

Isotopic niches of Mesopelagic fish on the southern Kerguelen Axis: variation and overlap

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Abstract

Mesopelagic fish are an important but poorly understood mid-trophic component of Southern Ocean food webs. This study aimed to investigate the trophic role of mesopelagic fish in the southern Kerguelen Plateau region. We used carbon and nitrogen stable isotopes to quantify the isotopic niches of key mesopelagic fish species (six from the family Myctophidae, and one from Bathylagidae), to investigate variation along the $\delta^{15}\text{N}$ and $\delta^{13}\text{C}$ axes between species, and to examine the relationship between fish body length and $\delta^{15}\text{N}$ within species and across the community. The assemblage of key mesopelagic fish occupied similar isotopic niche space with overlap among species in both $\delta^{13}\text{C}$ and $\delta^{15}\text{N}$ values. However, there were areas of non-overlapping isotopic niche space between species providing evidence of niche partitioning most likely driven by interspecific differences in diet and body size. At the community level, fish standard length was positively correlated with $\delta^{15}\text{N}$ suggesting size-related differences in diet between species. However, within-species relationships between fish standard length and $\delta^{15}\text{N}$ were weak. Overall, the findings from this study suggest that while there is a degree of trophic diversity among the taxa examined, this assemblage comprises a single energy pathway, which is informative for overall understanding of food-web architecture as well as development of trophically orientated ecosystem model for this region.

Niches isotopiques de poissons mésopélagiques dans le secteur sud de Kerguelen (Campagne Kerguelen Axis) : variation et chevauchement

Résumé

Les poissons mésopélagiques constituent un élément de niveau trophique intermédiaire important mais mal compris des réseaux trophiques de l'océan Austral. Cette étude visait à examiner le rôle trophique des poissons mésopélagiques dans la région sud du plateau de Kerguelen. À cet effet, elle a utilisé les isotopes stables du carbone et de l'azote pour quantifier les niches isotopiques des espèces clés de poissons mésopélagiques (six de la famille des Myctophidae et une des Bathylagidae), pour déterminer la variation interspécifique le long des deux axes $\delta^{15}\text{N}$ et $\delta^{13}\text{C}$, et pour examiner la relation entre la taille des poissons et $\delta^{15}\text{N}$ à l'échelle de l'espèce et à l'échelle de la communauté. L'assemblage des poissons mésopélagiques clés occupait un espace de niche isotopique similaire avec un recouvrement entre les espèces pour les valeurs de $\delta^{13}\text{C}$ et $\delta^{15}\text{N}$. Il existait toutefois des zones dans lesquelles les espèces ne partageaient pas l'espace de leur niche isotopique, ce qui met en évidence un partitionnement de la niche causé probablement par des différences interspécifiques de régime alimentaire et de taille. À l'échelle de la communauté, la longueur standard des poissons était positivement corrélée

avec $\delta^{15}\text{N}$, suggérant des différences de régime alimentaire entre espèces en fonction de la taille. Néanmoins, les relations intraspécifiques entre la longueur standard des poissons et $\delta^{15}\text{N}$ étaient faibles. Globalement, les résultats de cette étude suggèrent que, si les taxons examinés présentent un certain degré de diversité trophique, cet assemblage comprend une seule voie énergétique, ce qui est intéressant pour une compréhension générale de l'architecture des réseaux trophiques ainsi que pour le développement d'un modèle écosystémique trophique de la région.

Keywords: Trophodynamics, food webs, micronekton, prey field, midwater trawling

Introduction

Mesopelagic fish, found in the midwater zone (typically 200–1 000 m during the day, with many taxa moving to the surface waters at night), are important mid-trophic level components of pelagic food webs in the Southern Ocean (Kozlov, 1995). Lanternfish (family Myctophidae) are the dominant mesopelagic fish family of the oceanic ecosystem; and deep-sea smelt (family Bathylagidae) dominate in the lower mesopelagic zone at 400–1 000 m (Collins et al., 2012). Given the biomass of myctophids and bathylagids coupled with the vertical migrations of species, these fish are likely to play a key role in the transport of carbon from the surface waters to the deep ocean (Hulley and Duhamel, 2011; Collins et al., 2012). These small fish (<20 cm in length) are important prey for higher-trophic level predatory fish, some cephalopods, seabirds and marine mammals (Cherel et al., 2010; Stowasser et al., 2012), and are themselves important consumers of lower trophic level zooplankton species (Pakhomov et al., 1996; Gaskett et al., 2001; Shreeve et al., 2009). Further, fishes of both families are important prey for commercially valuable Patagonian toothfish (*Dissostichus eleginoides*; Gaskett et al., 2001). Energy pathways comprising mesopelagic fish are poorly understood in comparison to those dominated by krill, representing a key area of uncertainty in current ecosystem models (Murphy et al., 2012). Quantifying energy pathways mediated by these mid-trophic levels is central to the development and improvement of ecosystem models that are able to robustly predict the response of Southern Ocean food webs to environmental change. Such models are imperative for informing management of expanding fisheries and conservation of resources (Murphy et al., 2012).

Stable isotope analysis is increasingly being used to study trophic interactions and to delineate linkages in food webs (Peterson and Fry, 1987; Cherel et al., 2010; Phillips et al., 2014). Nitrogen

and carbon stable isotope values ($\delta^{15}\text{N}$ and $\delta^{13}\text{C}$ respectively) of consumer tissues reflect the biogeochemical processes that occur at the base of the food web (Minagawa and Wada, 1984; Post, 2002). In the marine environment, the nitrogen and carbon source utilised by primary producers influences their isotopic composition and can vary on spatial and temporal (seasonal) scales (Lourey et al., 2003, 2004). Consumer tissues preferentially retain the heavier ^{15}N isotope, resulting in an enrichment from one trophic step to the next (Minagawa and Wada, 1984), providing a proxy for trophic position (Post, 2002). Whereas $\delta^{13}\text{C}$ can be used to evaluate the major source of carbon for a consumer, such as pelagic (open ocean) production from phytoplankton (Post, 2002; Cherel and Hobson, 2007). Additionally, clear latitudinal variations in $\delta^{13}\text{C}$ of particulate organic matter (POM) have been observed in the Southern Ocean (Post, 2002; Cherel and Hobson, 2007). Isotopic gradients in the marine environment can therefore be utilised to investigate sources of primary productivity and foraging habitat of consumers.

The area occupied in bivariate (e.g. $\delta^{13}\text{C}$ versus $\delta^{15}\text{N}$) two-dimensional space provides an indicator of the 'realised ecological niche' of a species, with the dimensions of this isotopic niche reflecting a species' trophic ecology and habitat use (Peterson and Fry, 1987; Post, 2002; Newsome et al., 2007). Importantly, isotopic signatures of key consumers can be compared to determine whether they occupy distinct niches in stable isotope space which may highlight the presence of multiple distinct energy pathways (Jackson et al., 2011). Once individual niches are determined, the environmental predictors of these niches and associated energy pathways can be explored to provide further insight into community tropho-dynamics and drivers of energy pathways (Layman et al., 2012).

