

Feeding ecology of blue whiting (*Micromesistius poutassou*) in the NW Mediterranean: The important role of Myctophidae

Joan Mir-Arguimbau^{*}, Joan Navarro, Marc Balcells, Paloma Martín, Ana Sabatés

Institut de Ciències del Mar - CSIC, Passeig Marítim de la Barceloneta, 37-49, Barcelona, 08003, Spain

ARTICLE INFO

Keywords:

Stomach contents
Diet composition
Stable isotopes
Trophic position
NW Mediterranean

ABSTRACT

We investigated the feeding ecology of blue whiting (*Micromesistius poutassou*) in the NW Mediterranean living in two habitats, the shelf break and the continental slope, throughout the year, by combining two methodological approaches, stomach content characterization and stable isotope analyses. Stomach content indicated that blue whiting mainly fed on Myctophidae fish, decapods and euphausiids. Differences in diet were observed between areas and throughout the year, with a higher proportion of Myctophidae in individuals living over the shelf break (attaining values ~ 70% weight) than over the slope (attaining values ~ 50% weight). In both habitats Myctophidae, a highly energetic prey, were mainly consumed in spring and summer, which might allow the species to recover energy reserves after the reproductive period and supply the energetic demands of the fast growth season. MixSIAR models, which provide estimates of the relative contribution of each prey to the diet of the consumer by combining stable isotope values of the consumer with those of their potential prey, also indicated that Myctophidae were the main prey in the assimilated diet over the entire year, in both areas. The trophic niche, measured by isotope analyses, suggested segregation between individuals of the shelf break (mainly immatures) and the slope (mainly adults), which would reduce the intraspecific competition. The seasonal and spatial differences observed in the feeding ecology of the Mediterranean blue whiting are related to the energetic requirements of the species throughout the year and with changes in the spatial distribution of the different ontogenetic phases.

1. Introduction

Knowledge on the trophic ecology of marine organisms is essential for understanding their ecological role, the dietary relationships among species, and ultimately, the functioning of marine ecosystems (Braga et al., 2012; Brown et al., 2012). Empirical information on the trophic ecology of individual species is generally scarce or incomplete for many marine species and geographical areas (Dimarchopoulou et al., 2017). In addition, trophic data over different temporal and spatial scales provide comprehensive information on the diet variability (Fanelli et al., 2014; Reid et al., 2006) that is especially important for widely distributed species for which their functional role may differ depending on the habitat and region (Torres et al., 2015).

Blue whiting, *Micromesistius poutassou* (Risso, 1827), is a mesopelagic gadoid widely distributed in the North Atlantic and the Mediterranean Sea, inhabiting waters over the shelf edge and continental slope (Bailey, 1982; Heino et al., 2008). It is a species of commercial interest, exploited in the northern colder areas of the Mediterranean by bottom trawlers

(Martin et al., 2016) and also by pelagic trawlers in the Atlantic (Langøy et al., 2012; ICES, 2016). Despite its commercial significance, information on its biology and behavior is mostly restricted to the Atlantic waters. In the NW Mediterranean, blue whiting reproduces in winter (García et al., 1981; Serrat et al., 2019), when sea temperatures reach the minimum values (Calvo et al., 2011). Recent studies have reported that after the reproductive period, blue whiting increases its food intake allowing it to recover the energetic reserves invested in the reproduction and to start the fast growth season (Mir-Arguimbau et al., 2020).

Blue whiting plays a relevant role in the ecosystem as it is an important prey within three distinct food webs: deep demersal, shallow demersal, and pelagic (Silva et al., 1997). It is consumed by a wide range of predators, such as fish (*Merluccius*, *Lophius* spp. and *Scomber scombrus*) (Silva et al., 1997), sharks (*Squalus acanthias*), and flying squids (Bailey, 1982). As a consumer, blue whiting is considered a macro-planktivorous species feeding mainly on Euphausiacea and other pelagic decapods (Bachiller et al., 2016; Cabral and Murta, 2002; Dolgov et al., 2010; Keating et al., 2014; Langøy et al., 2012; Prokopchuk and Sentyabov,

^{*} Corresponding author.

E-mail address: joanmir@icm.csic.es (J. Mir-Arguimbau).

<https://doi.org/10.1016/j.dsr.2020.103404>

Received 19 April 2020; Received in revised form 22 September 2020; Accepted 22 September 2020

Available online 26 September 2020

0967-0637/© 2020 Elsevier Ltd. All rights reserved.

2006; Rault et al., 2017), although consumption of fish has also been reported in the Mediterranean (Macpherson, 1978; Papiol et al., 2014). Stomach content analysis (SCA) is the common methodology to infer diet, and it is very useful for determining the taxonomic identity of food web components (Choy et al., 2017). However, it provides a snapshot of an individual's recent diet, and the variability in the digestibility or assimilation of different prey items may lead to over- or under-estimations of the importance of a particular prey (Hyslop, 1980; Jackson et al., 1987). Stable isotope analysis (SIA) focuses on assimilated versus ingested prey material, providing a complementary method for investigating trophic relationships that integrates feeding across longer time scales, from weeks to months, depending on the tissue analyzed (Davis and Pineda-Munoz, 2016; Young et al., 2015). SIA is based on the fact that during the assimilation process, the lighter stable isotopes are preferentially excreted, meaning that consumers normally become isotopically enriched (heavy) relative to their prey (McCutchan et al., 2003), a phenomenon known as trophic discrimination. The stable isotopes of carbon (denoted as $\delta^{13}\text{C}$) and nitrogen (denoted as $\delta^{15}\text{N}$) are the most commonly used isotopes in trophic studies. $\delta^{13}\text{C}$ may vary substantially among primary producers and it is used as proxy of the main source of dietary carbon. $\delta^{15}\text{N}$ reflects stepwise enrichment with each trophic level and it is used as proxy of relative trophic position (Layman et al., 2012). Moreover, by combining stable isotope values from consumers with those from their potential prey, isotope mixing models can be applied to obtain estimates of the relative contribution of each prey item to the diet of the consumer (Parnell et al., 2013). Both approaches, conventional stomach content analysis and isotope analysis allow estimation of the trophic position of a species within the food web (Pauly and Palomares, 2000), which is a keystone in theoretical and applied ecology (Navarro et al., 2011; Post, 2002). The integration of diverse diet approaches provides new possibilities to understand complex trophic relationships in natural ecosystems, which are difficult to

untangle when using one single method (Nielsen et al., 2018).

Species investment of energy, either for growth or reproduction, changes seasonally, and along its life cycle. We hypothesized that the species food requirements will be met depending on prey type and abundance, which in turn will depend on variations in habitat and time of the year. The purpose of the present study was to investigate the trophic ecology of blue whiting in the NW Mediterranean in two different habitats, the shelf break and the slope, throughout the year, by combining two methodological approaches, stomach content and stable isotope analysis. The specific aims were i) to describe the diet at different temporal scales: in the short-term, through stomach content analysis, and in the long-term, by means of stable isotope analysis; ii) to analyze the trophic niche; and iii) to define the trophic position. This study provides detailed and updated knowledge on the trophic ecology of blue whiting in the Mediterranean that will allow a better understanding of its ecological role within the deep sea community.

2. Material and methods

2.1. Study area

The study was conducted in the NW Mediterranean, off Cap de Creus and Gulf of Roses (Fig. 1). The continental shelf width varies from ~2.6 km near the Cap de Creus canyon, to ~30 km in its wider part (Ribó et al., 2018). The bottom trawl fishing grounds encompass different habitats: the rather narrow continental shelf, the upper slope and the submarine canyon. In the NW Mediterranean, sea surface temperatures and primary production are characterized by a marked seasonal cycle. Water column seasonal stratification typically starts in spring around April, and it is not completely destroyed until late autumn (November–December) (Ribera d'Alcalà et al., 2004; Salat, 1996). The alternation of stratified and mixing periods confers strong seasonality to

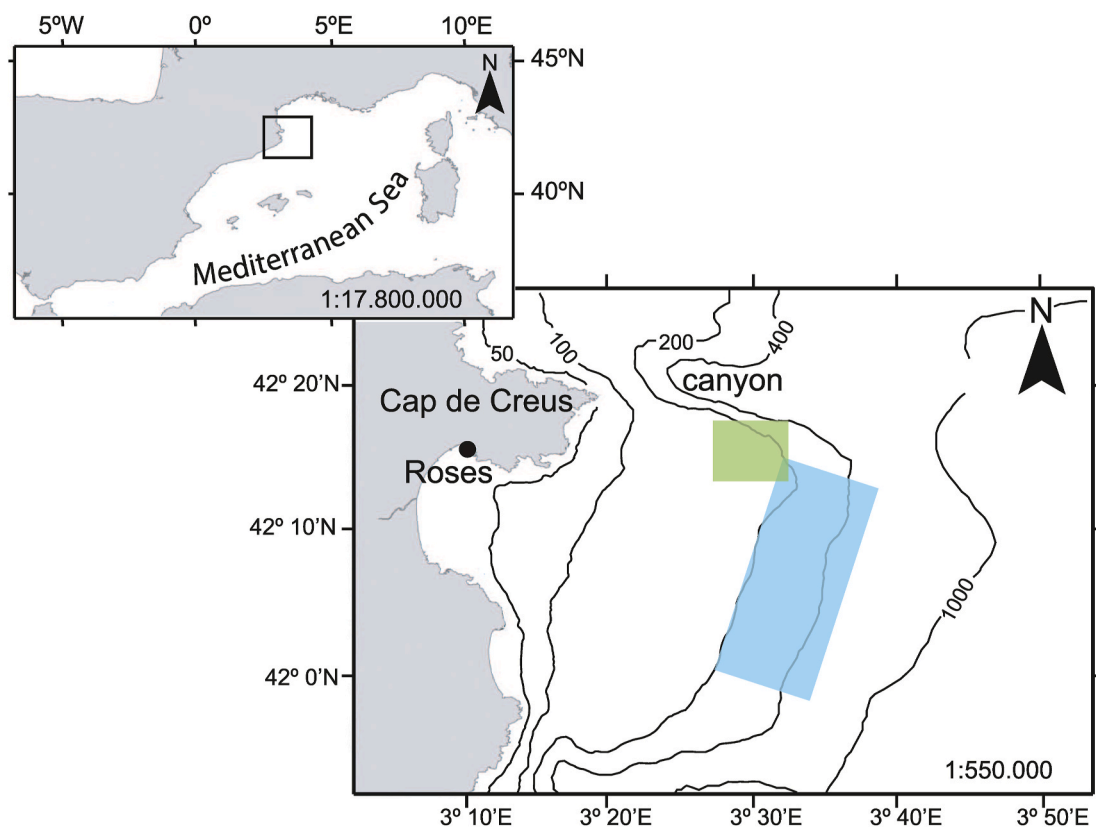


Fig. 1. Location of the study area. The green and blue boxes correspond to the shelf break and slope, respectively. The isobaths shown are 50, 100, 200, 400 and 1000 m. (For interpretation of the references to colour in this figure legend, the reader is referred to the Web version of this article.)

primary production. Plankton blooms occur typically at the end of winter, when surface waters begin to stabilize (Estrada et al., 1985; Saiz et al., 2014).

2.2. Field sampling and laboratory procedures

Blue whiting were collected on board a commercial bottom trawler based in the fishing port of Roses (Fig. 1). Two habitats were visited throughout the year, at the shelf break (130–200 m depth), and the upper slope (300–500 m depth, Fig. 1). Sampling was carried out on a monthly basis, from April 2017 to March 2018, except in February when a seasonal fishing closure was implemented in the study area. In total, 39 hauls were conducted (20 on the shelf break and 19 on the slope; Table S1) during day light hours, between 8 a.m. and 3 p.m. A total of 13,854 blue whiting individuals were measured to the nearest mm (total length, TL) to obtain the length frequency distribution over the sampling period in each habitat. From each haul, a subsample of ~25 individuals was placed in cooling containers on-board and transported to the laboratory for stomach content analysis. In addition, fish and crustacean species susceptible to be consumed by blue whiting were collected from the discarded fraction on board, placed immediately in cooling containers, and individually stored at -80°C in the laboratory for isotope analysis.

The diet of blue whiting was analyzed seasonally considering spring (April–June), summer (July–September), autumn (October–December) and winter (January and March). In the laboratory, between 10 and 15 individuals per month and habitat were selected for diet analyses. Total length (TL) was measured to the nearest mm, total weight (W) and eviscerated weight (We) to the nearest 0.1 g, and stomach weight (Ws) to the nearest 0.01 g. All stomachs were preserved in 5% formaldehyde buffered with sodium tetraborate solution.

To determine the potential effect of formalin preservation on the stomach content dry weight, 52 samples of unpreserved stomach contents from fresh individuals were weighed (wet weight) immediately after dissection and, after 24–48 h at 60°C , the dry weight was recorded to the nearest 0.001 mg. At the same time, 48 samples of stomach contents were weighed (wet weight) and preserved in buffered formalin. Four months later (the average time between the preservation and analysis of gut contents), the stomach contents were rinsed with distilled water and weighed after 24–48 h at 60°C (dry weight to the nearest 0.001 mg). No significant differences were found between preserved and unpreserved gut contents in the wet weight – dry weight relationships (unpreserved: Pearson correlation tests; $R = 0.97$, $p < 0.05$, $N = 52$; Formalin preserved: Pearson $R = 0.93$, $p < 0.05$, $N = 49$; t observed $< t$ tabulated 95%; $t_{\text{obs}} = 0.06$).

2.3. Stomach content analyses

Between 10 and 15 individuals per month and habitat were analyzed for SCA (Table S1). Stomach contents were examined under a binocular stereomicroscope (500x). Prey items were identified to the lowest possible taxonomic level, counted and pooled by taxonomic category. Prey groups were rinsed with distilled water and weighed after 24–48 h at 60°C (dry weight to the nearest 0.001 mg, Wd).

The feeding incidence (FI, the proportion of fish with prey in their guts) and the stomach fullness (F) ($F = 100 \cdot (Ws/We)$), an estimator of the feeding intensity that excludes the effect of the fish size (Hyslop, 1980), were calculated as a proxy of the feeding intensity. The Shannon index of diversity (H') was calculated for each season and habitat as:

$$H' = - \sum_{i=1}^r p_i \cdot \ln p_i \quad (1)$$

where p_i is the proportion of prey found in the studied group. The Fulton's condition factor (CF) ($CF = (We/TL^3) \cdot 100$) was determined as a proxy of fish condition and averaged by habitat and season.

