Macrozooplankton and micronekton diversity and associated carbon vertical patterns and fluxes under distinct productive conditions around the Kerguelen Islands

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Abstract

Mesopelagic communities are characterized by a large biomass of diverse macrozooplankton and micronekton (MM) performing diel vertical migration (DVM) connecting the surface to the deeper ocean and contributing to biogeochemical fluxes. In the Southern Ocean, a largely High Nutrient Low Chlorophyll (HNLC) and low carbon export region, the contribution of MM to the vertical carbon flux of the biological pump remains largely unknown. Furthermore, few studies have investigated MM communities and vertical flux in naturally iron fertilized areas associated with shallow bathymetry. In this study we assessed the MM community diversity, abundance and biomass in the Kerguelen Island region, including two stations in the HNLC region upstream of the islands, and two stations in naturally iron fertilized, one on the plateau, and one downstream of the plateau. The MM community was examined using a combination of trawl sampling and acoustic measurements at 18 and 38 kHz from the surface to 800m. A conspicuous vertical three-layers system was observed at all four stations: a shallow scattering layer (SSL, between 10 and 200 m), mid-depth scattering layers (MSL, between 200 and 500 m) and deep scattering layers (DSL, between 500 and 800 m). While salps (*Salpa thompsoni*) dominated the biomass at the productive Kerguelen plateau and the dowstream station, they were scarce at the HNLC stations upstream of the islands. In addition, crustaceans (mainly *Euphausia vallentini* and *Themisto gaudichaudii*) were particularly abundant over the plateau, representing a large, although varying, carbon stock in the 0-500 m water layer. Mesopelagic fish were prominent below 500m where they formed permanent or migrant layers accounting for the main source of carbon. Through these spatial and temporal sources of variability, complex patterns of the MM vertical distribution and associated carbon content were identified. The respiratory carbon flux mediated by migratory myctophids at the four stations was quantified and evaluated for possible inaccuracies. While the estimated levels are likely underestimated, this study highlights the importance of migrant biomass and size structure in the biological pump of the Southern Ocean regions affected by complex topography and land mass effects..

Keywords: macrozooplankton; micronekton; vertical patterns; migratory flux; spatio-temporal variability; acoustic; Kerguelen plateau; Southern ocean

Introduction

The mesopelagic community is composed of taxonomically and functionally diverse groups of organisms, including gelatinous organisms, crustaceans and mesopelagic fish, that occupy the 200-1000 m depth zone in the ocean. Through modelling and *in-situ* studies, mesopelagic organisms have gained an increasing attention from the ecological and biogeochemical communities (Davison et al., 2013, Anderson et al., 2018, Hernández-León et al., 2019) as well as from managers interested in the sustainable exploitation of potential new resources. This interest has primarily been stimulated by two characteristics of the mesopelagic zooplankton and micronekton. First, while logistical and technological difficulties in reliably estimating zooplankton and fish biomass still exist, recent assessments have pointed to a high likelihood of these populations being substantially underestimated (Irigoien et al., 2014, Hernández-León et al., 2020). Secondly, mesopelagic organisms are known to perform intensive diel vertical migration (DVM), described as the largest animal migration on Earth (Hays, Sutton). This DVM connects the mesopelagic zone (200-1000 m) where mesopelagic organisms reside during daytime to the surface epipelagicwaters (0-200 m) which they move up to for feeding at night. This vertical movement represents an important active contribution in the downward particle export, and particularly the transport of carbon (Bianchi et al., 2013, Ariza et al., 2015).

The Southern Ocean is the world ocean's largest high nutrient low chlorophyll (HNLC) area where the production is mainly limited by iron (de Baar et al., 1995). Naturally iron-fertilized sites generate highly productive regions in the Southern Ocean (Blain et al., 2007). The Kerguelen Plateau forms a large physical barrier to the eastward flowing Antarctic Circumpolar Current (ACC) and induces iron enrichment of shelf waters that are then entrained in the downstream area eastward of the AAC flux (Blain et al., 2007, Mongin et al., 2008). While upstream waters approaching the Kerguelen Islands are generally depleted in iron and chlorophyll (Jandel et al., 1998), a large bloom occurs over the Kerguelen plateau as well as in the downstream region, observed as a persistent and dynamical high-chlorophyll plume (d'Ovidio et al., 2015). An inverse relationship has been observed between production and export in this region, a typical feature of the Southern ocean (Maiti et al., 2013, Le Moigne et al., 2016). However, to date only passive export has been considered in this region, and the contribution of active carbon flux remains to be resolved. Given the prominent role of the Southern Ocean in the global carbon cycle, estimates of active carbon flux are important to consider with respect to the global carbon budget and it is fundamental to assess the contribution of the biological active community of mesopelagic organisms. A need to improve the knowledge on their role in ecosystems, including the diversity and their contribution in biogeochemical stocks and flux, has recently been stressed (Ratnarajah et al., 2020, Martin et al., 2020).

The Kerguelen area offers an ideal location to investigate the functioning of the pelagic ecosystem, including the biological pump, in contrasting production regimes with and without natural iron enhancement.. This region is also ecologically important as a foraging ground for several species of land-based marine top predators (Hindell et al., 2011). Their diet is largely comprised of macrozooplankton and micronekton (MM) and the estimated food consumption by the highest trophic level predators indicates the presence of a significant standing stock of mesopelagic micronekton, primarily myctophids, and macrozooplankton, including euphausiids and hyperiids (Guinet et al., 1996, Bocher et al., 2001, Bost et al., 2002, Cherel et al., 2002, Lea et al., 2002, Cherel et al., 2008). In this subantarctic area of the Southern Ocean, high abundances of intermediate trophic levels have been reported in association with either circumpolar frontal regions or local bathymetry-driven features (Pakhomov et al., 1994, Pakhomov and Froneman 1999, Behagle et al., 2017). For instance, the abundance of the subantarctic krill E*uphausia vallentini* was associated with the shelf topography and the location of the Polar Front, and it was reported to be more numerous in the eastern area than the western part of the Kerguelen region (Koubbi et al., 2011, Hunt et al., 2011). It has recently been reported that, on a global scale, zooplankton biomass in the whole water column increases with the average net primary production, implying an enhanced active export of carbon coupling the surface and deep layers (Hernández-León et al., 2020).

The comparative approach used in this study, targeting iron fertilized *vs* HNLC sites, originated from the scientific strategy of the KEOPS 1 and 2 campaigns (Queguiner et al., 2011). The objective of this study was to understand how mid-trophic level MM respond to contrasting production regimes (oligotrophic vs biologically-enriched zones). Specifically, we tested the hypothesis that high primary production implies high diversity and/or high abundance of MM. Deployment of midwater trawls allowed us to estimate the depth-stratified carbon content contributions of different taxonomic groups and qualitatively assess their contributions to the active carbon flux in the area. Quantitatively, the importance of mesopelagic fish to the active carbon transport was estimated using a recent compilation of myctophid respiration rates in the Southern Ocean (Belcher et al., 2019). Species composition and distribution patterns, including the derived fluxes, of MM from trawl data collections were supplemented with acoustic backscatter analyses. The temporal monitoring of acoustic densities using high-resolution measurements from the surface to 800 m appeared to be a powerful tool to assess the complex and diverse vertical patterns between the different areas of interests in the Kerguelen region.

Methods

- Survey

The Mobydick survey (DOI: https://doi.org/10.17600/18000403) was carried out in the area south of the Kerguelen Islands onboard the *R/V Marion Dufresne II*. From the 26th of February to the 19th of March 2018, hydrographic and acoustic data, as well as MM samples were collected at four stations (M1, M2, M3 and M4, Fig. 1). These stations were located based on knowledge from previous oceanographic cruises conducted in the area (e.g., Blain et al., 2007, d'Ovidio et al., 2015, Behagle et al., 2017). The M1 station was located east of the plateau in the area identified as the core foraging area of the king penguin, an important top predator in terms of consuming biomass (Scheffer et al., 2016). The M2 station located on the plateau (isobath 520m) corresponded to a reference station to study the naturally fertilised bloom on the Kerguelen plateau (Quéguiner et al. 2011). The stations M3 and M4 to the west of the plateau were chosen because HNLC conditions prevailed. While M1 was visited once, M4 was visited twice and M2 thrice. The first visit of the M3 station with a full sampling of all depths during daytime and nighttime was divided into two periods because of bad weather condition, so that M3-1 and M3-2 were separated by an 11-day period.

- Remote and in-situ oceanographic measurements

Hydrological casts were carried out at each visit of all stations (Fig. 1). Temperature and chlorophyll *a* concentration (Chl *a*) profiles were collected using SeaBird probes.
Sea surface chlorophyll data from Global Ocean Color products with a 1/24° resolution (from the Marine Copernicus data portal) was used to build time series of Chl *a* at each station. We considered the weekly averaged product (7 days) to describe the bloom temporal patterns since it represents a good compromise between the temporal resolution and the cloud coverage. We also estimated the Polar Front (PF) mean location in the Kerguelen area by using T and S profiles from the Global Ocean Reanalysis (Ferry et al., 2016), as described in Pauthenet et al., (2018).

- Acoustic measurements

Continuous acoustic measurements were made with a calibrated (Demer et al., 2015, Simrad EK80 documentation) Simrad EK80 echosounder operating at five frequencies: 18, 38, 70, 120 and 200 kHz. As we were interested to described acoustic scattering in epipelagic and mesopelagic waters, we only used the 18 and 38 kHz frequencies, with maximum acquisition ranges of 1000 and 800 m respectively.

Data used in this study were acquired with an average ping interval of 3 s, mostly during station time where the vessel was either immobile, or during trawling activity. See Table 1 for echosounder settings. The acoustic data were scrutinized, corrected and analysed using the “Movies3D” software developed at the “Institut Français de Recherche pour l'Exploitation de la Mer” (Ifremer; Trenkel et al., 2009) combined with the French “Institut de Recherche pour le Développement” (IRD) open source tool “Matecho” (Perrot et al., 2018), developed in MATLAB.

The noise from the surface (3 m deep from the transducer, that is 12 m deep from the surface) and the bottom ghost echoes were excluded and the bottom line was corrected. Single-ping interferences from electrical noise or other acoustic instruments (Le Bouffant, N., *comm. pers*.), and periods with either noise or attenuated signal due to inclement weather, were removed using the filters described by Ryan et al. (2015). Background noise was estimated and subtracted using methods described by De Robertis and Higginbottom (2007). The nautical area scattering coefficient (NASC in m^2 nmi^{-2}), an indicator of marine organisms biomass, and the volume backscattering strength (Sv in dB re $1m^{-1}$), an indicator of the marine organisms’ density, were calculated. Acoustic symbols and units used here follow MacLennan et al. (2002). Data were echo-integrated onto 0.5 m high layers over a 3 pings period giving one ESU (Elementary Sampling Unit) with a -100 dB threshold from 12 m down to 800 m depth.

The DVM is a common behaviour for zooplankton and micronekton that can be perceived at almost all spatial scales (Haury et al., 1978). Acoustic data were thus split into day, night and crepuscular periods (dawn and dusk). Day and night periods were defined based on the solar elevation angle with day when the altitude is >18° and night with altitude <-18° (as in Lehodey et al., 2014).

Acoustic data were also spatially split between stations by creating a 0.8° Longitude 0.5° Latitude rectangle around the GPS coordinate of each station (Fig. 1, blue rectangles). These rectangular areas at each station encompass the trawl operations area. Acoustic data recorded during transits (i.e. out of these spatial limits) were excluded from data analysis. The vertical profiles of mean acoustic density NASC were computed for each visit of each station for the daytime and nighttime periods (not only trawling time).

Data visualisation- Red Green Blue (RGB) composite images were generated in MATLAB based on the 18 and 38 kHz echo-integrated acoustic data as in Annasawmy et al. (2019). The acoustic volume backscattering strength Sv of the 18 kHz frequency was colour-coded in red while the 38 kHz was displayed in colder hue using both blue and green, with a high threshold scale of -60 dB and a low scale threshold of -90 dB. In the RGB composite image subsquently created, the hue gives the frequency with the highest backscatter and the luminance gives the intensity of the volume backscattering strength. A light cyan (combination of blue and green) colour indicates a dominant and high 38 kHz backscatter whereas a dark red colour indicates a dominant but low 18 kHz backscatter. A black hue indicates that all backscatters are under the low scale threshold or that no data are available, and a white hue indicates that all backscatters are above the high threshold scale. Using these two frequencies, the RGB echogram gave for each station, a clear and synthetic visual representation of the location and migration in the water column of acoustic communities of scatterers based on their most resonant frequency from 20 to 800 m.

