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Meso- and bathypelagic fish feeding ecology: A meta-analysis on fatty acids and stable isotope trophic studies

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ABSTRACT

Recent studies suggest that the global biomass of fish in the ocean is dominated by meso- and bathypelagic fish. However, despite their abundance and important role in marine ecosystems, their trophic ecology remains poorly understood. Feeding studies of meso-/bathypelagic fish are temporally and geographically scattered and apply different methodologies. A meta-analysis of published fatty acid and stable isotope data was conducted to determine the diet patterns of 23 meso-/bathypelagic fish species. The dataset was processed using logratio analysis resulting in a set of six biochemically important logratios which explained 91.5% of the total variance. The results demonstrate a gradient of feeding strategies from trophic level 2.17–3.38 and interspecific variation in the content of key fatty acid trophic markers indicated a potential gradient of meso-/bathypelagic consumers of herbivorous to carnivorous prey. Stable isotope analysis showed statistically significant differences in isotopic values of fish sampled in different locations and characterized by different fatty acid trophic markers, whereas trophic diversity and redundancy were explored based on six community metrics. Our study serves as a global perspective on the trophic ecology of meso-/bathypelagic fish based on currently available biochemical data. This type of studies, derived from the combination of fatty acid and stable isotope analyses could potentially be useful in large-scale comparisons of meso-/bathypelagic fish trophic ecology studies and that would ultimately better define their function in the global oceanic ecosystem.

1. Introduction

Meso- and bathypelagic fish, constitute a key component of global marine ecosystems (Bernal et al., 2015; Catul et al., 2011; Salvanes and Kristoffersen, 2001) due to their high abundance (Irigoien et al., 2014) and importance as prey for larger fish, cephalopods, birds, and marine mammals, making them a critical link to higher trophic levels (Bernal et al., 2015). With increasing interest in the exploitation of this biomass (Prellezo, 2019), there is a need for better understanding of their life history traits and feeding ecology which can further clarify the resource partitioning, habitat preferences, prey selection, and energy transfer within and between ecosystems. Our knowledge of the deep-water fish biology is limited due the challenges in accessing and assessing those populations living in and below the twilight zone (Saint-Béat et al., 2015; Silva et al., 2022).

Many mesopelagic fish, living at 200–1000 m depths, migrate to the surface layers to feed while some bathypelagic fish, living at 1000–2000 m depths, make migrations up to mesopelagic layers to capture their prey (Olivar et al., 2019; Silva et al., 2022). Meso- and bathypelagic fish, particularly of the family Myctophidae, have been characterized as opportunistic feeders, feeding on a range of different zooplankton prey; copepods, euphausiids, ostracods, amphipods, fish egg and larvae, while others are partially or fully piscivores (Bernal et al., 2015). There are several distinguishing traits that correlate with the migrating adaptation of mesopelagic fish between mesopelagic and epipelagic zone (Catul et al., 2011). Some of these traits have been used by Salvanes and Kristoffersen (2001) to categorise the fish, including feeding behaviour and the presence or absence of a swim bladder. Mouth morphology also gives an indication of their feeding behaviour and their prominent large extended jaws are considered an adaptation for feeding on larger prey (Salvanes and Kristoffersen, 2001).

Studies on the trophic ecology of marine organisms are important for assessing fish behaviour, population dynamics, habitat use, energy transfer, intra/inter-specific interactions within the marine food web and have ultimately contributed to fisheries management (Braga et al., 2012; Kido, 1996; Nakano and Murakami, 2001; Ross, 1986). Direct examination of individual gut contents has been the most common method used to determine fish feeding ecology (Hopkins and Baird,

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1973; Hyslop, 1980; Scotto di Carlo et al., 1982). However, over the years, other methodologies have emerged and been used either in parallel with gut content analysis or as standalone approaches (Silva et al., 2022). Primary among these methods is fatty acid analysis (FAA) which can be used to determine food selection with the aid of fatty acid trophic markers (FATM) (Seo et al., 1996; Stowasser et al., 2009) and stable isotope analysis (SIA) which can determine the trophic level of a species (Olivar et al., 2019; Richards et al., 2019; Valls et al., 2014). These methods are increasingly being applied in feeding ecology studies of meso-/bathypelagic fish (Bec et al., 2011; Braga et al., 2012).

Fatty acid trophic markers (FATM) are often used to establish past feeding of aquatic organisms, from zooplankton to mammals and the concept of using fatty acids (FA) as trophic markers, is based on the principle of a conservative transfer of specific fatty acids from primary producers to higher trophic levels (Dalsgaard et al., 2003a). Phytoplankton are the primary producers of fatty acids, and the different genera have distinct fatty acid profiles and many of their fatty acids can be traced into their grazers (Jónasdóttir, 2019). Most of the published FATM studies focus on herbivorous zooplankton (Dalsgaard et al., 2003a; Teuber et al., 2014; Bode et al., 2015; Kopprio et al., 2015) where the phytoplankton diet can be adequately detected. Many studies also focus on FATMs in higher trophic level organisms, but the dietary source signal does get more muddled, partly due to fatty acid alterations such as desaturations and elongations levels (Dahl et al., 2003; Raclot et al., 1998). Some fatty acids are selectively withheld (e.g. the omega-3 fatty acids) resulting in different fatty acid profiles relative to their basal carbon source (Galloway and Budge, 2020). Only very few of the specific phytoplankton fatty acid biomarkers remain unaltered and are suitable trophic markers (Dalsgaard et al., 2003a; Jónasdóttir, 2019) and can therefore be used as FATMs at higher trophic levels. For example, the 16:1n-7 is an indicator of diatom diet of the prey and 18 carbon length polyunsaturated fatty acids are indicators of dinoflagellate in the diet (Jónasdóttir 2019). The fatty acid 18:1n-7 is of phytoplankton origin, elongated from the 16:1n-7. Odd chain fatty acids suggest bacterial content in the diet (Perry et al., 1979) and 16, 18 and 22 carbon length saturated fatty acids (SFA) are indicative of detritus (Zhukova, 2019). The long chain monounsaturated fatty acids (MUFAs), such as 20:1n-9 and 22:1n-11 are indicative of lipid rich copepod prey (Dalsgaard et al., 2003; Stowasser et al., 2009). The fatty acid 18:1n-9 is a common FA in most marine animals and has been used as an indication of carnivory (Falk-Petersen et al., 2000; Sargent and Falk-Petersen 1981), therefore, high values of the ratio 18:1n-9/18:1n-7 is considered indicative of carnivory (Cripps et al., 1999; Hagen et al., 1995). Docosahexaenoic acid 22:6n-3 (DHA) is essential and retained in the membranes of organisms and elevated amounts of DHA can be used as an indicator of carnivory as well as high PUFA/SFA ratio (Stevens et al., 2004). Therefore, use of these FATMs can help us understand the trophic ecology of meso-/bathypelagic fishes. Several mesopelagic fish feeding studies compare the FATM found in the fish to the fatty acid signatures of their potential prey (Petursdottir et al., 2008; Seo et al., 1996; Stowasser et al., 2009; F. Wang et al., 2019). This direct transfer makes FATM a valuable tool in investigating trophic ecology and food selection of meso-/bathypelagic fish but requires information on the fatty acid composition of a wide variety of potential prey.

DeNiro and Epstein (1978) were the first to investigate and evaluate the distribution of stable isotopes (SI) of carbon and nitrogen based on the organisms' diet. They state that the $\delta^{13}C$ and the $\delta^{15}N$ values of a consumer reflect their diets in a predictable manner. The $\delta^{13}C$ is defined as the measure of the ^{13}C over ^{12}C ratio relative to Pee Dee Belemnite standard and likewise, $\delta^{15}N$ is the measure of the ratio of the ^{15}N over ^{14}N relative to the N_2 air standard (Coplen, 2011; Wieser and Brand, 2016). SIA has become a useful tool in describing the trophic structure of the marine food web (Valls et al., 2014). SIA provides an indication of the trophic level (TL) through the $\delta^{15}N$ values, physiology (biochemical production of essential compounds such as proteins and lipids) (Whiteman et al., 2019) and accounts for the width of the trophic niche and geographical foraging range (Bearhop et al., 2004). The variance of N and C stable isotopes is only dependent on the tissue turnover rate, regardless of the digestion stage (Bearhop et al., 2004; Post et al., 2007; Richards et al., 2019). SIA has been applied on a broad range of organisms from plankton to planktivorous consumers and top pelagic predators such as dolphins (Bode et al., 2003, 2007). The spatial variability in isotopic composition of $\delta^{13}C$ in marine food webs could be indicative of the relative contributions of different carbon pools to a consumer, i.e. different prey inputs from varying spatial scales such coastal or offshore habitats (Bearhop et al., 2004). An important factor in SIA is the isotopic composition of a reference baseline, which is highly variable in time and space, and essential for the TL estimation (Olivar et al., 2019; Post, 2002). Different baselines have been used, including the average of sampled copepods, nauplii, euphausiids, salps or particulate organic matter (POM) (Bode et al., 2015; Richards et al., 2019; Stowasser et al., 2012; Valls et al., 2014). During *de-novo* synthesis of molecules using the C and N building blocks from the diet, the isotopic signature changes due to metabolic processes e.g. a balance between nitrogen assimilation and excretion. The offset is called the trophic discrimination factor, mirroring the physiological fractionation of isotopes with increasing trophic level (Whiteman et al., 2019). Nitrogen diet-tissue fractionation ($\Delta\delta^{15}N$) has been shown not to be constant, but decreasing with higher trophic levels (Hussey et al., 2013; Olivar et al., 2019; Valls et al., 2014; Whiteman et al., 2019).

