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Trophic ecology of pelagic fish species off the Iberian coast: diet overlap, cannibalism and intraguild predation

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ABSTRACT: This work presents, for the first time, a comparative study of the feeding ecology of the most abundant pelagic fish (PF) species (sardines, anchovies, chub mackerel, horse mackerel, bogue, jack mackerel, Mediterranean horse mackerel) in the Western Iberian Upwelling Ecosystem (WIUE). Special attention is given to understanding how the trophic ecology of PF can affect sardine population dynamics, which have been declining in recent years. Diet composition was estimated for juvenile and adult fish collected off the western and southern Iberian coasts during spring by determining the contribution of different prey types and prey size-classes to total dietary carbon. Results show that PF have highly diversified diets, with mesozooplankton and prey ranging from 1000 to 2000 µm being the major contributors to total dietary carbon. Calanoid copepods were important prey for all PF. Despite these similarities, there were significant differences in diet composition between areas, species, and maturity stages. Small prey such as phytoplankton, crustacean eggs, nauplii and small copepods were particularly important for the diet of sardines and juvenile chub mackerel. Prey >1500 µm (including decapod larvae, euphausiids and mysids) were mostly important for anchovies, adult chub mackerel, bogue, horse mackerel, jack mackerel and Mediterranean horse mackerel. Chub mackerel juveniles had the highest diet overlap with sardines. Sardine and chub mackerel juveniles, followed by bogue, were the main predators of fish eggs, particularly those of sardines, suggesting further investigation of their role in egg mortality and recruitment strength. This is particularly relevant given the recent northward expansion of chub mackerel into the main spawning grounds of sardines off the WIUE.

KEY WORDS: Pelagic fish · Pelagic foodweb · Trophic ecology · Stomach contents · Cannibalism · Intraguild predation

INTRODUCTION

Small pelagic fish (PF) such as sardines and anchovies are generally key species in the most productive regions of the world's oceans, particularly in upwelling regions, where they occupy an intermediate trophic level in the coastal marine trophic web fundamental to a wide range of predators (Bakun 2006). The dominant PF in the Western Iberian Upwelling Ecosystem (WIUE) is the European sardine *Sardina pilchardus*, and its spawning area is almost continuous throughout the continental shelf up to the 150 m depth contour (Bernal et al. 2007). The Iberian sardine stock has decreased substantially since 2006 due to prolonged low recruitment (ICES 2014). Sardine total biomass reached historical minimum values in 2012–2013, which led to drastic reductions of annual catch (ICES 2014).

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Population fluctuations of short-lived small PF species are known to be the result of recruitment variability, and food supply is considered the main cause of such variability, either by affecting the intensity of reproduction or by directly impacting the growth and survival of the early life stages (Garrido & van der Lingen 2014). Former studies have shown that sardines are highly opportunistic planktonic feeders whose diet compositions vary ontogenetically, spatially and temporally, and they are to a large degree dependent on prevailing food availability (Garrido et al. 2007a, 2008a). Regional differences in productivity related to distinct oceanographic and topographic features were shown to have a significant effect on sardine trophic ecology (Garrido et al. 2008a, Costalago et al. 2015). Moreover, spatial differences of the feeding ecology of sardines were shown to affect their lipid composition and also the fatty acid reserves transferred to their progeny (Garrido et al. 2007b, 2008b).

The availability of food for sardines depends not only on plankton productivity, but also on the competition with other planktivorous PF species sharing the same area of distribution and which often occur in mixed shoals with several species. Other abundant PF species in the WIUE are horse mackerel *Trachurus trachurus*, Atlantic chub mackerel *Scomber colias*, mackerel *Scomber scombrus*, anchovy *Engraulis encrasicolus*, bogue *Boops boops* and jack mackerel *Trachurus picturatus* (ICES 2013). These are known to be completely, or at least partially, planktivorous during most of their life cycles and to co-occur with sardine, mainly as juveniles and young adults, potentially competing with sardines. Recent studies show a high degree of diet overlap between PF species (Bachiller & Irigoien 2015). However, the feeding ecology of most PF species in the WIUE is unknown.

A vast number of planktivorous PF species are known to cannibalize their own eggs and larvae. Cannibalism was proposed to be a density-dependent, self-regulatory mechanism (Valdés et al. 1987) and also as a way to compensate for reduced food availability (Smith & Reay 1991). Estimates of egg mortality due to cannibalism or intraguild predation vary greatly for different PF species and areas of distribution (Garrido & van der Lingen 2014), but accurate assessment of the impact of intraguild predation on these species is highly important because it might be a significant source of mortality and may be sufficient to cause fluctuations in recruitment strength (Smith & Reay 1991).

