



Interannual trophic behaviour of a pelagic fish predator in the western Mediterranean Sea

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ABSTRACT

The exploitation of forage fish species can modify the functioning of marine ecosystems potentially impacting the population status of predators. This may be the case for the western Mediterranean Sea, where a reduction in the biomass of two key pelagic forage fish (European anchovy *Engraulis encrasicolus* and European sardine *Sardina pilchardus*) could produce a change in the diet composition of their main predators, which would consume alternative preys or change the size of the prey consumed. Here, we aimed to investigate the potential effect of biomass reduction of sardine and anchovy in the western Mediterranean Sea on the trophic preferences of the little tunny (*Euthynnus alletteratus*), a medium-sized predator that present a high consumption of these forage fish. We compared its interannual trophic ecology by combining the analysis of stomach contents and stable isotopes. Specifically, we examined if the diet of little tunny changed in its main trophic habits (diet composition, prey size, and trophic niche) during a 6-year period. We found that small pelagic fish, especially clupeiformes, were the most important prey group for the little tunny during the study period. However, we found changes in the body size of anchovy and the relative importance of sardine in recent years, probably reflecting the reported reduction in the biomass and body size of these two forage fish in the study area. In addition to these changes, we found an increase in some demersal and benthopelagic species in the diet of little tunny, which could act as an alternative diet resource.

1. Introduction

The exploitation of marine resources is considered an important factor that can alter the functioning of marine ecosystems, especially when it affects forage fish species (Cury et al., 2011). In this situation and due to resource depletion, some predators could suffer a great impact on their population status (Buren et al., 2019; Myers and Worm, 2003). This effect could be more severe for predators with high preference for particular marine resources as they are more sensitive to changes than generalist species (Clavel et al., 2011; Devictor et al., 2008; Wilson et al., 2008). Disturbance, habitat destruction and changing environmental conditions can cause an increase in competition between species that can lead to population reductions if species are unable to adapt to these new conditions (Clavel et al., 2011).

Marine resources in the Mediterranean Sea have been exploited since

ancient times, but during the last few decades due in part to the increase in fishing exploitation and improvements in fishing technology, the stocks of different marine resources are now considered overfished (Fernandes et al., 2017; Vasilakopoulos et al., 2014). In addition, other factor such as bottom-up processes, climate driven changes, pathogens or increase of natural predation are impacting species in the Mediterranean Sea in a cumulative fashion (Brosset et al., 2016, 2017; Ramírez et al., 2021; Saraux et al., 2019; Van Beveren et al., 2016b). A clear example of this is the reduction in the population and biomass of ecologically important forage fish, such the European anchovy (*Engraulis encrasicolus*) and European sardine (*Sardina pilchardus*) in the western Mediterranean Sea (Coll et al., 2019; Coll and Bellido, 2019; Quattrocchi and Maynou, 2017; Saraux et al., 2019; Van Beveren et al., 2016a). Both species are key species in the Mediterranean Sea as they present wasp-waist effects, exerting bottom-up and top-down control of

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marine organisms (Coll et al., 2008; Palomera et al., 2007; Piroddi et al., 2015, 2017). For this reason, it is expected that the observed reduction in the availability of these prey would produce a change in the diet composition of their main predators, which would consume alternative prey or change the size of prey consumed (Calado et al., 2020; Gulka et al., 2017). However, there is scarce information about the potential effect of changes in the populations of these pelagic forage fish species on the trophic ecology of marine predators inhabiting the Mediterranean Sea (Gómez-Campos et al., 2011; Queiros et al., 2018; Van Beveren et al., 2017). This lack of knowledge prevents an understanding of the real impacts that a biomass reduction of both sardine and anchovy may have on their main predators (Coll et al., 2019; Piroddi et al., 2015). For these reasons, considering the ecological importance of this type of studies, further investigations that include multi-year data on the feeding habits of marine predators are needed to obtain a complete overview of the potential effect of the variation of particular prey resources.

The study of feeding ecology of marine predators has traditionally relied on stomach content analysis (SCA) (Stergiou and Karpouzi, 2002). Although SCA data permits high levels of taxonomic resolution, this methodology presents some shortcomings, as SCA results are often skewed towards those prey that are difficult to digest (Hyslop, 1980). Moreover, SCA generally requires large sample sizes to accurately quantify long-term feeding patterns (Hyslop, 1980). As a complement to SCA, stable isotope analysis (SIA) of nitrogen ($\delta^{15}\text{N}$) and carbon ($\delta^{13}\text{C}$) has become an effective way to examine the trophic ecology of marine organisms (Newsome et al., 2010). SIA is based on the fact that $\delta^{15}\text{N}$ and $\delta^{13}\text{C}$ values are transformed from dietary sources to consumers in a predictable manner (Layman et al., 2012). Moreover, by combining SIA values for consumers with those of their potential prey, isotopic mixing models can be applied to interpret the isotopic values by estimating the relative contribution of each prey group to the diet of the consumer (Phillips et al., 2014). For this reason, the combination of SCA and SIA can be useful to better understand the trophic ecology of marine predators (Giménez et al., 2017; Navarro et al., 2017; Phillips et al., 2014; Shiffman et al., 2012).

