



Trophic structure of pelagic species in the northwestern Mediterranean Sea



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ABSTRACT

Ecological knowledge of food web interactions within pelagic marine communities is often limited, impairing our capabilities to manage these ecologically and economically important marine fish species. Here we used stable isotope analyses to investigate trophic interactions in the pelagic ecosystem of the northwestern Mediterranean Sea during 2012 and 2013. Our results suggest that European sardine, *Sardina pilchardus*, and anchovy, *Engraulis encrasicolus*, are consumers located at relatively low levels of the pelagic food web. Unexpectedly, the round sardinella, *Sardinella aurita*, appeared to be located at a higher trophic level than the other small pelagic fish species, although previous studies found similarity in their diets. Isotope data suggested that trophic niches of species within the genera *Trachurus* spp. and *Scomber* spp., were distinct. Atlantic bonito *Sarda sarda*, European hake *Merluccius merluccius* and European squid *Loligo vulgaris*, appeared to feed at higher trophic levels than other species. Despite some intraspecific seasonal variability for some species, community trophic structure appeared relatively stable through the year. These data provide an important step for developing models of food web dynamics in the northwestern Mediterranean Sea.

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1. Introduction

Marine pelagic fisheries account for 26% of the world's total protein consumption (Tacon and Metian, 2009). With exploitation of these stocks increasing, there is a need to understand how the trophic structure may be shifting in pelagic systems (Pikitch et al., 2014). Yet, relative to coastal ecosystems, we have less knowledge of pelagic food webs and the trophic role of pelagic species (Miller et al., 2010). This is particularly true for small- and medium-sized pelagic fishes, which are ecologically and economically important species in marine ecosystems worldwide and represent >50% of the total landings in the Mediterranean Sea (Cury et al., 2000; Leonart and Maynou, 2003).

Small pelagic fish species, such as *Sardina pilchardus* (European sardine) and *Engraulis encrasicolus* (European anchovy), account for

significant biomass at intermediate trophic levels of Mediterranean Sea food webs and are the main prey resource for several marine predators (Coll et al., 2006; Cury et al., 2000; Pikitch et al., 2012, 2014). Medium pelagic fishes, such as mackerels and horse-mackerels, are also abundant in many pelagic food webs (Juan-Jordá et al., 2013; Leonart and Maynou, 2003). These species can be prey species for higher trophic levels, as well as having top-down effects on small pelagic fish populations (Bayhan et al., 2013; Meneghesso et al., 2013; Trenkel et al., 2014).

Previous studies have described food web dynamics of the pelagic ecosystem in the Mediterranean Sea (see Bănaru et al., 2013; Coll et al., 2006; Corrales et al., 2015); however, little information about specific trophic interactions between small- and medium-sized pelagic fishes has been published. Likewise, although seasonal environmental variability has been shown to affect the population dynamics of small pelagic fishes, few studies have taken into account how this could affect trophic interactions (França et al., 2011; Lloret et al., 2001, 2004; Palomera et al., 2007). In this study we used stable isotope analysis to describe the overall community structure and examine the potential

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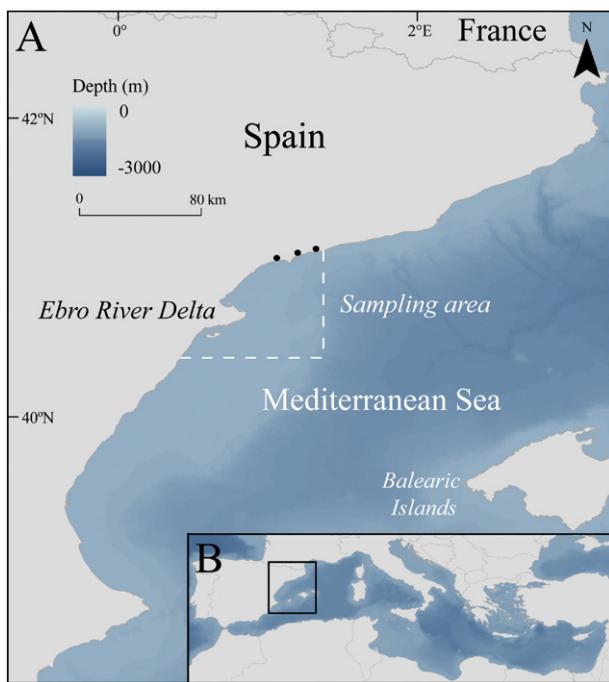


Fig. 1. (A) Map of the study area where the individuals were collected on the Ebro Delta continental shelf, northwestern Mediterranean. The sampling area (dashed line) and the fishing harbors where most of the samples were landed are indicated with (●). (B) Position of the study area in the Mediterranean Basin.

seasonal shifts in trophic interactions of 11 abundant pelagic species in the northwestern Mediterranean Sea. The main objectives were to analyze the specific trophic relationships between species and to compare the relative niche positions among seasons.

2. Material and methods

2.1. Study area

The study was conducted in the continental-shelf and upper slope area associated with the Ebro River Delta, from Cape Salou to Castelló de la Plana (Fig. 1; northwestern Mediterranean Sea). As a consequence of particular oceanographic conditions, including vertical mixing and river discharges, this area is an important fishing ground in the Mediterranean Sea (Coll et al., 2006; Lloret et al., 2004; Navarro et al., 2016). Moreover, it is an important area for threatened animals, including Balearic shearwater, *Puffinus mauretanicus*, Audouin's gull, *Larus audouinii* and loggerhead turtle *Caretta caretta* as well as other predators that also prey on small pelagic fishes (Arcos et al., 2009; Coll et

al., 2015; Tomas et al., 2001). From May to October the ecosystem is characterized by a distinct thermocline and stratification of the water column, resulting in a reduction of nutrients in the photic zone (Salat, 1996). During the stratified season, riverine inputs are the main source of nutrients at the surface (Palomera et al., 2007; Salat et al., 2002). In contrast, from November to April, the water temperature is lower and the water column mixed, leading to higher nutrient availability at the surface (Salat et al., 2002).

