Trophic ecology of mesopelagic fishes in the northern and southern Benguela Upwelling Systems revealed through stable isotope patterns

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ABSTRACT: Mesopelagic fishes are important components of marine food webs as trophic links between primary consumers and higher trophic levels, but their trophic ecology is poorly understood. We used stable isotopes ($\delta^{13}C$ and $\delta^{15}N$) to compare the trophic position, trophic enrichment factor, and isotopic niche among feeding guilds of mesopelagic fishes (including myctophids, stomiids) during different seasons in the northern and southern Benguela Upwelling Systems. These subsystems are influenced by differing water masses with various physical and biological properties, which can lead to changes in the marine food web. We aimed to determine if and how the trophic ecology of mesopelagic fishes differs between seasons and subsystems. When separating fishes into guilds based on dietary preferences (zooplanktivores vs. piscivores) and migration patterns (migrating vs. non-migrating), the trophic position was highest during winter in the south for non-migrating piscivores (4.5), but the trophic positions of piscivores (3.2–4.4) were not always higher than those of zooplanktivores (3.1–4.5). This may indicate different isotopic enrichment between species or a very generalist diet from zooplanktivores such as myctophids and their prey. Trophic enrichment factors for $\delta^{15}N$ among guilds ranged from 3.8 to 7.5‰ between the baseline and zooplanktivores and from −0.8 to 1.6‰ between zooplanktivores and piscivores. Previously, mesopelagic fishes have been incorporated into food web models in the Benguela Upwelling Systems, but only as a single entity. Elucidating the complex seasonal and regional trophodynamics of various mesopelagic feeding guilds may contribute to more accurate assessments of trophic transfer efficiencies and higher-resolution models in these systems.

KEY WORDS: Isotopic niche · Trophic enrichment factor · Trophic level · $\delta^{13}C$ · $\delta^{15}N$ · Myctophidae · SIBER

1. INTRODUCTION

Mesopelagic fishes play a vital role in the pelagic food web through their high biomass (Kaartvedt et al. 2012, Irigoien et al. 2014), position in the food web (Choy et al. 2013, Gloeckler et al. 2018, Romero-Romero et al. 2019), and contribution to the ocean's biological carbon pump (Davison et al. 2013). Every day, micronekton, including mesopelagic fishes, perform extensive diel vertical migrations (DVMs), actively ascending from the mesopelagic layer to the upper layers of the water column to feed on smaller animals such as zooplankton and fish (Klevjer et al. 2012, 2016). These mesopelagic fishes are consumed by top predators such as tuna (Valls et al. 2022), hake (Pillar & Barange 1997, Durholtz et al. 2015), sharks

(Carrassón et al. 1992, Filmalter et al. 2017), and seals (Naito et al. 2013). Hence, they interlink the food and nutrient supply in the epipelagic layer with deeper ocean layers (Davison et al. 2013). The mesopelagic zone is an important ecosystem for carbon sequestration (Le Moigne 2019). In the Gulf of Mexico, for example, fecal contribution by mesopelagic fishes contributes up to 25.3% of the particulate organic carbon standing stock in the water column (Woodstock et al. 2022).

The Benguela Upwelling System (BUS) is a highly productive region and 1 of the 4 major eastern boundary currents of the world (Hutchings et al. 2009). It is divided into 2 subsystems, the northern (nBUS) and southern (sBUS) Benguela Upwelling Systems. The subsystems are separated by the permanent Lüderitz upwelling cell at 26°S (Rae 2005, Kirkman et al. 2016) (see Fig. 1). The subsystems exhibit different physical and biological properties and differ in their water mass composition. In austral summer (December–February), the sBUS is dominated by Eastern South Atlantic Central Water (ESACW) and the nBUS by the South Atlantic Central Water (SACW). During the upwelling season in austral winter, ESACW prevails on the nBUS shelf (Mohrholz et al. 2008, Flohr et al. 2014, Tim et al. 2018). These subsystems also differ in their oxygen content throughout the water column. The nBUS has an oxygen minimum zone (OMZ) on the shelf, which is pronounced during austral summer (Mohrholz et al. 2008, Hutchings et al. 2009, Ekau et al. 2018), when the OMZ extends offshore. In contrast, oxygen concentrations in the sBUS are higher throughout the entire water column (Duncan et al. 2022). The main upwelling season in the sBUS is during the summer and fall, with peaks between December and May (Field & Shillington 2005). The region from about 15 to 30°S has year-round upwelling; however, upwelling in the nBUS peaks during August and September (Chavez & Messié 2009, Martin et al. 2015). Martin et al. (2015) documented that maximum chlorophyll concentrations occur in September, with the highest biomass of zooplankton occurring in December. These differences in physical properties have also led to differences in the assemblage structure of mesopelagic fishes in the BUS, where communities differ between subsystems and also between the shelf and offshore (Duncan et al. 2022).

Myctophidae, which dominate the biomass of mesopelagic fishes (Gjøsaeter & Kawaguchi 1980), are known to feed mainly on mesozooplankton such as — but not limited to — copepods, euphausiids, and ostracods (Williams et al. 2001, Pusch et al. 2004).

DVM is a differentiating trait between mesopelagic fishes; while most of the night-time surface scattering layer in the upper 100 m is made up of migrant species, deeper waters still contain a significant portion of mesopelagic fishes that are characterized as non-migrating or semi-migrating (Gjøsaeter & Kawaguchi 1980, Hulley 1981, Ariza et al. 2016). For example, the myctophid *Diaphus hudsoni* feeds in the upper 100 m of the water column, while *D. meadi* or *D. osternfeldi* exhibit partial migrations and feed below 150 m at night (Hulley 1981). Similarly, piscivores of the family Stomiidae include species that migrate vertically, such as *Chauliodus sloani* (Eduardo et al. 2020b), as well as species that do not perform DVM, such as *Neonesthes microcephalus* (Barton et al. 2019).

For a more holistic approach to dietary studies, stable isotope analysis can be combined with stomach content data to relate diets to vertical migration patterns of fishes. Fishes that perform DVM and feed in the epipelagic layer consume more freshly produced nitrogen sources, whereas those in deeper waters feed on remineralized nitrogen sources and consequently show higher $\delta^{15}N$ signatures (Richards et al. 2020, Bode et al. 2021). Thus, higher $\delta^{15}N$ values indicate that the respective organisms tend to spend more time at depth and/or represent a higher trophic level (Richards et al. 2020, Bode et al. 2021, Massing et al. 2022). Species-specific information on diet and vertical migration patterns can be used to assign each species to functional groups (Czudaj et al. 2020). The use of functional groups has been widely applied to compare communities and their trophic ecology among ecosystems (Benedetti et al. 2016, Czudaj et al. 2020, Eduardo et al. 2020a). In the Canary Current ecosystems, for example, species composition differs between low- and high-oxygen habitats; however, both habitats contain planktivores and piscivores, as well as migrators and non-migrators. These species can be assigned to different functional groups, and comparisons in trophic ecology can be made among regions and functional groups (Czudaj et al. 2020). Aggregating data by functional groups can also increase the power of statistical analyses when catches of individual species are low (Czudaj et al. 2020, Duncan et al. 2022).

In upwelling regions, the transfer of energy between trophic levels (trophic transfer efficiency) is higher than in oligotrophic regions (Ryther 1969, Sommer et al. 2002). Hence, food web studies can lead to a better understanding of ecosystem functioning, energy flux and assemblage structure (Polis & Strong 1996, Richards et al. 2019). Traditionally,

stomach content analysis has been used in food web studies; however, this provides only a 'snapshot' of an organism's trophic ecology, and the analysis itself can be very time-consuming (Baker et al. 2014). Alternatively, the use of stable isotopes such as $\delta^{15}N$ and $d^{13}C$ provides longer-term information on the trophodynamics of an organism, as the signal is integrated over a longer period, such as several weeks or months (Sweeting et al. 2005, Chen et al. 2012, Thomas & Crowther 2015). $\delta^{15}N$ undergoes a higher rate of trophic fractionation between predators and their prey (2.4–3.8‰), whereas fractionation is less pronounced in $\delta^{13}C$ (0.4–1.8‰) (Fry 2006, Barton et al. 2019). Consequently, the primary organic carbon source can be assessed from $\delta^{13}C$ and the trophic level can be derived from the $\delta^{15}N$ signatures.

To our knowledge, no comprehensive studies have compared the trophic ecology of mesopelagic fishes in the BUS, including taxa besides myctophids (Erasmus & Iitembu 2019), such as the species-rich families Stomiidae and Sternoptychidae, among others. Moreover, seasonal and regional differences in the physical and biological properties of a system can lead to changes in the marine food web structure (Vargas et al. 2007, Szczepanek et al. 2021). This study aimed to elucidate the trophic ecology of mesopelagic fishes in the BUS and to explore regional and seasonal differences within and among functional groups. We combined stable isotope analyses ($\delta^{13}C$ and $\delta^{15}N$) with published data on stomach contents and vertical migration patterns to compare the isotopic niches of feeding guilds, as well as the trophic positions and trophic enrichment factors between the subsystems and between summer and winter. Furthermore, we assessed relationships between $\delta^{15}N$ and morphometrics such as standard length and gape size of mesopelagic fishes and compared these relationships among different taxa based on body shape. We hypothesized that there would be niche partitioning in the isotopic niches of 4 feeding guilds (migrating zooplanktivores, non-migrating zooplanktivores, migrating piscivores, non-migrating piscivores). Non-migrators were expected to have higher $\delta^{15}N$ signatures than migrators because the latter feed on regenerated nitrogen sources. Due to seasonal differences in physical and biological properties of the subsystems (e.g. more constant upwelling in the nBUS and seasonal upwelling in the sBUS), we predicted that $\delta^{15}N$ signatures and isotopic niches would differ between seasons and between subsystems: trophic niches would likely be more similar between seasons in the nBUS than in the sBUS, where seasonal variability in isotopic signatures is probably more pronounced.

