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Trophic niche overlap of sprat and commercial small pelagic teleosts in the Gulf of Lions (NW Mediterranean Sea)

Le Bourg B. [1], Banaru Daniela [1, *], Saraux Claire [2], Nowaczyk A. [1, 3], Le Luherne E. [1, 4], Jadaud Angelique [2], Bigot Jean-Louis [2], Richard P. [5]

[1] Aix Marseille Univ, CNRS INSU, IRD, MIO, F-13288 Marseille, France.
[2] IFREMER, CRH, UMR MARBEC IRD IFREMER UM CNRS, F-34203 Sete, France.
[3] Univ Bordeaux, UMR CNRS EPOC OASU 5805, F-33120 Arcachon, France.
[4] Agrocampus Ouest, ESE Ecol & Sante Ecosyst UMR985, F-35042 Rennes, France.
[5] Univ La Rochelle, UMR CNRS LIENSs 7266, F-17000 La Rochelle, France.

* Corresponding author: Daniela Banaru, email address : daniela.banaru@univ-amu.fr ;

lebourg.bap@orange.fr ; Claire.Saraux@ifremer.fr ; a.nowaczyk@epoc.u-bordeaux1.fr ; emilie.leluherne@agrocampus-ouest.fr ; Angelique.Jadaud@ifremer.fr ; Jean-Louis.Bigot@ifremer.fr ; pierre.richard01@univ-lr.fr

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Abstract :

Increasing abundance of non-commercial sprats and decreasing biomass and landings of commercial anchovies and sardines justify the need to study the feeding ecology and trophic niche overlap of these planktivorous species in the Gulf of Lions. Their diet has been investigated on the basis of stomach content and stable isotope analyses in 2011 and 2012 according to different depths and regions in the study area. The main prey were Corycaeidae copepods, Clauso/Paracalanus, Euterpina acutifrons and Microsetella, for sprats and small copepods, such as Microsetella, Oncaea and Corycaeidae, for anchovies and sardines. This is the first time that the diet of sprats is described in the Gulf of Lions. Sprats fed on a larger size spectrum of prey and seem to be more generalist feeders compared to anchovies and sardines. Ontogenetic changes as well as spatial and temporal variations of the diet occurred in the three species. Stable isotope analysis revealed mobility of sardines and sprats among feeding areas while anchovies exhibited preferred feeding areas. Sprats showed a higher relative condition assessed by C/N ratios than sardines and anchovies. Our results showed an overlap of the trophic niches for the three species, indicating a potential trophic competition in the Gulf of Lions.

Highlights

► Sprats' diet was described for the first time in the NW Mediterranean Sea. ► There was a high trophic overlap for sardines, anchovies and sprats. ► Spatio-temporal and ontogenetic variations of their diet were described. ► Sprats were more generalist than sardines and anchovies and fed on larger prey. ► Diet particularities may explain the better relative condition of sprats.

Keywords : Anchovies, Sardines, Sprats, North-western Mediterranean sea, Stomach contents, Stable isotopes

1. Introduction

Small pelagic teleosts are key species in ecological systems as they ensure the transfer of organic matter from zooplankton to higher trophic levels (Banaru et al., 2013). They may exert different types of control in marine systems such as bottom-up (Cury et al., 2011), top-down (Köster and Möllmann, 2000; Verheye and Richardson, 1998) or wasp-waist control (Cury et al., 2000).

Traditionally, anchovies (Engraulis encrasicolus; Linnaeus, 1758) and sardines (Sardina pilchardus; Walbaum, 1792) were the two main pelagic teleosts in the Gulf of Lions (North-West Mediterranean Sea) in terms of biomass and represent target and commercial species for the fishing industry (Banaru et al., 2013). However, anchovy and sardine landings have declined since 2005 and fishing activity has been reduced to an exploratory activity in 2010. Anchovies and sardines are still abundant but their biomasses and size have decreased, which lowers their commercial value. Furthermore, there has been an unusual increase of non-commercial sprat (Sprattus sprattus; Linnaeus, 1758) abundance since 2008 (Van Beveren et al., 2014). A recent decline was reported in body condition and growth of anchovies and sardines (Van Beveren et al., 2014) which might be linked to changes in their diet compared to past studies (Costalago and Palomera, 2014; Plounevez and Champalbert, 2000) and/or to trophic interactions with sprats. Indeed, the abundance of prey seems to be one of the main environmental drivers of body condition in these species (Brosset et al., in press). The three species are zooplanktivorous and may be competitors for food in the study area. Moreover, there is significant overlap in their spatial distribution (Saraux et al., 2014) but no data are available concerning their trophic interactions in this area. No qualitative or quantitative data on the zooplankton community are available to show eventual changes in the availability of the resources during the last period. Consequently, studies on their feeding behaviour and interactions are necessary to understand the origin of the recent shifts in the pelagic ecosystem of the Gulf of Lions.

Stomach content analysis is a well-known method to study the trophic ecology of teleosts and provides a qualitative and quantitative snapshot of the diet (Hyslop, 1980). Ratios of nitrogen and carbon isotopes (^{14}N:^{15}N , $\delta^{15}N$; ^{12}C:^{13}C , $\delta^{13}C$) are used to determine feeding areas and primary sources of carbon in food-web (Hobson, 1999; Michener and Kaufman, 2007). Stable isotope analyses allow longer-term study of the diet of organisms and identification of changes in feeding sources and areas. Carbon/nitrogen (C/N) ratios measured with stable isotope ratios are a proxy of the lipid content of organisms (Dempson et al., 2010; Logan et al., 2008; Post et al., 2007; Sweeting et al., 2006) and thus can be used as indicators of the relative condition.

Some studies on the trophic ecology of small pelagic teleosts of the European coasts have been previously conducted using stomach content analyses (e.g. Costalago and Palomera, 2014; Costalago et al., 2014; Garrido et al., 2008; Plounevez and Champalbert, 2000; Tičina et al., 2000) and stable isotopes (e.g. Bode et al., 2004; Chouvelon et al., 2014; Costalago et al., 2012), but few studies have combined the two approaches (Pasquaud et al., 2008) and none of them in the study area. Moreover, the last diet studies based on stomach content analysis of adult anchovies and sardines in the Gulf of Lions were performed in 1995-1996 by Plounevez and Champalbert (2000), and in 2007 by Costalago and Palomera (2014), when these species had higher condition values (Brosset et al., in press; Van Beveren et al., 2014) and before the fall of their biomass. No data on the trophic ecology of *S. sprattus* is available for the North-Western Mediterranean Sea.

The aim of this study was to combine the methods of stomach content analysis and stable isotopes to describe the trophic ecology, niche width and diet overlap of anchovies (*E. encrasicolus*), sardines (*S. pilchardus*) and sprats (*S. sprattus*) in the Gulf of Lions to infer the potential interactions between the three species. In addition, this is the first time that spatial variations in the diet of these species related to their stable isotope ratios were described in the North-Western Mediterranean Sea.

2. Material and methods

2.1. Study area and sampling

The Gulf of Lions has a wide continental shelf. It is a mesotrophic area influenced by Rhône river inputs and the northern current flowing southwestwards along the continental slope (Espinasse et al., 2014a). Consequently, concentrations of nutrients in water and sediments decrease from east to west and from coast to continental shelf (Cruzado and Velasquez, 1990; Denis and Grenz, 2003; Van Den Broeck and Moutin, 2002). Furthermore, river inputs influence isotopic ratios of particulate organic matter and phytoplankton with higher $\delta^{15}N$ and lower $\delta^{13}C$ in waters influenced by the Rhône plume (Harmelin-Vivien et al., 2008). Espinasse et al. (2014a) divided the gulf into three habitat types: the western part of the coast, most of the eastern area of the gulf influenced by Rhône river (the coast and a part of the continental shelf), and the continental shelf (except in eastern areas where river inputs are high). In the present study, the gulf has been divided into two depth zones (coastal areas and continental shelf) separated by the 50 metres isobath and three regions (west, centre and east) according to the spatial changes of environmental conditions (Espinasse et al., 2014a; Harmelin-Vivien et al., 2008 Fig. 1).

Teleosts were sampled in June and July 2011 and 2012 during the IFREMER MEDITS and PELMED campaigns aboard the IFREMER R.V. ‘l’Europe’. In addition, small juvenile sardines were sampled in May 2011 by beach seining near the Rhône estuary. Sampled teleosts were immediately frozen to avoid digestion. In the laboratory, the following measurements were taken on each teleost: total length (TL) to the nearest 1 mm and total body weight (TW). Stomachs were extracted and preserved in 95° alcohol. Eviscerated body weight (EW) was measured. Anterior dorsal muscles of teleosts were sampled and freeze-dried for subsequent stable isotope analyses.