2.2. Sampling

We sampled eleven species of small and medium pelagic fishes, squids and potential predators of small pelagic fishes (see Table 1). We only sampled adult individuals to avoid potential ontogenetic differences in the isotopic values, since fish species often have ontogenetic niche shifts (Bode et al., 2004; Chouvelon et al., 2012). A total of 443 individuals were collected (spring 2012, summer 2012, fall 2012 and winter 2013) from commercial vessels of the harbors of Tarragona, Torredembarra and Cambrils (Fig. 1), as well as from an experimental oceanographic cruise in winter 2013 (ECOTRANS Project, Institut de Ciències del Mar, CSIC). All individuals were immediately frozen after capture and stored at -20°C and then the morphological measurements (total body weight and total body length) and tissue collection were conducted in the laboratory. During the experimental oceanographic cruise in winter 2013, samples of microplankton were collected with a calVET net (53–200 μm) and frozen and stored at -20°C .

2.3. Stable isotope analyses

Over the last few decades, stable isotope analyses have been broadly used to study the structure of food webs and trace energy and mass flows in ecosystems (Layman et al., 2012). Particularly, ^{13}C and ^{15}N are stable isotopes commonly used to study trophic pathways. $\delta^{13}\text{C}$ may vary substantially among primary producers, but shows little change from prey to consumers; alternatively, $\delta^{15}\text{N}$ reflects stepwise enrichment with each trophic level. Therefore, $\delta^{13}\text{C}$ is often used as a proxy of the original source of dietary carbon and $\delta^{15}\text{N}$ as a proxy of relative trophic position (Layman et al., 2012).

A small portion of the dorsal muscle from fish species, and of the mantle from squid species, was dissected from each individual. All samples were freeze-dried, powdered and 0.28–0.33 mg of each sample was packed into tin capsules. Isotopic analyses were performed at the Laboratory of Stable Isotopes of the Estación Biológica de Doñana (www.ebd.csic.es/lie/index.html). 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 analyser interfaced with a Delta V Advantage mass spectrometer. Stable isotope ratios were expressed in the standard δ -notation (‰) where $\delta^{13}\text{C}$ or $\delta^{15}\text{N} = ([R_{\text{sample}} / R_{\text{standard}}] - 1) \cdot 1000$ where R is $^{13}\text{C} : ^{12}\text{C}$ or $^{15}\text{N} : ^{14}\text{N}$ relative to Vienna Pee Dee Belemnite ($\delta^{13}\text{C}$) and atmospheric N_2 ($\delta^{15}\text{N}$). Based on laboratory standards, the measurement error was ± 0.1 and ± 0.2

Table 1

Main prey of focal species as based on previous literature reports in the Mediterranean Sea.

Species name	Main prey	References
<i>Engraulis encrasicolus</i>	Copepods, cladocerans	Costalago et al., 2012; Tudela and Palomera, 1997
<i>Sardina pilchardus</i>	Copepods, cladocerans, diatoms	Costalago and Palomera, 2014; Nikolioudakis et al., 2012
<i>Sardinella aurita</i>	Copepods, decapods larvae, fish larvae	Karache and Stergiou, 2014; Lomiri et al., 2008
<i>Trachurus mediterraneus</i>	Copepods, euphasiids, fish	Bayhan et al., 2013; Yankova et al., 2008
<i>Trachurus trachurus</i>	Copepods, euphasiids, fish	Jardas et al., 2004; Šantić et al., 2005
<i>Scomber scombrus</i>	Euphasiids, decapod larvae, fish	Olaso et al., 2005
<i>Scomber colias</i>	Copepods, mysids, decapod larvae, fish	Castro, 1993; Keč et al., 2012
<i>Illex coindetii</i>	Fish, crustaceans	Martínez-Baena et al., 2016; Rosas-Luis et al., 2014
<i>Loligo vulgaris</i>	Fish, crustaceans, cephalopods	Valls et al., 2015
<i>Merluccius merluccius</i>	Benthopelagic and pelagic fish, decapods, euphausiids	Bozzano et al., 1997; Cartes et al., 2004
<i>Sarda sarda</i>	Small pelagic fish	Campo et al., 2006; Navarro et al., in press

Table 2

Mean and standard deviation of $\delta^{15}\text{N}$ and $\delta^{13}\text{C}$ values, total body length values (BL; cm) and estimated trophic level (TL) of small pelagic fish, medium pelagic fish, squids and large pelagic and demersal fish species during spring, summer, fall, and winter, along with the number of specimens sampled (n). Cells corresponding to *T. trachurus* not sampled in summer are indicated with nd (no data).