In this study, our main aim was to investigate the potential effect in the biomass reduction of sardine and anchovy recorded in the western Mediterranean Sea on the trophic preferences of the little tunny (*Euthynnus alletteratus*), an example of a pelagic predator with a high preference in the consumption of these forage fish (Campo et al., 2006; Falautano et al., 2007; Navarro et al., 2017, 2020). For this purpose, we compared its interannual trophic ecology between 2012, 2015, 2016 and 2017 by combining SCA and SIA methodologies on individuals sampled in a same area of the northwestern Mediterranean Sea. Specifically, we aimed to evaluate if the diet of this pelagic fish predator showed an interannual change in its main trophic habits (diet composition, prey size, and trophic niche). We expected a decline in the occurrence of forage fish species in the diet of the little tunny, a reduction of prey size consumed, and/or a replacement with other species consumed.

2. Material and methods

2.1. Sampling procedures

Between 2012 and 2017, a total of 73 individuals of little tunny were sampled in Tarragona (northwestern Mediterranean Sea). The study area is one of the most important fishing grounds in the Mediterranean Sea (Leonart and Maynou, 2003). The oceanographic features are controlled by a south-westward current that follows the continental slope close to the coast in the northern part of the area where the continental shelf is narrow and influences the circulation features over the continental shelf in the southern part, which presents a wider continental shelf (Salat, 1996). Over this continental shelf, anticyclonic eddies may develop and local events like wind stress, vertical mixing,

upwellings and inputs of freshwater, can have a major influence on the circulation patterns (Salat, 1996).

All little tunny individuals were collected in the same pelagic area by sport fishing activities (years 2015, 2016 and 2017) and from commercial fisheries (year 2012; Navarro et al., 2017). After the capture, the body mass (± 0.1 g) and fork length (± 0.1 cm) were measured. Also, the stomach and a small portion of the liver of each individual were extracted and frozen at -20°C until their analysis. Liver was chosen as it presents a shorter isotopic turnover rate if compared with other tissues such as muscle or fin (Davis and Pineda Munoz, 2016) and it is more suitable for comparison with traditional stomach content analysis (Navarro et al., 2020).

2.2. Stomach content analysis

The contents of each stomach were carefully separated by filtering using three different sieves (1 mm, 300 μm , and 500 μm). Prey items retained in these sieves were identified at the minimum taxonomic resolution possible. Otoliths were used to identify species using the AFORO database (aforo.cmima.csic.es, Lombarte et al. (2006)). Cephalopods and crustaceans were identified as general groups. We also measured the length and width of all otoliths, by using a stereomicroscope fitted with a digital camera LASV4.9 with Leica software (<https://leica-geosystems.com/>). The length and width of otoliths were used to estimate the fish length of the different individuals found in the stomachs using standard regression algorithms to reconstruct the size of each fish individual (Giménez et al., 2016). Estimated fish length was used to estimate the weight of each fish individual using fish length–fish weight published equations (see Table S1; e.g. Torres et al. (2012); Moutopoulos and Stergiou (2002)).

Four trophic metrics based on the number of non-empty stomachs were calculated: i) the frequency of occurrence (%FO; *i.e.* calculated as the number of stomachs where prey *i* was found divided by the total number of stomachs), ii) the frequency in number (%N; *i.e.* numerical percentage of each prey *i* in relation to the total number of prey individuals found in the stomachs), iii) the percentage of reconstructed weight (%W) and iv) the Index of Relative Importance (%IRI; Pinkas (1971), Hyslop (1980)) of each prey as a measure of overall importance in the diet ($\text{IRI} = (\%N + \%W) + \%F$), calculated as a modified version using %W instead of %V. This modification has been previously done in other studied where %V was not available (Bittar and di Benedetto, 2009; Hacunda, 1981; Krishnan et al., 2008; Marçalo et al., 2018; Pedà et al., 2015).

