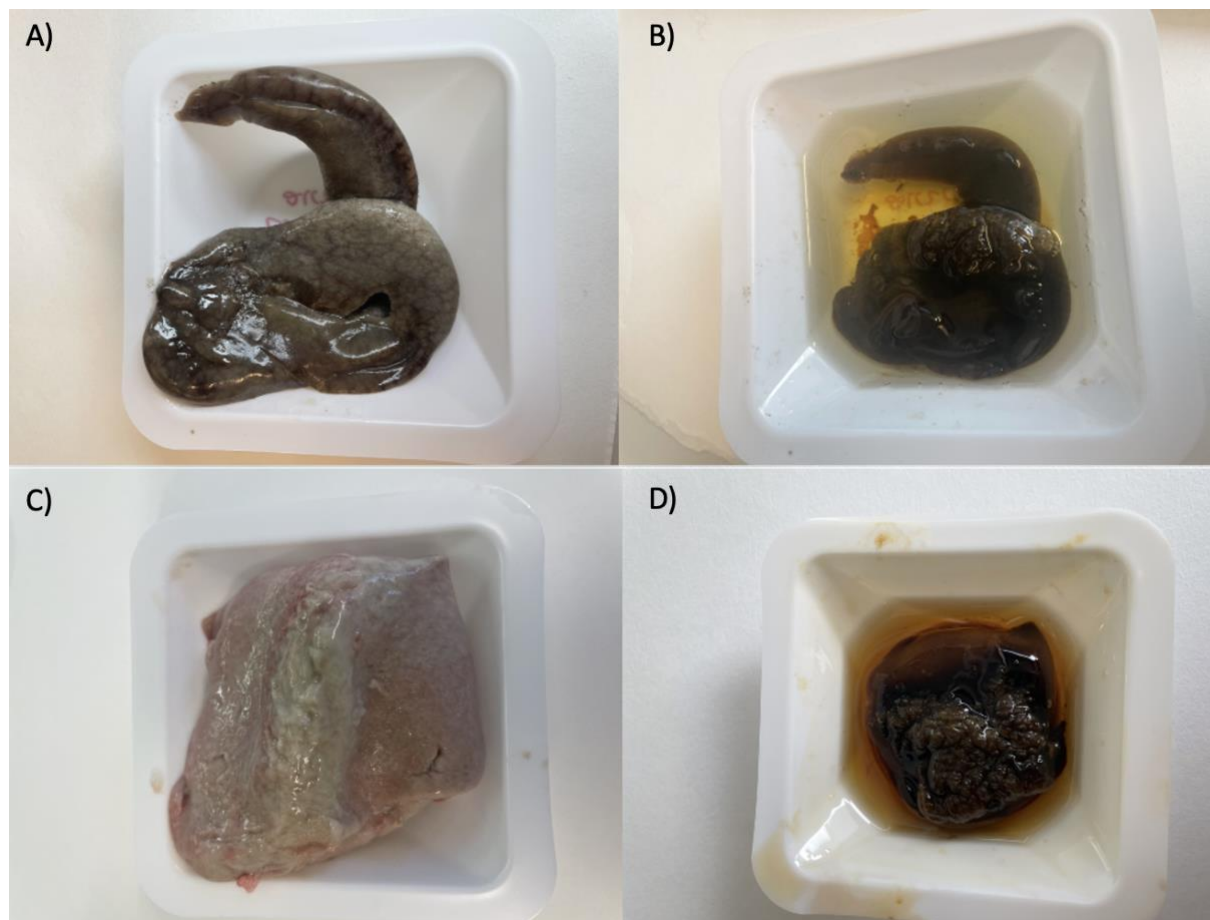


Figure 24: Pictures of: A) Liver of *E. spinax* before drying; B) liver of *E. spinax* after drying; C) Liver of *G. melastomus* before drying; and D) liver of *G. melastomus* after drying.

G. melastomus had a high proportion of water in their livers which ranged from 15-50%, whereas *E. spinax* had a water content of only 5-35%. In Masfjord there was large individual variation in water loss especially for *G. melastomus* (glm; deviance = 1.44, $p \ll 0.05$; Figure 25; Model summary in Appendix F; Table F5). Additionally, there was a big increase in water between February and September for *G. melastomus* and a slight increase for *E. spinax* (glm; deviance = 0.03, $p < 0.05$; Figure 25). While it was not possible to test for *G. melastomus* due to low sample size, no difference in liver water content was observed between fjords for *E. spinax* (lm; deviance = -0.08, $p = 0.37$; Appendix E; Figure E3, Model summary in Appendix F; Table F6).

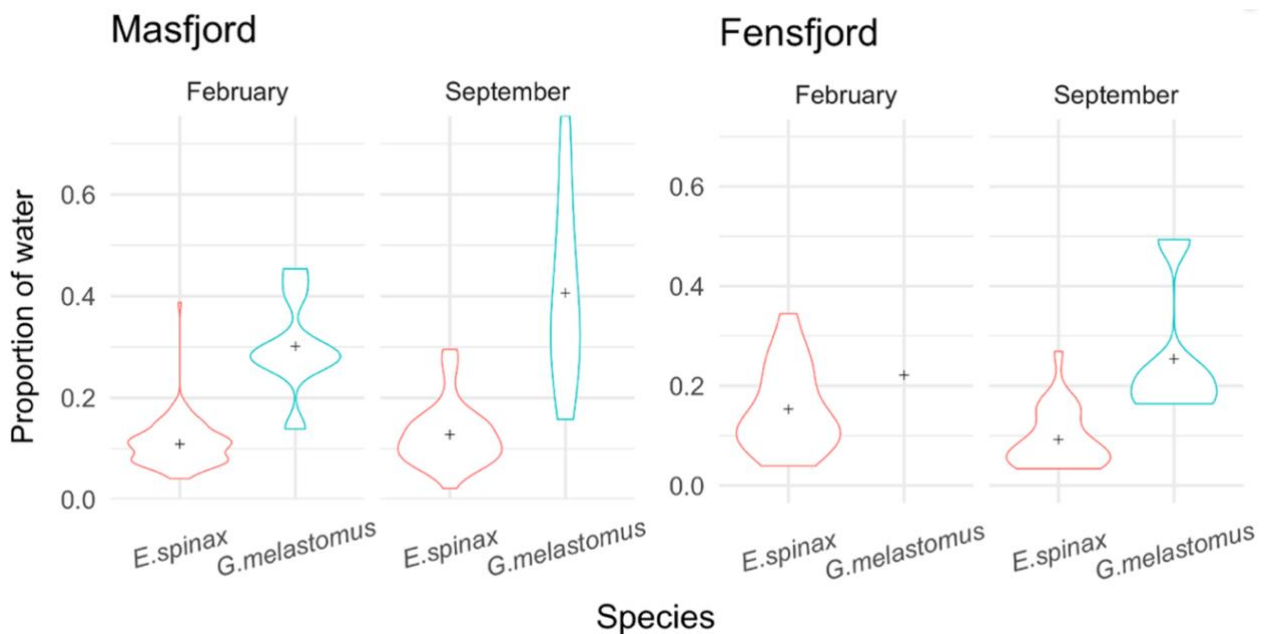


Figure 25: The total proportion (0-1) of water in the livers of *E. spinax* and *G. melastomus* were plotted separately for February and September for both Fensfjord and Masfjord. The water content was calculated using Equation 3, and the black symbol “+” shows the mean value.

4 Discussion

This study aimed to explore and compare the spatial and trophic ecology, energetic status, and hypoxia tolerance of two common sharks in western Norwegian fjords: *Etmopterus spinax* and *Galeus melastomus*. Our data show that *E. spinax* utilizes both benthic and pelagic habitats, with a spatial distribution that extends from the seafloor to about 200 m below the sea surface. Contrastingly, the distribution of *G. melastomus* is limited to the seafloor. *E.*

spinax has a more pelagic diet and feeds on mesopelagic fishes and crustaceans, whereas *G. melastomus* feeds on more bottom-associated prey. In addition to both sharks feeding more extensively on bait from longlines in Masfjord, both species also showed a higher proportion of empty stomachs in that fjord, suggesting Masfjord as a less favorable food environment. Moreover, *E. spinax* had a higher HSI and lower liver water content suggesting a more energetically efficient liver compared to *G. melastomus*. Lower HSI in Masfjord compared to Fensfjord further indicates that Masfjord supports a less favorable food environment. No intraspecific differences in HSI were found between maturation stages or sex, surprisingly since different maturation stages requires different energy investment. Interestingly, except for minor differences observed between fjords altogether, our results indicate that the low oxygen levels in Masfjord had little effect on either species' ecology.

4.1 Distribution

Pelagic trawls, bottom trawls, longlines, and traps sample at different depths and different parts of the ecosystem. The different sampling gears can thus provide information about the habitat use of the species caught. We know that *E. spinax* emits bioluminescence on its ventral side, which causes counterillumination when they are higher up in the water column (Claes et al. 2010). It is thus not surprising that their distribution extends further up in the pelagic zone compared to *G. melastomus* which does not have this ability.

Bottom trawl data from Masfjord between 2011-2015 display a view of how the species were distributed along the seafloor prior to the period of hypoxia, and our results found that both species had a similar distribution on the seabed. Only smaller individuals (< 40 cm) of both species were caught using bottom trawl and larger individuals were caught further up in the water column using longlines. This suggests that only larger individuals emerge from the seabed and utilize more pelagic associated resources. Most demersal species exhibit an ontogenetic migration and move into deeper waters as they grow. As such, larger individuals are typically caught deeper, which often is referred to as the bigger-deeper phenomenon (Massutí and Moranta 2003). However, our results with these sharks show the opposite, where larger individuals come further up from the bottom. It is important to note that most studies reporting the bigger-deeper phenomenon use bottom trawls and not pelagic sampling gear. Our study includes both bottom and pelagic sampling gears to study the ecology of demersal species, showing that the water column is also an important part of the habitat especially for *E. spinax*.

Although our results show that larger individuals are more likely to come off the bottom to feed in the midwater, it is uncertain why this is the case. It may be that food quality is higher in the water column compared to the bottom, and there is a tradeoff to the energetic cost of swimming up. Larger individuals are less susceptible to predators, and if the predators are pelagic species, it may be too dangerous for smaller individuals to migrate up to feed.

4.2 Dietary differences

A species' habitat can be revealed by its diet, and stomach content can thus tell a lot about the ecology of a species. Fanelli et al. (2008) presented a low, although small, dietary overlap between the species, mostly caused by a stronger pelagic diet of *E. spinax* compared to *G. melastomus*. It was also reported by Fanelli et al. (2008) that *G. melastomus* had a slightly more specialistic behavior while *E. spinax* was described as a generalist. Although this was the case in the Mediterranean, our results from Norwegian fjords show the opposite and *G. melastomus* was found to have a more diverse and generalistic diet than *E. spinax* who fed on fewer unique prey items and presented a more specialistic behavior. Although *G. melastomus* had a higher contribution of brown stomach contents than *E. spinax*, they also had a fair contribution of red coloration. Based on our methods, a high number of both brown- and red-colored stomach contents would indicate a combination of benthic and pelagic feeding. However, using stomach content coloration as a method to describe diet is not bullet-proof, which becomes apparent as *D. bonnieri* and *Mysida* cause red coloration but are indeed demersal species. It was therefore necessary with a more thorough examination of the stomach content than only looking at the coloration to be able to discuss and compare dietary preferences and comment on habitat use.

Some dietary overlap was observed between the species which coincide with the results of Fanelli et al. (2008). Both species fed on mesopelagic species like krill and *Sergestes sp.*, but despite this a clear diet separation was observed between species, and it was obvious that *G. melastomus* had a more heterogenous and benthic associated diet, whereas the diet of *E. spinax* is influenced by more pelagic prey items. A high contribution of mysids in addition to a fair amount of rocks, sand, and plant residues in the stomach of *G. melastomus* further confirmed benthic feeding. Additionally, an unidentified teleost head was found in one *G. melastomus* stomach, which strongly indicated scavenging. Scavengers feed on dead organic material falling onto the seafloor and is a common feeding strategy for benthos.

Furthermore, a higher proportion of empty stomachs was found in Masfjord compared to Fensfjord, and in addition to this, more stomachs from Masfjord had bait from longlines and traps in them. Traps and longlines are passive sampling gears, and consumers must thus actively seek bait. This suggests that individuals in Masfjord must actively search for food, indicating a poorer feeding habitat compared to Fensfjord. A potential difference was also observed in the number of unique prey types found in Masfjord compared to Fensfjord. While both species fed on a higher total number of unique prey types in Masfjord, the cumulative prey curves from Fensfjord are steeper (Figure 15), suggesting a more heterogeneous diet in that fjord. However, this may be caused by a sample bias between fjords and could only be confirmed with a higher sample size in Fensfjord.

4.3 Trophic interactions

Stable isotope analysis (SIA) has been increasingly used (e.g., Logan and Lutcavage 2010; Valls et al. 2014; Stewart et al. 2017) to supplement stomach content analysis in investigating trophic interactions. In this study, SIA allowed us to compare an integrated diet signature of the two sharks for the past 5-6 months (long-term diet), and while stomach content analysis only reveal diet the past day (short-term diet), these methods in combination provide a strong perception of their diet. According to SIA, it is clear that *E. spinax* and *G. melastomus* utilize different parts of the ecosystem, which was also validated by stomach content data. The $\delta^{13}\text{C}$ -signature describes what type of prey a consumer has been feeding on and overlapping $\delta^{13}\text{C}$ -signatures can thus expose dietary similarities. Findings of Barria et al. (2018) show that *E. spinax* had a lower $\delta^{13}\text{C}$ -signature than *G. melastomus* in the Gulf of Lyons, which coincides with our results in Norwegian fjords. However, their findings in the Catalan Sea show very similar $\delta^{13}\text{C}$ -signatures between both species, which is different from what we found. This deviance between regions suggests that the sharks can show different isotopic signatures in different habitats, and our results therefore fills knowledge gaps about their isotopic signatures in western Norwegian fjords. The $\delta^{15}\text{N}$ -signature describes the trophic position of an organism and increases up the food chain. Our study found that *G. melastomus* fed on one trophic level higher than *E. spinax*, evidenced by a 2.5 per mill higher $\delta^{15}\text{N}$ -signature of *G. melastomus*. Previous work of Albo-Puigserver et al. (2015) also found that *G. melastomus* feed at a higher trophic position than *E. spinax*, which coincide with our results. *S. acanthias* was investigated as a third species, but only a few samples of this species were analyzed. No dietary overlap was found between *S. acanthias* and the two species of primary interest, suggesting that although *S. acanthias* is

present in the same fjords, it utilizes different resources than *E. spinax* and *G. melastomus*. Jac et al. (2022) found that *G. melastomus* and *S. acanthias* fed at the same trophic level and mainly on teleosts, and hypothesized that the two species were in direct competition. However, our study clearly shows a trophic separation between *S. acanthias* and *G. melastomus* making them less likely to be competitors.