There is a clear advantage in running SI and FA analyses in parallel for better assessment of the feeding ecology (Petursdottir et al., 2008; Richards et al., 2019; Teuber et al., 2014; Wang et al., 2019). The two methods complement each other with FAA describing the long-term trends in dietary habits and SIA that perform well in tracking the origin and pathways of energy within the food web. This offers an advantage over conventional stomach content analysis that accounts for the recent (days) feeding history (Mahesh et al., 2018).

Determining the diet patterns of meso-/bathypelagic fish on a global scale will facilitate our understanding of energy flow and the interrelation among the different components of the marine food webs in this large least-known fish biomass. This is particularly valuable as studies on feeding habits of deep-sea fish are relatively limited and geographically skewed (Bernal et al., 2015). In this review, we have compiled published information on fatty acid and stable isotope content of meso- and bathypelagic fish to evaluate their feeding ecology on a global scale, though the identification of key FATMs for each species, their TL estimation and the assessment of their trophic niche width and overlap. We focused on species on which both analyses have been applied, not necessarily though on the same individuals or at the same point in time and space. This resulted in a large-scale statistical analysis on the trophic ecology of 23 species of meso- and bathypelagic fish.

2. Materials and methods

2.1. Database

Published papers containing information on fatty acids or/and stable isotope content of meso-/bathypelagic fish were mined and two respective databases were constructed. The search was performed using Google Scholar, and by searching for references cited in the papers found. The most popular terms used were "fatty acids"/"FATM"/"stable isotope analysis"/"feeding ecology" and "mesopelagic" or "bathypelagic fish" for the lipid and SIA databases. The lipid database (Sigrún Jónasdóttir, unpublished compilation) contains fatty acid measurements for 147 different meso-/bathypelagic fish species obtained from 29 different studies published between 1969 and 2020. The fatty acid compilation from the North Atlantic studies can be found in Silva et al. (2022). A SIA database containing $\delta^{13}C$ and $\delta^{15}N$ values was similarly compiled, resulting in 101 different meso-/bathypelagic fish species. The SIA database, including isotopic values of Copepoda, Chaetognaths and Euphausiacea was compiled from 10 SIA studies spanning from

2010 to 2019. The selection of the fatty acid studies for the analysis was based on the availability of complimentary stable isotope data for the same meso-/bathypelagic species. This resulted in a total number of 23 meso-/bathypelagic fish species for the meta-analysis (Table 1) with data from 21 overall published studies representing most of the world-ocean basins (Fig. 1). Each publication has a unique way of presenting the data. They all provide a single averaged value for different FA (%) and/or SIA (‰) per species but the number of individuals (n) behind the mean values varies (Table 1). In the present analysis, for each fish species, we generated a species average based on all the respective publication averages.

2.2. Data analysis

The FA values come from a compilation of different studies and the sum of the relative FA proportions presented does not necessarily represent the total (100%) fatty acid content of each species (Appendix; Fig. A1). Not all authors report the same specific fatty acids, and some do not report the specific detail on location of the double bond. In our database, the sum of reported fatty acids ranges from a minimum of 76.7% for *D. dumerilii* to a maximum of 99% for *S. affinis* (Fig. A1). With the aim of dealing with this sub-compositional incoherence in the fatty acid dataset, we applied a logratio analysis (LRA). LRA is an approach to Principal Component Analysis (PCA), i.e. a PCA applied to a matrix of logratios (Aitchison, 1990; Greenacre, 2018), given that ratios of components are considered suitable for compositional data analysis. LRA analysis was used to identify the interspecies variability of FA profiles of the pooled sample of meso-/bathypelagic fish. Prior to the LRA, the FA percentages were rounded to two decimals, zero values were replaced with half the minimum value for each FA and the dataset was renormalized to sum to one. The FAs were weighted (Greenacre, 2019) with the default built-in weights set of the easyCODA package in R Studio (Greenacre, 2018). Bi-plots were created as a function of the first two dimensions. All 23 meso -/bathypelagic fish have been associated with three main FATMs, as resulted from the LRA results (Copepod-C, Diatom-D and DHA FATMs).

Stable isotope data were analysed separately, and not inserted into the LRA. One-way analysis of variance (ANOVA) was performed to test for statistically significant differences in δ^{15}N and δ^{13}C values between meso-/bathypelagic fish sampled in the Atlantic and Southern Oceans and between fish represented by the copepod and DHA FATMs. Fish from Mediterranean and associated with diatom FATMs were excluded from the tests, due to very low number of representative species. ANOVA tests met the assumptions of normality tested with Shapiro-Wilk test and of homoscedasticity tested with Levene's test and with visual inspection of residual and qq plots. Additionally, to provide a comprehensive framework for analysing stable isotope data, we estimated the isotopic niche width and overlap, by comparing six community metrics (Layman metrics) according to Layman et al. (2007). These metrics demonstrate significant aspects of the trophic structural diversity as well as redundancy within a food web and include: the δ^{15}N range (NR) as representative of the vertical structure and diversity within a community, the range in δ^{13}C values (CR) providing information on niche diversification of the basal resources, the total area/convex hull (TA) representing the total niche width occupied by the community users, the mean Euclidean distance (CD) of each species within a community to the δ^{15}N – δ^{13}C centroid (mean value for all the species) in the bi-plot space, as another measure of trophic diversity in the food web. Finally, the mean nearest neighbour Euclidean distance (NND) and its standard deviation (SDNND) reflecting the density within the community and the evenness of the species packing, respectively (Layman et al., 2007; Czudaj et al., 2020).

Table 1
Meso- and bathypelagic fish species of which published fatty acids (FA) and/or stable isotope (SI) are used in the meta-analysis. SC: Species code. Location of sampling in parenthesis A: Atlantic Ocean (North and tropical), M: Mediterranean Sea, P: Pacific Ocean, S: Southern Ocean. Total number (n) of fish sampled for each of FAA and SIA publication. Average total lipids as % of dry weight (TL % DW), wax ester (WE) and Triacylglycerol (TAG) as % total lipids. Dash indicates unknown value. Reference numbers are detailed in the footnote of the table.

SC	Species	FAA n	SIA n	TL % DW	WE %	TAG %	Reference
Ba	*Benthosema glaciale* (A, M)	16	15	52	71	17	3, 4, 5, 7, 17, 19
Cw	*Ceratoscopelus warmingi* (A, P)	22	15	36	0.1	61	1, 2, 7, 8, 18
Cp	*Cyclothone pseudopallida* (A, P)	5	10	14	38	29	6, 8, 18
Db	*Diaphus brachycephalus* (A, P)	5	6	–	0	59	2, 7
Dd	*Diaphus dumerilii* (A)	1	3	–	–	Main lipid type	7, 16
Ea	*Electrona antarctica* (S)	35	32	41	73	8	10, 11, 13, 15, 20
Ec	*Electrona carlsbergi* (S)	21	22	35	4	74	9, 10, 11, 15, 20
Ge	*Gonostoma elongatum* (A, M)	8	12	–	0	Main lipid type	16, 18
Gbo	*Gymnoscopelus bolini* (S)	8	12	41	–	–	9, 10
Gbr	*Gymnoscopelus braueri* (S)	8	37	40	–	–	9, 10, 13
Gf	*Gymnoscopelus fraseri* (S)	12	12	23	0	59	10, 13, 15
Gn	*Gymnoscopelus nicholsi* (S)	29	20	40	9	73	9, 10, 11, 13, 15
Gp	*Gymnoscopelus piabilis* (S)	7	12	–	–	–	10, 12, 15
Hm	*Hygophum machrochir* (A)	1	3	–	–	Main lipid type	7, 16
Ka	*Krefftichthys andersoni* (S)	1	27	32	67	0	9, 10, 11, 13
La	*Lampanyctus alatus* (A)	4	6	–	–	Main lipid type	7, 16, 18
Mm	*Maurolicus muelleri* (A, M)	22	6	47	5	74	3, 5, 17
Nr	*Notoscopelus resplendens* (A, P)	3	6	6	5	52	1, 7
Pb	*Protomyctophum bolini* (S)	12	29	19	5	60	9, 10, 11, 12, 13
Pc	*Protomyctophum choriodon* (S)	20	27	31	–	–	9, 13
Pg	*Protomyctophum gemmatum* (S)	2	4	14	–	–	9, 10
Pt	*Protomyctophum tenisoni* (S)	6	16	21	0	55	10, 13, 17
Sa	*Stomias affinis* (A, P)	2	26	24	–	–	8, 14
	Reference organisms						
	Chaetognatha (A, S, M)	–	64	–	–	–	7, 13, 18, 21
	Euphausiacea (A, S, M)	–	122	–	–	–	5, 13, 18, 21
	Reference baseline						
	Copepoda (A, S, M)	–	238	–	–	–	7, 13, 18, 21