2.3. Stable isotope analyses

All liver samples were freeze-dried and powdered, and 0.3–0.4 mg of each sample was packed into tin capsules. Isotopic analyses were performed at the Laboratory of Stable Isotopes of the Biological Station of Doñana (Sevilla, Spain). Samples were combusted at 1020°C using a continuous flow isotope-ratio mass spectrometry system (Thermo Electron) by means of a Flash HT Plus elemental analyzer interfaced with a Delta V Advantage mass spectrometer. Stable isotope ratios were expressed in the standard δ -notation (‰) relative to Vienna Pee Dee Belemnite ($\delta^{13}\text{C}$) and atmospheric N_2 ($\delta^{15}\text{N}$). The laboratory standards were previously calibrated with international standards supplied by the International Atomic Energy Agency (IAEA, Vienna). The %C and %N of all samples were determined. Because lipid contents could affect the $\delta^{13}\text{C}$ values by depleting the real values, we checked the C:N ratio (a proxy of lipid content) and the individuals with a ratio higher than 3.5‰ were corrected following (Logan et al., 2008). To investigate interannual differences in stable isotope values, while accounting for differences in fish length, we conducted an analysis of covariance (ANCOVA) using fish length as a covariate. We corrected *p*-values to account for the effect of conducting multiple comparisons over the same sample using the Bonferroni procedure using the *rstatix* package in R (Kassambara, 2020).

2.4. Stable isotopic metrics and diet reconstruction

Based on the liver turnover, stable isotopic values in this tissue reflect the diet of little tunny individuals during the 5 weeks prior to the sampling (Gómez-Campos et al., 2011; Navarro et al., 2020). As a proxy to the trophic niche, we calculated the isotopic niche using the standard ellipses area corrected for small sample sizes (SEA_c) for each year using the package *SIBER* (Jackson et al., 2011). Each SEA_c contains 40% of the data (Jackson et al., 2011). We also estimated the Bayesian standard ellipses area (SEA_b) to obtain the uncertainty associated with this metric (Jackson et al., 2011). The Bayesian framework takes into account the uncertainty in the sampled data and incorporates the error arising from the sampling process, propagating it through to the derived metric (Jackson et al., 2011). Furthermore, the estimation via Bayesian inference allows robust comparisons to be made among data sets comprising different sample sizes (Jackson et al., 2011). SEA_b was estimated

through 10,000 iterations of the analysis. Furthermore, we calculated the overlap among SEA_b between the sampling years.

To estimate the contribution of the different potential prey to the diet of little tunny, we used a Bayesian stable isotope mixing model (MixSIAR, Stock and Semmens (2016)). Potential preys were identified through the results of stomach content analysis obtained in the present study. Those prey detected in the diet with more than 2% IRI were included as potential prey in the MixSIAR models. In addition, gelatinous species were included since they have been suggested as important prey for little tunny in the western Mediterranean Sea (Cardona et al., 2012). Stable isotope data from potential prey species were obtained from published datasets from the same studied area (Isolibrary, Barría et al. (2015); Table S2). Ward's hierarchical cluster analysis was used to group prey species in isotopically similar clusters based on their mean stable isotope values as recommended by Phillips et al. (2014). MixSIAR models were fitted with diet-to-tissue discrimination factors of 1.2 ±

Table 1

Stomach content analysis of little tunny from the northwestern Mediterranean Sea during the years 2012, 2015, 2016 and 2017. N%: Numerical percentage, F%: Frequency of occurrence, W%: Weight percentage, IRI %: Index of relative importance percentage. The total stomachs examined each year (n), the vacuity index (VI %) and the mean ± standard deviation of the forkal length are also indicated for each year.