- Trawling

Forty-eight trawls were performed, consisting of three night trawls and three day trawls at each station (Table 2). Macrozooplankton and micronekton (MM) were collected during daytime and nighttime using a Mesopelagos trawl, designed by Ifremer (fisheries biology and technology laboratory, LTBH, Lorient, France) (Meillat, 2012). This trawl has a 7 m mean vertical opening and 12 m horizontal opening, with a 65 m^2 mouth area and 44 m length. The trawl has a mesh size of 30 mm in the wings, reducing to 4 mm in the codend. Trawl depth was monitored in real time with a Scanmar (Åsgårdstrand, Norway) depth sensor attached to the trawl headline. We adopted a semi-stratified/adaptive strategy in trawl sampling. As the aim was to provide the most complete picture of the micronekton community at each station, the whole water column from the surface to 650 m was sampled at different strata corresponding to the sound scattering layers at different depths: the shallow scattering layers (SSL, between 10 and 200 m), the mid-depth scattering layers (MSL, between 200 and 500 m) and the deep scattering layers (DSL, between 500 and 800 m). At each layer, hauls were performed at targeted depths according to the observations of the different scattering structures (patches or layers) provided by the echosounders. The towing speed was maintained near 2 knots, with effective fishing times of 30 minutes.

Once on board, the total wet mass (WM) in grams was weighed. Organisms were firstly sorted into broad taxonomic groups (fish, crustaceans, gelatinous organisms and cephalopods), then identified at the species level. All organisms were counted and weighed; fish and salps were also measured.

The allocated temperature estimate for each trawl was performed by using the temperature profile from the CTD cast closest to the trawl location in space and time, and by taking the estimated temperature at the trawl depth (during the fishing period).

- Estimates of C content

Carbon biomass was estimated using conversion factors to convert WM in dry mass (DM) and DM in carbon biomass for the four main taxonomic groups, gelatinous organisms, fish, molluscs and crustaceans. Water content for each of the group was estimated based on available data from the literature as follow: 94% for gelatinous organisms (Larson 1986, Huntley et al 1989), 75% and 80% for fish and molluscs, respectively, (Schaafsma et al., 2018) and 75% for crustaceans (Schaafsma et al., 2018, Harris et al., 2000). The carbon content of dry biomass was provided in the context of stable isotopes analysis (Hunt et al., this issue) carried out on all the main taxa. The percentage of C in DM was then averaged for each group such as gelatinous organisms 15%, fish 50%, molluscs 35% and crustaceans 40%.

- Migrant biomass and carbon flux

Additionally, biomass and carbon flux were estimated for migratory fish of the family Myctophidae. This group was targeted as migratory layers found at night near surface, and more importantly, because it was possible to estimate carbon flux using metabolic predictive equations specifically developed for this family (Belcher et al., 2019).

We assumed that all myctophids found at nighttime in the epipelagic layer would return to the mesopelagic at day. Migration was then calculated as the abundance and biomass of myctophids in the nocturnal shallow trawls 5, 6, 11, 19, 20, 21, 31, 35, 37, 39, and 48. This was standardized for the volume filtered by the net, and it was integrated by the thickness of the sound scattering layer (from echograms) where net was located. Abundance and biomass was expressed as the number of individuals or the milligrams of carbon weight by square metre (ind m^{-2}, mg C m^{-2}).

Carbon flux mediated by respiration was estimated by calculating the amount of carbon dioxide exhaled by myctophids below the thermocline. For this, the respiration rate for each individual was estimated using body mass and environmental temperature as predictors, following the respiration regression developed for myctophid fish in Belcher et al. (2019):

$$\mathrm{Ln}(R_{WM}) = -1.315 - 0.2665 \times \mathrm{Ln}(WM) + 0.0848 \times T \qquad \textit{Eq. 1}$$

where R_{WM} is the mass-specific respiration rate per hour (µl O_2 mg WM^{-1} h^{-1}), *WM* is the individual wet mass (mg), and *T* is the environmental temperature (ºC). Individual wet mass was estimated using the length-weight relationships provided for the family Myctophidae by Kwong et al. (2020). Respiration was computed for 2.2 ºC, corresponding to the average temperature in waters between 400 and 500 m depth. This interval was assumed as the end of migration, according to the daytime migrant layer depth registered with the echosounder. The total respiration for each trawl was calculated by standardising the volume filtered by the net (considering a cylinder with the surface of the trawl opening and the distance traveled during the haul), and summing for all myctophid individuals captured in that trawl. Similarly to the abundance and biomass measurements, total respiration was integrated by the thickness of the sound scattering layer where net was located. This was then converted to units of carbon per square meter and day (mg C m^{-2} d^{-1}) using a respiratory quotient of 0.90 for fishes (Brett and Groves, 1979, Ariza et al., 2015) and the stoichiometric relationship between carbon and oxygen (22.4 L O_2 = 12 g carbon). Since carbon export to the mesopelagic zone only occur during daytime, only 12 hours of the day were considered for calculations.

Results

- Environmental conditions around Kerguelen plateau

In addition to their location relative to the plateau (on the plateau *vs* upstream/downstream areas), the stations were also situated within the area of a particular oceanographic feature, the PF, which crossed the plateau just south of the Kerguelen Islands (Fig. 1). The M1, M2 and M4 stations were located south of the PF, with varying distances to the PF mean location, while the M3 station was located north of this front.

During the cruise, the concentration of Chl *a* was higher at station M2 on the plateau compared to the downstream and upstream stations (Fig. 2). Overall, the concentrations (both over and outside the plateau) during the survey were considered low (<0.4 $mg.m^{-3}$) compared to the concentrations observed during the spring/summer period from October to January. Throughout this period, the highest Chl *a* was measured on the plateau in mid-January. Medium values occurred upstream (M3 and M4) with a simultaneous peak. An earlier (late November) maximum was observed downstream.

- Description of the macrozooplancton/micronekton community from trawl collection.

Over the whole study area, the dominant biomass obtained from the trawl samples was attributed to gelatinous organisms (Fig. 3). In most trawls, they constituted a major part of the absolute biomass, i.e. an average weight per sample of 3497 g (±7837 g) corresponding to a mean proportion of 63 % (±33.35 %) of the total weight (Fig. 4). This was followed by crustaceans, with an average weight per sample of 312 g (±275 g) corresponding to a mean proportion of 30 % (±31 %), and fish with an average weight per sample of 133 g (±193 g) corresponding to a mean proportion of 6.5 % (±10.4 %).

In trawls with a low total biomass (<1000 g), the gelatinous dominance was challenged by a higher relative biomass of crustaceans (Fig. 4), particularly for samples carried out during daytime at depths shallower than 300 m. This trend was supported by the high relative abundance of crustaceans, which contributed more than half of the total organisms in 75 % of the 48 trawls (Fig. 5).

In terms of biomass, the most important gelatinous contributors were salps (S*alpa thompsoni*) followed by siphonophores (especially *Rosacea plicata*) (Fig. 6 and Table 3). Notably, *S. thompsoni* was only abundant at stations M1 and M2. Chaetognathes were also often found in trawls with a relatively low biomass. Ctenophores (*Bolinopsis* sp.) and jellyfish (mostly scyphozoans) contributed variably in the proportion of gelatinous organisms with species occurring in half of the trawls (e.g., *Calycopsis borchgrevinki*) and contributing weakly to moderately to biomass (such as *Atolla wyvillei* and *Periphylla periphylla*).

For crustaceans, the most common species in terms of occurrence and abundance were the euphausiid *E. vallentini* and the hyperiid amphipod *Themisto gaudichaudii* (Fig. 7 and Table 4). The latter was the only species among all taxonomic groups found in all trawls, but it was particularly abundant at M2 over the shelf. The euphausiid *Euphausia triacantha* was also frequently found, though with a lower abundance than *E. vallentini*. Other hyperiid amphipods, e.g. *Cyllopus magellanicus* and *Primno macropa*, often occurred in trawls albeit at relatively low abundances.

The dominant fish family was Myctophidae with 3367 individuals belonging to 14 species (Fig. 8 for myctophids only, Table 5 and supplemental material 1 for the main fish species). The most abundant species within the whole fish community was *Krefftichthys anderssoni*, which represents half of the fish caught when merging adults and post-larvae. *Electrona antarctica* was also an abundant species and the most frequent fish in all trawls. Other myctophids, such as *Gymnoscopelus braueri* and *Protomyctophum bolini* had a high occurrence but were low to moderately abundant. Other fish families were characterized by either a high occurrence (i.e., *Notolepis coatsi*) or locally a high abundance (e.g., *Bathylagus tenuis, Cyclothone* sp.).

- Variability in vertical patterns from acoustic and trawl records

-Diel variability-

Diel variability in biomass and acoustic densities: A strong variability was observed in the vertical distribution of both biomass and acoustic densities between nighttime and daytime. Very low biomass was sampled in the SSL during daytime (Fig. 3). However, acoustic profiles indicated that densities, organized in relatively thin peaks, occurred in this layer at ~100 m depth during both nighttime and daytime (Fig. 9). At depth, diel differences regarding biomass was less clear and acoustic densities was variable. Recurrent medium densities were observed between 400-500 m during daytime and between 250-400 m during night-time. The 38 kHz backscatter is globally lower than the 18kHz between the surface and 500 m, while an opposite pattern occurred at depths >500 m. Despite acoustic structures moved vertically between daytime and nighttime and variable patches and layers were observed in the RGB echograms, a conspicuous 3-layers system characterized the whole area (Fig. 10). During daytime, clear scattering layers appeared and various patches were observed whereas acoustic scattering features were more consistent in the horizontal axis. Transition periods (dusk and dawn) evidenced different patterns of vertical migrations between the surface and the underlying deeper layers, including vertical movements deeper than 800 m. Migratory organisms were more responsive at 18kHz, while a permanent non-migratory layer was observed at 600 m, which was characterized by an intense 38kHz signal (in dB).

Diel variability in communities: The most important diel variability in communities and relative biomass/abundance was observed in the SSL (i.e. above 200m) (Fig. 3, 4, 5). The gelatinous MM (mainly salps) dominated biomass at nighttime at M1 and M2 and abundance at M1. During the night at M2, gelatinous groups and crustaceans were rather balanced in terms of relative abundance in the top 200 m layer. Crustaceans (mainly euphausiids at M1, M3 and M4 at night, Fig. 7) were lower in biomass but more abundant than gelatinous organisms. Myctophids (mainly *E. antarctica*, Fig. 8) were only present in this surface layer during nighttime.Between 200 and 500 m, gelatinous MM (mostly salps), contributed the most to total MM biomass during nighttime and a mixture with other gelatinous during daytime at M1 and M2, while siphonophores dominates the biomass in this layer at M3 and M4 (Fig. 6). Crustaceans (mainly euphausiids and hyperiids, Fig. 7) were also proportionally abundant during both periods of the day (Fig. 5), while numerous at this depth only at M2 (Fig. 7). Fish mainly occurred in this MSL during night-time (Fig. 8). Below 500 m (excluding the station M2), the biomass volume was shared between the three main taxonomic groups, with a higher contribution of fish than in the upper layers (Fig. 4, 5). This corresponded with higher myctophid abundance and also more bathylagids and cyclothones (supplemental material 1). Similar (relative) biomass and abundance were observed during night-time and daytime within this DSL. Gelatinous organisms were similar to the MSL previously described with an increased proportion of jellyfish occurring during night-time (Fig. 6). Crustaceans presented similar biomass between night-time and daytime.

-*Inter-station variability*- Lower biomass were reported for M3 and M4 stations during the nighttime in the (sub-)surface (shallower than 200 m). This main difference was mostly attributed to gelatinous organisms. While salps were abundant at M1 and M2 stations, they represented a low percentage of the gelatinous community at M3 and M4 (Table 3 and Fig. 6). The biomass at these latter stations were consequently considerably lower with a higher contribution of the other taxa, particularly siphonophores (occurring only deeper than 300m, including at M2) and to a lesser extent, ctenophores and jellyfish.

Crustacean abundances between stations exhibited a different pattern. They were numerous at the M2 station with a large proportion of the hyperiid *T. gaudichaudii* (Table 4 and Fig. 7). At other stations, euphausiids dominated the crustacean community, especially in surface waters during nighttime where large quantities were collected (at stations M1 and M4).

Conversely to the crustacean pattern, the lowest abundances of fish, including the dominant myctophids, were found at M2. Despite a low fish biomass at this station, a high diversity was found and *E. antarctica* was the most abundant species at all depths. At other stations, *K. anderssoni* was the dominant species, particularly in mid-depth and deeper waters during nighttime. However, *E. antarctica* was the most common species found in surface waters during the nighttime and at depth during the daytime.

Finally, the main contrast observed in acoustic densities where reported between M2 and the other stations (Fig. 9). The more similar pattern in the trawl results is observed for the fish, that are less abundant at M2.

