

Trophic interactions in the mesopelagic layer along the continental slope in the Norwegian Sea

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Research Article

Keywords: fish diet, Calanus, Myctophids, stomach contents, stable isotopes

Posted Date: September 30th, 2026

DOI: <https://doi.org/10.21203/rs.3.rs-11063133/v1>

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Additional Declarations: No competing interests reported.

Abstract

Mesopelagic layers are arguably one of the least documented components of marine ecosystems, especially regarding the nature and scale of the biological processes occurring there. Large amounts of biomass transit through the mesopelagic layer, where trophic interactions involve species from different pelagic zones, and vertical fluxes transfer biomass into the deeper layers. Characterizing these processes requires extensive datasets that are severely lacking, especially in polar areas. Here, we gathered gut contents and stable isotope data from zooplankton to fish in a subpolar mesopelagic layer along the northern Norwegian coast. We highlighted the key roles played by a few species in this ecosystem, especially at the lower trophic levels. Higher in the trophic chain, some fish species exhibited strong prey selectivity, potentially resulting in a reduced capacity to cope with environmental change. This kind of information is relevant to the sustainable management of these ecosystems.

INTRODUCTION

Over the past decades, the anthropogenic pressure on marine ecosystems has intensified (Halpern et al., 2019). In polar areas, climate change has been shown to be particularly pronounced, with an increase in water temperature well above the world average (Post et al., 2019). In the Arctic, ice retreat might also result in the development of potentially harmful practices such as fuel and mineral exploitation, as well as an extension of fishing effort, with expected ecological and social consequences (Hanaček et al., 2022). These multiple stressors and their interactions affect both directly and indirectly all components of the marine food web, including the mesopelagic communities (Doney et al., 2011, Heneghan et al., 2021, Henson et al., 2017, Hoegh-Guldberg & Bruno, 2010). Significant changes in population phenology and spatial distribution are likely (Hazen et al., 2013, Heneghan et al., 2023, Kortsch et al., 2015), as well as alterations of biomass transfer along the trophic chain (Arimitsu et al., 2021, Atkinson et al., 2024).

Changes in biomass production and its subsequent transfer can result in dramatic consequences. For example, the biological pump, which currently buffers the increase in carbon dioxide in the atmosphere, was altered over the last decades (Brun et al., 2019). This process consists in biomass synthesized by autotrophic organisms in the epipelagic layer and then sedimenting both passively and actively towards the sea bottom (Volk & Hoffert, 1985). The active part of the biological pump relies on species migrating vertically along the water column (Brierley, 2014, Kobari et al., 2008). Diel vertical migration of herbivorous zooplankton and mesopelagic fishes is an integral part of this sinking process (Brun et al., 2019, Davison et al., 2013, Sarmiento-Lezcano et al., 2022). The overall abundance of mesopelagic fishes, and their importance regarding the biological pump, has been significantly revised upward (Irigoién et al., 2014). Through their vertical migrations, these species actively transport biomass from the epipelagic to the mesopelagic zone. In the mesopelagic, remineralization of marine snow by bacteria occurs at lower rates than in the surface layers, hence allowing more biomass to sediment (Marsay et al., 2015).

A good understanding of the trophic structure is required to identify the mechanisms driving biomass transfer along the food web as well as toward the ocean depths. However, describing trophodynamics is a challenging process that requires high resolution observations that are often lacking in polar areas (Murphy et al., 2016). This is due to the challenges associated with sampling deeper layers in the ocean, especially in regions which are already notoriously difficult to monitor all year round. The lack of fundamental ecological data is hampering our efforts to reveal major trophic pathways and identify crucial links within these pathways, where any disruption could lead to collapse in predator populations and / or changes in biomass sinking rates (Wassmann et al., 2011). Different approaches can provide information on trophic structure. Traditionally, analysis of stomach contents was used to describe recent food items ingested by predators. As a complementary approach, biogeochemical tracers, such as stable isotopes (SI), have proven useful to describe trophic structure across a larger part of the trophic chain (Post, 2002). While $\delta^{15}\text{N}$ is used to reveal the trophic levels due to its enrichment between levels, $\delta^{13}\text{C}$ is primarily used to define the sources of the studied food chain (e.g., benthos vs pelagic, coastal vs offshore). Used together, they allow the isotopic niche of a population to be defined, which gives information on its diet flexibility (e.g., Matich et al., 2011).

The continental margin along the northern Norwegian coast lies at the transition between temperate and polar conditions, providing favourable conditions for life development. This very productive area is characterized by large stocks of pelagic fish, including cod, capelin, herring and mackerel, supporting some of the world's largest fisheries (Skjoldal et al., 2004). In this study, we utilize a dataset that combines isotopic composition and stomach content description of samples collected along the continental slope in Northern Norway. Our aims were to describe the trophic structure and interactions from zooplankton to fish in the mesopelagic layer, characterize fish feeding behavior, and identify key species within the biomass pathway.

MATERIALS AND METHODS

Research cruise and study site

The samples were collected during a scientific cruise within the NRC-financed project STRESSOR conducted from April 27 to May 12, 2019 on board the RV Helmer Hanssen. A total of 11 stations were visited, distributed as follows: one coastal station, nine slope stations and one offshore station (Fig. 1). In addition, three transects crossing the shelf from the coast to the open ocean were sampled for environmental data. The study area was located in the northern Norwegian Sea at about 69°N. The area is characterized by a relatively wide and deep continental shelf (average depth ca. 200 m) separating a coastline cut by fjords and a steep slope leading to the open ocean (bottom depth ca 3000 m). The oceanic circulation in the area includes the Norwegian Coastal Current, which flows northward in the surface layer along the coast and the Norwegian Atlantic Current, also flowing northward along the continental slope further offshore and occupying the mid-depth layer. The Norwegian Atlantic Current is a branch of the North Atlantic Current transporting warmer and saltier waters northward. It plays an important role in the life dynamics of several species, including arguably the most important food source

at the base of the food web in the North Atlantic Ocean, the *Calanus* spp. copepods (Pershing & Stamieszkin, 2020).