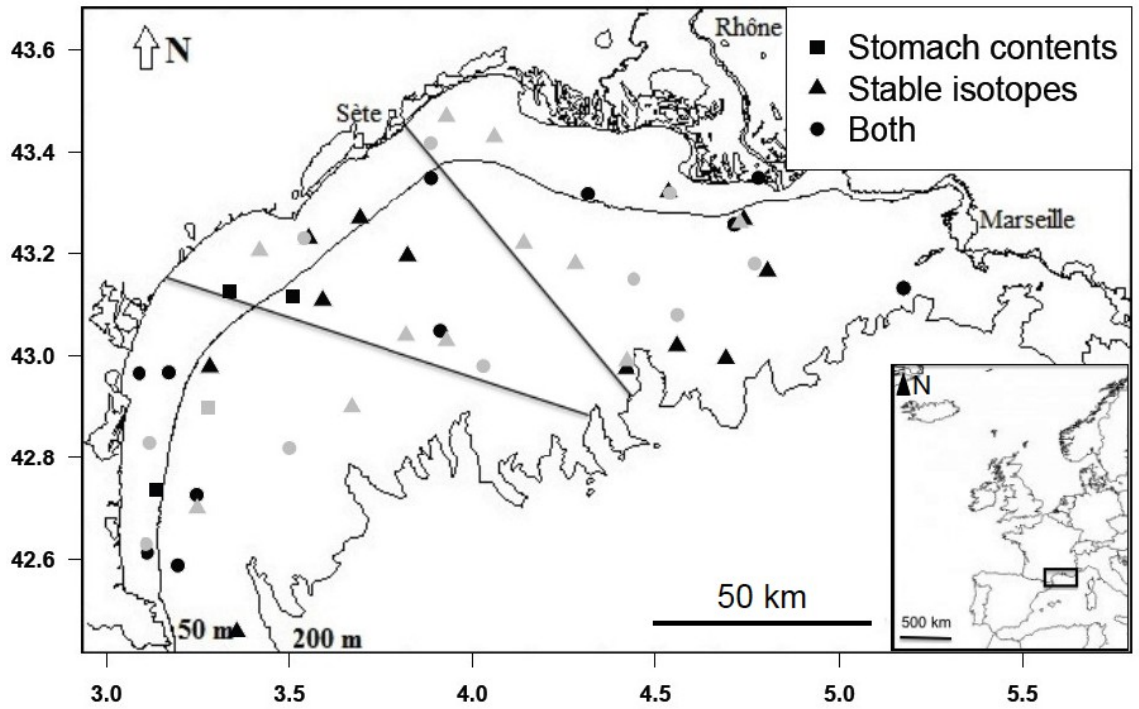

Fig. 1. Location of sampling stations in the Gulf of Lions selected for stomach content analysis and/or stable isotope analysis in 2011 (black) and 2012 (grey). The 50 metre isobath separates coastal areas and the continental shelf. The lines separate the regions west, centre and east.

2.2. Stomach content analysis

We chose individuals of the different available size classes (1 cm interval) for each depth and region. Selected stomach contents (117 anchovies, 145 sardines, 166 sprats) (Fig. 1; Table 1.a) were weighted. In each stomach, ingested organisms were identified to genus level (if possible) and counted. Dry weight (DW) of ingested organisms was obtained from the literature (Table A.1). Food composition was expressed by frequency of occurrence (%O; percentage of non-empty stomachs containing a given prey item), numerical percentage (%N; mean percentage per stomach of the number of a given prey item as a proportion of the total number of all prey in each stomach), weight percentage (%W; mean percentage per stomach of the weight of a given prey item as a proportion of the total weight of all prey in each stomach). The index of relative importance (IRI) (Pinkas et al., 1971) was then calculated according to the formula:

$$IRI = \%O \times (\%N + \%W)$$

IRI was then transformed in percentage by dividing it by the sum of IRI for each prey item (%IRI; Cortés, 1997). Niche width (B_G) and diet overlap (%T; Schoener, 1970) were calculated according to formulas:

$$B_G = e^{H'} \text{ with } H' = -\Sigma\ (IRI_{xi} \times \log_2 IRI_{xi})$$

$$\%T = (1-0.5\ \Sigma\ |\%IRI_{xi} - \%IRI_{yi}|) \times 100$$

where $\%IRI_{xi}$ and $\%IRI_{yi}$ are %IRI for the prey item i in the teleost species x and y. Overlap is considered as significant if %T exceeds 60% (Arculeo et al, 1993). %T was also calculated using %W.

Prey were measured for subsamples of the three studied species (82 anchovies, 64 sardines, 58 sprats) for different size classes. Predator/prey size ratios were also estimated for each species.

2.3. Stable isotope analysis

For each species, depth and region, stable isotope ratios were studied in muscle samples of fish collected in various sampling stations (104 anchovies, 101 sardines, 116 sprats) (Fig. 1; Table 1.b). Selected muscle were freeze-dried and then ground into a fine powder. Subsamples were weighed (0.4 to 0.5 mg) in 5×8 tin cups and analysed with a continuous-flow isotope-ratio mass spectrometer (Delta V Advantage, Thermo Scientific) coupled to an elemental analyser (Flash EA 1112, Thermo Scientific). $\delta^{15}N$ and $\delta^{13}C$ were expressed in ‰ according to the formula:

$$\delta X_{sample} = [(R_{sample}/R_{standard}) - 1] \times 1000$$

where X is ^{13}C or ^{15}N, R_{sample} is the isotopic ratio of sample and $R_{standard}$ is the isotopic ratio of standards (atmospheric nitrogen for $\delta^{15}N$ and Pee Dee Belemnite for $\delta^{13}C$).

$\delta^{13}C$ values were corrected for the effects of lipids when the C/N ratio was higher than 3.5 according to the formula developed by Post et al. (2007):

$$\delta^{13}C_{normalised} = \delta^{13}C_{sample} - 3.32 + 0.99 \times C/N$$

In order to study isotopic niches of the three species, standard ellipses were generated and the Standard Ellipse Areas (SEA) were corrected for sample size (SEA_C) using the SIAR package (Stable Isotope Analysis in R, Parnell et al., 2010). The overlap between the ellipses was then determined. Isotopic niche of the three species was estimated by determining areas of the ellipses using the bayesian method (SEA_B) (Jackson et al., 2011).

The relative condition factor was estimated using C/N ratios related to the lipid content.

Table 1

Number and size range (in brackets, cm) of the analysed individuals in the study area for a) stomach content and b) stable isotopes samples.

a)

Species	West		Centre		East	
	Coast	Shelf	Coast	Shelf	Coast	Shelf
E. encrasicolus	26 (9.4-12.5)	18 (8.5-12.3)	22 (8.4-11.6)	7 (9.8-12.7)	15 (8.5-11.7)	29 (9.4-14.0)
S. pilchardus	20 (10.5-14.2)	16 (7.5-14.2)	28 (9.3-12.5)	0	47 (3.9-13.1)	34 (10.4-16.5)
S. sprattus	56 (6.3-10.8)	20 (7.4-10.5)	15 (7.1-10.0)	10 (9.3-10.8)	23 (7.3-10.2)	42 (7.3-11.2)

b)

Species	West		Centre		East	
	Coast	Shelf	Coast	Shelf	Coast	Shelf
E. encrasicolus	11 (8.0-10.3)	16 (8.5-11.6)	9 (3.5-10.3)	12 (9.5-11.1)	15 (8.6-10.3)	41 (8.7-14.0)
S. pilchardus	16 (11.0-13.1)	12 (11.2-15.0)	8 (9.3-12.5)	8 (11.6-14.1)	24 (3.8-14.2)	33 (9.3-16.5)
S. sprattus	11 (6.3-10.7)	24 (8.0-10.2)	15 (7.5-10.3)	12 (9.3-10.1)	18 (6.3-10.0)	36 (8.0-11.0)

2.4. Data analyses

All data analyses were performed with the R statistical software (version 2.15.0).

Classifications (based on Bray-Curtis dissimilarity index) were performed on %IRI in each total length class (1 cm interval) to study ontogenetic shifts in the diet of each species. The same classifications were also applied on %IRI in each zone (defined by region, depth and year of sampling) for each species to study spatial and temporal variations in their diet.

Normality of residuals and homoscedasticity were checked by Shapiro tests, Q-Q plots and Levene tests. Ontogenetic changes in the size classes of prey consumed by anchovies, sardines and sprats were studied with Spearman rank correlation tests (rho) between teleosts total length and individual prey length for each of the three species. Predator/prey size ratios were compared between the three species by Kruskal-Wallis tests (H).

Stable isotope and C/N ratios were compared between the three species by Kruskal-Wallis tests. For each species, Student's t-tests (t), or Wilcoxon tests (W) if data did not fit to a normal distribution pattern, were performed to compare isotopic and C/N ratios between the years 2011 and 2012. Subsequent analyses were performed on separate years or the pooled two years if the year factor was not significant.

Type III analyses of covariances (ANCOVA; F) were performed with the factors length, region, depth and their interaction on isotopic and C/N ratios. The teleosts total length covariate was deleted from the models if its effect on the isotopic and C/N ratios was non-significant. Scheffé post-hoc tests were performed when the region significantly influenced isotopic or C/N ratios.

3. Results

3.1. Diet composition

Proportions of empty stomachs were 11.11% for anchovies, 18.62% for sardines 30.72% for sprats. Fifty-five prey items were identified in the stomachs (anchovies: 43, sardines: 33, sprats: 37). The three species fed mainly on copepods (%IRI = 93.91 for anchovies, 92.08 for sardines and 97.29 for sprats, diet detailed in Table A.2).