The importance of each prey in the diet of blue whiting was described based on different trophic indexes calculated with the non-empty stomachs, including the percentage of numerical abundance (%N), the percentage of frequency of occurrence (%FO), the gravimetric percentage (%W), the Index of Relative Importance (IRI) expressed in percentage (%IRI) (Hyslop, 1980). IRI for each prey category was calculated following the equation:

$$IRI_i = FO_i(W_i + N_i) \quad (2)$$

Furthermore, %PSIRI (Brown et al., 2012) was calculated following the equation:

$$\%PSIRI_i = \frac{\%FO_i \cdot (\%PN_i + \%PW_i)}{2} \quad (3)$$

Where %PNi is the prey specific abundance in number, and %PWi is the prey specific abundance in weight. The prey specific abundance is defined as:

$$\%PA_i = \frac{\sum_{j=1}^n \%A_{ij}}{ni} \quad (4)$$

where %A_{ij} is the abundance (by counts or weights) of prey category i in stomach sample j , ni is the number of stomachs containing prey i , and n is the total number of stomachs.

Differences in stomach contents (based on Wd) between habitats (shelf break vs. slope) and seasons (spring, summer, autumn and winter) were compared using 2-way semi-parametric permutational multivariate analyses of variance (PERMANOVA) based on a Bray-Curtis distance matrix (Anderson et al., 2008) on square root-transformed biomass (Wd) data. Wd was used because this trophic index has been suggested as the best proxy of the energy provided by a prey to a predator (Tyler, 1972). For the analyses the most important taxa were considered (higher than 10% in %W in one season) and all the other taxa were grouped as "other groups". Factors (season and habitats) were crossed and factor levels were fixed. Significance was set at $P = 0.05$; P -values were obtained using 999 permutations of residuals under a reduced model (Anderson, 2001). When significant differences were detected, pairwise tests were performed. To analyze the average dissimilarity between habitats at each season and to identify which prey made the greatest contribution to the observed differences in diet composition, an analysis of similarity percentages (SIMPER) was performed (Clarke and Gorley, 2006). PERMANOVA test and SIMPER were conducted with PRIMER-E 6 & PERMANOVA + software (Clarke and Gorley, 2006).

Relationships between fish size and prey number, stomach content dry weight, and F were explored through Pearson correlation tests. Seasonal and spatial differences in F, FI and prey number were tested with the Man Whitney U test and Kruskal-Wallis One Way Analysis of Variance on Ranks in Sigma Plot.

2.4. Stable isotope analyses

Stable isotopes of carbon ($\delta^{13}\text{C}$) and nitrogen ($\delta^{15}\text{N}$) were analyzed in the muscle of 77 blue whiting individuals (~10 individuals per habitat and season; Table S1). Whenever possible, isotope analyses were performed on the same individuals considered for stomach content analyses or, otherwise, collected in the same hauls. Stable isotopes were also analyzed on the blue whiting main prey, based on SCA, including fish (*Benthosema glaciale*, *Ceratoscopelus maderensis*, *Lampanyctus* spp.), and crustaceans (*Gennadas elegans*, Euphausiacea order, Sergestidae family, *Solenocera membranacea*) (Table S2). Also, pools of Salpidae family and *Pyrosoma atlanticum* collected during the sampling were analyzed as isotopic baseline values. Isotope analyses were carried out at the Laboratorio de Isótopos Estables de the Estación Biológica de Doñana (LIE-EBD, Spain; www.ebd.csic.es/lie/index.html). All tissues were freeze-dried and powdered, and 0.28–0.33 mg of the powdered tissue was packed into tin capsules. Samples were combusted at 1020°C using a

continuous flow isotope-ratio mass spectrometry system by means of Flash HT Plus elemental analyzer coupled to a Delta-V Advantage isotope ratio mass spectrometer via a CONFLO IV interface (Thermo Fisher Scientific, Bremen, Germany). The isotopic composition was reported in the conventional delta (δ) per mil notation (‰), relative to Vienna Pee Dee Belemnite ($\delta^{13}\text{C}$) and atmospheric N_2 ($\delta^{15}\text{N}$). The analytical measurement error was $\pm 0.1\text{‰}$ and $\pm 0.2\text{‰}$ for $\delta^{13}\text{C}$ and $\delta^{15}\text{N}$, respectively. The standards used were: EBD-23 (cow horn, internal standard), LiE-BB (whale baleen, internal standard) and LiE-PA (feathers of Razorbill, internal standard). Laboratory standards were previously calibrated with international standards supplied by the International Atomic Energy Agency (IAEA, Vienna). Before statistical comparisons, $\delta^{13}\text{C}$ values of samples with a C:N ratio of >3.5 were lipid-corrected following Logan et al. (2008). The C:N relation was used as a proxy of blue whiting condition (Dempson et al., 2010; Schmidt et al., 2003), and differences in C:N between seasons and habitat were tested using ANOVA.

Differences in $\delta^{15}\text{N}$ and $\delta^{13}\text{C}$ values between seasons and habitats were tested using a 2-way semi-parametric PERMANOVA based on a Euclidean distance matrix (Anderson et al., 2008) using PRIMER-E 6&PERMANOVA + software (Clarke and Gorley, 2006). To provide insight into species trophic niche widths, and to assess the degree of isotopic niche overlap between habitats and seasons, we calculated Bayesian isotopic standard ellipse areas corrected for sample size (SEAc) (Jackson et al., 2011). SEAc and their overlap were calculated using the routine Stable Isotope Bayesian Ellipses in the SIAR library in R3.6.0 (R Core Team, 2018; Jackson et al., 2011).

To estimate the contribution of the different potential prey types to the diet of blue whiting in each season and habitat, we adopted a Bayesian stable isotope mixing model (MixSIAR, Stock and Semmens, 2013). Prey were grouped into functional groups (filter feeders, Myctophidae fish family, pelagic shrimps, benthic shrimps and Euphausiacea). As the isotopic signal of filter feeders showed seasonal variation (see Table S2) this variation was considered for the MixSIAR. All the

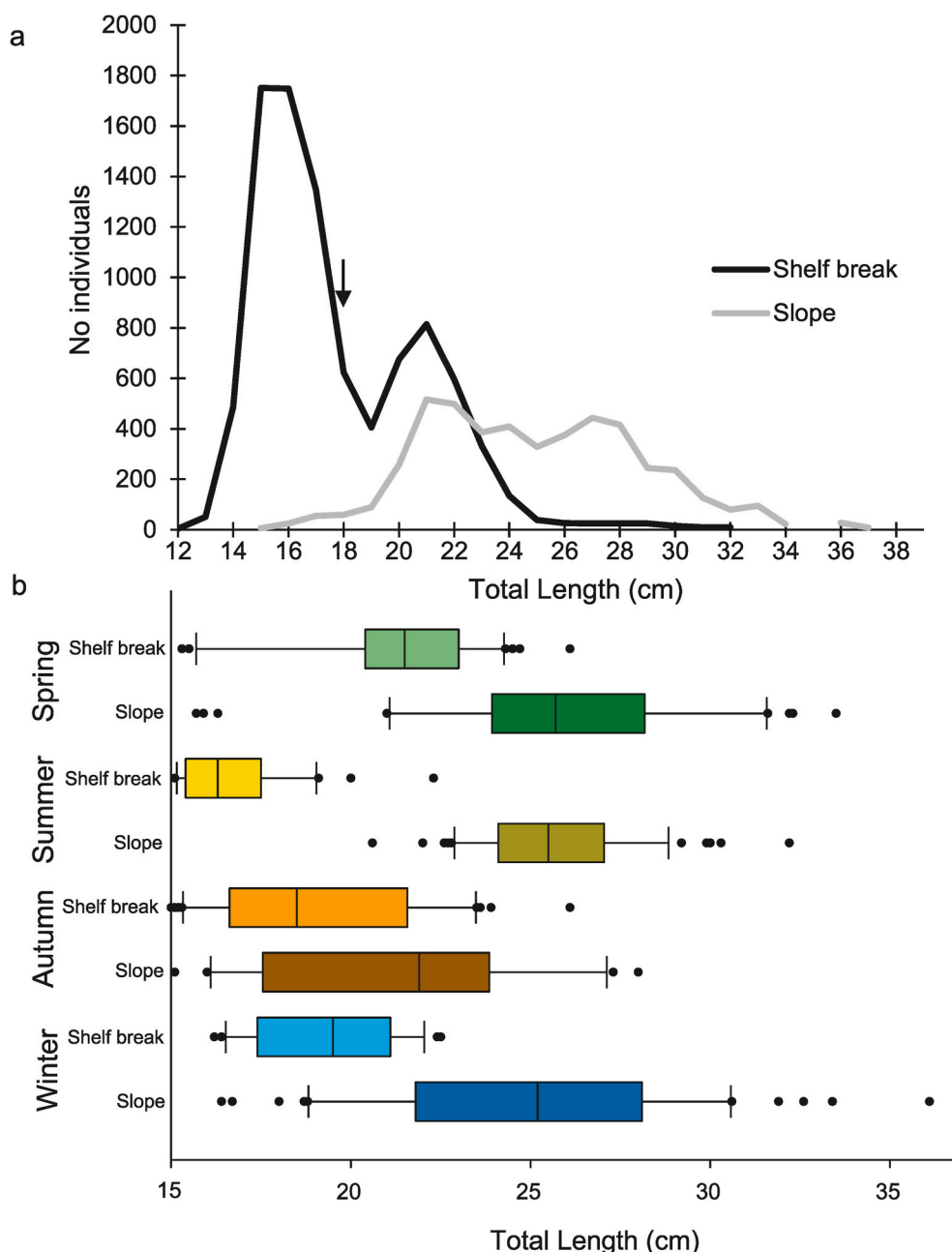


Fig. 2. a) Length frequency distribution of blue whiting collected in the shelf break and over the slope during the sampling period (April 17- March 18). The arrow indicates the size at first maturity of the species reported in Mir-Arguimbau et al. (2020). b) Total length of blue whiting individuals analyzed for the stomach content analyses, by season and habitat (shelf break and slope). Box length represents interquartile range (25th to 75th percentiles), bar length represents size range (10th and 90th percentiles) and vertical lines inside the boxes represent median values. The black circles indicate the values under 10th and above 90th percentile. (For interpretation of the references to colour in this figure legend, the reader is referred to the Web version of this article.)

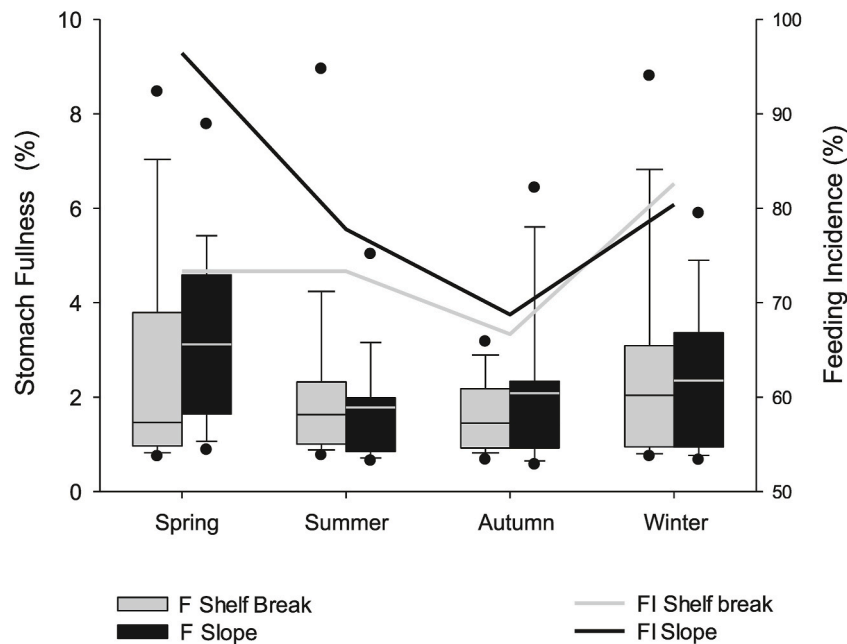


Fig. 3. Stomach Fullness Index (box-plots) and Feeding incidence (lines) for individuals over the shelf break (grey) and slope (black), by season. Box length represents interquartile range (25th to 75th percentiles), bar length represents 10th–90th percentiles and vertical line within the boxes represents median values. The black circles indicate 5th and 95th percentile.

isotopic values of the different functional groups are shown in Table S2. MixSIAR models were fitted with diet-to-tissue discrimination factors of $1.3 \pm 0.1\%$ for C and $3.35 \pm 0.2\%$ for N, according to Caut et al. (2009), to obtain adequate discrimination factors. MixSIAR was run with three MCMC chains, and a burn-in of 300,000 draws, followed by 200,000 draws to calculate the posterior distribution to compute credible Bayesian intervals. To provide a quantitative basis for model acceptance or rejection, a mixing polygon simulation was constructed based on a frequentist probability that allows knowing whether the proposed mixing model can correctly estimate sources contribution to the consumer's isotopic value (Smith et al., 2013).

2.5. Trophic position based on stomach content and stable isotope values

The trophic position (TP) of blue whiting in the food web was estimated through stomach content (TP_{sca}) and stable isotope analysis (TP_{sia}). TP of aquatic consumers can take any value between 2.0, for herbivorous/detritivorous, and 5.0, for piscivorous/carnivorous organisms (Pauly et al., 1998).

TP_{sca} of blue whiting was estimated for each season and habitat, based on the %W of each prey item in their diet, using the following equation (Cortés, 1999):

$$TP_i = 1 + \sum_{j=1}^G DC_{ij} * TP_j \quad (5)$$

where TP_j is the fractional trophic position of prey (j), P_{ij} represents the fraction of prey j in the diet of i and G is the total number of prey species. The TP_j used are shown in Table S3.

To estimate the TP_{sia} of each individual we used the equation proposed by Zanden and Rasmussen (2001):

$$TP_{\text{consumers}} = TP_{\text{basal}} + (\delta^{15}\text{N}_{\text{consumer}} - \delta^{15}\text{N}_{\text{basal}}) / \Delta\delta^{15}\text{N} \quad (6)$$

Where $\delta^{15}\text{N}_{\text{consumers}}$ was the $\delta^{15}\text{N}$ values of blue whiting and $\delta^{15}\text{N}_{\text{basal}}$ was $\delta^{15}\text{N}$ values of filter feeders (Table S2). We applied a basal trophic position (TP_{basal}) of 2 assuming that filter feeders are typically primary consumers (Ménard et al., 2014; Cherel et al., 2010; Fanelli and Cartes, 2010). The discrimination factor used ($\Delta\delta^{15}\text{N}$) was the one calculated for the MixSIAR.