Sampling at discrete stations

The mesopelagic layer was sampled on 14 occasions across 11 stations (i.e., three duplicates) using a Harstad pelagic trawl with an 8 mm mesh net towed at three knots for 20 minutes (Table 1). The opening of the trawl was 8 by 12 m resulting in a total volume of water sampled of ca 180 000 m³ for each sampling event. The location of the mesopelagic layer (biomass peak usually occurring between 200 and 400 m depth) along the water column was identified based on 38 kHz echosounder data displayed live onboard. Trawl samples were directly processed onboard in the laboratory facilities. Most fish and macrozooplankton were counted and measured to estimate abundance and biomass. If a large number of individuals from the same species were caught, only a sub-sample was processed. In addition, the mesozooplankton community was sampled using a Multinet midi (180 µm mesh size, 0.25 m² mouth area; Hydrobios) that was deployed vertically from 600 m depth (or bottom) to the surface. Stage V copepodites of *Calanus finmarchicus* were identified and counted under a microscope. They were specifically targeted because they were the most numerous organisms among all samples (both in terms of abundance and occurrence) and they are suitable as trophic / isotopic baseline (Espinasse et al., 2022).

Sampling along transects

Temperature and salinity were measured along three transects crossing the continental shelf using a MVP-LOPC-CTD-F system (Herman et al., 2004). A fluorometer (F) was used to provide an index of chlorophyll a concentrations (chl_a). *In situ* fluorescence values were calibrated against laboratory analyses of discrete water sampling along the water column. The Laser Optical Plankton Counter (LOPC) concurrently provided quasi continuous distribution of particles and plankton along the transect. The abundance of large copepods (mostly *Calanus*) was determined based on the size and opacity of the particles (Basedow et al., 2014).

Table 1. Description of sampling stations. Station numbering: C - continental shelf; S - slope; O - offshore; from 1 to 9 going eastward. * Sampled twice.

Stations	Date	Latitude (°N)	Longitude (°E)	Bottom depth (m)	Sampling depth (m)	Multinet
C1	29.04.2019	68.28	13.28	151	135	Yes
S1	30.04.2019	68.90	12.08	2572	290	Yes
*S2	30.04.2019	68.74	12.43	306	200/600	Yes
S3	03.05.2019	69.01	12.91	1953	230	Yes
S4	09.05.2019	69.05	13.23	2390	265	No
S5	08.05.2019	68.98	13.46	443	200	No
S6	09.05.2019	69.02	13.61	718	200	No
*S7	09.05.2019	69.21	13.91	1995	300/375	Yes
*S8	05.05.2019	69.10	14.03	908	220/300	Yes
S9	10.05.2019	69.11	14.24	597	300	No
O1	04.05.2019	69.50	13.33	2771	280	Yes

Stomach content analysis

The stomachs of most predators were processed on board in order to identify, count and weigh ingested items. Taxonomic identification was done to the lowest taxonomic level possible. When it was not possible to process all the fish, the stomachs were conserved in ethanol for further analyses at university facilities.

Stable isotope analysis

Selected predator and prey samples were conserved in a freezer at -20°C for stable isotope analysis. The samples were then processed at the university laboratory. For small-sized organisms, the entire body was used for analyses. For the fish, a piece of muscle was excised from the dorsal part. All samples were dried for 48 h at 50°C in an oven before being ground to a homogeneous powder using a mortar and pestle. The samples were packed in tin caps and sent to LIENSs Stable Isotope Facility for analysis. Isotopic ratios of carbon ($\delta^{13}\text{C}$) and nitrogen ($\delta^{15}\text{N}$) were measured with a continuous-flow isotope ratio mass spectrometer (DeltaV Advantage, Thermo Scientific, Bremen, Germany) coupled to an elemental analyzer (Flash EA1112 Thermo Scientific, Milan, Italy). Isotope values were expressed in parts per thousand (‰) relative to Vienna PeeDee Belemnite and atmospheric N_2 for $\delta^{13}\text{C}$ and $\delta^{15}\text{N}$, respectively, using the equation: $\delta x = ((R_{\text{sample}}/R_{\text{standard}}) - 1) \times 1000$, where x is ^{13}C or ^{15}N and R is the isotope ratio $^{13}\text{C}/^{12}\text{C}$ or $^{15}\text{N}/^{14}\text{N}$, respectively. The calibration of the isotope ratio mass spectrometer was done by measuring the secondary reference material USGS61 and USGS62, provided by the International Atomic Energy Agency (IAEA, Vienna). For both $\delta^{13}\text{C}$ and $\delta^{15}\text{N}$, the measurement precision was < 0.1‰.

RESULTS

Environmental conditions

The influence of coastal waters, characterized by relatively low salinity (< 34.8), was found in the surface layer from the shelf to the slope along the T2 transect and even further offshore along the T3 transect (Fig. 2). In the top 300 m, water temperature was slightly higher over the slope for the three transects ($> 6^{\circ}\text{C}$) and decreased below 500 m depth ($< 4^{\circ}\text{C}$) (Fig. S1). Chla concentrations were generally higher in the epipelagic layer over the slope and further offshore, with higher values occurring in the southern part of the study area where a bloom event occurred ($> 5 \text{ mg m}^{-3}$).