The warming trend observed in the WIUE (Relvas et al. 2009) may explain the northward expansion of several PF with southern affinities, such as Atlantic chub mackerel and jack mackerel (ICES 2008). Martins et al. (2013) observed an inverse correlation between sardine and chub mackerel recruitment and suggested it may be a consequence of feeding competition and intraguild predation, but no study has addressed this hypothesis so far. Given that chub mackerel have been invading the major spawning area of sardines off the Iberian coast (northwestern coast) in recent years (Martins et al. 2013), it is important to know what the impact competition and intraguild predation between these species may be, throughout their ontogeny. Knowledge of the spatial and seasonal variability in the trophic ecology of PF will enable a better understanding of the influence of the environment on the dynamics of these species.

The aim of this work was, for the first time, to study the trophic relationships (diet composition and overlap, cannibalism, intraguild predation) between PF of the WIUE and to understand how these can affect sardine population dynamics.

MATERIALS AND METHODS

PF samples were collected with a pelagic trawl (20 mm mesh size in the codend) towed at depths between 16 and 50 m during a research cruise (PELAGO14) conducted by the RV 'Noruega' from Instituto Português do Mar e da Atmosfera (IPMA). The main purpose of the cruise was to acoustically estimate the abundance of European sardine and anchovy (ICES 2013) . It was carried out off western and southern coasts of Iberia (Fig. 1) from the April 3 to May 12 in 2014 (for details of the cruise see ICES 2014). Samples of PF species collected in 19 different trawl hauls were selected to conduct stomach content analysis (see Table 1). Samples were selected (1) to maximize the number of different PF species collected in the same trawl and (2) to have several length classes available for each species. Biological data of the fish was recorded onboard and included total length (cm), total and gutted weight (fish weight minus viscera, to the nearest 0.1 mg), sex and maturity stage (maturity scales: sardine and anchovy, Afonso-Dias et al. 2008; horse mackerel, jack mackerel, chub mackerel and mackerel, Walsh et al. 1990; bogue, Gordo 1995). After this, stomachs were removed and kept frozen to be analysed in the laboratory.

The stomach of each fish was weighed individually, its content removed and weighed, and the empty stomach weighed again. Only the contents of the cardiac stomach and the fundulus of the stomach were

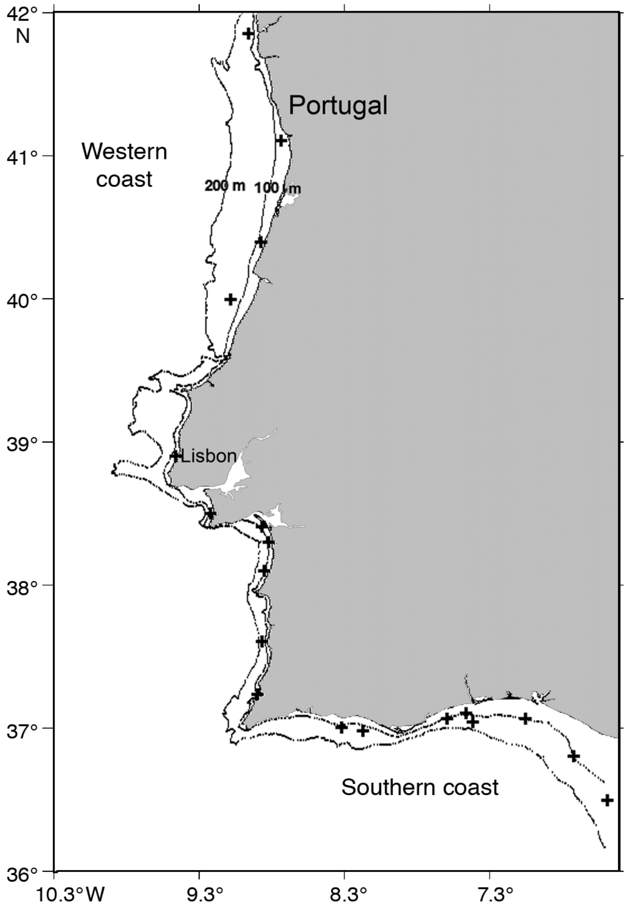

Fig. 1. Map of the Portuguese continental coast, showing the sampling locations (+) off western and southern Iberia where pelagic fish were caught during the PELAGO14 research cruise

analysed, while the contents of the oesophagus, pyloric stomach and intestine were not extracted to avoid bias due to differential rates of prey digestion, gut passage times and codend feeding. All weight measurements were made to the nearest 0.1 mg using a Sartorius BP 61S scale.