2. MATERIALS AND METHODS

2.1. Sampling and sample preparation

Sampling took place on board the RV 'Meteor' (cruise M153) during austral summer (February and March) of 2019 (Ekau 2019) and the RV 'Sonne' (cruise SO285) during austral winter (September and October) of 2021 (Rixen 2021) in the northern and southern subsystems of the BUS (Fig. 1). A rectangular midwater trawl (RMT 8) with an 8 m² opening, a mesh size of 4.5 mm, and a 1 mm cod-end (Baker et al. 1973) was towed at each station for about 30 min at a ship speed of 2.5–3.0 kn. The RMT was deployed obliquely to a maximum water depth of ca. 650 m (Table S1 in the Supplement at www.int-res.com/articles/suppl/m725p075_supp.pdf).
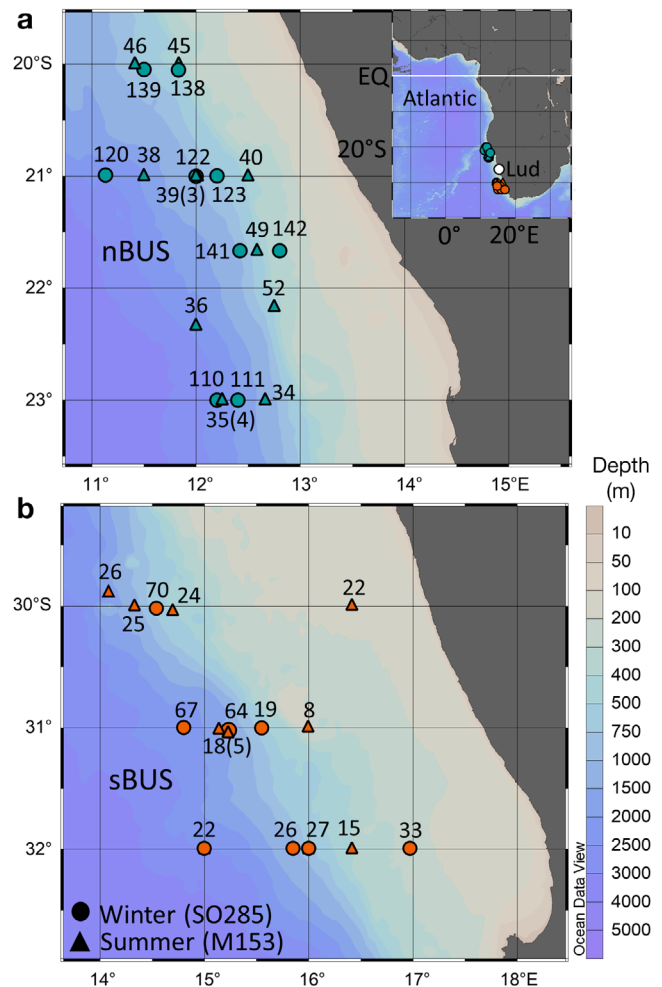

Fig. 1. Sampling stations in the (a) northern (nBUS) and (b) southern (sBUS) Benguela Upwelling Systems in summer and winter using a rectangular midwater trawl (RMT 8). Colour scale indicates bottom depth. Lüderitz (Lud) upwelling cell is shown in the inset in panel (a)

After removal of the cod-end buckets, we flushed samples from the cod-ends and placed them on ice. Species identification was supported by various taxonomic references (Nafpaktitis 1977, Smith & Heemstra 2003, Richards 2005, Sutton et al. 2020). We identified organisms to the lowest possible taxonomic level, usually to species. Specimens were then randomly selected, and standard length (SL) and gape size were measured to the nearest mm. SL was measured from the tip of the jaw to the beginning of the caudal fin (at the last fleshy portion) because caudal rays were often damaged or broken off from trawling. As gape size constrains prey size and has been used in many trophic studies (e.g. Schmitt & Holbrook 1984, Contreras et al. 2019), we measured the upper maxilla length (Araújo et al. 2011) as a proxy for gape size. This was the distance from the tip of the snout to the tip of the maxillary (Poulet et al. 2004). For stable isotope analysis, muscle tissue was removed from the anterior dorsal region of each fish, placed in a −80°C freezer, and shipped to the Thünen Institute for Sea Fisheries (Bremerhaven, Germany) for freeze-drying and further analysis. For baseline determination, specimens of the copepod *Nannocalanus minor* were also frozen for analysis of stable isotopes ($\delta^{15}N$, $\delta^{13}C$). This primarily herbivorous copepod was best suited as a baseline organism to calculate trophic levels (TLs) for mesopelagic fishes because its TL in the northern Benguela is 2.0–2.1, the lowest $\delta^{15}N$ values among 18 common species in the region (Schukat et al. 2014). These isotopic data were provided by Maya Bode-Dalby (Marine Zoology, University of Bremen). A subsample of *N. minor* was obtained from stratified vertical hauls using a HydroBios Multinet Midi that had a net opening of 0.25 m^2 and 5 opening/closing nets with a mesh size of 200 µm. Stations overlapped with those sampled by the RMT survey.

2.2. Hydrography

Data on temperature, salinity, oxygen concentration, and fluorescence (as a proxy for chlorophyll *a* concentration) were collected at each station where fishes were sampled, using a CTD (Sea Bird Scientific, PLUS SBE 9). No hydrographic data were collected at Stn 52 of the SO285 cruise and at Stn 26 of the M153 cruise. The hydrographic data were used to create depth profiles and a potential temperature–salinity (T–S) plot for each season. Water masses were assigned based on previously described water mass properties (Poole & Tomczak 1999, Rae 2005, Mohrholz et al. 2008, Flohr et al. 2014). Depth pro-

files and T–S plots showing parameter limits for each water mass were visualized in Ocean Data View (ODV) v.5.2.1 (Schlitzer 2018).

2.3. Stable isotope analysis ($\delta^{15}N$ and $\delta^{13}C$)

Fish tissue samples and copepods were freeze-dried for 24 h. Tissues were then homogenized into a powder, and samples of 1.0–1.5 mg dry mass were transferred into tin capsules. Lipids were not removed prior to stable isotope analysis, and a lipid correction was performed for those individuals with a C:N ratio >3.5, as described by Post et al. (2007) for aquatic organisms.

Analysis of $\delta^{15}N$ and $\delta^{13}C$ took place at Agroisolab GmbH (Jülich, Germany). Samples were analyzed using an elemental analyzer (EA3000 EuroVector) in combination with an isotope ratio mass spectrometer (IRMS New Horizon) and helium as the carrier gas. For calibration and to ensure proper functioning, 8 laboratory standards were used before measuring the samples. In addition, 2 laboratory standards were measured after every 12 samples. For $\delta^{13}C$, the laboratory standard L-leucin was calibrated against international standards (IAEA-CH7, USGS-54, USGS-61, and USGS-62 for $\delta^{13}C$; NIAEA-N1, IAEA-N2, and USGS61 for $\delta^{15}N$) and used to determine the isotope ratios of carbon and nitrogen (C:N).

2.4. Characterization of diet and vertical migration patterns

Using the feeding guild approach (Hopkins et al. 1996, Sutton & Hopkins 1996, Czudaj et al. 2020), literature analysis was completed for each species to characterize the diet and vertical migration patterns of mesopelagic fishes (Table S2). They belonged to the feeding groups zooplanktivores (zp) and piscivores (pisc). The diet of zooplanktivores included organisms such as copepods, euphausiids, ostracods, and amphipods. Examples of piscivores are fishes of the family Stomiidae, which feed primarily on myctophids. Because of small sample sizes for most species, we were not able to provide more refined separations in diets (and migration patterns), so zooplanktivores also included opportunistic feeders, which may feed on non-crustacean zooplankton. Nevertheless, they have a smaller gape size than most stomiids and other piscivores and would not necessarily be able to, nor are they known to, consume fish. Vertical migration patterns included the categories migrator (m)

and non-migrator (nm). Migrating species perform DVMs, stay in mesopelagic layers during the day, and feed in the epipelagic layer at night. Those classified as non-migrators either migrate partially or do not perform DVMs and feed in the mesopelagic zone (200–1000 m). For example, partial migrators may inhabit the ca. 500 m zone during the day and ascend to ca. 200 m at night to feed. Piscivorous species (Williams et al. 2001), such as the stomiids *Stomias boa* or *Chauliodus* spp., were classified as zooplanktivores if they were smaller than 60 mm SL since smaller specimens also feed on zooplankton such as euphausiids (Eduardo et al. 2020b, Froese & Pauly 2000, S. E. Duncan and A. F. Sell unpubl. data).