3. Results

The length frequency distribution showed that smaller blue whiting (<19 cm) were more abundant over the shelf break whereas larger fish (>22 cm) were generally found on the slope (Fig. 2), although some size overlap was observed.

3.1. Stomach content analyses

The size of the individuals used for the SCA, collected in each season, reflected the segregation by size in the two habitats. This was more evident in summer, while size overlapping was highest in autumn, when the largest individuals were not observed (Fig. 2b). A positive relationship was found between fish size and stomach content dry weight (Pearson Correlation test; $r = 0.36$; $p < 0.05$; $n = 238$) and between fish size and number of prey ($r = 0.28$; $p < 0.05$; $n = 238$). However, no significant relationship was found between fish size and stomach fullness F ($r = 0.05$, $p > 0.05$, $n = 295$).

A total of 306 individuals were examined for stomach content analyses, 1173 prey items were counted and 32 taxa were identified. All seasons and habitats combined, feeding incidence, FI, was 76.52%. Within seasons, FI was similar in the two habitats, although seasonal differences were observed, with minimum FI values in autumn (66.7% and 68.8% on the shelf break and the slope, respectively) and maximum FI in spring (96.4% on the slope) and winter (82.6% on the shelf break and 80% on the slope) (Fig. 3; Table S4). Stomach content (dry weight) was, in all four seasons, higher in the slope than in the shelf break, although in autumn and winter differences were not significant. The highest stomach content values along the year were attained in spring in both habitats. The maximum stomach fullness index was attained in spring over the slope; significant differences between habitats were observed in spring and summer (Table S4). According to the Shannon diversity index, H', prey diversity exhibited the lowest values in winter ($H' = 1.6$), both over the shelf break and the slope. Prey diversity during the rest of the year was similar ($H' > 2$), except in autumn over the slope ($H' = 1.8$) (Table S4). Fulton's Condition Factor showed maximum values in spring in both habitats. Over the shelf break a significant decrease in condition was observed from spring to summer, remaining

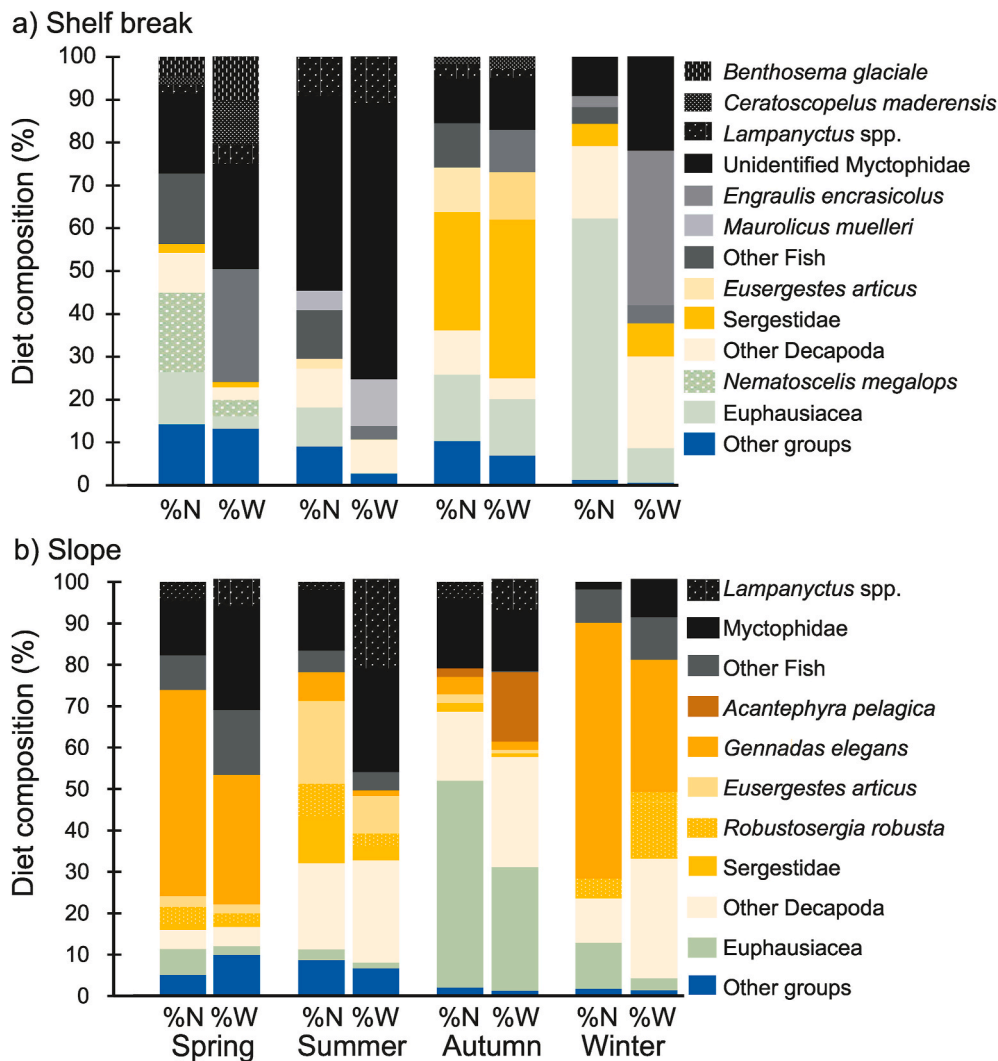


Fig. 4. Diet composition of blue whiting in number (%N) and weight (%W) for each season for individuals from the shelf break (a) and individuals from the slope (b). Only taxa with more than 10% in %N or in %W have been considered. (For interpretation of the references to colour in this figure legend, the reader is referred to the Web version of this article.)

similar from summer to winter, while over the slope the condition decreased from spring to winter (Fig. S1, Table S5).

Blue whiting mainly feeds on myctophid fishes, Decapoda (such as *Gennadas elegans* and Sergestidae shrimps) and Euphausiacea (Table S6), although significant differences in the diet composition were found among habitats, seasons, and their interaction (Table S7). Pair-wise comparison tests showed significant differences between habitats in all seasons ($p < 0.001$) (see Table S8). Furthermore, significant differences were found between seasons at the habitat level (Table S9), except when comparing autumn and winter over the shelf break ($t = 1.18$, $p = 0.2$) (Table S9a), and summer and autumn on the slope ($t = 1.32$, $p = 0.1$) (Table S9b). SIMPER analysis showed that Decapoda (notably the species *Gennadas elegans* and the Sergestidae), and the myctophid fishes, were the main groups that explained the dissimilarity between habitats at each season (Table S10).

Generally, fishes were the dominant prey in the blue whiting diet on the shelf break, with much lower importance on the slope, where pelagic crustaceans predominate. In particular, on the shelf break the most important prey in spring and summer were mesopelagic fish, mainly Myctophidae, attaining values around 50 %N and 80% W (Fig. 4a; Table 1). Within the Myctophidae, *Benthoosema glaciale* and *Ceratoscopelus maderensis* were the most important preys in spring (10.4% W and 10% W, respectively) and *Lampanyctus* spp. in summer (10.8% W). In

autumn crustacean Sergestidae became the most important prey (37.9 % N and 48.3 %W). In winter, while Euphausiacea (58.4 %N) were the most abundant prey in number, anchovy, *Engraulis encrasicolus*, was the dominant prey in weight (36.2% W), although it appeared in a small number of individuals (10.6 %O) (Table 1).

As for blue whiting inhabiting the slope, pelagic crustaceans were the main prey throughout the year (>60 %N and >50 %W), and in spring and summer mesopelagic fish were also relatively important (~20 %N and 50 %W) (Fig. 4b). Regarding pelagic crustaceans, *Gennadas elegans* was the dominant prey in winter (61.8 %N, 31.8 %W) and in spring (49.8 %N and 31.8 %W) (Table 2). In summer Sergestidae became the most important prey (39.1 %N and 15.5 %W) as well as other Decapoda (16.7 %N and 26.5 %W) that included the Pasiphaeidae, Pandalidae and Processidae families. In autumn, Euphausiacea was the dominant prey (50 %N, 29.8 %W), while other Decapoda (26.5 %W) and *Acantheephyra pelagica* (16.8 %W) were also important in %W (Table 2).

3.2. Stable isotope analyses

Blue whiting isotopic values ranged between -18.92‰ and -19.82‰ for $\delta^{13}\text{C}$, and between 8.28‰ and 9.54‰ for $\delta^{15}\text{N}$ (Table 3), and significant differences were observed between seasons and habitats (pseudo- $F_{2,715} = 5.74$, $p < 0.001$). Individuals from the shelf break

Table 1

Diet composition of blue whiting over the Shelf break. Numerical percentage (%N), percentage of frequency of occurrence (%FO), gravimetric percentage (%W), percentage of Relative Importance Index (%IRI) and percentage of Prey-specific index of relative importance (%PSIRI) for each season.

Shelf break			Spring					Summer					Autumn					Winter				
			%N	%O	%W	%IRI	%PSIRI	%N	%O	%W	%IRI	%PSIRI	%N	%O	%W	%IRI	%PSIRI	%N	%O	%W	%IRI	%PSIRI
Pisces																						
Actinopterygii																						
	Sternoptychidae	<i>Argyropelecus hemigymnus</i>																				
		<i>Maurolicus muelleri</i>						4.5	4.0	10.9	1.0	7.7										
	Stomiidae	<i>Chauliodus sloani</i>																				
	Gonostomatidae	<i>Cyclothone</i> spp.																				
	Engraulidae	<i>Engraulis encrasicolus</i>																2.6	10.5	36.2	9.1	19.4
	Gadidae																					
	Myctophidae	<i>Benthoema glaciale</i>	4.3	12.1	10.4	4.0	7.4															
		<i>Ceratoscopelus maderensis</i>	2.1	6.1	10.0	1.7	6.1						1.7	3.7	2.8	0.5	2.3					
		<i>Diaphus holti</i>	0.7	3.0	1.5	0.1	1.1															
		<i>Lampanyctus crocodilus</i>	0.7	3.0	3.2	0.3	2.0						3.4	3.7	2.2	0.6	2.8					
		<i>Lampanyctus pusillus</i>	1.4	6.1	1.5	0.4	1.4	6.8	8.0	10.1	2.1	8.5										
		<i>Lampanyctus</i> spp.						2.3	4.0	0.7	0.2	1.5										
		<i>Notoscopelus elongatus</i>																				
	Unidentified		17.9	36.4	23.1	33.7	20.5	45.5	52.0	64.7	90.1	55.1	10.3	22.2	12.1	14.5	11.2	9.1	26.3	22.0	18.4	15.6
	Myctophidae																					
	Unidentified fish		12.9	33.3	18.6	23.8	15.8	2.3	4.0	0.6	0.2	1.4	10.3	18.5	9.9	10.9	10.1	2.6	5.3	4.0	0.8	3.3
	Fish remains		3.6	15.2	7.8	3.9	5.7	9.1	16.0	2.6	2.9	5.9						1.3	5.3	0.3	0.2	0.8
Crustaceans																						
	Euphausiacea																					
	Unidentified	<i>Meganyctiphanes norvegica</i>	2.9	9.1	1.6	0.9	2.2						8.6	11.1	9.7	5.9	9.1	1.3	5.3	1.6	0.3	1.5
	Euphausiacea	<i>Nematoscelis megalops</i>	18.6	9.1	3.7	4.6	11.2															
		<i>Nyctiphanes couchii</i>																1.3	5.3	1.7	0.4	1.5
			9.3	15.2	1.3	3.6	5.3	9.1	4.0	0.2	0.6	4.6	6.9	11.1	3.5	3.4	5.2	58.4	36.8	4.7	52.2	31.6
Decapoda																						
	Acanthephyridae	<i>Acanthephyra pelagica</i>																				
	Axiidae	<i>Calocaris macandreae</i>																				
	Benthescymidae	<i>Gennadas elegans</i>											3.4	3.7	2.4	0.6	2.9	2.6	10.5	0.7	0.8	1.6
	Pasiphaeidae	<i>Pasiphaea multidentata</i>						2.3	4.0	6.4	0.5	4.3										
		<i>Pasiphaea sivado</i>																1.3	5.3	0.2	0.2	0.7
		<i>Pasiphaea</i> spp.																				
	Pandalidae	<i>Plesionika antgai</i>																				
		<i>Plesionika edwardsii</i>																				
		<i>Plesionika martia</i>																				
		<i>Plesionika</i> spp.																				
	Processidae	<i>Processa acutirostris</i>																				
	Sergestidae	<i>Eusergestes arcticus</i>						2.3	4.0	0.1	0.1	1.2	10.3	11.1	11.1	6.9	10.7					
		<i>Deosergestes corniculum</i>																1.3	5.3	3.6	0.6	2.4
		<i>Robustosergia robusta</i>	0.7	3.0	0.1	0.1	0.4															
		Unidentified	1.4	6.1	1.2	0.4	1.3						27.6	25.9	37.2	48.8	32.4	3.9	10.5	3.4	1.7	3.7
	Solenoceridae	<i>Solenocera membranacea</i>	0.0	0.0	0.0	0.0	0.0											1.3	5.3	8.1	1.1	4.7

(continued on next page)

Table 1 (continued)

Shelf break	Spring						Summer						Autumn						Winter					
	%N	%O	%W	IRI	%	PSIRI	%N	%O	%W	IRI	%	PSIRI	%N	%O	%W	IRI	%	PSIRI	%N	%O	%W	IRI	%	PSIRI
Unidentified shrimp	8.6	21.2	2.8	5.5	5.7		6.8	8.0	1.3	1.0	4.0		5.2	11.1	2.3	2.4	3.7		10.4	26.3	13.2	13.9	11.8	
Decapoda remains	0.7	3.0	0.2	0.1	0.5								1.7	3.7	0.2	0.2	0.9		1.3	5.3	0.0	0.2	0.7	
Amphipoda																								
Crustacean remains	7.1	30.3	4.4	7.9	5.8		2.3	4.0	0.1	0.1	1.2		6.9	14.8	3.7	4.6	5.3							
Mollusca							4.5	8.0	2.2	0.9	3.4													
Cephalopoda																								
<i>Histioteuthis reversa</i>																								
Cephalopoda beak	0.7	3.0	0.2	0.1	0.5		2.3	4.0	0.1	0.1	1.2		1.7	3.7	1.1	0.3	1.4		1.3	5.3	0.3	0.2	0.8	
Gelatinous remains																								
Unidentified remains	6.4	27.3	8.4	9.1	7.4								1.7	3.7	2.0	0.4	1.8							

showed minimum $\delta^{13}\text{C}$ isotope values in summer (-19.82 ± 0.14) and the highest in winter (-18.92 ± 0.25), while the $\delta^{15}\text{N}$ values increased from 8.28 ± 0.36 in spring to 9.54 ± 0.69 in winter (Table 3). However, no differences were observed among seasons for individuals from the slope (Table 3, Table S11). Differences between habitats were observed in each season, except in winter. Overall, $\delta^{15}\text{N}$ values were always lower over the shelf break while $\delta^{13}\text{C}$ values were similar in both areas except in summer, when they were lower over the shelf break ($\delta^{13}\text{C} = -19.82 \pm 0.14\text{‰}$ and $\delta^{13}\text{C} = -19.06 \pm 0.27\text{‰}$ over the shelf break and slope respectively) (Table 3; Table S11). The ratio C:N was always around 3.2 and no statistical differences between habitats and seasons were observed (Table 3).