-*Intra-station variability*- For stations visited twice (M4) or three times (M2 and M3), patterns of vertical distributions were coherent despite some variability was observed. The variability is mostly observed in terms of biomass and abundance at similar depths, while the composition of the MM community was similar between visits. Acoustic profiles indicated some changes observed between visits. Densities observed during daytime at M2 decreased between the first (highest daytime biomass, Fig. 3) and the second visit. At M3 and M4, a global deepening of densities from MSL to DSL (highest fish biomass reported during the 2^{nd} visit of M3) as well as an increase in the surface layer occurred between the first and the second visit, especially during nighttime.

- Description of the carbon content in each taxonomic group

Due to low carbon content, the contribution of gelatinous plankton to total carbon biomass was important but decreased significantly in comparison with their contribution to wet biomass (Fig. 11). At most of the stations (M1, M3 and M4), fish dominated carbon biomass in the DSL, especially for the night trawls. In surface layers, crustaceans were usually the major contributors to carbon biomass, except for a few stations where gelatinous organisms were dominant.

- Respiratory carbon flux

The abundance, biomass, and respiratory carbon flux from myctophids entering the mesopelagic zone ranged from 0.001 to 0.163 ind m^{-2}, from 0.04 to 15.08 mg C m^{-2} d^{-1}, and from 0 to 0.045 mg C m^{-2} d^{-1}, respectively. According to Fig. 12, the stations M1 and M4 that were located over the ocean basin, exhibited the highest values of abundance, biomass, and carbon export, while M2 and M3 (over and close to the plateau, respectively) resulted in the lowest values. Averaged Chl *a*, from 20 to 100 m depth, ranged from 0.19 to 0.60 mg m^{-3} during the visits at which carbon flux was estimated (Fig. 12a-b). As a result of the varying hydrographic conditions found at each visit, the distribution of migratory scattering layers changed, and the depth range of trawling was adjusted to target these layers (e-h). The highest values on abundance, biomass, and carbon export coincided with intermediate Chl *a* values in M1 and M4, in migratory layers sampled between 50 and 170 m depth (trawls 11, 21, 31 in Fig. 12), while the lowest with Chl *a* maxima at M2, in migratory layers sampled between 30 and 90 m (trawls 37, 39 in Fig. 12). Carbon flux was fundamentally driven by biomass, which was in turn driven by the total number of individuals in the catch. This resulted from the overall similar size distributions between trawls, with individuals mostly ranging from 10 to 70 mm standard length (see supplementary material 2). Exceptionally, in trawls 6 and 20 at M2 station, the occurrence of a few individuals larger than 100 mm increased the total biomass, but decreased carbon export as result of lower metabolic rates of large fish (see equation 1).

Discussion

The waters surrounding the Kerguelen Islands encompassed variable communities of MM, with respect to their biomasses, proportional contributions, and vertical patterns. Because vertical active fluxes are generally driven by biomass and composition, this has important implications for the regional and global biological pump (Ariza et al., 2015, Gorgues et al., 2019, Hernández-León et al., 2019). The MM variability had been revealed in this study in response to the particular physical features and biological characteristics of this dynamic area. While the combination of trawl and acoustic sampling clearly benefited the description of the MM community, it is crucial to bear in mind the specificities of each methodology (Ariza et al., 2016). Despite the possibility of contamination of deep hauls by upper organisms due to the use of a non-closing trawl, we reduced this effect through fast launch and haul out during trawl operations. Moreover, while numerous species were sampled we only focus on the most abundant species. This precaution is particularly adapted in our study area where the dominant species were limited and represent a very high proportion in terms of biomass-abundance, consequently contributing significantly to the backscatter. In turn, acoustic measurements are based on the properties of the dominant species in a volume containing many organisms, either in terms of relative backscatter intensity dominated by the strongest reflector or due to the frequency-dependent response. It implies that gas-bearing organisms such as fish with air-filled swimbladders or siphonophores dominated small fluid-like organisms at 18kHz and 38kHz (Ariza et al., 2016, Behagle et al., 2017).

1. Macrozooplankton-micronekton communities within the Kerguelen seascape and spatial variability.

Our results provide a comprehensive picture of the macrozooplankton-micronekton (MM) communities following a longitudinal gradient across the Kerguelen plateau, and serves as a case study of an area of the Southern Ocean where contrasted production regions occur. The set of four stations visited during the survey represented different environments describing the various seascape around the Kerguelen Islands. These environments differed in terms of bathymetry (downstream vs upstream location relative to the plateau), level of biological production (Chl *a*) and northern vs southern location in relation to the PF.

- M1 was representative of the Kerguelen plume downstream of the plateau. At this location close to the PF, the primary production peaked three months earlier and was very low during the cruise. Salps largely dominated the biomass, especially during night-time in the SSL and MSL. Euphausiids, mainly *E. vallentini*, was abundant in surface layers during night-time. Significant abundance of the fish species *K. anderssoni* and *E. antarctica* were found within the SSL to DSL, according to their diel cycle (Duhamel et al. 2000). This area on the eastern flank of the Kerguelen plateau is a well-known foraging area for top predators such as king penguins, macaroni penguins and fur seals, which predominantly forage within the SSL on crustaceans and myctophids (Bost et al., 2002, Lea and Dubroca 2003, Sato et al., 2004)

- M2 was representative of the productive plateau area, even if relatively low Chl *a* was estimated during the sampling period, it was preceded by a strong bloom. Indeed, this area is characterized by a reoccurring large phytoplankton bloom induced by naturally iron-fertilized waters from the plateau (Blain et al., 2007). Trawl estimated MM biomass was high at this station with salps being the main contributors. Crustaceans were numerous at M2, with a large proportion of *T. gaudichaudii*, as previously reported (Carlotti et al., 2015), followed by *E. vallentini*. Fish densities were the lowest at M2 compared to other stations, while their diversity was the highest. Sustained blooms as observed on the plateau station favour a high secondary production rate and a general increase in herbivory in zooplankton, as observed during the KEOPS2 survey (Carlotti et al., 2015).

- **M3 was the first HNLC upstream station north of the PF**; it was located close to the plateau and corresponded to the previous KERFIX station (Jeandel et al. 1998). The lowest overall biomass was reported at this station mainly due to low salp densities. However, the gelatinous group had a relatively high diversity, with a contribution of siphonophores, jellyfish and ctenophores. Crustacean abundance was low and dominated by euphausiids. As a consequence of the low contribution of other groups, fish made a relatively high contribution to biomass at M3. Their densities were highly variable and they were more diverse, with less *E. antarctica* and a higher proportion of bathylagids and *Cyclothone* sp. The observed community corresponded to warmer waters north of the PF delimiting the northern extent of the distribution area of the endemic Antarctic *E. antarctica* (Duhamel et al., 2014).

- **M4 was the second HNLC upstream station south of the PF**. This station was located further west from the plateau. The gelatinous group dominated the total biomass, with siphonophores ranking first, salps showing the lowest contribution, and jellyfish being significant in the deeper layers. Euphausiids dominated crustaceans and their total densities within the SSL. Fish made a larger contribution at night than during the day, and *K. anderssoni* and *E. antarctica* were equally important contributors. Within the M3 and M4 areas, upstream of the plateau, the PF location is highly variable and undergoes a large seasonal change (Pauthenet et al., 2018). These authors reported that the PF is located at its southern position in March, i.e., during the survey period. As a consequence, the location of station M3 in relation to the PF may have shifted in the previous months and resulted in different physical and biogeochemical conditions. Moreover, the purported HNLC upstream M3/M4 stations presented similar levels of Chl *a* than the downstream M1 station. The production at M3/M4 was abnormally high when compared to the averaged Chl *a* (Christaki et al., this issue), potentially influencing the densities of the MM populations.

2. Diel cycles and intra-station variability as sources of time varying patterns

Despite clear differences in vertical distribution of both acoustic densities and biomass-abundance between daytime and nighttime, a consistent three-layers system occurred over the whole Kerguelen area from upstream to downstream regions of the plateau. Here we describe and interpret the temporal variability due to this diel cycle, together with the variability observed between visits at the same stations

- Diel vertical patterns of macrozooplankton-micronekton:

While a higher total biomass was observed during nighttime, particularly in the surface layer, acoustic densities were remarkably similar between daytime and nighttime.

- This acoustic peculiarity is especially noticeable in the SSL where various densities were reported at the two frequencies. Here, very few gelatinous organisms and fish were collected and nearly-only crustaceans were trawled during daytime. The combination of trawl avoidance from myctophids during daylight and of their diurnal behaviour in the structuring could explain why biomass of these organisms are undersampled in the surface layer (Kaartvedt et al., 2012). Indeed, fish schooling is a diurnal behaviour leading to a patchy distribution during the day that vanishes at night (Saunders et al., 2013). The peak in acoustic densities above 100 m during daytime is likely to correspond to a thin layer where small schools of myctophids probably occurred. This is suggested by both previous acoustic measurements carried out in the area east of the plateau corresponding to the station M1 (Behagle et al., 2017), and the diving depth of king penguins that feed mostly on *K. anderssoni* during daytime (Scheffer et al., 2016). Few fish species were caught at shallow depths in offshore Kerguelen waters during the day, with the shallow acoustic densities being likely *K. andersson*i (Duhamel et al., 2000). The vertical distribution of this non-migratory species is based on age-segregation: juveniles are intensively feeding in the warm and productive surface waters while adults were found deeper (Lourenço et al., 2017).

- The diel cycle in the upper layer was the largest contrast we observed, with the invasion of gelatinous, crustaceans and mesopelagic fish from mid- and deep layers to the epipelagic. The daily difference in biomass and in the RGB echograms evidenced the migratory pattern of numerous species, including:

i) salps, which were found deeper than 200 m in the morning and performed a first migration to subsurface at mid-day, before moving up to the surface layer at night (Nishikawa and Tsuda 2001, Henscke et al., 2021).
ii) the main crustacean species, i.e. *E. vallentini* that performed DVM from subsurface-deep waters (100 m to 600 m depth) during daytime to the surface layer during night-time (Mauchline and Fisher, 1969, Boden and Parker, 1986), and *T. gaudichaudii* that also displayed DVM through a more complex pattern due to an ontogenetic component, with juveniles moving in the upper 100 m whereas adults descended to depths below 200 m during daytime (Pakhomov and Froneman, 1999).
iii) the myctophid *E. antarctica* exhibits a typical DVM, occurring within the surface waters during the night and descending below 300 m during daytime, with a size component (larger individuals found deeper than 600 m at night, while small fish were located at 300-400 m during the day; Hulley and Duhamel, 2011). Meanwhile, other important contributors are non- or slightly migratory species, such as *K. anderssoni* (see above) and the siphonophore *R. plicata* that exhibits a quasi-permanent distribution below 300 m with minor diel movements (as suggested in Pugh 1984).

- Multiple layers and patches and diverse DVM during the transition periods were observed on the RGB echograms. This bi-frequency visualization is particularly insightful to understand the vertical patterns of averaged acoustic profiles that appeared relatively similar during both day and night periods. Here we attempt to interpret this three-layer system based on the combination of bi-frequency responses and trawl sampling obtained during our survey and on the already known diel vertical distribution:

- SSL: During daytime, this layer was dominated by juveniles of *K. anderssoni* and of *T. gaudichaudii*, while it was invaded by numerous species at night from deeper waters, including salps, *E. antarctica*, and *E. vallentini*. First preliminary results from the four frequency comparison (but limited to the surface layer) indicated a more complex pattern with layers presenting multi-acoustic responses indicative of multi-species structures.

- MDL: During daytime, salps distributed in the upper part (~200 m) of this layer at M1 in the morning, before moving up at mid-day, as indicated by a strong response at 18kHz (Wiebe et al., 2010). A mix of the main crustacean species (*E. vallentini* and adults *T. gaudichaudii* between 200 m and 300 m) was found at M2. The lower part was attributed to siphonophores collected below 300 m, combined with crustaceans. During night-time, crustaceans mainly migrated to the SSL, while siphonophores constituted a permanent layer below 300 m, slightly moving upward at night. At the M2 station, waters just above the bottom were characterized by a permanent layer that was found deeper (~600 m) at the other stations.

- DSL: During daytime, the permanent 38kHz-dominated layer centred at 600 m was probably characterized by the main fish species in the area, i.e., large specimens of *E. antarctica*, adults of *K. anderssoni*, and bathylagids and *Cyclothone* sp. together with siphonophores and euphausiids. During the night, a part of this fish community, probably juveniles or the smallest individuals, move upward together with euphausiids. However, a 600 m-depth layer remained permanently, with the same combination of organisms that was acoustically dominated by fish. The higher 38kHz acoustic levels compared to the 18kHz at the DSL could originate from this fish dominance, since larger non-migrant *E. antarctica* individuals have a reduced gaseous swimbladder relative to the smaller individuals that have a large air-filled swimbladder (Dornan et al. 2019). Other acoustic layers occurred deeper, at the limit of the 38kHz vertical range, where just two trawls were carried out and reported a similar community with more deep-sea species such as jellyfish.