2.5. Trophic positions and trophic enrichment factors

Many studies assume that the increase in $\delta^{15}N$ is constant between predators and their prey; however, this is not always the case (Hussey et al. 2014). Similarly, only using a single method to assess TPs can lead to inaccurate determinations and biased conclusions, so it is recommended to apply and compare several methods to obtain the most accurate results (Kjeldgaard et al. 2021). Therefore, we applied 3 approaches to assess the trophic positions (TP, TPC, and TPS; see below) of mesopelagic fishes and one to determine the trophic enrichment factor (TEF_{calc}) between trophic levels. TP and TPC are both additive models, and TPS uses a scaled method where TEF decreases with increasing TP (Hussey et al. 2014).

The first approach was to calculate the TP using a constant TEF of 3.4‰ that is commonly applied. The TP was calculated for each individual using the following equation:

$$TP = TL_{baseline} + \frac{(\delta^{15}N_{consumer} - \delta^{15}N_{baseline})}{TEF} \quad (1)$$

where $TL_{baseline}$ represents the set trophic level of the baseline, for which we used the herbivorous copepod *Nannocalanus minor* and set it to a TL of 2.0 (this baseline of 2.0 is also applied for Eqs 2. and 3 below). $\delta^{15}N_{consumer}$ is the $\delta^{15}N$ value of the consumer, $\delta^{15}N_{baseline}$ is the $\delta^{15}N$ value of the baseline *N. minor*, and the TEF is constant at 3.4‰. We report the mean $\delta^{15}N$ value across all individuals within a trophic guild for this and the following methods.

The second method used to calculate the TP (TPC) is similar to the first. However, the TEF (TEF_v) differs between seasons and subsystems as a function of the

baseline value for $\delta^{15}N$. This approach was used for myctophids by Olivar et al. (2019). It was established from a meta-analysis and described by Caut et al. (2009), where the following equations were used for muscle tissue:

$$TEF_v = -0.281\ (\delta^{15}N_{baseline}) + 5.879 \quad (2)$$

$$TPC = TL_{baseline} + \frac{(\delta^{15}N_{consumer} - \delta^{15}N_{baseline})}{TEF_v} \quad (3)$$

where TEF_v is the variable TEF based on the mean $\delta^{15}N_{baseline}$ values for *N. minor* for the specific season and subsystem (TEF_v values: nBUS summer 3.58‰, sBUS summer 3.59‰, nBUS winter 4.54‰, sBUS winter 4.58‰).

The third method that we used to calculate trophic level, the scaled trophic position (TPS), was a scaled approach, where the TEF decreases with increasing TP, as described by Hussey et al. (2014) and applied to zooplanktivorous mesopelagic fishes by Olivar et al. (2019). The following equation was used:

$$TPC = TL_{baseline}$$
$$+ \frac{[\log(\delta^{15}N_{lim} - \delta^{15}N_{baseline}) - (\delta^{15}N_{lim} - \delta^{15}N_{baseline})]}{k} \quad (4)$$

where $\delta^{15}N_{lim} = 21.926$, the saturating isotope limit as the TL increases, and $k = 0.137$, the rate at which $\delta^{15}N_{consumer}$ approaches $\delta^{15}N_{lim}$ (Olivar et al. 2019). Values used were described by Hussey et al. (2014).

Lastly, because the TEF is not always 3.4‰ and has been shown to decrease with higher TLs (Hussey et al. 2014), we assigned the TLs ($TL_{assigned}$) based on the literature of each species' diet and then determined the enrichment factor (TEF_{calc}) between guilds. *N. minor* was set to 2.0 ($TL_{baseline}$), zooplanktivores were set to TL 3.0 ($TL_{assigned}$), and piscivores were set to TL 4.0 since they mostly feed on smaller fish such as zooplanktivorous myctophids ($TL_{assigned}$).

$$TEF_{calc} = \frac{(\delta^{15}N_{consumer} - \delta^{15}N_{baseline})}{TL_{assigned} - TL_{baseline}} \quad (5)$$

As an alternative, because many copepod species vary in their trophic positions from 2.0 to 3.9 (those in upper 700 m) (Schukat et al. 2014), we set zooplanktivores to 3.5 and piscivores to 4.5 as a sensitivity analysis.

2.6. Statistical analysis

Data analysis was carried out with R v.4.0.2 (R Core Team 2021) and the package 'Pipe-Friendly Frame-

work for Basic Statistical Tests (rstatix)' v.0.7.0 (Kassambara 2021). Stable isotope data ($\delta^{13}C$ and $\delta^{15}N$) were tested for normality using a Shapiro-Wilk normality test, prior to further analysis. Because data were not normally distributed, non-parametric tests were selected for further analysis. One outlier was removed from the analysis for *Triplophos hemingi*.

Samples comprised 11 families and 54 species (Table S3). These samples were composed of 132 individuals from the nBUS summer community, 107 from the nBUS winter community, 90 from the sBUS summer community, and 59 from the sBUS winter community. To determine the difference in $\delta^{15}N$ and $\delta^{13}C$ between seasons and subsystems, all species in each of the 4 communities were pooled and a Kruskal-Wallis test was used to determine the difference in the mean values of $\delta^{13}C$ and $\delta^{15}N$ between the 4 communities. Means were calculated as an average of all individuals within each community. Pairwise comparisons between groups were then made using a Wilcoxon rank sum test with correction for multiple testing. A separate pairwise comparison was made for each of the 2 stable isotopes (with 4 communities within each test).

To test for differences between the trophic position of feeding guilds within a community, we applied Kruskal-Wallis analysis, because data were either not normally distributed and/or did not meet the assumption of homogeneity of variance based on Levene's test. For each community that had significant differences in trophic position among feeding guilds, pairwise comparisons were made using a Wilcoxon rank sum test. Statistical analyses were carried out separately for each method that was used to assess the trophic position (TP, TPC, and TPS). A separate TP/TPC/TPS was calculated for every individual, and means were calculated by averaging the values of individuals for each trophic guild, season, and subsystem.

To compare the isotopic niches of feeding guilds between subsystems and seasons, the package 'SIBER' (Stable Isotope Bayesian Ellipses in R; Jackson et al. 2011) was used to calculate Bayesian ellipses to quantify the spread of the isotopic data. The 'SIBER' package uses stable isotope data ($\delta^{13}C$ and $\delta^{15}N$) to infer the niche width and community characteristics by comparing metrics among communities (e.g. regional or seasonal assemblages) or among groups such as feeding guilds. The metrics used in our analysis were the convex hull area (TA), the standard ellipse area (SEA), and the standard ellipse area corrected for small sample size (SEAc) (Jackson et al. 2011). The SEA encompasses 40% of the data, compared to the convex hull area, which encompasses the most ex-

treme points. Because some trophic guilds, such as the piscivorous groups, had very small sample sizes, the focus was placed in these cases on the SEAc, and this was used to calculate the proportion of overlap between isotopic niches of feeding guilds. Isotope data were not normally distributed (left skewed); however, previous studies have successfully implemented the SIBER analysis with non-normally distributed data (Daly et al. 2013, Eckrich et al. 2020, Nemec et al. 2021). Syväranta et al. (2013) also compared the TA, SEA, and SEAc using both normally and non-normally distributed data in fishes, and only found minimal differences in the estimates of niche size.

We grouped species based on their body shapes, which were 'fusiform', 'short–deep', or 'elongated' (López-Pérez et al. 2020, Czudaj et al. 2022) (Table S3). To determine how SL and gape size are related to $\delta^{15}N$ and $\delta^{13}C$, we used Kendall's tau correlation coefficient as a robust, rank-based measure of association. The outliers we removed for this analysis were 1 individual each of *Lepidopus caudatus*, *Leptostomias longibarbatus*, and Nemichthyidae, as they had a much higher SL than other species and skewed all other data.

3. RESULTS

3.1. Hydrography

Depth profiles showed that during both seasons, the nBUS was dominated by SACW and the sBUS was mostly composed of ESACW during both seasons (Fig. S1), consistent with Duncan et al. (2022). During both seasons, nBUS waters had a lower oxygen concentration than sBUS waters, but there were more pronounced differences in oxygen concentration between the subsystems during summer than during winter (Fig. S1). Oxygen concentrations in the nBUS were higher on average in winter than in summer. Maximum oxygen concentrations throughout the water column (but especially in deeper waters) during winter occurred at Stns 110, 111, and 120 (3.7–3.8 ml l^{-1} at 500 m). These stations were also the furthest offshore in the nBUS. Fluorescence, salinity, and temperature were similar between seasons and subsystems (Fig. S1).

3.2. Community comparisons of $\delta^{13}C$ and $\delta^{15}N$

A comparison of the mesopelagic fish communities revealed a shift in the $\delta^{13}C$ (Kruskal-Wallis, χ^2 =

127.56, df = 3, p < 0.001) and δ^{15}N (Kruskal-Wallis, χ^2 = 53.406, df = 3, p < 0.001) signatures among spatio-temporal groups in the BUS (Fig. 2). δ^{15}N values were higher in summer than in winter for both regions (Fig. 2; Table S4). In contrast, δ^{13}C values were significantly higher in the nBUS compared to the sBUS, but showed a similar seasonal pattern with lower values in winter, particularly in the sBUS (Fig. 2).