1: Saito and Murata (1996), 2: Seo et al. (1996); 3: Petursdottir et al. (2008), 4: Fanelli et al. (2014), 5: Valls et al. (2014), 6: Maar et al. (2023), 7: Olivar et al. (2019), 8: Wang et al. (2019), 9: Stowasser et al. (2009), 10: Cherel et al. (2010), 11: Connan et al. (2010), 12: Raclot et al. (1998), 13: Stowasser et al. (2012), 14: Richards et al. (2019), 15: Lea et al. (2002), 16: Culkin and Morris (1970), 17: Falk-Petersen et al. (1986), 18: McClain-Counts et al. (2017), 19: Geoffroy et al. (2019), 20: Phleger et al. (1997), 21: Fanelli et al. (2011)..

Trophic levels of a consumer TL_C were calculated as

$$TL_c = \frac{\delta^{15}N_C - \delta^{15}N_B}{\Delta\delta^{15}N} + 2 \tag{1}$$

where $\delta^{15}N_C$ is the $\delta^{15}N$ value of the consumer i.e. mesopelagic fish, $\delta^{15}N_B$ is the $\delta^{15}N$ reference baseline set at trophic level two and $\Delta\delta^{15}N$ is the mean nitrogen diet-tissue fractionation for fish muscle, and was set to 3.15‰ according to findings of (Sweeting et al., 2007). Calanoid copepods, mainly herbivores, were set as the reference baseline for the TL estimations and different $\delta^{15}N_B$ values were considered for species originally sampled in the Atlantic ($\delta^{15}N_B = 5.97$‰), Southern ($\delta^{15}N_B = 5.55$‰) oceans and the Mediterranean Sea ($\delta^{15}N_B = 5.03$‰). The isotopic values of Euphausiidae and Chaetognatha were also incorporated into SIA, to serve as a comparison to the mesopelagic fish. The trophic level can vary among different studies for the same species and is highly dependent on the selection of the reference baseline and the $\Delta\delta^{15}N$ values. Here, we propose a general overview of the TL of many different species, to interpret the relative differences among the species on a larger scale. Corrections to address the variability on $\Delta\delta^{15}N$ among biological systems have been suggested to improve the accuracy of the TL estimation but have not been applied to our analysis and a fixed $\Delta\delta^{15}N$ value was used (McMahon and McCarthy, 2016; Olivar et al., 2019; Whiteman et al., 2019).

The interpretation of $\delta^{13}C$ values can be significantly biased by the lipid content present in fish and zooplankton (Post et al., 2007). The majority of the studies, where $\delta^{13}C$ values were extracted from, had the lipids removed from the fish samples (Petursdottir et al., 2008; Stowasser et al., 2012; Czudaj et al., 2020). In other studies, $\delta^{13}C$ values were provided after numerical lipid normalization in order to avoid significant loss of material (Valls et al., 2014). According to Post et al. (2007), C:N ratios in aquatic organisms could be used to correct $\delta^{13}C$ values for lipids, in agreement with the following equation:

$$\delta^{13}C_{normalized} = \delta^{13}C_{raw} - 3.32 + 0.99 \times C : N \tag{2}$$

In some other cases, $\delta^{13}C$ values were left uncorrected, since the C:N ratio of the fish was low (C:N < 4), and thus it was suggested that lipids would not significantly affect the $\delta^{13}C$ interpretation (Richards et al., 2019, 2020). When $\delta^{13}C$ values were provided in some studies uncorrected with C:N > 4, we applied lipid normalization applying Eq. (2) (Post et al., 2007). Therefore, the analysis of the SI data in our study was conducted with lipid-corrected $\delta^{13}C$ values. All the statistical analysis were performed in RStudio 1.2.5033 (R Core Team 2020) with the packages easyCODA (Greenacre, 2018), ggbreak (Xu et al., 2021) and SIBER (Jackson et al., 2011).

3. Results

3.1. Fatty acid profiles and logratio analysis

The relative proportions of the FA profiles among the different species are presented in Figure A1 and Table A1 (online Appendix). There are clear differences among species in the proportions of specific long-chain polyunsaturated and monounsaturated FAs (PUFAs and MUFAs, respectively), including 22:6n-3, 22:1n-9 and 22:1n-11. Possible groupings of fish with similar fatty acid profiles were identified from the LRA biplot (Fig. 2). FA with high contribution to the solution (logratio variance) are highlighted in red whereas the ones contributing less are represented with a smaller font, closer to the centre (Fig. 2). The total logratio variance (total inertia) equals 0.552, whereas the first two dimensions account for 75.8% of the total variance (Table 2). In LRA, FAs are not treated as regular variables, but they are reported in their pairwise positions, since the variables of interest are the constructed logratios (Greenacre, 2021). A set of six logratios with the highest biochemical impact explains 91.51% of the total dataset variance, consisting eight out of 15 FAs of the full dataset, whereas the

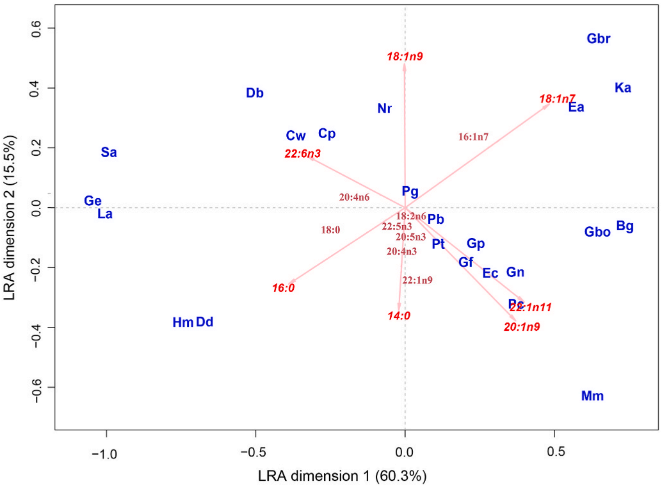

Fig. 2. Contribution LRA biplot indicating the logratio contribution of FAs. Species codes are defined in Table 1.

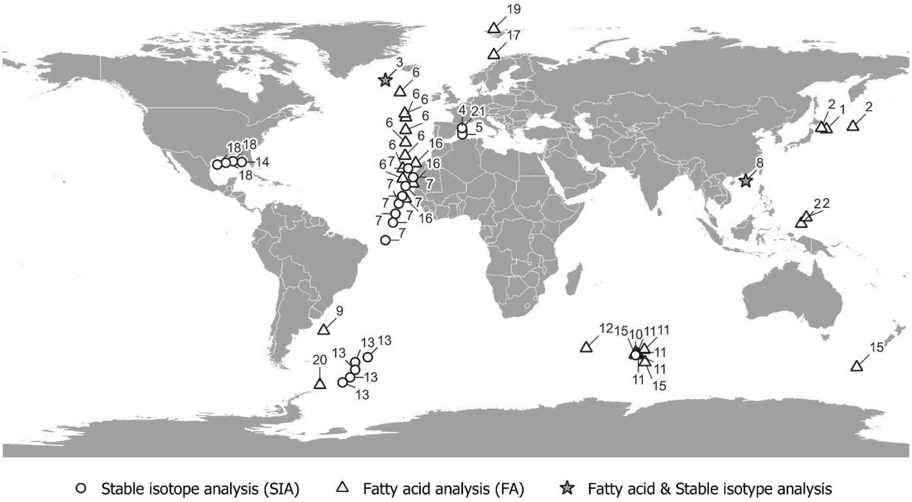

Fig. 1. Map of sampling locations. Numbers next to the station symbols refer to the reference numbers in Table 1. Upward triangles indicate studies reporting on fatty acids, bullets on stable isotopes, and stars on both fatty acids and stable isotopes in meso-/bathypelagic fish.