Microscopic analysis of food items was conducted in pools of 2 to 10 stomachs (depending on fish availability) per trawl, species and species size class (see Table 1). Analysing pools of stomachs of fish caught in the same haul to describe the diet is a common methodology for planktivorous fish (e.g. van der Lingen 2002, Garrido et al. 2008a, Nikolioudakis et al. 2012, Costalago et al. 2015) since differences in prey number and composition are expected to be minimal (Garrido 2002). Contents from these pools were diluted in a known volume of water (proportional to the weight of the aliquot), filtered through a 200 µm sieve and the resulting 2 size fractions were analysed separately; those <200 µm were identified using an inverted microscope at a magnification of 400×, whereas those >200 µm were examined using a stereomicroscope at a magnification of 80×. All prey were identified to the lowest possible taxa. Digital pictures of prey were taken using the software Visilog Expert 6.300 on the inversion microscope and on the stereomicroscope, and the major and minor axes of each prey item were recorded and converted into volumetric estimates using equations that approximated the appropriate shape (generally spherical or ellipsoidal). In order to determine the relative importance of prey, their carbon content was estimated using equations given in the literature and described in Garrido et al. (2008a) and Garrido & van der Lingen (2014). The percentage contribution by number and by dietary carbon of each prey type was then calculated, as well as its frequency of occurrence (FO), defined as the number of pooled stomachs where a given prey type was found relative to the total number of pooled stomachs analysed.

The maximum dimension of identified prey was used to group prey items into size classes; chain-forming diatoms were assigned to a size class based on the maximum dimension of single cells, since most phytoplankton cells were found as individuals in stomach contents and the length of the chain was unknown. The percentage contribution to dietary carbon of each prey size class was then calculated.

Feeding intensity (FI) was standardized in order to account for differences in the size of the stomach in relation to fish size, being calculated as:

$$\mathrm{FI} = \frac{\text{Stomach content weight}}{\text{Total weight}} \tag{1}$$

Mean number of prey per stomach was estimated as the number of prey identified in each of the stomach pools divided by the number of stomachs of the respective pool. Differences of mean prey number per stomach content between PF species and of the mean prey size contribution to dietary carbon were tested using nonparametric Kruskal-Wallis rank tests followed by an *a posteriori* pairwise test for multiple comparisons of mean rank sums (Nemenyi-tests). Diversity of prey inside the stomachs was assessed using the species richness (estimated as the number of prey types in each pooled stomach sample) and the Shannon-Wiener diversity index (H'), calculated as:

$$H' = \sum_{i}^{R} p_i \ln(p_i) \tag{2}$$

where R is the number of prey types found in the pooled stomachs and p_i is the relative abundance of a given prey type i. This index was subsequently standardized by dividing by the natural logarithm of the total number of prey types identified in this study to enable comparison among different studies of the diet composition of PF.

ANOVA was used to test for differences in feeding intensity and in prey diversity between species, areas (western or southern coasts off the Iberian peninsula) and maturity stages (juvenile or adult). Only those species sufficiently represented in each of the areas and maturity stage levels were included in the analysis (sardine, anchovy, chub mackerel, horse mackerel). Maturity stages were defined by considering fish smaller than the mean size of first maturity (L_{50}) as juveniles and those larger as adults. Species-specific L_{50} values were taken from the literature (12 cm for anchovy, Millán 1999; 22 cm for chub mackerel, Vasconcelos et al. 2012; 19 cm for horse mackerel, Abaunza et al. 2003; 26 cm for mackerel, Dorel 1986; 14 cm for bogue, Gordo 1995; 22 cm for jack mackerel, Jurado Ruzafa & García Santamaría 2013; and 16 cm for Mediterranean horse mackerel, Viette et al. 1997), using data from the western and southern Iberian coasts when possible, given the latitudinal differences in L_{50}. For sardines, L_{50} off western and southern Iberia is defined as 15 cm (Silva et al. 2006), but we separated the larger and smaller fish at the 16 cm length class given that previous dietary studies describe the length class at which sardine diet changes with ontogeny as 18 cm (Bode et al. 2003).