3.3. Trophic positions and TEFs

We found considerable overlap in the trophic position (TP, TPC, TPS) among feeding guilds within each community (Fig. 3), but also significant differences in 3 of the feeding guilds. During summer, there was no difference in trophic position between feeding guilds in the nBUS, in contrast to the sBUS (Tables 1 & 2). Pairwise comparisons in summer showed that the guild with the highest trophic position was zooplanktivorous migrators, whereas the guild with the lowest trophic position was zooplanktivorous non-migrators (Table 2, Fig. 3). During winter, there were differences in the feeding guilds in both subsystems. In the nBUS, the guilds with the highest trophic position were zooplanktivorous non-

Fig. 2. Distribution of (a) δ^{15}N and (b) δ^{13}C values for mesopelagic fish communities from the northern (nBUS) and southern (sBUS) Benguela Upwelling Systems during austral winter and summer. All specimens were pooled across species. Letters below bars represent significantly different groups based on the Wilcoxon rank sum test. Boxplot shows the median (thick line), interquartile range (colored region), minimum and maximum (whiskers) and outliers (points)

migrators and piscivorous migrators. While the ranges and means varied slightly depending on the respective method we used to calculate the trophic position, differences between guilds were similar within all groups. TP tended to produce higher trophic positions than TPC and TPS regardless of the method applied, and the choice of method did not influence the main results or conclusions. For example, piscivores (migrating and non-migrating) ranged between 3.1 and 4.5 when using 3.4‰ as the TEF, while TPS produced a range between 3.0 and 4.1, and TPC between 3.1 and 3.8.

When we assigned TLs based on published fish diets (Table S2) and calculated the TEF between each feeding guild (Fig. 4, Table 3), the TEF for δ^{15}N ranged from 3.8 to 7.5‰ between the baseline and zooplanktivores and from −0.8 to 1.6‰ between zooplanktivores and piscivores. When we assessed the TEF with zooplanktivores set to TL 3.5 and piscivores to 4.5, relationships did not change between zooplanktivores and piscivores (since they were still only 1 TL apart), but the TEF decreased between the baseline and zooplanktivores (Table 3b).

3.4. Feeding guilds and isotopic niche size

Most species belonged to the feeding guild of zooplanktivorous migrators (zp-m) in both the nBUS (46.7%) and the sBUS (55.5%), followed by zooplanktivorous non-migrators (zp-nm) in the sBUS (25.9%) and piscivorous migrators (pisc-m) in the nBUS (22.0%). The guilds that contained the lowest number of species in the nBUS were zp-nm (20.0%) and piscivorous non-migrators (pisc-nm) (11.1%). Feeding guilds with the lowest number of species in the sBUS were pisc-m (11.0%) and pisc-nm (7.4%). The nBUS contained a higher number of species in all categories.

The trophic niche size was compared between guilds within each community (subsystem and season) (Fig. 5, Table 4). In the nBUS, the guild with the largest trophic niche size was the pisc-m guild during the summer (SEAc). This guild comprised almost double the area of all other guilds. During winter, the guild in the nBUS with the largest isotopic niche was pisc-m. However, all groups had wider isotopic niches in winter than in summer (Table 4a), excluding pisc-nm due to the insufficient sample size to calculate an isotopic niche. The overlap between groups was smaller in winter than in summer, with the exception of zp-nm and pisc-m. The isotopic niche sizes were smaller in the sBUS than in the nBUS. In
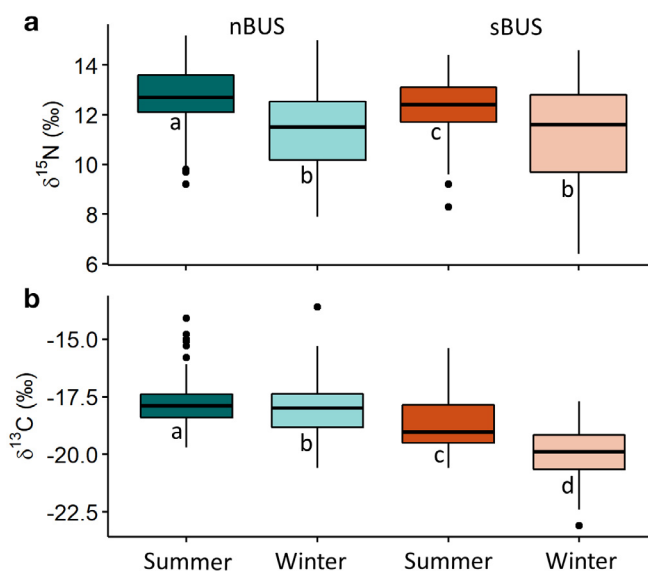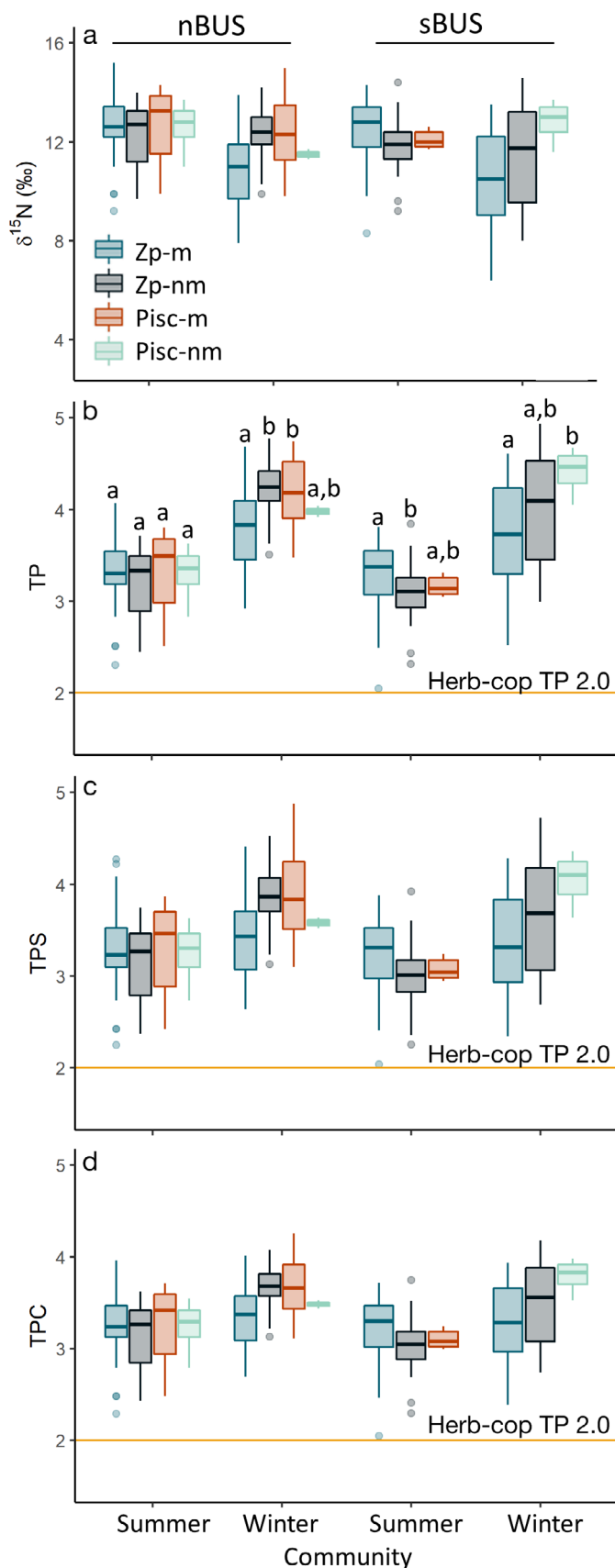
Fig. 3. (a) $\delta^{15}N$ of mesopelagic fish communities from the northern (nBUS) and southern (nBUS) Benguela Upwelling Systems during austral winter. Calculations of trophic positions based on the (b) literature-derived fixed trophic enrichment factor of 3.4‰, (c) variable trophic enrichment factors for each subsystem and season (Caut et al. 2009), and (d) scaled trophic enrichment factors between subsystems, seasons, and trophic positions (Hussey et al. 2014). Letters above bars in panel b represent significantly different groups from the Wilcoxon rank sum test (same letters in all 3 panels). Zp: zooplanktivore; pisc: piscivore; m: migrator; nm: non-migrator; herb-cop: herbivorous copepod

Table 1. Results of the Kruskal-Wallis analysis used to test differences between feeding guilds within a community. A separate test was performed for each community and for each method used to calculate the trophic position (TP: additive, using 3.4 ‰ as the enrichment factor; TPC: additive, using enrichment factors based on subsystem and season; TPS: scaled trophic position); nBUS (sBUS): northern (southern) Benguela Upwelling System. *Statistically significant at p ≤ 0.01

Community	Method	χ^2	df	p
nBUS Summer	TP	1.78	3	0.62
	TPC	1.83	3	0.61
	TPS	1.78	3	0.62
sBUS Summer	TP	8.56	2	0.01*
	TPC	8.56	2	0.01*
	TPS	8.56	2	0.01*
nBUS Winter	TP	23.74	3	<0.01*
	TPC	23.74	3	<0.01*
	TPS	23.74	3	<0.01*
sBUS Winter	TP	10.96	2	<0.01*
	TPC	10.96	2	<0.01*
	TPS	10.96	2	<0.01*

the sBUS, the group with the largest niche during summer was zp-m and that with the smallest niche during summer was pisc-m (Table 4c). The overlap of isotopic niches was also smaller than in the nBUS. Overall there was high variation in trophic signatures within feeding guilds and this was also the case even within single species within a each guild (Fig. S2)

3.5. Morphometrics and isotopic signatures

Within the 3 body shape groupings, most species fell into the category 'fusiform'. There were few individual groups that showed strong relationships between length or gape size and $\delta^{15}N$ or $\delta^{13}C$ within a single season or subsystem, and patterns were not