Spatial distribution

Calanus abundances were found to be generally higher in the northern part of the study area, based on both transect and discrete sampling data (Fig. 3). Dense aggregations occurred within thin layers in the coastal area in the south, and spread offshore going northward. The krill species *Meganyctiphanes norvegica* was ubiquitous over the study area and was observed at every sampling occasion but one (Table 2; Fig. 3). Higher concentrations were found above the continental slope. Smaller krill of the genus *Thysanoessa* were found at only half of the slope stations and was absent offshore. Higher abundances were measured at the coastal station (C1). Blue whiting (*Micromesistius poutassou*) was the most commonly found fish species, occurring at most slope stations and the offshore station (Table 3). Among the mesopelagic fishes, *Benthoosema* sp. occupied the southwestern part of the study area while *Maurolicus* sp. occurred mainly in the northeastern part as well as at the coastal station. None of these species were found at the offshore station.

Table 2

Description of the zooplankton community sampled using Multinet (i.e., *Calanus* and *Paraeuchaeta*) and trawl.

Species	Abbreviation	# isotope samples	# observations (# trawls)	Total biomass (g)	Average density (ind m^{-3})
<i>Calanus finmarchicus</i>	Calanus	3	na	na	39.65
<i>Paraeuchaeta</i> spp.	Paraeuchaeta	1	na	na	0.07
<i>Thysanoessa</i> spp.	Thysanoessa	4	26556 (8)	2156	$6.20 \cdot 10^{-3}$
<i>Meganyctiphanes norvegica</i>	Meganyctiphanes	7	19654 (13)	4278	$7.87 \cdot 10^{-3}$
<i>Themisto</i> spp.	Themisto	3	449 (10)	52	$0.17 \cdot 10^{-3}$
<i>Clione limacina</i>	Clione limacina	3	143 (5)	10	-
<i>Pasiphae</i> spp.	Pasiphae	2	84 (7)	-	$0.03 \cdot 10^{-3}$
<i>Pandalus</i> spp.	Pandalus	1	33 (2)	-	-
<i>Periphylla periphylla</i>	Periphylla	1	17 (10)	8200	$0.006 \cdot 10^{-3}$
<i>Siphonophore</i>	Siphonophore	2	-	-	-

Table 3

Description of the nekton community sampled over 14 trawls conducted in the bioacoustic mesopelagic layer. Information related to stable isotope analysis and stomach content is shown.

Species	Abbreviation	# observations (# trawls)	# isotope samples	Total # stomach analysed (% empty)	Total stomach content composition
<i>Micromesistius poutassou</i>	Blue whiting	131 (9)	5	26 (46%)	Thysanoessa (47), Themisto (8), Meganyctiphanes (1)
<i>Pollachius virens</i>	Saithe	9 (5)	4	9 (44%)	Thysanoessa (392), Meganyctiphanes (34), Fish spine (9), Clione (6), Myctophid (1)
<i>Merlangius merlangus</i>	Whiting	8 (1)	1	8 (62%)	Meganyctiphanes (4), Thysanoessa (3), Blue whiting (1)
<i>Clupea harengus</i>	Herring	6 (4)	3	6 (16%)	Thysanoessa (16)
<i>Melanogrammus aeglefinus</i>	Haddock	3 (2)	1	3 (66%)	Meganyctiphanes (26)
<i>Sebastes mentella</i>	Sebastes	1 (1)	1	1 (100%)	na
<i>Reinhardtius hippoglossoides</i>	Greenland halibut	1 (1)	1	1 (0%)	Pandalus (3)
<i>Gadus morhua</i>	Atlantic cod	2 (2)	1	2 (50%)	Meganyctiphanes (3)
<i>Arctozenus rissoi</i>	Barracudina	1 (1)	1	1 (0%)	unidentified
<i>Benthoosema glaciale</i>	Benthoosema	406 (10)	4	0	na
<i>Maurolicus muelleri</i>	Maurolicus	243 (9)	5	0	na
<i>Notoscopelus kroyeri</i>	Lancet fish	1 (1)	1	0	na

Diet characteristics

The feeding preference of organisms was investigated using stomach contents and isotopic composition of predators and prey. Euphausiids were the most common and abundant prey found in stomach contents (Table 3). The herring diet relied solely on *Thysanoessa*. Blue whiting fed mainly on

Thysanoessa, also occasionally foraging on other prey. Saithe and whiting showed a wider range of prey including pteropods and other fish. These tendencies were supported by the description of the isotopic niches of these species (Fig. 4). Herring (*Clupea harengus*), *Benthosema* and blue whiting showed small dispersion in their isotopic values (albeit one outlier for blue whiting, corresponding to the deep trawl at S2) (Fig. 4). On the other hand, saithe and *Maurolicus* had larger isotopic niches implying foraging on a wider range of food sources.

Trophic structure

Ranking species or groups of species based on their nitrogen isotopic composition (i.e., $\delta^{15}\text{N}$) can be used to determine the trophic structure. The trophic level (TL) of a given species is calculated using an isotopic baseline and a trophic fractionation or trophic discrimination factor. We present results based on two different estimations of the trophic discrimination factor (TDF), the linear estimation (Post, 2002) and the narrowing estimation (Hussey et al., 2014). *Calanus spp.* were situated at the base of the food web with $\delta^{15}\text{N}$ values slightly below 7‰ (Fig. 5). As herbivorous zooplankton, they were assumed to belong to the trophic level 2. Euphausiids and Themisto were found half a trophic level higher. Herring and blue whiting were estimated to occupy TL 3 or slightly higher using linear or narrowing increments, respectively. Mesopelagic fish, *Benthosema* and *Maurolicus* were found at TL 3.5. Saithe and Atlantic cod were estimated to occupy TL 4 using the narrowing TDF. Trophic positions can also be estimated based on stomach content. Saithe and whiting, partly feeding on other fish species, occupied the top of the trophic chain (Table 3). Based on isotopic values, among euphausiid species *Meganyctiphanes* stood slightly above *Thysanoessa*. Herring, which only fed on *Thysanoessa*, were therefore the fish with the lowest trophic position, with blue whiting being slightly above. This is consistent with results based on isotopic composition.