In order to explore whether the differences in the diet could be explained by the area, maturity stage and fish species, a multivariate regression tree (De'ath 2001) was fitted to the data, using percentage contribution of prey types to dietary carbon as an independent variable, and area, maturity stage and species as covariates. Only the 13 prey species or groups with the highest relative importance in the whole data set (phytoplankton, crustacean eggs and nauplii, small copepods, calanoids, cirripeds, decapods, euphausiids, mysids, polichaets, other zooplankton, anchovy eggs, sardine eggs, other fish eggs) were used for the multivariate regression tree. Prey groups were considered important when the percent contribution to total dietary carbon was >30% at least for one stomach sample, and less important zooplankton prey were then grouped as 'other zooplankton'.

Diet overlap was estimated using the Schoener's index (S), defined as

$$S = 1 - 0.5(\sum_{i=1}^{n} |C_{i\mathrm{A}} - C_{i\mathrm{B}}| \qquad (3)$$

where $C_{i\mathrm{A}}$ and $C_{i\mathrm{B}}$ are the relative contribution to total carbon content of prey type i in the diet of fish species A and B, respectively (Linton et al. 1981). Values of diet overlap vary between 0 (no food is shared) and 1 (same proportional use of all food resources). Values >0.6 are considered to be correspondent of a biologically significant overlap (Wallace & Ramsay 1983).

All statistical analyses and data manipulations were performed using the open source software R version 2.14.2 (R Development Core Team; www.r-project.org) and the package mvpart version 1.6.0 (De'ath 2001).

RESULTS

A total of 571 PF stomachs (grouped in 106 stomach pools) were analysed from the following species (hereafter referred to by the FAO code): 148 of sardine (*Sardina pilchardus*, pil), 202 of anchovy (*Engraulis encrasicolus,* ane), 79 of chub mackerel (*Scomber colias*, mas), 62 of horse mackerel (*Trachurus trachurus*, hom), 44 of bogue (*Boops boops*, bog), 21 of mackerel (*Scomber scombrus*, mac), 10 of Mediterranean horse mackerel (*Trachurus mediterraneus*, hmm) and 5 of jack mackerel (*Trachurus picturatus*, jaa) (Table 1). With the exceptions of mac and jaa, which were only sampled off the western coast, and hmm, which was only sampled off southern Iberia, all the other species occurred at both studied areas (western and southern Iberian coasts). Regarding maturity stages, for most species the juvenile and adult stages were analysed, except for bog and hmm for which only adults were sampled, and jaa, only represented by juveniles (Table 1).

Feeding intensity

Stomach content weight of the PF ranged from 0.01 to 7.22 g, corresponding to a feeding intensity from 0.05 to 6.7 (Fig. 2). Results of the ANOVA comparing fish species (pil, ane, mas and hom) represented in all areas and maturity stage levels revealed significant differences between areas, species and maturity stages and the interactions between species, maturity stage and area were also significant ($p < 0.001$, $R^2 = 0.26$, $N = 447$). Juvenile fish had a higher feeding intensity than adults (Tukey test $p < 0.001$) and fish from the west coast had stomachs slightly but significantly fuller than those from the south ($p < 0.001$). Regarding the differences in feeding intensity between species, ane had significantly higher feeding intensity than pil, mas and hom ($p < 0.005$), while feeding intensity was not significantly different between the other species.

Table 1. Pelagic fish species, maturity stage (juveniles and adults), fish length classes (cm), number of stomachs analysed (n) per area and number of trawls. Species are represented by FAO codes—pil: *Sardina pilchardus*; ane: *Engraulis encrasicolus*; mas: *Scomber colias*; hom: *Trachurus trachurus*; bog: *Boops boops*; mac: *Scomber scombrus*; jaa: *Trachurus picturatus*; hmm: *Trachurus mediterraneus*

Species	Maturity	Western Iberia			Southern Iberia		
		Size classes (cm)	n	Trawls	Size classes (cm)	n	Trawls
pil	Juvenile	13, 14, 15, 16	46	3	14, 16	22	3
	Adult	19, 20, 21, 22, 23	19	4	18, 19, 20, 21	61	7
ane	Juvenile	9, 10, 11	27	2	9, 10, 11	18	2
	Adult	12, 13, 14, 15, 16, 17, 18	101	3	12, 13, 14	52	4
mas	Juvenile	19, 20, 21		4	20, 21	22	4
	Adult	22, 23, 24, 27	28	5	22, 24	14	2
mac	Juvenile	22, 23, 24, 25	27	3			
	Adult	36	1	1			
bog	Juvenile						
	Adult	20, 21, 22, 24	28	2	16, 19, 22, 24	17	2
hom	Juvenile	13, 15, 17, 18	23	2	18	5	1
	Adult	19, 21, 22, 24	19	3	21	5	1
jaa	Juvenile	18	5	1			
	Adult						
hmm	Juvenile						
	Adult				19	10	1