Species	Spring 2012				Summer 2012					
	n	$\delta^{15}\text{N}(\text{\textperthousand})$	$\delta^{13}\text{C}(\text{\textperthousand})$	BL (cm)	TL	n	$\delta^{15}\text{N}(\text{\textperthousand})$	$\delta^{13}\text{C}(\text{\textperthousand})$	BL (cm)	TL
<i>E. encrasiculus</i>	14	8.0 ± 0.4	-19.3 ± 0.3	13.9 ± 1.9	2.9 ± 0.1	10	8.1 ± 0.3	-19.0 ± 0.2	14.5 ± 1.2	2.9 ± 0.1
<i>S. pilchardus</i>	10	7.8 ± 0.6	-19.6 ± 0.6	17.9 ± 0.6	2.8 ± 0.2	11	8.1 ± 0.3	-20.0 ± 0.4	15.7 ± 1.2	2.9 ± 0.1
<i>S. aurita</i>	10	8.7 ± 0.4	-18.7 ± 0.2	23.6 ± 1.5	3.1 ± 0.1	14	9.0 ± 0.4	-18.7 ± 0.1	20.7 ± 3.5	3.2 ± 0.1
<i>T. trachurus</i>	10	9.0 ± 0.4	-19.0 ± 0.3	24.5 ± 1.9	3.2 ± 0.1	nd	nd	nd	nd	nd
<i>T. mediterraneus</i>	17	10.0 ± 0.6	-18.4 ± 0.3	26.3 ± 4.4	3.5 ± 0.2	10	10.5 ± 0.3	-18.2 ± 0.3	33.4 ± 2.0	3.6 ± 0.1
<i>S. scombrus</i>	7	9.9 ± 0.4	-18.6 ± 0.3	31.5 ± 5.3	3.5 ± 0.1	19	10.6 ± 0.4	-19.2 ± 1.4 ^a	28.4 ± 3.5	3.7 ± 0.1
<i>S. colias</i>	11	9.0 ± 0.3	-19.1 ± 0.6	33.4 ± 3.6	3.2 ± 0.1	10	10.0 ± 0.2	-18.4 ± 0.3 ^a	35.1 ± 1.6	3.5 ± 0.0
<i>I. coindetii</i>	11	8.0 ± 0.5	-19.2 ± 0.3	17.1 ± 1.7	2.9 ± 0.1	4	9.6 ± 0.3	-18.4 ± 0.1	13.3 ± 0.4	3.4 ± 0.1
<i>L. vulgaris</i>	12	11.4 ± 0.6	-18.0 ± 0.3	20.3 ± 3.6	3.9 ± 0.2	6	11.3 ± 0.4	-17.9 ± 0.4	17.2 ± 1.4	3.9 ± 0.1
<i>M. merluccius</i>	7	10.7 ± 0.6	-18.5 ± 0.3	49.3 ± 2.8	3.7 ± 0.2	6	10.4 ± 0.5	-18.3 ± 0.5	43.2 ± 6.2	3.6 ± 0.2
<i>S. sarda</i>	13	10.8 ± 1.0	-17.7 ± 0.4	47.3 ± 3.5	3.7 ± 0.3	9	11.4 ± 0.5	-17.9 ± 0.8 ^a	47.7 ± 7.5	3.9 ± 0.1
Fall 2012										
Species	n	$\delta^{15}\text{N}(\text{\textperthousand})$	$\delta^{13}\text{C}(\text{\textperthousand})$	BL (cm)	TL	n	$\delta^{15}\text{N}(\text{\textperthousand})$	$\delta^{13}\text{C}(\text{\textperthousand})$	BL (cm)	TL
<i>E. encrasiculus</i>	10	8.1 ± 0.2	-18.8 ± 0.2	14.0 ± 1.3	2.9 ± 0.1	11	8.2 ± 0.2	-19.3 ± 0.2	14.0 ± 0.8	3.0 ± 0.1
<i>S. pilchardus</i>	8	8.2 ± 0.3	-19.4 ± 0.6	17.7 ± 1.0	3.0 ± 0.1	9	8.1 ± 0.4	-19.2 ± 0.4	12.9 ± 0.5	2.9 ± 0.1
<i>S. aurita</i>	10	9.2 ± 0.2	-18.2 ± 0.2	24.0 ± 1.8	3.3 ± 0.1	10	9.2 ± 0.5	-18.5 ± 0.1	23.2 ± 1.1	3.2 ± 0.1
<i>T. trachurus</i>	10	9.3 ± 0.2	-18.6 ± 0.1	24.4 ± 1.9	3.3 ± 0.1	10	9.4 ± 0.8	-19.0 ± 0.4	28.9 ± 4.3	3.3 ± 0.2
<i>T. mediterraneus</i>	19	10.3 ± 0.6	-18.1 ± 0.5	27.6 ± 5.9	3.6 ± 0.2	11	10.6 ± 0.5	-18.4 ± 0.5	29.6 ± 4.5	3.7 ± 0.1
<i>S. scombrus</i>	12	10.3 ± 0.3	-18.6 ± 0.5	31.2 ± 3.1	3.6 ± 0.1	12	9.9 ± 0.5	-18.4 ± 0.3	27.7 ± 1.6	3.5 ± 0.2
<i>S. colias</i>	7	9.9 ± 0.3	-18.0 ± 0.2	35.9 ± 3.2	3.5 ± 0.1	10	9.2 ± 0.3	-18.3 ± 0.5	33.9 ± 3.0	3.2 ± 0.1
<i>I. coindetii</i>	9	9.3 ± 0.4	-18.2 ± 0.3	15.2 ± 1.4	3.3 ± 0.1	12	9.7 ± 0.7	-18.6 ± 0.6	18.2 ± 2.1	3.4 ± 0.2
<i>L. vulgaris</i>	9	10.9 ± 1.0	-17.3 ± 0.6	20.5 ± 2.0	3.8 ± 0.3	12	11.2 ± 0.8	-17.6 ± 0.5	20.1 ± 3.2	3.8 ± 0.2
<i>M. merluccius</i>	8	10.4 ± 1.0	-18.4 ± 0.4	52.0 ± 15.4	3.6 ± 0.3	9	10.4 ± 0.8	-18.4 ± 0.4	39.1 ± 6.3	3.6 ± 0.2
<i>S. sarda</i>	5	10.8 ± 1.3	-18.1 ± 0.9 ^a	46.2 ± 9.2	3.7 ± 0.4	9	11.4 ± 0.3	-18.0 ± 0.7 ^a	44.5 ± 1.0	3.9 ± 0.1