- Intra-station variability of vertical patterns:

The vertical patterns in biomass and communities together with the diel cycles were coherent between visits at the M2 station and at the two upstream M3/M4 stations. While M1 appeared to be a physical dynamic area and the other stations showed a low horizontal transport (Henschke et al., 2021), the trawl data indicate that the same MM populations were sampled at each station. The occasional variability in biomass and abundance in the same layers could indeed be attributed either to the known MM patchiness (i.e., spatial variability) or to the development of trophic interactions (i.e., temporal variability).

Noticeable variability was observed between the first and following two visits to M2, with a decrease in daytime acoustic density at 200 m and an overall larger biomass of crustaceans during the second visit. An increase and deepening of densities from the MSL to DSL was observed at M3 during night-time, which was confirmed by a higher biomass of all taxa, i.e. *K. anderssoni*, *E. vallentini* and siphonophores.

3. Variability in vertical distribution of carbon content and active flux associated with macrozooplankton-micronekton.

For consistency, we used an average of water carbon content computed for each of the groups, based on available data from the literature. However, we acknowledge that variability can be observed between species of the groups and between different estimates within the same species. Such variability can be explained by the different geographic area where the same species occurred and the samples obtained at different seasons, both potentially affecting the body composition of organisms (Schaafsma et al 2018). Although gelatinous groups dominated the wet biomass in the majority of trawls, it is the energy content that is important to sustain the development of higher trophic levels. For example, crustaceans are higher quality food than gelatinous organisms, such as salps (Harmelin-Vivien et al 2019). Considering C content allows a better estimate of the relative contribution of the different groups in terms of their roles in the energy transfer along the food web. Mesopelagic fish represented the main source of carbon stock in the DSL. They were shown to play an important role in active transfer of carbon from the intermediate layers to deep waters (Irigoien et al 2014). The extent of the active carbon flux driven by fish depends on the species composition, with not all species performing DVM (Romero-Romero et al 2019, Klevjer et al 2020). In our study, some of the highest fish C biomasses were measured at the station M3, where relatively low abundances of crustacean were found in the upper layer (including zooplankton, see Hunt et al this issue), potentially implying some top down control. However, primary productivity in surface waters at this upstream station was low, which may have contributed to the low crustacean biomass, and further, it is questionable whether such low biomass of fish can impact crustacean abundance (Pepin et al 2013). Crustacean and gelatinous organisms represented a large, although varying C stock at the 'productive' station M2, but they were not associated with a high mesopelagic fish biomass, possibly due to depth limitation (ca 550 m depth over the shelf).

Additionally, we only estimated the respiratory carbon flux mediated by migratory fish from the family Myctophidae, a major component in the Southern Ocean food web (Pakhomov et al., 1996; Saunders et al., 2019), which is known to play an important role in the active transport of carbon to the deep ocean (Davison et al., 2013; Ariza et al., 2015; Belcher et al., 2019; Kwong et al., 2020). Interestingly here, myctophids ranked as the fourth group contributing to migrant biomass, after gelatinous organisms and crustaceans, mainly salps, euphausiids, and hyperiids (Fig. 3-8). Without discrediting the important role of these groups in the Antarctic food webs (Perissinoto et al., 1998; Pakhomov et al., 2002), it should be taken into account that our results on relative biomass among groups might be strongly affected by the catchability and selectivity performance of our trawling net (Meillat, 2012, Béhagle et al., 2017). Myctophids are fast swimmers and they are expected to efficiently avoid trawling nets (Kaartvedt et al., 2012), especially when compared to quasi-drifting life forms like salps, or to smaller organisms such as euphausiids or hyperiids (Skjoldal, et al. 2013). Trawl avoidance can make a difference, considering that we used a net with a 65 m^2 mouth area. Hence, we presumed that myctophids were undersampled and are an overwhelmingly important component of the DVM in the study region. This, along with the extraordinary migration extent of organisms, often beyond 700-800 m depth when they are larger than 40 mm (Badcock and Merret, 1976), made pertinent the estimation of carbon flux on this group which required further investigations.

Our carbon flux estimation relies on individual body mass and environmental temperature, using a respiration rate predictive equation for myctophids, implemented by Belcher et al (2019). As discussed by the authors of this work, species-specific metabolism variance is not accounted for by this predictive equation and this should be added, along with the capture efficiency of the net, as factors potentially influencing our results. Capture efficiency and metabolic models are a common source of uncertainty to estimate carbon flux in micronekton, and this might explain why results generated over the last two decades still differ by up to three orders of magnitude (see Table 6). Our respiratory carbon flux estimations, ranging from 0.001 to 0.045 mg C m^{-2} d^{-1}, are for instance one order or magnitude lower than those obtained by Belcher et al. (2019) in the Atlantic sector of the Southern Ocean, using the same predictive equation, and based on non-corrected catch data, as we did (see Table 6). This demonstrates the urgent need to perform further inter-calibration experiments on micronekton samplers and acoustics (Pakhomov et al., 2010, Kaartvedt et al., 2012), and to work towards obtaining more accurate metabolic models for species involved in DVM (Becher et al., 2019, 2020). In the particular case of this study, the mesopelagos net is known to strongly undersample large fish (Meillat, 2012, Béhagle et al., 2017). Respiration is also expected to be underestimated in cold temperature environments, because the predictive equation was partially built from respiration rates calculated for temperate and tropical species (Belcher et al., 2020). Our carbon flux estimations might therefore be underestimated to an unknown degree, but until these uncertainties are resolved, the results should be interpreted with caution in absolute terms. Indeed, the most recent inter-comparison of carbon fluxes between epi- and mesopelagic zones using a linear inverse ecosystem model suggested that estimates of zooplankton active transport using conservative estimates of standard metabolism are grossly underestimated (Kelly et al. 2020). Relative values among stations and visits were however revealing about how environmental factors and population dynamics can affect carbon flux. For instance, Figure 12 illustrates how carbon flux is strongly driven by the total migrant biomass, but that this biomass will be more efficiently converted into carbon dioxide when the size structure of the community is small. This results from higher metabolic rates occurring in small fish (Equation 1). On the other hand, the migration range in small myctophid fishes used to be shorter and shallower (Badcock and Merrett, 1976), and this should be taken into account when modelling fish-mediated carbon export. Overall, the ocean-basin and slope-boundary stations M1 and M4, situated south off the PF, had greater migrant biomass, larger species, and from twofold to threefold higher respiratory carbon fluxes. This highlights the importance of patchiness when assessing carbon export, and demonstrate a strong bottom up structuring on this mechanism.

Conclusion

We used a complementary collection of trawl and acoustic data to elucidate MM biodiversity and its organisation in the different primary production regimes in the Kerguelen region. We identified a variable three-layer system common to the zones over and around the Kerguelen plateau, a shallow scattering layer (SSL, between 10 and 200 m), mid-depth scattering layers (MSL, between 200 and 500 m) and deep scattering layers (DSL, between 500 and 800 m). This integrated trawl–acoustic approach is needed to collect the necessary information to understand the patterns of variability in mesopelagic ecosystems, including diversity and vertical distribution, and their consequences in terms of trophic interactions and biogeochemical fluxes. Next steps will be to use the full range of acoustic frequencies (18 kHz to 200 kHz) to better resolve the complexity of the various groups, despite limited to the SSL. The biophysical links also deserve investigations to describe the influence of physical features such as the stratification of water masses, the PF and the plateau vs offshore areas. Finally, estimates of active C fluxes should be made to other groups in addition to fish, to reach an assessment of the combined active contribution of mid-trophic levels on the biological carbon pump.

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Table 1. EK80 echosounder settings.

Frequency (kHz)	Max. acquistion range (m)	Power (W)	Pulse length (μs)
18	1000	2000	1024
38	800	1000	2048

Table 2. Summary of trawl samples.

Station	Visit	Date	Day/Night	Latitude/Longitude	Max depth (m)	Trawl ID
M1	1st	08/03/18	Night	49°50 S / 74°54 E	51	21
		08/03/18	Night	49°50 S / 74°54 E	290	22
		08/03/18	Night	49°50 S / 74°54 E	617	23
		09/03/18	Day	49°50 S / 74°54 E	400	24
		09/03/18	Day	49°50 S / 74°54 E	50	25
		09/03/18	Day	49°50 S / 74°54 E	632	26
M2	1st	26/02/18	Day	50°36 S / 72°S	318	1
		26/02/18	Day	50°30 S / 72°01 E	210	2
		26/02/18	Day	50°27 S / 72° E	350	3
		27/02/18	Night	50°35 S / 71°55 E	346	4
		27/02/18	Night	50°35 S / 71°52 E	55	5
		27/02/18	Night	50°34 S / 71°50 E	158	6
	2nd	07/03/18	Day	50°39 S / 71°57 E	170	15
		07/03/18	Day	50°39 S / 71°57 E	70	16
		07/03/18	Day	50°39 S / 71°57 E	350	17
		07/03/18	Night	50°40 S / 71°59 E	317	18
		07/03/18	Night	50°40 S / 71°59 E	50	19
		07/03/18	Night	50°40 S / 71°59 E	175	20
	3rd	16/03/18	Night	50°36 S / 71°59 E	65	37
		16/03/18	Night	50°36 S / 71°59 E	377	38
		16/03/18	Night	50°36 S / 71°59 E	30	39
		17/03/18	Day	50°36 S / 71°59 E	105	40
		17/03/18	Day	50°36 S / 71°59 E	340	41
		17/03/18	Day	50°36 S / 71°59 E	190	42
M3	1st	04/03/18	Day	50°45 S / 68°03 E	55	13
		04/03/18	Day	50°47 S / 68°01 E	460	14
	2nd	15/03/18	Day	50°41 S / 68°03 E	683	33
		15/03/18	Night	50°41 S / 68°03 E	610	34
		15/03/18	Night	50°41 S / 68°03 E	90	35
		15/03/18	Night	50°36 S / 67°58 E	415	36
	3rd	18/03/18	Day	50°39 S / 67°45 E	814	43

		18/03/18	Day	50°39 S / 67°45 E	600	44
		18/03/18	Day	50°39 S / 67°45 E	65	45
		19/03/18	Night	50°39 S / 67°45 E	802	46
		19/03/18	Night	50°39 S / 67°45 E	650	47
		19/03/18	Night	50°39 S / 67°45 E	73	48
M4	1st	01/03/18	Day	52°36 S / 67°11 E	93	7
		01/03/18	Day	52°35 S / 67°08 E	575	8
		01/03/18	Day	52°33 S / 67°00 E	425	9
		02/03/18	Night	52°36 S / 67°11 E	400	10
		02/03/18	Night	52°39 S / 67°07 E	96	11
		02/03/18	Night	52°42 S / 67°05 E	575	12
	2nd	14/03/18	Day	52°37 S / 67°09 E	85	27
		14/03/18	Day	52°37 S / 67°09 E	610	28
		14/03/18	Day	52°37 S / 67°09 E	410	29
		14/03/18	Night	52°35 S / 67°11 E	600	30
		14/03/18	Night	52°35 S / 67°11 E	80	31
		14/03/18	Night	52°35 S / 67°11 E	400	32

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Table 3. Proportion and occurrence of gelatinous species caught during trawl operations. Main contributions are in bold.

FAMILY	Species	% occurrence	% all stations	% M1	% M2	% M3	% M4
CHAETOGNATHS	*Sagitta gazellae*	**93.62**	0.77	0.43	0.62	3.56	1.34
CTENOPHORES	*Beroe cucumis*	31.91	0.89	0.75	0.21	2.33	2.95
	Bolinopsis sp.	29.79	0.74	0.24	0.09	**11.98**	0.09
	Leucothea sp.	2.13	0.01	0.00	0.00	0.17	0.00
MEDUSAE	*Atolla wyvillei*	17.02	1.53	0.62	0.00	**14.36**	**4.42**
	Calycopsis borchgrevinki	**51.06**	0.35	0.28	0.14	1.66	0.71
	Calycopsis sp. 2	6.38	0.02	0.00	0.00	0.31	0.00
	Halicreas minimum	2.13	0.00	0.00	0.00	0.05	0.00
	Haliscera conica	4.26	0.02	0.00	0.00	0.35	0.00
	Medusa unknown B	4.26	0.03	0.00	0.00	0.51	0.00
	Periphylla periphylla	29.79	1.02	0.05	0.19	**5.92**	**5.00**
	Rhopalonema sp.	2.13	0.01	0.00	0.00	0.00	0.05
	Scyphomedusae	2.13	0.05	0.00	0.00	0.00	0.40
	Solmissus sp. *(Medusa unknown A)*	36.17	0.37	0.27	0.00	1.38	1.47
	Stygiomedusa gigantea	0.00	0.00	0.00	0.00	0.00	0.00
NEMERTEANS	*Pelagonemertes rollestoni*	8.51	0.01	0.00	0.00	0.20	0.00
POLYCHAETES	*Tomopteris carpenteri*	17.02	0.01	0.01	0.02	0.03	0.00
SALPS	*Salpa thompsoni*	**85.11**	**73.63**	**89.74**	**86.88**	**10.63**	**2.75**
SIPHONOPHORES	*Diphyes* sp.	4.26	0.00	0.00	0.00	0.01	0.00
	Rosacea plicata	**55.32**	**20.59**	**7.60**	**11.85**	**46.55**	**80.83**

Table 4. Proportion and occurrence of crustaceans species caught during trawl operations. Main contributions are in bold.