	2012				2015				2016				2017			
	N%	F%	W%	IRI%	N%	F%	W%	IRI%	N%	F%	W%	IRI%	N%	F%	W%	IRI%
	n = 4, forkal length = 90.98 ± 3.67 cm, VI = 0%				n = 31, forkal length = 85.47 ± 6.79 cm, VI = 83.87%				n = 25, forkal length = 93.82 ± 4.18 cm, VI = 84%				n = 13, forkal length = 93.82 ± 4.18 cm, VI = 69.23%			
ACTINOPTERYGII	81.08	100	100		85.40	100	100		73.10	80.95	100		96.49	100	100	
Argentinidae																
Unidentified Argentinidae									1.02	4.76	0.12	0.07				
Atherinidae																
<i>Atherina</i> sp.									0.51	4.76	0.16	0.04				
Carangidae																
<i>Trachurus</i> sp.									1.02	9.52	23.59	3.04				
Carapidae																
<i>Echiodon dentatus</i>	1.35	25.00														
Cepolidae																
<i>Cepola macrophthalma</i>									1.02	9.52	1.59	0.32				
Clupeidae																
<i>Sardina pilchardus</i>	18.92	75.00	20.79	31.98	7.76	23.08	16.07	4.61	1.52	4.76	1.81	0.21	3.51	11.11	13.55	1.26
<i>Sardinella aurita</i>					1.24	11.54	5.47	0.65	2.03	14.29	10.63	2.35				
<i>Sprattus sprattus</i>	5.41	50.00	3.39	4.72												
Echeneidae																
Unidentified Echenidae									0.51	4.76						
Engraulidae																
<i>Engraulis encrasicolus</i>	40.54	50.00	74.82	61.94	70.50	96.15	43.33	91.68	45.18	76.19	41.76	85.99	89.47	88.89	75.89	97.70
Gadidae																
<i>Micromesistius poutassou</i>	2.70	25.00	0.44	0.84					12.69	28.57	4.19	6.26				
<i>Trisopterus capelanus</i>	1.35	25.00	0.56	0.51	1.55	15.38	3.19	0.61	2.03	14.29	1.26	0.61				
Gobiidae																
<i>Gobius</i> sp.					0.31	3.85	1.50	0.06	0.51	4.76	7.03	0.47				
<i>Gobius cobitis</i>					0.93	11.54	10.03	1.06								
<i>Gobius niger</i>					0.62	7.69	1.02	0.11								
<i>Lesueurigobius friessi</i>					0.31	3.85	0.03	0.01								
Labridae													1.75	11.11		0.13
Unidentified Labridae																
Merlucciidae																
<i>Merluccius merluccius</i>					0.31	3.85	3.74	0.13	0.51	4.76	0.85	0.08				
Myctophidae																
<i>Notoscopelus elongatus</i>									0.51	4.76	0.12	0.04				
Sparidae																
<i>Boops boops</i>					0.62	7.69	6.96	0.49	1.02	4.76	5.67	0.41				
<i>Pagellus erythrinus</i>																
<i>Sarpa salpa</i>					0.62	7.69	8.28	0.57					1.75	11.11	10.56	0.91
<i>Spondyliosoma cantharus</i>									0.51	4.76	1.21	0.11				
<i>Spicara</i> sp.					0.31	3.85	0.38	0.02								
Unidentified Sparidae					0.31	3.85			2.54	9.52						
Syngnathidae																
<i>Syngnathus phlegon</i>	10.81	25.00														
CEPHALOPODA	1.35	25.00							6.60	19.05						
CRUSTACEA	17.57	50.00			14.60	30.77			20.30	28.57			3.51	11.11		

0.3‰ for $\delta^{13}\text{C}$ and $1.1 \pm 0.6\%$ for $\delta^{15}\text{N}$ (Madigan et al., 2012). MixSIAR were run on long setting with three MCMC chains, and a burn-in of 300,000 draws, followed by 2,000,000 draws to calculate the posterior distribution to compute credible Bayesian intervals. Model convergence was assessed with the Gelman-Rubin diagnostic, which compares estimates of variance between and within Markov chains, with values < 1.01 indicating convergence (Gelman et al., 2013). Two different MixSIAR models were run, one without covariates (model 1) and another with year a fixed covariate (model 2). The *compare_models* function from the *MixSIAR* package (Stock and Semmens, 2016) was used to compare the predictive accuracy of the models constructed. The function uses the 'loo' package to compute LOO (leave-one-out cross-validation) for different fitted models. LOO is a method to estimate pointwise out-of-sample prediction accuracy from a fitted Bayesian model using the log-likelihood evaluated at the posterior simulations of the parameter values (Vehtari et al., 2017). In addition, the relative support for each model was calculated using LOO weights. Finally, to provide a quantitative basis for model acceptance or rejection, a mixing polygon simulation was constructed based on a frequentist probability that shows if the proposed mixing model can correctly estimate source contribution to the consumer's isotopic value (Smith et al., 2013).

3. Results

3.1. Diet based on stomach content analysis

Based on the stomach contents, we found that the diet of little tunny was mainly composed of fish, followed, in very low proportion, by crustaceans, cephalopods, and gastropods (Table 1). Among the different fish species, European anchovy and three species of clupeids, especially European sardine, were the most important species consumed along the different sampling years (Table 1). Between years, the importance of anchovy in the stomach contents was always high (between 61.94% and 97.70% of %IRI; Table 1). Sardine was more important in the diet in the early years analysed (in 2012, %IRI = 31.98%) (Table 1). In 2015 and 2016, we recorded an increase in the % IRI of some species, such as mackerels (*Trachurus* sp) or some demersal species such as the blue whiting (*Micromesistius poutassou*) or the poor cod (*Trisopterus capelanus*) (Table 1).

3.2. Size of anchovy and sardine in the diet of little tunny

Reconstructed body length of anchovy and sardine present in the stomach contents of little tunny changed significantly between years for both species (ANOVA tests; anchovy, $F_{3, 675} = 54.85$ p-value < 0.001; sardine, $F_{3, 57} = 8.34$ p-value < 0.001; Fig. 1, Table S3). For anchovy, Tukey post hoc tests showed that body length differed between the years 2014, 2015, 2017 and 2012–2016, with the individuals found in 2017 being the smallest (Fig. 1, Table S3). In the case of sardine, post hoc tests showed differences between 2012 and 2015 ($p < 0.05$), with the largest body sizes found in 2017 and the smallest sizes found in 2012 (Fig. 1, Table S3).