Table 2. Trophic positions of feeding guilds. Results are from the Wilcoxon rank sum analysis and include the median ± interquartile range and the mean ± SD for the 3 methods used to calculate the trophic position (abbreviations as in Table 1), and sample size in each group (n). Pairwise comparisons between feeding guilds were made for all groups except the northern Benguela Upwelling System (nBUS) summer community, where the Kruskal-Wallis test did not show significant results. Pairwise comparisons that could not be made because of missing groups within a community are marked with 'na' (not analysed). Zp: zooplanktivore; pisc: piscivore; m: migrator; nm: non-migrator

Community	Feeding guild	Sample size n	TP Median	TP Mean	TPC Median	TPC Mean	TPS Median	TPS Mean	Pairwise comparisons	Test p
nBUS Summer	zp-m	76	3.3 ± 0.4	3.4 ± 0.4	3.2 ± 0.3	3.3 ± 0.3	3.2 ± 0.4	3.3 ± 0.4	zp-m & zp-nm	No signi-
	zp-nm	23	3.3 ± 0.6	3.2 ± 0.4	3.3 ± 0.6	3.2 ± 0.4	3.3 ± 0.7	3.2 ± 0.4	zp-m & pisc-m	ficant Kruskal-
	pisc-m	26	3.5 ± 0.7	3.4 ± 0.4	3.4 ± 0.7	3.3 ± 0.4	3.5 ± 0.8	3.3 ± 0.4	zp-m & pisc-nm	Wallis test
	pisc-nm	12	3.4 ± 0.3	3.3 ± 0.3	3.3 ± 0.3	3.2 ± 0.3	3.3 ± 0.4	3.3 ± 0.3	zp-nm & pisc-m	
									zp-nm & pisc-nm	
									pisc-m & pisc-nm	
sBUS Summer	zp-m	56	3.4 ± 0.5	3.3 ± 0.4	3.3 ± 0.5	3.2 ± 0.3	3.3 ± 0.6	3.3 ± 0.4	zp-m & zp-nm	0.018
	zp-nm	29	3.1 ± 0.3	3.1 ± 0.3	3.0 ± 0.3	3.1 ± 0.3	3.0 ± 0.4	3.0 ± 0.4	zp-m & pisc-m	0.245
	pisc-m	5	3.1 ± 0.2	3.2 ± 0.1	3.1 ± 0.2	3.1 ± 0.1	3.0 ± 0.2	3.1 ± 0.1	zp-m & pisc-nm	na
	pisc-nm	na	na	na	na	na	na	na	zp-nm & pisc-m	0.559
									zp-nm & pisc-nm	na
									pisc-m & pisc-nm	na
nBUS Winter	zp-m	65	3.8 ± 0.7	3.8 ± 0.5	3.4 ± 0.5	3.3 ± 0.3	3.4 ± 0.6	3.4 ± 0.4	zp-m & zp-nm	<0.001
	zp-nm	21	4.2 ± 0.3	4.2 ± 0.3	3.7 ± 0.2	3.7 ± 0.3	3.9 ± 0.4	3.9 ± 0.4	zp-m & pisc-m	0.002
	pisc-m	20	4.2 ± 0.7	4.2 ± 0.4	3.7 ± 0.5	3.7 ± 0.3	3.8 ± 0.7	3.9 ± 0.5	zp-m & pisc-nm	0.696
	pisc-nm	2	4.0 ± 0.1	4.0 ± 0.1	3.5 ± 0.0	3.5 ± 0.1	3.6 ± 0.1	3.6 ± 0.1	zp-nm & pisc-m	0.865
									zp-nm & pisc-nm	0.281
									pisc-m & pisc-nm	0.696
sBUS Winter	zp-m	30	3.7 ± 0.9	3.7 ± 0.6	3.3 ± 0.7	3.3 ± 0.4	3.3 ± 0.9	3.3 ± 0.6	zp-m & zp-nm	0.151
	zp-nm	20	4.1 ± 1.1	4.0 ± 0.6	3.6 ± 0.8	3.5 ± 0.4	3.7 ± 1.1	3.6 ± 0.6	zp-m & pisc-m	na
	pisc-m	na	na	na	na	na	na	na	zp-m & pisc-nm	0.002
	pisc-nm	9	4.5 ± 0.3	4.4 ± 0.2	3.8 ± 0.2	3.8 ± 0.2	4.1 ± 0.4	4.1 ± 0.2	zp-nm & pisc-m	na
									zp-nm & pisc-nm	0.109
									pisc-m & pisc-nm	na

consistent across groups (Figs. 6 & 7). For example, in the nBUS, there was a significant negative relationship between SL and $\delta^{15}N$ during summer, for fusiform fishes ($\tau = -0.26$, p < 0.014), while during winter, there was a slight increase ($\tau = 0.35$, p < 0.001). In the sBUS there were also not very strong relationships between standard length or gape size and $\delta^{15}N$. The strongest relationship was for short-deep fishes, which showed an increase in $\delta^{15}N$ with increasing standard length ($\tau = 0.74$, p < 0.012).

4. DISCUSSION

4.1. Spatial and seasonal variation in isotopic signatures between communities

Our study revealed regional and seasonal variability in the isotopic signatures of mesopelagic fish communities in the northern and southern BUS. $\delta^{15}N$ was highest during summer in both subsystems. This could be attributed to changes in the $\delta^{15}N$ signatures of primary producers. Our baseline organism, the copepod species *Nannocalanus minor*, which has a TL of 2.0–2.1 (Schukat et al. 2014), had a $\delta^{15}N$ signature of about 8.0‰ during summer and 4.0‰ during winter in both subsystems, suggesting that the increased $\delta^{15}N$ values in summer are a result of increases at the base of the food web. For the sBUS, this may be explained by increased coastal upwelling during the summer, which increases the particle flux (Romero et al. 2002). In the sBUS, $\delta^{15}N$ of particulate organic matter (POM), which reflects $\delta^{15}N$ in primary producers, was higher in summer than in winter (7.2 vs. 4.3‰) (Romero et al. 2002), very similar to the differences in our baseline. We found seasonal differences in $\delta^{15}N$ signals in the nBUS as well, with the highest $\delta^{15}N$ signatures in summer for *N. minor* and fishes. Fishes show a delay in the $\delta^{15}N$ signals due to the rate of isotopic fractionation between TLs. This can range from days up to a year, depending on the size or growth rate, among other factors, but for smaller fish this would typically require several weeks to months (Sweeting et al. 2005, Chen et al.
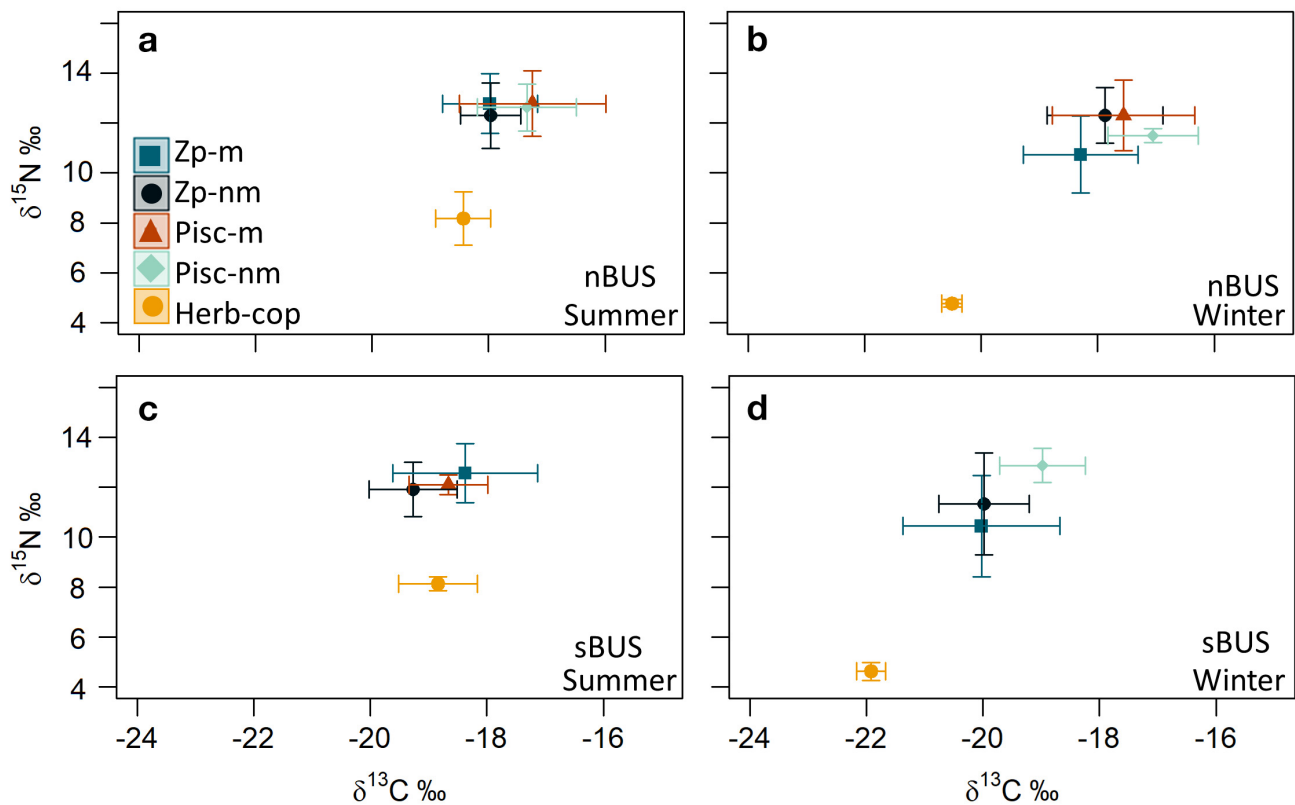
Fig. 4. Means of $\delta^{15}N$ and $\delta^{13}C$ of mesopelagic fish communities from the (a,b) northern (nBUS) and (c,d) southern (sBUS) Benguela Upwelling Systems during austral winter (cruise SO285) and summer (cruise M153). Error bars: SE. Community abbreviations as in Fig. 3