Anchovies had the lowest niche width (B_G = 15.52) and their diet was dominated by the copepods *Microsetella* (%IRI = 32.06), *Oncaea* (%IRI = 25.25) and the Corycaeidae family (%IRI = 16.62). *Microsetella* (%IRI = 28.63), *Oncaea* (%IRI = 23.70) and the Corycaeidae family (%IRI = 20.25) also dominated the diet of sardines. Sardines had a higher niche width (B_G = 16.67) than anchovies. Sprats had a more diversified diet (B_G = 17.87) dominated by *Clauso/Paracalanus* (%IRI = 23.41), the Corycaeidae family (%IRI = 19.04), *Euterpina acutifrons* (%IRI = 14.61) and *Microsetella* (%IRI = 10.08).

3.2. Ontogenetic variations in diet

Cluster analyses of teleosts diets (based on %IRI) by size classes are shown in Fig. 2.

Stomach contents show that *Oncaea* was the main prey for 8-10 cm long anchovies, which also fed on *Microsetella*, Corycaeidae copepods and on some unidentified copepods. Anchovies with a 10-12 cm body size consumed mainly *Microsetella*, but also Corycaeidae copepods and *Oncaea*. Larger anchovies (12-13 cm) consumed mainly copepods from the Corycaeidae family (%IRI = 23.05), but also large diatoms (%IRI = 14.67) and the copepod species *Centropages typicus* (%IRI = 12.40). In fact, contribution of diatoms and *Centropages typicus* increased with body length while that of *Oncaea* decreased.

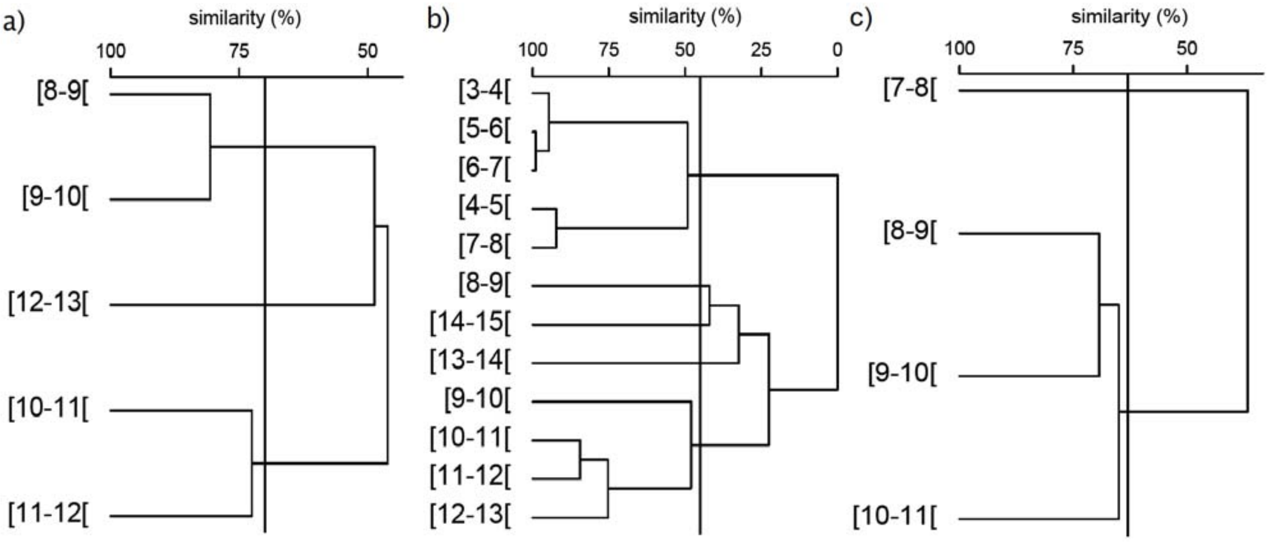

Fig. 2. Cluster analyses of diet similarities (based on %IRI) among size classes (cm) in a) anchovies, b) sardines, c) sprats. The vertical line separates the clusters.

Sardines between 3 and 8 cm consumed mainly suprabenthic mysids (genus *Paramysis*). Unidentified copepods were also consumed by 4-5 and 7-8 cm sardines. Sardines between and 9 and 13 cm fed on *Microsetella* and *Oncaea*. Among those sardines, 9-10 cm individuals fed also on *Euterpina acutifrons* (%IRI = 24.48) and bivalve larvae (%IRI = 12.26) while 10-13 cm sardines fed on Corycaeidae. The size classes 8-9 cm, 13-14 cm and 14-15 cm had unusual diets. The first size class fed on *Microsetella* (%IRI = 36.01) but had high contribution of *Acartia* (%IRI = 16.40) and unidentified copepods (%IRI = 37.06) in its diet. The second size class fed on Corycaeidae (%IRI = 18.85) but also on *Acartia* (%IRI = 25.46), diatoms (%IRI = 21.47) and unidentified copepods (%IRI = 12.24). The last size class fed on *Microsetella* (%IRI = 50.00) but also on diatoms (%IRI = 37.09).

The main prey of small sprats (7-8 cm) were unidentified copepods (%IRI = 48.09). Nevertheless, *Euterpina acutifrons* (%IRI = 16.13), *Oncaea* (%IRI = 11.82) were the most important identified prey items for this body size. Sprats between 8 and 11 cm had a diet dominated by two prey: *Clauso/Paracalanus* and the Corycaeidae. Among 8-11 cm sprats, *Euterpina acutifrons* was also an important prey for sprats between 8 and 10 cm. In fact, the contribution of the Corycaeidae copepods (%IRI from 4.33 to 33.95) increased for larger sprats while that of *Oncaea* decreased (%IRI from 11.82 to 3.51).

3.3. Class lengths of the consumed prey

Anchovies and sardines consumed mainly 0.2-0.6 mm prey (62.97% of all measured prey for anchovies and 52.93% for sardines), the most consumed size class being the 0.4-0.5 mm (20.45% of all measured prey for anchovies and 15.99% for sardines). Sprats fed on slightly larger prey as they consumed mainly 0.3-0.7 mm prey (77.22% of all measured prey) (Fig. 3). The 0.4-0.5 mm size class was once again the most consumed one, but this size class was consumed in larger proportions by sprats than by the two other species (32.31% of all measured prey). Furthermore, the 0.5-0.6 mm size class was also more strongly represented in the diet of sprats (21.94% of all measured prey) than in that of anchovies (10.29%) and sardines (10.23%). There was a peak of occurrence in sardines for the 1.0-1.1 mm size class (9.24% of measured prey) (Fig. 3). Nevertheless, only 11 sardines fed on this size class and the peak resulted from a high number of anchovy eggs (more than 10) in stomachs of 4 sardines in one sampling site. No ontogenetic changes of prey length consumed by anchovies (rho = -0.008, P = 0.738) and sprats (rho = 0.008, P = 0.791) occurred for the analysed individuals. In contrast, size classes consumed by sardines slightly decreased when sardines were larger (rho = -0.276, $P < 0.001$).

Sprats had the lowest predator/prey size ratios (mean ± SD = 176.45 ± 71.14) followed by anchovies (236.67 ± 133.66) and sardines (259.47 ± 191.69) (H = 135.458, $P < 0.001$) (Table 2). Anchovies consumed the largest prey compared to their own size and sardines the smallest. Sardines showed the highest variation between the minimum and the maximum predator/prey size ratios (Table 2).

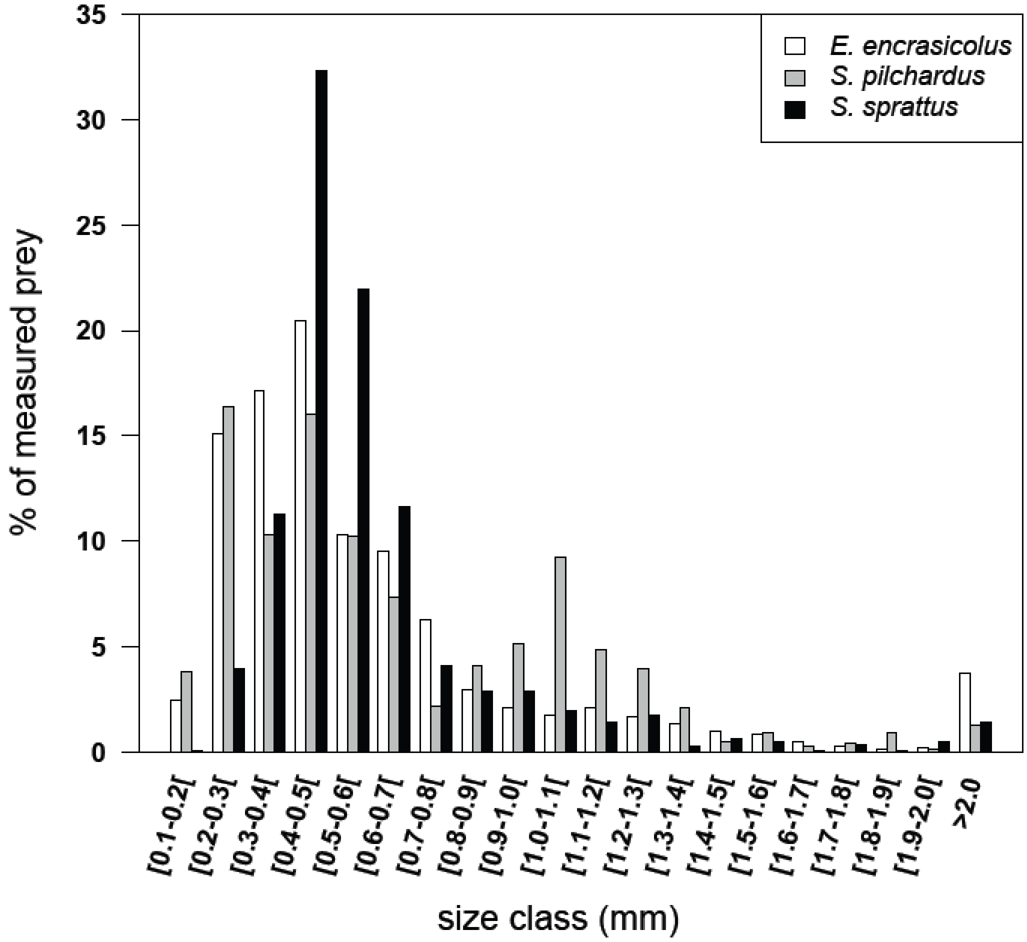

Fig. 3. Proportions of the prey size classes in the stomach content of anchovies, sardines and sprats.