Despite the ecological importance of the Kerguelen Plateau and nearby Antarctic continent

(hereafter ‘Kerguelen Axis’), and of mesopelagic fish communities in the region, only one previous study has examined the isotopic ecology of myctophids in this area (Cherel et al., 2010). This study focused on the northern Kerguelen Plateau, in the vicinity of the Kerguelen Islands. The study found qualitative evidence for isotopic niche differentiation along either the $\delta^{15}\text{N}$ (trophic position) or the $\delta^{13}\text{C}$ (habitat) axis, suggesting trophic partitioning within the fish assemblage (Cherel et al., 2010). The average size of fish was positively correlated with trophic position ($\delta^{15}\text{N}$) at the species level; and foraging habitat and migratory behaviours influenced carbon isotope signatures, both factors determinants of trophic niche differentiation (Cherel et al., 2010). It is unclear whether the patterns described in Cherel et al. (2010) are representative of the entire region, or are characteristic only of the area in the immediate vicinity of the Kerguelen Islands.

The objectives of this study are to: (1) quantitatively assess variation along the $\delta^{15}\text{N}$ (resource use) and $\delta^{13}\text{C}$ (habitat use) axes between key mesopelagic fish species; and (2) investigate the relationship between fish body length and relative trophic position as inferred by $\delta^{15}\text{N}$ values within species and across the community. This study is part of a large-scale program assessing the influence of different environmental drivers on the ecosystem, associated marine food webs and key energy pathways.

Methods

Sample collection

Samples were collected from nine sampling stations along a latitudinal transect from the Antarctic continental shelf to the BANZARE Bank over the Kerguelen Plateau during the Kerguelen Axis voyage of the RSV *Aurora Australis* in January–February 2016 (Figure 1). Mesopelagic fish were sampled from the surface to 1 000 m depth using an International Young Gadoid Pelagic Trawl (IYGPT) net equipped with a MIDwater Open and Closing (MIDOC) multiple codend device. The MIDOC allowed the haul to be split into individual codends for different depth strata in 200 m bands between 1 000 m and the surface (0–200, 200–400, 400–600, 600–800 and 800–1 000 m). Catches from each haul were sorted on board then frozen whole at -20°C for further analysis in the laboratory.

Stable isotope analysis

The realised ecological niches of key mesopelagic fish species in the southern Kerguelen Axis region were investigated using $\delta^{15}\text{N}$ and $\delta^{13}\text{C}$ values. This study focused on taxa from the Myctophidae family of the genera *Electrona*, *Gymnoscopelus*, *Krefflichthys* and *Protomyctophum*, and the Bathylagidae family of the genera *Bathylagus* given that these are dominant genera in the Southern Ocean (Pusch et al., 2004; Hulley and Duhamel, 2011; Collins et al., 2012).

In the laboratory, fish were thawed, measured, weighed and identified to species level based on external features and otolith morphology, using published guides (Gon and Heemstra, 1990; Duhamel et al., 2005). Where available, for each fish species, five replicates per station were selected for stable isotope analysis. A sample of white dorsolateral muscle tissue from each fish was analysed for $\delta^{15}\text{N}$ and $\delta^{13}\text{C}$ at the Central Science Laboratory (CSL), University of Tasmania, Hobart, Australia. Muscle samples were oven-dried (at 60°C), delipidated (using cyclohexane) and ground to a homogeneous powder prior to analysis. Isotope compositions were measured using an Isoprime100 mass spectrometer coupled to an Elementar vario PYRO cube elemental analyser. Stable isotope values are presented in δ notation as parts per thousand (‰; relative to international standards of PeeDee belemnite and atmospheric N_2 for $\delta^{13}\text{C}$ and $\delta^{15}\text{N}$ respectively). Measurement precision values were 0.02‰ for $\delta^{13}\text{C}$ and 0.1‰ for $\delta^{15}\text{N}$ based on replicates of sulphanilamide as an internal laboratory standard run on every 12th sample.

Data analysis

To quantify and compare the isotopic niche space occupied by key mesopelagic fish species, we used multivariate ellipse-based metrics within the Stable Isotope Bayesian Ellipses in R (SIBER) package (Jackson et al., 2011). SIBER presents isotope data in multivariate space (e.g. $\delta^{13}\text{C}$ versus $\delta^{15}\text{N}$ plot) with standard ellipses overlaid on the data defining a consumer’s isotopic niche (Newsome et al., 2007; Jackson et al., 2011). The $\delta^{13}\text{C}$ axis was a proxy for the environmental components, and the $\delta^{15}\text{N}$ axis was used to represent the trophic components of niche space (Hutchinson, 1978). The isotopic niche width and isotopic niche overlap were calculated using Bayesian standard ellipse areas (SEA_b) and

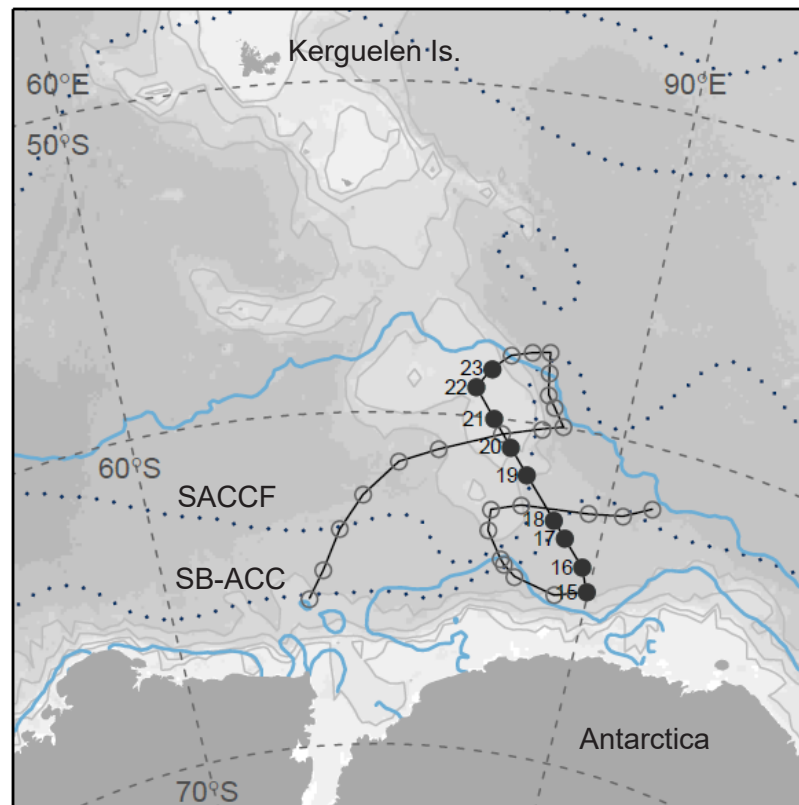


Figure 1: Location of the MIDOC sampling stations (black circles) in 2016 on the southern Kerguelen Axis. Station 15 was on the Antarctic continental shelf, stations 16 to 18 were south of the Southern Boundary of the Antarctic Circumpolar Current (SB-ACC) and stations 19 to 23 were north of the Southern Antarctic Circumpolar Current Front (SACCF) over the Kerguelen Plateau. The dotted lines with labels indicate the SB-ACC and the SACCF (Orsi et al., 1995). The blue lines indicate the northern extent of winter sea-ice for January and November (minimum and maximum for the season respectively, at 15% concentration).

sample size corrected standard ellipse areas (SEA_c) respectively, as outlined in Jackson et al. (2011). The quantitative assessment of the variation in niche space between and within species allowed us to make inferences for the ‘realised ecological niche’ of a species (Newsome et al., 2007). Standard ellipse areas were scaled to contain approximately 40% of the data. The isotopic niche width of each group was compared by calculating the SEA on the posterior distribution of the covariance matrix for each group to generate SEA_b . The probability that one group’s posterior distribution was smaller or larger than another group’s was calculated to determine significant differences between groups, a significant difference was considered as >95%. Overlap of SEA_c was calculated as a proportion of the sum of the non-overlapping area, where a completely distinct ellipse was equal to zero and a completely coincidental ellipse was equal to one.