Table 2

FAs as logratios; percentages of the total variance (0.552) explained by each FA logratio, accumulated percentage and the Procrustes correlations in the stepwise process. Bold font represents step six where the total variance explained and the Procrustes correlation equals 95% and 0.95, respectively.

Step	FA logratio	% variance explained	% variance explained (accum.)	Procrustes correlation
1	16:1n7/20:4n-6	55.95	55.95	0.748
2	18:1n-9/20:1n9	14.98	70.94	0.706
3	18:1n-9/18:1n-7	10.22	81.16	0.821
4	18:1n-9/22:6n-3	5.85	87.02	0.898
5	16:0/22:1n11	4.48	91.51	0.939
6	**14:0/22:1n9**	**3.42**	**94.93**	**0.951**
7	14:0/18:1n-9	2.14	97.07	0.96
8	16:0/22:1n9	1.13	98.2	0.967
9	16:0/16:1n7	0.65	98.86	0.97
10	20:5n-3/22:6n-3	0.44	99.3	0.972
11	18:1n-9/18:2n-6	0.26	99.57	0.973
12	16:0/22:5n3	0.21	99.78	0.975
13	18:0/20:4n-3	0.13	99.91	0.976
14	16:0/18:0	0.08	1	0.98

contribution of the rest logratios to the total variance was relatively small with no further substantial biological interpretation. Meso-/-bathypelagic fish appear to form small groups of two or three species in the LRA biplot, such as *H. machrochir* and *D. dumerilii* towards the direction of SFA 16:0 (detritus), or *E. antartica, G. braueri* and *K. andersoni* towards 18:1n-7 (phytoplankton FATM). A larger clustering of species is observed from the centre of the biplot toward the long-chain monounsaturated FAs (MUFAs), such as 22:1n-9 and 22:1n-11, which are identified as copepods FATMs.

The logratio 16:1n-7/20:4n-6 explained a slightly more than half of the total variance (56%; Table 2). The logratio with the second highest explanatory value was 18:1n-9/20:1n-9. The logratio 18:1n-9/18:1n-7 which exhibits the contrast between possible carnivorous and herbivorous prey, contributes 10.22% to the total variance (Table 2). Procrustes correlation at the sixth step reaches 0.95 (95% of the variance explained) and indicates the similarity of the FA ratios with their corresponding configuration based on logratios.

3.2. Stable isotopes

Geographically influenced variability was observed for reference baseline SI values, with Mediterranean copepods having the lowest δ^{15}N (5.02 ± 0.79‰) and highest δ^{13}C (21.29 ± 1.00‰) values compared to Atlantic and Southern Ocean baselines (Table 3). Copepods from the Southern Ocean showed the lowest δ^{13}C values, however with the highest variability (−22.72 ± 1.70‰), while copepods from the Atlantic Ocean had the highest δ^{15}N values (5.96 ± 1.11‰). Euphausiacea from Atlantic Ocean appeared to have slightly lower δ^{15}N and less depleted δ^{13}C values compared to copepods from the same geographical region, resulting in a TL estimate of 1.96, while the reference TL for copepods is set to 2. Even though among Copepoda and Chaetognaths the Mediterranean species had the lowest δ^{15}N enrichment, within Euphausiacea, the species from the Mediterranean region had the highest δ^{15}N values.

The δ^{15}N values for mesopelagic fish ranged from 6.53 ± 0.12‰ for *H. machrochir* to 9.98 ± 0.89‰ for *S. affinis*, with *G. bolini* though having the highest TL estimate (TL range: 2.17–3.38, Table 3), resulting from regional differences in $\delta^{15}N_B$ values. The δ^{13}C values ranged from −22.90 ± 0.85‰ for *G. braueri* to −17.50 ± 0.50‰ for *H. machrochir*. Meso-/bathypelagic fish that ranked with TL three and above, could potentially be predators of the species lying one trophic level below (Tables 3 and 4). Most of the meso-/bathypelagic fish included in the SIA originated from Atlantic and Southern Oceans (Table 3), whereas only 2 species sampled in Mediterranean Sea. δ^{15}N values did not show any statistically significant differences between the location and FATM groups tested (Table 3; Fig. 3). It is observed that most of the Atlantic meso-/bathypelagic species tend to have slightly lower δ^{15}N ($p = 0.05$) but higher δ^{13}C values ($p < 0.01$) (Fig. 3). Regarding the differences in SI grouped by FATMs, species tagged with copepod FATMs scored relatively higher in δ^{15}N ($p = 0.08$), while species with DHA FATMs had significantly higher δ^{13}C values compared to species with copepod FATMs (Table 3; Fig. 3).

The analysis of the Layman metrics aimed to better define the structure of the isotopic niche for the 23 meso-/bathypelagic fish studied. The overall TA, for all the 23 meso-/bathypelagic fish, excluding the reference organisms and baseline, was calculated 9.92 (Fig. 4). CD ranged from: 0.67 (D) to 1.04 (C), CR and NR: 0.25 (D) – 3.16 (C) and 0.94 (Copepoda baseline) – 3.45 (DHA) respectively, TA: 0.11 (D) – 3.13 (C), NND: 0.40 (C) – 0.78 (Copepoda baseline) and SDNND: 0.16 (Copepoda baseline) – 0.41 (D) (Fig. 4). Even though the meso-/bathypelagic fish with diatom FATMs included only three species in total, NR ranked the second highest among the rest of the FATM groups. Comparing the DHA and C groups was relatively simpler, due to similar number of observations (n) for each category and the calculated values for TA and CD were similar between C and DHA but considerably lower for D and Copepoda baseline.

4. Discussion

4.1. Fatty acid profiles

S. affinis and *C. pseudopallida* display the highest proportions of DHA which suggests carnivorous prey (Wang et al., 2019), whereas *B. glaciale* and *M. muelleri* contain higher proportions of the calanoid long chain MUFAs indicating potential feeding on herbivorous prey (Fig. A1). In the LRA, *E. antarctica, G. braueri* and *K. anderssoni* cluster together on the LRA axis with the phytoplankton FATM; 16:1n-7 (diatom) and 18:1n-7 (elongated diatom fatty acid 16:1n7; Sargent and Falk-Petersen 1988). However, on the TL listing (Table 3) *E. antarctica* and *G. braueri* are at a similar trophic level (3.17 and 3.33 while *K. anderssoni* is at level 2.77). All three have wax esters as the main lipid type (Table 1).

The MUFA 16:1n-7 is a diatom and/or ice algae biomarker and is therefore linked to diatom eating organisms, in this case zooplankton that are the prey of the fish. Arachidonic acid (20:4n-6) is one of the essential fatty acids, that is preferably accumulated unchanged from their diet into their phospholipid membrane (Graeve and Greenacre, 2020). Oleic acid (18:1n-9) is considered a FA synthesized *de-novo* and indicates carnivory whereas the long-chain monounsaturated FA 20:1n-9 is a copepod diet biomarker (Falk-Petersen et al., 1986; Dalsgaard et al., 2003b; Graeve and Greenacre, 2020). *Calanus* copepods constitute an important link between primary producers and higher trophic levels due to their rich lipid content (Sargent and Falk-Petersen, 1988). The long-chain monounsaturated fatty acids and alcohols 20:1n-9 and 22:1n-11 are characteristic of lipid rich calanoid copepods and frequently used as FATMs for them in higher trophic levels (Dalsgaard et al., 2003). The fatty acid 18:1n-7 most often derives from elongation of 16:1n-7 and, is usually found in large quantities in marine

Table 3

Average ± standard deviation $\delta^{13}C$ (lipid-corrected) and $\delta^{15}N$ values along with the TL for each of the mesopelagic fish species, the reference organisms and baseline. Reference numbers detailed in the footnote. A: Atlantic Ocean (North and tropical), M: Mediterranean Sea, S: Southern Ocean. Results from one-way ANOVA on the SI between the FATMs and location groups are presented at the lower part of the table. F-value is the variance ratio for the ANOVA. All tests had df = 1. Asterisks indicate statistically significant relationships. FATM: Copepod-related (n = 11) and DHA (n = 9), Location: Atlantic (n = 10) and Southern Oceans (n = 12).