Table 2

Predator/prey size ratios in anchovies, sardines and sprats (N = number of individuals, SD = standard deviation).

Species	Predator lengths (cm)	N predators	N prey	Mean ± SD	Range
E. encrasicolus	Total	82	1604	236.67 ± 133.66	7.15-806.22
	[8-10[	27	640	223.40 ± 123.79	31.92-700.14
	[10-12[	50	865	245.50 ± 137.21	7.15-806.22
	[12-13[	5	99	245.26 ± 156.24	41.52-773.51
S. pilchardus	Total	64	1007	259.47 ± 191.69	13.00-1621.29
	[3-8[	6	33	34.23 ± 26.67	13.00-138.24
	[8-15[	58	974	267.10 ± 190.24	33.87-1621.29
S. sprattus	Total	58	1080	176.45 ± 71.14	21.47-517.05
	[7-8[	6	170	150.91 ± 45.41	21.47-359.45
	[8-11[	52	910	181.22 ± 74.02	26.88-517.05

3.4. Spatial and temporal variations in diet

Dendrograms resulting from hierarchical clustering on teleosts diet similarities (based on %IRI) among region, depth and year are shown in Fig. 4.

Five clusters appeared for anchovies. The first cluster contained all the coastal stations sampled in 2011 and depicted a diet dominated by *Oncaea* (%IRI > 40). The second cluster contained anchovies only sampled in the west, on the shelf in 2011, feeding on Euphausiacean larvae (%IRI = 58.48), *Microsetella* (%IRI = 12.43) and *Clauso/Paracalanus* (%IRI = 11.48). The third cluster contained only zones sampled on the shelf, in 2011 and 2012, and where the diet was dominated by *Microsetella* (and Corycaeidae in the zone Centre-Shelf-2011). The fourth cluster contained anchovies sampled in the west, on the coast in 2012, feeding almost exclusively on diatoms (%IRI = 97.26). The fifth cluster had stations sampled in 2012 but unidentified copepods were the main prey. These results show that year and depth were the most important parameters influencing diet.

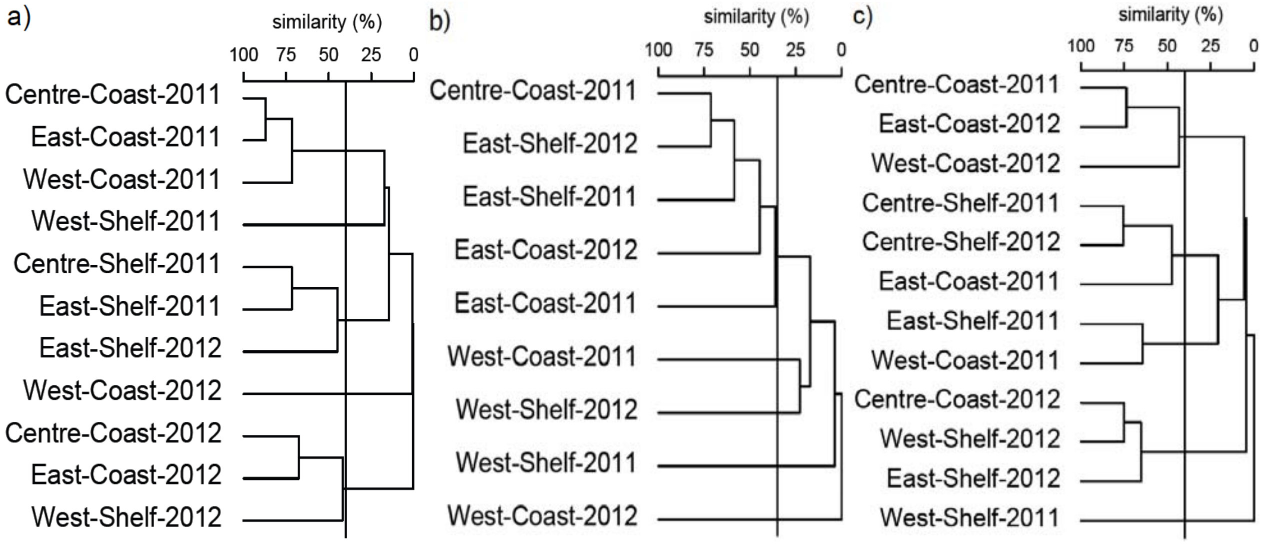

Fig. 4. Cluster analyses of diet similarities (based on %IRI) among region, depth and year in a) anchovies, b) sardines, c) sprats. The vertical line separates the clusters.

For sardines, five clusters appeared. The first cluster contained all sardines sampled at the centre and east of the gulf. The other clusters contained the zones sampled in the west. These results show that the region has influenced the diet, sardines sampled in the west feeding on various dominating (but there is only one sardine in the cluster West-Shelf-2011) prey among zones (eggs on the coast in 2011, diatoms on the coast in 2012 and unidentified copepods on the shelf in 2012), while sardines of the other regions fed mainly on the copepods usually observed in this study of their diet (*Microsetella*, *Oncaea* and Corycaeidae).

Five clusters appeared for sprats. The first contained sprats only sampled on the coast with a diet characterised by *Euterpina acutifrons* and diverse secondary prey (*Oncaea* at the centre in 2011, *Clauso/Paracalanus* in the east in 2012 and Diatoms and *Oncaea* in the west in 2012). The second contained two zones on the shelf and one on the coast where the diet was characterised by Corycaeidae copepods and *Microsetella*. The third cluster contained two zones on the coast and on the shelf and in the west and the east. Sprats of this cluster fed on *Clauso/Paracalanus* and on Corycaeidae. The fourth cluster contained two zones on the shelf and one on the coast but the diet was characterised by unidentified copepods. The last cluster contained the zone West-Shelf-2011 where sprats fed on decapod larvae (%IRI = 98.24). These results suggest that depth may have influenced sprat diet, with *Euterpina acutifrons* being a widely consumed prey in coastal zones.

3.5. Stable isotope analysis

Isotopic values were significantly different among the three species ($H = 64.028$, $P < 0.001$ for $\delta^{15}N$, $H = 44.843$, $P < 0.001$ for $\delta^{13}C$). Anchovies had the lowest $\delta^{15}N$ value (mean ± SD = 7.5 ± 0.5‰), followed by sprats (7.8 ± 0.4‰) and sardines (8.1 ± 0.5‰). Anchovies had the highest $\delta^{13}C$ value (-19.4 ± 0.3‰) while sprats and sardines had similar $\delta^{13}C$ values (-19.8 ± 0.6‰ for both species). Nevertheless, sprats had a wider range of $\delta^{13}C$ (from -21.1 to -17.2‰) than sardines (from -21.2 to -19.0, Fig. 5). Anchovies had the smallest isotopic niche (mean $SEA_B = 0.60$) while sardines and sprats had similar isotopic niche width (mean $SEA_B = 0.75$ for sardines and 0.79 for sprats).

The influence of the different factors on $\delta^{15}N$ and $\delta^{13}C$ are detailed in Table A.3a and b. In anchovies, $\delta^{15}N$ ($t = 5.919$, $P < 0.001$) and $\delta^{13}C$ ($t = 6.398$, $P < 0.001$) were dependent on the year of sampling. In 2011, the highest $\delta^{15}N$ was observed in the west (7.5 ± 0.4‰), the lowest in the centre (7.1 ± 0.4‰) and the intermediate value in the east (7.3 ± 0.5‰). $\delta^{13}C$ slightly increased when the body length increased and was higher in the centre (-19.4 ± 0.3‰), lower in the east (-19.6 ± 0.3‰) and intermediate in the west (-19.5 ± 0.3‰). The interaction between depth and region showed that offshore anchovies had a higher $\delta^{13}C$ than coastal anchovies except in the east where coastal anchovies had a higher $\delta^{13}C$. In 2012, depth had an effect on $\delta^{15}N$, with higher $\delta^{15}N$ for individuals caught in coastal areas (8.1 ± 0.5‰) than on the shelf (7.7 ± 0.4‰) and the interaction between depth and region also influenced $\delta^{15}N$ (greater difference between coastal $\delta^{15}N$ and offshore $\delta^{15}N$ in the centre region). No factor had a significant effect on $\delta^{13}C$.