In all seasons, trophic niche width of blue whiting from the slope was wider than that of the individuals from the shelf break according to the Bayesian isotopic ellipses areas (Fig. 5; Table 3). In spring and summer, there was no overlap between isotopic niches of the two habitats. In autumn, the isotopic niches partially overlapped (55% and 16% for individuals of the shelf break and slope, respectively), and in winter the overlap was the highest (99% and 27% for the shelf break and the slope, respectively). It is worth noting that the overlap, when exists, always represented a higher proportion of the SEAc for individuals of the shelf break due to its smaller trophic niche width.

The mixing polygon simulation allowed accepting and validating the MixSIAR models, since the blue whiting individuals values fell inside the 95% mixing region in all seasons (Fig. 6). MixSIAR outputs showed that myctophid fishes were the main contributor to the blue whiting diet in the shelf break in autumn and winter (77.6% and 76.7%, respectively), while in spring and summer, in addition to Myctophidae (47.7% and 35.4% respectively), filter feeders were also relatively important (39.8% in spring and 52.1% in summer). However, for blue whiting on the slope, Myctophidae were the main prey throughout the year (70.8% in spring, 69.4% in summer, 82.8% in autumn and 80.6% in winter) (Fig. 6). Other prey, such as pelagic shrimps and Euphausiacea, showed a low contribution to the diet, with values always lower than 15% in both habitats.

3.3. Trophic position

The average TP_{sca} considering all seasons and habitats was 4.11 ± 0.07 . The highest TP_{sca} values corresponded to winter (4.22) and the lowest to autumn (4.03) (Table 4).

The TP_{sia} was similar in the shelf break (mean TL_{sia} = 3.94) and as in the slope (mean TL_{sia} = 4.05). Seasonally, TP_{sia} increased throughout the year in both habitats, with the lowest value in spring (3.41) and the highest in winter (TL_{sia} = 5.08).

4. Discussion

This study provides new trophic information of blue whiting in the Mediterranean, and highlights differences throughout the year between individuals living in two close areas, the shelf break and the slope. An increase in blue whiting size with depth was observed, with a certain overlap between the two habitats. This pattern had been previously reported in the north Atlantic, where larger blue whiting individuals tend to be in deeper areas (Bailey, 1982). Taking into account that in the study area the size at first maturity for this species has been established at around 18 cm TL (Mir-Arguimbau et al., 2020; Serrat et al., 2019), blue whiting over the shelf break would mainly correspond to immature individuals, and over the continental slope, to adults.

Throughout the year, feeding indicators (FI and stomach content Wd) attained the highest values in spring. This seasonal pattern has already been reported for other species in the western Mediterranean, such as hake, and has been related to the high availability of prey one month after the peak of primary production (Cartes et al., 2009, 2004). Conversely, the low values of feeding indicators and stomach fullness (F) in summer, and especially in autumn, suggest potential food limitation in this period. Regarding habitats, feeding indicators were higher in

Table 2

Diet composition of blue whiting over the Slope. Numerical percentage (%N), percentage of frequency of occurrence (%FO), gravimetric percentage (%W), percentage of Relative Importance Index (%IRI) and percentage of Prey-specific index of relative importance (%PSIRI) for each season. for each season.

Slope			Spring					Summer					Autumn					Winter				
			%N	%O	%W	% IRI	% PSIRI	%N	%O	%W	% IRI	% PSIRI	%N	%O	%W	% IRI	% PSIRI	%N	%O	%W	% IRI	% PSIRI
Pisces																						
Actinopterygii																						
	Sternoptychidae	<i>Argyropelecus hemigymnus</i>																0.4	2.4	0.7	0.1	0.6
		<i>Maurolicus muelleri</i>	0.2	2.6	1.8	0.1	1.0															
	Stomiidae	<i>Chauliodus sloani</i>																0.4	2.4	3.4	0.2	1.9
	Gonostomatidae	<i>Cyclothone</i> spp.	0.2	2.6	0.1	0.0	0.2											5.8	2.4	0.7	0.3	3.3
	Engraulidae	<i>Engraulis encrasicolus</i>	0.2	2.6	1.1	0.0	0.7											0.4	2.4	3.5	0.2	2.0
	Gadidae		0.2	2.6	1.1	0.0	0.7															
	Myctophidae	<i>Benthosema glaciale</i>	2.2	17.9	7.5	2.0	4.9	0.9	2.8	2.6	0.4	1.8						0.4	2.4	0.3	0.0	0.4
		<i>Ceratoscopelus maderensis</i>	0.9	7.7	2.1	0.3	1.5	0.9	2.8	2.1	0.4	1.5						0.4	2.4	2.9	0.1	1.7
		<i>Diaphus holti</i>																				
		<i>Lampanyctus crocodilus</i>	0.9	7.7	0.9	0.2	0.9															
		<i>Lampanyctus pusillus</i>	2.6	12.8	5.1	1.1	3.9						2.1	6.7	2.1	0.7	2.1					
		<i>Lampanyctus</i> spp.	1.1	5.1	0.5	0.1	0.8	1.7	2.8	21.5	2.9	11.6	2.1	6.7	5.3	1.3	3.7					
		<i>Notoscopelus elongatus</i>	0.2	2.6	0	0.0	0.1															
		Unidentified	9.9	33.3	15.4	9.7	12.7	13	11.1	20.3	16.7	16.7	16.7	53.3	14.8	44.2	15.8	0.9	4.9	6	0.6	3.5
	Myctophidae																					
	Unidentified fish		6	38.5	9	6.6	7.5	0.9	2.8	1.2	0.3	1.1						0.4	2.4	1.9	0.1	1.2
	Fish remains		1.5	17.9	2.5	0.8	2.0	4.3	13.9	3.2	4.7	3.8	0	6.7	0.2	0.0	0.1	0.4	2.4	0.1	0.0	0.3
Crustaceans																						
Euphausiacea																						
		<i>Meganyctiphanes norvegica</i>	2.6	17.9	1.3	0.8	2.0											0.4	2.4	0.3	0.0	0.4
		<i>Nematoscelis megalops</i>	1.1	5.1	0.4	0.1	0.8											3.6	2.4	0.5	0.2	2.1
		<i>Nyctiphanes couchii</i>											4.2	6.7	1.9	1.1	3.1					
	Unidentified Euphausiacea		2.6	10.3	0.4	0.4	1.5	2.6	8.3	1.4	1.5	2.0	45.8	13.3	27.9	25.9	36.9	7.1	7.3	2	1.2	4.6
Decapoda																						
	Acanthephyridae	<i>Acanthephyra pelagica</i>											2.1	6.7	16.8	3.3	9.5					
	Axiidae	<i>Calocaris macandreae</i>	0.2	2.6	0.1	0.0	0.2															
	Benthescymidae	<i>Gennadas elegans</i>	49.8	74.4	31.3	69.3	40.6	7	13.9	1.4	5.2	4.2	4.2	13.3	1.9	2.1	3.1	61.8	51.2	31.8	83.1	46.8
	Pasiphaeidae	<i>Pasiphaea multidentata</i>	0.2	2.6	0.2	0.0	0.2	1.7	2.8	4.5	0.8	3.1										
		<i>Pasiphaea sivado</i>	1.5	7.7	0.7	0.2	1.1						4.2	6.7	4.7	1.6	4.5	0.4	2.4	1.7	0.1	1.1
		<i>Pasiphaea</i> spp.						7	13.9	8.4	9.6	7.7						1.3	7.3	3	0.6	2.2
	Pandalidae	<i>Plesionika antgai</i>																0.4	2.4	2.9	0.1	1.7
		<i>Plesionika edwardsii</i>	0.4	5.1	0.4	0.1	0.4															
		<i>Plesionika martia</i>	0.2	2.6	0.2	0.0	0.2															
		<i>Plesionika</i> spp.	0.2	2.6	0.1	0.0	0.2	1.7	2.8	0.9	0.3	1.3						0.4	2.4	1.8	0.1	1.1
	Processidae	<i>Processa acutirostris</i>						0.9	2.8	1.3	0.3	1.1										
	Sergestidae	<i>Eusergestes arcticus</i>	2.6	25.6	2.1	1.4	2.4	20	22.2	9	29.0	14.5	2.1	6.7	0.9	0.5	1.5					
		<i>Deosergestes corniculum</i>																0.4	2.4	0.4	0.0	0.4
		<i>Robustosergia robusta</i>	4.1	20.5	2.5	1.5	3.3	7.8	11.1	3.1	5.4	5.5						4.4	14.6	15.8	5.1	10.1
		Unidentified	1.5	10.3	0.8	0.3	1.2	11.3	8.3	3.4	5.5	7.4	2.1	6.7	0.8	0.5	1.5					
	Sergestidae																					
	Solenoceridae	<i>Solenocera membranacea</i>																				
		Unidentified shrimp	1.3	7.7	1.9	0.3	1.6	7	11.1	5	6.0	6.0	12.5	20	21.8	18.1	17.2	5.3	17.1	15.4	6.1	10.4
	Decapoda remains		0.4	5.1	1	0.1	0.7	2.6	8.4	4.5	1.3	3.6						2.7	14.6	4	1.7	3.4

(continued on next page)

Table 2 (continued)

Slope	Spring						Summer						Autumn						Winter					
	%N	%O	%W	IRI	%	PSIRI	%N	%O	%W	IRI	%	PSIRI	%N	%O	%W	IRI	%	PSIRI	%N	%O	%W	IRI	%	PSIRI
Amphipoda	2.2	20.5	3.8	1.4	3.0	3.0	5.2	16.7	4.2	7.1	4.7	4.7	2.1	6.7	0.8	0.5	1.5	1.5	0.4	2.4	0.1	0.0	0.3	0.3
Crustacean remains																								
Mollusca	0.2	0	0	0.0	0.0	0.0													0.9	4.9	0.8	0.1	0.9	0.9
Cephalopoda																								
<i>Histioteuthis reversa</i>																								
Cephalopoda beak																								
Gelatinous remains	2.8	33.3	5.6	3.22	4.2	4.2	3.5	11.1	2	2.72	2.75	2.75							0.4	2.4	0.1	0.02	0.25	0.25
Unidentified remains																								

individuals over the slope in spring and summer. Considering the observed segregation by size in these seasons, these differences are in line with the positive relation between blue whiting size and feeding indicators reported by [Bachiller et al. \(2016\)](#) in the Atlantic. These authors related their results with a higher success in predation upon large prey with increasing blue whiting length.

The diet of blue whiting consisted mainly of mesopelagic organisms. Although some benthic species were identified in the stomach contents, their frequency of occurrence was quite low. Overall, blue whiting feeds on mesopelagic fish, pelagic Decapoda, and Euphausiacea, as previously reported in the NW Mediterranean ([Macpherson, 1978](#); [Papiol et al., 2014](#)), and no evidence of cannibalism was detected, as also pointed out in other studies conducted in the N Atlantic and the Mediterranean ([Bailey, 1982](#); [Macpherson, 1978](#); [Plekhanova and Soboleva, 1982](#)). In contrast to the Atlantic, where mesozooplankton constitutes an important part of the blue whiting diet (e.g. [Langøy et al., 2012](#); [Bachiller et al., 2016](#)), in the present study these prey only appeared in four individuals (a total of $n = 16$ copepods) that always had Myctophidae fish in their guts. Copepods might have been previously ingested by these mesopelagic fish as part of their diet ([Bernal et al., 2013](#); [Contreras et al., 2020](#)) and hence were not considered as prey.

The two methodologies used to analyze the blue whiting diet, suggested a high importance of myctophid fishes as prey. The most consumed species were *Benthosema glaciale*, *Ceratoscopelus maderensis* and *Lampanyctus* spp., some of the most abundant Myctophidae species in the NW Mediterranean ([Oliver et al., 2012](#)). These fish are usually the dominant micronekton organisms, in terms of biomass and abundance, in oceanic waters of all temperate and tropical regions around the world ([Brodeur and Yamamura, 2005](#); [De Forest and Drzen, 2009](#)), and constitute an important component of the food webs in these ecosystems ([Bernal et al., 2015](#); [Hazen and Johnston, 2010](#); [Valls et al., 2011](#)). While Myctophidae were the most important assimilated prey throughout the year according to MixSIAR models, the presence of Myctophidae in the stomachs was particularly high in spring and summer, with a higher importance in individuals from the shelf break than in those from the slope. This seasonal pattern in the Myctophidae intake has also been reported for different species in the western Mediterranean ([Battaglia et al., 2013](#); [Cartes et al., 2008](#); [Fanelli and Cartes, 2008, 2010](#); [Giménez et al., 2018](#)). To our knowledge, there is a lack of information on the spatial and seasonal variability of Myctophidae species composition and abundance in the western Mediterranean that would allow relating the stomach content variability with the availability of Myctophidae in the field. However, it is worth noting that in spring and summer is when the highest abundance of larvae of the most consumed species (*B. glaciale*, *C. maderensis* and *Lampanyctus* spp.) occurs ([Oliver et al., 2014](#); [Sabatés and Masó, 1990](#)) which would suggest a greater vulnerability of these species to predation during their spawning period. The higher consumption of Myctophidae in the shelf break might seem surprising considering the oceanic habitat of these fishes. The study area is located close to the Cap de Creus canyon, with an abrupt slope, that would allow blue whiting to prey on oceanic mesopelagic organisms commonly found in submarine canyons ([Auster, 1992](#)). In this line, [Cartes et al. \(2009\)](#) already reported that the mesopelagic community sustained the trophic requirements of hake living over the shelf break in the NW of Mallorca Island, an area of bathymetric characteristics similar to our study area. These authors suggested that the consumption of these prey could be explained by oblique migrations of the mesopelagic community along the slope, as reported in other geographic areas ([Reid et al., 1991](#)).