In addition to investigating interspecific differences, SIA allowed us to examine potential intraspecific differences related to the reproduction cycle or changes in the physical environment. A slight difference between sex was found in the $\delta^{13}\text{C}$ -signature, suggesting that males and females may feed on different prey items. These results contrast with those of Albo-Puigserver et al. (2015), who found no difference between sex in either isotopic signature in either species. Sex was hypothesized to have a significant impact on the isotope signatures due to an extensive reproductive investment of females compared to males. Surprisingly, females who invest large amounts of energy and time into reproduction have almost no dietary divergence from males. There has been reported segregation by sex in other regions (Porcu et al. 2020), and if such segregation is present in Norwegian fjords it may explain the observed differences in carbon signature, assuming that such segregation means that they utilize different prey items. Moreover, our dataset showed no differences in either isotopic signature concerning maturation stage, meaning that even *E. spinax* that develop and carry pups in their abdomen for several months have no dietary divergence from immature females. It could, however, be that females had stocked up with energy over a longer period before they were ready to mature and reproduce, and as maturation started and progressed between February and September, they kept feeding in the same manner as always but canalized the energy from the liver and into reproduction.

4.4 Energetic physiology

Hepatosomatic index (HSI) was calculated to examine the energetic status of *E. spinax* and *G. melastomus* since chondrichthyans store lipids in the liver and uses it as energy storage (Corner et al. 1969). HSI responds quickly to changes in feeding pattern and feeding intensity and can thus indicate how well fed an individual is or how favorable the feeding environment is (Ordines et al. 2021). *E. spinax* was found to have a higher HSI than *G. melastomus*, suggesting more efficient energy storage in *E. spinax*. However, sharks also use their liver to regulate buoyancy (Corner et al. 1969), and the differences in HSI that we are observing could be

associated with *E. spinax* having a clearly wider vertical distribution than *G. melastomus*. Pinte et al. (2019) found that *E. spinax* not only had a higher HSI than *G. melastomus*, but the lipid composition of *E. spinax* also consisted of lipids providing more hydrostatic force important for buoyancy control. This further suggests that *E. spinax* uses the liver for buoyancy as well as energy reserve and thus requires a bigger liver. There was found no difference in HSI in relation to either sex or maturation stage, which is surprising since the reproductive investment is very different between sex and at different stages in the reproduction cycle. However, as there was found no difference in feeding rate between different maturation stages either, this may explain why no changes were observed in the energy storage. However, Aranha et al. (2009) show that HSI indeed differed between different maturation stages of *E. spinax* and that HSI increased while maturing while decreasing during the development of embryos and pups. There is an increased energy investment as they start to produce embryos, and the liver may therefore lose weight in the process.

While it was hypothesized that *E. spinax* had bigger energy reserves due to an extensive energy investment into reproduction, it did not affect the HSI in our study. However, the water content in the livers had a slight increase from February to September in Masfjord, suggesting that although HSI remained the same throughout the seasons, the energetic efficiency of the livers suffered a decline. Water content can also provide insights into the energy efficiency of the liver since water adds weight to the liver but is energetically ineffective. Significant differences in both liver size and water content make a big difference in the energetic efficiency of the livers, and smaller and water-rich livers could be an indicator of starvation. There was also a large individual variation in the water loss of *G. melastomus* in Masfjord. However, this was not caused by differences in length or sex, suggesting that other factors influence the energetic status of these individuals. It may be related to individual variations in their adaptability to changing oxygen conditions, and that this is affecting the energetic status of the liver.

4.5 Hypoxia tolerance

Low catches of *E. spinax* were presented in the pelagic zone in Masfjord until 2017 before an increase in catches from 2018-2021. While Masfjord suffered deoxygenation from 2011-2018, the waters were only hypoxic (dissolved oxygen $>1.4 \text{ ml l}^{-1}$) between 2017-2018. It may be that decreasing oxygen levels in the basin water caused *E. spinax* to migrate up to shallower and more oxygenated waters. There were, however, no bottom trawls conducted in the same period

that can validate the absence of *E. spinax* at the seafloor in this period, and we can only speculate if this is the reason for the sudden increase in catches in the pelagic zone after 2018.

We know that there was a rise in oxygen levels of the basin water in Masfjord between February and September, and that this reoxygenation event allowed us to investigate whether potential changes in the species' ecology could be related to seasonal changes or ambient oxygen levels. Our findings that the vertical distribution was not affected by hypoxia in either species coincide with previous studies on teleost fishes. Sato et al. (2016) found no change in either horizontal or vertical distribution of Pacific Herring and Pacific Hake in Washington fjords with moderately low oxygen levels. Although the study of Sato et al. (2016) focused on teleost fishes, there may be similarities in how Herring and Hake and our species of interest behave in poorly oxygenated waters. It may be that the distribution of *E. spinax* and *G. melastomus* remains the same across different levels of oxygen due to an increased number of predators in shallower and more oxygenated waters, meaning that the low oxygen basin water is the safest habitat to occupy. Another explanation may be related to decreased competition for food and space in poorer environments (due to e.g., habitat compression). No changes in their distribution with low oxygen levels indicate other factors to influence their distribution, and whether this is related to predation, competition, food accessibility, or environmental factors is uncertain. *G. melastomus* was found to have a lower oxygen threshold of 1.8 ml l⁻¹ (Encyclopedia of Life Accessed 16. May 2022), and in the 11-year time series in Masfjord oxygen levels rarely went below this. It could therefore be that *G. melastomus* was not affected by the period of deoxygenation because it could still tolerate the oxygen levels it experienced. *E. spinax*, however, which has been found to have a lower oxygen threshold of 3.4 ml l⁻¹ (Encyclopedia of Life Accessed 16. May 2022) experienced oxygen levels well below their tolerance. Hypoxia was thus hypothesized to have a bigger impact on the ecology of *E. spinax* than what our results presented.

If reduced oxygen conditions in the basin water cause diel vertical migration organisms to visit deep waters less frequently, it can affect the feeding rate of demersal species. *E. spinax*, who has a broader vertical migration than *G. melastomus*, has a better opportunity to migrate to more oxygenated waters to feed on pelagic resources. In contrast, *G. melastomus*, who lives along the seafloor, relies on benthic food items. While it was not possible to examine seasonal differences by looking at stomach contents, differences between fjords were visible. Stomachs of both species in Masfjord contained a considerably higher amount of bait. It may be that

Masfjord is a poorer food environment due to lower oxygen conditions in the fjord, making *E. spinax* and *G. melastomus* seek bait from longlines more frequently. However, stable isotopes revealed no difference between February and September, indicating that lower oxygen conditions don't affect the feeding intensity of either *E. spinax* or *G. melastomus*.

G. melastomus undergoes an increase in liver water weight between February and September in Masfjord, and even though less obvious, this is possibly the case for *E. spinax* too. An increase in liver water weight indicates a decline in energy reserves, meaning that energy reserves decrease between the months. In Fensfjord, however, the liver water content declined for *E. spinax* in the same period, suggesting an increase in liver reserves. Since there is a difference between fjords, this increase or decrease in energy reserves is assumably not related to seasonality. That individuals from Masfjord have a lower energy reserve is an indicator of starvation, suggesting that Masfjord is a poorer food environment which may be due to lower oxygen levels. Individuals in Masfjord were also suggested to be hungrier due to a significant contribution of bait in their stomach content.

4.6 Limitations of the study

Bottom trawls were conducted in Masfjord between 2011-2015, but due to cables laid on the seafloor and the increasing number of fish farms in the area, bottom trawling was prohibited after 2015. Additionally, bottom trawling was not allowed in Fensfjord in any years between 2011-2021 due to the high number of fish farms and no places to trawl. This inconsistency in samples shortened our dataset and only made it possible to compare catches between fjords from 2020-2021 when sampling was consistent. Despite this limitation, bottom trawl data provided valuable information on the distribution of *E. spinax* and *G. melastomus* along the seafloor prior to the period of hypoxia in Masfjord.

Moreover, it was not possible to compare length data between species since removing years with no consistency considerably shortened our length dataset. The shortened dataset made it challenging to investigate a potential length-segregation reported for these species in other areas (Fanelli et al. 2008). Regardless, our data showed that *G. melastomus* generally reaches a larger size than *E. spinax*, providing further insights into their ecology.

Stomachs used in stomach content analysis were dominated by *E. spinax* from Masfjord. Additionally, most individuals used in the analysis was sampled in September, which made it challenging to explore the effects of seasonality and hypoxia. Despite this, stomach content analysis provided reliable results that show a clear difference in the diet of the two sharks, which was also confirmed by stable isotopes. Evidence also point to a strong ecological niche separation between *E. spinax* and *G. melastomus* regardless.

4.7 Future research

A lot is known about *E. spinax* and *G. melastomus* across the Mediterranean Sea, and our study contributes to the current knowledge on these species in Norwegian waters by looking at their ecology in fjord systems. However, little is known about the ecology of the two sharks across the broad latitudinal gradient that both species span. To study these species elsewhere will widen our knowledge on how the spatial and trophic ecology change, or doesn't change, across different ecosystems and climates. The stable isotope signature of *E. spinax* and *G. melastomus* is shown to vary between regions and at different depths. Although our study provides information about the isotopic signature of the sharks in western Norwegian fjords, information about this is missing across many areas within their habitat range. Future research should aim to establish their isotopic signature in other regions where information is lacking.

Future research on spatial and trophic interactions in Norwegian fjords could aim to include *S. acanthias* as a third species of interest. *S. acanthias* is present in many Norwegian fjords, including Masfjord and Fensfjord. Although a few samples of *S. acanthias* were included in the stable isotope analysis and it revealed a clear trophic separation between *S. acanthias* and the two species of primary interest, only two individuals of *S. acanthias* were represented in the analysis and a bigger sample size could have strengthened our conclusion.

Future studies should aim to compare the diet of chondrichthyans present in Norwegian fjords that differ in oxygen conditions, to widen our knowledge on the effect of hypoxia on the diet of the species. If we know more about how oxygen loss affects the diet of these species, we are better prepared for the consequences of deoxygenation as climate change accelerates. Significant differences were observed in the livers of *E. spinax* and *G. melastomus* in our study, not just in size but also during the drying process. While *E. spinax* had large amounts of oily residue that leaked from the livers when drying, the livers of *G. melastomus* were completely

dry in many cases. Including methods that describe and compare the lipid composition of the livers in these populations could help explain the big differences observed in the livers. The sharks use livers as energy storage but also to regulate buoyancy, and because *E. spinax* performs diel vertical migration and *G. melastomus* lives along the bottom, there are reasons to believe that the lipid composition of the liver differs. Studies on the energetic physiology of *E. spinax* and *G. melastomus* in other regions within their habitat range would also be beneficial in order to understand their energy requirements across different climates. Understanding the energetic physiology of these species better is crucial when trying to understand their reproductive requirements and energetic status better.

Other studies have found that low temperatures could mitigate the effects of low oxygen levels due to reduced metabolic rate following lower temperatures (Schurmann and Steffensen 1992). Temperature was not included as an environmental variable in our study, and future studies should aim to investigate temperature as a potential explanation to their distribution in hypoxic regions.

4.8 Conclusion

The general conclusion is that *E. spinax* and *G. melastomus* hold a different ecological niche regarding what they eat and where they live. While *E. spinax* has a broad vertical distribution and feeds on more pelagic associated prey, *G. melastomus* lives along the bottom, feeds at a higher trophic level, and utilizes benthic associated prey. Although intraspecific differences were not as apparent in the energetic physiology and hepatosomatic index, clear interspecific differences were observed where *E. spinax* has a more energetically efficient liver. Surprisingly low oxygen conditions did not have any significant effects on either species' spatial or trophic ecology.

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Appendix

Appendix A – Catch data from 2011-2021

Table A: Every sampling haul conducted in Fensfjord and Masfjord between 2011-2021. “*E. spinax*” and “*G. melastomus*” refers to the number of individuals of that species caught in the respective haul. Table also includes calculated catch per hour from Equation 4. “*E.s* CPUE” refers to the CPUE of *E. spinax* whereas “*G.m* CPUE” refers to the CPUE of *G. melastomus*. CPUE is standardized catches per hour.

Year	Fjord	Station	Sample type	Sampling time (min)	Depth (m)	E. spinax	E.s CPUE	G. melastomus	G.m CPUE
2011	Masfjord	2011115	Bottom trawl	22	475.0	1.0	2.7	7.0	19.1
2011	Masfjord	2011127	Bottom trawl	19	468.0	8.0	25.3	43.0	135.8
2012	Masfjord	2012366	Bottom trawl	3	470.0	2.0	40.0	0.0	0.0
2012	Masfjord	2012372	Bottom trawl	7	478.0	2.0	17.1	0.0	0.0
2013	Masfjord	2013188	Bottom trawl	16	485.0	39.0	146.3	21.0	78.8
2013	Masfjord	2013198	Bottom trawl	8	462.0	139.0	1042.5	83.0	622.5
2014	Masfjord	2014258	Bottom trawl	5	469.0	2.0	24.0	85.0	1020.0
2014	Masfjord	2014259	Bottom trawl	7	472.0	13.0	111.4	52.0	445.7
2014	Masfjord	217	Fixed depth range	8	250.0	1.0	7.5	0.0	0.0
2015	Masfjord	121	Deep pelagic trawl	37	335.0	3.0	4.9	0.0	0.0
2015	Masfjord	2015111	Bottom trawl	29	400.0	31.0	64.1	11.0	22.8
2015	Masfjord	2015115	Bottom trawl	20	340.0	34.0	102.0	6.0	18.0
2015	Masfjord	2015118	Bottom trawl	17	430.0	25.0	88.2	117.0	412.9
2015	Masfjord	2015120	Bottom trawl	29	425.0	41.0	84.8	16.0	33.1
2015	Masfjord	2015128	Bottom trawl	22	425.0	24.0	65.5	16.0	43.6
2017	Lustrafjord	2017438	Deep pelagic trawl	30	323.0	1.0	2.0	0.0	0.0
2017	Masfjord	2017415	Follow echo layer	9	305.0	0.0	0.0	1.0	6.7
2018	Fordefjord	2018015	Follow echo layer	11	94.0	4.0	21.8	0.0	0.0
2018	Fordefjord	2018016	Fixed depth range	10	147.0	3.0	18.0	0.0	0.0
2018	Fordefjord	2018016	Fixed depth range	10	247.0	3.0	18.0	0.0	0.0
2018	Fordefjord	2018018	Follow echo layer	10	262.0	1.0	6.0	0.0	0.0