In sardines, the year of sampling had no effect on $\delta^{15}N$ ($W = 1123.5$, $P = 0.428$) but influenced $\delta^{13}C$ ($W = 702$, $P < 0.001$). $\delta^{15}N$ decreased when body length increased. In 2011, $\delta^{13}C$ increased when the body length increased. In 2012, no factor had a significant effect on $\delta^{13}C$.

In sprats, the year of sampling influenced $\delta^{13}C$ (W = 458, P < 0.001) but not $\delta^{15}N$ (t = 0.080, P = 0.936). $\delta^{15}N$ slightly increased when the body length increased. $\delta^{13}C$ slightly decreased when body length increased in 2011 but influence of body length on $\delta^{13}C$ was weak in 2012.

3.6. Interactions between species

Diet overlap estimated on %IRI and %W was significant for anchovies and sardines (%T = 83.91 for %IRI and 76.92 for %W). For sprats and anchovies (%T = 55.06 for %IRI and 65.34 for %W) and for sprats and sardines (%T = 58.51 for %IRI and 64.00 for %W), the overlap was nearly significant when estimated using %IRI and was significant when using %W. Diet overlap between length classes is detailed in Table A.4. Anchovies share only 17.12% of their isotopic niche with sardines (and sardines 12.92% with anchovies) and 48.46% with sprats (and sprats 34.48% with anchovies). Sardines share 48.28% of their isotopic niche with sprats (and sprats 45.50% with sardines) (Fig. 5).

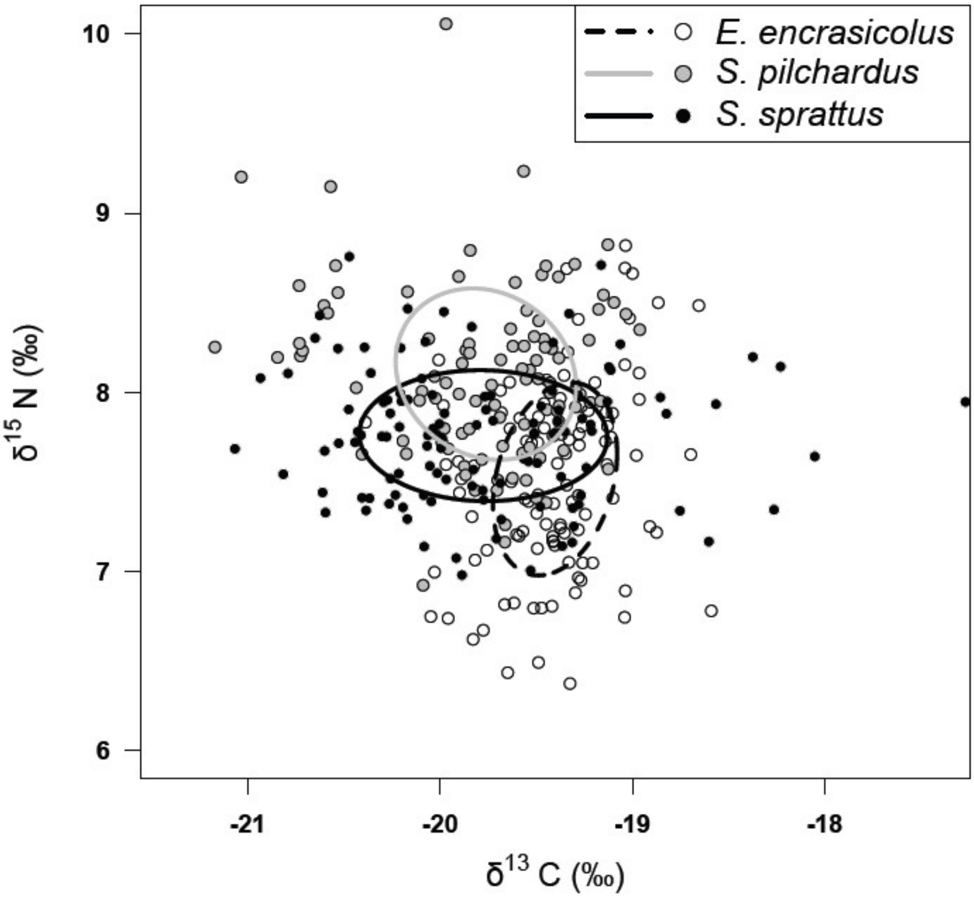

Fig. 5. Isotopic values in muscles of anchovies, sardines and sprats and depiction of their niche area using standard ellipses.

3.7. Relative condition factor

Sprats had the highest C/N ratios (mean ± SD = 4.38 ± 1.12), followed by sardines (3.31 ± 0.14) and anchovies (3.20 ± 0.09) (H = 148.931, P < 0.001). The C/N ratios of anchovies were only influenced by the interaction between depth and region (Table A.3c) while C/N ratios of sardines were not dependent on any factor. For anchovies, C/N ratio did not differ between coastal and offshore regions except in the centre where coastal C/N is higher than offshore C/N. For sprats, C/N ratios differed between 2011 and 2012 (W = 1093.5, P = 0.002), C/N ratios being higher in 2012 (4.83 ± 1.36) than in 2011 (4.03 ± 0.74). The C/N ratios of sprats in 2011 and 2012 were higher when body length increased but the other factors were not significant.

4. Discussion

4.1. Diet composition and ontogenetic shifts

Anchovies fed mainly on *Microsetella*, *Oncaea* and Corycaeidae copepods. Consumption of *Microsetella* has been previously observed in the Gulf of Lions during summer (Plounevez and Champalbert, 2000), *Oncaea* is a usual prey in other regions of the Mediterranean Sea during other seasons (Bacha and Amara, 2009; Borme et al., 2009; Tudela and Palomera, 1997) and high Corycaeidae copepods consumption has been reported near the Gironde estuary (Plounevez and Champalbert, 1999). Our results contrast with those of Costalago et al. (2012) based on stable isotope analysis where adult anchovies sampled in summer 2008 fed on cladocerans and appendicularians. This contrast suggests that anchovies' summer diet changed between 2007 and 2011-2012. Nevertheless, results on stomach contents of adult anchovies sampled in the 2007-2008 period have not been published yet to confirm the qualitative change in the diet of this age class. Thus, this interpretation should be taken with caution as stomach contents and stable isotopes do not provide the same information.

Anchovies had the lowest $\delta^{15}N$ and the highest $\delta^{13}C$. As detritus discharged by the Rhône reduces $\delta^{13}C$ and increases $\delta^{15}N$ of phytoplankton and particulate organic matter in eastern and coastal areas (Harmelin-Vivien et al., 2008), this result indicates that anchovies fed primarily on the continental shelf or in western regions of the Gulf of Lions, far from the Rhône outflow, similarly to what was found in the Bay of Biscay (Chouvelon et al., 2014). The study of the spatial distribution of anchovies in the Gulf of Lions (Saraux et al., 2014) confirms this hypothesis. Anchovies consumed more diatoms and *Centropages typicus* and less *Oncaea* when their body length increased. Consumption of *Oncaea* by small anchovies is in accordance with Costalago et al. (2014) where juveniles sampled in the Gulf of Lions during summer 2007 fed on some *Oncaea*, even if the dominant prey groups in their study were cladocerans and copepods such as Clauso/Paracalanidae and *Centropages typicus*. It is the first time that a high contribution of diatoms in the diet of large anchovies was observed in the Gulf of Lions but this has been observed in the Baltic Sea (Schaber et al., 2010). Nevertheless, high diatom consumption has been only observed in one sampling station in 2012 and thus cannot be considered as a general phenomenon. Furthermore, copepods remained the main prey items for anchovies of all length classes. No changes of stable isotope ratios with body length have been detected in anchovies except a slight increase for $\delta^{13}C$ in 2011, suggesting few ontogenetic changes in the preferred feeding area.

Microsetella, *Oncaea* and the Corycaeidae family were also the main prey of sardines. The *Oncaea* genus was an important prey of adult sardines in the Gulf of Lions during summer 2007 (Costalago and Palomera, 2014) and in other regions (e.g. Garrido et al., 2008; Sever et al., 2005). Our stomach contents results are similar with those of Costalago and Palomera (2014) but cladocerans were an important prey in adult sardines in 2007 (highest %IRI), which suggests that the dominant prey in the summer diet of sardines might have changed between 2007 and 2011-2012.