^a Indicates species with lipid corrected $\delta^{13}\text{C}$ values in the corresponding season.

for $\delta^{13}\text{C}$ and $\delta^{15}\text{N}$, respectively. Following Post et al. (2007), a correction to the $\delta^{13}\text{C}$ values was made to account for the presence of lipids on individuals with a C:N ratio higher than 3.5. Three species of the family Scombridae required this correction (5 individuals of *S. scombrus*, $\Delta\delta^{13}\text{C} = 1.11 \pm 0.34$; 4 of *S. colias*, $\Delta\delta^{13}\text{C} = 1.64 \pm 0.85$; and 8 of *S. sarda*, $\Delta\delta^{13}\text{C} = 1.56 \pm 0.19$).

2.4. Estimated trophic level

To estimate the trophic level (TL) of each individual based on isotopic values we used the equation proposed by Vander Zanden and Rasmussen (2001):

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

where $\delta^{15}\text{N}_{\text{consumer}}$ and $\delta^{15}\text{N}_{\text{basal}}$ were, respectively, the $\delta^{15}\text{N}$ values of each individual sampled and the $\delta^{15}\text{N}$ values of microplankton sampled in the oceanographic cruise in winter 2013 (ECOTRANS Project, Institut de Ciències del Mar, CSIC) ($\delta^{15}\text{N}_{\text{basal}} = 3.25 \pm 0.62$). Microplankton samples for other seasons were not available. We applied a basal trophic level (TL_{basal}) of 1.5 assuming that the microplankton is mostly composed by phytoplankton (primary producers; TL = 1) and micro- and mesozooplankton (typically primary consumers; TL = 2) (Costalago et al., 2012). Due to the lack of specific diet tissue discrimination factors associated with trophic transfers ($\Delta\delta^{15}\text{N}$) for the species studied in the present study, we used a conventional $\Delta\delta^{15}\text{N}$ of 3.4 (Post, 2002) to keep our results comparable with previous works in the northwestern Mediterranean Sea (e.g., Polunin et al., 2001; Valls et al., 2014; Costalago et al., 2012). We are aware that using a single isotopic baseline and $\Delta\delta^{15}\text{N}$ induces sources of potential bias into our data set. Yet, we are not attempting herein to make definitive estimates of trophic positions. We instead are interested in relative comparisons among species and to identify apparent general patterns in trophic structure (see Layman et al., 2005 for a similar general approach). We hope that

these preliminary data will help generate new hypotheses that can be more rigorously tested with refined baseline values and species-specific tissue turnover data.

2.5. Seasonal variability

Differences in $\delta^{15}\text{N}$ and $\delta^{13}\text{C}$ values among seasons for each species were tested using one-way semi-parametric permutation multivariate analyses of variance tests (PERMANOVA test) on the Euclidean distance matrix (Anderson et al., 2008). PERMANOVA allows for the analysis of complex designs (multiple factors and their interaction) without the constraints of multivariate normality, homoscedasticity, and when there are a greater number of variables than in traditional ANOVA tests. The method calculates a pseudo-F statistic directly analogous to the traditional F-statistic for multifactorial univariate ANOVA models, using permutation procedures to obtain P-values for each term in the model (Anderson et al., 2008). In the case of a significant result, pairwise tests were performed. PERMANOVA tests were carried out with PRIMER-E 6 software (Clarke and Gorley, 2006). The significance level for all tests was adopted at $P < 0.05$.

2.6. Trophic niche width

To provide insight into species' trophic niche width, and to estimate the degree of isotopic niche overlap between species, we calculated Bayesian isotopic ellipse areas corrected by sample size (SEA_B) (Jackson et al., 2011). This metric represents a measure of the core isotopic niche with higher values indicating broader trophic niche breadth (Layman et al., 2012). Isotopic standard ellipse areas and their overlap were calculated using the routine Stable Isotope Bayesian Ellipses in the SIAR library (SIBER; Jackson et al., 2011).

The isotopic niche position (centroid location) of the species was evaluated to determine whether isotopic niche position differed between species. To obtain measures of central tendency of each species we used nested linear models and residual permutation procedures.

Then, Euclidian distances between centroids (bivariate means) were calculated. Two species can be assumed to occupy a different isotopic niche position if the Euclidian distance is significantly greater than zero (for additional details and R code for the test see Turner et al., 2010).

We also used the isotope data to explore potential predators on the anchovy and sardine. All $\delta^{15}\text{N}$ and $\delta^{13}\text{C}$ values for each sardine and anchovy species were corrected by diet tissue discrimination factors of +3.4 and +1.3 for $\delta^{15}\text{N}$ and $\delta^{13}\text{C}$ values, respectively (Post, 2002). The convex hull polygon containing all the corrected $\delta^{15}\text{N}$ and $\delta^{13}\text{C}$ isotopic values of sardine and anchovy was then plotted. Predator species that had an ellipse overlap with a convex hull polygon were assumed to be potential predators of sardine and anchovy.