To investigate the relationship between fish standard length (mm) and $\delta^{15}N$, we fitted linear regression models to the data using the R package lme4 (Bates et al., 2015). The dependent variable, $\delta^{15}N$, was modelled as a function of fish standard length for each taxonomic group to show within-species relationships, and with all taxonomic groups pooled together to show relationships at the community level. Data met the assumptions of homoscedasticity and normality. All statistics were evaluated using R version 3.4.3 with $\alpha = 0.05$ (R Core Team, 2017).

Results

Isotopic compositions of key taxonomic groups

We measured the $\delta^{13}C$ and $\delta^{15}N$ values of white muscle tissue from six species of the Myctophidae family and one species of the Bathylagidae family

($n = 172$; for details see Woods, 2017). The $\delta^{15}\text{N}$ values ranged from 6.6 to 11.1‰ between taxonomic groups (Figure 2a), with *Kreftlichthys anderssoni* showing the lowest $\delta^{15}\text{N}$ values (mean: $7.6 \pm 0.7\text{‰}$) and *Bathylagus* sp. the highest $\delta^{15}\text{N}$ values (mean: $9.6 \pm 0.6\text{‰}$). *Kreftlichthys anderssoni* showed the widest range in $\delta^{15}\text{N}$ values from 6.63 to 9.34‰ (a difference of 2.71‰), while *Protomyctophum bolini* showed the narrowest range in $\delta^{15}\text{N}$ values from 7.64 to 9.00‰ (a difference of 1.36‰). At the species level, $\delta^{15}\text{N}$ values were relatively evenly spread between stations (Figure 2a). The exception was for *K. anderssoni* which showed a gradual decline in $\delta^{15}\text{N}$ values from sampling station 15 to station 23. Further, it must also be noted that *P. bolini* was predominantly present at sampling stations north of the Southern Antarctic Circumpolar Current Front (SAACF).

The $\delta^{13}\text{C}$ values ranged from -26.5 to -21.9‰ between taxonomic groups (Figure 2b). Again, *K. anderssoni* showed the lowest $\delta^{13}\text{C}$ values (mean: $-25.6 \pm 0.7\text{‰}$) while *Gymnoscopelus nicholsi* showed the highest $\delta^{13}\text{C}$ values (mean: $-22.3 \pm 0.4\text{‰}$). *Gymnoscopelus* spp. showed the widest range in $\delta^{13}\text{C}$ values from -21.93 to -25.89‰ (a difference of 3.96‰), while *Electrona antarctica* showed the narrowest range in $\delta^{13}\text{C}$ values from -26.20 to -23.88‰ (a difference of 2.32‰). At the species level, there were some notable differences in $\delta^{13}\text{C}$ values between stations (Figure 2b). Firstly, the spread of $\delta^{13}\text{C}$ values was broader at station 23 compared to all other sampling stations for *Bathylagus* sp. The $\delta^{13}\text{C}$ values for *Gymnoscopelus* spp. appeared to increase gradually from sampling station 15 in the south to sampling station 23 in the north. Finally, there were comparatively higher $\delta^{13}\text{C}$ values at station 17 compared to other associated stations for *K. anderssoni*.

Isotopic niches of key taxonomic groups

Isotopic niches of the five taxonomic groups were tightly clustered on both the $\delta^{15}\text{N}$ and $\delta^{13}\text{C}$ axes and showed overlapping niche boundaries for some groups (Figure 3a). *Bathylagus* sp. and *Gymnoscopelus* spp. occupied isotope space at the highest $\delta^{15}\text{N}$ values within the community. Conversely, *K. anderssoni* occupied isotope space at the lowest $\delta^{15}\text{N}$ values. Further, *E. antarctica* and *P. bolini* were positioned at intermediate values on the $\delta^{15}\text{N}$ axis. Taxonomic groups occupied similar space along the $\delta^{13}\text{C}$ axis. Although,

K. anderssoni also occupied space at more negative $\delta^{13}\text{C}$ values while *P. bolini* predominantly occupied space at higher $\delta^{13}\text{C}$ values. *Gymnoscopelus* spp. appeared to occupy broader space along the $\delta^{13}\text{C}$ axis compared to other taxonomic groups. There were also areas of shared niche space or overlap between different taxonomic groups. *Kreftlichthys anderssoni* and *E. antarctica* showed the largest proportion of overlapping area (proportion = 0.18; Figure 3a). *Gymnoscopelus* spp. showed overlap with both *Bathylagus* sp. (proportion = 0.17) and *P. bolini* (proportion = 0.13). Conversely, *Gymnoscopelus* spp. showed negligible overlap with *E. antarctica* (proportion = 0.002). Further, the isotopic niche of *E. antarctica* was also distinct from *Bathylagus* sp. and *P. bolini*, while *Bathylagus* sp. was distinct from *K. anderssoni* and *P. bolini*, and *K. anderssoni* was distinct from *P. bolini* and *Gymnoscopelus* species. Isotopic niche width was similar across the taxonomic groups (Figure 3c).

Isotopic niches of three *Gymnoscopelus* species

Isotopic niches of three species belonging to the *Gymnoscopelus* genera differed along the $\delta^{13}\text{C}$ axis, but occupied similar space along the $\delta^{15}\text{N}$ axis (Figure 3b). *Gymnoscopelus opisthopterus* and *G. braueri* shared some niche space shown as overlap of ellipse areas (proportion = 0.05). However, *G. nicholsi* was distinct from *G. braueri* and *G. opisthopterus* showing no overlap of ellipse areas. Isotopic niche widths were similar between species (Figure 3d). It should also be noted that only four *G. nicholsi* were available for stable isotope analysis.

Fish standard length and $\delta^{15}\text{N}$

The standard length of fish ranged from a minimum value of 28.4 mm for *E. antarctica* to a maximum value of 192.5 mm for *Bathylagus* sp. *Bathylagus* sp. showed the widest range in length from 80.3 to 192.5 mm (a difference of 112.2 mm), while *G. nicholsi* showed the narrowest range in length from 135.0 to 147.6 mm (a difference of 12.6 mm). However, this narrow range is likely to be influenced by small sample size. The three smallest species in this study were *P. bolini*, *E. antarctica* and *K. anderssoni*, conversely the largest species were *Bathylagus* sp., *G. nicholsi* and *G. opisthopterus* (Figure 4a).