Sardines had the highest $\delta^{15}N$ and a low $\delta^{13}C$, indicating that this species fed mainly on coastal or eastern areas of the Gulf of Lions (Harmelin-Vivien et al., 2008), similarly to what was found in the Bay of Biscay (Chouvelon et al., 2014). The study of the spatial distribution of sardines in the Gulf of Lions (Saraux et al., 2014) confirms this hypothesis. High consumption of benthic mysids *Paramysis* by small sardines in our study shows that juveniles of this species may feed in coastal and benthic habitats. Nevertheless, small juvenile sardines have been sampled only at one station near the Rhône plume and consumption of *Paramysis* cannot be considered as a general phenomenon in the Gulf of Lions. Costalago and Palomera (2014) and Costalago et al. (2014) have reported that juvenile sardines of the Gulf of Lions fed mainly on cladocerans and decapod larvae during summer 2007. Like anchovies, sardines consumed more diatoms when their body length increased but this observation is limited to one sampling station. A high contribution of photosynthetic organisms in the diet of adult sardines has been previously observed (e.g. Garrido et al., 2008) but these prey are poorly assimilated (Bode et al., 2004; Costalago and Palomera, 2014; Nikolioudakis et al., 2012). Copepods remained the main prey items for large juvenile and adult sardines. High consumption of *Paramysis* by small sardines and consumption of diatoms by large sardines explain the decrease of the size of the prey when the sardines are growing and may be linked to the acquisition of filter feeding ability thanks to gill rakers development (Costalago and Palomera, 2014). $\delta^{13}C$ increased while $\delta^{15}N$ decreased when body length increased in 2011, indicating that juvenile sardines fed in areas influenced by the Rhône inputs while adult sardines fed in more oligotrophic areas with marine phytoplankton being the main carbon source.

Sprats were more generalist and fed on *Clauso/Paracalanus*, the Corycaeidae family, *Euterpina acutifrons* and *Microsetella*. By contrast, adult sprats feed mainly on the copepods *Calanus* and *Temora* in the Adriatic Sea (Tičina et al., 2000) but important consumption of *Microsetella* was detected in term of number in a Norwegian fjord (Falkenhaug and Dalpadado, 2014). Sprats also had the lowest predator/prey ratios compared to sardines and anchovies, indicating that they fed on the largest prey relative to their size. The consumption of larger prey compared to its own size may be explained by the fact that sampled sprats are mostly juveniles (de

Silva, 1973) and thus have a lesser filter-feeding capacity. The absence of changes in prey sizes for anchovies and sprats is thus likely the result of a lower size range available for these species.

Sprats had an intermediate $\delta^{15}N$ and a $\delta^{13}C$ value very similar to the $\delta^{13}C$ value of sardines but with a wider range. Consequently, the mean $\delta^{13}C$ value indicates that sprats fed mainly on coastal or eastern areas of the Gulf of Lions, probably in the same areas as sardines, but the range also indicate that they may feed on the shelf.

Whatever their size, sprats fed more on larger copepods. The contribution of *Oncaea* to the diet decreased with increasing body length while the contribution of Corycaeidae increased. $\delta^{15}N$ increased with body length, indicating increasing trophic level while growing as they fed less on omnivorous *Oncaea* (Wu et al., 2004) and more on the predatory Corycaeidae copepods (Landry et al., 1985; Turner et al., 1984). $\delta^{13}C$ decreased in 2011, indicating that sprats may exploit food webs influenced by Rhône inputs while growing as $\delta^{13}C$ is lower in waters influenced by the Rhône plume (Harmelin-Vivien et al., 2008).

4.2. Spatial and temporal variations of diet

Diet of anchovies differed between 2011 and 2012 and between coast and shelf. In 2011, coastal anchovies fed mainly on *Oncaea* while *Microsetella* was the main prey on the shelf. Only few anchovies were sampled in coastal areas by Plounevez and Champalbert (2000), which may explain the high importance of *Microsetella* and the low importance of *Oncaea* in the general diet of anchovies sampled in their study. Diet of anchovies in the western region was quite unusual, with high consumption of Euphausiacean larvae on the shelf in 2011 and of diatoms on the coast in 2012. Plounevez and Champalbert (2000) observed differences of feeding between west and east for offshore anchovies, with Euphasiacean larvae being an important prey for western anchovies in 1995 and *Microsetella* being an important prey for eastern anchovies in 1995 and 1996. In 2011, stable isotope ratios were dependent on the region of sampling and, in 2012, $\delta^{15}N$ was influenced by depth. Anchovies sampled in 2011 in the eastern region showed higher $\delta^{13}C$ in the coastal area than on the shelf. This result was not in accordance with low $\delta^{13}C$ observed in particulate organic matter (Harmelin-Vivien et al., 2008) but was in accordance with high values of $\delta^{13}C$ recorded in zooplankton sampled near the Rhône river as this zooplankton previously fed in an offshore area characterised by higher $\delta^{13}C$ values (Espinasse et al., 2014b). No spatial pattern was found in the Bay of Biscay, indicating high mobility of anchovies in this region (Chouvelon et al., 2014). In the Gulf of Lions, different stable isotope ratios between regions in 2011 or between depths in 2012 may indicate that anchovy schools may have preferences in feeding areas.

Diet of sardines differs among regions of the Gulf of Lions. Sardines sampled in the centre and the east fed mainly on *Microsetella*, *Oncaea* and Corycaeidae, while sardines sampled in the west had a more diverse diet (eggs on the coast in 2011, diatoms on the coast in 2012). As in the Bay of Biscay (Chouvelon et al., 2014), stable isotope ratios of sardines did not vary among regions or depths of sampling, except in 2011 on the eastern coast where $\delta^{13}C$ was low, suggesting high mobility of sardines.

Diet of sprats differs between coastal areas and continental shelf and diet was dominated by decapod larvae on the western shelf. In 2012, diatoms are a secondary prey in the west and on the coast, suggesting that sprat is more carnivorous than anchovies and sardines. This result is in accordance with those of Pethybridge et al. (2014) where sprat sampled during winter 2011 had higher fatty acid markers of carnivory than anchovies and sardines. No spatial variations of stable isotope ratios were observed in sprats, indicating high mobility of sprat schools in the Gulf of Lions. Higher diversity and variability of dominating prey in the west of the Gulf of Lions for the three species may be the result of differences of habitat conditions (Espinasse et al., 2014a).

4.3. Interaction between planktivorous teleost species

Trophic competition has been speculated in areas where planktivorous teleost species co-occur (Casini et al., 2004; Raab et al., 2012). Our stomach contents results indicate high trophic interactions between anchovies, sardines and sprats in the Gulf of Lions as diet overlap occurs in their general diet, notably between anchovies and sardines. δ^{13}C values indicate that sardines and sprats fed in the same areas. In contrast, trophic interactions of anchovies with sardines and sprats are potentially reduced considering their differences in δ^{13}C. The isotopic niche of sprats based on both δ^{13}C and δ^{13}N ratios highly overlapped with those of anchovies and sardines, suggesting that sprats compete with the two other species, while the isotopic niches of anchovies and sardines poorly overlapped, suggesting that they fed in different areas considering their distribution (Saraux et al., 2014). Pethybridge et al. (2014) have also observed reduced competition between anchovies and sardines by using lipid biomarkers. Consequently, contrasting results were obtained on trophic interactions between anchovies and sardines with stomach content and stable isotopes, suggesting overlap for the recently ingested prey but not for the previously ingested prey and/or the feeding areas. However, results on stable isotope ratios should be considered with caution as these potentially migratory species feed in an area subjected to high inputs and hydrological variations (Espinasse et al., 2014a; Harmelin-Vivien et al., 2008). These factors may also explain the high differences noticed in the trophic niche overlap when using diet indices (%IRI and %W) and stable isotope ratios.

Differences of δ^{15}N in anchovies between coast and continental shelf in 2012 indicate that some anchovies may sometimes exploit mainly coastal areas with sardines and sprats instead of the continental shelf, leading to high local trophic overlap between the three species. Adult anchovies of the Bay of Biscay feed primarily in offshore habitats (Chouvelon et al., 2014) but Pasquaud et al. (2008) observed that small anchovies can also feed along with sprats in estuarine habitats of the Gironde. If competition between the three species occurs in the Gulf of Lions, sprats should have an advantage considering their larger niche width, the feeding on slightly larger, and thus, more energetic prey (Gerking, 1994; van Deurs et al., 2015) than anchovies and sardines, their lowest predator/prey size ratios and because they seem to recover well after the spawning period (Pethybridge et al., 2014).

Even if studies on stomach contents and stable isotopes do not exactly provide the same information, the changes in the diets of anchovies and sardines reported from 1995-1996 (Plounevez and Champalbert, 2000) to 2007-2008 (Costalago et al., 2012; Costalago and Palomera, 2014) and to 2011-2012 (this study) may have been a contributing factor to the decline of anchovies and sardines. Consumption of cladocerans by the three species is variable among regions with, for examples, a good representation of this group in the general diet of sardines of the Aegean sea (Nikolioudakis et al., 2012) and sprats of the Baltic Sea and of the North Sea (Casini et al., 2004; Raab et al., 2012) but a low importance in western Mediterranean Sea (Borme et al., 2009; Plounevez and Champalbert, 2000; Tičina et al., 2000) except at local scale (Tudela and Palomera, 1997). Furthermore, cladocerans are considered to have lower energetic value than copepods (Bodt and Haldorson, 2002). Consequently, unusual consumption of cladocerans in 2007-2008, while it was rare in 1995-1996 and 2011-2012, may have had a negative impact on the body condition of adult anchovies and sardines, leading to the decreasing biomass observed for these species since 2008. Decreasing biomass of anchovies and sardines after such events may have led to an increase in sprat biomass and competition may have prevented the recovery of anchovies and sardines, leading to persistence of the phenomenon. However, competition only occurs when food resources are limited for the predators and no information regarding this factor exists for the study area or elsewhere for these species. Furthermore, body condition of anchovies and sardines was still low in 2011 and 2012 despite the fact that they ate more copepods and less cladocerans than in the past years (Van Beveren et al., 2014). Consequently, other environmental and/or physiological factors (Cury and Roy, 1989; Takasuka et al., 2007) may have acted in interaction with the trophic one to influence the body condition and/or biomass of small pelagic teleosts. However, the relationship between body condition of anchovies and sardines and mesozooplankton concentration (Brosset et al., in press) indicates that the decline of these species is mainly explained by the trophic ecology of these species. The importance of competition may possibly vary seasonally. In the Gulf of Lions, Pethybridge et al. (2014) reported that no competition of sprats with anchovies and sardines during winter 2011 was apparent on the basis of lipid biomarkers. In the Bay of Biscay, Chouvelon et al.