Decapod crustaceans occurred frequently throughout the year in the blue whiting stomach contents, with a higher relative importance in individuals from the slope. The different species that make up this group showed a seasonal presence that corresponds to their seasonal abundance in the field. Thus, *Gennadas elegans*, the most important decapod prey, mainly appeared in winter and spring in specimens from the slope, the periods of maximum abundance of the species at these depths ([Cartes et al., 1994](#)). Sergestidae were present throughout the year in

Table 3

Mean values and standard deviation of $\delta^{13}\text{C}$ (‰) and $\delta^{15}\text{N}$ (‰) values, the C:N relation and the isotope niche metrics for blue whiting, by season, in the shelf break and the slope. The PERMANOVA pair-wise test results for the combined $\delta^{13}\text{C}$ - $\delta^{15}\text{N}$ values are indicated by letters, seasons with the same letter were not significantly different (see details in Table S8); TA: total area; SEAc: corrected standard ellipses area; Overlap: percentage of the ellipse area overlapped.

	Spring		Summer		Autumn		Winter	
	Shelf break	Slope	Shelf break	Slope	Shelf break	Slope	Shelf break	Slope
n	10	10	10	10	9	7	10	10
$\delta^{13}\text{C}$ (‰)	-19.34 ± 0.19	-19.18 ± 0.43	-19.82 ± 0.14	-19.06 ± 0.27	-19.4 ± 0.24	-19.13 ± 0.27	-18.92 ± 0.25	-18.85 ± 0.31
$\delta^{15}\text{N}$ (‰)	8.28 ± 0.36	8.91 ± 0.46	8.75 ± 0.21	9.19 ± 0.55	9.03 ± 0.18	9.37 ± 0.43	9.54 ± 0.69	9.44 ± 1.33
PERMANOVA	A	ce	b	cde	c	de	d	cd
C:N	3.20 ± 0.021	3.201 ± 0.019	3.202 ± 0.047	3.209 ± 0.037	3.194 ± 0.015	3.197 ± 0.023	3.184 ± 0.050	3.203 ± 0.113
TA(‰ ²)	0.2	0.3	0.3	0.5	0.2	0.5	0.7	2.3
SEAc (‰ ²)	0.1	0.3	0.2	0.3	0.1	0.3	0.4	1.4
Overlap	1%	2%	0	0	55%	16%	99%	27%

individuals from the slope, while over the shelf break became important only in autumn. These results are consistent with the observations of Cartes et al. (1994) that reported the presence of this group over the slope, and in autumn also over the shelf break. The presence of Euphausiacea in the stomach contents was constant throughout the year (around 20% O; Table S6), although its importance in W% was only relevant in autumn both in the shelf break and the slope. In this season, FI values were the lowest along the year, suggesting that the high relative importance of Euphausiacea would be related to the absence of the main prey. In any case, the Euphausiacea relative importance, both in %W and in O%, was lower than previously reported in the area (Macpherson, 1978). Unlike the SCA, MixSIAR models showed a low contribution of crustaceans to the diet, not only Euphausiacea but also pelagic shrimps (Sergestidae and *Gennadas elegans*). These differences between both approaches could be explained by the longer digestion time of crustaceans because of their chitinous exoskeleton (Berens and

Murie, 2008), that would overestimate crustaceans with respect to other more digestible prey in the SCA (Hyslop, 1980).

Planktonic gelatinous filter feeders were important in the assimilated diet of individuals from the shelf break in spring and summer according to MixSIAR models. In the NW Mediterranean, the seasonal abundance peak of filter feeders takes place at the end of winter and spring, just after the seasonal phytoplanktonic bloom (Licandro et al., 2006; Saiz et al., 2014). Thus, the high contribution of filter feeders to the blue whiting assimilated diet in spring and summer would be related to the period of their maximum abundance in the field with a certain delay due to the time period of isotopic integration. These gelatinous organisms are hardly observable in the SCA and their relevance as prey has been usually underestimated (Henschke et al., 2016; Revelles et al., 2007). However, recent studies have reported the importance of gelatinous organisms in the diet of different fish species (Albo-Puigserver et al., 2019; Henschke et al., 2016; Logan and Dodge, 2013; Mir-Arguimbau

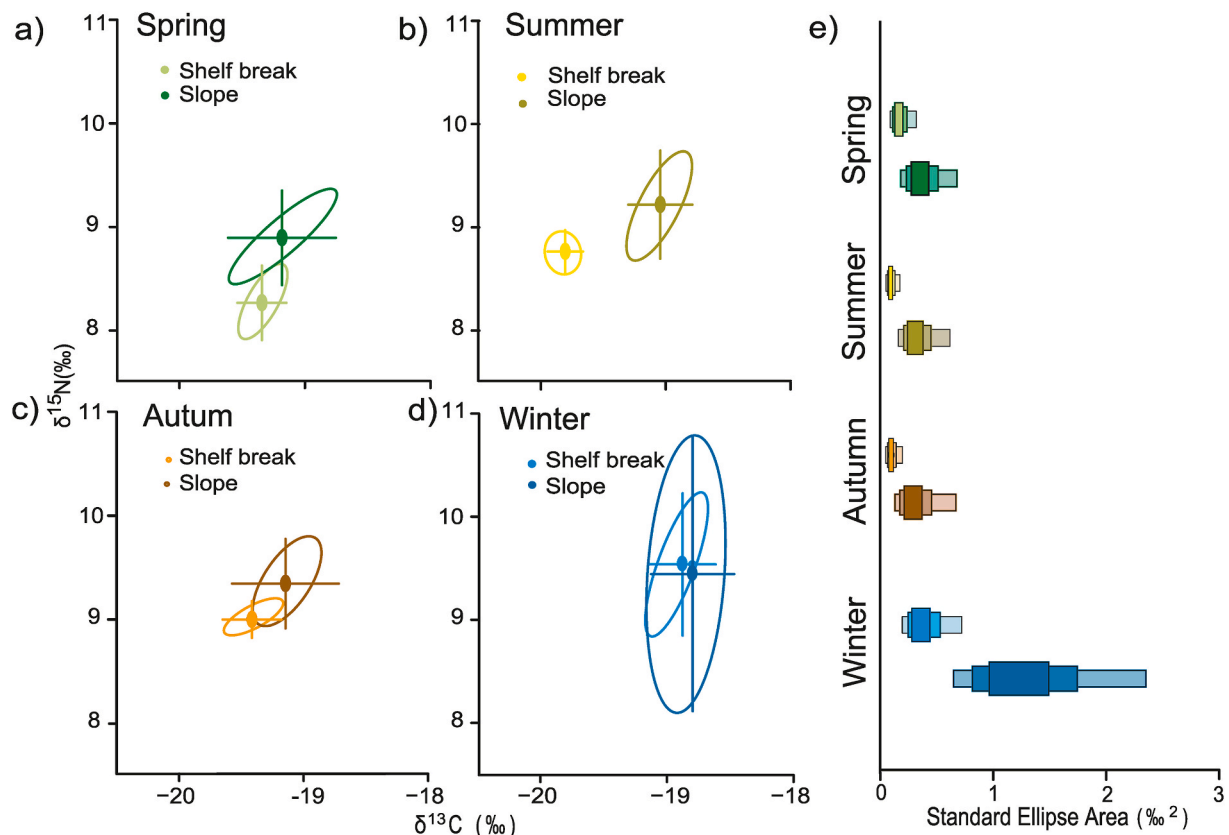


Fig. 5. Blue whiting trophic niche. Mean \pm standard deviation of $\delta^{15}\text{N}$ and $\delta^{13}\text{C}$ and Bayesian standard ellipses (SEAc) for each season and habitat (shelf break and slope) (a-d, left and central panels). Standard Ellipse Area of Bayesian Ellipses (95, 75 and 50% credibility intervals) for each season and habitat (e, right panel). (For interpretation of the references to colour in this figure legend, the reader is referred to the Web version of this article.)

Table 4

Trophic level of Mediterranean blue whiting, by season and habitat, calculated based on the %W of each prey item in the stomach content (TLsca) and on isotopic values (TLsia, mean and Standard deviation).

Trophic level	Shelf break				Slope			
	Spring	Summer	Autumn	Winter	Spring	Summer	Autumn	Winter
TLsca	4.16	4.19	4.03	4.22	4.05	4.12	4.05	4.05
TLsia (mean)	3.41	3.55	3.73	5.06	3.60	3.67	3.84	5.08
TLsia (SD)	0.11	0.06	0.05	0.19	0.14	0.17	0.13	0.40

et al., 2019; Tilves et al., 2018). Applying genetic techniques in further studies will provide relevant information about prey taxa that are usually underestimated in SCA. It should be considered that if blue whiting over the shelf break fed on gelatinous organisms in spring, the FI would be underestimated which would explain the lower FI in that area. The possibility that filter feeders may have been an important prey at earlier blue whiting developmental stages should also be considered, since MixSIAR integrates information of assimilated diet during the most recent months. The seasonal presence of the different prey groups in the stomachs of blue whiting is related with their seasonality in the

environment, suggesting that the species is an opportunistic predator. Further studies should go into more detail exploring concurrently fish diet and prey availability in the field.

The energetic content of the diet varied along the year, being higher in spring and summer due to the high abundance of Myctophidae. According to Spitz et al. (2010), the energetic content of Myctophidae (average = 6.6 KJg^{-1}) is higher than that of crustacean prey (Euphausiacea = 3.9 KJg^{-1} and pelagic shrimps = 4.3 KJg^{-1}). The C:N ratios observed for these groups in the present study also suggested a higher lipid content for Myctophidae than for crustaceans. The high energy

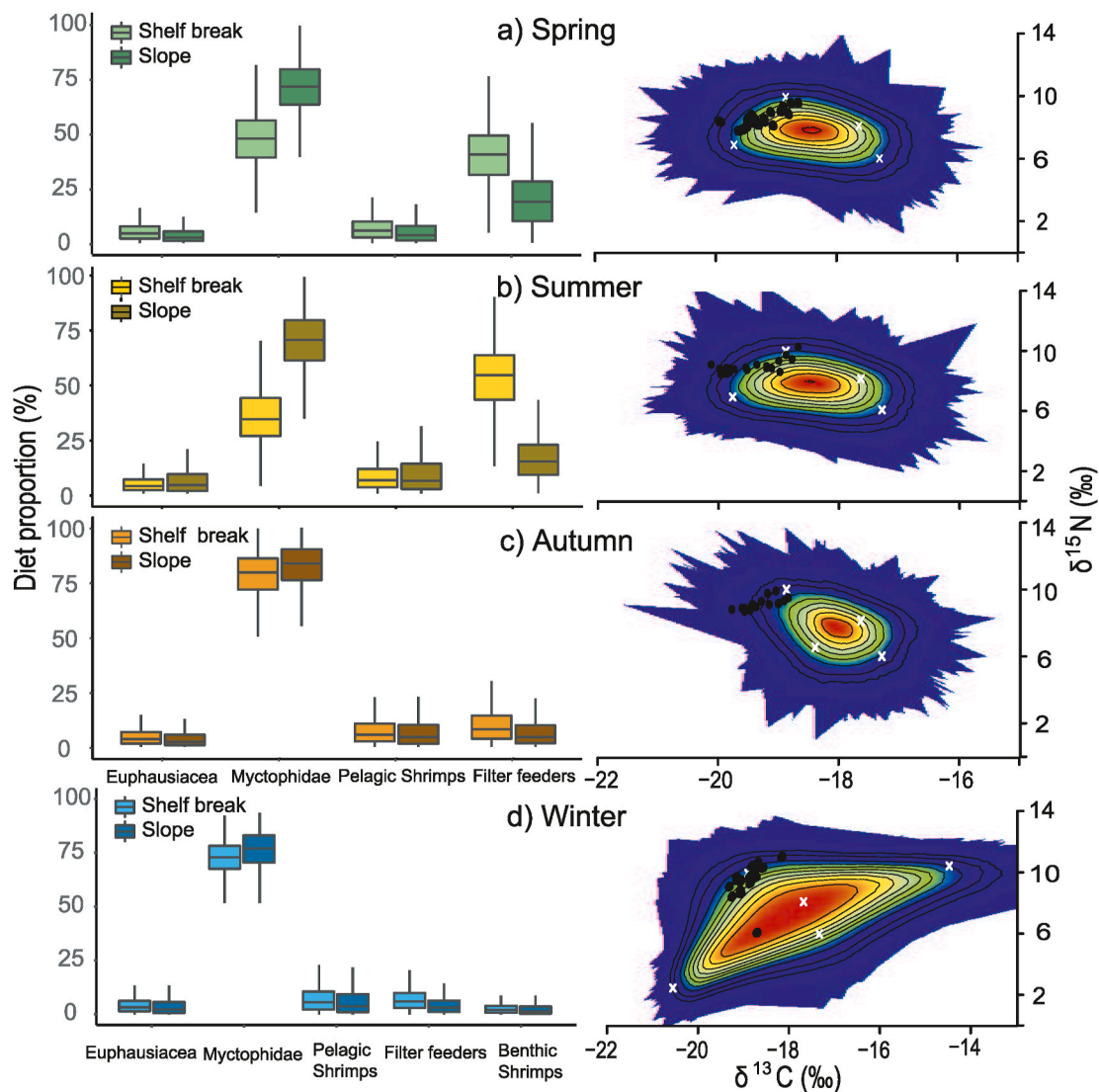


Fig. 6. Diet composition of blue whiting according to MixSIAR models (95, 75 and 50% credibility intervals) for each season and habitat (shelf break and slope) (a-d; left panel). Mixing polygon of stable isotopes values of blue whiting (black dots) and potential dietary sources represented with the mean isotopic value (white crosses) for each season (a-d; right panel). The probability contours are drawn every 10% confidence level. (For interpretation of the references to colour in this figure legend, the reader is referred to the Web version of this article.)

content of the diet in this period, in combination with the high FI, coincided with the highest fish condition (Fulton's condition index) and would be related with the biological cycle of the species. At the end of winter, when the blue whiting spawning season finished, the energy reserves and fish condition were at their lowest levels (Mir-Arguimbau et al., 2020). Later on, in spring, the energy reserve and fish condition rapidly recovered and reached the maximum values (Mir-Arguimbau et al., 2020; Serrat et al., 2019) as a result of the high feeding intensity (also observed by Papiol et al. (2014)) and the intake of highly energetic prey. In that period of high energetic reserves, the fast growth season started and extended until the end of summer (Mir-Arguimbau et al., 2020). Fish condition variation during the year in each habitat could be related with the investment of energy throughout the ontogeny. Thus, while individuals over the shelf break (mainly immatures) would invest their energy in growth, which would lead to a decrease in their condition in summer, the slope individuals (mainly adults) invest energy in reproduction, resulting in an important decrease in their condition in winter. Unlike Fulton's condition index, the ratio C:N, also considered a proxy of organism condition (Dempson et al., 2010; Papiol et al., 2014; Schmidt et al., 2003), did not vary in the blue whiting white muscle tissue along the year. Other tissues, such as liver, a lipid reservoir in blue whiting (Mir-Arguimbau et al., 2020), could provide a more accurate information on the fish condition.