2012, Thomas & Crowther 2015). Assuming that $\delta^{15}N$ in POM increases between December and March in the water column (Holmes et al. 2002), $\delta^{15}N$ values in fish should be higher during our summer sampling period (February/March). Cruise SO285 sampling took place during September (late winter) prior to decreases in POM detected by Holmes et al. (2002), which may be reflected in the lower $\delta^{15}N$ signatures in both *N. minor* and mesopelagic fishes. Peaks in $\delta^{15}N$ in primary producers and POM may differ between years and depths, requiring station-specific $\delta^{15}N$ data for primary producers to assess their role in explaining the observed seasonal differences. Nevertheless, while the delay between primary producers and consumers is unknown, the observed increases in $\delta^{15}N$ during summer in the baseline most likely reflect the increase in $\delta^{15}N$ of primary producers.

The $\delta^{13}C$ signatures differed between all seasons and subsystems in our study, and the largest differences occurred between summer and winter in the sBUS, with a lower $\delta^{13}C$ in winter than in summer. This may be attributed to differences in the phytoplankton communities between seasons. Species compositions

of coccolithophores and diatoms differ between winter and summer, and during winter, there is also a higher diversity of Foraminifera (Romero et al. 2002). These differences in assemblage structure at the base of the food web would result in shifts of the $\delta^{13}C$ signals for higher TLs, as $\delta^{13}C$ is determined by the production source. However, to substantiate these conclusions, phytoplankton communities and their $\delta^{13}C$ signatures would need to be compared between seasons and subsystems. We did observe large differences in the $\delta^{13}C$ signatures of the baseline species *N. minor* and feeding guilds of mesopelagic fishes. For example, the difference in $\delta^{13}C$ ranged from −0.4 to 2.6‰ (Table 3a) between *N. minor* and zooplanktivores, depending on the subsystem, season, and migration pattern. These are larger differences than expected, since $\delta^{13}C$ has been reported to show little fractionation between TLs (Barton et al. 2019). This may therefore be attributed not only to phytoplankton communities at the base of the food web but also to deviating metabolic pathways in the respective taxa, since differing amino acids show different rates of fractionation in $\delta^{13}C$ (Takizawa et al. 2020).

Table 3. Calculated trophic enrichment factor (TEF) between trophic guilds of mesopelagic fishes. The copepod *Nannocalanus minor* was used as the baseline species and set to a trophic level (TL) of 2. Zooplanktivores (zp) were set to TL 3 and piscivores (pisc) to TL 4 in panel (a) and set to TL 3.5 and 4.5, respectively, in panel (b). Values used to calculate TEF from differences in TL between guilds are presented in Table 4. m: migrator; nm: non-migrator; herb-cop: herbivorous copepod. Colors match those of feeding guilds in Figs. 4 & 5

a

TL = 2.0, 3.0, 4.0

$\delta^{15}N$

		Herb-cop → Zp-m	→ pisc-m	Herb-cop → Zp-nm	→ pisc-nm
nBUS Summer		4.6‰	<0.1‰	4.1‰	0.3‰
nBUS Winter		6.0‰	1.6‰	7.5‰	−0.8‰
sBUS Summer		4.4‰	0.5‰	3.8‰	na (na)
sBUS Winter		5.8‰	na (na)	6.7‰	1.5‰

$\delta^{13}C$

		Herb-cop → Zp-m	→ pisc-m	Herb-cop → Zp-nm	→ pisc-nm
nBUS Summer		0.5‰	−0.7‰	0.5‰	−0.6‰
nBUS Winter		2.2‰	−0.7‰	2.6‰	−0.8‰
sBUS Summer		0.5‰	0.3‰	−0.4‰	na (na)
sBUS Winter		1.9‰	na (na)	1.9‰	−1.0‰

b

TL = 2.0, 3.5, 4.5

$\delta^{15}N$

		Herb-cop → Zp-m	→ pisc-m	Herb-cop → Zp-nm	→ pisc-nm
nBUS Summer		3.1‰	<0.1‰	2.8‰	0.3‰
nBUS Winter		4.0‰	1.6‰	5.5‰	−0.8‰
sBUS Summer		3.0‰	0.5‰	2.5‰	na (na)
sBUS Winter		3.9‰	na (na)	4.5‰	1.5‰

$\delta^{13}C$

		Herb-cop → Zp-m	→ pisc-m	Herb-cop → Zp-nm	→ pisc-nm
nBUS Summer		0.3‰	−0.7‰	0.3‰	−0.6‰
nBUS Winter		1.5‰	−0.7‰	1.7‰	−0.8‰
sBUS Summer		0.3‰	0.3‰	−0.3‰	na (na)
sBUS Winter		1.3‰	na (na)	1.3‰	−1.0‰

4.2. Trophic position and niche size

Differences in the trophic position of feeding guilds within a community occurred in both subsystems during winter, and also in the sBUS during summer. Since stomiids (the majority of the piscivore group) generally feed on fish such as myctophids (the majority of the zooplanktivore group), we expected zooplanktivores to have a lower calculated trophic position than piscivores. However, this was not always the case; while migrating zooplanktivores had a lower trophic position than migrating piscivores in the nBUS during winter, zooplanktivores did not have significantly lower trophic positions than piscivores in all other communities. Similarities in trophic positions of piscivores and zooplanktivores have also been reported by Choy et al. (2012) based on stomach content data and compound-specific isotope analysis of amino acids (CSIA). For myctophids, stomach con-

tent data resulted in a trophic position of around 3.2, while CSIA indicated 2.9. For stomiids, stomach contents pointed to a trophic position of 4.1, but CSIA indicated 3.2 (Choy et al. 2012). These CSIA estimates of 2.9 and 3.2 for myctophids and piscivorous stomiids are very similar to each other and to our findings.

Our results may be explained by a number of factors. For instance, stomiids may have fed on mycto-phids that had consumed omnivorous euphausiids, while smaller myctophids may have ingested carnivorous copepods with a higher trophic position than the euphausiids. Depending on the environmental conditions and availability of prey, many species of euphausiids are opportunistic omnivores that can switch between herbivory and omnivory (Pillar et al. 1992, Zhou et al. 2021). In the BUS, the dominant species of euphausiids are *Euphausia hanseni* and *Nematoscelis megalops* (Pillar et al. 1992). These 2 species partition their resources based on size, with *E. hanseni* feeding
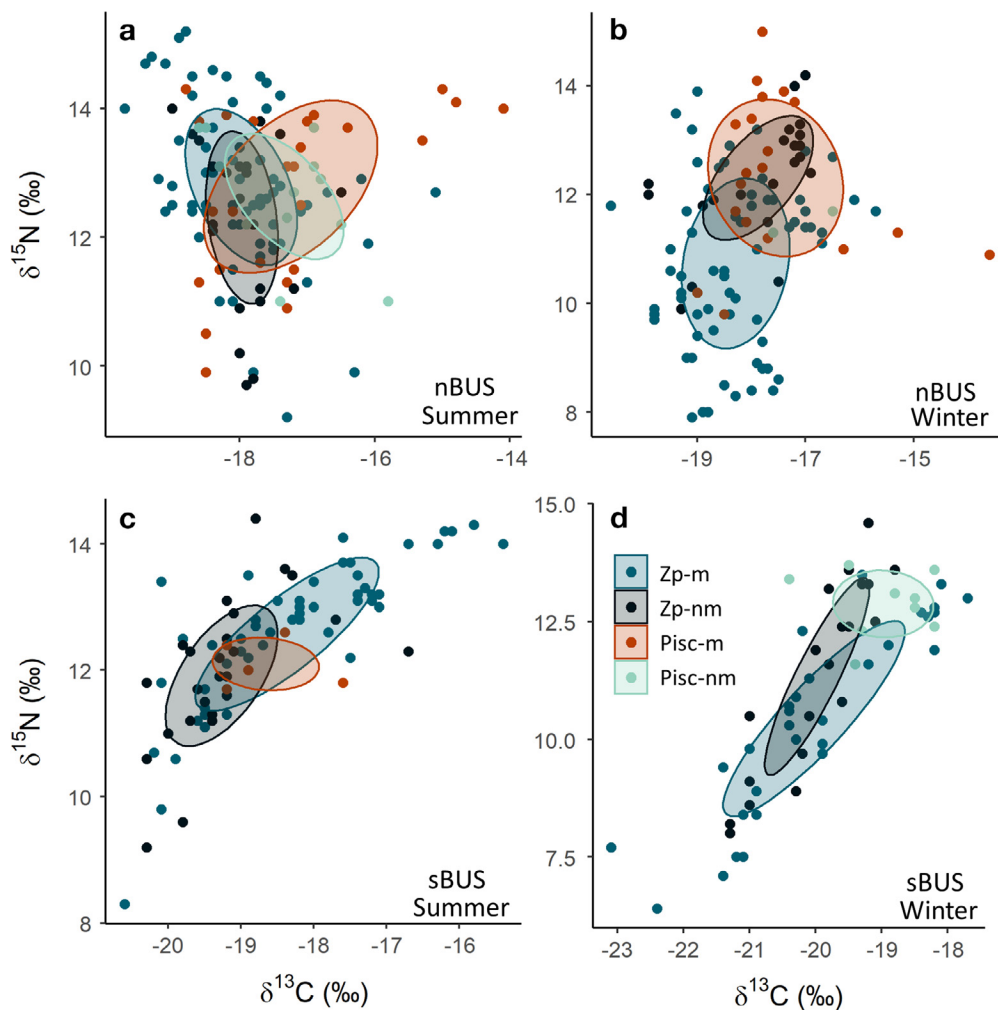
Fig. 5. Isotopic niches of mesopelagic fish feeding guilds for the (a,b) northern (nBUS) and (c,d) southern (sBUS) Benguela Upwellng Systems in summer and winter. Community abbreviations as in Fig. 3. Ellipses represent the maximum liklihood standard ellipse for each feeding guild, corrected for small sample size (SEAc) which encompasses about 40% of the data