Species	Location	$\delta^{13}C$ (‰)	$\delta^{15}N$ (‰)	TL	References
H. machrochir	A	−17.50 ± 0.50	6.53 ± 0.12	2.17	3
C. warming	A	−19.30 ± 0.26	6.66 ± 0.40	2.22	3, 8
C. pseudopallida	A	−19.00 ± 0.36	7.83 ± 0.20	2.59	8
G. elongatum	A	−18.85 ± 0.20	8.10 ± 0.25	2.67	8
L. alatus	A	−18.06 ± 0.15	8.17 ± 0.27	2.70	3, 8
K. andersoni	S	−22.65 ± 0.40	8.00 ± 0.35	2.77	5, 6
N. resplendens	A	−19.13 ± 0.47	8.46 ± 0.16	2.79	3
P. tenisoni	S	−20.75 ± 0.35	8.40 ± 0.30	2.90	5, 6
B. glaciale	A	−17.78 ± 0.29	8.95 ± 0.27	2.94	1, 2, 3, 10
D. brachycephalus	A	−18.22 ± 0.16	8.96 ± 0.30	2.95	3
P. gemmatum	S	−22.10 ± 0.10	8.70 ± 0.40	3.00	5
E. carlsbergi	S	−22.15 ± 0.40	8.75 ± 0.40	3.01	5, 6
G. piabilis	S	−19.80 ± 0.30	8.80 ± 0.20	3.03	5
P. choriodon	S	−19.55 ± 0.35	8.80 ± 0.25	3.03	5, 6
B. glaciale	M	−18.15 ± 0.59	8.40 ± 0.58	3.07	1, 2, 3, 10
M. muelleri	M	−19.05 ± 0.17	8.40 ± 0.35	3.07	2
G. fraseri	S	−21.10 ± 0.40	9.00 ± 0.40	3.09	5
D. dumerilii	A	−18.71 ± 0.60	9.50 ± 0.60	3.12	3
E. antarctica	S	−22.70 ± 0.75	9.25 ± 0.40	3.17	5, 6
P. bolini	S	−22.65 ± 1.05	9.50 ± 0.55	3.25	5, 6
S. affinis	A	−19.38 ± 0.84	9.98 ± 0.89	3.27	4, 7
G. braueri	S	−22.90 ± 0.85	9.75 ± 0.45	3.33	5, 6
G. nicholsi	S	−21.00 ± 0.55	9.75 ± 0.31	3.33	5, 6
G. bolini	S	−20.50 ± 0.40	9.90 ± 0.50	3.38	5
Copepoda	A	−21.54 ± 0.68	5.96 ± 1.11	2	3, 6, 8, 9
Copepoda	M	−21.29 ± 1.00	5.02 ± 0.79	2	
Copepoda	S	−22.72 ± 1.70	5.55 ± 0.86	2	
Chaetognaths	A	−20.67 ± 0.58	8.03 ± 0.99	2.65	3, 6, 8, 9
Chaetognaths	M	−20.38 ± 0.50	5.65 ± 0.50	2.19	
Chaetognaths	S	−22.90 ± 1.50	7.40 ± 0.90	2.58	
Euphausiacea	A	−19.31 ± 0.16	5.86 ± 0.40	1.96	2, 6, 8, 9
Euphausiacea	M	−19.68 ± 0.33	6.91 ± 0.74	2.59	
Euphausiacea	S	−21.58 ± 2.22	5.78 ± 0.96	2.07	

	Mean Square	F-value	*p*-value
$\delta^{13}C$ - FATM **	19.94	15.44	<0.01
$\delta^{13}C$ - Location ***	28.90	37.83	<0.01
$\delta^{15}N$ - FATM	2.66	3.38	0.08
$\delta^{15}N$ - Location	3.10	4.06	0.05

1: Fanelli et al. (2014), 2: Valls et al. (2014), 3: Olivar et al. (2019), 4: Wang et al. (2019), 5: Cherel et al. (2010), 6: Stowasser et al. (2012), 7: Richards et al. (2019), 8: McClain-Counts et al. (2017), 9: Fanelli et al. (2011), 10: Petursdottir et al. (2008).

animal lipids, but also in some phytoplankton groups (Jónasdóttir, 2019). Therefore, it is also likely that indicates diatom/phytoplankton input and therefore herbivorous prey when found at higher trophic levels.

A high content of DHA is often used as a proxy that indicates carnivorous diet (Dalsgaard et al., 2003a; Jónasdóttir, 2019; Wang et al., 2019). This is based on accumulation of DHA at higher trophic levels and is relatively high in fish (Wang et al., 2019). It is likely that DHA is being absorbed after digestion, as it consists of an important building block of structural lipids (Graeve and Greenacre, 2020). DHA and Oleic acid (18:1n-9) were correlated which strongly suggests carnivorous prey (Table 2), but could also suggest different types of carnivorous feeding (e.g. dinoflagellate-based diet versus piscivory). Another significant ratio that emerged in LRA was 16:0/22:1n-11 (Table 2). Palmitic acid (16:0) and Stearic acid (18:0) have been both associated with detritus-based diet (Suhr et al., 2003; Zhukova, 2019). The logratio 16:0/22:1n-11 represents the contrast of a detritus signal, linked to the long chain 22:1n-11 typical for lipid rich copepods such as *Calanus* (Dalsgaard et al., 2003b). Bode et al. (2021) showed that even piscivorous species rely on detritus consumption to a significant extent e.g. fish of genus *Stomias* and microbial contribution has proven to have an important influence on the overall TL of the consumers. The last logratio is the combination of the structural *de-novo* synthesized short chained 14:0 and long-chained MUFA 22:1n-9 that derives from elongation of the 20:1n-9 and is also, as stated before, typical of lipid rich copepods.

4.2. Stable isotopes

Spatial variation of isotopic values is expected at different geographical locations, reflecting different oceanographic conditions such as temperature and, salinity as well as available nutrients and primary production (Stowasser et al., 2012). Carbon and nitrogen stable isotope composition of POM and zooplankton is highly coupled to the hydrographic conditions (Lee et al., 2013). As a result of this and the extent of the geographical area of the SI database, it is anticipated that there will be a high degree of variation in isotopic values, even if regional $\delta^{15}N_B$ values are employed. Richards et al. (2019) have reported significant correlation of $\delta^{13}C$ values with geographical location in their sampling area. Table 3 reveals that Copepoda and Euphausiacea from the Atlantic and Southern Ocean, respectively, exhibited comparable $\delta^{15}N$ and $\delta^{13}C$ values and any differences in regional $\delta^{15}N_B$ values could have an important effect in the final TL ranking of the meso-/-bathypelagic fish. However, as illustrated in Table and Fig. 3, meso-/-bathypelagic fish and Copepoda from the Southern Ocean displayed

Table 4

Summary table of FA and SI findings for all 23 examined mesopelagic fish along with key information on the pre-existing literature knowledge. TL ranking: High >3.00, Intermediate 2.60–3.00, Low <2.60. $\delta^{13}C$ ranking: Low $< -22‰$, Intermediate $-22‰ < \delta^{13}C < -20‰$, High $> -20‰$. FATM were assigned according to LRA results.