$\delta^{13}\text{C}$ and $\delta^{15}\text{N}$ values obtained for blue whiting in the present study were similar to those previously reported in the Mediterranean Sea (Barría et al., 2015; Louzao et al., 2017; Papiol et al., 2013). Overall the $\delta^{15}\text{N}$ values for Mediterranean were lower than those for the Atlantic blue whiting (Chouvelon et al., 2012; Pinnegar et al., 2002). This is a common trend that occurs in a large number of marine organisms along the food web (e.g. Graham et al., 2010; Louzao et al., 2017; Navarro et al., 2009) since in oligotrophic ecosystems, such as the Mediterranean Sea, nitrogen fixation by diazotrophs provides a source of organic matter with low $\delta^{15}\text{N}$ values (Montoya et al., 2002). The seasonal differences in isotopic values of individuals over the shelf break would be related with the ontogenetic development of the species. The smallest sizes of blue whiting living in that area (Fig. 2b), especially in summer, corresponded to age 0 individuals (Mir-Arguimbau et al., 2020). Important changes occur during the first developmental stages of the fish (dietary, physiological and recruitment to the adult habitat) (Bailey, 1982; Bernal et al., 2013; Mir-Arguimbau et al., 2020), which could explain the differences in the isotopic values observed among seasons. Conversely, blue whiting living over the slope, that is, larger individuals in which ontogenetic changes are not so marked, did not show significant differences in the isotopic values throughout the year. Bayesian ellipses showed trophic niche segregation between the shelf break and slope in spring and summer, while in autumn and winter trophic niches overlapped. As discussed above, this trophic segregation would be related to the size of the individuals in each habitat avoiding intraspecific competition between immature and adult individuals. A wider trophic niche (higher SEA) was always observed in individuals from the slope, particularly in winter. This wider niche could be explained by possible migration movements of oldest individuals disappearing from the study area in summer and autumn (when food limitation could exist) until winter when they became again vulnerable to fishing (Mir-Arguimbau et al., 2020). This migration would allow the larger individuals to feed on different isotopic sources, either by consuming different prey, or the same prey but with different $\delta^{13}\text{C}$ and $\delta^{15}\text{N}$ basal values. This is an interesting point of the feeding ecology of this species that should be further explored in future research.

Variability in the blue whiting diet has been observed throughout the distribution area of the species. Euphausiacea were the most important prey from the Barents Sea to the south of Portugal (e.g. Bailey, 1982; Cabral and Murta, 2002; Bachiller et al., 2016, 2018). Also, high importance of zooplanktonic prey, as mysids and Calanoida copepods, was reported in the Norwegian Sea (Langøy et al., 2012; Bachiller et al., 2016, 2018), in the Celtic Sea (Bailey, 1982) and in the Portuguese coast

(Cabral and Murta, 2002). Only Dolgov et al. (2010) reported a relatively important consumption of fish (polar cod) in the Barents Sea. This suggests that in the North Atlantic blue whiting has a crustacean-based diet, in contrast to what has been observed in the Mediterranean, where Myctophidae are the most important prey. The role of Euphausiacea and myctophid fish in marine food webs have recently discussed by Saunders et al. (2019). These authors reported that in the Scotia Sea, a krill-dominated system, under low-krill scenarios myctophids can maintain food web stability and sustain higher predator populations, becoming an alternative trophic pathway. The trophic position calculated from SCA (TP_{sca} = 4.1) was similar to that reported for the adult Mediterranean blue whiting (TP of ~4; Stergiou and Karpouzi, 2002; Karchle and Stergiou, 2017) and higher than that for the Atlantic (TP = 3.7; Jiming (1982)). Trophic position estimation based on the stable isotope values (TP_{sia} = 3.9) was lower than that obtained based on the diet, although it is still higher in the Mediterranean than in the Atlantic (TP_{sia} = 3.14) (Pinnegar et al., 2002). It should be noted that TP_{sia} values estimated in winter were high compared to the values obtained for the other seasons and to the TP_{sca} values in the shelf break and the slope. Although we expected that TP_{sca} and TP_{sia} followed a similar pattern, on occasions, differences between both TP estimations occur (Fanelli et al., 2010; Navarro et al., 2011) considering that TP_{sia} values are vulnerable to the $\delta^{15}\text{N}$ values of the basal sources used (Olin et al., 2013). In our study, the high TP_{sia} values detected in winter could be an artifact of the extremely low $\delta^{15}\text{N}$ values of the basal groups (filter feeders) obtained in winter. These groups are very sensitive to seasonal variation of $\delta^{15}\text{N}$ caused by primary producers (Bănuaru et al., 2013; Costalago et al., 2012), though in higher trophic levels this seasonal variation is not so evident (Costalago et al., 2012; Fanelli et al., 2011, 2009; Valls et al., 2014). It should also be taken into account that, although filter feeders are commonly considered as primary consumers, the trophic position could be slightly overestimated since filter feeders are not completely primary consumers because they can also predate on heterotrophic organisms (Vargas et al., 2004). In any case, even if winter was not considered, the mean TP_{sia} value (3.63) was still higher for the Mediterranean blue whiting. Thus, both approaches strengthen the idea that in the Mediterranean the species is a secondary carnivore (TP = 4), while in the Atlantic is closer to a primary carnivore (TP = 3). The differences in the blue whiting diet and in the trophic position between Atlantic and Mediterranean could be related to their different productivity. In the Mediterranean, where primary and secondary production are lower than in the N Atlantic (Estrada, 1996; Strömberg et al., 2009) and Euphausiacea and zooplanktonic organisms have lower lipid content (Mayzaud et al., 1999), feeding on high energetic prey, such as Myctophidae, would satisfy the blue whiting energetic demands. In contrast, the higher mesozooplankton biomass in the N Atlantic (Isa et al., 2004; Strömberg et al., 2009) and their higher energy content (Percy and Fife, 1981; Barroeta et al., 2017) would allow a diet based on Euphausiacea and zooplanktonic crustaceans.

5. Conclusions

This study characterized the trophic ecology of blue whiting in the NW Mediterranean Sea throughout the year, in the shelf break and the slope. The seasonal variability in the consumed prey is related with their seasonal presence in the environment, suggesting that blue whiting is an opportunistic predator. The combined approach, stomach content and isotope analyses, evidenced the importance of Myctophidae in the diet in both habitats despite the seasonal and spatial variability in the prey intake. Myctophidae, highly energetic prey, were mainly consumed in spring and summer, which might allow the species recovering the energetic reserves after the reproductive period and supply the energetic demands of the fast growth season. The estimated trophic niche suggested a segregation between individuals of the shelf break (mainly immatures) and the slope (adults) that would reduce the intraspecific competition. Finally, this work evidenced that, in the Mediterranean,

blue whiting has a more fish-based diet than in the Atlantic Ocean, where its diet is based on Euphausiacea and zooplanktonic crustaceans. Accordingly, the trophic position of blue whiting in the Mediterranean is higher than in the Atlantic Ocean.

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.

Acknowledgements

We greatly appreciate the assistance of the crew of the fishing vessel Medan during the samplings. We especially thank M.P. Olivar and J. E. Cartes for their advice in some taxa identification and for their useful suggestions. We acknowledge the constructive comments and suggestions of the reviewers that were very helpful for the improvement of the manuscript. J.M.-A. was supported by a predoctoral fellowship of the FI program of the Secretaria d'Universitats i Recerca de la Generalitat de Catalunya, Spain, and Fons Social Europeu (FSE) [2019FI_B2 00183]. JN was funded by the Spanish National Program Ramón y Cajal (RYC-2015-17809), Ministry of Science and Innovation, Spain. This work was supported by the Spanish Ministry of Economy and Competitiveness [CTM2015-68543-R], Spain. The authors declare that all experimental procedures were conducted in strict accordance with good animal practice as defined by the current Spanish, Catalanian and European legislation.

Appendix A. Supplementary data

Supplementary data to this article can be found online at <https://doi.org/10.1016/j.dsr.2020.103404>.