Linear regression models were fitted to the data for all species groups (Figure 4a). In general, most groups showed weakly negative relationships where

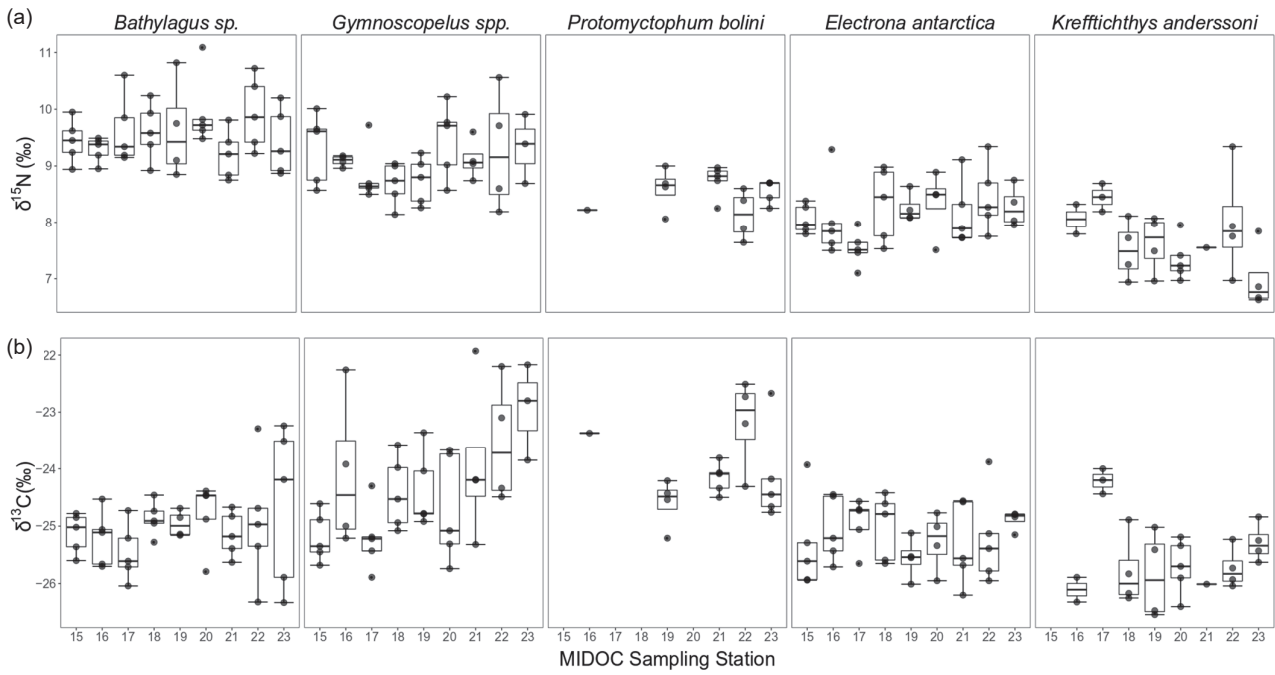


Figure 2: Box and whisker plots of the (a) $\delta^{15}\text{N}$ and (b) $\delta^{13}\text{C}$ values for each taxonomic group at each of the nine stations. Whiskers represent the minimum and maximum values that are not outliers, the ends of box plots are the quartiles and the middle vertical line in each box plot is the median value.

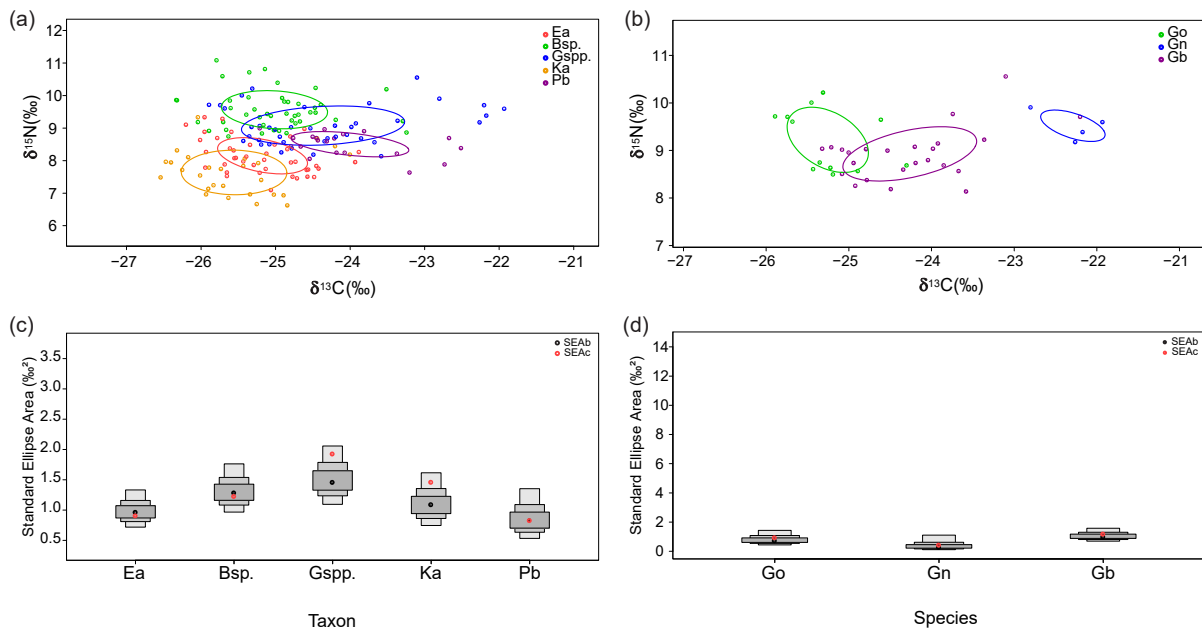


Figure 3: Sample size-corrected ellipse areas (SEA_c) for (a) each taxonomic group (in all panels, names are abbreviated as: Ea – *Electrona antarctica*; Bsp. – *Bathylagus* sp.; Gspp. – *Gymnoscopelus* spp.; Ka – *Krefftichthys anderssoni*; Pb – *Protomyctophum bolini*) and (b) *Gymnoscopelus* spp. (in all panels, names are abbreviated as: Go – *Gymnoscopelus opisthopterus*; Gn – *Gymnoscopelus nicholsi*; Gb – *Gymnoscopelus braueri*) plotted in two-dimensional $\delta^{13}\text{C} \sim \delta^{15}\text{N}$ space depicting isotopic niche position and overlap; SIBER density plot showing the Bayesian estimates of standard ellipse areas (SEA_b) depicting the isotopic niche width for (c) each taxonomic group and (d) *Gymnoscopelus* spp. Black dots represent the mode values of SEA_b , red dots represent the mode values of SEA_c and the different areas of grey shading represent the 50, 75 and 95% credible intervals.