DISCUSSION

Despite being some of the richest environments in the marine realm, interactions in the mesopelagic layer of polar regions are poorly documented. In this study, we provided some insights into the feeding habits of the main species dwelling along the Norwegian coast in a subpolar mesopelagic layer. Main findings, including spatial niche partitioning, characteristics of trophic interactions and feeding selectivity, will be discussed from lower to higher trophic levels.

Zooplankton distribution and trophic interactions

As a key source of food for the entire trophic chain, *Calanus* ecology has been extensively studied over the past decades (e.g., Falk-Petersen et al., 2009, Heath et al., 2000, Melle et al., 2014). Along the Norwegian coast, several species of fish rely at different points of their life cycle on *Calanus* availability. The timing, location and intensity of *Calanus* blooms are crucial factors determining recruitment success, body condition or migration pathways of fish and fish larvae (Beaugrand et al., 2003, Melle et al., 2020). They are also a major food source for mesopelagic fish (Pepin, 2013). Continental slopes are

known to be extremely productive environments (Levin & Dayton, 2009), and along the northern Norwegian coast the inputs of *Calanus* both from offshore deep water and from the coastal area ensure a large supply of prey over an extended period for predators (Basedow et al., 2024, Espinasse et al., 2016). The cross-shelf / offshelf exchanges of water are a major mechanism in shaping *Calanus* distribution (Dong et al., 2021, Halvorsen et al., 2003). Particular bathymetrical features such as canyons often play a role as entry / exit points (Eiane et al., 2018, Espinasse et al., 2017). While the focus is usually placed on transport of offshelf populations onto the shelf and the fish spawning grounds, individuals dwelling in the surface layer can also be advected offshore (Weidberg et al., 2022). During our survey, *Calanus* abundances were the highest in the top 100 m and their horizontal distribution appeared to follow low salinity waters, implying an offshore transport. The highest abundances were found in front of the Hola trough, an area known for its occasional cross shelf circulation patterns (Eiane et al., 2018).

While *Thysanoessa* individuals were not identified to species level, they are assumed to be mainly *T. inermis*, which is the common species occurring in subpolar shelf ecosystems (Dalpadado, 2006). Together with *Meganyctiphanes norvegica*, these two krill species occupied the study area, with *T. inermis* dominating on the shelf and *M. norvegica* over the continental slope. *T. inermis* is considered mainly herbivorous while *M. norvegica* is known to feed frequently on copepods (Dalpadado et al., 2008). This is consistent with the slightly higher $\delta^{15}\text{N}$ values measured in *M. norvegica* compared to *T. inermis*.

Planktivorous fish

Myctophid fish, represented by *Benthosema glaciale* and *Maurolicus muelleri*, were the most abundant fish species collected during our survey. Both species usually dominate the abundances within the mesopelagic layers in the North Atlantic (Dalpadado et al., 1998, Klevjer et al., 2020). *M. muelleri* is a pseudo-oceanic species found frequently near the shelf, while *B. glaciale* is widely distributed across the pelagic realm. This is in line with our results as *Benthosema* occurred at the deepest stations over the shelf break and *M. muelleri* was found at shallower stations and onto the shelf. Interestingly, while *Benthosema* are known to feed on copepods (Knutzen et al., 2023, Pepin, 2013), their distributions did not match *Calanus* distributions but rather areas of higher phytoplankton concentration. In the Northeast Atlantic, *B. glaciale* was reported to start spawning in May (Gjøsæter, 1981), matching phytoplankton bloom development, which could provide favourable conditions for larval development, as larvae feed on smaller prey than adults (Dove et al., 2021).

Together with blue whiting, herring were the only small pelagic fish collected during our survey. Individuals were caught on four different occasions and all of them fed exclusively on *Thysanoessa* spp.. This is rather peculiar for a species which is known to feed on an extensive range of prey (Bachiller et al., 2016, Prokopchuk & Sentyabov, 2006, Trenkel et al., 2014), but not unprecedented (Dalpadado et al., 2000). Blue whiting were found widely across our study area (9 out of 14 trawls) and showed a broader diet including euphausiids and amphipods, which is in agreement with previous observations (Bachiller et al., 2016, Prokopchuk & Sentyabov, 2006, Trenkel et al., 2014).

Large-sized fish

Saithe were collected on five occasions with individual length ranging from 41 to 80 cm. Potentially due to the wide size range, they showed the broadest diet among fish, including euphausiids, pteropods and small fish, which is in agreement with the literature (Homrum et al., 2012). They also have the widest range of SI values (taking into account both $\delta^{15}\text{N}$ and $\delta^{13}\text{C}$), implying variations in prey trophic levels. Interestingly, a myctophid was found in the stomach of one of the saithe. Saithe distribution along the water column overlaps with the vertical distribution of myctophids (Rosen & Holst, 2013) and the latter could represent an interesting alternative source of food when other prey are scarce. At the deepest trawl (600 m depth), one saithe (length of 42 cm) was caught with its stomach 90% full, containing exclusively *Thysanoessa* (174 individuals). The average length for intact individuals in the stomach was 16.7 mm ($n = 90$; SD: 2.8 mm) compared to 23.0 mm ($n = 28$; SD: 3.0 mm) for the individuals caught in the field. Saithe are able to feed on prey of length up to 20% of their body length (Floeter & Temming, 2005, Scharf et al., 2000) and have therefore the physical ability to feed on larger euphausiids. We suggest that when prey abundance is not a limiting factor, this specific size of euphausiids could represent, for a 42 cm-long fish, the optimal balance between the amount of energy required to catch the prey relative to the amount of energy provided by its ingestion (Pinnegar et al., 2003).