References

- Albo-Puigserver, M., Borne, D., Coll, M., Tirelli, V., Palomera, I., Navarro, J., 2019. Trophic ecology of range-expanding round sardinella and resident sympatric species in the NW Mediterranean. *Mar. Ecol. Prog. Ser.* 620, 139–154.
- Anderson, M.J., 2001. A new method for non-parametric multivariate analysis of variance. *Austral Ecol.* 26, 32–46.
- Anderson, M., Gorley, R., Clarke, K., 2008. PERMANOVA for PRIMER: Guide to Software and Statistical Methods. PRIMER-E, Plymouth.
- Auster, P.J., Griswold, C.A., Youngbluth, M.J., Bailey, T.G., 1992. Aggregations of myctophid fishes with other pelagic fauna. *Environ. Biol. Fish.* 35, 133–139. <https://doi.org/10.1007/BF00002187>.
- Bachiller, E., Skaret, G., Nøttestad, L., Slotte, A., 2016. Feeding ecology of Northeast Atlantic Mackerel, Norwegian spring-spawning herring and blue whiting in the Norwegian Sea. *PLoS One* 11. <https://doi.org/10.1371/journal.pone.0149238>.
- Bachiller, E., Utne, K.R., Jansen, T., Huse, G., 2018. Bioenergetics modelling of the annual consumption of zooplankton by pelagic fish feeding in the Northeast Atlantic. *PLoS One* 13 (1), e0190345.
- Bailey, R.S., 1982. The population biology of blue whiting in the north atlantic. *Adv. Mar. Biol.* 19, 257–355. [https://doi.org/10.1016/S0065-2881\(08\)60089-9](https://doi.org/10.1016/S0065-2881(08)60089-9).
- Bănuș, D., Mellon-Duval, C., Roos, D., Bigot, J.L., Souplet, A., Jadaud, A., Beaubrun, P., Fromentin, J.M., 2013. Trophic structure in the Gulf of Lions marine ecosystem (north-western Mediterranean Sea) and fishing impacts. *J. Mar. Syst.* 111–112, 45–68. <https://doi.org/10.1016/j.jmarsys.2012.09.010>.
- Barriá, C., Coll, M., Navarro, J., 2015. Unravelling the ecological role and trophic relationships of uncommon and threatened elasmobranchs in the western Mediterranean Sea. *Mar. Ecol. Prog. Ser.* 539, 225–240. <https://doi.org/10.3354/meps11494>.
- Barroeta, Z., Olivar, M.P., Palomera, I., 2017. Energy density of zooplankton and fish larvae in the southern Catalan Sea (NW Mediterranean). *J. Sea Res.* 124, 1–9. <https://doi.org/10.1016/j.seares.2017.04.008>.
- Battaglia, P., Andaloro, F., Consoli, P., Esposito, V., Malar, D., Musolino, S., Pedà, C., Romeo, T., 2013. Feeding habits of the atlantic bluefin tuna, *Thunnus thynnus* (L. 1758), in the central Mediterranean Sea (strait of messina). *Helgol. Mar. Res.* 67, 97–107. <https://doi.org/10.1007/s10152-012-0307-2>.
- Berens, E.J., Murie, D.J., 2008. Differential digestion and evacuation rates of prey in a warm-temperate grouper, gag *Mycteroperca microlepis* (Goode & Bean). *J. Fish. Biol.* 72, 1406–1426. <https://doi.org/10.1111/j.1095-8649.2008.01806.x>.
- Bernal, A., Olivar, M.P., Maynou, F., Fernández de Puellas, M.L., 2015. Diet and feeding strategies of mesopelagic fishes in the western Mediterranean. *Prog. Oceanogr.* 135, 1–17. <https://doi.org/10.1016/j.pocean.2015.03.005>.
- Bernal, A., Olivar, M.P., de Puellas, M.L.F., 2013. Feeding patterns of *Lampanyctus pusillus* (Pisces: Myctophidae) throughout its ontogenetic development. *Mar. Biol.* 160, 81–95. <https://doi.org/10.1007/s00227-012-2064-9>.
- Braga, R.R., Bornatowski, H., Vitule, J.R.S., 2012. Feeding ecology of fishes: an overview of worldwide publications. *Rev. Fish. Biol. Fish.* 22, 915–929. <https://doi.org/10.1007/s11160-012-9273-7>.
- Brodeur, R., Yamamura, O., 2005. Micronekton of the north pacific. *PICES Sci. Rep.* 30, 1–115.
- Brown, S.C., Bizzarro, J.J., Cailliet, G.M., Ebert, D.A., 2012. Breaking with tradition: redefining measures for diet description with a case study of the Aleutian skate *Bathyraja aleutica* (Gilbert 1896). *Environ. Biol. Fish.* 95, 3–20. <https://doi.org/10.1007/s10641-011-9959-z>.
- Cabral, H.N., Murta, A.G., 2002. The diet of blue whiting, hake, horse mackerel and mackerel off Portugal. *J. Appl. Ichthyol.* 18, 14–23. <https://doi.org/10.1046/j.1439-0426.2002.00297.x>.
- Calvo, E., Simó, R., Coma, R., Ribes, M., Pascual, J., Sabatés, A., Gili, J.M., Pelejero, C., 2011. Effects of climate change on Mediterranean marine ecosystems: the case of the Catalan Sea. *Clim. Res.* 50, 1–29. <https://doi.org/10.3354/cr01040>.
- Cartes, J.E., Company, J.B., Maynou, F., 1994. Deep-water decapod crustacean communities in the Northwestern Mediterranean: influence of submarine canyons and season. *Mar. Biol.* 120, 221–229. <https://doi.org/10.1007/BF00349682>.
- Cartes, J.E., Hidalgo, M., Papiol, V., Massutí, E., Moranta, J., 2009. Changes in the diet and feeding of the hake *Merluccius merluccius* at the shelf-break of the Balearic Islands: influence of the mesopelagic-boundary community. *Deep. Res. Part I Oceanogr. Res. Pap.* 56, 344–365. <https://doi.org/10.1016/j.dsr.2008.09.009>.
- Cartes, J.E., Madurell, T., Fanelli, E., López-Jurado, J.L., 2008. Dynamics of suprabenthic-zooplankton communities around the Balearic Islands (western Mediterranean): influence of environmental variables and effects on the biological cycle of *Aurelia aurita*. *J. Mar. Syst.* 71, 316–335.
- Cartes, J.E., Rey, J., Lloris, D., Gil De Sola, L., 2004. Influence of environmental variables on the feeding and diet of European hake (*Merluccius merluccius*) on the Mediterranean Iberian coasts. *J. Mar. Biol. Assoc. U. K.* 84, 831–835. <https://doi.org/10.1017/S0025315404010021h>.
- Caut, S., Angulo, E., Courchamp, F., 2009. Variation in discrimination factors ($\Delta^{15}\text{N}$ and $\Delta^{13}\text{C}$): the effect of diet isotopic values and applications for diet reconstruction. *J. Appl. Ecol.* 46, 443–453. <https://doi.org/10.1111/j.1365-2664.2009.01620.x>.
- Cherel, Y., Fontaine, C., Richard, P., Labat, J.P., 2010. Isotopic niches and trophic levels of myctophid fishes and their predators in the Southern Ocean. *Limnol. Oceanogr.* 55, 324–332. <https://doi.org/10.4319/lo.2010.55.1.0324>.
- Chouvelon, T., Spitz, J., Caurant, F., Méndez-Fernández, P., Chappuis, A., Laugier, F., Le Goff, E., Bustamante, P., 2012. Revisiting the use of $\delta^{15}\text{N}$ in meso-scale studies of marine food webs by considering spatio-temporal variations in stable isotopic signatures - the case of an open ecosystem: the Bay of Biscay (North-East Atlantic). *Prog. Oceanogr.* 101, 92–105. <https://doi.org/10.1016/j.pocean.2012.01.004>.
- Choy, C.A., Haddock, S.H.D., Robison, B.H., 2017. Deep pelagic food web structure as revealed by in situ feeding observations. *Proceedings. Biol. Sci.* 284 <https://doi.org/10.1098/rspb.2017.2116>.
- Clarke, K., Gorley, R., 2006. "Primer v6." User Manual/tutorial, Plymouth Routine in Multivariate Ecological Research.
- Contreras, T., Olivar, M.P., González-Gordillo, J.I., Hulley, P.A., 2020. Feeding patterns of transforming and juvenile myctophids that migrate into neustonic layers. *Mar. Ecol. Prog. Ser.* <https://doi.org/10.3354/meps13234>. AV3.
- Cortés, E., 1999. Standardized diet compositions and trophic levels of sharks. *ICES J. Mar. Sci.* 56, 707–717. <https://doi.org/10.1006/jmsc.1999.0489>.
- Costalago, D., Navarro, J., Álvarez-Calleja, I., Palomera, I., 2012. Ontogenetic and seasonal changes in the feeding habits and trophic levels of two small pelagic fish species. *Mar. Ecol. Prog. Ser.* 460, 169–181. <https://doi.org/10.3354/meps09751>.
- Davis, M., Pineda Muñoz, S., 2016. The temporal scale of diet and dietary proxies. *Ecol. Evol.* 6, 1883–1897. <https://doi.org/10.1002/ece3.2054>.
- De Forest, L., Drazen, J., 2009. The influence of a Hawaiian seamount on mesopelagic micronekton. *Deep. Res. Part I Oceanogr. Res. Pap.* 56, 232–250. <https://doi.org/10.1016/j.dsr.2008.09.007>.
- Dempson, J.B., Braithwaite, V.A., Doherty, D., Power, M., 2010. Stable isotope analysis of marine feeding signatures of Atlantic salmon in the North Atlantic. *ICES J. Mar. Sci.* 67, 52–61. <https://doi.org/10.1093/icesjms/fsp227>.
- Dimarchopoulou, D., Stergiou, K.I., Tsikliras, A.C., 2017. Gap analysis on the biology of Mediterranean marine fishes. *PLoS One* 12, 1–16. <https://doi.org/10.1371/journal.pone.0175949>.
- Dolgov, A.V., Johannessen, E., Heino, M., Olsen, E., 2010. Trophic ecology of blue whiting in the Barents Sea. *ICES J. Mar. Sci.* 67, 483–493. <https://doi.org/10.1093/icesjms/fsp254>.
- Estrada, M., Vives, F., Alcaraz, M., 1985. Life and the productivity of the open sea. *Key Environ. West. Mediterr.* 148–197.
- Estrada, M., 1996. Primary production in the northwestern Mediterranean, 60 (Supl. 2). In: Palomera, I., Rubiés, P. (Eds.), *The European Anchovy and its Environment*. Scientia Marina, Barcelona, pp. 55–64.
- Fanelli, E., Badalamenti, F., D'anna, G., Pipitone, C., Romano, C., 2010. Trophodynamic effects of trawling on the feeding ecology of pandora, *Pagellus erythrinus*, off the northern sicily coast (Mediterranean Sea). *Mar. Freshw. Res.* 61, 408–417. <https://doi.org/10.1071/MF09049>.
- Fanelli, E., Cartes, J.E., 2010. Temporal variations in the feeding habits and trophic levels of three deep-sea demersal fishes from the western Mediterranean Sea, based on stomach contents and stable isotope analyses. *Mar. Ecol. Prog. Ser.* 402, 213–232. <https://doi.org/10.3354/meps08421>.

- Fanelli, E., Cartes, J.E., 2008. Spatio-temporal changes in gut contents and stable isotopes in two deep Mediterranean pandalids: influence on the reproductive cycle. *Mar. Ecol. Prog. Ser.* 355, 219–233. <https://doi.org/10.3354/meps07260>.
- Fanelli, E., Cartes, J.E., Papiol, V., 2011. Food web structure of deep-sea macrozooplankton and micronekton off the Catalan slope: insight from stable isotopes. *J. Mar. Syst.* 87, 79–89. <https://doi.org/10.1016/j.jmarsys.2011.03.003>.
- Fanelli, E., Papiol, V., Cartes, J.E., Rodríguez-Romeu, O., 2014. Trophic ecology of *Lamparyctus crocodilus* on north-west Mediterranean Sea slopes in relation to reproductive cycle and environmental variables. *J. Fish. Biol.* 84, 1654–1688. <https://doi.org/10.1111/jfb.12378>.
- García, L., Lucena, J., Sánchez, F.J., Hernández, J., 1981. *Biología de la bacaladilla («Micromesistius poutassou» risso 1826) del mediterráneo Occidental* 169–198.
- Giménez, J., Marçal, A., García-Polo, M., García-Barón, I., Castillo, J.J., Fernández-Maldonado, C., Saavedra, C., Santos, M.B., de Stephanis, R., 2018. Feeding ecology of Mediterranean common dolphins: the importance of mesopelagic fish in the diet of an endangered subpopulation. *Mar. Mamm. Sci.* 34, 136–154. <https://doi.org/10.1111/mms.12442>.
- Graham, B.S., Koch, P.L., Newsome, S.D., McMahon, K.W., Auriolo, D., 2010. Using isoscapes to trace the movements and foraging behavior of top predators in oceanic ecosystems. In: West, J.B., Bowen, G.J., Dawson, T.E., Tu, K.P. (Eds.), *Isoscapes: Understanding Movement, Pattern, and Process on Earth through Isotope Mapping*. Springer Science & Business Media, Dordrecht, pp. 299–318.
- Hazen, E.L., Johnston, D.W., 2010. Meridional patterns in the deep scattering layers and top predator distribution in the central equatorial Pacific. *Fish. Oceanogr.* 19, 427–433. <https://doi.org/10.1111/j.1365-2419.2010.00561.x>.
- Heino, M., Engelhard, G.H., Godø, O.R., 2008. Migrations and hydrography determine the abundance fluctuations of blue whiting (*Micromesistius poutassou*) in the Barents Sea. *Fish. Oceanogr.* 17, 153–163. <https://doi.org/10.1111/j.1365-2419.2008.00472.x>.
- Henschke, N., Everett, J.D., Richardson, A.J., Suthers, I.M., 2016. Rethinking the role of salps in the ocean. *Trends Ecol. Evol.* 31, 720–733. <https://doi.org/10.1016/j.tree.2016.06.007>.
- Hyslop, E.J., 1980. Stomach contents analysis—a review of methods and their application. *J. Fish. Biol.* 17, 411–429. <https://doi.org/10.1111/j.1095-8649.1980.tb02775.x>.
- ICES, 2016. Report of the Inter-benchmark Protocol for Blue Whiting (IBPBLW), 10 March–10 May 2016, by Correspondence. ICES CM 2016/ACOM, 36. 118 pp.
- Isla, J.A., Llope, M., Anadón, R., 2004. Size-fractionated mesozooplankton biomass, metabolism and grazing along a 50°N–30°S transect of the Atlantic Ocean. *J. Plankton Res.* 26, 1301–1313. <https://doi.org/10.1093/plankt/fbh121>.
- Jackson, A.L., Inger, R., Parnell, A.C., Bearhop, S., 2011. Comparing isotopic niche widths among and within communities: SIBER - stable Isotope Bayesian Ellipses in R. *J. Anim. Ecol.* 80, 595–602. <https://doi.org/10.1111/j.1365-2656.2011.01806.x>.
- Jackson, A.S., Duffy, D.C., Jenkins, J.F.G., 1987. Gastric Digestion in Marine Vertebrate Predators: in Vitro Standards Published by: British Ecological Society Stable. <http://www.jstor.org/stable/2389433> Gastric digestion in marine vertebrate predators: in vitro standards 1, 287–291.
- Jiming, Y., 1982. A tentative analysis of the trophic levels of north sea fish. *Mar. Ecol. Prog. Ser.* 7, 247–252. <https://doi.org/10.3354/meps007247>.
- Karachle, P.K., Stergiou, K.I., 2017. An update on the feeding habits of fish in the Mediterranean Sea (2002–2015). *Mediterr. Mar. Sci.* 18, 43–52. <https://doi.org/10.12681/mms.1968>.
- Keating, J.P., Brophy, D., Officer, R.A., Mullins, E., 2014. Otolith shape analysis of blue whiting suggests a complex stock structure at their spawning grounds in the Northeast Atlantic. *Fish. Res.* 157, 1–6. <https://doi.org/10.1016/j.fishres.2014.03.009>.
- Langøy, H., Nøttestad, L., Skaret, G., Broms, C., Fernø, A., 2012. Overlap in distribution and diets of Atlantic mackerel (*Scomber scombrus*), Norwegian spring-spawning herring (*Clupea harengus*) and blue whiting (*Micromesistius poutassou*) in the Norwegian Sea during late summer. *Mar. Biol. Res.* 8, 442–460. <https://doi.org/10.1080/17451000.2011.642803>.
- Layman, C.A., Araujo, M.S., Boucek, R., Hammerschlag-Peyer, C.M., Harrison, E., Jud, Z. R., Matich, P., Rosenblatt, A.E., Vaudou, J.J., Yeager, L.A., Post, D.M., Bearhop, S., 2012. Applying stable isotopes to examine food-web structure: an overview of analytical tools. *Biol. Rev.* 87, 545–562. <https://doi.org/10.1111/j.1469-185X.2011.00208.x>.
- Licandro, P., Ibañez, F., Etienne, M., 2006. Long-term fluctuations (1974–1999) of the salps *Thalia democratica* and *Salpa fusiformis* in the northwestern Mediterranean Sea: relationships with hydroclimatic variability. *Limnol. Oceanogr.* 51, 1832–1848. <https://doi.org/10.4319/lo.2006.51.4.1832>.
- Logan, J.M., Dodge, K.L., 2013. Comment on “Stable isotopes challenge the perception of ocean sunfish *Mola mola* as obligate jellyfish predators. *J. Fish. Biol.* 82, 1–9. <https://doi.org/10.1111/j.1095-8649.2012.03432.x>.
- Logan, J.M., Jardine, T.D., Miller, T.J., Bunn, S.E., Cunjak, R.A., Lutcutave, M.E., 2008. Lipid corrections in carbon and nitrogen stable isotope analyses: comparison of chemical extraction and modelling methods. *J. Anim. Ecol.* 77, 838–846. <https://doi.org/10.1111/j.1365-2656.2008.01394.x>.
- Louza, M., Navarro, J., Delgado-Huertas, A., de Sola, L.G., Forero, M.G., 2017. Surface oceanographic fronts influencing deep-sea biological activity: using fish stable isotopes as ecological tracers. *Deep. Res. Part II Top. Stud. Oceanogr.* 140, 117–126. <https://doi.org/10.1016/j.dsr2.2016.10.012>.
- Macpherson, E., 1978. Régimen alimentario de *Micromesistius poutassou* (Risso, 1810) y *Gadilucus argenteus argenteus* Guichenot, 1850 (Pisces, Gadidae) 42.
- Martin, P., Maynou, F., Recasens, L., Sabatés, A., 2016. Cyclic fluctuations of blue whiting (*Micromesistius poutassou*) linked to open-sea convection processes in the northwestern Mediterranean. *Fish. Oceanogr.* 25, 229–240. <https://doi.org/10.1111/fog.12147>.
- Mayzaud, P., Virtue, P., Albessard, E., 1999. Seasonal variations in the lipid and fatty acid composition of the euphausiid *Meganyctiphanes norvegica* from the Ligurian Sea. *Mar. Ecol. Prog. Ser.* 186, 199–210. <https://doi.org/10.3354/meps186199>.
- McCutchan Jr., J.H., Lewis, W.M., Kendall, C., McGrath, C.C., 2003. Variation in trophic shift for stable isotope ratios of carbon, nitrogen, and sulfur. *Oikos* 102, 378–390.
- Ménard, F., Benivary, H.D., Bodin, N., Coffineau, N., Le Loc'h, F., Mison, T., Richard, P., Potier, M., 2014. Stable isotope patterns in micronekton from the Mozambique Channel. *Deep Sea Res. Part II Top. Stud. Oceanogr.* 100, 153–163. <https://doi.org/10.1016/j.dsr2.2013.10.023>.
- Mir-Arguimbau, J., Balcells, M., Raventós, N., Martín, P., Sabatés, A., 2020. Growth, reproduction and their interplay in blue whiting (*Micromesistius poutassou*, Risso, 1827) from the NW Mediterranean. *Fish. Res.* 227, 105540. <https://doi.org/10.1016/j.fishres.2020.105540>.
- Mir-Arguimbau, J., Sabatés, A., Tilves, U., 2019. Trophic ecology of *Trachurus mediterraneus* juveniles associated with the jellyfish *Rhizostoma pulmo* and *Cotylorhiza tuberculata*. *J. Sea Res.* 147, 28–36. <https://doi.org/10.1016/j.seares.2019.02.004>.
- Montoya, J.P., Carpenter, E.J., Capone, D.G., 2002. Nitrogen fixation and nitrogen isotope abundances in zooplankton of the oligotrophic North Atlantic. *Limnol. Oceanogr.* 47, 1617–1628. <https://doi.org/10.4319/lo.2002.47.6.1617>.
- Navarro, J., Coll, M., Louza, M., Palomera, I., Delgado, A., Forero, M.G., 2011. Comparison of ecosystem modelling and isotopic approach as ecological tools to investigate food webs in the NW Mediterranean Sea. *J. Exp. Mar. Biol. Ecol.* 401, 97–104. <https://doi.org/10.1016/j.jembe.2011.02.040>.
- Nielsen, J.M., Clare, E.L., Hayden, B., Brett, M.T., Kratina, P., 2018. Diet tracing in ecology: method comparison and selection. *Methods Ecol. Evol.* 9, 278–291. <https://doi.org/10.1111/2041-210X.12869>.
- Olin, J.A., Hussey, N.E., Grgicak-Mannion, A., Fritts, M.W., Wintner, S.P., Fisk, A.T., 2013. Variable $\delta^{15}\text{N}$ diet-tissue discrimination factors among sharks: implications for trophic position, diet and food web models. *PLoS One* 8, 1–11. <https://doi.org/10.1371/journal.pone.0077567>.
- Olivar, M.P., Bernal, A., Molí, B., Peña, M., Balbín, R., Castellón, A., Miquel, J., Massutí, E., 2012. Vertical distribution, diversity and assemblages of mesopelagic fishes in the western Mediterranean. *Deep. Res. Part I Oceanogr. Res. Pap.* 62, 53–69. <https://doi.org/10.1016/j.dsr.2011.12.014>.
- Olivar, M.P., Sabatés, A., Alemany, F., Balbín, R., Fernández de Puelles, M.L., Torres, A. P., 2014. Diel-depth distributions of fish larvae off the Balearic Islands (western Mediterranean) under two environmental scenarios. *J. Mar. Syst.* 138, 127–138. <https://doi.org/10.1016/j.jmarsys.2013.10.009>.
- Papiol, V., Cartes, J.E., Fanelli, E., 2014. The role of food availability in regulating the feeding dynamics and reproductive cycles of bathyal benthopelagic fish in the northwestern Mediterranean slope. *Limnol. Oceanogr.* 59, 1779–1794. <https://doi.org/10.4319/lo.2014.59.5.1779>.
- Papiol, V., Cartes, J.E., Fanelli, E., Rumolo, P., 2013. Food web structure and seasonality of slope megafauna in the NW Mediterranean elucidated by stable isotopes: relationship with available food sources. *J. Sea Res.* 77, 53–69.
- Parnell, A.C., Phillips, D.L., Bearhop, S., Semmens, B.X., Ward, E.J., Moore, J.W., Jackson, A.L., Grey, J., Kelly, D.J., Inger, R., 2013. Bayesian stable isotope mixing models. *Environmetrics* 24, 387–399. <https://doi.org/10.1002/env.2221>.
- Pauly, D., Palomares, M.L., 2000. Approaches for dealing with three sources of bias when studying the fishing down marine food web phenomenon. *Fish. down Mediterr. food webs* 12, 61–66.
- Pauly, D., Trites, A.W., Capuli, E., Christensen, V., 1998. Diet composition and trophic levels of marine mammals. *ICES J. Mar. Sci.* 55, 467–481. <https://doi.org/10.1006/jmsc.1997.0280>.
- Percy, J.A., Fife, F.J., 1981. The biochemical composition and energy content of arctic marine macrozooplankton. *Arctic* 34, 307–313. <https://doi.org/10.14430/arctic2533>.
- Pinnegar, J.K., Jennings, S., O'Brien, C.M., Polunin, N.V.C., 2002. Long-term changes in the trophic level of the Celtic Sea fish community and fish market price distribution. *J. Appl. Ecol.* 39, 377–390. <https://doi.org/10.1046/j.1365-2664.2002.00723.x>.
- Plekhanova, N.V., Sobleva, M.S., 1982. Peculiarities of Blue Whiting Feeding on Copepods and Plankton Development in Open Areas of the the Norwegian Sea in 1979 to 1981. *ICES, CM*, 19821.
- Post, D.M., 2002. Using stable isotopes to estimate trophic position: models, methods, and assumptions. *Ecology* 83, 703–718. [https://doi.org/10.1890/0012-9658\(2002\)083\[0703:USITET\]2.0.CO;2](https://doi.org/10.1890/0012-9658(2002)083[0703:USITET]2.0.CO;2).
- Prokopcuk, I., Sentyabov, E., 2006. Diets of herring, mackerel, and blue whiting in the Norwegian Sea in relation to *Calanus finmarchicus* distribution and temperature conditions. *ICES J. Mar. Sci.* 63, 117–127. <https://doi.org/10.1016/j.icesjms.2005.08.005>.
- R Core Team, 2018. R: a Language and Environment for Statistical Computing. R Foundation for Statistical Computing, Vienna.
- Rault, J., Le Bris, H., Robert, M., Pawlowski, L., Denamiel, M., Kopp, D., 2017. Diets and trophic niches of the main commercial fish species from the Celtic Sea. *J. Fish. Biol.* 91, 1449–1474. <https://doi.org/10.1111/jfb.13470>.
- Reid, K., Davis, D., Staniland, I.J., 2006. Spatial and temporal variability in the fish diet of Antarctic Fur seal (*Arctocephalus gazella*) in the Atlantic sector of the Southern Ocean. *Can. J. Zool.* 84, 1025–1037. <https://doi.org/10.1139/Z06-071>.
- Reid, S.B., Hirota, J., Y R, E., H L, E., 1991. Marine biology. *Mar. Biol.* 109, 427–440. <https://doi.org/10.1038/164914a0>.
- Revelles, M., Cardona, L., Aguilar, A., Fernández, G., 2007. The diet of pelagic loggerhead sea turtles (*Caretta caretta*) off the Balearic archipelago (western