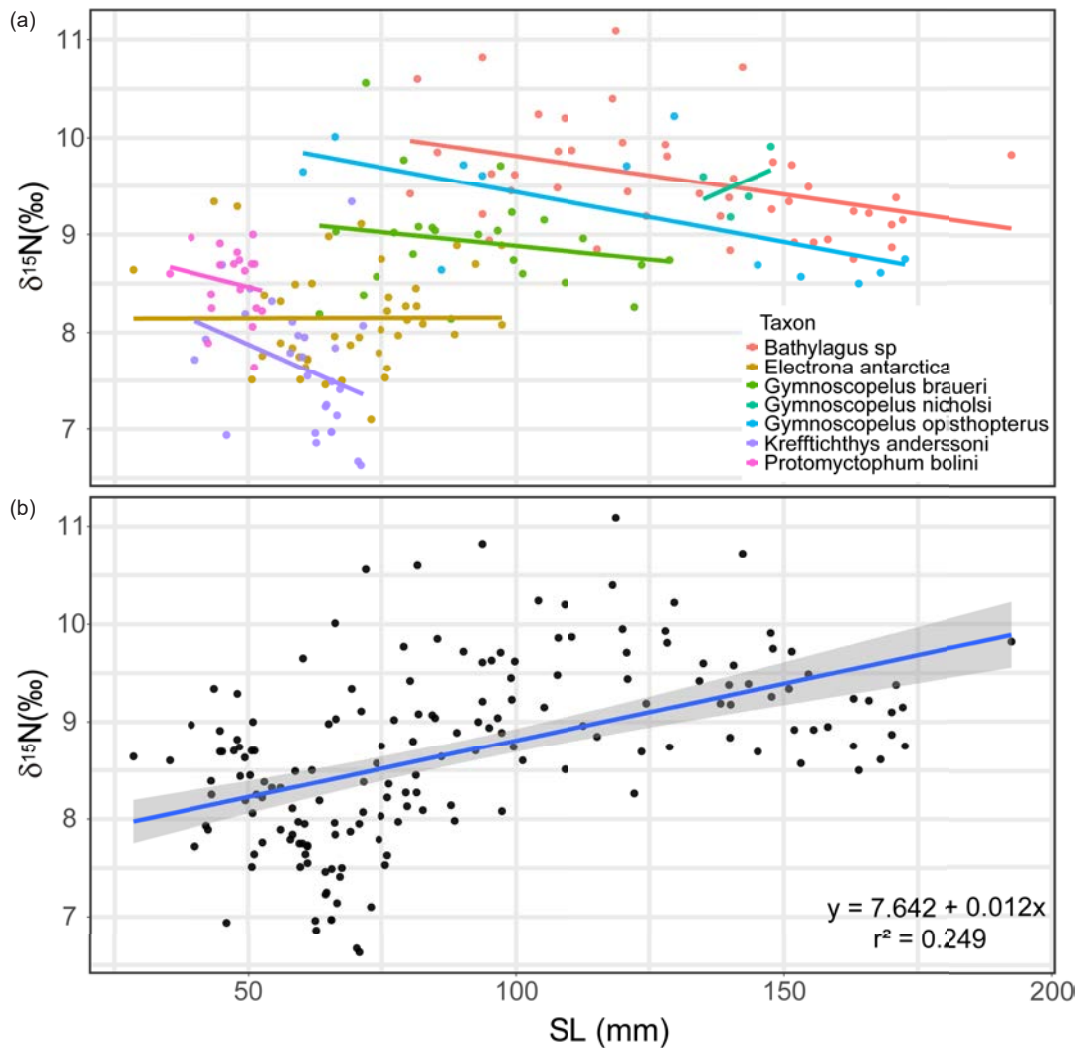


Figure 4: Linear regression models with $\delta^{15}\text{N}$ (‰) as the dependent variable and standard length (mm) as the independent variable for (a) species groups and (b) all species pooled to form a community showing 95% confidence interval in grey shading. Significance level was set to <0.05 .

$\delta^{15}\text{N}$ (‰) decreased with increasing length (mm). The exception was for *G. nicholsi*, which showed a positive relationship, and *E. antarctica* which showed no relationship. Linear regression models showed a statistically significant result for only two of the seven species. The length of *Bathylagus* sp. showed a negative relationship with $\delta^{15}\text{N}$ (‰) which was a relatively weak relationship (linear regression: $F_{1,42} = 8.311$, $r^2 = 0.165$, $p = 0.006$). Likewise, the length of *G. opisthopterus* showed a statistically significant negative relationship with $\delta^{15}\text{N}$ (‰), although this was also a weak relationship (linear regression: $F_{1,10} = 6.941$, $r^2 = 0.165$, $p = 0.006$). This relationship changed when pooling all species together (Figure 4b). This showed a statistically significant positive relationship where $\delta^{15}\text{N}$ (‰) increased with increasing fish standard

length (linear regression: $F_{1,170} = 56.37$, $r^2 = 0.249$, $p = 3.23 \times 10^{-12}$). However, this was again a relatively weak relationship with a low r^2 of 0.249.

Discussion

Our study provides the first detailed isotopic analysis of the mesopelagic fish assemblage in the southern Kerguelen Plateau region in the Indian Ocean sector of the Southern Ocean. Key mesopelagic taxa occupied similar isotopic niche space with significant overlap in both $\delta^{13}\text{C}$ and $\delta^{15}\text{N}$ values. This suggests that species have similar trophic roles within the ecosystem, comprising a single energy pathway. The non-overlapping areas in isotopic niche space between taxonomic groups observed in this study suggest inter-specific

differences in resource and habitat use demonstrating a degree of trophic diversity (Hopkins and Gartner, 1992).

Resource use

In the present study, the muscle tissue of *K. anderssoni* showed the lowest $\delta^{15}\text{N}$ values followed by *E. antarctica* and *P. bolini*. This is in agreement with previous studies investigating the trophic ecology of myctophids which have found the same species to occupy the lower trophic levels within Southern Ocean myctophid communities (Cherel et al., 2010; Stowasser et al., 2012). The diets of the three species are dominated by copepods, amphipods (Pakhomov et al., 1996; Gaskett et al., 2001) and small euphausiid species such as *Thysanoessa* spp. and *Euphausia frigida* (Shreeve et al., 2009). We found evidence of some niche partitioning with areas of non-overlapping isotopic niche space between species. This was indicated firstly by *K. anderssoni* which occupied isotope space at the lowest position on the $\delta^{15}\text{N}$ axis, suggesting the lowest relative trophic position. Followed by *E. antarctica* and *P. bolini* which were positioned progressively higher on the $\delta^{15}\text{N}$ axis. Studies have found evidence of dietary specialisation in some myctophid species, which may permit resource partitioning (Pakhomov et al., 1996; Gaskett et al., 2001; Pusch et al., 2004; Shreeve et al., 2009; Saunders et al., 2015). Dietary preferences or the partitioning of resources in this way is largely driven by a species' ability to access and utilise these different prey resources. One factor shaping this is fish body size (Pusch et al., 2004; Shreeve et al., 2009; Cherel et al., 2010; Saunders et al., 2015; Clarke et al., 2018). *Krefflichthys anderssoni* is one of the smallest species of myctophid in this study. Smaller myctophid species have consistently been found to consume smaller prey (Shreeve et al., 2009; Cherel et al., 2010; Stowasser et al., 2012). A study by Shreeve et al. (2009) demonstrated a change in diet from copepods to euphausiids and amphipods as myctophid size increased. Gape size of marine fishes has been shown to increase linearly with length (Scharf et al., 2000) which influences diet selectivity (Shreeve et al., 2009). The fact that *E. antarctica* reaches larger body size than *K. anderssoni*, allows it to access a wider variety of prey resources, possibly explaining the observed difference in niche space occupied by species in this study.