Species	FATM	SI indicators	Main suggested ecology	Previous knowledge
Benthosema glaciale (Bg)	Calanoid FATM	-Intermediate/High TL (Atlantic/ Mediterranean) -High $\delta^{13}C$	Herbivorous prey – lipid rich copepods Narrow niche	Herbivorous prey - Canaloid copepods, amphipods, euphausids and ostracods [1, 2, 3]
Ceratoscopelus warmingi (Cw)	DHA	-Low TL -High $\delta^{13}C$	Herbivorous prey Narrow niche	Herbivorous prey and direct diatom feeding [4]
Cyclothone pseudopallida (Cp)	DHA	-Intermediate TL -High $\delta^{13}C$	Carnivorous prey Narrow niche	Carnivorous prey [6], piscivory [7], zooplanktivore [5]
Diaphus brachycephalus (Db)	DHA	-Intermediate TL -High $\delta^{13}C$	Carnivorous prey Narrow niche	Carnivorous prey – Chaetognaths and fish [12]
Diaphus dumerilii (Dd)	DHA + Detritus FATM	-High TL -High $\delta^{13}C$	Omnivorous occasionally carnivorous prey Narrow niche	Copepoda, Euphausiacea, Amphipoda, and Decapoda [12]
Electrona antarctica (Ea)	Diatom FATM	-High TL -Low $\delta^{13}C$	Opportunistic Broad niche	Carnivorous amphipods, herbivorous salps [9, 11]
Electrona carlsbergi (Ec)	Calanoid FATM	- High TL -Low $\delta^{13}C$	Herbivorous prey Broad niche	Herbivorous prey; amphipods, calanoid copepods [10]
Gonostoma elongatum (Ge)	DHA + structural FAs	-Intermediate TL -High $\delta^{13}C$	Carnivorous prey Narrow niche	Crustacean consumer and copepods as juvenile [8]
Gymnoscopelus bolini (Gbo)	Calanoid and diatom FATMs	-High TL -Intermediate $\delta^{13}C$	Carnivorous prey Narrow niche	Piscivory and krill [7, 9, 10]
Gymnoscopelus braueri (Gbr)	Diatom FATM	-High TL -Low $\delta^{13}C$	Carnivorous and herbivorous prey Broad niche	Carnivorous amphipods, herbivorous salps [9, 11]
Gymnoscopelus fraseri (Gf)	Calanoid FATM	-High TL -Intermediate $\delta^{13}C$	Opportunistic – herbivorous prey Broad niche	Omnivorous copepods and krill [10]
Gymnoscopelus nicholsi (Gn)	Calanoid FATM	-High TL -Intermediate $\delta^{13}C$	Opportunistic – herbivorous prey Broad niche	Diverse diet; euphausids, copepods [15]
Gymnoscopelus piabilis (Gp)	Calanoid FATM	-Intermediate TL -High $\delta^{13}C$	Opportunistic – herbivorous prey Narrow niche	No information found
Hygophum machrochir (Hm)	DHA + Detritus FATM	-Low TL -High $\delta^{13}C$	Herbivorous prey + detritus Narrow niche	Herbivorous copepods, crustacean macrozooplankton, seston [12]
Krefftichthys andersoni (Ka)	Diatom FATM	-Intermediate TL -Low $\delta^{13}C$	Herbivorous prey Broad niche	Copepods, euphasids, amphipods [15, 16]
Lampanyctus alatus (La)	DHA	Intermediate TL -High $\delta^{13}C$	Carnivorous prey Narrow niche	Crustacean-based zooplankton diet; ostracods and calanoid copepods [5, 12]
Maurolicus muelleri (Mm)	Calanoid FATM	-High TL -High $\delta^{13}C$	Herbivorous prey Narrow niche	Calanoid copepods [2]
Notoscopelus resplendens (Nr)	DHA	-Intermediate TL -High $\delta^{13}C$	Carnivorous prey Narrow niche	Seston and herbivorous copepods [12]
Protomyctophum bolini (Pb)	Calanoid FATM	-High TL -Low $\delta^{13}C$	Herbivorous prey Broad niche	Copepods and krill [9]
Protomyctophum choriodon (Pc)	Calanoid FATM	-High TL -High $\delta^{13}C$	Herbivorous prey Narrow niche	Herbivorous and omnivorous copepods [12]
Protomyctophum gemmatum (Pg)	Calanoid FATM DHA	-Intermediate TL -Low $\delta^{13}C$	Opportunistic Broad niche	Herbivorous copepods and euphausiid [10]
Protomyctophum tenisoni (Pt)	Calanoid FATM	-Intermediate TL -Intermediate $\delta^{13}C$	Opportunistic Broad niche	Herbivorous and omnivorous copepods [13, 14]
Stomias affinis (Sa)	DHA	-High TL -High $\delta^{13}C$	Carnivorous prey Narrow niche	Carnivorous prey [6], Piscivory [7, 10]

1: Pepin (2013), 2: Petursdottir et al. (2008), 3: Pakhomov and Perissinotto (1996), 4: Robison (1984), 5: McClain-Counts et al. (2017), 6: Wang et al. (2019), 7: Wang and Zhang (2020), 8: Lancraft et al. (1988), 9: Shreeve et al. (2009), 10: Stowasser et al. (2009), 11: Kruse et al. (2015), 12: Olivar et al. (2019), 13: Williams (1985), 14: Cherel et al. (2010), 15: Connan et al. (2010), 16: Lourenço et al. (2016).

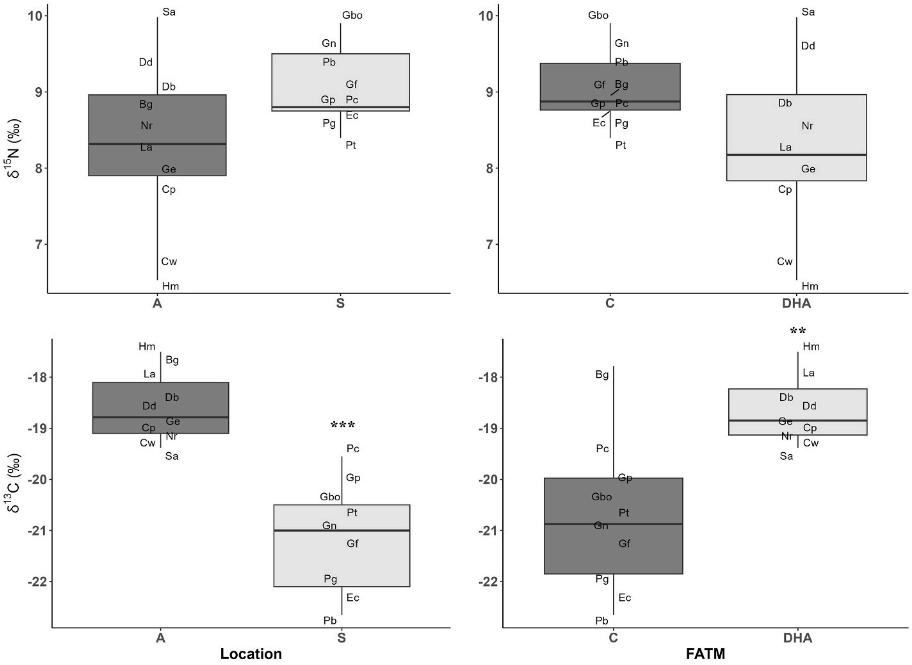

Fig. 3. Boxplots depicting interspecific differences in mean δ15N and δ13C (upper and lower panel, respectively) values for different factors, A: Atlantic, S: Southern Oceans, C: Copepod and DHA FATMs. Asterisks denote significant differences. Species codes defined in Table 1.

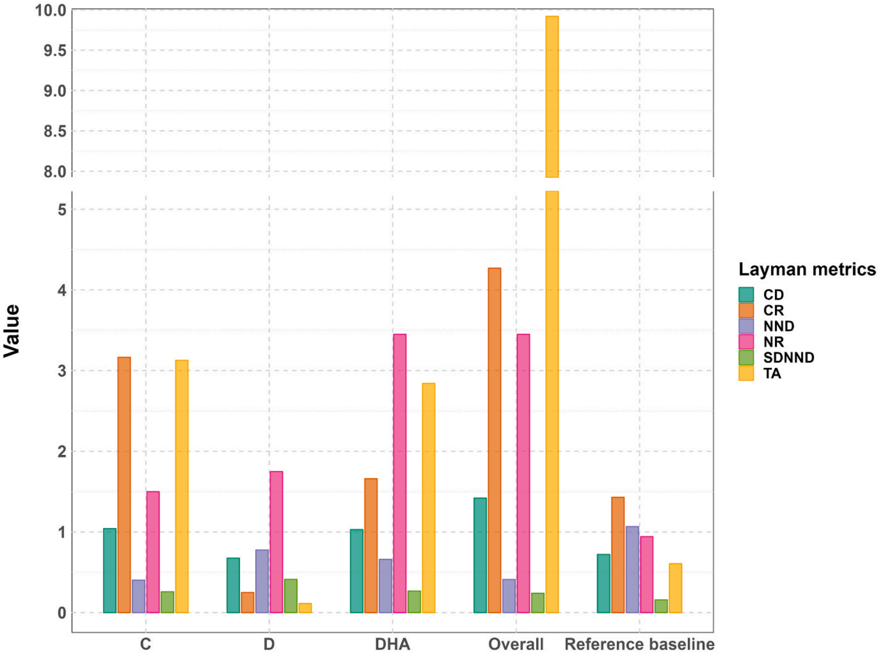

Fig. 4. Bar chart representing the Layman metrics calculated for the meso-/bathypelagic fish assigned in three FATM categories. C: Copepod, D: Diatom, DHA FATMs. Reference baseline refers to Copepoda. Overall: all the 23 meso-/bathypelagic fish. Layman metrics abbreviations are defined in the section 2.2. *Data analysis*.

significant lower $\delta^{13}C$ values, which suggests a diverse dietary pattern, wide trophic niche, and possibly opportunistic feeding behaviour for the fish species. Data was available for *B. glaciale* from two sampling locations and the Atlantic Ocean *B. glaciale* exhibited more enriched values both in $\delta^{15}N$ and $\delta^{13}C$, possibly indicating narrower niche than the population of the Mediterranean Sea. However, the Mediterranean *B. glaciale*'s TL was calculated higher than the corresponding species sampled in Atlantic Ocean, reflecting the regional differences of the $\delta^{15}N$ values of the reference baselines. According to Agersted et al. (2014), the $\delta^{15}N$ baseline signal in *Calanus* spp. was found to be highest inshore and lowest offshore, likely due to increased nitrate supply and local nitrogen transformations, e.g. estuaries having higher $\delta^{15}N$ values compared to marine waters (Alkhatib et al., 2012; Agersted et al., 2014). Additionally, differences in $\delta^{13}C$ in the baseline signal suggest varying food sources in different areas (Perry et al., 1999; Agersted et al., 2014).