2018	Fordefjord	2018019	Fixed depth range	10	252.0	4.0	24.0	0.0	0.0
2018	Fordefjord	2018021	Fixed depth range	13	156.0	11.0	50.8	0.0	0.0
2018	Fordefjord	2018022	Fixed depth range	10	148.0	1.0	6.0	0.0	0.0
2018	Fordefjord	2018022	Fixed depth range	10	251.0	2.0	12.0	0.0	0.0
2018	Fordefjord	2018024	Deep pelagic trawl	26	305.0	2.0	4.6	0.0	0.0
2018	Masfjord	2018010	Deep pelagic trawl	20	378.0	0.0	0.0	1.0	3.0
2018	Masfjord	2018012	Fixed depth range	10	253.0	5.0	30.0	0.0	0.0
2018	Masfjord	2018013	Fixed depth range	10	250.0	3.0	18.0	0.0	0.0
2018	Masfjord	610	Follow echo layer	15	60.0	1.0	4.0	0.0	0.0
2018	Masfjord	610	Follow echo layer	15	297.5	5.0	20.0	0.0	0.0
2018	Masfjord	611	Fixed depth range	12	50.0	1.0	5.0	0.0	0.0
2018	Masfjord	611	Fixed depth range	18	150.0	2.0	6.7	0.0	0.0
2018	Masfjord	612	Fixed depth range	16	250.0	3.0	11.3	0.0	0.0
2018	Masfjord	616	Fixed depth range	40	400.0	1.0	1.5	4.0	6.0
2018	Masfjord	617	Fixed depth range	36	400.0	2.0	3.3	1.0	1.7
2019	Masfjord	2019014	Fixed depth range	11	253.0	1.0	5.5	0.0	0.0
2019	Masfjord	2019015	Fixed depth range	12	242.0	11.0	55.0	0.0	0.0
2019	Masfjord	2019017	Fixed depth range	13	251.0	1.0	4.6	0.0	0.0
2019	Masfjord	2019020	Follow echo layer	14	267.0	1.0	4.3	0.0	0.0
2019	Masfjord	2019022	Follow echo layer	11	232.0	1.0	5.5	0.0	0.0
2019	Masfjord	2019024	Deep pelagic trawl	20	390.0	5.0	15.0	0.0	0.0
2020	Fensfjord	249	Fixed depth range	15	150.0	1.0	4.0	0.0	0.0
2020	Fensfjord	249	Fixed depth range	16	250.0	1.0	3.8	0.0	0.0
2020	Fensfjord	250	Follow echo layer	15	315.0	3.0	12.0	0.0	0.0
2020	Fensfjord	251	Fixed depth range	21	250.0	1.0	2.9	0.0	0.0
2020	Masfjord	2020001	Follow echo layer	11	232.0	3.0	16.4	0.0	0.0
2020	Masfjord	2020008	Fixed depth range	10	250.0	2.0	12.0	0.0	0.0
2020	Masfjord	2020009	Follow echo layer	11	297.0	1.0	5.5	0.0	0.0
2020	Masfjord	2020022	Fixed depth range	10	250.0	1.0	6.0	0.0	0.0

2020	Masfjord	2020028	Deep pelagic trawl	20	370.0	0.0	0.0	1.0	3.0
2020	Masfjord	242	Fixed depth range	16	250.0	7.0	26.3	0.0	0.0
2020	Masfjord	243	Fixed depth range	13	250.0	5.0	23.1	0.0	0.0
2020	Masfjord	243	Fixed depth range	18	150.0	1.0	3.3	0.0	0.0
2020	Masfjord	252	Fixed depth range	15	250.0	7.0	28.0	0.0	0.0
2020	Masfjord	254	Fixed depth range	16	250.0	2.0	7.5	0.0	0.0
2020	Masfjord	254	Fixed depth range	16	150.0	5.0	18.8	0.0	0.0
2020	Masfjord	255	Fixed depth range	15	150.0	4.0	16.0	0.0	0.0
2020	Masfjord	255	Fixed depth range	17	250.0	5.0	17.6	0.0	0.0
2021	Fensfjord		Pelagic trawl	10	440.0	0.0	0.0	0.0	0.0
2021	Fensfjord	1	Traps	4320	356.0	0.0	NA	0.0	NA
2021	Fensfjord	151	Fixed depth range	15	266.0	2.0	8.0	0.0	0.0
2021	Fensfjord	151	Pelagic trawl	15	266.0	2.0	8.0	0.0	0.0
2021	Fensfjord	153	Pelagic trawl	12	50.0	0.0	0.0	0.0	0.0
2021	Fensfjord	154	Pelagic trawl	10	440.0	4.0	24.0	0.0	0.0
2021	Fensfjord	154	Deep pelagic trawl	61	440.0	4.0	3.9	0.0	0.0
2021	Fensfjord	155	Pelagic trawl	10	464.0	0.0	0.0	0.0	0.0
2021	Fensfjord	2	Traps	4320	356.0	0.0	NA	0.0	NA
2021	Fensfjord	203	Fixed depth range	10	59.0	0.0	0.0	0.0	0.0
2021	Fensfjord	204	Fixed depth range	10	150.0	0.0	0.0	0.0	0.0
2021	Fensfjord	204	Fixed depth range	10	250.0	2.0	12.0	0.0	0.0
2021	Fensfjord	205	Fixed depth range	11	65.0	0.0	0.0	0.0	0.0
2021	Fensfjord	206	Fixed depth range	10	59.0	0.0	0.0	0.0	0.0
2021	Fensfjord	207	Fixed depth range	10	50.0	0.0	0.0	0.0	0.0
2021	Fensfjord	208	Fixed depth range	11	50.0	0.0	0.0	0.0	0.0
2021	Fensfjord	213	Fixed depth range	10	595.0	0.0	0.0	0.0	0.0
2021	Fensfjord	4	Traps	4320	433.0	0.0	NA	0.0	NA
2021	Fensfjord	5	Traps	4320	433.0	0.0	NA	0.0	NA
2021	Fensfjord	6	Traps	4320	433.0	0.0	NA	0.0	NA

2021	Fensfjord	LL10	Longline	720	363.2	0.0	NA	0.0	NA
2021	Fensfjord	LL10	Longline	720	501.2	0.0	NA	1.0	NA
2021	Fensfjord	LL10	Longline	720	503.5	1.0	NA	0.0	NA
2021	Fensfjord	LL10	Longline	720	512.7	0.0	NA	1.0	NA
2021	Fensfjord	LL11	Longline	720	208.3	1.0	NA	0.0	NA
2021	Fensfjord	LL11	Longline	720	238.2	1.0	NA	0.0	NA
2021	Fensfjord	LL11	Longline	720	242.8	1.0	NA	0.0	NA
2021	Fensfjord	LL11	Longline	720	263.5	1.0	NA	0.0	NA
2021	Fensfjord	LL11	Longline	720	272.7	1.0	NA	0.0	NA
2021	Fensfjord	LL11	Longline	720	277.3	1.0	NA	0.0	NA
2021	Fensfjord	LL11	Longline	720	284.2	1.0	NA	0.0	NA
2021	Fensfjord	LL11	Longline	720	311.8	1.0	NA	0.0	NA
2021	Fensfjord	LL11	Longline	720	325.6	0.0	NA	1.0	NA
2021	Fensfjord	LL11	Longline	720	350.9	1.0	NA	0.0	NA
2021	Fensfjord	LL11	Longline	720	353.2	1.0	NA	0.0	NA
2021	Fensfjord	LL11	Longline	720	357.8	1.0	NA	0.0	NA
2021	Fensfjord	LL12	Longline	720	183.0	1.0	NA	0.0	NA
2021	Fensfjord	LL12	Longline	720	187.6	1.0	NA	0.0	NA
2021	Fensfjord	LL12	Longline	720	189.9	1.0	NA	0.0	NA
2021	Fensfjord	LL12	Longline	720	192.2	1.0	NA	0.0	NA
2021	Fensfjord	LL12	Longline	720	199.1	0.0	NA	0.0	NA
2021	Fensfjord	LL12	Longline	720	201.4	0.0	NA	0.0	NA
2021	Fensfjord	LL12	Longline	720	219.8	0.0	NA	0.0	NA
2021	Fensfjord	LL12	Longline	720	226.7	1.0	NA	0.0	NA
2021	Fensfjord	LL12	Longline	720	238.2	1.0	NA	0.0	NA
2021	Fensfjord	LL12	Longline	720	252.0	1.0	NA	0.0	NA
2021	Fensfjord	LL12	Longline	720	263.5	1.0	NA	0.0	NA
2021	Fensfjord	LL12	Longline	720	265.8	1.0	NA	0.0	NA
2021	Fensfjord	LL12	Longline	720	268.1	1.0	NA	0.0	NA

2021	Fensfjord	LL12	Longline	720	272.7	0.0	NA	1.0	NA
2021	Fensfjord	LL12	Longline	720	279.6	0.0	NA	0.0	NA
2021	Fensfjord	LL12	Longline	720	288.8	1.0	NA	0.0	NA
2021	Fensfjord	LL12	Longline	720	295.7	1.0	NA	0.0	NA
2021	Fensfjord	LL5	Longline	720	328.0	0.0	NA	1.0	NA
2021	Fensfjord	LL5	Longline	720	395.0	0.0	NA	1.0	NA
2021	Fensfjord	LL5	Longline	720	406.0	1.0	NA	0.0	NA
2021	Fensfjord	LL5	Longline	720	408.0	0.0	NA	0.0	NA
2021	Fensfjord	LL6	Longline	720	390.0	0.0	NA	0.0	NA
2021	Fensfjord	LL6	Longline	720	417.0	1.0	NA	0.0	NA
2021	Fensfjord	LL6	Longline	720	458.0	0.0	NA	1.0	NA
2021	Fensfjord	LL7	Longline	720	242.0	1.0	NA	0.0	NA
2021	Fensfjord	LL7	Longline	720	247.0	1.0	NA	0.0	NA
2021	Fensfjord	LL7	Longline	720	346.0	1.0	NA	0.0	NA
2021	Fensfjord	LL7	Longline	720	415.0	0.0	NA	1.0	NA
2021	Fensfjord	LL7	Longline	720	417.0	1.0	NA	0.0	NA
2021	Fensfjord	LL8	Longline	720	287.0	1.0	NA	0.0	NA
2021	Fensfjord	LL8	Longline	720	451.0	1.0	NA	0.0	NA
2021	Fensfjord	LL9	Longline	720	476.7	0.0	NA	0.0	NA
2021	Fensfjord	LL9	Longline	720	479.0	1.0	NA	0.0	NA
2021	Fensfjord	LL9	Longline	720	485.9	1.0	NA	0.0	NA
2021	Fensfjord	LL9	Longline	720	490.5	0.0	NA	1.0	NA
2021	Fensfjord	LL9	Longline	720	495.1	0.0	NA	0.0	NA
2021	Fensfjord	LL9	Longline	720	504.3	1.0	NA	0.0	NA
2021	Fensfjord	LL9	Longline	720	508.9	0.0	NA	1.0	NA
2021	Fensfjord	LL9	Longline	720	520.4	1.0	NA	0.0	NA
2021	Fensfjord	Trap1	Traps	4320	451.0	6.0	NA	0.0	NA
2021	Haugsvaerfjord	218	Deep pelagic trawl	19	50.0	0.0	0.0	0.0	0.0
2021	Masfjord	10	Traps	4320	344.0	0.0	NA	0.0	NA

2021	Masfjord	11	Traps	4320	344.0	0.0	NA	0.0	NA
2021	Masfjord	12	Traps	4320	344.0	0.0	NA	0.0	NA
2021	Masfjord	148	Pelagic trawl	10	240.0	0.0	0.0	0.0	0.0
2021	Masfjord	149	Pelagic trawl	10	225.0	0.0	0.0	0.0	0.0
2021	Masfjord	149	Pelagic trawl	11	50.0	0.0	0.0	0.0	0.0
2021	Masfjord	150	Follow echo layer	11	222.0	11.0	60.0	0.0	0.0
2021	Masfjord	150	Pelagic trawl	11	222.0	11.0	60.0	0.0	0.0
2021	Masfjord	157	Pelagic trawl	10	466.0	3.0	18.0	0.0	0.0
2021	Masfjord	157	Deep pelagic trawl	55	466.0	3.0	3.3	0.0	0.0
2021	Masfjord	158	Pelagic trawl	10	435.0	2.0	12.0	0.0	0.0
2021	Masfjord	158	Deep pelagic trawl	59	435.0	2.0	2.0	0.0	0.0
2021	Masfjord	190	Fixed depth range	9	250.0	0.0	0.0	0.0	0.0
2021	Masfjord	190	Fixed depth range	10	250.0	0.0	0.0	0.0	0.0
2021	Masfjord	191	Fixed depth range	11	50.0	0.0	0.0	0.0	0.0
2021	Masfjord	191	Fixed depth range	11	150.0	0.0	0.0	0.0	0.0
2021	Masfjord	192	Fixed depth range	11	150.0	0.0	0.0	0.0	0.0
2021	Masfjord	193	Follow echo layer	11	125.0	0.0	0.0	0.0	0.0
2021	Masfjord	193	Follow echo layer	12	25.0	0.0	0.0	0.0	0.0
2021	Masfjord	194	Fixed depth range	10	59.0	0.0	0.0	0.0	0.0
2021	Masfjord	194	Follow echo layer	10	150.0	0.0	0.0	0.0	0.0
2021	Masfjord	194	Follow echo layer	10	250.0	1.0	6.0	0.0	0.0
2021	Masfjord	195	Fixed depth range	11	50.0	0.0	0.0	0.0	0.0
2021	Masfjord	195	Fixed depth range	11	150.0	0.0	0.0	0.0	0.0
2021	Masfjord	195	Fixed depth range	11	250.0	0.0	0.0	0.0	0.0
2021	Masfjord	196	Follow echo layer	11	25.0	0.0	0.0	0.0	0.0
2021	Masfjord	197	Follow echo layer	11	40.0	0.0	0.0	0.0	0.0
2021	Masfjord	198	Fixed depth range	10	59.0	0.0	0.0	0.0	0.0
2021	Masfjord	199	Follow echo layer	10	155.0	0.0	0.0	0.0	0.0
2021	Masfjord	199	Follow echo layer	10	185.0	0.0	0.0	0.0	0.0