3.3. Stable isotope results

Isotopic values differed between years in the case of carbon (ANCOVA test: $F_{3, 48} = 5.79$; $p = 0.002$) but not for nitrogen (ANCOVA test: $F_{3, 48} = 0.912$; $p = 0.44$) (Table 2). Based on Tukey post hoc tests, differences in $\delta^{13}\text{C}$ values were found between 2012 and 2017 and between 2016 and 2017 (Table 2). SEA_a and SEA_b increased between 2012 and 2017 (Fig. 2 and Table 3). SEA_b overlap was found between some years (Fig. 2, Table 4). We found especially high overlap between 2015 and 2017 (Fig. 2, Table 4), while the largest SEA_b segregation was between 2012 and 2015 and between 2012 and 2017 (Fig. 2, Table 4).

Regarding potential preys, the cluster analysis clustered four species (*M. poutassou*, *E. encrasicolus*, *S. pilchardus* and *Sprattus sprattus*) in a

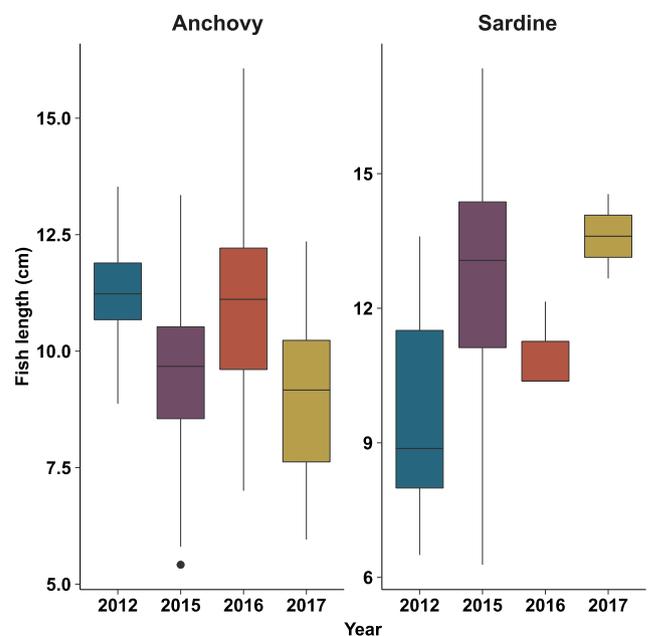


Fig. 1. Box plots showing the fish length (cm) of anchovy and sardine found in the stomachs of the little tunny (*Euthynnus alletteratus*) between years.

Table 2

Mean and standard deviation of $\delta^{13}\text{C}$ and $\delta^{15}\text{N}$ values from little tunny for each sampling year. The number of individuals analysed is also indicated (n).

Year	n	$\delta^{13}\text{C}$ (‰)	$\delta^{15}\text{N}$ (‰)
2012	3	-18.79 ± 0.61	9.33 ± 0.60
2015	12	-17.85 ± 0.48	8.85 ± 0.64
2016	25	-18.46 ± 0.53	8.93 ± 0.89
2017	13	-17.61 ± 0.84	9.09 ± 0.93

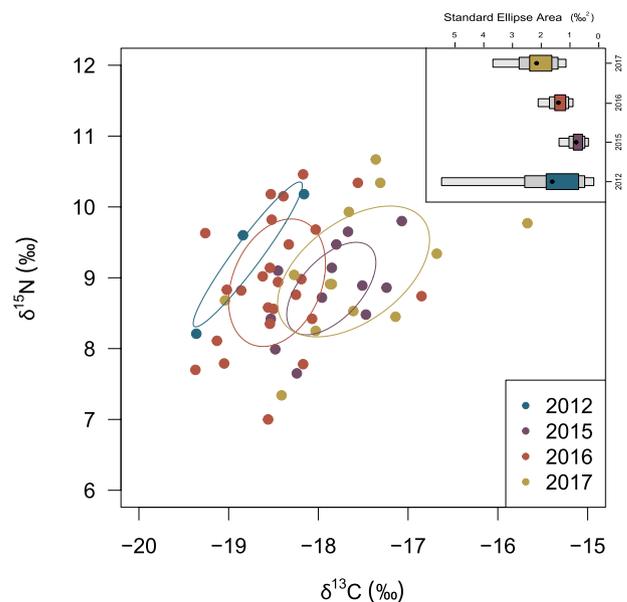


Fig. 2. Individual $\delta^{13}\text{C}$ and $\delta^{15}\text{N}$ values and Standard Ellipse Area (SEAc) and niche width (SEAb; subplot) of little tunny (*Euthynnus alletteratus*) in the western Mediterranean Sea for different years.

single group (Fig. 3) due to their isotopic similarity. They were then grouped and used as a single end-member in the Bayesian isotopic mixing model.