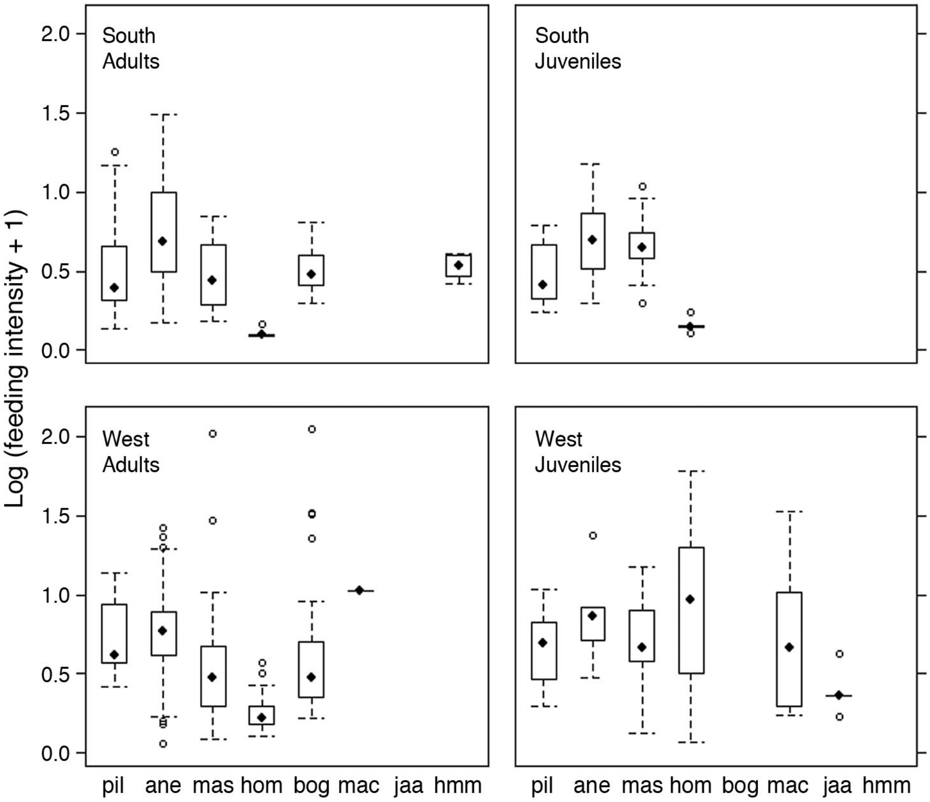

Fig. 2. Feeding intensity of pelagic fishes per area (western and southern Iberian coasts), species (FAO codes as in Table 1) and maturity stages (adults and juveniles). Boxplots show the first and third quartile and 95% confidence interval of the median and points represent outliers

Prey composition and diet overlap

Mean number of identified prey in the stomachs of PF varied between 2 prey per stomach for one hmm stomach pool and 1 944 724 prey per stomach for one pil stomach pool. The comparison of the mean number of prey per stomach of the different PF species showed no significant differences between them, except for hmm, which had a significantly lower number of prey than pil, ane and mas (Table 2, Table S1 in the Supplement at www.int-res.com/articles/suppl/m539p271_supp.pdf). Species richness of prey taxa in PF stomachs was similar between areas and maturity stages but was significantly different between fish species (ANCOVA, $p < 0.001$, $R^2 = 0.43$, $N = 70$). Particularly, species richness

Table 2. Results (p-values) of the pairwise test for multiple comparisons of mean rank sums (Nemenyi-tests) comparing mean prey number (log-transformed) estimated in the stomach contents of different pelagic fish species captured during the PELAGO14 cruise. See Table 1 for species FAO codes. Statistically significant values ($p < 0.05$) are in **bold**

	pil	ane	mas	hom	bog	mac	jaa
ane	0.206	–	–	–	–	–	–
mas	0.820	0.996	–	–	–	–	–
hom	**0.000**	**0.023**	**0.005**	–	–	–	–
bog	0.161	0.998	0.923	0.379	–	–	–
mac	0.987	0.999	1.000	0.088	0.973	–	–
jaa	0.358	0.794	0.662	1.000	0.914	0.692	–
hmm	0.398	0.828	0.704	1.000	0.933	0.731	1.000

(mean ± SD) in pil stomachs (17.6 ± 4.45) was significantly higher than that of ane (12.92 ± 2.70, $p < 0.0001$) and hmm (10.85 ± 3.21, $p = 0.01$) and similar to that of mas (14.94 ± 3.84, $p = 0.08$). bog and jaa, captured off the western Iberian coast, had a species richness of 13.27 ± 2.90 and 14, respectively, while juvenile hmm captured off the southern coast had a species richness of 12. The standardized Shannon-Wiener diversity index of prey determined for each stomach pool varied between 0.02 and 0.61 (Fig. 3) and the ANCOVA of most abundant species (pil, ane, mas and hom) showed that there were no significant differences of prey diversity between areas, maturity stages and species ($p = 0.21$, $R^2 = 0.21$, $N = 70$).