2021	Masfjord	209	Deep pelagic trawl	21	370.0	0.0	0.0	0.0	0.0
2021	Masfjord	210	Deep pelagic trawl	12	375.0	0.0	0.0	0.0	0.0
2021	Masfjord	215	Deep pelagic trawl	11	269.9	7.0	38.2	0.0	0.0
2021	Masfjord	216	Deep pelagic trawl	20	460.0	0.0	0.0	1.0	3.0
2021	Masfjord	217	Deep pelagic trawl	11	390.0	0.0	0.0	0.0	0.0
2021	Masfjord	7	Traps	4320	248.0	1.0	NA	0.0	NA
2021	Masfjord	8	Traps	4320	248.0	0.0	NA	0.0	NA
2021	Masfjord	LL1	Horizontal longline	255	264.0	6.0	NA	2.0	NA
2021	Masfjord	LL1	Longline	720	353.0	1.0	NA	0.0	NA
2021	Masfjord	LL1	Longline	720	396.0	1.0	NA	0.0	NA
2021	Masfjord	LL1	Longline	720	398.0	1.0	NA	0.0	NA
2021	Masfjord	LL1	Longline	720	418.0	0.0	NA	1.0	NA
2021	Masfjord	LL1	Longline	720	434.0	1.0	NA	0.0	NA
2021	Masfjord	LL2	Horizontal longline	255	264.0	12.0	NA	3.0	NA
2021	Masfjord	LL2	Longline	720	310.0	0.0	NA	0.0	NA
2021	Masfjord	LL2	Longline	720	348.0	0.0	NA	0.0	NA
2021	Masfjord	LL2	Longline	720	362.0	1.0	NA	0.0	NA
2021	Masfjord	LL2	Longline	720	400.0	0.0	NA	0.0	NA
2021	Masfjord	LL2	Longline	720	429.0	0.0	NA	1.0	NA
2021	Masfjord	LL2	Longline	720	447.0	0.0	NA	1.0	NA
2021	Masfjord	LL2	Longline	720	454.0	0.0	NA	1.0	NA
2021	Masfjord	LL2	Longline	720	456.0	0.0	NA	1.0	NA
2021	Masfjord	LL3	Horizontal longline	165	402.0	0.0	NA	2.0	NA
2021	Masfjord	LL3	Longline	720	275.0	1.0	NA	0.0	NA
2021	Masfjord	LL3	Longline	720	286.0	1.0	NA	0.0	NA
2021	Masfjord	LL3	Longline	720	320.0	1.0	NA	0.0	NA
2021	Masfjord	LL3	Longline	720	322.0	1.0	NA	0.0	NA
2021	Masfjord	LL3	Longline	720	340.0	1.0	NA	0.0	NA
2021	Masfjord	LL3	Longline	720	349.0	1.0	NA	0.0	NA

2021	Masfjord	LL3	Longline	720	365.0	1.0	NA	0.0	NA
2021	Masfjord	LL3	Longline	720	387.0	1.0	NA	0.0	NA
2021	Masfjord	LL3	Longline	720	397.0	0.0	NA	1.0	NA
2021	Masfjord	LL3	Longline	720	401.0	1.0	NA	0.0	NA
2021	Masfjord	LL3	Longline	720	403.0	0.0	NA	1.0	NA
2021	Masfjord	LL3	Longline	720	408.0	1.0	NA	0.0	NA
2021	Masfjord	LL3	Longline	720	423.0	1.0	NA	0.0	NA
2021	Masfjord	LL4	Horizontal longline	165	402.0	1.0	NA	0.0	NA
2021	Masfjord	LL4	Longline	720	336.0	0.0	NA	0.0	NA
2021	Masfjord	LL4	Longline	720	377.0	1.0	NA	0.0	NA
2021	Masfjord	LL4	Longline	720	384.0	0.0	NA	0.0	NA
2021	Masfjord	LL4	Longline	720	422.0	0.0	NA	0.0	NA
2021	Masfjord	LL4	Longline	720	424.0	0.0	NA	1.0	NA
2021	Masfjord	LL4	Longline	720	440.0	1.0	NA	0.0	NA
2021	Masfjord	LL4	Longline	720	442.0	1.0	NA	0.0	NA
2021	Masfjord	LL4	Longline	720	447.0	0.0	NA	1.0	NA
2021	Masfjord	LL4	Longline	720	449.0	0.0	NA	1.0	NA
2021	Masfjord	LL4	longline	720	451.0	1.0	NA	0.0	NA
2021	Masfjord	LL5	Longline	720	297.7	0.0	NA	0.0	NA
2021	Masfjord	LL5	Longline	720	398.9	1.0	NA	0.0	NA
2021	Masfjord	LL5	Longline	720	405.8	1.0	NA	0.0	NA
2021	Masfjord	LL5	Longline	720	428.8	1.0	NA	0.0	NA
2021	Masfjord	LL5	Longline	720	431.1	0.0	NA	1.0	NA
2021	Masfjord	LL5	Longline	720	433.4	0.0	NA	1.0	NA
2021	Masfjord	LL5	Longline	720	440.3	1.0	NA	0.0	NA
2021	Masfjord	LL5	Longline	720	442.6	0.0	NA	1.0	NA
2021	Masfjord	LL5	Longline	720	454.1	0.0	NA	1.0	NA
2021	Masfjord	LL6	Longline	720	213.8	1.0	NA	0.0	NA
2021	Masfjord	LL6	Longline	720	216.1	1.0	NA	0.0	NA

2021	Masfjord	LL6	Longline	720	241.4	1.0	NA	0.0	NA
2021	Masfjord	LL6	Longline	720	266.7	1.0	NA	0.0	NA
2021	Masfjord	LL6	Longline	720	271.3	1.0	NA	0.0	NA
2021	Masfjord	LL6	Longline	720	298.9	1.0	NA	0.0	NA
2021	Masfjord	LL6	Longline	720	303.5	1.0	NA	0.0	NA
2021	Masfjord	LL6	Longline	720	308.1	1.0	NA	0.0	NA
2021	Masfjord	LL6	Longline	720	310.4	1.0	NA	0.0	NA
2021	Masfjord	LL6	Longline	720	317.3	1.0	NA	0.0	NA
2021	Masfjord	LL6	Longline	720	326.5	1.0	NA	0.0	NA
2021	Masfjord	LL6	Longline	720	328.8	1.0	NA	0.0	NA
2021	Masfjord	LL6	Longline	720	338.0	1.0	NA	0.0	NA
2021	Masfjord	LL6	Longline	720	342.6	1.0	NA	0.0	NA
2021	Masfjord	LL6	Longline	720	347.2	1.0	NA	0.0	NA
2021	Masfjord	LL6	Longline	720	365.6	0.0	NA	1.0	NA
2021	Masfjord	LL6	Longline	720	374.8	0.0	NA	1.0	NA
2021	Masfjord	LL6	Longline	720	377.1	1.0	NA	0.0	NA
2021	Masfjord	LL7	Longline	720	277.1	1.0	NA	0.0	NA
2021	Masfjord	LL7	Longline	720	293.2	1.0	NA	0.0	NA
2021	Masfjord	LL7	Longline	720	316.2	1.0	NA	0.0	NA
2021	Masfjord	LL7	Longline	720	339.2	1.0	NA	0.0	NA
2021	Masfjord	LL7	Longline	720	341.5	1.0	NA	0.0	NA
2021	Masfjord	LL7	Longline	720	357.6	1.0	NA	0.0	NA
2021	Masfjord	LL7	Longline	720	366.8	1.0	NA	0.0	NA
2021	Masfjord	LL7	Longline	720	373.7	1.0	NA	0.0	NA
2021	Masfjord	LL7	Longline	720	419.7	0.0	NA	0.0	NA
2021	Masfjord	LL8	Longline	720	359.6	0.0	NA	0.0	NA
2021	Masfjord	LL8	Longline	720	437.8	1.0	NA	0.0	NA
2021	Masfjord	LL8	Longline	720	453.9	1.0	NA	0.0	NA
2021	Masfjord	LL8	Longline	720	456.2	1.0	NA	0.0	NA

2021	Masfjord	LL8	Longline	720	465.4	0.0	NA	1.0	NA
2021	Masfjord	Trap2	Traps	4320	473.0	98.0	NA	4.0	NA
2021	Osterfjord	147	Pelagic trawl	19	245.0	0.0	0.0	0.0	0.0
2021	Osterfjord	159	Pelagic trawl	11	68.0	0.0	0.0	0.0	0.0
2021	Osterfjord	189	Follow echo layer	42	145.0	0.0	0.0	0.0	0.0
2021	Sorfjord	160	Pelagic trawl	11	250.0	0.0	0.0	0.0	0.0
2021	Sorfjord	160	Pelagic trawl	12	67.0	0.0	0.0	0.0	0.0
2021	Sorfjord	160	Pelagic trawl	13	179.0	0.0	0.0	0.0	0.0
2021	Sorfjord	161	Pelagic trawl	10	146.0	0.0	0.0	0.0	0.0
2021	Sorfjord	161	Pelagic trawl	12	254.0	0.0	0.0	0.0	0.0
2021	Sorfjord	161	Pelagic trawl	18	40.0	0.0	0.0	0.0	0.0
2021	Sorfjord	162	Pelagic trawl	10	330.0	0.0	0.0	0.0	0.0
2021	Sorfjord	163	Pelagic trawl	10	329.0	0.0	0.0	0.0	0.0
2021	Sorfjord	LL10	Longline	720	246.0	0.0	NA	1.0	NA
2021	Sorfjord	LL10	Longline	720	373.0	0.0	NA	0.0	NA
2021	Sorfjord	LL9	Longline	720	359.0	1.0	NA	0.0	NA
2021	Sorfjord	LL9	Longline	720	384.0	1.0	NA	0.0	NA
2021	Sorfjord	LL9	Longline	720	386.0	1.0	NA	0.0	NA

Appendix B – Length distribution

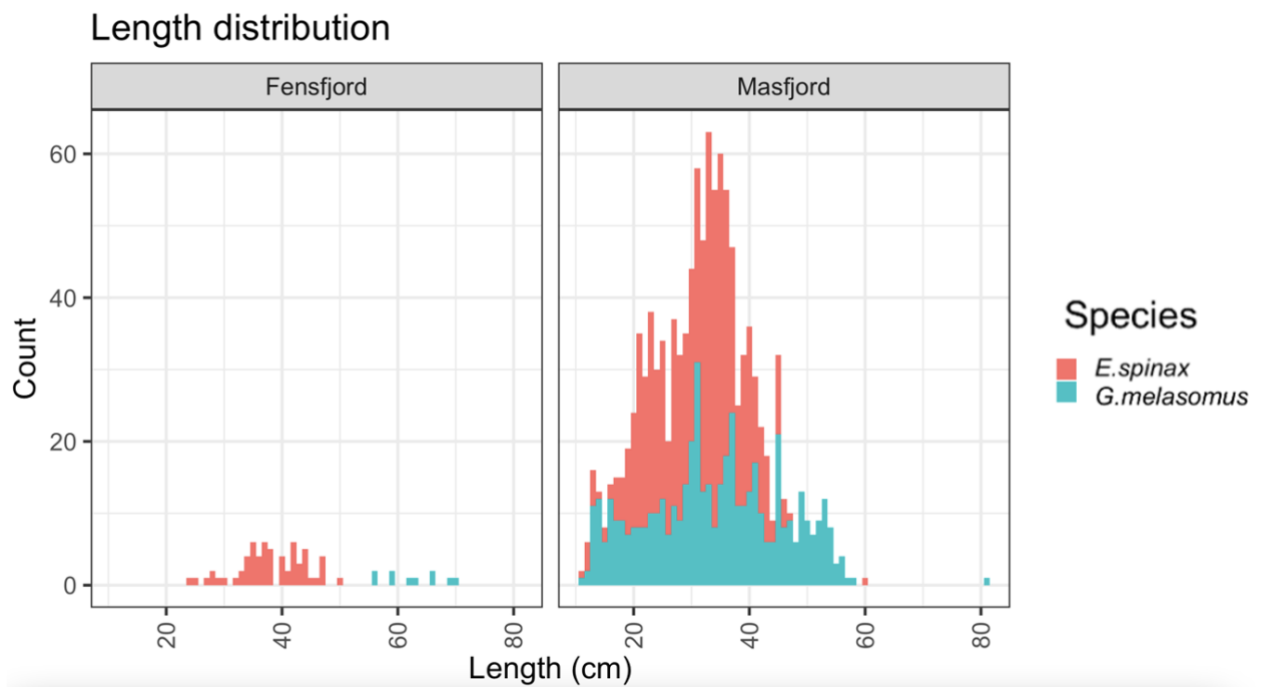


Figure B: Total length (cm) distribution of all sampled individuals of *E. spinax* (red) and *G. melastomus* (blue). Data is collected between 2011-2021 and includes bottom trawls, pelagic trawls with (Fixed depth range + follow echo layer) and without (periphylla haul + deep pelagic trawls) a Multisampler attached, vertical longlines and traps. Data is separated by Fensfjord and Masfjord. Note that data from bottom trawls is only available from Masfjord.

Appendix C – Stomach content analysis samples

Table C: Samples used for stomach content analysis and the sample type they were caught using. Stomach content was noted as y/n where; y = yes, n= no.

N	fjord	Month	species	Sample type	Stomach content (y/n)
1	Masfjord	2	<i>G. melastomus</i>	Longline	y
2	Masfjord	2	<i>G. melastomus</i>	Longline	n
3	Masfjord	2	<i>E. spinax</i>	Traps	n
4	Masfjord	2	<i>E. spinax</i>	Traps	n
5	Masfjord	2	<i>G. melastomus</i>	Traps	n
6	Masfjord	2	<i>E. spinax</i>	Traps	n
7	Masfjord	2	<i>E. spinax</i>	Traps	n
8	Masfjord	2	<i>E. spinax</i>	Traps	n
9	Masfjord	2	<i>E. spinax</i>	Traps	n
10	Masfjord	2	<i>E. spinax</i>	Traps	n
11	Masfjord	2	<i>G. melastomus</i>	Longline	y
12	Fensfjord	2	<i>G. melastomus</i>	Longline	y
13	Masfjord	2	<i>G. melastomus</i>	Longline	y
14	Masfjord	2	<i>G. melastomus</i>	Longline	n
15	Fensfjord	2	<i>G. melastomus</i>	Longline	y
16	Masfjord	2	<i>G. melastomus</i>	Traps	y
17	Fensfjord	2	<i>G. melastomus</i>	Longline	y
18	Fensfjord	2	<i>E. spinax</i>	Longline	n
19	Fensfjord	2	<i>E. spinax</i>	Longline	y
20	Fensfjord	2	<i>E. spinax</i>	Longline	y
21	Fensfjord	2	<i>E. spinax</i>	Longline	y
22	Masfjord	2	<i>E. spinax</i>	Traps	y
23	Masfjord	2	<i>E. spinax</i>	Traps	y
24	Masfjord	2	<i>E. spinax</i>	Traps	n
25	Masfjord	2	<i>E. spinax</i>	Longline	n
26	Masfjord	2	<i>E. spinax</i>	Longline	y
27	Masfjord	9	<i>E. spinax</i>	Traps	y
28	Masfjord	9	<i>E. spinax</i>	Longline	y
29	Fensfjord	9	<i>E. spinax</i>	Pelagic	y
30	Fensfjord	9	<i>E. spinax</i>	Longline	y
31	Masfjord	9	<i>E. spinax</i>	Pelagic	y
32	Masfjord	9	<i>E. spinax</i>	Pelagic	y
33	Fensfjord	9	<i>E. spinax</i>	Longline	y
34	Fensfjord	9	<i>E. spinax</i>	Longline	y
35	Masfjord	9	<i>E. spinax</i>	Longline	y
36	Masfjord	9	<i>E. spinax</i>	Pelagic	y
37	Masfjord	9	<i>E. spinax</i>	Longline	y
38	Masfjord	9	<i>E. spinax</i>	Longline	n
39	Fensfjord	9	<i>E. spinax</i>	Pelagic	y
40	Masfjord	9	<i>E. spinax</i>	Longline	y
41	Fensfjord	9	<i>G. melastomus</i>	Longline	y
42	Fensfjord	9	<i>G. melastomus</i>	Longline	y
43	Fensfjord	9	<i>G. melastomus</i>	Longline	y