Table 3

Standard ellipses area correct (SEAc) and median Bayesian SEA (SEAb) for each sampling year for little tunny. For SEAb the 25% and 75% credible intervals are given in parenthesis.

	2012	2015	2016	2017
N	3	12	25	13
SEAc (% ²)	1.17	0.84	1.49	2.30
SEAb (% ²)	1.64 (1.12–2.5)	0.82 (0.68–1.02)	1.47 (1.28–1.68)	2.18 (1.83–2.66)

Table 4

Median SEAb overlap of little tunny between years (percentage of overlap of the isotopic area of species in the first column versus the ones of the first row). 25% and 75% Bayesian credible intervals are given in parenthesis.

	2012	2015	2016	2017
2012		1.69 (0–7.62)	24.85 (0–70.21)	7.42 (0–48.01)
2015	2.55 (0–20.62)		23.18 (0–78.62)	73.82 (25.95–100)
2016	26.62 (0–71.99)	13.75 (0–50.44)		33.73 (0–85.78)
2017	5.7 (0–25.71)	28.85 (9.76–49.89)	22.87 (0–52.58)	

3.4. Diet reconstruction by Bayesian isotopic mixing models

All little tunny isotopic data, except two extreme data points (excluded from further analysis), were inside the mixing region delimited by the mixing polygon of potential prey adjusted by the DTDF (Fig. 3). Two different models were tested (see Table S4) and the best model included year as a covariate (Model weight: 66.8%, Model 2). The other model without any covariates (Model 1) also had some weight (33.2%). According to the best MixSIAR model, the clustered group including *M. poutassou*, *E. encrasicolus*, *S. pilchardus* and *S. sprattus* contributed on average to the diet of little tunny between 59% and 83% (Fig. 4, Table S5). The other prey always contributed less than 14% to the diet (Fig. 4, Table S5). In the second model, the contribution of the

clustered group contributed $65 \pm 10\%$, while the rest of the groups contributed less than 11% (Fig. 4, Table S5).

4. Discussion

In this study, we describe the feeding ecology of little tunny in the years 2012 and 2015, 2016 and 2017 in the northwestern Mediterranean Sea using two complementary methodologies, stomach content and stable isotopic analyses. The results of this trophic study revealed an evident consistence in the importance of clupeiformes in the diet of this pelagic predator. The importance of these forage fish species in the diet of little tunny is similar to previous information for the species (Campo et al., 2006; Navarro et al., 2017, 2020).

Based on the stomach content analysis, we found that the importance of European anchovy in the diet of little tunny was very high during all years, in comparison to the other species. However, although European sardine is the second most important prey for little tunny in all years (except for 2016 where *M. poutassou* stands as the second most important species), we found a reduction in the presence of this species in the little tunny diet (31.98%, 4.61%, 0.21%, 1.26%IRI respectively for 2012, 2015, 2016, and 2017). The decrease in sardine could be associated with the recorded reduction in the biomass of this species in the northwestern Mediterranean Sea in recent years (Coll and Bellido, 2019; Quattrocchi and Maynou, 2017; Van Beveren et al., 2014). In the case of anchovy, although there is evidence of a reduction in its population biomass in the study area associated with overfishing (Coll and Bellido, 2019; Quattrocchi and Maynou, 2018; Van Beveren et al., 2014), this reduction apparently was not sufficient to affect the consumption of this resource for little tunny. However, we detected a decreasing trend in the body length of anchovies consumed, with the smallest lengths found in the last year of the study. In general, the presence of populations composed of small individuals is a sign of overfishing (Pauly et al., 1998), and is in line with a decline in biomass but an increase in abundance that has been observed for anchovy in some areas of the western Mediterranean Sea (Coll and Bellido, 2019). For this reason, the apparent reduction in the body size of anchovy in the diet of little tunny in the last year could be an indicator of the impact of fisheries on anchovy in the western Mediterranean Sea. However, further studies