Prey composition, estimated as the relative contribution of different prey types to dietary carbon, was significantly different between species, areas and maturity stages (Table S2 in the Supplement, Figs. 4 & 5). The prey composition of ane, hom, mac and hmm in particular was very different from prey composition of pil, mas, bog and jaa. Prey composition of adult ane, hom and mac from the western coast were dominated by calanoid copepods, followed by decapods and cirripeds, whereas the diet of juvenile ane and hom was dominated by calanoid copepods, decapods and polychaeta. For ane, hom and hmm captured off the southern coast, no differences occurred between juveniles and adults and the stomachs were dominated by calanoid copepods and euphausiids. However, for ane and hmm, mysids and small copepods were also important prey whereas for hom, sardine eggs were the third most important prey type.

Both pil and mas presented similar prey composition, particularly notable is the high importance of sardine eggs for dietary carbon of both species (Table S2, Figs. 4 & 5). Prey composition for these species was different for fish captured off the western and southern coasts. In the south, pil diet composition of juveniles was dominated by fish eggs (unidentified, anchovy eggs and sardine eggs) followed by copepods (calanoids and small harpacticoid, poecilostomatoid and cyclopoids) while adult pil stomachs were dominated by calanoid copepods and sardine eggs, followed by small copepods, crustacean eggs and nauplii and phytoplankton species. Regarding mas off the southern coast, calanoid copepods, decapods and sardine eggs were the most important contributors to dietary carbon. Off the western coast, prey composition of juveniles and adults of pil and mas were similar and dominated by calanoid copepods (>70% dietary carbon), followed by sardine eggs, phytoplankton, cirripeds, decapods and unidentified fish eggs. Finally, the diet of bog was similar to the diet of jaa off the western coast, being dominated by decapods, followed by calanoids and fish eggs, including those of sardines and anchovies, whereas the diet of bog captured in the south was dominated by calanoid copepods and sardine eggs (Table 2, Figs. 4 & 5).

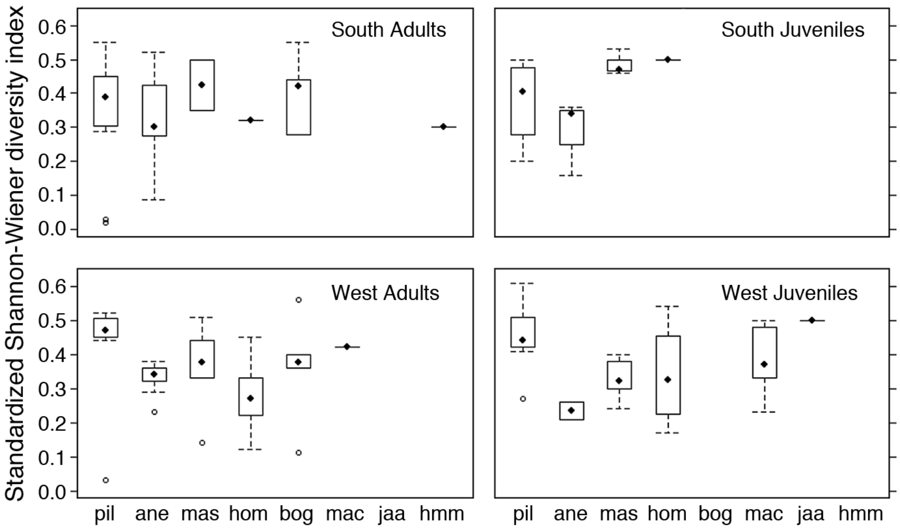

Fig. 3. Standardized Shannon-Wiener diversity index of prey taxa in stomachs of pelagic fishes. Data are divided per area (western and southern Iberian coasts), species (FAO codes as in Table 1) and maturity stages (adult and juvenile). Boxplots show the first and third quartile and 95% confidence interval of the median and points represent outliers

Significant diet overlap was found between several fish species and maturity stages when considering the mean frequency of prey groups to total dietary carbon. Particularly,