44	Masfjord	9	<i>G. melastomus</i>	Longline	y
45	Fensfjord	9	<i>G. melastomus</i>	Longline	y
46	Fensfjord	9	<i>G. melastomus</i>	Longline	n
47	Masfjord	9	<i>G. melastomus</i>	Pelagic	y
48	Masfjord	9	<i>G. melastomus</i>	Longline	y
49	Masfjord	9	<i>G. melastomus</i>	Longline	y
50	Fensfjord	9	<i>G. melastomus</i>	Longline	y
51	Masfjord	9	<i>G. melastomus</i>	Longline	y
52	Masfjord	9	<i>G. melastomus</i>	Longline	y
53	Masfjord	9	<i>G. melastomus</i>	Longline	y
54	Masfjord	9	<i>E. spinax</i>	Pelagic	y
55	Masfjord	9	<i>E. spinax</i>	Pelagic	y
56	Masfjord	9	<i>E. spinax</i>	Pelagic	y
57	Fensfjord	9	<i>E. spinax</i>	Longline	y
58	Masfjord	2	<i>E. spinax</i>	Traps	n
59	Masfjord	2	<i>E. spinax</i>	Traps	n
60	Masfjord	2	<i>E. spinax</i>	Traps	n
61	Masfjord	2	<i>E. spinax</i>	Traps	n
62	Masfjord	2	<i>E. spinax</i>	Traps	n
63	Masfjord	2	<i>E. spinax</i>	Traps	n
64	Masfjord	2	<i>E. spinax</i>	Traps	n
65	Masfjord	2	<i>E. spinax</i>	Traps	n
66	Masfjord	2	<i>E. spinax</i>	Traps	n
67	Masfjord	2	<i>E. spinax</i>	Traps	n
68	Masfjord	2	<i>E. spinax</i>	Traps	n
69	Masfjord	2	<i>E. spinax</i>	Traps	n
70	Masfjord	9	<i>E. spinax</i>	Longline	n
71	Masfjord	9	<i>E. spinax</i>	Longline	y
72	Masfjord	9	<i>E. spinax</i>	Longline	n
73	Masfjord	9	<i>E. spinax</i>	Longline	y
74	Masfjord	9	<i>E. spinax</i>	Longline	n
75	Masfjord	9	<i>E. spinax</i>	Longline	y
76	Masfjord	9	<i>E. spinax</i>	Longline	y
77	Masfjord	9	<i>E. spinax</i>	Longline	y
78	Masfjord	9	<i>E. spinax</i>	Longline	n
79	Masfjord	9	<i>E. spinax</i>	Longline	n
80	Masfjord	9	<i>E. spinax</i>	Longline	y
81	Masfjord	2	<i>E. spinax</i>	Deep pelagic	n
82	Masfjord	2	<i>E. spinax</i>	Longline	n
83	Masfjord	2	<i>E. spinax</i>	Pelagic	n
84	Masfjord	2	<i>E. spinax</i>	Pelagic	n
85	Masfjord	2	<i>E. spinax</i>	Deep pelagic	n
86	Masfjord	2	<i>E. spinax</i>	Traps	n
87	Masfjord	2	<i>E. spinax</i>	Pelagic	n
88	Masfjord	9	<i>E. spinax</i>	Longline	n
89	Masfjord	9	<i>E. spinax</i>	Longline	y
90	Masfjord	9	<i>E. spinax</i>	Longline	n
91	Masfjord	9	<i>E. spinax</i>	Longline	y
92	Masfjord	9	<i>E. spinax</i>	Longline	n
93	Masfjord	9	<i>E. spinax</i>	Longline	y

94	Masfjord	9	<i>E. spinax</i>	Longline	y
95	Masfjord	9	<i>E. spinax</i>	Longline	n
96	Masfjord	9	<i>E. spinax</i>	Longline	n
97	Masfjord	9	<i>E. spinax</i>	Longline	y
98	Masfjord	9	<i>E. spinax</i>	Longline	n
99	Masfjord	9	<i>G. melastomus</i>	Longline	y
105	Masfjord	9	<i>E. spinax</i>	Longline	n
106	Masfjord	9	<i>E. spinax</i>	Longline	y
107	Masfjord	9	<i>E. spinax</i>	Longline	y
108	Masfjord	9	<i>E. spinax</i>	Longline	n
109	Masfjord	9	<i>E. spinax</i>	Longline	n
110	Fensfjord	2	<i>E. spinax</i>	Pelagic (T1)	y
111	Fensfjord	2	<i>E. spinax</i>	Pelagic (T1)	y
112	Fensfjord	2	<i>E. spinax</i>	Pelagic (T1)	y
113	Fensfjord	2	<i>E. spinax</i>	Pelagic	y
114	Fensfjord	2	<i>E. spinax</i>	Pelagic	n
115	Fensfjord	2	<i>E. spinax</i>	Pelagic	y
116	Fensfjord	2	<i>E. spinax</i>	Pelagic	n
117	Masfjord	9	<i>G. melastomus</i>	Longline	n
118	Masfjord	9	<i>G. melastomus</i>	Longline	y
119	Masfjord	9	<i>G. melastomus</i>	Longline	y
120	Masfjord	9	<i>G. melastomus</i>	Longline	y
121	Masfjord	9	<i>G. melastomus</i>	Longline	y
122	Masfjord	9	<i>G. melastomus</i>	Longline	y
123	Fensfjord	2	<i>E. spinax</i>	Pelagic	y
124	Fensfjord	2	<i>E. spinax</i>	Pelagic	y
125	Fensfjord	2	<i>E. spinax</i>	Pelagic	y
126	Fensfjord	2	<i>E. spinax</i>	Pelagic	y
127	Fensfjord	2	<i>E. spinax</i>	Pelagic	y
128	Fensfjord	2	<i>E. spinax</i>	Longline	n
129	Fensfjord	2	<i>E. spinax</i>	Longline	y
130	Fensfjord	2	<i>E. spinax</i>	Longline	n
131	Fensfjord	2	<i>E. spinax</i>	Longline	y
132	Fensfjord	2	<i>G. melastomus</i>	Longline	y
125	Fensfjord	2	<i>E. spinax</i>	Pelagic	y
126	Fensfjord	2	<i>E. spinax</i>	Pelagic	y
127	Fensfjord	2	<i>E. spinax</i>	Pelagic	y
128	Fensfjord	2	<i>E. spinax</i>	Longline	n
129	Fensfjord	2	<i>E. spinax</i>	Longline	y
130	Fensfjord	2	<i>E. spinax</i>	Longline	n
131	Fensfjord	2	<i>E. spinax</i>	Longline	y
132	Fensfjord	2	<i>G. melastomus</i>	Longline	y

Appendix D – Stable isotope analysis samples

Table D: Samples used for stable isotope analysis and for life history characteristics (sex, length (cm), weight (g), and maturity stage) of each individual, and results from isotope analysis ($\delta^{15}N$ and $\delta^{13}C$). Wet mass (mg) and Dry mass (mg) refer to the weight of the tissue before and after drying.

Fjord	Month	Species	Sex	Length (cm)	Weight (g)	Maturation stage	Wet mass (mg)	Dry mass (mg)	d15N	d13C
Masfjord	9	<i>E. spinax</i>	Male	32	127.27	Maturing	15.695	0.811	12.74	-19.54
Masfjord	9	<i>E. spinax</i>	Female	40	355.84	Maturing	17.056	1.192	13.75	-18.46
Masfjord	9	<i>E. spinax</i>	Male	31	136.63	Not mature	14.223	0.813	13.58	-18.20
Masfjord	9	<i>E. spinax</i>	Female	36	252.27	Maturing	18.556	0.757	12.68	-19.58
Masfjord	9	<i>E. spinax</i>	Female	40	244.72	Not mature	16.009	1.476	12.66	-18.51
Masfjord	9	<i>E. spinax</i>	Female	25	257.01	Mature	11.149	0.748	11.97	-19.71
Masfjord	9	<i>E. spinax</i>	Female	33	204.72	Mature	13.622	0.967	14.09	-18.43
Masfjord	9	<i>E. spinax</i>	Female	38	207.06	Mature	21.118	0.92	13.08	-18.69
Fensfjord	2	<i>E. spinax</i>	Female	31	124.79	Immature	10.412	0.849	13.37	-18.87
Fensfjord	2	<i>E. spinax</i>	Female	34	132.05	Immature	20.377	1.109	14.22	-17.73
Fensfjord	2	<i>E. spinax</i>	Male	38	336.98	No info.	11.986	1.041	13.42	-18.57
Fensfjord	2	<i>E. spinax</i>	Female	38	336.98	Developed babies	14.008	0.887	14.25	-17.64
Fensfjord	2	<i>E. spinax</i>	Male	33	156.1	Maturing	13.277	0.937	13.79	-17.98
Sorfjord	2	<i>S. acanthias</i>	Female	28	68	No info.	5.158	0.899	10.87	-21.36
Sorfjord	2	<i>S. acanthias</i>	Female	28	68	No info.	8.142	0.848	10.69	-21.44
Fensfjord	2	<i>G. melastomus</i>	Male	53	603.78	Mature	15.259	0.956	16.36	-16.95
Masfjord	9	<i>G. melastomus</i>	Female	51	275.95	No info.	19.226	0.711	15.44	-17.49
Masfjord	9	<i>G. melastomus</i>	Female	44	246.3	Not mature	15.039	0.807	15.05	-17.62
Masfjord	9	<i>G. melastomus</i>	Male	52	341.12	Maturing	32.503	1.361	15.43	-16.78

Masfjord	9	<i>G. melastomus</i>	Male	51	411.55	No info.	27.104	1.686	15.03	-15.75
Masfjord	9	<i>G. melastomus</i>	Male	46	266.1	No info.	23.282	1.316	15.46	-16.82
Masfjord	2	<i>G. melastomus</i>	Female	50	282	No info.	16.842	0.891	15.07	-17.80
Masfjord	2	<i>G. melastomus</i>	Female	38	136	No info.	34.644	1.18	14.43	-17.60
Fensfjord	2	<i>G. melastomus</i>	Female	66	815	No info.	18.925	1.096	16.67	-17.09
Fensfjord	2	<i>G. melastomus</i>	Male	59	569	No info.	25.022	1.234	16.82	-16.24
Masfjord	2	<i>G. melastomus</i>	Male	57	436	No info.	17.717	1.177	15.75	-16.79
Masfjord	2	<i>G. melastomus</i>	Male	57	436	No info.	15.214	0.904	15.70	-17.21
Masfjord	2	<i>G. melastomus</i>	Female	36	104	NA	27.019	0.846	14.35	-17.92
Masfjord	2	<i>G. melastomus</i>	Female	53	362	No info.	36.912	0.892	15.31	-17.28
Fensfjord	2	<i>E. spinax</i>	Female	33	167	No info.	12.189	1.121	14.27	-18.10
Fensfjord	9	<i>G. melastomus</i>	Male			No info.	13.084	0.794	14.69	-18.47
Fensfjord	2	<i>G. melastomus</i>	Female	69	934	2 eggs in oviduct	11.215	1.03	14.55	-17.97
Masfjord	2	<i>G. melastomus</i>	Male	53	359	No info.	12.969	0.777	14.18	-18.87
Masfjord	9	<i>E. spinax</i>	Male	34	150.34	Maturing	6.503	0.22	11.78	-20.13
Masfjord	9	<i>E. spinax</i>	Female	39	226.65	Not mature	3.842	0.378	12.00	-19.49
Masfjord	9	<i>E. spinax</i>	Male	36	173.25	Maturing	7.637	0.603	12.29	-19.01
Masfjord	9	<i>E. spinax</i>	Male	32	126.22	Not mature	12.749	0.616	13.54	-18.75
Masfjord	9	<i>E. spinax</i>	Male	36	154.7	Not mature	8.497	0.406	12.67	-19.49
Masfjord	9	<i>E. spinax</i>	Female	27	82.67	Not mature	9.531	0.73	14.44	-18.47
Masfjord	9	<i>E. spinax</i>	Female	35	253.73	8 embryos	8.352	0.307	12.19	-20.10
Masfjord	9	<i>E. spinax</i>	Male	35	137.33	Not mature	3.844	0.155	13.29	-19.37
Masfjord	9	<i>E. spinax</i>	Female	36	222.38	6 embryos	6.567	0.174	12.92	-20.13
Masfjord	9	<i>E. spinax</i>	Male	28	100.01	Not mature	8.815	0.288	13.49	-19.14
Masfjord	9	<i>E. spinax</i>	Female	38	218.3	Mature	11.377	0.463	13.10	-19.44
Masfjord	9	<i>E. spinax</i>	Female	36	239.32	Mature	7.884	0.349	13.29	-19.80

Fensfjord	2	<i>E. spinax</i>	Female	44	463.37	No info.	8.303	0.476	13.45	-18.95
Fensfjord	2	<i>E. spinax</i>	Female	28	81.16	No info.	9.451	0.425	13.10	-19.67
Fensfjord	2	<i>E. spinax</i>	Female	43	333.72	Maturing	7.703	0.305	12.46	-19.52
Fensfjord	2	<i>E. spinax</i>	Female	36	193.94	Maturing	5.58	0.448	11.99	-20.57
Fensfjord	2	<i>E. spinax</i>	Male	37	200.98	Maturing	12.246	0.632	13.92	-18.33
Fensfjord	2	<i>E. spinax</i>	Female	32	133.66	Immature	8.925	0.223	11.77	-20.10
Fensfjord	2	<i>E. spinax</i>	Female	41	335.53	Maturing	11.142	0.608	12.89	-19.10
Fensfjord	2	<i>E. spinax</i>	Female	38	336.98	Developed babies	15.731	0.689	14.15	-18.02
Fensfjord	2	<i>E. spinax</i>	Female	38	336.98	Developed babies	8.879	0.262	13.33	-19.03
Sorfjord	2	<i>S. acanthias</i>	Female	28	68	No info.	5.282	0.705	10.61	-21.53
Sorfjord	2	<i>S. acanthias</i>	NA	NA	NA	NA	9.843	0.644	10.98	-20.21
Masfjord	9	<i>E. spinax</i>	Male	34	155.09	Maturing	13.559	0.6	13.07	-18.75
Masfjord	9	<i>G. melastomus</i>	Male	53	430.92	Maturing	11.533	0.651	15.51	-17.50
Masfjord	9	<i>G. melastomus</i>	Male	52	342.38	Maturing	20.585	0.629	15.07	-17.47
Masfjord	2	<i>G. melastomus</i>	Male	57	436	No info.	14.869	0.605	15.37	-17.40
Fensfjord	2	<i>E. spinax</i>	Male	35	176	No info.	15.454	0.379	14.98	-17.83
Masfjord	9	<i>G. melastomus</i>	Male	45	240	No info.	18.846	0.17	16.67	-17.26
Masfjord	2	<i>G. melastomus</i>	Male	42	175	No info.	21.389	0.437	16.15	-17.56
Masfjord	2	<i>G. melastomus</i>	Female	43	180	No info.	17.73	0.024	13.89	-19.31