3. Results

3.1. Trophic structure

Across sampling periods the relative position of species appeared fairly consistent; there were no major shifts in the relative position of species across seasons. *S. pilchardus* and *E. encrasicolus* had the lowest estimated trophic levels with the lowest $\delta^{15}\text{N}$ and $\delta^{13}\text{C}$ values and mean estimated trophic levels in both species of 2.9 ± 0.1 (Table 2; Fig. 2). *S. aurita* had higher $\delta^{15}\text{N}$ and $\delta^{13}\text{C}$ values than the other two small pelagic fishes (a mean estimated trophic level of 3.2 ± 0.1 ; Table 2; Fig. 2). Mackerels and horse mackerels, *T. trachurus* and *S. colias* both had a mean estimated trophic level of 3.3 ± 0.2 , while *T.*

mediterraneus and *S. scombrus* had an estimated trophic level of 3.6 ± 0.2 and 3.6 ± 0.1 , respectively. The two squid species seemed to have different isotopic niches, with *I. coindetii* having lower values of $\delta^{15}\text{N}$ and $\delta^{13}\text{C}$ than *L. vulgaris* (estimated TL = 3.2 ± 0.3 for *I. coindetii* and TL = 3.8 ± 0.2 for *L. vulgaris*; Fig. 2; Table 2). *M. merluccius*, *S. sarda* and *L. vulgaris* had the highest $\delta^{15}\text{N}$ values of the species studied, with estimated trophic levels close to 4 (Table 2; Fig. 2).

3.2. Species seasonal variability

Only the predators *L. vulgaris*, *M. merluccius* and *S. sarda* did not have distinct seasonal differences in $\delta^{15}\text{N}$ and $\delta^{13}\text{C}$ values (Table 3). Differences for other species were small suggesting no major seasonal shifts in trophic structure. For each species, the range of seasonal variation was 0.2 to 0.7 for $\delta^{15}\text{N}$ and of 0.2 to 0.8 for $\delta^{13}\text{C}$, with the exception of *S. colias* ($\Delta\delta^{15}\text{N} = 1.0$; $\Delta\delta^{13}\text{C} = 1.1$) and *I. coindetii* ($\Delta\delta^{15}\text{N} = 1.7$; $\Delta\delta^{13}\text{C} = 1.0$) (Fig. 3). In most species the mean seasonal variability in the estimated trophic level was not >0.2 . *I. coindetii* had the highest change, a mean difference of 0.5 between spring and the rest of the seasons (Fig. 3). Data for $\delta^{15}\text{N}$, $\delta^{13}\text{C}$, body length and estimated trophic level are reported in Table 2.

3.3. Isotopic niche overlap

Isotopic niche width seemed larger for species positioned higher in the food web (Fig. 4). The epipelagic fish *S. sarda* had the largest isotopic niche width, while *E. encrasicolus* and *S. aurita* had relatively small ones (Fig. 4). The four medium pelagic fish species and *M. merluccius* had

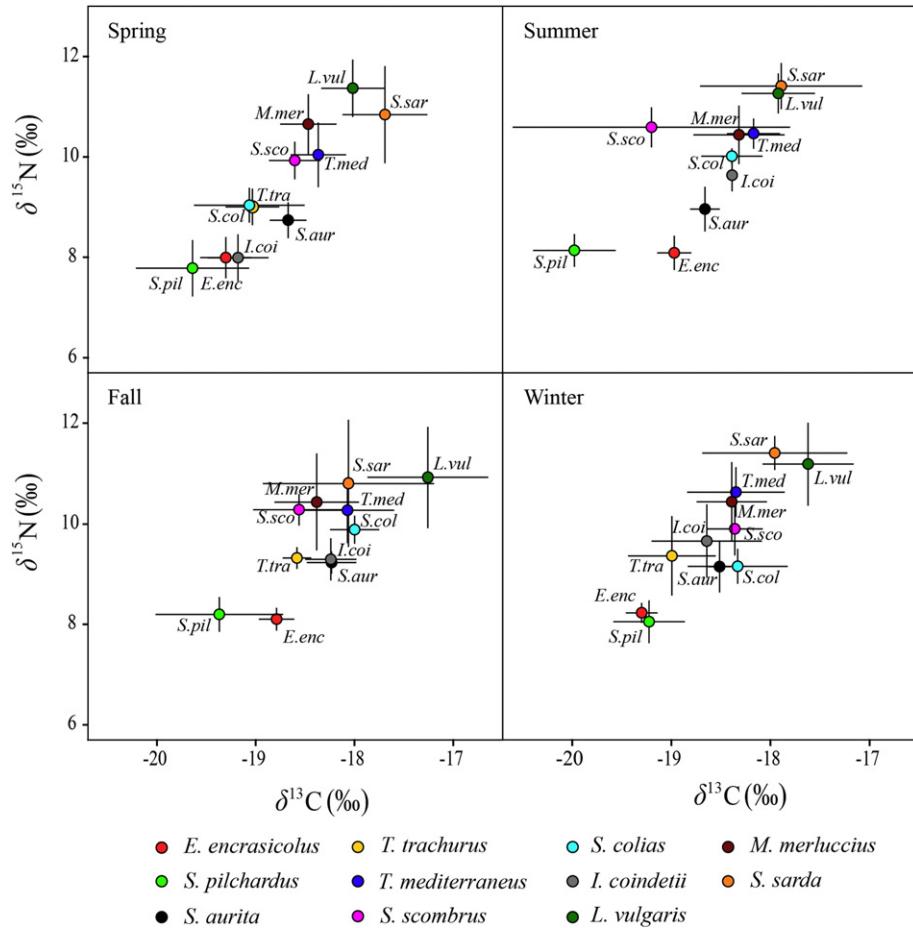


Fig. 2. Mean and standard deviation of $\delta^{13}\text{C}$ and $\delta^{15}\text{N}$ values of each species during spring, summer, fall, and winter.

similar isotopic niche widths across seasons, with the exception of *T. trachurus* and *S. scombrus* which had a larger isotopic niche width in winter and in summer, respectively (Fig. 4). For squid, the niche width of *L. vulgaris* was larger than that of *I. coindetii* (Fig. 4).