Fig. 5 presents the scatterplot of the distribution of $\delta^{15}N$ and $\delta^{13}C$ for all the 23 meso-/bathypelagic fish, reference organisms and Copepoda baselines, where the FATMs and location groups are clearly clustered with distinct isotopic properties. The utilization of Layman metrics offered a thorough and comprehensive analysis on the isotopic niche of

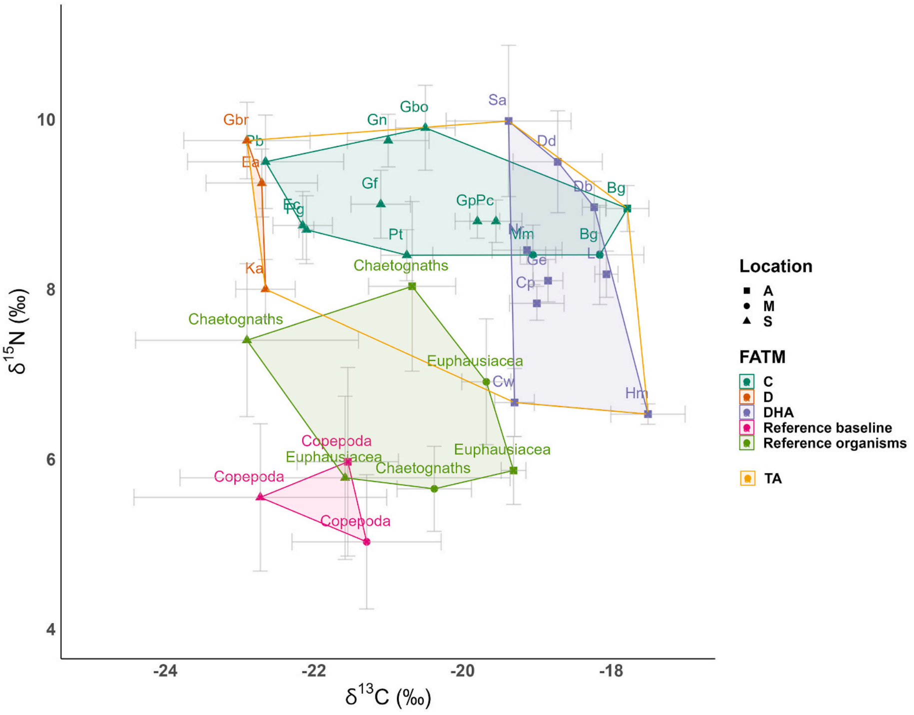

Fig. 5. Scatterplot of mean ± SD literature compiled stable isotope values (δ^{15}N and δ^{13}C) for 23 meso-/bathypelagic species, reference organisms and baselines. δ^{13}C values are lipid corrected. Colors correspond to the FATM groups; C: copepod, D: diatoms and DHA FATMs. Polygons represent the overall (yellow) and FATM sub-group TAs. Shape corresponds to location; A (square): Atlantic Ocean, M (circle): Mediterranean, S (triangle): Southern Ocean.

meso-/bathypelagic fish. It has yielded valuable insights into the feeding behaviour of the species studied in the current research, as well as the community dynamics within the food web (Layman et al., 2007). Fish species with extreme isotopic values towards both δ^{15}N and δ^{13}C directions (e.g. *G. braueri, H. machrochir*), tend to increase the overall TA resulting in an elevated trophic diversity within the entire food web (Fig. 5). Potential exclusion of species laying on the borderline of the overall TA or of the FATM sub-groups, would result in reduced TA, NR, CR and consequently decreased trophic diversity in the overall and diet-specific meso-/bathypelagic fish communities. Except for the TA, the community metrics for the other groups, such as DHA and copepod FATMs, exhibited similarities (Fig. 4). This suggests that the trophic community in our study is largely composed of fish that feed on either copepods or on carnivorous copepods and piscivores. Species such as *G. piabilis* (copepod FATM) or *G. elongatum* (DHA) are species with similar isotopic signature to *P. choriodon* and *C. pseudopallida*, respectively and neither of them is critical for defining the TA of the FATM sub-groups. In this sense, species like these are redundant and thus their exclusion from the meso-/bathypelagic fish pool of this study would not affect neither the overall nor the FATM sub-group specific trophic diversity (Layman et al., 2007). The copepod FATM group shows higher levels of CR, indicating a greater variety of food sources at the bottom of the food chain and more diverse basal resources, as shown in Fig. 4. On the other hand, the DHA group ranks higher in NR, which suggests a wider range of feeding habits among the fish, leading to more trophic levels within the group. Copepod FATM group exhibit the smallest NND, which as measure of the community density, indicates that the fish included in this group are characterized by similar feeding ecologies, whereas the individual species of the diatom FATM group had the highest NND and SDNND values, revealing more diverse and distinct trophic ecologies within the group.

4.3. Dietary preference of meso- and bathypelagic fish

Many of the meso-/bathypelagic fish in the present meta-analysis have unknown dietary preference. One of the best dietary information is available for *E. antarctica*, *G. braueri* and *K. anderssoni.* It has been reported that the hyperiid amphipod *Themisto gaudichaudii* and the salp *Salpa thompsoni* play a significant role in the diet of Southern Ocean meso-/bathypelagic fish species (Kruse et al., 2015; Shreeve et al., 2009). *E. antarctica* and *G. braueri* are specifically reported to prey on *T. gaudichaudii* (Shreeve et al., 2009) which itself is a carnivorous amphipod that feeds on copepods, chaetognaths and pteropods (Kruse et al., 2015; Lange, 2006), explaining the higher TL for *E. antarctica* and *G. braueri.* The other potential dietary input, the salp (*S. thompsoni*) feeds directly on phytoplankton, especially diatoms (Kruse et al., 2015) which could explain the high influence of 16:1n-7 and 18:1n7-related logratios found in *E. antarctica* and *G. braueri* due to which they were categorized in the diatom FATM group in SIA (Fig. 5). In turn the diet of *K. anderssoni* is reported to be copepods, small euphausids and amphipods (Lourenço et al., 2016) and due to its lower TL is likely to be copepods feeding on diatoms. One of such candidates is *Calanus simillimus* that indeed is reported to have high 16:1n-7 signal (Ward et al., 1996) and has been often identified as a prey of both *K. anderssoni* and *T. gaudichaudii* in South Georgia waters (Lourenço et al., 2016; Pakhomov and Perissinotto, 1996). This observation is also supported by the SIA, which shows that this group *E. antarctica, G. braueri and K. anderssoni* that occupy the Southern Ocean, have low mean values of δ^{13}C with large variability indicating a diverse dietary pattern and perhaps broad trophic niche supporting mostly an opportunistic feeding behaviour in Southern Ocean meso-/bathypelagic species.

Another cluster at the lower right panel of the fatty acid LRA biplot (Fig. 2) with high zooplankton signals (20:1n-9 and 22:1n11) highlight the zooplanktivores *M. muelleri, P. choriodon, G. nicholsi, E. carlsbergi* and *B. glaciale.* As these long chain MUFAs are typical of lipid rich copepods, this clustering may separate the fish feeding on the mesopelagic or/and diapausing copepods. In the same clustering are *G. fraseri* and *P. bolini* for which stomach content analysis have shown that the main preys are the copepods *Metridia* spp. and *Rhincalanus gigas* and the krill *Euphausia frigida* (Shreeve et al., 2009). The δ^{13}C values for *G. fraseri* and *G. nicholsi* in this cluster are similar with slight difference in δ^{15}N values resulting in higher trophic level for *G. nicholsi* (Table 3).