- Mediterranean): relevance of long-line baits. *J. Mar. Biol. Assoc. U. K.* 87, 805–813. <https://doi.org/10.1017/S0025315407054707>.
- Ribera d'Alcalá, M., Conversano, F., Corato, F., Licandro, P., Mangoni, O., Marino, D., Mazzocchi, M.G., Modigh, M., Montresor, M., Nardella, M., Saggiomo, V., Samo, D., Zingone, A., 2004. Seasonal patterns in plankton communities in a pluriannual time series at a coastal Mediterranean site (Gulf of Naples): an attempt to discern recurrences and trends. *Sci. Mar.* 68, 65–83. <https://doi.org/10.3989/scimar.2004.68s165>.
- Ribó, M., Durán, R., Puig, P., Van Rooij, D., Guillén, J., Masqué, P., 2018. Large sediment waves over the Gulf of Roses upper continental slope (NW Mediterranean). *Mar. Geol.* 399, 84–96. <https://doi.org/10.1016/j.margeo.2018.02.006>.
- Sabatés, A., Masó, M., 1990. Effect of a shelf-slope front on the spatial distribution of mesopelagic fish larvae in the western Mediterranean. *Deep Sea Res. Part A, Oceanogr. Res. Pap.* 37, 1085–1098. [https://doi.org/10.1016/0198-0149\(90\)90052-W](https://doi.org/10.1016/0198-0149(90)90052-W).
- Saiz, E., Sabatés, A., Gili, J.-M., 2014. The zooplankton. In: Goffredo, S., Dubinsky, Z. (Eds.), *The Mediterranean Sea: its History and Present Challenges*. Springer, Netherlands, Dordrecht, pp. 183–211.
- Salat, J., 1996. Review of hydrographic environmental factors that may influence anchovy habitats in northwestern Mediterranean. *Sci. Mar.* 60, 21–32.
- Saunders, R.A., Tarling, G.A., Hill, S., Murphy, E.J., 2019. Myctophid fish (family Myctophidae) are central consumers in the food web of the Scotia Sea (Southern Ocean). *Front. Mar. Sci.* 6, 530. <https://doi.org/10.3389/fmars.2019.00530>.
- Schmidt, K., Atkinson, A., Stübing, D., McClelland, J.W., Montoya, J.P., Voss, M., 2003. Trophic relationships among Southern Ocean copepods and krill: some uses and limitations of a stable isotope approach. *Limnol. Oceanogr.* 48, 277–289. <https://doi.org/10.4319/lo.2003.48.1.0277>.
- Serrat, A., Lloret, J., Frigola-Tepe, X., Muñoz, M., 2019. Trade-offs between life-history traits in a coldwater fish in the Mediterranean Sea: the case of blue whiting *Micromesistius poutassou*. *J. Fish. Biol.* 1–16. <https://doi.org/10.1111/jfb.13993>.
- Silva, A., Azevedo, M., Cabral, H., Machado, P., Murta, A., Silva, M.A., 1997. Blue whiting. (*Micromesistius poutassou*) as a forage fish in Portuguese waters. *Proc. Internat. Symp. Role of forage fishes in marine ecosystems. Alaska Sea Grant College Program* 127–146.
- Smith, J.A., Mazumder, D., Suthers, I.M., Taylor, M.D., 2013. To fit or not to fit: evaluating stable isotope mixing models using simulated mixing polygons. *Methods Ecol. Evol.* 4, 612–618. <https://doi.org/10.1111/2041-210X.12048>.
- Spitz, J., Mourocq, E., Schoen, V., Ridoux, V., 2010. Proximate composition and energy content of forage species from the Bay of Biscay: high- or low-quality food? *ICES J. Mar. Sci.* 67, 909–915. <https://doi.org/10.1093/icesjms/fsq008>.
- Stergiou, K.I., Karpouzi, V.S., 2002. Feeding habits and trophic levels of Mediterranean fish. *Rev. Fish Biol. Fish.* 11, 217–254.
- Stock, B.C., Semmens, B.X., 2013. MixSIAR GUI user manual. version 1.0. Accessible online at. <http://conserver.iugo-cafe.org/user/brice.semmens/MixSIAR>.
- Strömberg, K.H.P., Smyth, T.J., Allen, J.I., Pitois, S., O'Brien, T.D., 2009. Estimation of global zooplankton biomass from satellite ocean colour. *J. Mar. Syst.* 78, 18–27. <https://doi.org/10.1016/j.jmarsys.2009.02.004>.
- Tilves, U., Fuentes, V.L., Milisenda, G., Parrish, C.C., Vizzini, S., Sabatés, A., 2018. Trophic interactions of the jellyfish *Pelagia noctiluca* in the NW Mediterranean: evidence from stable isotope signatures and fatty acid composition. *Mar. Ecol. Prog. Ser.* 591, 101–116. <https://doi.org/10.3354/meps12332>.
- Torres, L.G., Sutton, P.J.H., Thompson, D.R., Delord, K., Weimerskirch, H., Sagar, P.M., Sommer, E., Dilley, B.J., Ryan, P.G., Phillips, R.A., 2015. Poor transferability of species distribution models for a pelagic predator, the grey petrel, indicates contrasting habitat preferences across ocean basins. *PLoS One* 10, 1–18. <https://doi.org/10.1371/journal.pone.0120014>.
- Tyler, A.V., 1972. Food resource division among northern, marine, demersal fishes. *J. Fish. Res. Board Can.* 29, 997–1003. <https://doi.org/10.1139/f72-144>.
- Valls, M., Olivar, M.P., Fernández de Puelles, M.L., Molí, B., Bernal, A., Sweeting, C.J., 2014. Trophic structure of mesopelagic fishes in the western Mediterranean based on stable isotopes of carbon and nitrogen. *J. Mar. Syst.* 138, 160–170. <https://doi.org/10.1016/j.jmarsys.2014.04.007>.
- Valls, M., Quetglas, A., Ordines, F., Moranta, J., 2011. Ecología alimentaria de elasmobranchios demersales de plataforma y talud en aguas de las islas baleares (Mediterráneo Occidental). *Sci. Mar.* 75, 633–639. <https://doi.org/10.3989/scimar.2011.75n4633>.
- Vargas, C.A., Madin, L.P., 2004. Zooplankton feeding ecology: clearance and ingestion rates of the salps *Thalia democratica*, *Cyclosalpa affinis* and *Salpa cylindrica* on naturally occurring particles in the Mid-Atlantic Bight. *J. Plankton Res.* 26, 827–833. <https://doi.org/10.1093/plankt/fbh068>.
- Young, J.W., Hunt, B.P.V., Cook, T.R., Llopiz, J.K., Hazen, E.L., Pethybridge, H.R., Ceccarelli, D., Lorrain, A., Olson, R.J., Allain, V., Menkes, C., Patterson, T., Nicol, S., Lehodey, P., Kloser, R.J., Arrizabalaga, H., Anela Choy, C., 2015. The trophodynamics of marine top predators: current knowledge, recent advances and challenges. *Deep. Res. Part II Top. Stud. Oceanogr.* 113, 170–187. <https://doi.org/10.1016/j.dsr2.2014.05.015>.
- Zanden, M.J. Vander, Rasmussen, J.B., 2001. Variation in $\delta^{15}\text{N}$ and $\delta^{13}\text{C}$ trophic fractionation: implications for aquatic food web studies. *Limnol. Oceanogr.* 46, 2061–2066. <https://doi.org/10.4319/lo.2001.46.8.2061>.