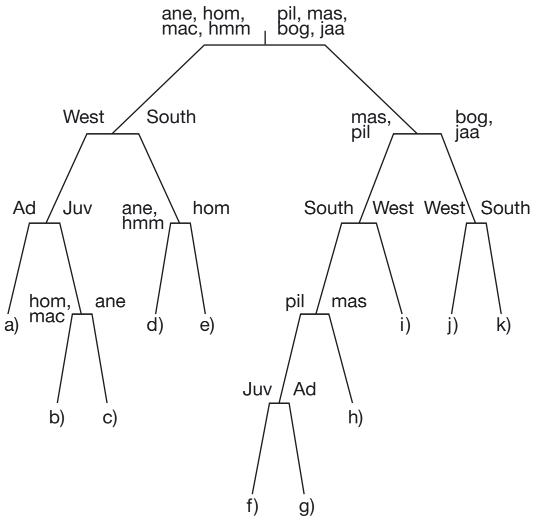

Fig. 4. Regression tree of the percentage contribution of different prey types to total dietary carbon of pelagic fishes sampled during the PELAGO14 survey. Data are divided per area (western and southern Iberian coasts), species (FAO codes as in Table 1) and maturity stages (Ad: adult; Juv: juvenile). Prey compositions (letters) are presented in Fig. 5

for fish captured off the western coast, overlap was high between juvenile ane and adult mac ($S = 0.68$), adult ane and juvenile mas ($S = 0.95$), adult bog and juvenile hom ($S = 0.98$), pil and mas juveniles ($S = 0.62$) and adult and juvenile pil ($S = 0.68$). For fish captured of the southern coast, diet overlap was high between adult pil and juvenile mas ($S = 0.77$) and between adult bog and 3 other species; adult pil ($S = 0.79$), juvenile mas ($S = 0.73$) and juvenile hom ($S = 0.62$). All the other comparisons resulted in overlap index values below 0.6.

Prey size

The comparison of the mean prey size contribution to dietary carbon in the stomachs of the different PF species showed significant differences between the species (N = 1495, $p < 0.0001$, Fig. 6). Particularly, mean prey size was significantly different between pil and all other fish species except for mas and mac, with pil having smaller prey sizes than the other fish species