Comparison of SI and stomach content results

Stomach content and SI approaches have been used extensively in monitoring programs over the last decades. Each has its own strengths and weaknesses, but they are overall very complementary and are particularly efficient to detail trophic structure and interactions when used in combination (Davis et al., 2012, Parzanini et al., 2019). Very briefly, gut content analysis has the advantage of providing species identification but is time consuming and only shows a snapshot of the individual's diet. On the other hand, SI analyses are relatively easy to perform and they provide information integrated over different time periods depending on the type of tissue analyzed but the interpretation of the values can be somewhat difficult. During our study, both approaches produced broadly consistent results. Using the narrowing increment to calculate TL based on $\delta^{15}\text{N}$ enrichment (Hussey et al., 2014) resulted in a better fit to the trophic structure outlined by stomach content analysis. In addition, the SI values proved useful to establish the TL of macrozooplankton species, usually representing the TL3 of the food web and for which no gut contents data can be obtained. It allows differentiation between species whose diets tend toward either planktivory or herbivory (e.g., *Meganyctiphanes* vs *Thysanoessa*), and in turn to explain differences in the TLs of fish feeding on them.

Conclusion

This study illustrates the value of combining these two complementary approaches and highlights the potential of this type of data, which are currently scarce in polar areas. Although a larger dataset will be needed to get an exhaustive view of the mesopelagic system, our data highlight feeding preferences and trophic linkages for some of the most abundant fish species. A good understanding of fish specific feeding behaviour is required to assess how resilient a given species will be when facing a stressor. Fish species with a narrow diet, identified as specialist species, are indeed more likely to be affected by

changes in their prey field. Accounting for this vulnerability is necessary to develop adequate management plans.

Declarations

ACKNOWLEDGEMENTS

We thank Guillaume Schuler for help with the sample collection. The captain and crew of R/V 'Helmer Hanssen' are thanked for great support.

FUNDING

This study was funded by the Norwegian Research Council as part of the project 'Collaborative Studies of Two Resource Ecosystems in Shelf, Slope and Oceanic Regions of the Norwegian and South-China Seas (STRESSOR)', project number 287042.

Author Contribution Statement

BE processed the samples, analyzed the data, and wrote the first draft of the manuscript. **SB** collected the samples, polished the manuscript, and secured the funding. All authors have read and agreed to the published version of the manuscript.

Conflict of interest

The authors declare that they have no conflict of interest.

Data availability statements

Data will be made available upon request to the corresponding author.