Protomyctophum bolini was predominantly found at sampling stations over the Kerguelen Plateau. Given that $\delta^{15}\text{N}$ values vary on spatial and temporal scales at the base of the food web (Lourey et al., 2003), the observed position of *P. bolini* on the $\delta^{15}\text{N}$ axis may be representative of the different productivity regimes north of SACCF and south of the Southern Boundary. Cross-basin differences in $\delta^{15}\text{N}$ of POM were found in a study of the Tasman Sea abyssal basin which propagated through the food web to higher trophic levels (Flynn and Kloser, 2012). In this study, spatial variation in $\delta^{15}\text{N}$ values at the base of the food web cannot be ruled out as the reason for observed differences in $\delta^{15}\text{N}$ values for *P. bolini* compared to the other myctophid species. This highlights the importance of considering spatial differences in $\delta^{15}\text{N}$ signatures across different productivity regimes.

The isotopic niche position of *Gymnoscopelus* spp. was higher on the $\delta^{15}\text{N}$ axis compared to *K. anderssoni*, *E. antarctica* and *P. bolini* indicating a higher relative trophic position. Our findings are consistent with a reportedly higher trophic level for *G. nicholsi* and *G. braueri* in previous studies (Cherel et al., 2010; Stowasser et al., 2012). *Gymnoscopelus* spp. are larger myctophid species often with a broader size range (this study; Shreeve et al., 2009; Cherel et al., 2010). This gives species of this genera a wider range of prey resources which it can access. This is reflected in previous dietary studies which have demonstrated a diet composed of a range of copepods, amphipods and euphausiids (Pakhomov et al., 1996; Gaskett et al., 2001; Shreeve et al., 2009; Clarke et al., 2018). In general, larger myctophids consume larger prey items (Pusch et al., 2004; Shreeve et al., 2009; Clarke et al., 2018). The larger sized *Gymnoscopelus* spp. have been shown to consume high proportions of euphausiids. In the region of the South Shetland Islands and the Scotia Sea, the diet of *G. nicholsi* is predominantly composed of *E. superba* (Pusch et al., 2004; Shreeve et al., 2009). Further, DNA-based dietary analysis of the three *Gymnoscopelus* spp. from our study region has shown the dominance of euphausiids, particularly *E. superba* and *T. macrura*, as prey sources (Clarke et al., 2018). A separate study has also shown evidence of fish predation by the larger *G. nicholsi* species which was found to prey on other mesopelagic fish, *Neopageotopsis ionah* and *P. bolini* (Pusch et al., 2004). The higher $\delta^{15}\text{N}$ values and consequently higher relative trophic position observed for

Gymnoscopelus spp. compared to the other myctophid species in this study reflects the ability of larger myctophid species to access larger-sized prey such as *E. superba* and other mesopelagic fish species.

Fishes of the Bathylagidae family are deep-dwelling species dominating the lower mesopelagic zone (Collins et al., 2012). Common Southern Ocean Bathylagidae species include *Bathylagus antarcticus* and *Bathylagus tenuis* (Collins et al., 2012). In this study, one bathylagid species was commonly found, however, species-specific identification was difficult. The isotopic niche of *Bathylagus* sp. was positioned higher on the $\delta^{15}\text{N}$ axis compared to all other taxonomic groups in this study. Stomach content analysis of *B. antarcticus* from the Macquarie Island region showed that this species was primarily ingesting amphipods (Gaskett et al., 2001). However, DNA-based dietary analysis of *Bathylagus* sp. from our study region has shown the importance of gelatinous species in their diet (Clarke et al., 2018). This is verified by an earlier dietary study of *B. antarcticus* from the Weddell Sea, where gelatinous species such as *Salpa thompsoni* dominated (Geiger et al., 2000). *Salpa thompsoni* are filter-feeding tunicates that graze on microplankton typically showing low $\delta^{15}\text{N}$ values consistent with primary consumers (Stowasser et al., 2012). Subsequently, the high $\delta^{15}\text{N}$ values observed in this study for *Bathylagus* sp. do not reflect the findings of stomach content analysis. Unexpectedly high $\delta^{15}\text{N}$ values for the deep-dwelling *Bathylagus* sp. have also been documented in previous studies (Cherel et al., 2011; Choy et al., 2015). Laakmann and Auel (2010) demonstrated an enrichment in ^{15}N of POM with increasing depth. Further, this enrichment is reflected in suspension feeders (Mintenbeck et al., 2007) as well as some zooplankton species (Laakmann and Auel, 2010) with depth. Higher $\delta^{15}\text{N}$ values with depth is largely linked to microbial degradation of POM which results in a loss of the lighter isotope, ^{14}N , leading to an increase in $\delta^{15}\text{N}$ values as particles sink through the water column (Mintenbeck et al., 2007; Laakmann and Auel, 2010). This suggests that although *Bathylagus* sp. undertake diel vertical migrations from depths of 400 to 1 000 m (Collins et al., 2012), they may be accessing prey resources at deeper depths compared to other taxonomic groups in this study.

Foraging habitat

Although isotopic niche space was mostly similar on the $\delta^{13}\text{C}$ axis for the five taxonomic groups, *P. bolini* showed higher $\delta^{13}\text{C}$ values compared to other community members. The difference in $\delta^{13}\text{C}$ values seen in this study for *P. bolini* may be attributed to a different foraging area with differing basal resources. *Protomyctophum bolini* was mostly found in stations north of the SACCF, directly over the Kerguelen Plateau, consistent with its known distribution (Collins et al., 2012). Accordingly, the higher $\delta^{13}\text{C}$ values seen here may have been driven by enriched basal $\delta^{13}\text{C}$ over the plateau (Trull et al., 2008).

The *Gymnoscopelus* spp. group in this study consisted of three different species of the *Gymnoscopelus* genera. Our study showed a separation in isotopic niche position on $\delta^{13}\text{C}$ axis for the three *Gymnoscopelus* species. This suggests that niche partitioning between species of this genera appear to be through the use of different foraging habitat in the study area. The isotopic niche of *Gymnoscopelus nicholsi* was distinct from the other *Gymnoscopelus* species. The higher $\delta^{13}\text{C}$ values seen here may represent some of the assemblages from sampling stations north of the SACCF reflecting the latitudinal gradient in $\delta^{13}\text{C}$ values at the base of the food web. Similar findings were reported for five *Gymnoscopelus* species in the region of the Kerguelen Islands where species differed either by their habitat, where species from higher latitudes showed lower $\delta^{13}\text{C}$ values compared to those at lower latitudes, or food resources highlighting the different mechanisms for niche segregation (Cherel et al., 2010).

Despite being a deep-dwelling species from a different taxonomic family, *Bathylagus* sp. showed a high degree of overlap in $\delta^{13}\text{C}$ values with other community members. It appears that *Bathylagus* sp. may share basal resources with that of the myctophid species in this study. Research investigating the basal resources of mesopelagic fishes from the North Pacific Subtropical Gyre ecosystem demonstrated energy flows across epipelagic, mesopelagic and bathypelagic zones (Choy et al., 2015). This is attributed to the transport of organic material by diel vertically migrating species in addition to sinking POM (Choy et al., 2015). The findings presented for *Bathylagus* sp. here suggest similar

connectivity of the pelagic food web through overlapping habitat with myctophid species in the Southern Ocean.