The FATMs characterised for carnivory are the fatty acids 18:1n-9 and 22:6n-3 (DHA). The FATM 18:1n-9 is used for indication of animal dietary input but is also synthesized *de-novo* by most organisms (S. Falk-Petersen et al., 2000; Graeve and Greenacre, 2020). The use of DHA fatty acid as a marker of carnivory results from all organisms' preferential retention of this essential fatty acid in bio-membranes (Stübing and Hagen, 2003). The δ^{15}N analyses revealed high tropic level values for *G. bolini, G. braueri, G. nicholsi* and *S. affinis*. However, those did not cluster together in the fatty acid LRA analysis, which could be an indication of different types of carnivory or de novo DHA synthesis. *S. affinis* and *G. bolini* have been reported to be piscivorous (Stowasser et al., 2009; J. Wang and Zhang, 2020), while krill, *Euphausia superba* has been identified as major prey of *G. bolini* and *G. nicholsi* in the Scotia Sea (Shreeve et al., 2009; Stowasser et al., 2009). *C. pseudopallida* has also been classified as a piscivore by Wang and Zhang (2020). However, McClain-Counts et al. (2017) lists it as true zooplanktivore, which is in concert with the TL estimation of 2.59 from our analysis. Bode et al. (2021) have obtained TL estimations for *C. pseudopallida* using CSIA, targeting the natural abundance of δ^{15}N of alanine and mixtures of glutamine and glutamic acid. Results showed that CSIA yielded TLs for *C. pseudopallida* higher than TLs calculated by "bulk" SIA, and thus it is possible that the microbial food web's contribution to the trophic position of meso-/bathypelagic fish has been underestimated (Gloeckler et al., 2018; Basedow et al., 2016; Richards et al., 2020). The remaining species in this study were mostly reported to be zooplanktivorous or have unidentified diets (Richards et al., 2019; J. Wang and Zhang, 2020). *G. elongatum* has been reported to be a crustacean consumer, with preference for copepods during its juvenile stages (Lancraft et al., 1988). No statistically significant differences were observed in the δ^{15}N values among species that were marked by Copepod and DHA FATMs (Fig. 3). This lack of significance may be explained by the greater variability of δ^{15}N seen in species marked by DHA, since DHA can be indicative of a broad range of carnivory. The inclusion of piscivorous species in the DHA marked group leads to higher δ^{15}N values, similar to those observed in the Copepod marked species. The species primarily responsible for the distribution's skewness towards the lower quartile are *H. macrochir* and *C. warming*, since they had the lowest δ^{15}N values, indicating the lowest trophic level among the meso-/bathypelagic fishes. *C. warmingi* is reported to feed on diatoms, when other food sources are scarce (Robison, 1984), however the positioning of *H. machrochir* at the LRA biplot also towards detritus FATM, could potentially also explain the low trophic level of *H. machrochir* suggested by the SIA.

Based on all the data we analysed in this study, we can presume that the gradient from the bottom-right to the upper left on the fatty acid LRA biplot (Fig. 2) indicates a shift from predation on herbivorous copepods (salps, Calanoids, krill) to a more omnivorous (*Metridia*) and finally carnivore zooplankton diet (*Pareuchaeta*, *Themisto*, Chaetognatha). Piscivory is likely to be in the direction furthest left where *S. affinis* is located. Myctophids that are positioned at a lower TL than Stomiidae could well have a prey-predator relationship, consistent with the reported piscivorous feeding behaviour of *S. affinis*. Fish with prevailing phytoplankton FATM are most likely migratory feeding at the surface. This gradient could then be indicative of the dietary preference of the meso-/bathypelagic fish with unknown dietary requirements that lie around the diagonal connecting the two end-members of herbivorous and carnivorous diet, in combination with the evaluation of the trophic niche diversity and redundancy assessed by SIA (Fig. 5).

The different methodologies and analyses result in different information on the feeding of the meso-/bathypelagic fish. Fatty acids reveal the potential dietary sources while stable isotopes provide an insight on trophic level and niche. For example, copepods have very diverse dietary habits, ranging from omnivores feeding on phytoplankton and ciliates to fully carnivorous copepods. Some of the mesopelagic copepods are also suspected to be detritivorous feeding on marine snow (Bathmann et al., 1993; Gloeckler et al., 2018; Zhukova, 2019; Bode et al., 2021). A copepod/zooplankton signal in the fatty acid profile, may give different trophic SI signal in the consumer and thus, the two analyses could complement each other. Published observations on gut content can further "ground truth" the SIA and FAA results. Due to the large biomass of meso-/bathypelagic fish, a better understanding of their diet and feeding habits is crucial for determining the dynamics of the marine food web. The combination of FAA and SIA has been shown to be effective in estimating long-term diets, when comparing the signatures of species with known and unknown diets and defining intra-specific and ontogenetic differences (Stowasser et al., 2009, 2012). Other methods are used and evolving such as, compound-specific SIA (CSIA) of δ^{13}C in FAs (Wang et al., 2019), and amino acids (Chikaraishi et al., 2009; Gloeckler et al., 2018; Bode et al., 2021) shed light into the contribution of energy flow through the microbial food web into the entire meso-/bathypelagic community. High-throughput DNA sequencing is also another approach, which enhances the importance of gelatinous prey in the diet of meso-/bathypelagic fish (Clarke et al., 2020). Parameters such as age, feeding depth, length, season, weight and ontogenetic stage of meso-/bathypelagic fish are not taken into account in the present analysis, due to lack of information from the data sources. Such species-targeted FA and/or SI analyses can show more detailed feeding preferences based on location (Choy et al., 2012; McClain-Counts et al., 2017). For example, ontogenetic intra-specific differences in FATM with increasing size for *B. glaciale* and *M. muelleri* is reported by Petursdottir et al. (2008) with those species shifting from phytoplankton based FATMs (probably mainly phytoplankton grazers) to the lipid richer calanoid FATM, indicating that the fish may change their diet as they grow.

4.4. Methodological challenges

In this review only two studies performed both fatty acid analysis and stable isotope analysis on the same samples (Petursdottir et al., 2008; Wang et al., 2019), while the rest of the studies analysed the meso-/bathypelagic fish either for stable isotopes or fatty acids, which in fact could introduce several biases into the statistical analysis of the present study. The different analytical methods used in the different studies may introduce variability in the SI and FA along with the fact that different studies may have sampled different fish populations for FAA and SIA and thus, could affect the overall comparability and representativeness of the data for the entire meso-/bathypelagic ecosystem. Another methodological constraint included the employment of regional $\delta^{15}N_B$ for Copepoda. Ideally, the $\delta^{15}N_B$ value for the TL calculation should reflect the sampling station-specific reference value for Copepoda. Since, not of all the studies analysed the samples both for SI and FA, the acquisition of high resolution $\delta^{15}N_B$ values was not possible in the present study. We considered the best alternative being the employment of three overall greater regional categories for the Atlantic, Southern Oceans and Mediterranean Sea. Alterations in nutrient and basal sources, can occur rapidly due to changes in the phytoplankton community, which could be reflected to the isotopic signatures of plankton and therefore of the reference baselines which meso-/bathypelagic fish TL estimates are based on (Agersted et al., 2014). Finally, as discussed earlier, microbial contribution is rather invisible for the "bulk" SIA, whereas CSIA could efficiently trace microbial and detritus trophic steps (Gloeckler et al., 2018; Bode et al., 2021). However, FAA can effectively complement "bulk" SIA into deciphering and gaining a better insight into bacterial and detritus FATMs. In the present study, we carefully considered the comparability of the data from different studies to eliminate to the greatest extent feasible the potential statistical biases, improve the reliability and validity of our statistical analysis and finally provide an interpretation of the trophic ecology of meso-/bathypelagic species as accurate as possible.

5. Conclusions and perspectives

The present study has demonstrated the utility of a large-scale meta-analysis in providing a general overview of meso-/bathypelagic fish feeding ecology from geographically and temporally scattered data, despite the limitation of attaining paired FA and SI data for the fish species. The present analysis has validated the utility of LRA as a suitable statistical methodology to address the sub-compositional incoherence of FA datasets as well as the utility of combining FATMs with isotopic niche analysis of the species with the aim of gaining a more comprehensive understanding of the trophic pathways and food sources that support the meso-/bathypelagic food web. The current study establishes a framework for an optimized interactive meso-/bathypelagic trophic map, which would incorporate fatty acid and isotopic signatures of newly sampled species with unknown diets into a species "cloud". Along with community metrics, this map would enable easier interpretation and understanding of trophic interactions, diversity, redundancy, basal sources, and baseline alterations. This approach could potentially help to assess the impact of environmental changes, including the anthropogenic climate crisis, on the meso-/bathypelagic food web.

It is essential to understand the existing interactions in the marine food web, with the aim to proceed into modelling the fluxes from plankton and microbial loops to top predators and recycling processes. Research on meso-/bathypelagic fish, as a potential harvestable resource, has been gaining attention over the last years, yet studying life in this ocean zone has been limited despite its ecological importance. Therefore, a deeper insight on the linkage of deep-sea fish to other components of the food web, by resolving the energy fluxes between meso-/bathypelagic and epipelagic zone is of great importance. Multivariate biomarker methodologies and large-scale analyses are promising tools for diet assessments and can provide accurate and robust knowledge of the dietary patterns of meso-/bathypelagic fish.

CRediT authorship contribution statement

Maria Papadimitraki: Conceptualization, Investigation, Data Curation, Formal analysis, Writing - Original Draft, Review and Editing. **Kristian Maar:** Formal analysis Writing - Review & Editing. **Sigrún Huld Jónasdóttir:** Conceptualization, Data Curation, Supervision, Writing - Review & Editing, Funding acquisition.

Declaration of competing interest

The authors declare that they have no known competing financial interests or personal relationships that could have appeared to influence the work reported in this paper.

Data availability

Data will be made available on request.

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Appendix A. Supplementary data

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