FAMILY	Species	% occurrence	% all stations	% M1	% M2	% M3	% M4
EUPHAUSIIDS	*Euphausia longirostris*	10.64	0.30	1.85	0.00	0.00	0.00
	Euphausia triacantha	**82.98**	**11.28**	**15.71**	**7.20**	**20.03**	**9.99**
	Euphausia vallentini	**87.23**	**43.12**	**43.28**	**28.16**	**41.55**	**74.39**
	Thysanoessa macrura/vicina	**51.06**	2.78	**4.99**	2.67	0.06	3.30
GAMMARID AMPHIPODS	*Cyphocaris richardi*	31.91	0.12	0.01	0.00	0.22	0.39
	Danaela mimonectes	10.64	0.01	0.00	0.00	0.01	0.02
	Eurythenes obesus	6.38	0.00	0.01	0.00	0.01	0.00
	Eusiroides stenopleura	19.15	0.03	0.02	0.00	0.10	0.07
	Parandania boecki	40.43	0.89	1.55	0.08	2.22	1.11
HYPERIID AMPHIPODS	*Cyllopus magellanicus*	**80.85**	0.87	2.27	0.89	0.25	0.24
	Hyperia spinifera	12.77	0.01	0.01	0.01	0.01	0.00
	Hyperia macrocephala	6.38	0.00	0.00	0.01	0.00	0.00
	Hyperiella antarctica	21.28	0.01	0.01	0.01	0.03	0.01
	Hyperoche luetkenides	44.68	0.07	0.11	0.09	0.03	0.02
	Pegohyperia princeps	2.13	0.00	0.00	0.00	0.00	0.00
	Physosomata sp. 1	6.38	0.00	0.00	0.00	0.02	0.00
	Physosomata sp. 2	4.26	0.00	0.01	0.00	0.00	0.00
	Primno macropa	**87.23**	1.65	2.07	1.52	**3.44**	0.44
	Scinidae sp.	0.00	0.00	0.00	0.00	0.00	0.00
	Themisto gaudichaudii	**100.00**	**37.77**	**25.49**	**59.06**	**29.42**	**9.68**
	Vibilia antarctica	**72.34**	0.59	2.44	0.25	0.40	0.05
MYSIDS	*Neognathophausia gigas*	8.51	0.01	0.00	0.00	0.04	0.00
	Mysida sp.	17.02	0.25	0.00	0.05	1.44	0.00
	Mysida sp. (red)	4.26	0.04	0.00	0.00	0.27	0.00
NATANTIA	*Acanthephyra pelagica*	4.26	0.00	0.00	0.00	0.01	0.00
	Campylonotus sp. (red)	21.28	0.01	0.02	0.00	0.03	0.00
	Pasiphaea scotiae	25.53	0.04	0.03	0.00	0.08	0.09
	Gennada sp./*Natantia* sp.	6.38	0.01	0.01	0.00	0.03	0.00
	Sergestidae sp.	6.38	0.01	0.03	0.00	0.00	0.00
	Decapoda larvae	10.64	0.01	0.02	0.00	0.02	0.00
OSTRACODS	*Gigantocypris muelleri*	21.28	0.10	0.07	0.00	0.30	0.19

Table 5. Proportion and occurrence of fish species caught during trawl operations. Main contributions are in bold.

FAMILY	Species	% occurrence	% all stations	% M1	% M2	% M3	% M4
BATHYLAGIDAE	*Bathylagus tenuis*	23.40	**5.52**	3.58	0.00	**7.94**	4.69
GONOSTOMATIDAE	*Cyclothone* sp. A	25.53	3.18	0.68	0.00	2.65	**6.93**
	Cyclothone sp. B	2.13	0.06	0.00	0.00	0.13	0.00
STOMIIDAE	*Stomias boa/gracilis*	21.28	0.83	1.87	0.00	0.97	0.22
ASTRONESTHIDAE	*Borostomias antarcticus*	2.13	0.03	0.00	0.00	0.06	0.00
IDIACANTHIDAE	*Idiacanthus atlanticus*	2.13	0.03	0.17	0.00	0.00	0.00
SCOPELARCHIDAE	*Bentalbella macropinna*	8.51	0.18	0.17	0.00	0.06	0.45
PARALEPIDIDAE	*Notolepis coatsi*	**48.94**	3.03	1.70	**12.20**	1.87	2.46
MYCTOPHIDAE	*Electrona antarctica*	**65.96**	**27.71**	**29.64**	**37.50**	**17.62**	**40.22**
	Electrona subaspera	2.13	0.03	0.17	0.00	0.00	0.00
	Gymnoscopelus bolini	2.13	0.03	0.00	0.00	0.06	0.00
	Gymnoscopelus braueri	**44.68**	4.07	3.24	2.68	**5.62**	2.46
	Gymnoscopelus fraseri	4.26	0.27	0.00	0.60	0.00	0.78
	Gymnoscopelus nicholsi	14.89	0.27	0.17	1.79	0.06	0.11
	Krefftichthys anderssoni	**55.32**	**28.10**	**20.61**	**18.15**	**41.06**	**14.30**
	Krefftichthys anderssoni (postlarvae)	**55.32**	**21.18**	**32.54**	**4.17**	**18.85**	**24.13**
	Nannobrachium achirus	8.51	0.39	0.00	0.00	0.65	0.34
	Protomyctophum andriashevi	4.26	0.12	0.68	0.00	0.00	0.00
	Protomyctophum bolini	**38.30**	1.54	1.19	**6.55**	0.19	2.23
	Protomyctophum gemmatum	2.13	0.03	0.17	0.00	0.00	0.00
	Protomyctophum parallelum	4.26	0.06	0.00	0.00	0.13	0.00
	Protomyctophum tenisoni	19.15	0.45	0.85	2.38	0.13	0.00
	Myctophidae (postlarvae)	4.26	0.09	0.00	0.00	0.19	0.00
MURAENOLEPIDAE	*Muraenolepis marmoratus*	27.66	0.83	0.51	**5.95**	0.26	0.11
MACROURIDAE	Macrouridae sp.	2.13	0.03	0.00	0.00	0.06	0.00
MELANONIDAE	*Melanonus gracilis*	4.26	0.12	0.51	0.00	0.06	0.00
MELAMPHAIDAE	*Poromitra crassiceps*	2.13	0.33	0.00	0.00	0.71	0.00
LIPARIDAE	*Paraliparis thalassobathyalis*	2.13	0.03	0.00	0.00	0.06	0.00
NOTOTHENIIDAE	*Notothenia rossii* (blue fingerling)	10.64	0.18	0.00	0.89	0.19	0.00
	Postlarvae type A	25.53	0.95	1.53	**6.55**	0.06	0.00
GEMPYLIDAE	*Paradiplospinus gracilis*	4.26	0.06	0.00	0.60	0.00	0.00
ACHIROPSETTIDAE	*Achiropsetta tricholepis*	6.38	0.12	0.00	0.00	0.26	0.00
Larvae (unidentified)		6.38	0.18	0.00	0.00	0.06	0.56

Table 6. Comparison of respiratory carbon fluxes (mg C m^{-2} d^{-1}) estimated in this study and in other sites.

Source	Location	Site	Migrant biomass (mg C m^{-2} d^{-1})	Respiratory flux at 2°C (mg C m^{-2} d^{-1})
This study[a§]	Kerguelen Islands	Station M1	14,676	0,043
		Station M2	1.761 (0.041 - 5.987)	0.004 (0.000 – 0.012)
		Station M3	1.255 (0.201 - 2.309)	0.005 (0.001 - 0.008)
		station M4	10.072 (5.067 - 15.077)	0.031 (0.016 - 0.045)
Kwong et al. (2020)[a§]	Southeast Australia	Cold core eddy “B-CCE”	0,5	0,17
		Warm core eddy “R-WCE”	4,1	0,56
		Warm core eddy “WCE”	10,6	2,75
Belcher et al. (2019)[a‡]	Scotia Sea	JR 161 WSS	49,8	0,05
		JR161 NSS	520,6	0,28
		JR177 GB	238,5	0,13
		JR177 MSS	407,1	0,33
Ariza et al. (2015)[b†]	Canary Islands	North of Gran Canaria	168	0,69
Hudson et al. (2014)[b†]	North Azores	Reykjanes Rdige	5,2	0.003-0.014
		Azorean Zone	40	0.012-0.071
Hidaka et al. (2001)[b§]	Western equatorial Pacific	Station 15	462,5	0,73
		Station 16	248,9	0,39
		Station 8	539,5	0,86
		Station 10	406,5	0,64
		Station 13	726,92	1,1

[a]Uncorrected for capture efficiency
[b]Assumes 14% of capture efficiency
[†]Small framed trawl
[‡]Medium framed trawl
[§]Large pelagic trawl

Fig. 1. Locations of the four stations (M1, M2, M3 and M4) in the Kerguelen region during the MOBYDICK survey. Acoustic and trawl data areas are indicated by blue squares. The dotted line indicates the mean location of the Polar Front during the study period.

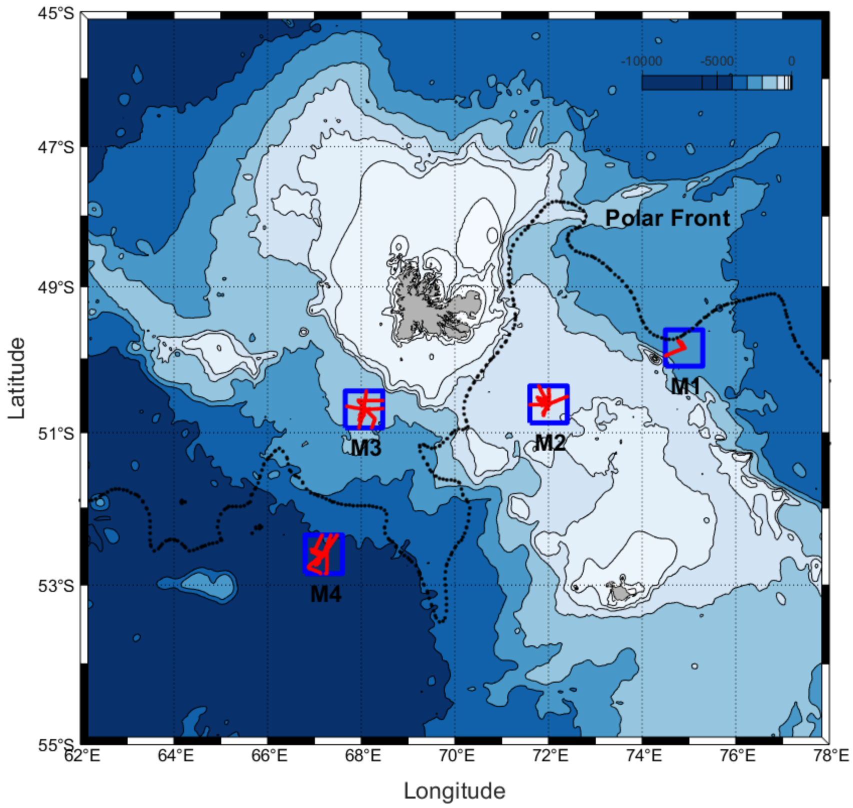


Fig. 2. Time series of weekly-averaged chlorophyll a concentration (mg · m^{-3}) at each MOBYDICK station (blue squares in Figure 1) from October 2017 to March 2018.