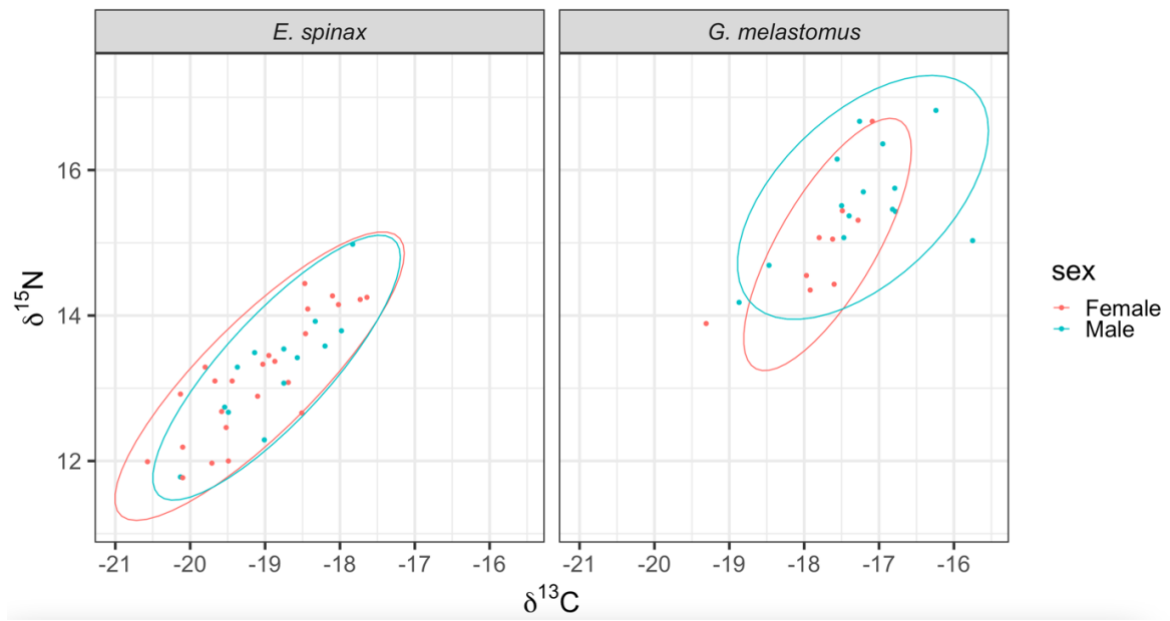


Figure D1: Isotope biplot showing the $\delta^{13}\text{C}$ and $\delta^{15}\text{N}$ values of *E. spinax* and *G. melastomus*, separated by sex.

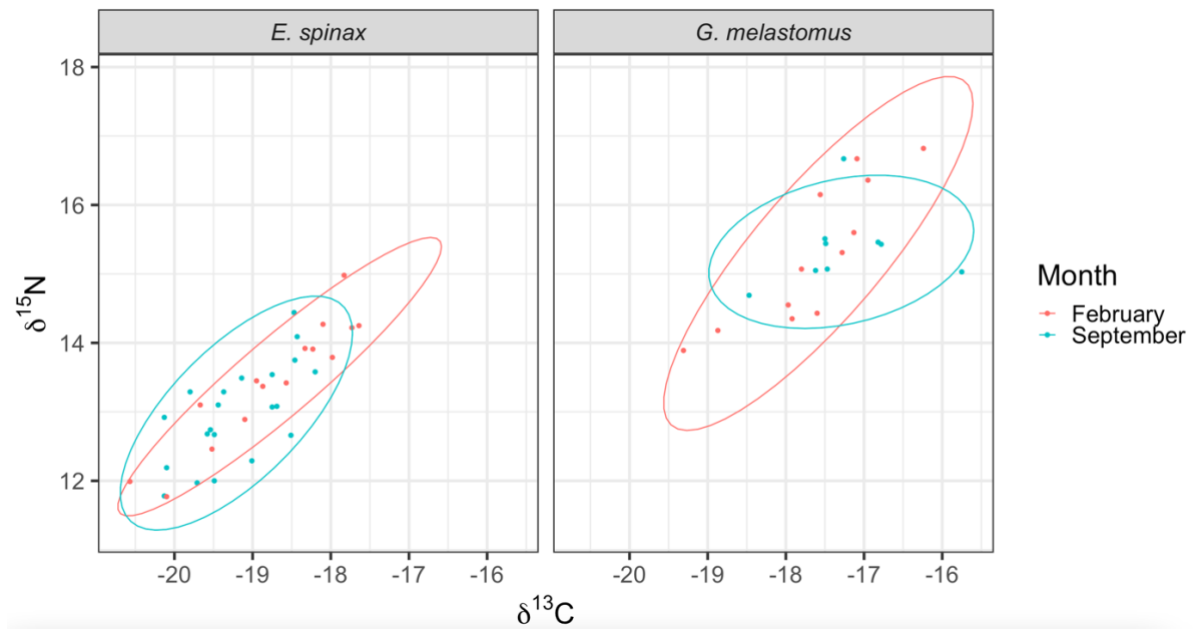


Figure D2: Isotope biplot showing the $\delta^{13}\text{C}$ and $\delta^{15}\text{N}$ values of *E. spinax* and *G. melastomus*, separated by month (“2” = February, “9” = September)

Appendix E – Liver analysis

Table E: Individuals used for liver analysis, including the sample type they were caught using and fish-ID. Table also includes liver wet weight (g) and results from liver analysis; liver dry weight (g)

Fjord	Year	Month	Species	Sample type	Fish-ID	Liver wet weight (g)	Liver dry weight (g)
Masfjord	2021	2	<i>G. melastomus</i>	Longline	LL2-76	17.65	12.51
Masfjord	2021	2	<i>G. melastomus</i>	Longline	LL2-77	9.86	7.17
Masfjord	2021	2	<i>G. melastomus</i>	Traps	Trap2-4.gm	4.9	2.91
Masfjord	2021	9	<i>G. melastomus</i>	Pelagic	216-66-1	20.54	15.57
Masfjord	2021	9	<i>G. melastomus</i>	Longline	LL5-63	9.36	4.29
Masfjord	2021	9	<i>G. melastomus</i>	Longline	LL5-68	11.53	6.77
Masfjord	2021	9	<i>G. melastomus</i>	Longline	LL5-73	6.91	2.19
Masfjord	2021	9	<i>G. melastomus</i>	Longline	LL2-52_LD	13	8.92
Masfjord	2021	9	<i>G. melastomus</i>	Longline	LL1-42_LD	9.26	4.3
Masfjord	2021	9	<i>G. melastomus</i>	Longline	LL1-54_LD	15.82	11.03
Masfjord	2021	9	<i>G. melastomus</i>	Longline	LL2-54_LD	17.43	10.43
Masfjord	2021	9	<i>G. melastomus</i>	Longline	LL2-12_LD	12.67	7.32
Masfjord	2021	9	<i>G. melastomus</i>	Longline	LL6-68_LD	39.74	32.69
Masfjord	2021	9	<i>G. melastomus</i>	Longline	LL6-72_LD	14.16	7.39
Fensfjord	2021	2	<i>G. melastomus</i>	Longline	LL7-78_LD	48.02	37.38
Masfjord	2021	9	<i>G. melastomus</i>	Longline	LL5-64	5.1	1.25
Masfjord	2021	9	<i>G. melastomus</i>	Longline	LL3-63	12.22	8.51
Masfjord	2021	9	<i>G. melastomus</i>	Longline	LL3-26	14.73	10.44
Masfjord	2021	9	<i>G. melastomus</i>	Longline	LL5-62	35.22	32.92
Masfjord	2021	2	<i>G. melastomus</i>	Longline	LL3-76	15.2	11.11
Masfjord	2021	2	<i>G. melastomus</i>	Longline	LL3-61	13.79	7.53
Masfjord	2021	2	<i>G. melastomus</i>	Longline	LL4-76	13.02	9.09
Masfjord	2021	2	<i>G. melastomus</i>	Longline	LL4-75	22.51	19.39
Masfjord	2021	2	<i>G. melastomus</i>	Longline	LL4-65	18.73	13.54
Masfjord	2021	9	<i>G. melastomus</i>	Longline	LL8-74	36.13	30.44
Fensfjord	2021	9	<i>G. melastomus</i>	Longline	LL11-58	41.46	21.01
Fensfjord	2021	9	<i>G. melastomus</i>	Longline	LL10-70	49.49	41.28
Fensfjord	2021	9	<i>G. melastomus</i>	Longline	LL10-75	38.85	32.47
Fensfjord	2021	9	<i>G. melastomus</i>	Longline	LL9-69	42.84	33.71
Fensfjord	2021	9	<i>G. melastomus</i>	Longline	LL9-61	40.68	31.18
Masfjord	2021	2	<i>E. spinax</i>	Traps	Trap2-67	23	20.62
Masfjord	2021	2	<i>E. spinax</i>	Traps	Trap2-39	23.29	20.85
Masfjord	2021	2	<i>E. spinax</i>	Traps	Trap2-97	16.7	13.63
Masfjord	2021	2	<i>E. spinax</i>	Traps	Trap2-17	25.36	22.75

Masfjord	2021	2	<i>E. spinax</i>	Traps	Trap2-95	25.72	23.26
Masfjord	2021	2	<i>E. spinax</i>	Traps	Trap2-38	23.05	20.22
Masfjord	2021	2	<i>E. spinax</i>	Traps	Trap2-62	19.43	16.37
Fensfjord	2021	2	<i>E. spinax</i>	Longline	LL8-3	30.57	27.84
Fensfjord	2021	2	<i>E. spinax</i>	Longline	LL8-76	60.48	58
Masfjord	2021	2	<i>E. spinax</i>	Traps	Trap2-5	27.99	26.25
Masfjord	2021	2	<i>E. spinax</i>	Longline	LL2-35	46.66	44.57
Masfjord	2021	9	<i>E. spinax</i>	Traps	Trap7-1	30.61	26.59
Masfjord	2021	9	<i>E. spinax</i>	Longline	LL8-70	24.06	20.55
Fensfjord	2021	9	<i>E. spinax</i>	Pelagic	204-44-1	38.99	32.99
Fensfjord	2021	9	<i>E. spinax</i>	Longline	LL11-35	39.61	36.03
Masfjord	2021	9	<i>E. spinax</i>	Pelagic	245-65-3	32.63	29.31
Masfjord	2021	9	<i>E. spinax</i>	Pelagic	215-65-6	26.49	22.81
Fensfjord	2021	9	<i>E. spinax</i>	Longline	LL9-56	30.67	25.75
Fensfjord	2021	9	<i>E. spinax</i>	Longline	LL11-52	49.29	41.68
Masfjord	2021	9	<i>E. spinax</i>	Longline	LL8-69	26.35	22.25
Masfjord	2021	9	<i>E. spinax</i>	Pelagic	194-13-1	51.05	46.13
Masfjord	2021	9	<i>E. spinax</i>	Longline	LL5-67	41.64	35.31
Masfjord	2021	9	<i>E. spinax</i>	Longline	LL7-41	54.74	48.17
Fensfjord	2021	9	<i>E. spinax</i>	Pelagic	204-44-2	8.59	7.17
Masfjord	2021	9	<i>E. spinax</i>	Longline	LL8-62	24.11	19.01
Masfjord	2021	9	<i>E. spinax</i>	Pelagic	215-65-5	25.99	23.16
Masfjord	2021	9	<i>E. spinax</i>	Pelagic	215-65-7	6.86	5.56
Masfjord	2021	9	<i>E. spinax</i>	Pelagic	215-65-2	50.6	48.5
Fensfjord	2021	9	<i>E. spinax</i>	Longline	LL11-20	87.11	82.54
Masfjord	2021	2	<i>E. spinax</i>	Traps	Trap2-68	6.41	5.32
Masfjord	2021	2	<i>E. spinax</i>	Traps	Trap2-96	23.22	20.7
Masfjord	2021	2	<i>E. spinax</i>	Traps	Trap2-79	23.9	19.93
Masfjord	2021	2	<i>E. spinax</i>	Traps	Trap2-83	26.53	24.58
Masfjord	2021	2	<i>E. spinax</i>	Traps	Trap2-54	27.65	24.06
Masfjord	2021	2	<i>E. spinax</i>	Traps	Trap2-87	18.84	16.33
Masfjord	2021	2	<i>E. spinax</i>	Traps	Trap2-51	29.51	26
Masfjord	2021	2	<i>E. spinax</i>	Traps	Trap2-90	25.34	22.69
Masfjord	2021	2	<i>E. spinax</i>	Traps	Trap2-89	20.13	17.72
Masfjord	2021	2	<i>E. spinax</i>	Traps	Trap2-34	26.62	23.49
Masfjord	2021	2	<i>E. spinax</i>	Traps	Trap2-47	16.54	15.2
Masfjord	2021	2	<i>E. spinax</i>	Traps	Trap2-14	25.4	21.82
Masfjord	2021	9	<i>E. spinax</i>	Longline	LL2-2_LD	11.49	9.75
Masfjord	2021	9	<i>E. spinax</i>	Longline	LL2-29_LD	53.14	50.42
Masfjord	2021	9	<i>E. spinax</i>	Longline	LL2-35_LD	34.17	30.55