Ethics declaration

Not applicable

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Figures

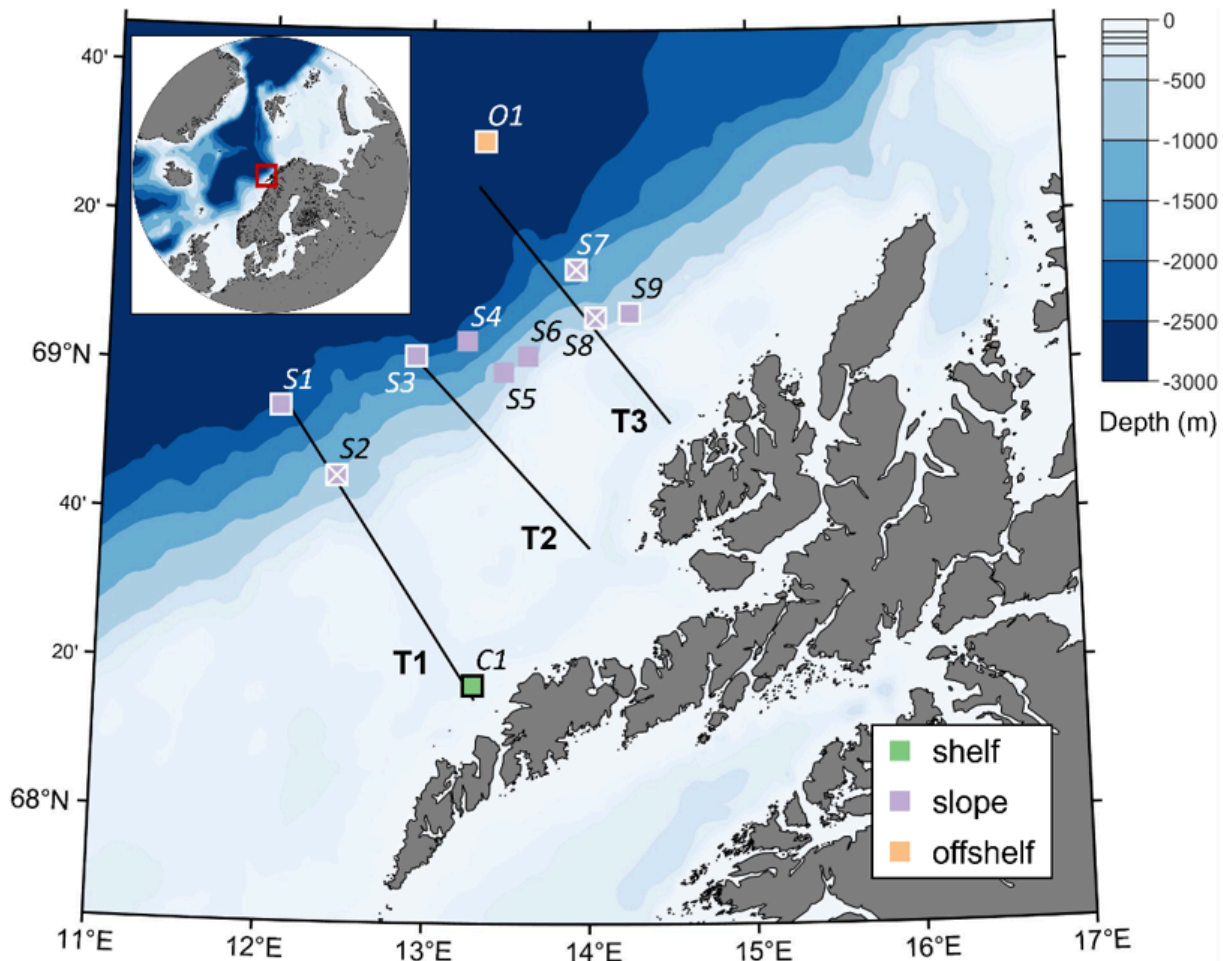


Figure 1

Map of the stations sampled during the STRESSOR cruise (May 2019) in Northern Norway. Temperature, salinity, chl-a concentrations and zooplankton density were sampled along 3 transects (T1-3) using a MVP-LOPC. In addition, 11 stations were sampled with a trawl, some of them two times (crossed square). At some of these stations (bordered squares) a multinet was used to sample mesozooplankton communities. The location of the study area at larger spatial scale is displayed in the embedded top left map (red frame).

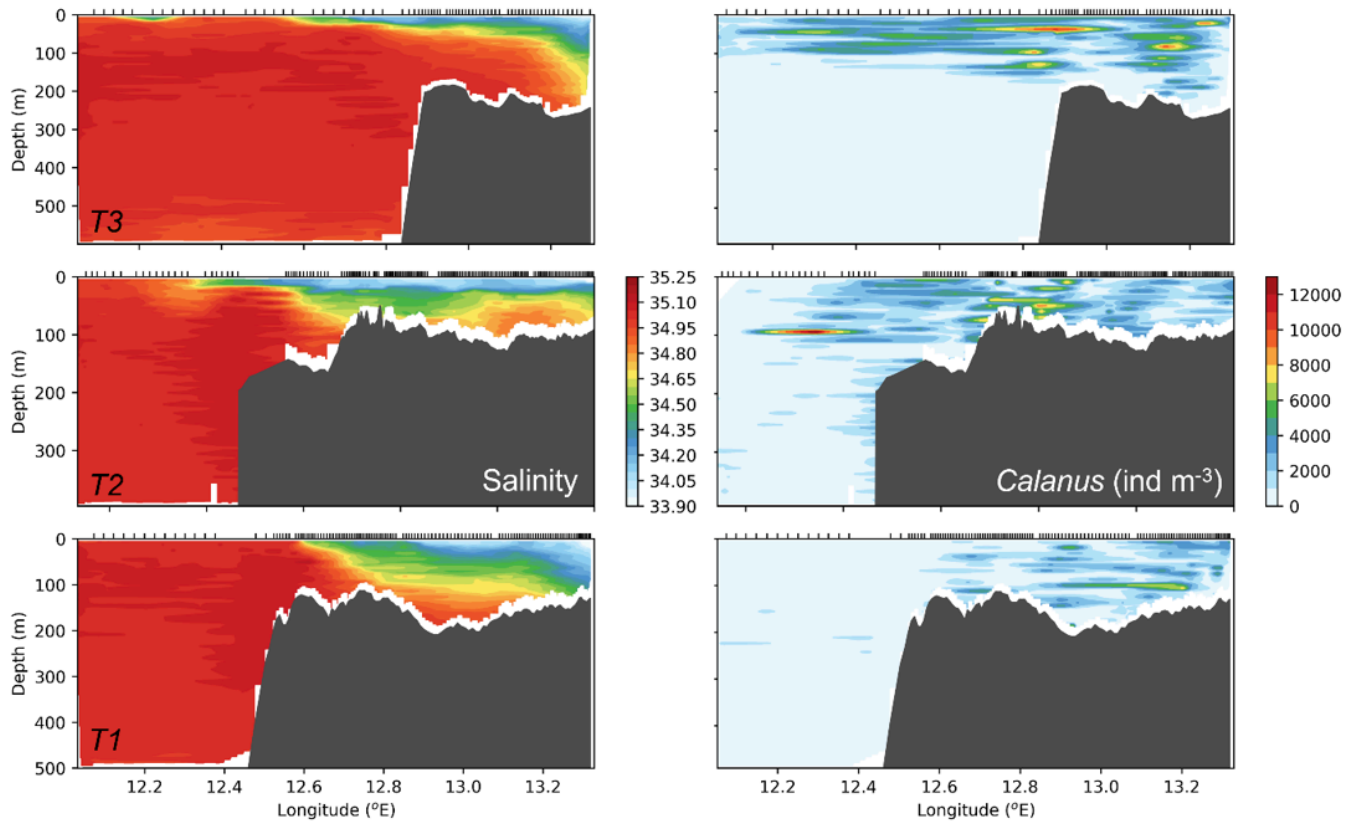


Figure 2

Salinity and *Calanus* density (ind m⁻³) sampled along three coast to offshore transects displayed from North (T3) to South (T1); see Fig.1 for locations, longitude data are only provided for T1 transect. Data were collected using a MVP equipped with a CTD and a LOPC. The ticks on the upper side of the plot frames show the location of the downward profiles used for the data extrapolation.