Standard length and trophic position

There was a positive relationship between length and $\delta^{15}\text{N}$ (trophic position) at the community level. This is consistent with the positive relationship seen for trophic position and standard length of the myctophid community near the Kerguelen Islands (Cherel et al., 2010). Further, this size-based trophic structure of fish communities is ubiquitous across a range of marine environments, including pelagic systems (Jennings et al., 2002) from polar regions (Cherel et al., 2010) to the tropics (Barnes et al., 2010) as well as reef systems (Trebilco et al., 2016). This is thought to be driven by increased gape size or a shift in foraging tactics with ontogeny increasing the range of prey sizes accessed (Scharf et al., 2000). However, in this study, the relationship between length and relative trophic position within species groups was significant for only two species. The standard length of *G. opisthopterus* and *Bathylagus* sp. increased with decreasing trophic position, as indicated by lower $\delta^{15}\text{N}$ values, although this relationship was relatively weak. This contrasts with the strong positive within-species relationships between fish standard length and trophic position commonly described for other ecosystems (Shreeve et al., 2009; Stowasser et al., 2012; Trebilco et al., 2016). Species-level trends were unable to be compared with research by Cherel et al. (2010) in the region of the Kerguelen Islands as analyses for the within-species relationships were not presented. However, weak or non-significant relationships at the species level have been reported in the northeast Atlantic (Jennings et al., 2002). There is evidence for ontogenetic shifts in habitat to deeper layers of the water column among some species, particularly for *E. antarctica* and *B. antarcticus* (Moteki et al., 2009). This can influence muscle tissue $\delta^{15}\text{N}$ values in these consumers (Choy et al., 2015) and further complicate the relationship between standard length and $\delta^{15}\text{N}$. Further research is required to ascertain if the within-species trends observed in our study are consistent with other ecosystems and the driving factors for observed weak and negative relationships at the species level.

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References

- Barnes, C., D. Maxwell, D.C. Reuman and S. Jennings. 2010. Global patterns in predator-prey size relationships reveal size dependency of trophic transfer efficiency. *Ecology*, 91 (1): 222–232, doi:10.1890/08-2061.1.
- Bates, D., M. Machler, B.M. Bolker and S.C. Walker. 2015. Fitting Linear Mixed-Effects Models Using lme4. *J. Stat. Softw.*, 67 (1): 1–48.
- Cherel, Y. and K.A. Hobson. 2007. Geographical variation in carbon stable isotope signatures of marine predators: a tool to investigate their foraging areas in the Southern Ocean. *Mar. Ecol. Prog. Ser.*, 329: 281–287, doi: 10.3354/meps329281.
- Cherel, Y., C. Fontaine, P. Richard and J.P. Labat. 2010. Isotopic niches and trophic levels of myctophid fishes and their predators in the Southern Ocean. *Limnol. Oceanogr.*, 55 (1), 324–332, doi: 10.4319/lo.2010.55.1.0324.
- Cherel, Y., P. Koubbi, C. Giraldo, F. Penot, E. Tavernier, M. Moteki, C. Ozouf-Costaz, R. Causse, A. Chartier and G. Hosie. 2011. Isotopic niches of fishes in coastal, neritic and oceanic waters off Adelie land, Antarctica. *Polar Sci.*, 5 (2): 286–297, doi: 10.1016/j.polar.2010.12.004.

- Choy, C.A., B.N. Popp, C.C.S. Hannides and J.C. Drazen. 2015. Trophic structure and food resources of epipelagic and mesopelagic fishes in the North Pacific Subtropical Gyre ecosystem inferred from nitrogen isotopic compositions. *Limnol. Oceanogr.*, 60 (4): 1156–1171, doi: 10.1002/lno.10085.
- Clarke, L.J., R. Trebilco, A. Walters A.M. Polanowski and B.E. Deagle. 2018. DNA-based diet analysis of mesopelagic fish from the southern Kerguelen Axis. *Deep-Sea Res. II*, 1–23, doi: 10.1016/j.dsr2.2018.09.001.
- Collins, M.A., G. Stowasser, S. Fielding, R. Shreeve, J.C. Xavier, H.J. Venables, P. Enderlein, Y. Cherel and A. Van de Putte. 2012. Latitudinal and bathymetric patterns in the distribution and abundance of mesopelagic fish in the Scotia Sea. *Deep-Sea Res. II*, 59: 189–198, doi: 10.1016/j.dsr2.2011.07.003.
- Duhamel, G., N. Gasco and P. Davaine. 2005. *Poissons des îles Kerguelen et Crozet: Guide régional de l'océan Austral* (424 pp.). Muséum national d'Histoire naturelle, Paris: Patrimoines naturels: 63.
- Flynn, A.J. and R.J. Kloser. 2012. Cross-basin heterogeneity in lanternfish (family Myctophidae) assemblages and isotopic niches ($\delta^{13}\text{C}$ and $\delta^{15}\text{N}$) in the southern Tasman Sea abyssal basin. *Deep-Sea Res. I*, 69: 113–127, doi: 10.1016/j.dsr.2012.07.007.
- Gaskett, A.C., C. Bulman, X. He and S.D. Goldsworthy. 2001. Diet composition and guild structure of mesopelagic and bathypelagic fishes near Macquarie Island, Australia. *New Zeal. J. Mar. Fresh.*, 35 (3): 469–476.
- Geiger, S.P., J. Donnelly and J.J. Torres. 2000. Effect of the receding ice-edge on the condition of mid-water fishes in the northwestern Weddell Sea: results from biochemical assays with notes on diet. *Mar. Biol.*, 137 (5-6): 1091–1104, doi: 10.1007/s002270000428.
- Gon, O. and P.C. Heemstra. 1990. *Fishes of the Southern Ocean*. J.L.B. Smith Institute of Ichthyology, Grahamstown: 462 pp.
- Hopkins, T.L. and J.V. Gartner. 1992. Resource-partitioning and predation impact of a low-latitude myctophid community. *Mar. Biol.*, 114 (2): 185–197, doi: 10.1007/bf00349518.
- Hulley, P.A. and G. Duhamel. 2011. Aspects of lanternfish distribution in the Kerguelen Plateau region. In: Duhamel, G. and D.C. Welsford (Eds). *The Kerguelen Plateau: marine ecosystems and fisheries*. Société Française d'Ichtyologie, Paris: 183–195.
- Hutchinson, G.E. 1978. *An Introduction to Population Ecology*. Yale University Press, New Haven: 260 pp.
- Jackson, A.L., R. Inger, A.C. Parnell and S. Bearhop. 2011. Comparing isotopic niche widths among and within communities: SIBER - Stable Isotope Bayesian Ellipses in R. *J. Anim. Ecol.*, 80 (3): 595–602, doi: 10.1111/j.1365-2656.2011.01806.x.
- Jennings, S., S.P.R. Greenstreet, L. Hill, G.J. Piet, J.K. Pinnegar and K.J. Warr. 2002. Long-term trends in the trophic structure of the North Sea fish community: evidence from stable-isotope analysis, size-spectra and community metrics. *Mar. Biol.*, 141 (6): 1085–1097, doi: 10.1007/s00227-002-0905-7.
- Kozlov, A. 1995. A review of the trophic role of mesopelagic fish of the family Myctophidae in the Southern Ocean ecosystem. *CCAMLR Science*, 2: 71–77.
- Laakmann, S. and H. Auel. 2010. Longitudinal and vertical trends in stable isotope signatures ($\delta^{13}\text{C}$ and $\delta^{15}\text{N}$) of omnivorous and carnivorous copepods across the South Atlantic Ocean. *Mar. Biol.*, 157 (3): 463–471, doi: 10.1007/s00227-009-1332-9.
- Layman, C.A., M.S. Araujo, R. Boucek, C.M. Hammerschlag-Peyer, E. Harrison, Z.R. Jud, P. Matich, A.E. Rosenblatt, J.J. Vaudo, L.A. Yeager, D.M. Post and S. Bearhop. 2012. Applying stable isotopes to examine food-web structure: an overview of analytical tools. *Biol. Rev.*, 87 (3): 545–562, doi:10.1111/j.1469-185X.2011.00208.x.
- Lourey, M.J., T.W. Trull and D.M. Sigman. 2003. Sensitivity of $\delta^{15}\text{N}$ of nitrate, surface suspended and deep sinking particulate nitrogen