Most species had some trophic niche overlap with at least one other species (Table 4; Fig. 5). However, the isotopic niche position between species overlapping was significantly different, suggesting distinct trophic roles within this food web (Table 4). In general, summer had the least, and winter the most, niche overlap between species pairs. In spring and winter, *E. encrasiculus* and *S. pilchardus* had a similar isotopic niche position, whereas they appeared rather different during summer. *S. aurita* was distinct from the other small pelagic fish species in all seasons (Table 4; Fig. 5).

Among the four species of medium pelagic fishes, *T. trachurus* had a high isotopic niche overlap with *S. colias* in spring, while *T. mediterraneus* overlapped substantially with *S. scombrus* in all seasons (Table 4; Fig. 5). The two squid species had distinct isotopic niches across all seasons. *I. coindetii* had high isotopic niche overlap with several species of small and medium pelagic fishes, depending on the season, whereas *L. vulgaris* had a more similar niche position to *S. sarda* (Table 4; Fig. 5).

Following correction for diet-tissue discrimination factors, the convex hull of anchovy and sardine partially overlapped the isotopic niche of *S. sarda*, *L. vulgaris*, and *M. merluccius* in almost all seasons, suggesting that these may be the most likely predators on sardine and anchovy (Fig. 5).

4. Discussion

Consistent with the fact that *S. pilchardus* and *E. encrasiculus* are plankton feeders (Costalago and Palomera, 2014; Costalago et al., 2012; Tudela and Palomera, 1997), our results indicated that they had the lowest trophic position of all the species studied. Similar to previous studies (Cardona et al., 2015; Costalago et al., 2012; Le Bourg et al., 2015), *S. pilchardus* and *E. encrasiculus* showed a similar trophic niche position with a large overlap of their core isotopic niches. However, during summer, the species seemed to partition resources, occupying different positions along the $\delta^{13}\text{C}$ axis. This is consistent with previous studies in the northwestern Mediterranean that have found that in summer *S. pilchardus* preyed more on cladocerans and appendicularians (with depleted values of $\delta^{13}\text{C}$), while *E. encrasiculus* prey more on copepods (Costalago et al., 2012, 2015; Tudela and Palomera, 1997). Moreover, lower dietary overlap between sardine and anchovy has been observed in areas and periods of high biological productivity (Chouvelon et al., 2015; Jemaa et al., 2015). Thus, the higher trophic niche segregation observed between sardine and anchovy in summer

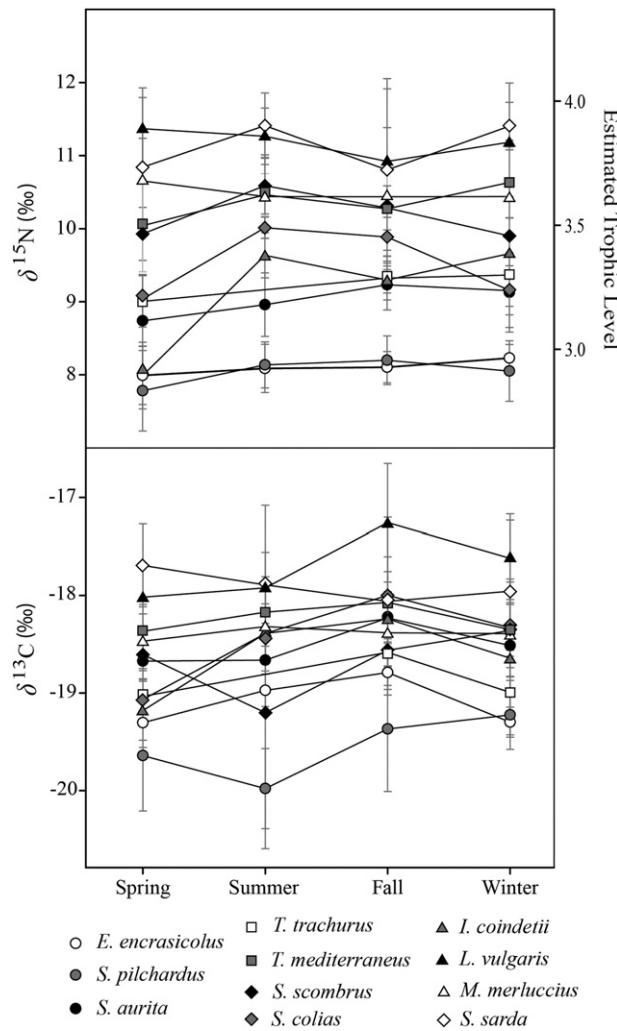


Fig. 3. Seasonal variation of the mean and standard deviation of $\delta^{15}\text{N}$, estimated trophic level and $\delta^{13}\text{C}$ values by season of each focal species.

may be explained by greater variety of food resources, largely as a consequence of the Ebro River discharges that contribute to the early spring phytoplankton bloom.