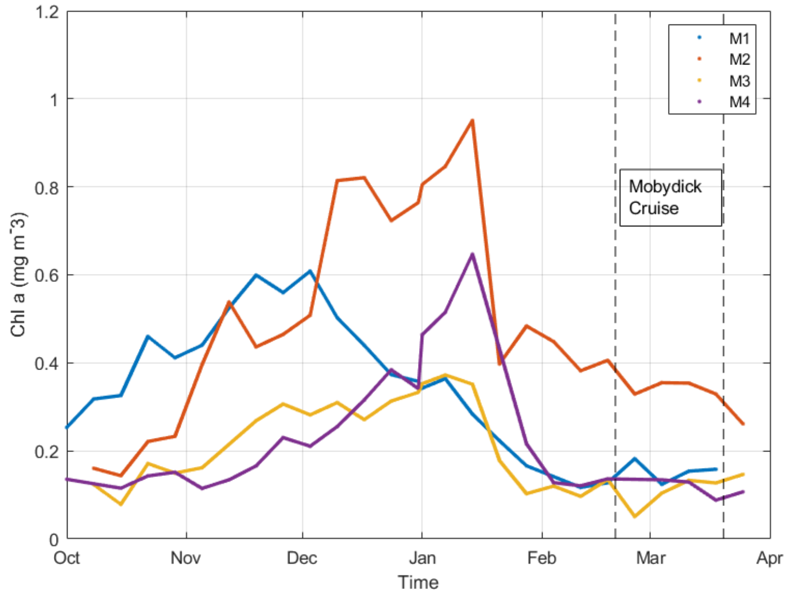


Fig. 3. Night-day (left-right) absolute biomass (in g · 1000m^{-3}) of macrozooplankton-micronekton from trawls.

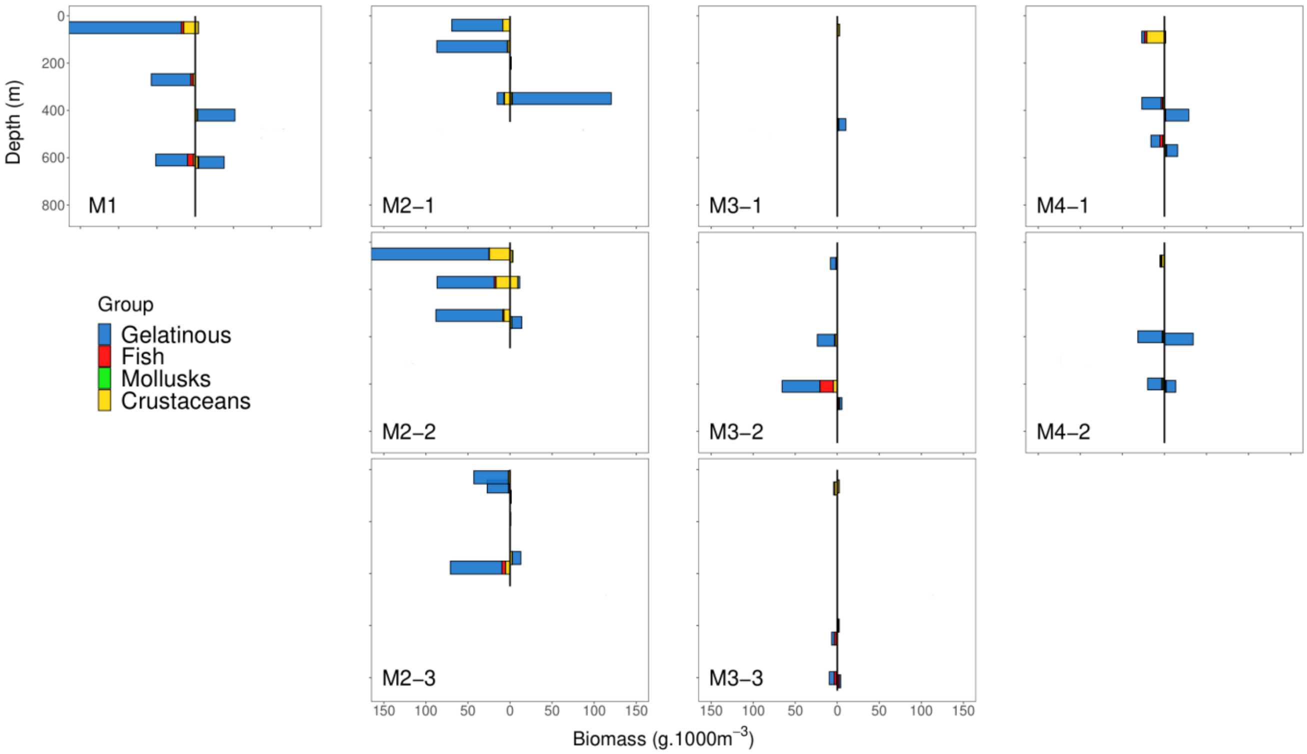


Fig. 4. Night-day (left-right) relative biomass of macrozooplankton-micronekton from trawls.

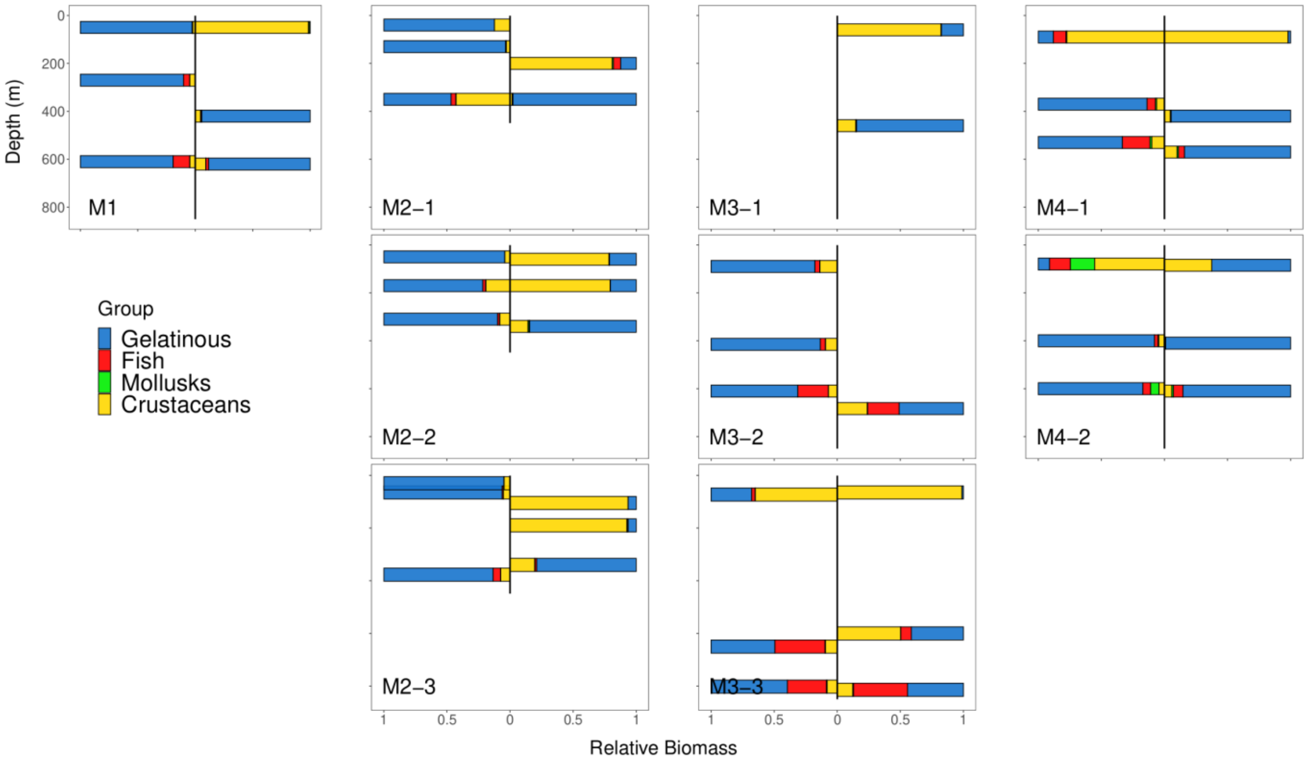


Fig. 5. Night-day (left-right) relative abundance of macrozooplankton-micronekton from trawls.

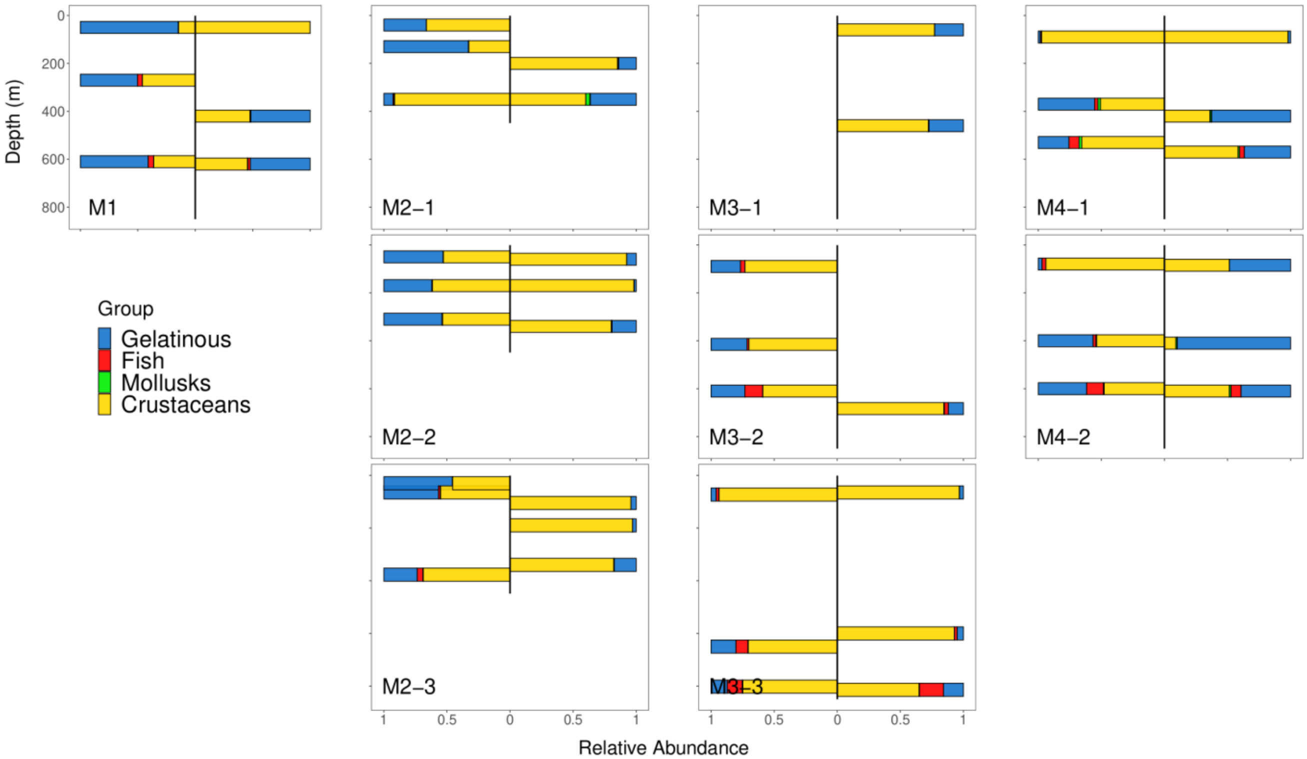


Fig. 6. Night-day (left-right) absolute biomass (in g · $1000m^{-3}$) of the main gelatinous organisms from trawls.

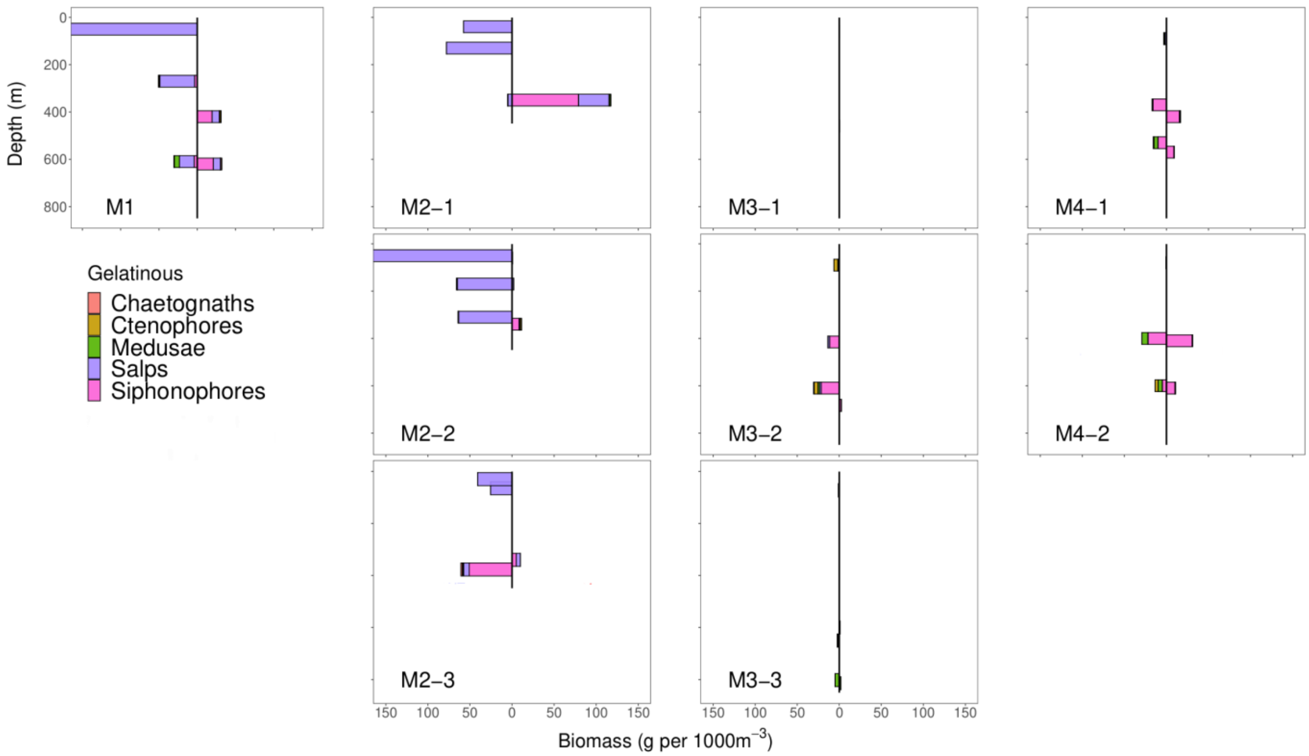


Fig. 7. Night-day (left-right) absolute abundance (in individual · $1000m^{-3}$) of the main crustaceans from trawls.