Table 4. (a) Area of the convex hull (TA), standard ellipse area (SEA), and standard ellipse area corrected for small sample size (SEAc) for each subsystem and season. (b,c) Portion of overlap of the feeding guild trophic niches between seasons (white portion) and within seasons (dark green: nBUS–summer; light green: nBUS–winter; red: sBUS–summer; pink: sBUS–winter) for the northern (nBUS) and southern (sBUS) Benguela Upwelling Systems. Zp: zooplanktivore; pisc: piscivore; m: migrator; nm: non-migrator; NA: not enough data for analysis

(a)		nBUS								sBUS						
		Summer				Winter				Summer				Winter		
	zp-m	zp-nm	pisc-m	pisc-nm	zp-m	zp-nm	pisc-m	pisc-nm	zp-m	zp-nm	pisc-m	pisc-nm	zp-m	zp-nm	pisc-m	pisc-nm
TA	14.7	5.4	11.1	4.5	17.6	7.9	14.0	0.0	13.0	9.0	1.0	NA	13.7	5.9	NA	3
SEA	2.8	2.1	4.6	2.1	4.7	2.8	5.4	0.0	2.7	2.1	0.8	NA	4	2.2	NA	1.6
SEAc	2.8	2.2	4.8	2.3	4.8	3.0	5.7	NA	2.7	2.2	1.1	NA	4.1	2.4	NA	1.8

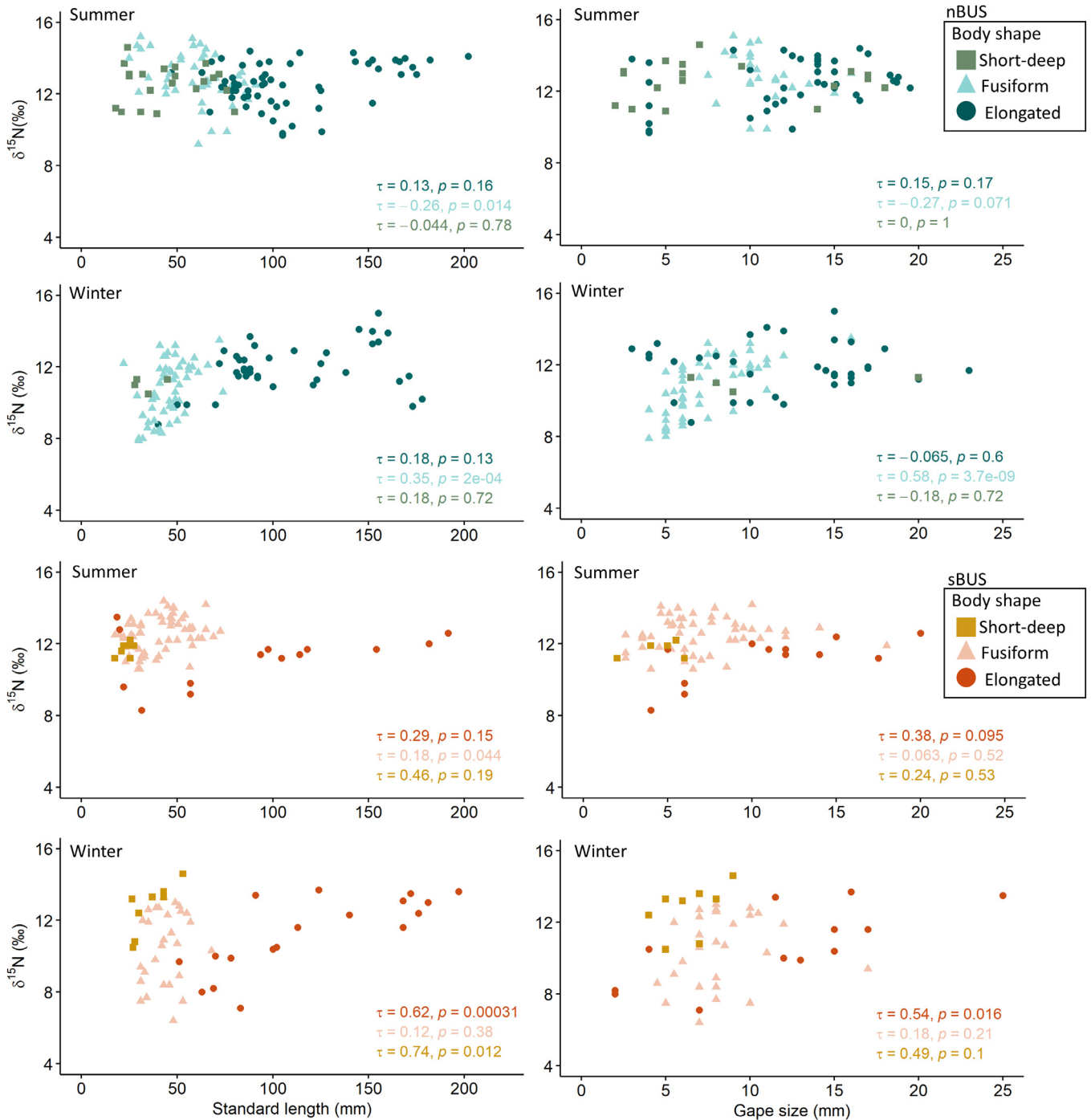| (b)	zp-m	zp-nm	pisc-m	pisc-nm	(c)	zp-m	zp-nm	pisc-m	pisc-nm
zp-m		0.06	0.50	0.33	0.33	zp-m	0.12	0.28	0.30	NA
zp-nm	0.18	0.43	0.30	0.21	zp-nm	0.24	0.18	0.23	NA
pisc-m	0.15	0.45	0.51	0.42	pisc-m	NA	NA	NA	NA
pisc-nm	NA	NA	NA	NA	pisc-nm	0.03	0.11	NA	NA

Fig. 6. Relationships between standard length or gape size versus $\delta^{15}N$ in the northern (nBUS) and southern (sBUS) Benguela Upwelling Systems during austral summer and winter for fusiform, elongated, and short–deep mesopelagic fishes. Kendall's tau and p-value reported for each group

on small copepods and *N. megalops* feeding on medium-sized copepods (Barange et al. 1991, Pillar et al. 1992). Stomach content analysis also showed diatoms in the stomachs of *E. hanseni* (Pillar et al. 1992). On the other hand, copepods such as *Pleuromamma*