Masfjord	2021	9	<i>E. spinax</i>	Longline	LL2-55_LD	45.22	42.98
Masfjord	2021	9	<i>E. spinax</i>	Longline	LL2-15_LD	34.53	30.48
Masfjord	2021	9	<i>E. spinax</i>	Longline	LL1-11_LD	37.39	35.28
Masfjord	2021	9	<i>E. spinax</i>	Longline	LL1-60_LD	21.66	19.31
Masfjord	2021	9	<i>E. spinax</i>	Longline	LL1-55_LD	69.3	60.74
Masfjord	2021	9	<i>E. spinax</i>	Longline	LL6-39_LD	41.23	37.7
Masfjord	2021	9	<i>E. spinax</i>	Longline	LL6-51_LD	17.04	14.81
Masfjord	2021	9	<i>E. spinax</i>	Longline	LL6-73_LD	34.05	29.38
Masfjord	2021	2	<i>E. spinax</i>	Deep pelagic	158-25-1	23.31	21.43
Masfjord	2021	2	<i>E. spinax</i>	Longline	LL1-72	24.57	22.98
Masfjord	2021	2	<i>E. spinax</i>	Pelagic	157-24-3	20.24	18.6
Masfjord	2021	2	<i>E. spinax</i>	Pelagic	157-24-1	39.91	37.96
Masfjord	2021	2	<i>E. spinax</i>	Deep pelagic	158-25-2	27.68	25.41
Masfjord	2021	2	<i>E. spinax</i>	Traps	Trap2-4.es	24.15	21.5
Masfjord	2021	2	<i>E. spinax</i>	Pelagic	157-24-2	39.75	37.41
Masfjord	2021	9	<i>E. spinax</i>	Longline	LL6-52_LD	21.12	14.88
Masfjord	2021	9	<i>E. spinax</i>	Longline	LL6-58_LD	21.38	20.92
Masfjord	2021	9	<i>E. spinax</i>	Longline	LL6-2_LD	19.7	17.15
Masfjord	2021	9	<i>E. spinax</i>	Longline	LL6-60_LD	11.41	9.67
Masfjord	2021	9	<i>E. spinax</i>	Longline	LL6-44_LD	14.6	12.25
Masfjord	2021	9	<i>E. spinax</i>	Longline	LL6-3_LD	33.77	30.99
Masfjord	2021	9	<i>E. spinax</i>	Longline	LL2-30_LD	22.8	20.39
Masfjord	2021	9	<i>E. spinax</i>	Longline	LL2-50_LD	28.27	25.67
Masfjord	2021	9	<i>E. spinax</i>	Longline	LL2-34_LD	42.84	40.46
Masfjord	2021	9	<i>E. spinax</i>	Longline	LL2-31_LD	60.83	56.26
Masfjord	2021	9	<i>E. spinax</i>	Longline	LL6-47_LD	18.92	15.3
Masfjord	2021	9	<i>E. spinax</i>	Longline	LL6-25_LD	19.14	16.11
Masfjord	2021	9	<i>E. spinax</i>	Longline	LL6-14_LD	21.35	19.02
Masfjord	2021	9	<i>E. spinax</i>	Longline	LL6-41_LD	14.32	10.54
Masfjord	2021	9	<i>E. spinax</i>	Longline	LL6-43_LD	41.65	37.95
Masfjord	2021	9	<i>E. spinax</i>	Longline	LL6-27_LD	49.41	46.99
Masfjord	2021	9	<i>E. spinax</i>	Longline	LL2-53_LD	34.14	24.07
Masfjord	2021	9	<i>E. spinax</i>	Longline	LL2-23_LD	57.02	51.34
Masfjord	2021	9	<i>E. spinax</i>	Longline	LL1-67_LD	32.41	29.18
Masfjord	2021	9	<i>E. spinax</i>	Longline	LL1-48_LD	13.56	11.29
Fensfjord	2021	2	<i>E. spinax</i>	Deep pelagic	152-14-1_LD	37.05	29.93
Fensfjord	2021	2	<i>E. spinax</i>	Deep pelagic	152-14-2_LD	28.31	20.75
Fensfjord	2021	2	<i>E. spinax</i>	Deep pelagic	152-14-3_LD	40.41	30.37
Fensfjord	2021	2	<i>E. spinax</i>	Pelagic	154-21-1_LD	88.52	79.15
Fensfjord	2021	2	<i>E. spinax</i>	Pelagic	154-21-2_LD	26.03	20.06

Fensfjord	2021	2	<i>E. spinax</i>	Pelagic	154-21-3_LD	41.05	34.38
Fensfjord	2021	2	<i>E. spinax</i>	Pelagic	154-21-4_LD	13.05	8.55
Fensfjord	2021	2	<i>E. spinax</i>	Pelagic	156-23-1_LD	50.67	42.49
Fensfjord	2021	2	<i>E. spinax</i>	Pelagic	156-23-2_LD	70.98	60.6
Fensfjord	2021	2	<i>E. spinax</i>	Pelagic	156-23-3_LD	21.36	17.75
Fensfjord	2021	2	<i>E. spinax</i>	Pelagic	156-23-4_LD	18.63	15.65
Fensfjord	2021	2	<i>E. spinax</i>	Pelagic	156-23-5_LD	41.22	32.99
Fensfjord	2021	2	<i>E. spinax</i>	Longline	LL7-3_LD	56.45	46.46
Fensfjord	2021	2	<i>E. spinax</i>	Longline	LL7-47_LD	62.21	34.11
Fensfjord	2021	2	<i>E. spinax</i>	Longline	LL7-77_LD	80.22	72.39
Fensfjord	2021	2	<i>E. spinax</i>	Longline	LL7-1_LD	37.35	34.43
Masfjord	2021	2	<i>E. spinax</i>	Traps	Trap2-94	28.7	25.1
Masfjord	2021	2	<i>E. spinax</i>	Traps	Trap2-84	20.54	17.94
Masfjord	2021	2	<i>E. spinax</i>	Traps	Trap2-86	10.46	8.89
Masfjord	2021	2	<i>E. spinax</i>	Traps	Trap2-98	33	28.52
Masfjord	2021	2	<i>E. spinax</i>	Traps	Trap2-80	21.52	19.08
Masfjord	2021	2	<i>E. spinax</i>	Traps	Trap2-92	50.28	42.7
Masfjord	2021	2	<i>E. spinax</i>	Traps	Trap2-53	15.05	12.77
Masfjord	2021	2	<i>E. spinax</i>	Traps	Trap2-72	53.22	47.32
Masfjord	2021	2	<i>E. spinax</i>	Traps	Trap2-48	24.3	20.57
Masfjord	2021	2	<i>E. spinax</i>	Traps	Trap2-15	31.28	27.5
Masfjord	2021	2	<i>E. spinax</i>	Traps	Trap2-91	14.01	12.14
Masfjord	2021	2	<i>E. spinax</i>	Traps	Trap2-81	27	23.71
Masfjord	2021	2	<i>E. spinax</i>	Traps	Trap2-93	26.93	23.07
Masfjord	2021	2	<i>E. spinax</i>	Traps	Trap2-41	13.19	11.22
Masfjord	2021	2	<i>E. spinax</i>	Traps	Trap2-75	15.68	13.77
Masfjord	2021	2	<i>E. spinax</i>	Traps	Trap2-32	24.11	21.1
Masfjord	2021	2	<i>E. spinax</i>	Traps	Trap2-82	12.4	10.81
Masfjord	2021	2	<i>E. spinax</i>	Traps	Trap2-64	19.55	5.93
Masfjord	2021	2	<i>E. spinax</i>	Traps	Trap2-78	26.53	23.68
Masfjord	2021	2	<i>E. spinax</i>	Traps	Trap2-36	25.92	22.13
Masfjord	2021	2	<i>E. spinax</i>	Traps	trap2-58	22.54	20.1
Masfjord	2021	2	<i>E. spinax</i>	Traps	Trap2-77	20.83	18.19
Masfjord	2021	2	<i>E. spinax</i>	Traps	Trap2-11	26.35	23.71
Masfjord	2021	2	<i>E. spinax</i>	Traps	Trap2-88	28.36	25.48
Masfjord	2021	2	<i>E. spinax</i>	Traps	Trap2-21	28.46	25.32
Masfjord	2021	2	<i>E. spinax</i>	Traps	Trap2-66	15.31	12.88
Masfjord	2021	2	<i>E. spinax</i>	Traps	Trap2-85	23.42	20.91
Masfjord	2021	2	<i>E. spinax</i>	Traps	Trap2-59	18	15.77
Masfjord	2021	2	<i>E. spinax</i>	Traps	Trap2-46	21.61	18.9

Fensfjord	2021	9	<i>E. spinax</i>	Longline	LL12-61	31.4	29.84
Fensfjord	2021	9	<i>E. spinax</i>	Longline	LL12-50	24.65	22.78
Fensfjord	2021	9	<i>E. spinax</i>	Longline	LL12-30	41.76	40.36
Fensfjord	2021	9	<i>E. spinax</i>	Longline	LL12-29	29.47	28.09
Masfjord	2021	9	<i>E. spinax</i>	Longline	LL7-55	23.87	21
Masfjord	2021	9	<i>E. spinax</i>	Longline	LL7-20	23.61	22.16
Masfjord	2021	9	<i>E. spinax</i>	Longline	LL5-52	35.84	33.47
Masfjord	2021	9	<i>E. spinax</i>	Longline	LL5-49	17.47	15.29
Fensfjord	2021	9	<i>E. spinax</i>	Longline	LL12-72	36.37	34.01
Masfjord	2021	9	<i>E. spinax</i>	Longline	LL7-52	19.44	17.84
Masfjord	2021	2	<i>E. spinax</i>	Traps	Trap2-45	10.12	9.02
Masfjord	2021	2	<i>E. spinax</i>	Traps	Trap2-42	25.55	23.8
Masfjord	2021	2	<i>E. spinax</i>	Traps	Trap2-16	6.58	5.51
Masfjord	2021	2	<i>E. spinax</i>	Traps	Trap2-23	17.5	15.51
Masfjord	2021	2	<i>E. spinax</i>	Traps	Trap2-70	21.58	20.06
Masfjord	2021	2	<i>E. spinax</i>	Traps	Trap2-69	22.03	20.36
Masfjord	2021	2	<i>E. spinax</i>	Traps	Trap2-24	25.42	23.42
Masfjord	2021	2	<i>E. spinax</i>	Traps	Trap2-31	21.96	20.12
Masfjord	2021	2	<i>E. spinax</i>	Traps	Trap2-74	23.45	21.98
Masfjord	2021	2	<i>E. spinax</i>	Traps	Trap2-71	44.01	42.22
Masfjord	2021	2	<i>E. spinax</i>	Traps	Trap2-57	22.54	20.76
Masfjord	2021	2	<i>E. spinax</i>	Traps	Trap2-22	23.17	21.44
Masfjord	2021	2	<i>E. spinax</i>	Traps	Trap2-13	22.21	20.41
Masfjord	2021	2	<i>E. spinax</i>	Traps	Trap2-6	15.91	13.77
Masfjord	2021	2	<i>E. spinax</i>	Traps	Trap2-49	30.03	27.69
Masfjord	2021	2	<i>E. spinax</i>	Traps	Trap2-9	23.42	21.38
Masfjord	2021	2	<i>E. spinax</i>	Traps	Trap2-12	25.67	23.67
Masfjord	2021	2	<i>E. spinax</i>	Traps	Trap2-61	22.52	20.78
Masfjord	2021	2	<i>E. spinax</i>	Traps	Trap2-7	18.11	16.42
Masfjord	2021	2	<i>E. spinax</i>	Longline	LL3-4	21.25	19.77
Masfjord	2021	2	<i>E. spinax</i>	Longline	LL3-54	19.33	17.21
Masfjord	2021	2	<i>E. spinax</i>	Longline	LL3-41	21.08	19.42
Masfjord	2021	2	<i>E. spinax</i>	Longline	LL3-70	29.05	26.44
Masfjord	2021	2	<i>E. spinax</i>	Longline	LL3-37	12.56	10.86
Masfjord	2021	2	<i>E. spinax</i>	Longline	LL3-24	22.47	18.54
Masfjord	2021	2	<i>E. spinax</i>	Pelagic	150-8-11	39.32	32.09
Masfjord	2021	2	<i>E. spinax</i>	Pelagic	150-8-7	39.23	34.84
Masfjord	2021	2	<i>E. spinax</i>	Pelagic	150-8-2	25.11	23.42
Masfjord	2021	2	<i>E. spinax</i>	Pelagic	150-8-10	31.36	29.25
Masfjord	2021	2	<i>E. spinax</i>	Pelagic	150-8-6	16.26	14.41

Masfjord	2021	2	<i>E. spinax</i>	Pelagic	150-8-4	26.79	23.74
Masfjord	2021	2	<i>E. spinax</i>	Pelagic	150-8-9	17.77	15.76
Masfjord	2021	2	<i>E. spinax</i>	Pelagic	150-8-8	22.72	20.4
Masfjord	2021	2	<i>E. spinax</i>	Longline	LL3-33	18.23	16.87
Masfjord	2021	2	<i>E. spinax</i>	Longline	2021.mas.LL3. E.s.63	21.88	19.61
Masfjord	2021	2	<i>E. spinax</i>	Longline	LL3-25	25.81	23.99
Masfjord	2021	2	<i>E. spinax</i>	Longline	LL3-60	17.89	15.12
Masfjord	2021	2	<i>E. spinax</i>	Longline	LL4-44	35.75	33.88
Masfjord	2021	2	<i>E. spinax</i>	Longline	LL4-73	15.43	13.17
Masfjord	2021	2	<i>E. spinax</i>	Longline	LL4-77	19.66	18.2
Fensfjord	2021	0	<i>E. spinax</i>	Longline	LL12-26	56.58	54.68
Masfjord	2021	9	<i>E. spinax</i>	Longline	LL7-13	29.7	26.38
Masfjord	2021	9	<i>E. spinax</i>	Longline	LL7-40	26.52	24.42
Masfjord	2021	2	<i>E. spinax</i>	Traps	trap2-60	21.94	19.7
Masfjord	2021	2	<i>E. spinax</i>	Traps	trap2-20	14.14	11.93
Masfjord	2021	2	<i>E. spinax</i>	Traps	trap2-18	43.99	41.64
Masfjord	2021	2	<i>E. spinax</i>	Traps	trap2-10	25.27	22.66
Masfjord	2021	2	<i>E. spinax</i>	Traps	trap2-50	21.46	19.61
Masfjord	2021	2	<i>E. spinax</i>	Traps	trap2-33	20.98	19.35
Masfjord	2021	2	<i>E. spinax</i>	Traps	trap2-19	50.5	47.67
Masfjord	2021	2	<i>E. spinax</i>	Traps	trap2-8	40.11	38.11
Masfjord	2021	2	<i>E. spinax</i>	Traps	trap2-76	27.76	25.47
Fensfjord	2021	2	<i>E. spinax</i>	Pelagic	151-11-1	21.6	19.25
Fensfjord	2021	2	<i>E. spinax</i>	Pelagic	151-11-2	31.9	28
Masfjord	2021	2	<i>E. spinax</i>	Longline	LL3-6	68.65	59.16
Masfjord	2021	2	<i>E. spinax</i>	Pelagic	150-8-3	56.19	51.96
Masfjord	2021	2	<i>E. spinax</i>	Pelagic	150-8-5	49	45.3
Masfjord	2021	2	<i>E. spinax</i>	Pelagic	150-8-1	69	56.63
Masfjord	2021	9	<i>E. spinax</i>	Longline	LL7-30	52.38	48.23
Masfjord	2021	9	<i>E. spinax</i>	Longline	LL7-48	55.79	51.77
Fensfjord	2021	9	<i>E. spinax</i>	Longline	LL12-28	62.27	57.66
Fensfjord	2021	9	<i>E. spinax</i>	Longline	LL9-59	84.53	80.64
Masfjord	2021	2	<i>E. spinax</i>	Traps	Trap2-25	9.03	7.65
Masfjord	2021	2	<i>E. spinax</i>	Traps	Trap2-52	21.19	19.01
Masfjord	2021	2	<i>E. spinax</i>	Traps	Trap2-65	23.36	21.95
Masfjord	2021	2	<i>E. spinax</i>	Traps	Trap2-35	20.53	18.53
Masfjord	2021	2	<i>E. spinax</i>	Traps	Trap2-40	28.21	26.09
Masfjord	2021	2	<i>E. spinax</i>	Traps	Trap2-37	22.37	20.19
Masfjord	2021	2	<i>E. spinax</i>	Traps	Trap2-55	17.3	15.96