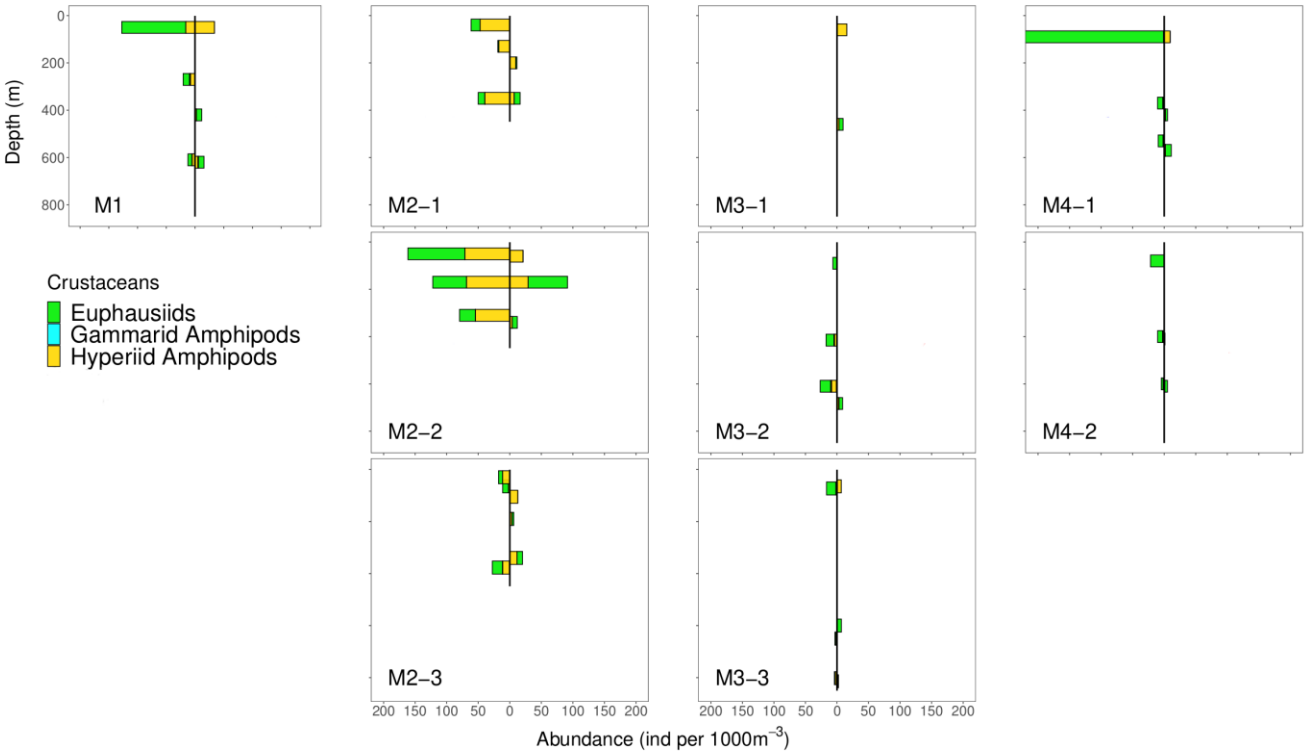


Fig. 8. Night-day (left-right) absolute abundance (in individual · $1000m^{-3}$) of the main myctophids from trawls.

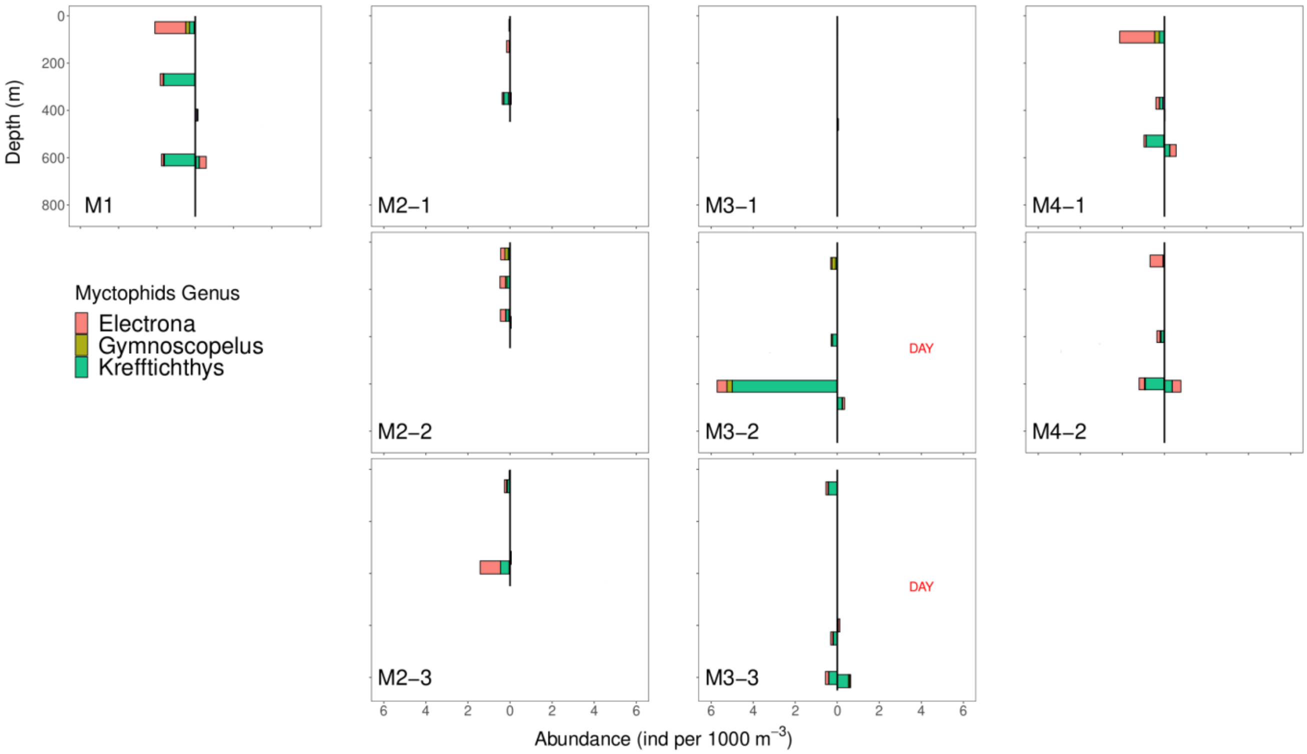


Fig. 9. Night-day (left-right) mean vertical NASC profiles at 18kHz (red) and 38 kHz (blue).

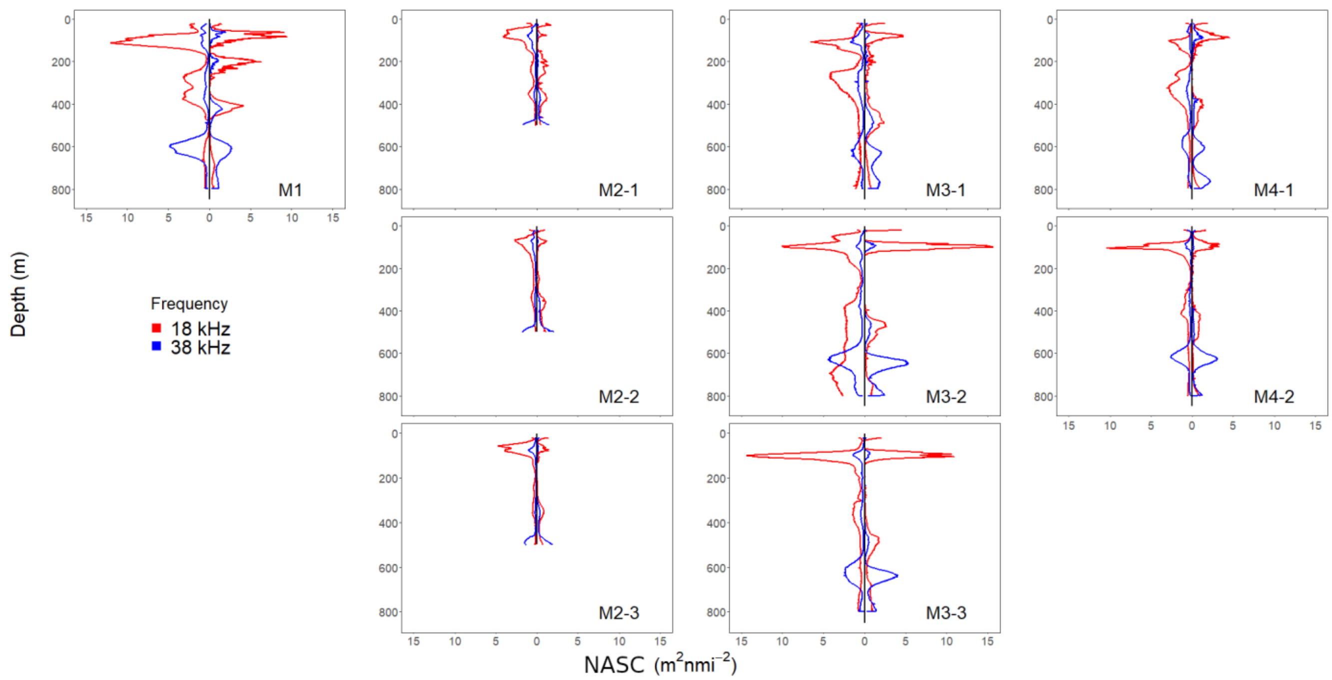


Fig. 10. Daily RGB composites of Sv values (dB re · $1m^{-1}$) from 12 to 800m for the four stations, with the 18 kHz displayed in red and the 38 kHz frequency displayed both in green and blue.