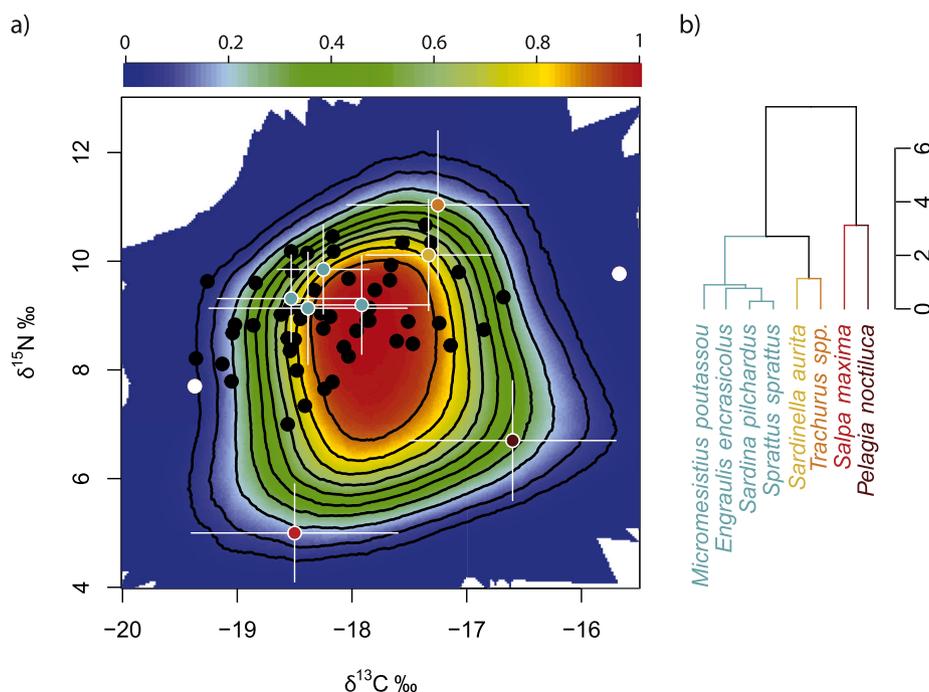


Fig. 3. a) Mixpolygon built with potential preys coloured by cluster results, b) Cluster analysis of potential preys.

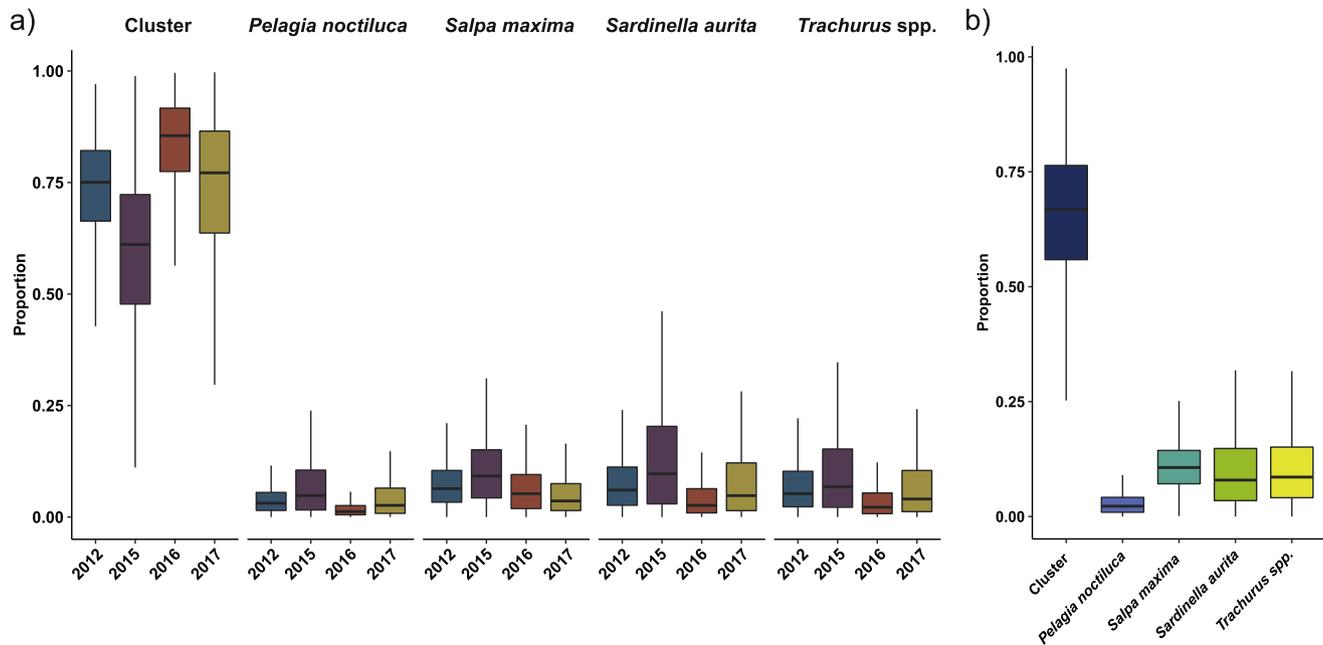


Fig. 4. a) MixSIAR model results using year as a covariate, b) MixSIAR model results without covariates.

should be conducted to evaluate this decreasing trend, as stomach contents of 2012 were gathered from only four stomachs and a temporal information gap is present from 2013 to 2014. A more continuous monitoring of the trophic habitats of little tunny and other similar pelagic predators is needed to confirm this decreasing trend.