The larger isotopic niche width of *S. pilchardus* suggests that it may feed on a broader range of prey. Previous studies showed that *S. pilchardus* is an opportunistic feeder with a greater filtering capacity than *E. encrasiculus* due to a higher number of gill-rakers that allow *S. pilchardus* to prey on diatoms, whereas diatoms have not been reported in the diet of *E. encrasiculus* at adult stages (Costalago and Palomera, 2014; Costalago et al., 2014; Pethybridge et al., 2014). *S. aurita* is a species that has been described as a plankton feeder similar to *S. pilchardus* and *E. encrasiculus* (Karachle and Stergiou, 2014; Lomiri et al., 2008). However, the clear trophic segregation and higher trophic position of *S. aurita* from *S. pilchardus* and *E. encrasiculus*, suggests that *S. aurita* may prey on larger zooplankton or larvae of other small pelagic fishes (Lomiri et al., 2008).

Contrary to what we expected, there were differences in the isotopic niches between species within the genera *Trachurus* and *Scomber*. This segregation between congeneric species could be explained by either differences in the feeding habits or differences in spatial distribution. A dietary difference may be more likely for *Scomber* species, as it has been described that *S. scombrus* in the Atlantic preyed mainly on euphausiids and fishes, whereas for *S. colias* one of the most important prey in the Mediterranean was mysids (Keč et al., 2012; Olaso et al.,

Table 3

PERMANOVA test results (Pseudo-F values) of significant differences for $\delta^{15}\text{N}$ and $\delta^{13}\text{C}$ values between seasons for each species. Means differing significantly ($P < 0.05$) by pairwise tests are indicated by the letters – seasons with the same letter were not significantly different. Cells corresponding to *T. trachurus* not sampled in summer are indicated with nd (no data). There were no differences among seasons for *L. vulgaris*, *M. merluccius* and *S. sarda*.

Species	Pseudo-F (p -value)	Spring	Summer	Fall	Winter
<i>E. encrasiculus</i>	6.32 (<0.01)	a	b	b	a
<i>S. pilchardus</i>	3.37 (<0.01)	a, b, c	a	b	c
<i>S. aurita</i>	5.07 (<0.01)	a	a, b	c	b,c
<i>T. trachurus</i>	2.90 (0.02)	a	nd	b	a,b
<i>T. mediterraneus</i>	2.58 (0.04)	a	a, b	a, b	b
<i>S. scombrus</i>	3.56 (<0.01)	a, b	a	a	b
<i>S. colias</i>	15.82 (<0.01)	a	b	c	d
<i>I. coindetii</i>	17.72 (<0.01)	a	b	b	b
<i>L. vulgaris</i>	1.97 (0.09)				
<i>M. merluccius</i>	0.15 (0.96)				
<i>S. sarda</i>	1.14 (0.35)				

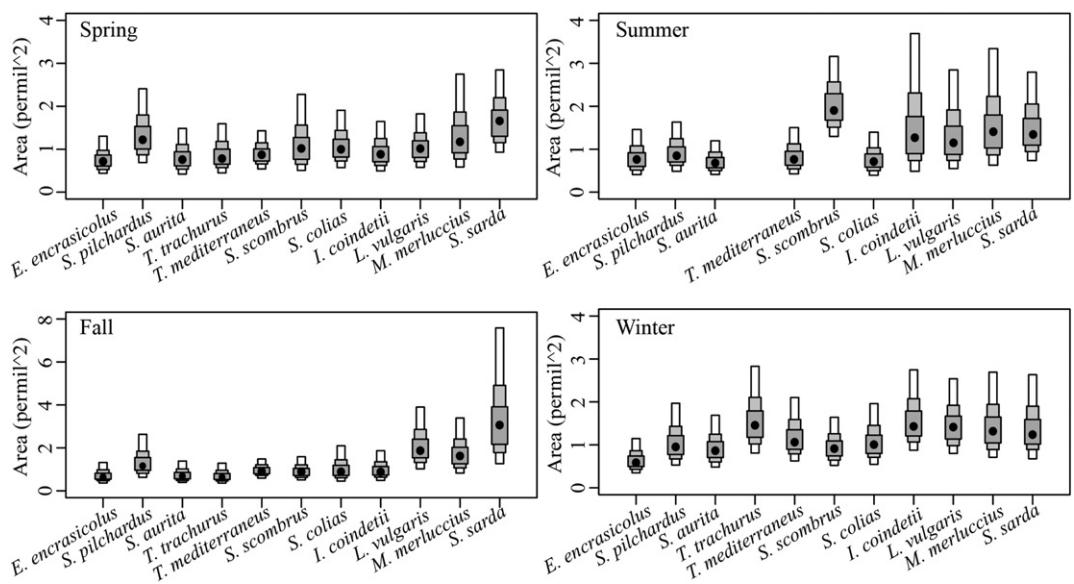


Fig. 4. Density plot of the standard ellipse areas of each species and for each season. Black points correspond to the mean standard ellipse area, while boxes show 50%, 75% and 95% credible intervals for mean estimates.

2005). If in the Mediterranean Sea *S. scombrus* has also a higher predation rate on fish than *S. colias*, then, this could explain the higher trophic level of *S. scombrus* (Polunin et al., 2001). Alternatively for the *Trachurus* species, Lloris and Moreno (1995) suggested that *T. mediterraneus* is located more commonly in shallow coastal areas, while *T. trachurus* has a wider distribution and often a more benthic behavior. Thus, the isotopic segregation between *Trachurus* spp. may be due to higher $\delta^{15}\text{N}$ of primary producers in coastal areas as a consequence of the dissolved nutrients and particulate organic matter (POM) in river plumes (Radabaugh

et al., 2013). Further dietary studies for both genera are needed to clarify the most plausible explanation(s).