(2015) hypothesised that anchovies and sardines are potential competitors for food in autumn, but not in spring.

4.4. C/N ratios as an indicator of relative condition

Sprats had the highest C/N ratios, followed by sardines and anchovies, suggesting that this species has the highest lipid levels and thus the best relative condition in the Gulf of Lions during summer. That does not imply the good "health" of this population over the time as sprats had a lower relative condition value and a small length when compared to previous years (Van Beveren et al., 2014). Low fat content in anchovies was related to the spawning activity that occurs in summer (Palomera et al., 2007). Higher fat content in sardines than in anchovies has been observed in various seasons (Sánchez et al., 2013; Zlatanos and Laskaridis, 2007).

Sprats sampled during winter 2011 had also higher lipid contents than anchovies and sardines (Pethybridge et al., 2014), suggesting that they had the best relative condition throughout the year when compared to sardines and anchovies. Slight increase of C/N ratios occurred only in sprats when they are growing, suggesting that larger sprats increase their chances of survival. As a result, sprats are at an advantage when they compete with anchovies and sardines. The greater niche width and the consumption of slightly larger prey may contribute to the better relative condition of sprats.

5. Conclusion

Combining stomach content analysis with stable isotopes is necessary to better understand trophic ecology of small pelagic teleosts within a region subjected to variable hydrological conditions, to different sources of particulate organic matter and variable plankton communities (Espinasse et al., 2014a). The studied species changed their summer diet compared to past studies. The trophic niche overlap between the three species sustains the hypothesis of their competition, but data on the quality and quantity of zooplankton are necessary to confirm or disprove the hypothesis on the limitation of food resources. However, the higher diversity and size of the consumed prey, trophic niche and C/N values of sprats indicate that they probably have a competitive advantage over anchovies and sardines and thus a trophic factor may be one of the explaining factors of the recent changes in small pelagic teleost communities of the Gulf of Lions.

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Supplementary material: Trophic niche overlap of sprat and commercial small pelagic teleosts in the Gulf of Lions (NW Mediterranean Sea)

B. Le Bourg, D. Banaru, C. Saraux, A. Nowaczyk, E. Le Luherne, A. Jadaud, J.L. Bigot, P. Richard

Table A.1. Dry weight (DW; µg) of prey and morphometric relationship used to calculate DW. TL = Total length (µm).

Prey		Dry weight (µg)	Reference
Protists			
Protists	Protists	DW = 30	This study
Crustaceans			
Copepods	*Clauso/Paracalanus*, *Pleuromamma* and copepods n.d.	Log DW = 2.285 log TL – 5.965	Mauchline (1998)
	Calanus	Log DW = 2.790 log TL – 7.370	Mauchline (1998)
	Microsetella	Ln DW = 1.15 ln TL – 7.79	Satapoomin (1999)
	Oncaea	DW = 1.34	Borme et al. (2009)
	Corycaeidae	DW = 62	Pitois & Fox (2006)
	Euterpina acutifrons	$\mathrm{DW} = 1.389*10^{-8}\ \mathrm{TL}^{2.857}$	Ara (2001)
	Macrosetella	Ln DW = 1.59 ln TL – 10.92	Satapoomin (1999)
	Centropages typicus	Log DW = 2.243 log TL – 5.568	Mauchline (1998)
	Centropages hamatus	DW = 14.7	Pitois & Fox (2006)
	Candacia	DW = 106.2	Pitois & Fox (2006)
	Oithona	DW = 2.2	Pitois & Fox, 2006
	Temora	Log DW = 2.179 log TL – 5.567	Mauchline (1998)
	Euchaeta	Log DW = 2.62 log TL – 6.47	Uye (1982)
	Acartia	Log DW = 3.208 log TL – 7.644	Mauchline (1998)
	Lucicutia	DW = 16.9	Delpy (2013)
	Clytemnestra	DW = 0.3	Delpy (2013)
Cladocerans	*Evadne*	$\mathrm{DW} = 3.946\ (\mathrm{TL}/1000)^{2.436}$	Borme et al. (2009)
	Podon	DW = 1.6	Borme et al. (2009)
	Cladocerans n.d.	mean *Evadne* and *Podon*	This study
Ostracods	Ostracods	DW = 6.036	Borme et al. (2009)
Mysids	*Paramysis*	Log DW = 3.08 log TL + 0.236	Uye (1982) (*Neomysis*)
Amphipods	*Phronima*	DW = 40; DW = 770	This study
	Other amphipods	DW = 40	This study
Isopods	Isopods	Ln DW = 1.69 ln (TL/1000) – 11.64	Borme et al. (2009)
Chaetognaths			
Chaetognaths	Chaetognaths	Log DW = 3.24 log TL – 0.975	Uye (1982)
Larvae			
Crustaceans	Copepodids	$\mathrm{DW} = 1.10*10^{-5}\ \mathrm{TL}^{1.89}$	Dumont et al. (1975)
	Nauplii	Log DW = 2.848 log TL – 7.265	Borme et al. (2009)
	Cirriped nauplii	DW = 0.67	Borme et al. (2009)
	Protozoea	DW = 27.798	Borme et al. (2009)
	Metazoea	DW = 27.798	Borme et al. (2009)
	Brachyurans	DW = 27.798	Borme et al. (2009)
	Decapods	DW = 27.798	Borme et al. (2009)
	Zoea	DW = 27.798	Borme et al. (2009)
	Trachelifer	DW = 27.798	Borme et al. (2009)
	Euphausiaceans	Log DW = 0.456 + 2.8 log TL	Lindley et al. (1999)
Molluscs	Gastropods	DW = 0.6	Borme et al. (2009)
	Bivalves	DW = 3.758	Borme et al. (2009)
Teleosts	Teleosts	DW = 7510	This study
Eggs			
Eggs	Anchovies eggs	DW = 30.1	Borme et al. (2009)

Table A.2. Frequency of occurrence (%O), numerical percentage (%N), weight percentage (%W) and percentage of the index of relative importance (%IRI) obtained in total stomach contents of anchovies, sardines and sprats.