Masfjord	2021	2	<i>E. spinax</i>	Traps	Trap2-63	17.42	16.07
Masfjord	2021	2	<i>E. spinax</i>	Traps	Trap2-73	27.33	26.06
Masfjord	2021	2	<i>E. spinax</i>	Traps	Trap2-43	18.52	17.12
Masfjord	2021	2	<i>E. spinax</i>	Traps	Trap2-44	21.49	19.81
Fensfjord	2021	2	<i>E. spinax</i>	Traps	Trap1-1	17.25	16.57
Fensfjord	2021	9	<i>E. spinax</i>	Longline	LL11-72	37.15	35.4
Fensfjord	2021	9	<i>E. spinax</i>	Longline	LL11-69	34.61	32.75
Fensfjord	2021	9	<i>E. spinax</i>	Longline	LL11-70	39.61	37.83
Masfjord	2021	9	<i>E. spinax</i>	Pelagic	215-65-4	34.24	31.79
Fensfjord	2021	2	<i>E. spinax</i>	Traps	Trap1-3	18.07	15.91
Fensfjord	2021	2	<i>E. spinax</i>	Traps	Trap1-5	36.98	32.63
Masfjord	2021	9	<i>E. spinax</i>	Longline	LL6-53_LD	48.65	46.23
Fensfjord	2021	9	<i>E. spinax</i>	Longline	LL11-22	47.39	45.36
Fensfjord	2021	9	<i>E. spinax</i>	Longline	LL11-30	52.56	50.57
Fensfjord	2021	2	<i>E. spinax</i>	Traps	Trap1-4	78.56	72.28
Fensfjord	2021	2	<i>E. spinax</i>	Traps	Trap1-6	68.08	63.09
Fensfjord	2021	9	<i>E. spinax</i>	Longline	LL9-74	53.85	47.6
Fensfjord	2021	9	<i>E. spinax</i>	Longline	LL9-67	27.47	20.08
Fensfjord	2021	9	<i>E. spinax</i>	Longline	LL10-71	57.06	51.4
Fensfjord	2021	2	<i>E. spinax</i>	Traps	Trap1-2	120.63	110.96
Masfjord	2021	9	<i>E. spinax</i>	Pelagic	215-65-1	67.72	63.08
Fensfjord	2021	9	<i>E. spinax</i>	Longline	LL11-7	57.84	53.96
Fensfjord	2021	9	<i>E. spinax</i>	Longline	LL11-40	86.84	72.82

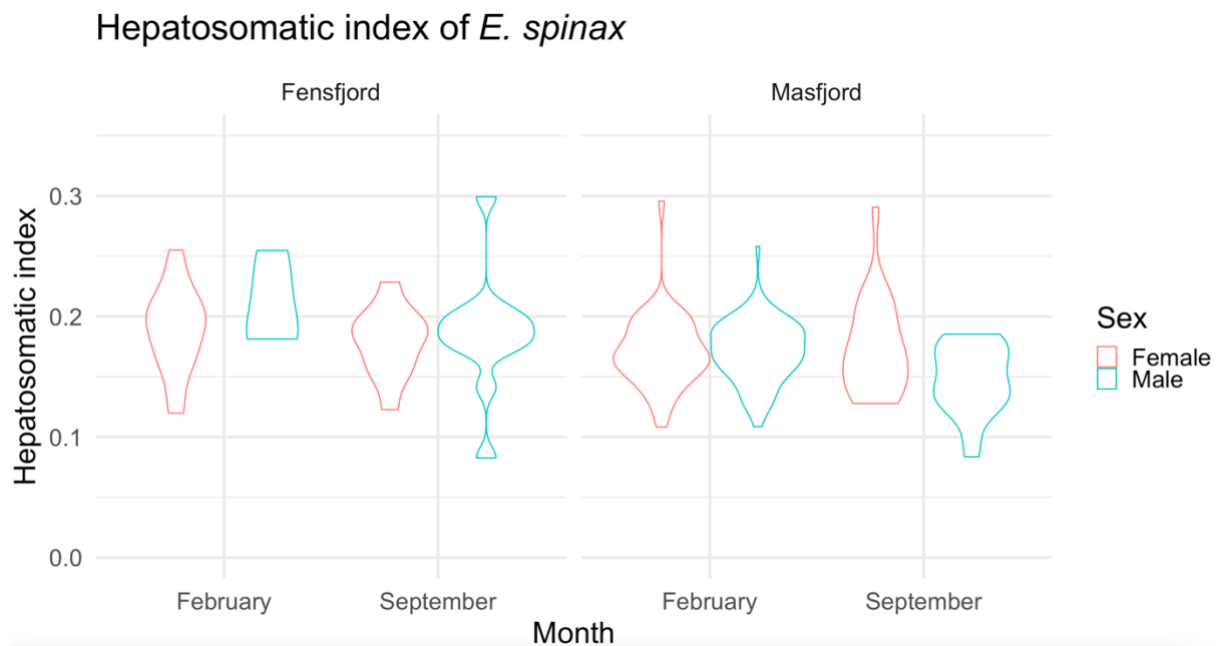


Figure E1: The hepatosomatic index (HSI) from equation 1 plotted for *E. spinax* and is separated by fjord, and sex.

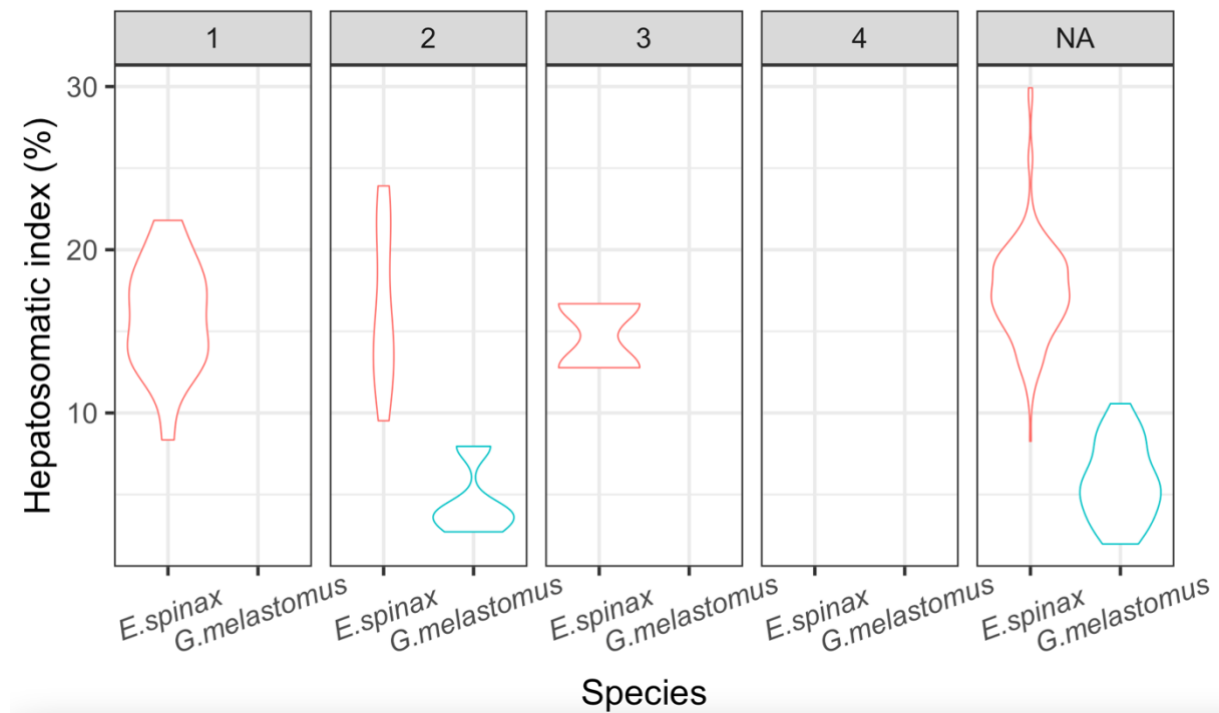


Figure E2: The hepatosomatic index (HSI) from equation 1 was plotted for *E. spinax* (red) and *G. melastomus* (blue), separated by maturation stages 1-4 +NA. Maturation stages are defined in Table 1.

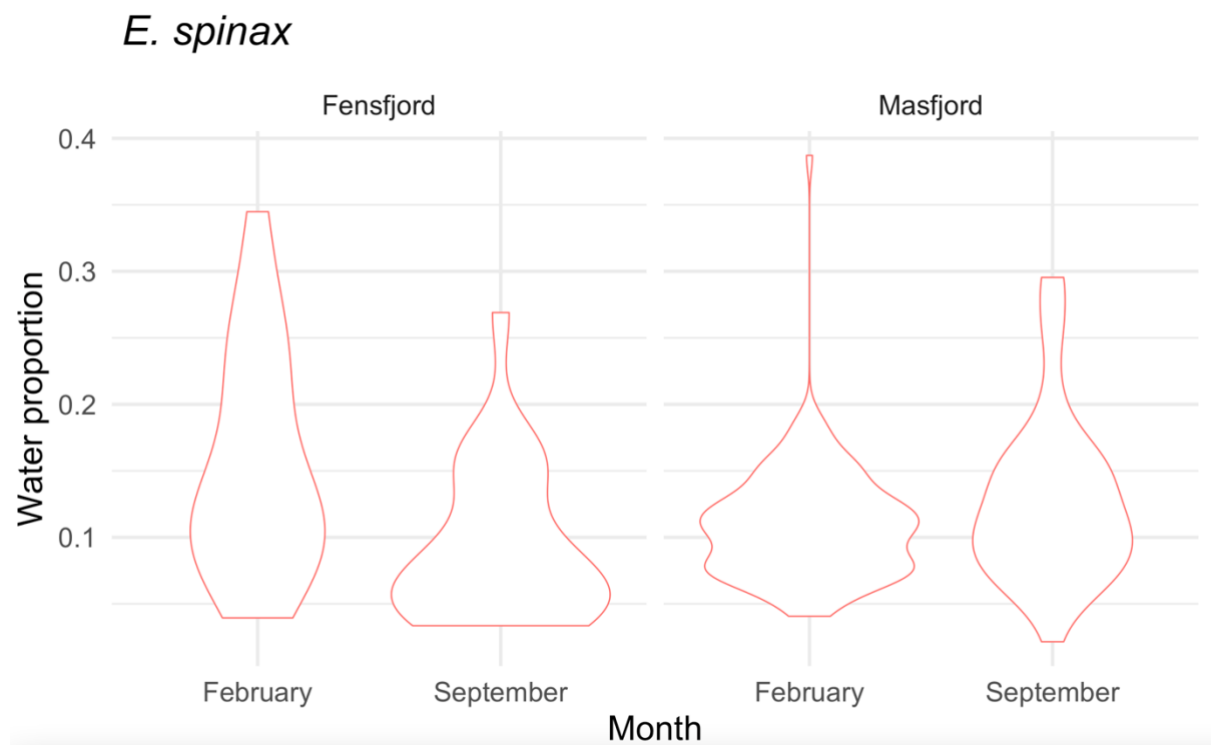


Figure E3: The total proportion of water in the livers of *E. spinax*, separated by fjord and month. The water content was calculated using Equation 2-3.

Appendix F – Statistical analyses

Table F1: Summary output of the best fitted linear model (lm) for $\delta^{13}C$ in Stable isotope analysis. Species, sex, and fjord were used as predictor variables.

Coefficients	Estimate	Std. error	t-value	p-value
(Intercept)	-18.9215	0.1768	-1.07E+02	2.00E-16***
SpeciesG.melastomus	1.5444	2.06E-01	7.503	5.10E-10***
fjordMasfjord	-0.4042	0.2061	-1.961	0.0549.
sexMale	0.4142	0.1992	2.079	0.0422*

Signif.codes: 0 '***' 0.001 '**' 0.01 '*' 0.05 '.' 0.1 ' ' 1

R-sq (adj) = 0.5357

Table F2: Summary output of the best fitted linear model (lm) for $\delta^{15}N$ in Stable isotope analysis. Species, sex, and fjord were used as predictor variables.

Coefficients	Estimate	Std. Error	t-value	p-value
(Intercept)	13.3733	0.1824	73.312	2.00E-16***
SpeciesG.melastomus	2.1787	0.2124	10.259	1.80E-14***
fjordMasfjord	-0.5656	0.2127	-2.659	0.0102*
sexMale	0.3882	0.2056	1.888	0.0642.

Signif.codes: 0 '***' 0.001 '**' 0.01 '*' 0.05 '.' 0.1 ' ' 1

R-sq (adj) = 0.6714

Table F3: Summary output from the best fitted linear model (lm) for liver weight (g) in liver analysis. Species, weight (g), and fjord were used as predictor variables, and an interaction term was included ($p < 0.05$).

Coefficients:	Estimate	Std. Error	t-value	p-value
(Intercept)	3.571154	1.839867	1.941	0.053487.
speciesG.melastomus	4.607698	3.155891	1.46E+00	0.145652
weight.g	0.175575	0.00644	2.73E+01	2.00E-16***
fjordMasfjord	-4.817985	1.258436	-3.829	0.000166***
speciesG.melastomus:weight.g	-0.130042	0.009068	-1.43E+01	2.00E-16***

Signif.codes: 0 '***' 0.001 '**' 0.01 '*' 0.05 '.' 0.1 ' ' 1

R-sq (adj) = 0.8258

Table F4: Summary output from the best fitted generalized linear model (glm) for HSI in liver analysis, with data from Masfjord only. Species, month sex and length (cm) were used as predictor variables.

Coefficients	Estimate	Std. Error	t-value	p-value
(Intercept)	-1.93853	0.131773	-14.711	<2e-16***
speciesG.melastomus	-1.196312	0.087211	-13.717	<2e-16***
month	-0.01204	0.004863	-2.476	0.0142*
sexm	-0.040558	3.02E-02	-1.344	0.1807
length.cm	0.006603	3.72E-03	1.78E+00	7.75E-02.
Signif.codes: 0 '***' 0.001 '**' 0.01 '*' 0.05 '.' 0.1 ' ' 1				

Table F5: Summary output from the best fitted generalized linear model (glm) for water proportion in liver analysis, with data from Masfjord only. Species, month sex and length (cm) were used as predictor variables.

Coefficients	Estimate	Std. Error	t-value	p-value
(Intercept)	-2.199227	0.341789	-6.434	1.13E-09***
speciesG.melastomus	1.448517	0.158304	9.15	2.00E-16***
month	0.038027	0.012427	3.06E+00	0.00256***
SexMale	0.125417	0.082178	1.53E+00	1.29E-01
length.cm	-0.00243	0.009715	-0.25	0.80276
Signif.codes: 0 '***' 0.001 '**' 0.01 '*' 0.05 '.' 0.1 ' ' 1				

Table F6: Summary output from the best fitted generalized linear model (glm) for water proportion from *E. spinax* only. Fjord, month, and sex were used as predictor variables.

Coefficients	Estimate	Std. Error	t-value	p-value
(Intercept)	-1.965593	0.109278	-17.987	<2e-16***
fjordMasfjord	-0.085638	0.096892	-0.884	0.378
month	-0.003133	0.012132	-0.258	7.97E-01
SexMale	0.022338	0.080002	0.279	0.78
Signif.codes: 0 '***' 0.001 '**' 0.01 '*' 0.05 '.' 0.1 ' ' 1				