robusta and *Gaussia princeps* in the northern Benguela subsystem have TPs of 3.9 and 4.5, respectively (Schukat et al. 2014). Hence, if a myctophid feeds on these copepods, the estimated trophic position of the stomiid and the myctophid could be very similar.
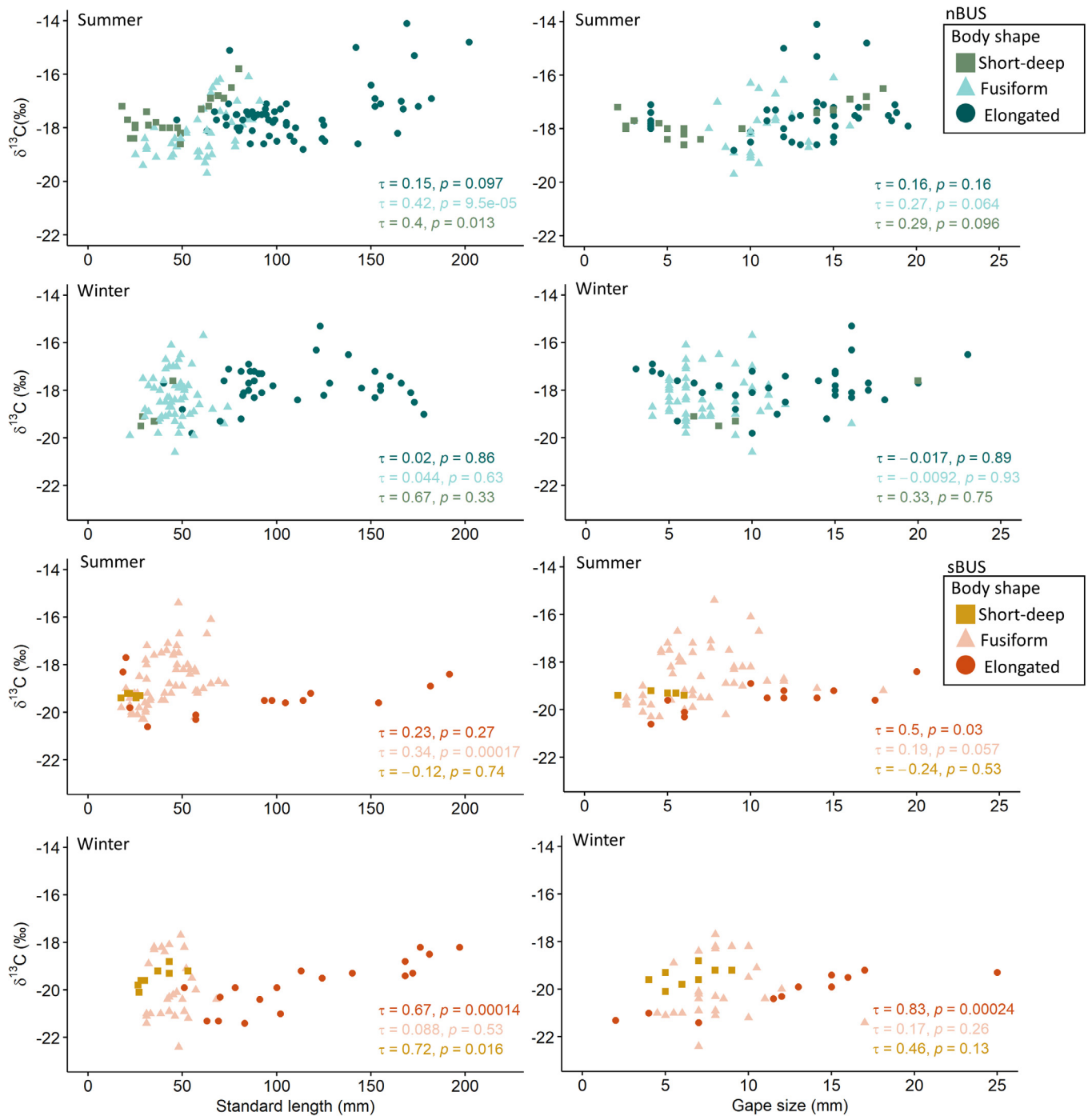
Fig. 7. Relationships between standard length or gape size versus $\delta^{13}C$ in the northern (nBUS) and southern (sBUS) Benguela Upwelling Systems during austral summer and winter for fusiform, elongated, and short–deep mesopelagic fishes. Kendall's tau and p-value reported for each group.

Overall, the high variability of the $\delta^{15}N$ data and of the estimated TPs of copepods and other crustaceans in the BUS (2.0–4.5) (Schukat et al. 2014) can lead to pronounced variations in the $\delta^{15}N$ signatures of higher TLs.

The high variation in $\delta^{15}N$ signatures of fishes was mirrored in the isotopic niche size in the present study. Migrating zooplanktivores occupied the largest trophic niches in the sBUS, and migrating piscivores had the largest isotopic niches in the

nBUS. The nBUS had a much higher diversity and sample size of migrating piscivores, whereas in the sBUS, our sample sizes were limited to 5 individuals during summer, possibly resulting in an underestimate of isotopic niche size, and no individuals during winter. The large trophic niche in the nBUS could partially be a result of the frequently found omnivory at the base of a complex food web, as indicated by copepods (Schukat et al. 2014). Interestingly, we found that the myctophid *Ceratoscopelus warmingii,* which we sampled in the sBUS in winter, had the lowest $\delta^{15}N$ signature of all fish species (7.0 ± 0.8). This species is a known zooplanktivore, but may also feed on mats of diatoms, demonstrating occasional herbivory (Robison 1984). Apparently, not only euphausiids can adapt to omnivory but even fishes, which expands the trophic niche area of an organism and its feeding guild (Pillar et al. 1992, Zhou et al. 2021). Niche size may be affected by the migration patterns of fishes. The majority of the zooplanktivores in the present study were migrating myctophids. They are active swimmers with high metabolic demands, whereas stomiids swim only sporadically and have lower metabolic needs (Torres et al. 1979, Choy et al. 2012). Migrating species may feed both in the epipelagic layer at night and opportunistically in the deeper layers, as they migrate vertically during the day. This opportunistic feeding behaviour would result in a larger isotopic niche, because organisms in deeper layers have higher $\delta^{15}N$ values than those at the surface, due to enriched $\delta^{15}N$ in the mesopelagic zone (Richards et al. 2020).

Differences in metabolic pathways between fish species with differing amino acid compositions may also affect the enrichment factor of $\delta^{15}N$ between TPs (Chikaraishi et al. 2009, Choy et al. 2012, Nuche-Pascual et al. 2021). In this case, the calculated trophic positions may not necessarily represent the true trophic position of a taxon. For example, myctophids are rich in lipids (Haque 1981, Lea et al. 2002), and not only the lipids but also the proteins may differ between myctophids and other taxa. Since differing amino acids have different enrichment factors between TPs, it may affect the trophic enrichment between zooplanktivores and piscivores (Chikaraishi et al. 2009, Choy et al. 2012). While amino acids such as alanine and glutamine have an enrichment factor of around 7‰, that of valine is around 5‰ (Nuche-Pascual et al. 2021). Hence, depending on the amino acid composition of a given species, the TP positions could vary greatly.

4.3. Differences between applied methods

When assigning trophic positions to taxa based on diet, in all groups there was a higher enrichment factor between the baseline and zooplanktivores than between zooplanktivores and piscivores. Hussey et al. (2014) demonstrated that a scaled approach is needed when calculating trophic positions because as the trophic position increases, the TEF decreases. Olivar et al. (2019) showed that the 3 methods used to calculate trophic positions were correlated. The methods differed in that the calculation of TPS showed lower values than other methods, due to the use of its scaled TEF between taxa. In our study, all 3 methods provided the same overall results. While the TP method tended to result in a slightly higher trophic position than the TPC and TPS methods, there were no significant differences between the 3 methods (Fig. 3, Table 2).

In some cases, we obtained a negative value for the TEF, e.g. between non-migrating zooplanktivores and non-migrating piscivores in the nBUS during winter (−0.8‰). Such negative values in $\delta^{15}N$ enrichment have also been found in other environments (DeNiro & Epstein 1981, McCutchan et al. 2003). For example, in controlled feeding experiments that included marine and terrestrial organisms and ranged from insects to mammals, $\delta^{15}N$ enrichment factors varied from −0.5 to 9.2‰, depending on the taxa (DeNiro & Epstein 1981, Chikaraishi et al. 2009). In future studies, CSIA should be performed on a subset of samples to compare the trophic enrichment between specific amino acids, due to their high variability. This approach has the advantage that it does not require a baseline (Chikaraishi et al. 2009), which can often be difficult to obtain; however, the CSIA method is time-consuming and expensive. In upwelling systems, the use of CSIA may be beneficial for untangling the complex food web and specific metabolic pathways in deeper layers.

Size-based approaches have shown that with increasing taxon size, there is an increase in $\delta^{15}N$ (Jennings et al. 2002, Jennings & Warr 2003, Hussey et al. 2014). We applied this to mesopelagic fishes and separated species based on their body shapes (fusiform, elongated, and short–deep). We found few significant positive relationships between size (length and gape size) and $\delta^{15}N$. Possibly, most mesopelagic fishes sampled were opportunistic feeders, especially fusiform fishes including myctophids. Another study conducted in the Mediterranean also did not find positive relationships between the SL of mesopelagic fishes and $\delta^{15}N$ (Valls et al. 2014). Bode et al. (2003)

showed that there was no difference in zooplankton size classes and $\delta^{15}N$ in the BUS when only looking at zooplankton. However, when zooplankton was combined with other taxa such as sardines and dolphins, there was a significant positive relationship between size and $\delta^{15}N$. Our analysis may have failed to find significant relationships due to the limited range of sizes sampled by the small trawl and high variability in $\delta^{15}N$.

Our study showed that in the highly productive northern and southern BUS, mesopelagic fish communities exhibit seasonal differences in their isotopic signatures, with increased $\delta^{15}N$ in summer in both subsystems and a seasonal shift in $\delta^{13}C$ in the sBUS. Feeding guilds within the BUS also show high trophic niche overlap, and zooplanktivores appear to feed very opportunistically based on their large isotopic niche size. This study emphasizes the complexity of TEFs between TLs. As a result, it is important to use different methods to compare trophic positions, not only the traditional value of 3.4‰ for $\delta^{15}N$. Mesopelagic fish occupy various TPs in the Benguela. As the majority of these species are migrating myctophids (Duncan et al. 2022, in combination with Table S2), they are an important component of the pelagic food web and energy flux in the BUS, e.g. as prey to the commercially important Cape hake, squids, and horse mackerel or even Cape fur seals (Pillar & Wilkinson 1995, Mecenero et al. 2006, Erasmus & Iitembu 2019). The northern and southern subsystems differ seasonally and regionally, and small changes at the base of the food webs could severely alter the trophic signatures of mesopelagic assemblages, and consequently affect upper TLs and the trophic transfer efficiency in the subsystems.

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