- to seasonal nitrate depletion in the Southern Ocean. *Global Biogeochem. Cy.*, 17 (3): 18, doi: 10.1029/2002gb001973.
- Lourey, M.J., T.W. Trull and B. Tilbrook. 2004. Sensitivity of delta C-13 of Southern Ocean suspended and sinking organic matter to temperature, nutrient utilization, and atmospheric CO₂. *Deep-Sea Res. I*, 51 (2): 281–305, doi: 10.1016/j.dsr.2003.10.002.
- Minagawa, M. and E. Wada. 1984. Stepwise enrichment of N-15 along food-chains: further evidence and the relation between delta-N-15 and animal age. *Geochim. Cosmochim. Ac.*, 48 (5): 1135–1140, doi: 10.1016/0016-7037(84)90204-7.
- Mintenbeck, K., U. Jacob, R. Knust, W.E. Arntz and T. Brey. 2007. Depth-dependence in stable isotope ratio delta N-15 of benthic POM consumers: The role of particle dynamics and organism trophic guild. *Deep-Sea Res. I*, 54 (6): 1015–1023, doi: 10.1016/j.dsr.2007.03.005.
- Moteki, M., N. Horimoto, R. Nagaiwa, K. Amakasu, T. Ishimaru and Y. Yamaguchi. 2009. Pelagic fish distribution and ontogenetic vertical migration in common mesopelagic species off Lutzow-Holm Bay (Indian Ocean sector, Southern Ocean) during austral summer. *Polar Biol.*, 32 (10): 1461–1472, doi: 10.1007/s00300-009-0643-0.
- Murphy, E.J., R.D. Cavanagh, E.E. Hofmann, S.L. Hill, A.J. Constable, D.P. Costa, M.H. Pinkerton, N.M. Johnston, P.N. Trathan, J.M. Klinck, D.A. Wolf-Gladrow, K. Daly, O. Maury and S.C. Doney. 2012. Developing integrated models of Southern Ocean food webs: Including ecological complexity, accounting for uncertainty and the importance of scale. *Prog. Oceanogr.*, 102: 74–92, doi: 10.1016/j.pocean.2012.03.006.
- Newsome, S.D., C.M. del Rio, S. Bearhop and D.L. Phillips. 2007. A niche for isotopic ecology. *Front. Ecol. Environ.*, 5 (8): 429–436, doi: 10.1890/060150.1.
- Orsi, A.H., T. Whitworth and W.D. Nowlin. 1995. On the meridional extent and fronts of the Antarctic Circumpolar Current. *Deep-Sea Res. I*, 42 (5): 641–673, doi: 10.1016/0967-0637(95)00021-w.
- Pakhomov, E.A., R. Perissinotto, R. and C.D. McQuaid. 1996. Prey composition and daily rations of myctophid fishes in the Southern Ocean. *Mar. Ecol. Prog. Ser.*, 134 (1-3): 1–14, doi: 10.3354/meps134001.
- Peterson, B.J. and B. Fry. 1987. Stable isotopes in ecosystem studies. *Annu. Rev. Ecol. Syst.*, 18: 293–320, doi: 10.1146/annurev.ecolsys.18.1.293.
- Phillips, D.L., R. Inger, S. Bearhop, A.L. Jackson, J.W. Moore, A.C. Parnell, B.X. Semmens and E.J. Ward. 2014. Best practices for use of stable isotope mixing models in food-web studies. *Can. J. Zool.*, 92 (10): 823–835, doi: 10.1139/cjz-2014-0127.
- Post, D.M. 2002. Using stable isotopes to estimate trophic position: Models, methods, and assumptions. *Ecology*, 83 (3): 703–718, doi: 10.2307/3071875.
- Pusch, C., P.A. Hulley and K.H. Kock. 2004. Community structure and feeding ecology of mesopelagic fishes in the slope waters of King George Island (South Shetland Islands, Antarctica). *Deep-Sea Res. I*, 51 (11): 1685–1708, doi: 10.1016/j.dsr.2004.06.008.
- R Core Team. 2017. R: A language and environment for statistical computing. R Foundation for Statistical Computing, Vienna, Austria. Retrieved from <https://www.R-project.org/>.
- Saunders, R.A., M.A. Collins, P. Ward, G. Stowasser, S.L. Hill, R. Shreeve and G.A. Tarling. 2015. Predatory impact of the myctophid fish community on zooplankton in the Scotia Sea (Southern Ocean). *Mar. Ecol. Prog. Ser.*, 541: 45–64, doi: 10.3354/meps11527.
- Scharf, F.S., F. Juanes and R.A. Rountree. 2000. Predator size – prey size relationships of marine fish predators: interspecific variation and effects of ontogeny and body size on trophic-niche breadth. *Mar. Ecol. Prog. Ser.*, 208: 229–248, doi: 10.3354/meps208229.
- Shreeve, R.S., M.A. Collins, G.A. Tarling, C.E. Main, P. Ward and N.M. Johnston. 2009. Feeding ecology of myctophid fishes in the northern Scotia Sea. *Mar. Ecol. Prog. Ser.*, 386: 221–236, doi: 10.3354/meps08064.

- Stowasser, G., A. Atkinson, R.A.R. McGill, R.A. Phillips, M.A. Collins and D.W. Pond. 2012. Food web dynamics in the Scotia Sea in summer: A stable isotope study. *Deep-Sea Res. II*, 59: 208–221, doi: 10.1016/j.dsr2.2011.08.004.
- Trebilco, R., N.K. Dulvy, S.C. Anderson and A.K. Salomon. 2016. The paradox of inverted biomass pyramids in kelp forest fish communities. *P. Roy. Soc. Lond. B. Bio.*, 283 (1833), doi: 10.1098/rspb.2016.0816 .
- Trull, T.W., D. Davies and K. Casciotti. 2008. Insights into nutrient assimilation and export in naturally iron-fertilized waters of the Southern Ocean from nitrogen, carbon and oxygen isotopes. *Deep-Sea Res. II*, 55 (5-7): 820–840, doi: 10.1016/j.dsr2.2007.12.035.
- Woods, B. 2017. *The role of mesopelagic fish in Southern Ocean food webs*. Master of Marine and Antarctic Science, The University of Tasmania, Hobart, Australia.