Our results are consistent with previous studies in showing that squids have a broad trophic width in marine food webs (Coll et al., 2013; Navarro et al., 2013). *I. coindetii* and *L. vulgaris* seem to have different trophic roles, with the former occupying lower positions in the food web with isotopic values closer to small pelagic fishes, and the latter apparently positioned higher in the food web and being a potential predator of anchovy and sardine. These differences are in accordance

Table 4
Percentage values of overlap of the Bayesian isotopic ellipses between each pair of species for each season. Overlaps of 0% are indicated with a dash. Pairs with isotopic niche positions that were not significant differently (see Materials and methods; $P > 0.05$) are indicated with a (*). Cells corresponding to *T. trachurus* not sampled in summer are indicated with nd (no data).

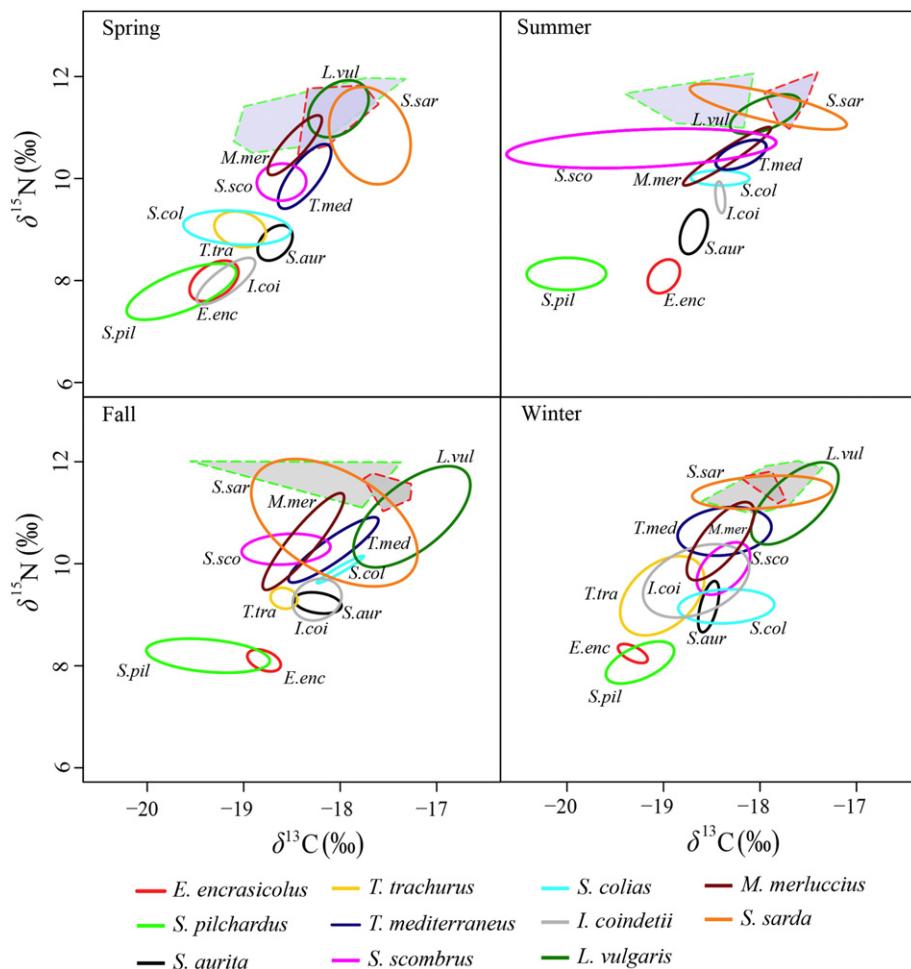


Fig. 5. Standard ellipses for each species during spring, summer, fall, and winter. The grey convex-hull represents the total isotopic area of potential predators of *Engraulis encrasicolus* (red dashed line) and *Sardina pilchardus* (green dashed line), accounting for prey–predator isotopic fractionation of 3.2‰ and 1.3‰ for $\delta^{15}\text{N}$ and $\delta^{13}\text{C}$ values, respectively.

with the dietary habits described for both species. *I. coindetii* has been reported to prey mainly on crustaceans, whereas fish have been described as the main prey of *L. vulgaris* (Martínez-Baena et al., 2016; Rosas-Luis et al., 2014; Valls et al., 2015).

High $\delta^{15}\text{N}$ values and trophic niche overlap for *M. merluccius*, *L. vulgaris* and *S. sarda* suggested that they feed at higher trophic levels than the other species. This is consistent with the fact that *M. merluccius* and *S. sarda* have been described primarily as piscivorous (Cresson et al., 2015; Harmelin-Vivien et al., 2012; Navarro et al. in press). Based on the discrimination corrected values, it is reasonable to infer that *L. vulgaris*, *M. merluccius* and *S. sarda* prey on small pelagic fishes. The three species had a large isotopic niche width probably due to their opportunistic feeding tendencies.

Despite intraspecific seasonal variability for some species, overall community trophic structure appeared relatively stable through the year. That is, *E. encrasiculus* and *S. pilchardus* were positioned at lower trophic levels than the other species studied, mackerels and horse mackerels occupy intermediate positions, and the large pelagic and demersal fish were highest in the web. This study is one of the first steps in understanding the seasonal food web dynamics of the pelagic species in the northwestern Mediterranean Sea, including novel data sets, e.g., some of the first isotope data on pelagic fishes and squids in the Mediterranean Sea that cover all seasons. More research is needed in this area, as many questions remained unanswered, especially according to how spatial variability affects the inferred trophic structure of this system. In particular, stronger isotopic baselines are needed, migratory behavior needs to be more well-documented, and abiotic drivers of

dietary patterns need to be developed. Such data are of upmost importance to better manage stocks of these species.

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