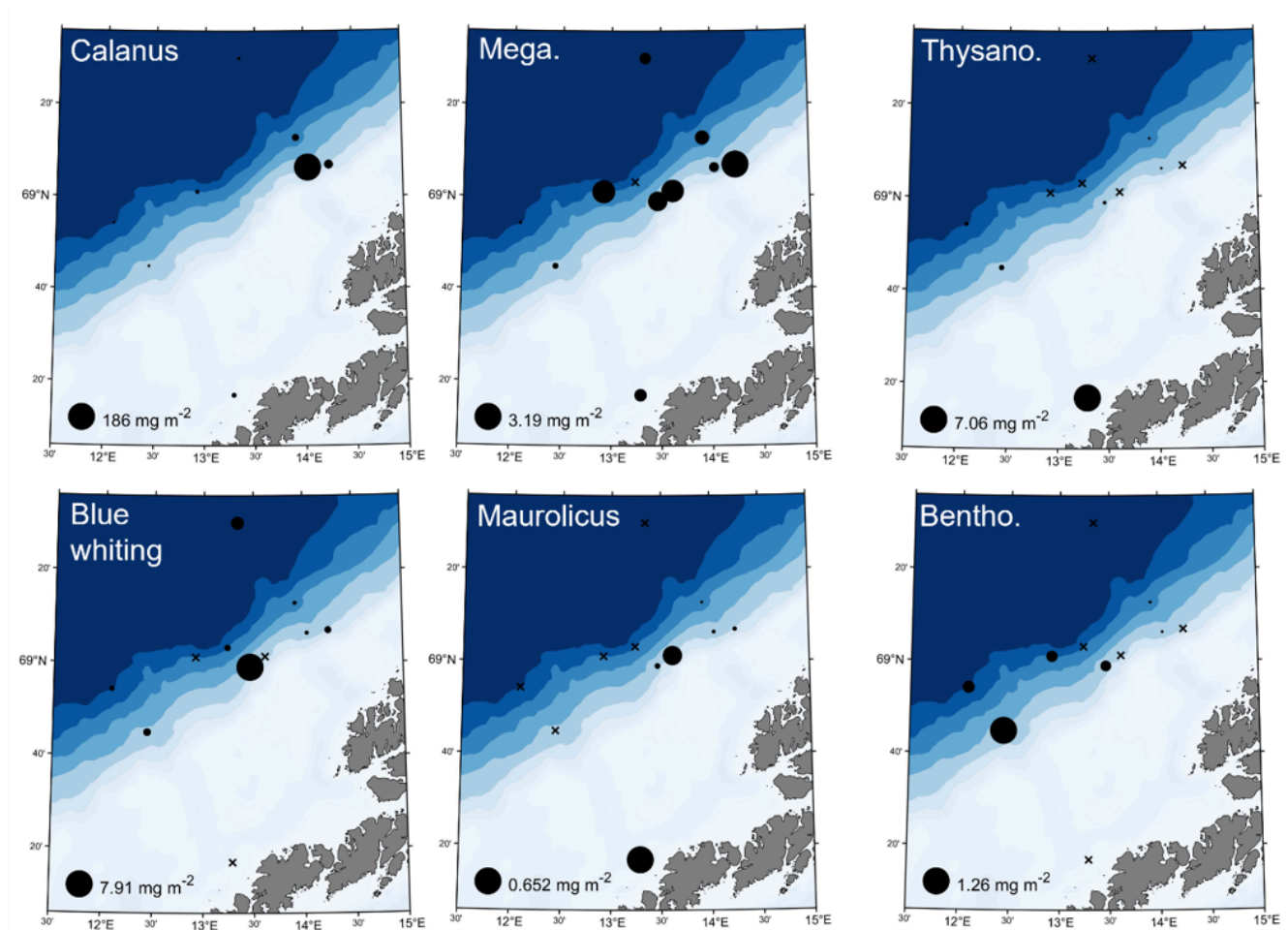


Figure 3

Spatial distribution of zooplankton species *Calanus*, *Meganyctiphanes*(Mega.) and *Thysanoessa* (Thysano.), Blue whiting fish, and Myctophid fishes *Benthosema* (Benthos.) and *Maurolicus*. *Calanus* were caught with a vertical multinet tow from bottom or 600 m depth. Other species were sampled by trawling in the mesopelagic layer.