		E. encrasicolus				*S. pilchardus*				*S. sprattus*			
		%O	%N	%W	%IRI	%O	%N	%W	%IRI	%O	%N	%W	%IRI
Protists													
Diatoms	Diatoms	9.62	9.21	9.58	2.31	10.17	5.25	8.21	2.01	7.83	1.07	2.89	0.36
Dinoflagellates	Peridinidae					3.39	0.14	0.22	0.02				
	Ceratium					0.85	0.02	0.03	< 0.01				
Foraminifera	Foraminifera	2.88	0.05	0.13	< 0.01					0.87	< 0.01	0.01	< 0.01
Crustaceans													
Copepods	*Calanus*	3.85	0.35	0.64	0.05								
	Acartia	19.23	2.66	8.70	2.79	11.02	3.24	7.58	1.75	21.74	2.17	8.96	2.84
	Clauso/Paracalanus	28.85	4.93	2.30	2.66	36.44	6.35	4.59	5.85	60.87	17.89	14.90	23.41
	Microsetella	74.04	25.18	8.76	32.06	62.71	22.17	8.98	28.63	56.52	13.30	1.90	10.08
	Oncaea	66.35	20.04	9.79	25.25	61.02	15.70	10.80	23.70	56.52	9.12	4.09	8.76
	Corycaeidae	43.27	4.31	25.79	16.62	40.68	7.63	26.35	20.25	47.83	7.36	26.58	19.04
	Euterpina acutifrons	36.54	2.08	0.34	1.13	32.20	8.17	3.97	5.73	52.17	17.20	6.68	14.61
	Macrosetella	0.96	< 0.01	< 0.01	< 0.01	0.85	0.01	< 0.01	< 0.01				
	Sapphirina					0.85	0.34	0.42	< 0.01				
	Pleuromamma	3.85	0.20	0.31	0.03	2.54	0.11	0.03	< 0.01	0.87	0.03	< 0.01	< 0.01
	Centropages typicus	21.15	3.54	5.28	2.38	11.02	1.34	1.37	0.44	22.61	1.44	2.72	1.10
	Centropages hamatus					0.85	0.02	0.03	< 0.01	1.74	0.02	0.02	< 0.01
	Candacia	10.58	0.89	3.34	0.57	2.54	0.11	0.93	0.04	4.35	0.36	1.34	0.09
	Oithona	5.77	0.11	0.02	< 0.01	3.39	0.17	0.04	0.01	8.70	0.29	0.09	0.04
	Temora	0.96	0.02	0.02	< 0.01					6.96	0.74	0.40	0.09
	Euchaeta									0.87	0.03	0.09	< 0.01
	Lucicutia									1.74	0.02	0.03	< 0.01
	Clytemnestra	1.92	0.07	< 0.01	< 0.01	2.54	0.28	0.09	0.01				
	Pareuchaeta									0.87	0.01	< 0.01	< 0.01
	Other harpacticoids					2.54	0.02	< 0.01	< 0.01				
	Other copepods	32.69	15.02	9.86	10.37	22.88	10.07	6.81	5.66	43.48	17.67	16.09	17.22
Cladocerans	*Evadne*	5.77	0.17	0.01	0.01	7.63	0.85	0.46	0.15	3.48	0.07	0.08	< 0.01
	Podon	6.73	0.15	0.03	0.02	3.39	0.15	0.11	0.01	0.87	0.06	0.05	< 0.01
	Other cladocerans									4.35	0.25	0.03	0.01
Ostracods	Ostracods	22.12	1.25	1.88	0.88	11.02	0.97	1.37	0.38	13.04	0.88	0.87	0.27
Mysids	*Paramysis*	0.96	0.27	0.24	< 0.01	10.17	7.97	8.71	2.49				
Amphipods	*Phronima*	1.92	0.16	0.88	0.03								
	Eusirus or *Synopia*	0.96	0.11	0.21	< 0.01								
	Other amphipods	0.96	< 0.01	0.02	< 0.01								
Isopods	Isopods	3.85	0.04	< 0.01	< 0.01					1.74	< 0.01	< 0.01	< 0.01
Chaetognaths													
Chaetognaths	Chaetognaths					0.85	< 0.01	< 0.01	< 0.01	0.87	0.07	0.01	< 0.01
Molluscs													
Pteropods	*Limacina*	2.88	0.07	< 0.01	< 0.01								
Appendicularians													
Appendicularians	Appendicularians	0.96	0.12	< 0.01	< 0.01								
Cnidarians													
Siphonophores	Calycophorae	1.92	0.03	< 0.01	< 0.01					0.87	0.43	0.03	< 0.01
Larvae													
Crustaceans	Copepodits					2.54	0.19	0.11	0.01	4.35	0.55	0.18	0.04
	Nauplii	0.96	0.02	< 0.01	< 0.01	5.08	0.04	< 0.01	< 0.01	5.22	0.05	< 0.01	< 0.01
	Cirripedia nauplii	0.96	< 0.01	< 0.01	< 0.01	2.54	0.12	< 0.01	< 0.01				
	Cirripedia cypris									0.87	0.01	< 0.01	< 0.01
	Protozoea	0.96	< 0.01	0.05	< 0.01								
	Metazoea	0.96	0.01	0.02	< 0.01					5.22	0.23	0.42	0.04
	Brachyoura	1.92	0.14	0.10	< 0.01	0.85	< 0.01	< 0.01	< 0.01	1.74	0.08	0.13	< 0.01
	Decapods	1.92	0.16	0.19	< 0.01					7.83	5.69	6.62	1.13
	Zoea	7.69	1.05	1.97	0.30	3.39	0.07	0.68	0.04	7.83	0.16	1.21	0.13
	Trachelifer	0.96	0.06	0.37	< 0.01								
	Euphausiaceans	7.69	2.84	3.90	0.66					1.74	0.95	1.06	0.04
Molluscs	Gasteropods	10.58	1.79	1.65	0.46	1.69	0.11	< 0.01	< 0.01	3.48	0.21	0.06	0.01
	Bivalves	24.04	1.59	1.00	0.79	8.47	1.03	0.95	0.25	14.78	0.80	1.76	0.44
Echinoderms	Ophiuroids	2.88	0.03	< 0.01	< 0.01								
Teleosts	Teleosts	0.96	0.07	0.92	0.01								
Eggs													
Eggs	Eggs	2.88	0.12	0.02	< 0.01	18.64	2.58	0.70	0.89	6.96	0.43	0.03	0.04
	Anchovy eggs	16.35	1.08	1.67	0.57	10.17	4.79	6.43	1.67	14.78	0.35	0.66	0.18

Table A.3. Effect of body length, depth and region of sampling on a) $\delta^{15}N$, b) $\delta^{13}C$, c) C/N in anchovies, sardines and sprats. Bold results are significant. The body length covariate was not included in the model if its effect was not significant (NC = not computed).

a)

	2011	2012	2011 and 2012	
Species	*E. encrasicolus*	*E. encrasicolus*	*S. pilchardus*	*S. sprattus*
Length	NC	NC	**$F_{1,94} = 7.495$** **$P = 0.007$**	**$F_{1,109} = 4.725$** **$P = 0.032$**
Depth	$F_{1,56} = 2.094$ $P = 0.154$	**$F_{1,30} = 16.890$** **$P < 0.001$**	$F_{1,94} = 0.060$ $P = 0.806$	$F_{1,109} = 0.741$ $P = 0.391$
Zone	**$F_{2,56} = 4.165$** **$P = 0.021$**	$F_{2,30} = 1.258$ $P = 0.299$	$F_{2,94} = 0.971$ $P = 0.382$	$F_{2,109} = 0.395$ $P = 0.675$
Depth*Zone	$F_{2,56} = 1.203$ $P = 0.308$	**$F_{2,30} = 3.630$** **$P = 0.039$**	$F_{2,94} = 0.345$ $P = 0.709$	$F_{2,109} = 0.826$ $P = 0.440$

b)

	2011			2012		
Species	*E. encrasicolus*	*S. pilchardus*	*S. sprattus*	*E. encrasicolus*	*S. pilchardus*	*S. sprattus*
Length	**$F_{1,55} = 20.274$** **$P < 0.001$**	**$F_{1,52} = 13.936$** **$P < 0.001$**	**$F_{1,59} = 6.253$** **$P = 0.015$**	NC	NC	**$F_{1,43} = 4.083$** **$P = 0.050$**
Depth	$F_{1,55} = 0.026$ $P = 0.873$	$F_{1,52} = 0.404$ $P = 0.528$	$F_{1,59} = 0.160$ $P = 0.691$	$F_{1,30} = 0.478$ $P = 0.495$	$F_{1,36} = 0.309$ $P = 0.582$	$F_{1,43} = 0.008$ $P = 0.929$
Zone	**$F_{2,55} = 4.998$** **$P = 0.010$**	$F_{2,52} = 1.531$ $P = 0.226$	$F_{2,59} = 1.850$ $P = 0.166$	$F_{2,30} = 1.761$ $P = 0.189$	$F_{2,36} = 1.183$ $P = 0.318$	$F_{2,43} = 2.090$ $P = 0.136$
Depth*Zone	**$F_{2,55} = 6.296$** **$P = 0.003$**	$F_{2,52} = 2.433$ $P = 0.098$	$F_{2,59} = 0.016$ $P = 0.984$	$F_{2,30} = 1.588$ $P = 0.221$	$F_{2,36} = 0.135$ $P = 0.874$	$F_{2,43} = 3.057$ $P = 0.057$

c)

	2011	2012	2011 and 2012	
Species	*S. sprattus*	*S. sprattus*	*E. encrasicolus*	*S. pilchardus*
Length	**$F_{1,59} = 33.903$** **$P < 0.001$**	**$F_{1,43} = 10.856$** **$P = 0.002$**	NC	NC
Depth	$F_{1,59} = 0.573$ $P = 0.452$	$F_{1,43} = 0.002$ $P = 0.966$	$F_{1,92} = 3.027$ $P = 0.085$	$F_{1,95} = 0.012$ $P = 0.913$
Region	$F_{2,59} = 0.646$ $P = 0.528$	$F_{2,43} = 1.279$ $P = 0.289$	$F_{2,92} = 1.296$ $P = 0.279$	$F_{2,95} = 0.054$ $P = 0.948$
Depth*Region	$F_{2,59} = 1.333$ $P = 0.271$	$F_{2,43} = 2.027$ $P = 0.144$	**$F_{2,92} = 5.709$** **$P = 0.005$**	$F_{2,95} = 2.618$ $P = 0.078$

Table A.4. Diet overlap (%T) between length class (cm) of anchovies, sardines and sprats using Schoener's formula (1970) on %IRI (upper diagonal) and %W (lower diagonal). Bold results are significant (%T ≥ 60).

		E. encrasicolus			*S. pilchardus*		*S. sprattus*	
		[8-10[	[10-12[	[12-13[	[3-8[	[8-15[	[7-8[	[8-11[
E. encrasicolus	[8-10[	-	**69.28**	55.38	14.00	**68.47**	57.90	53.44
	[10-12[	**68.46**	-	50.13	4.93	**81.34**	33.47	46.11
	[12-13[	52.21	53.55	-	14.21	54.64	39.19	**60.22**
S. pilchardus	[3-8[	19.19	9.03	12.48	-	3.96	13.99	14.04
	[8-15[	**70.06**	**74.44**	50.75	8.12	-	37.62	58.24
S. sprattus	[7-8[	**60.49**	38.24	31.80	20.85	44.33	-	52.19
	[8-11[	**63.84**	57.13	52.50	16.06	**66.49**	53.42	-

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