Due the reduction of small pelagic fish biomass in the study area, we expected an increase in alternative species consumed during the later years of the study. We found an increase in the presence of some demersal species such the blue whiting in the diet of little tunny. These changes in diet occurrence and composition based on the stomach content analysis likely explain the interannual variation in the isotopic niche metrics. In particular, the increase in trophic niche width observed in 2015 and 2016 seems to correspond to the increase in the isotopic niche metrics (*i.e.* SEA_b increase through time). The consumption of different prey implies greater variability in isotopic values of prey consumed and thus greater variability in the isotopic values of the predator (Layman et al., 2012). From a behavioural standpoint, the presence of pelagic and benthopelagic prey reflect the ability of the species to conduct vertical foraging movements to exploit the entire water column, as seen in other pelagic marine predators performing pronounced vertical movements (Abascal et al., 2010). This feeding pattern is an example of the importance of the pelagic-demersal coupling in Mediterranean marine ecosystems, already highlighted in previous studies of other pelagic fish predators (Coll et al., 2006; Navarro et al., 2017). This diet variation could result in a lower energetic diet due to the lower energy content of demersal species compared to the high energetic content of small pelagic fish (Albo-Puigserver et al., 2017, 2020) that, in turn, could affect the body condition of the little tunny (Lloret et al., 2014).

Opposite to the stomach content results, we did not detect this trend with stable isotope mixing models due to the lack of taxonomic resolution of the technique in our system. Isotopic similarity between sardine and anchovy precludes its differentiation as end-members in the mixing models and their contributions are confounded in the final results, as well as the contribution of alternative preys like blue whiting. Nevertheless, stable isotope mixing models showed that small pelagic species remain important in the diet of little tunny with some interannual variation. In addition, stable isotopes allow an examination of the importance of certain prey, which are generally underestimated in

stomach content analysis, such as the gelatinous species due to their fast digestion time (Hays et al., 2018). This soft-body prey was suggested as an important trophic resource for little tunny and other pelagic predators in the western Mediterranean (Cardona et al., 2012). However, we did not find any evidence that gelatinous species were important prey for little tunny during any of the study years. To fully test if this species predate on gelatinous organisms, genetic analysis of the stomach contents should be developed since soft-bodied species are difficult to find in visual examinations of the diets (Stergiou and Karpouzi 2002).

Stable isotope analysis allowed us to determine the diet of little tunny avoiding the limitations of traditional stomach content analysis such as the difficulty to identify the consumption of gelatinous prey, as well as overcoming the snapshot diet information provided. Nevertheless, this technique has also other limitations such as the low taxonomic resolution (*i.e.* several species were grouped due to isotopic similarity), the use of non-specific DTDf (*i.e.* Pacific Bluefin tuna (*Thunnus orientalis*) was used), and the overlook of spatiotemporal variation of isotopic differences in prey sources. For these reasons, the combination of techniques is a good proxy to overcome the limitations of each individual technique and provide a more comprehensive overview of trophic habits.

In conclusion, we found that small pelagic fish, especially clupeiformes, were the most important prey group for the little tunny during the study period in the northwestern Mediterranean Sea. However, we found changes in the body size of anchovy and the relative importance of sardine during the last years that are probably associated with the reported reduction in the biomass and body size of these two forage fish in the study area. In addition to these changes, we found an increase in some demersal and benthopelagic species in the diet of little tunny, which could act as alternative resources. Despite the high consumption of small pelagic fish, the ability to shift and consume other species points towards the opportunistic behaviour in diet habits. However, future research examining the energetic repercussions of a change from high energetic prey, such as sardine, to prey with less energetic content (Albo-Puigserver et al., 2017) could help understand the effect on the fitness of little tunny.

This study contributes to the monitoring of small pelagic fish changes through the study of their predators as recommended by Coll et al. (2019), as predators could act as suitable sources of information to

indirectly monitor changes in the pelagic food web. From a methodological perspective, our study provides evidence of the increased dietary inference when combining SIA and SCA, as both provide benefits and drawbacks. The best inferences are possible when local stomach content analysis is available to infer potential prey for isotopic mixing models (e.g. Giménez et al. (2017); Navarro et al. (2017)).

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.

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Appendix A. Supplementary data

Supplementary data to this article can be found online at <https://doi.org/10.1016/j.marenvres.2021.105288>.

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