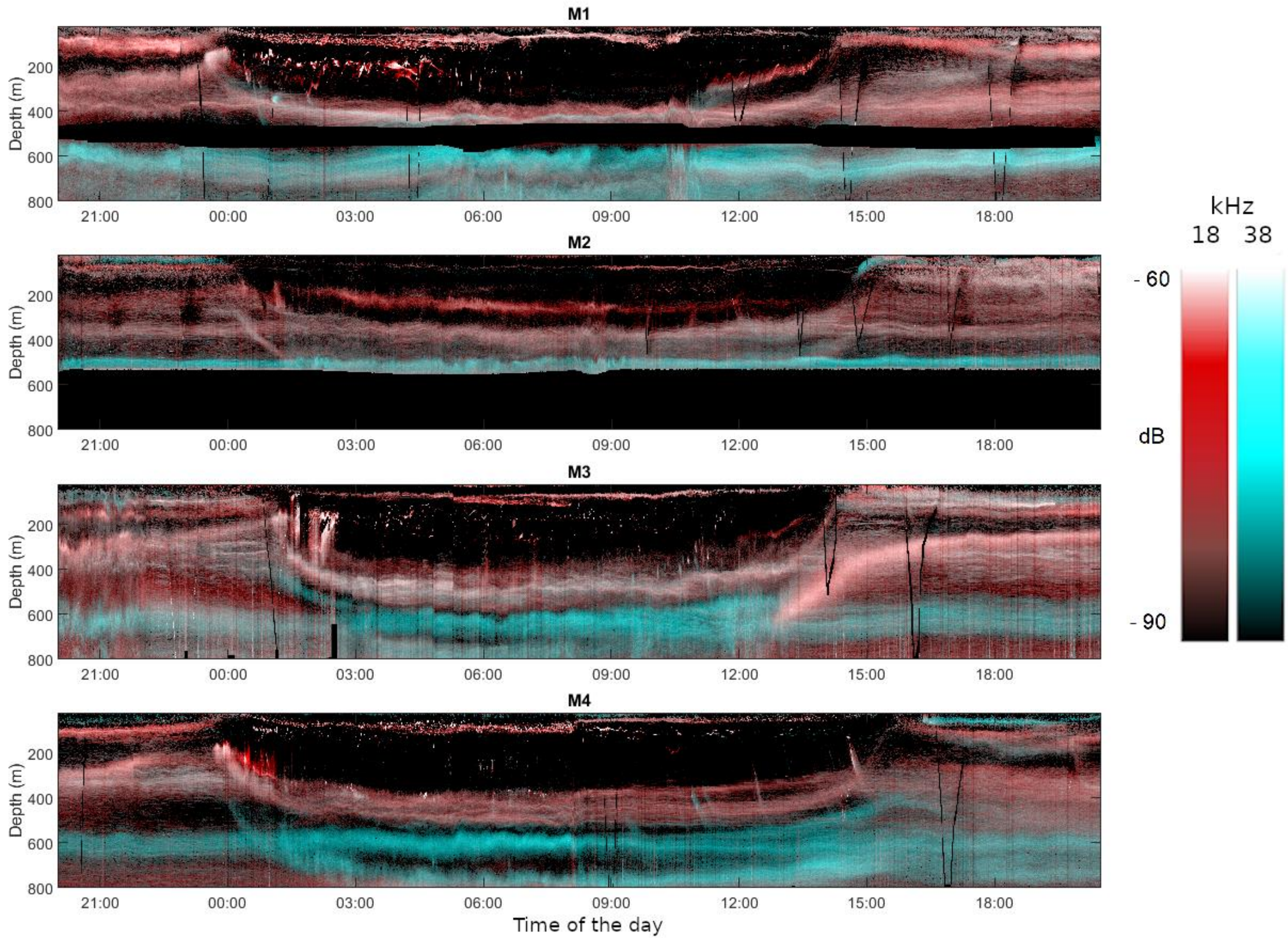


Fig. 11. Night-day (left-right) carbon content (in mg · m^{-3}) of macrozooplankton-micronekton from trawls.

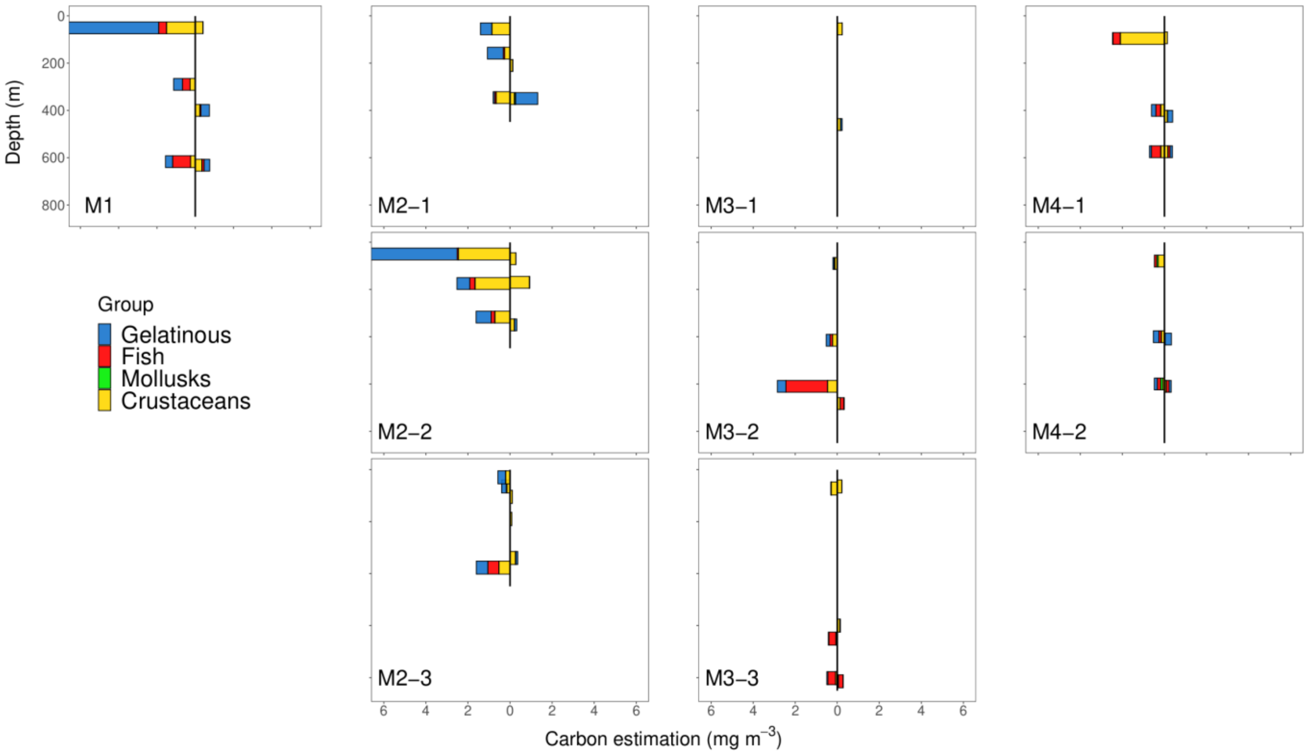
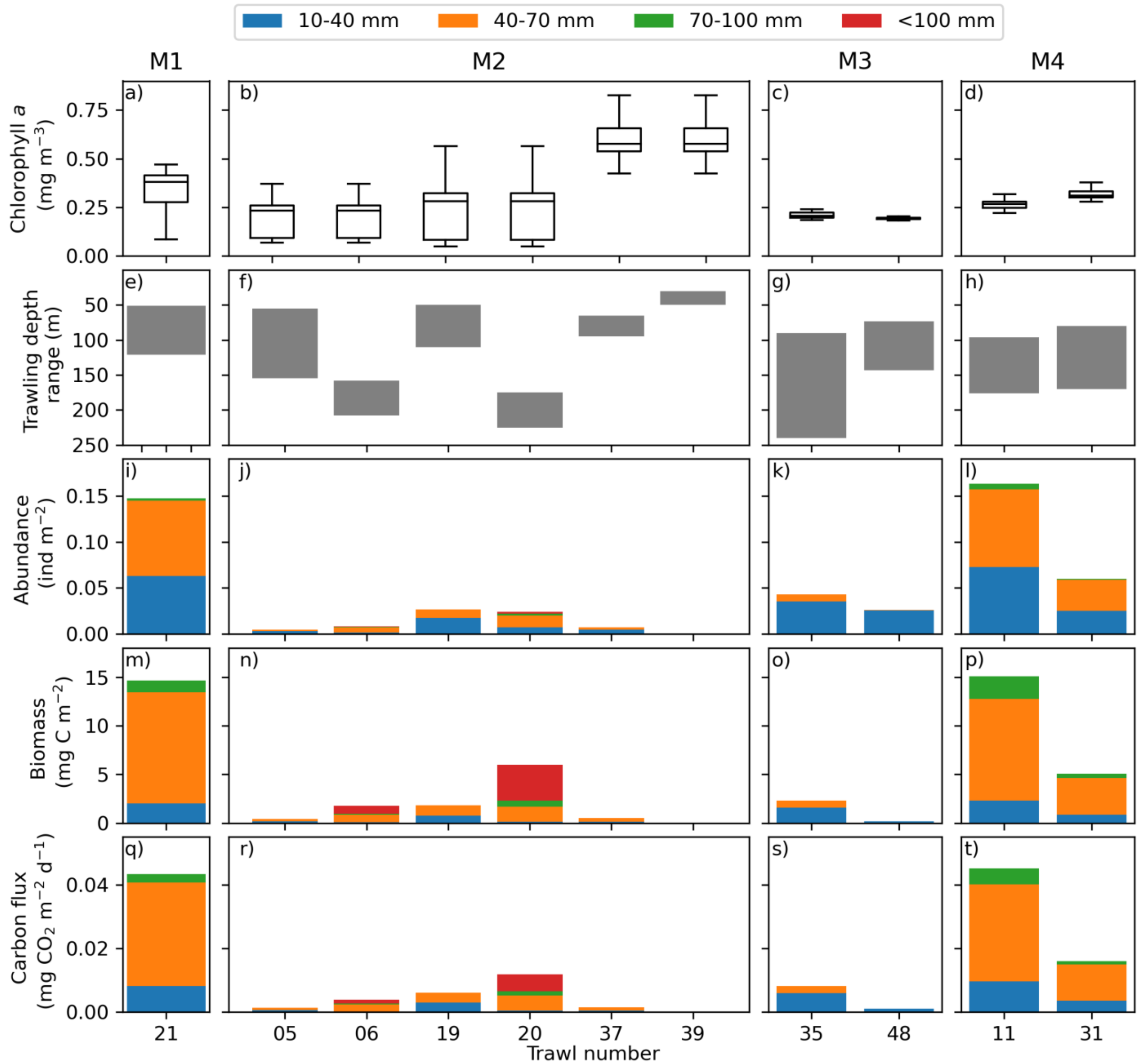
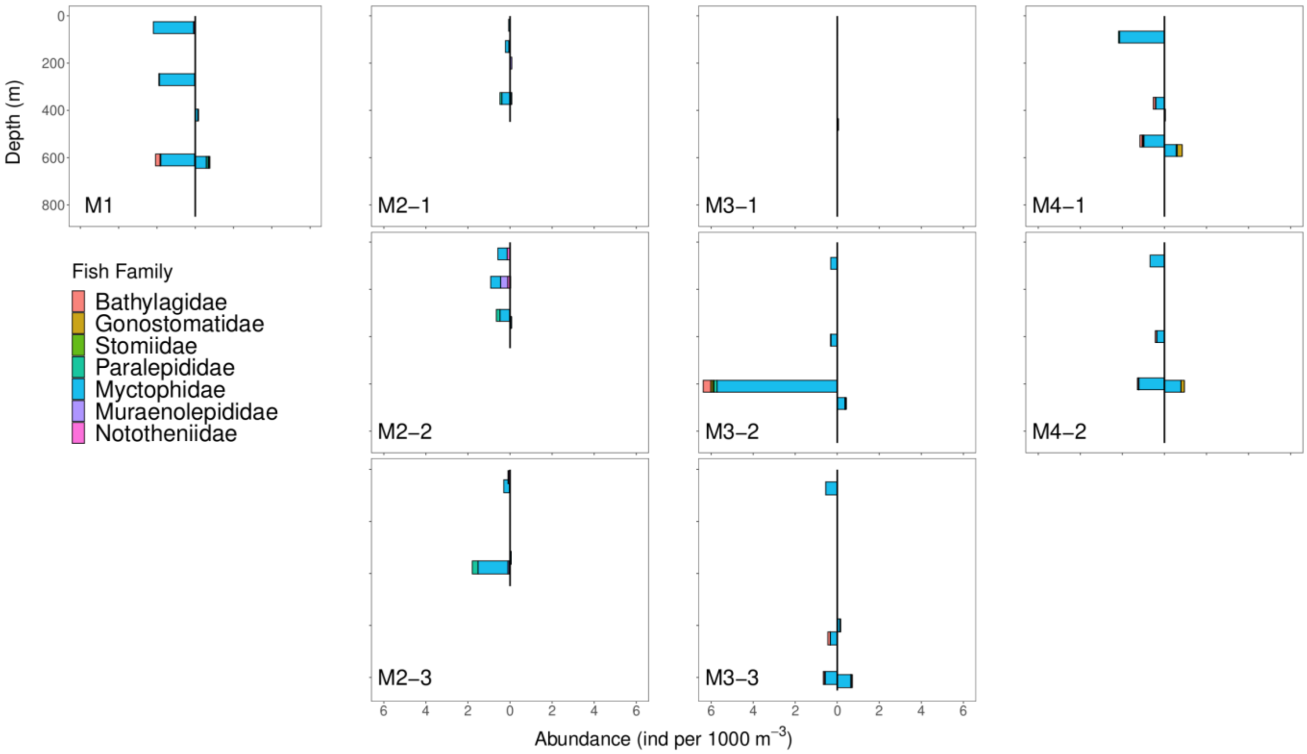


Fig. 12. Averaged chlorophyll *a* from 20 to 100 m depth (a-d), depth range of trawling used to target the migrant layers at each visit (e-h), and migrant abundance (i-j), biomass (m-p) and respiratory carbon flux (q-t) mediated by fish from the family Myctophidae.



Supplementary material 1

Night-day (left-right) absolute abundance (in individual · 1000m^{-3}) of fish from trawls.



Supplementary material 2

Size frequency densities for the two main fish species per station and depth strata.