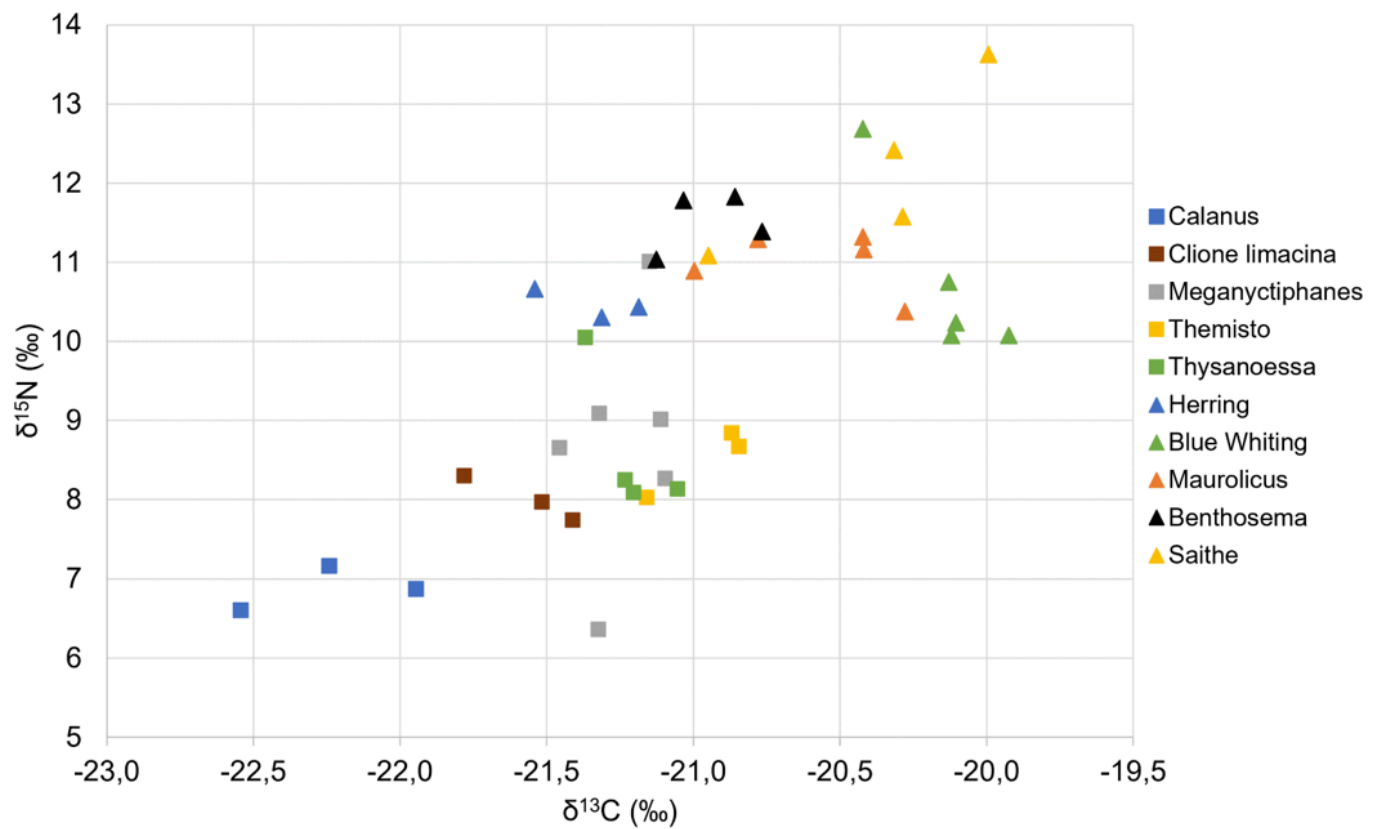


Figure 4

Scatter plot of $\delta^{15}\text{N}$ and $\delta^{13}\text{C}$ values measured in tissues of several plankton (square) and nekton (triangle) species. The level of dispersion of the datapoints for a given species defines its isotopic niche.

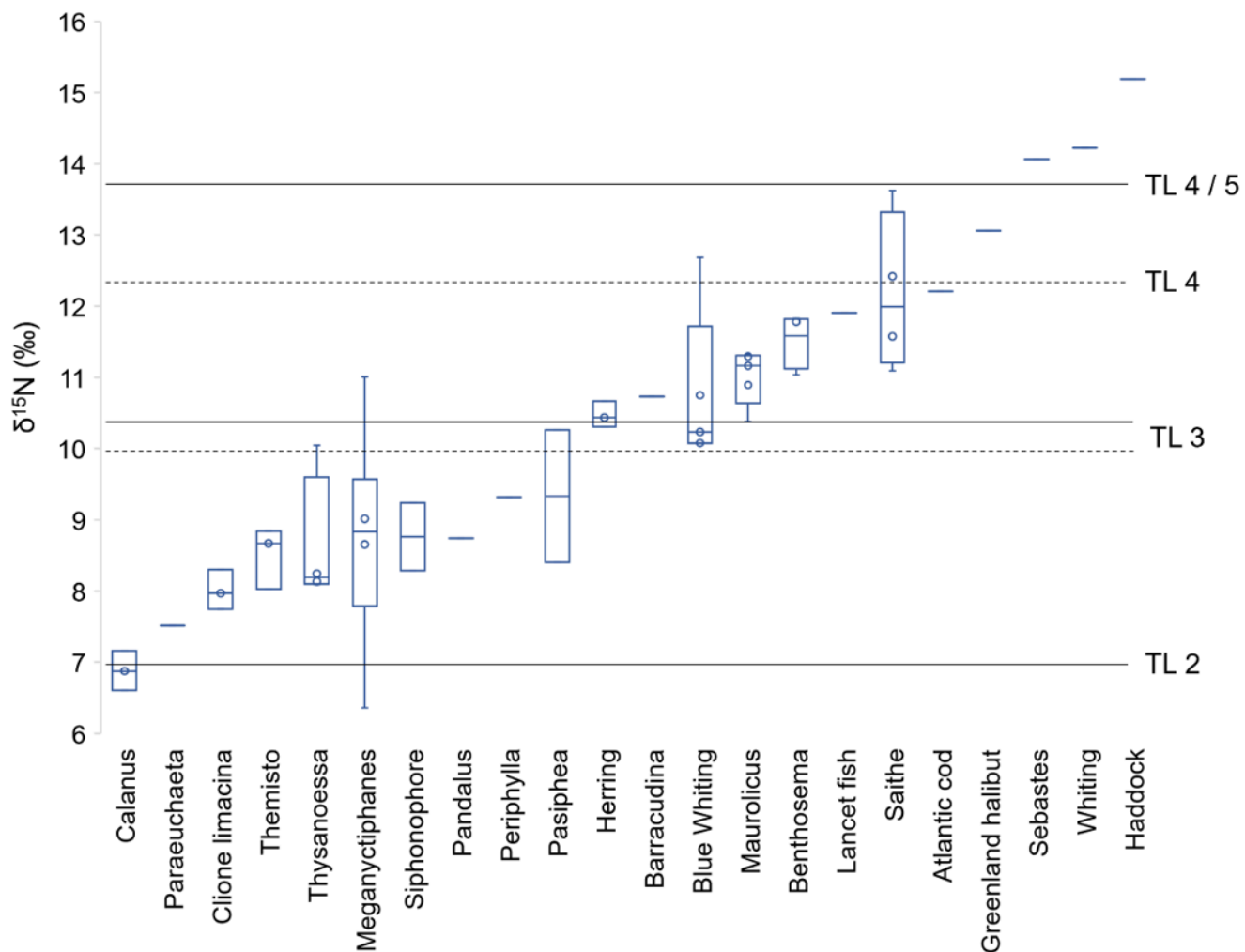


Figure 5

Ascending $\delta^{15}\text{N}$ values measured in tissues of several plankton and nekton species. *Calanus* were used as isotopic baseline (trophic level 2). Two methods were used to calculate the TL, the linear increment using a 3.4‰ increment (solid lines) and the narrowing increment (dashed lines).