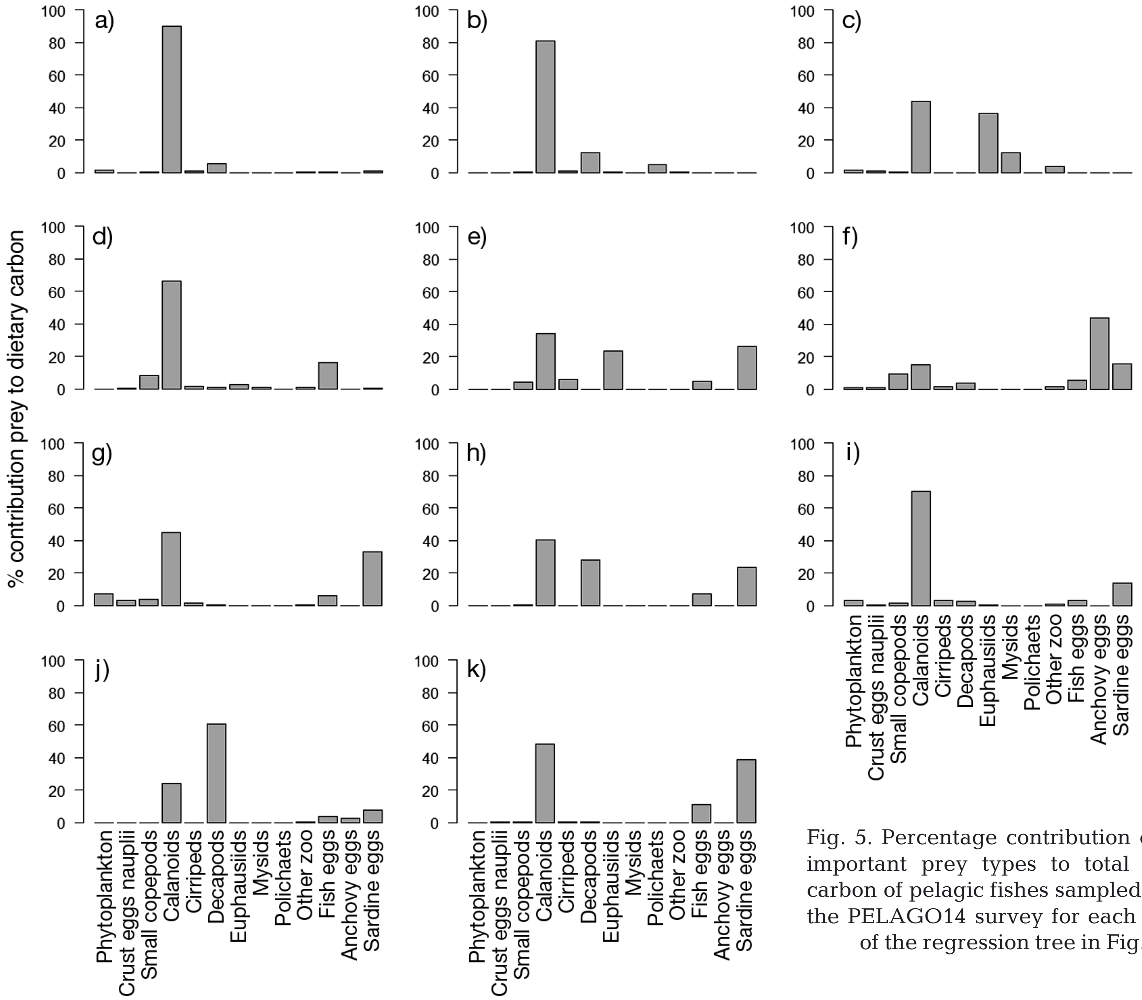

Fig. 5. Percentage contribution of most important prey types to total dietary carbon of pelagic fishes sampled during the PELAGO14 survey for each branch of the regression tree in Fig. 4

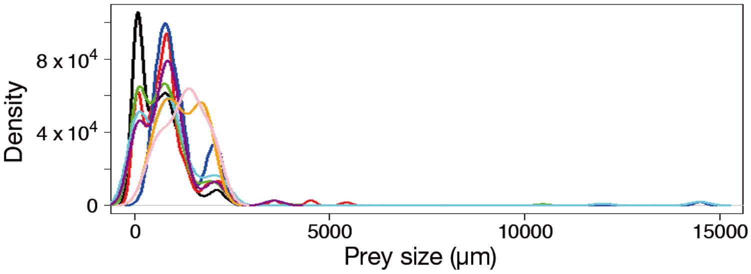

Fig. 6. Kernel density estimate of the distribution of prey size contribution to total dietary carbon of pelagic fishes sampled during the PELAGO14 survey. Species are represented by colors: sardine (black), anchovy (red), chub mackerel (green), horse mackerel (dark blue), bogue (light blue), mackerel (violet), jack mackerel (orange) and Mediterranean horse mackerel (pink)

(Table 3). Significant differences were also found between hom and ane, bog and mas, with hom and ane having larger mean prey size than bog and mas (Table 3).

The relative contribution of different prey size classes to dietary carbon was different between PF species, areas and maturity stages (Fig. 7). Most important prey size class for the majority of the PF species was 1000–2000 µm. This was the case in pil, mas, hom, bog, mac, jaa and hmm. For ane, there was a high and variable contribution of size classes ranging from 500 to >3000 µm, depending on the area and maturity stage. Prey ranging from 500–1000 µm were also important contributors to dietary carbon of all PF species except for jaa and hmm. Regarding the smallest prey size classes (<500 µm), these were abundant prey in the diet of pil, followed by ane and mas, and were absent or had a negligible contribution to dietary carbon for the other PF species. Regarding prey >2000 µm, these were particularly important for ane, mas and bog, representing >40% of total dietary carbon for ane and bog collected off the western coast and mas adults. For pil and hom, prey from 2000–3000 µm were also important, although representing <30% of total dietary carbon. For pil, hom, mac, jaa and hmm, prey >3000 µm had no significant contribution to dietary carbon. For those species where both maturity stages were sampled, there was no clear pattern of prey size class contribution to dietary carbon, except for mas, for which adults had a higher contribution of larger prey sizes (>2000 µm) than juveniles, in contrast to hom and mac, for which larger prey (>2000 µm) had a higher contribution to total dietary carbon for juvenile fish (Fig. 7).

Table 3. Results (p-values) of the pairwise test for multiple comparisons of mean rank sums (Nemenyi-tests) comparing mean prey size contribution to dietary carbon estimated in the stomach contents of different pelagic fish species captured during the PELAGO14 cruise. See Table 1 for species FAO codes. Statistically significant values ($p < 0.05$) are in **bold**

	ane	bog	hmm	hom	jaa	mac	mas
bog	1.000	–	–	–	–	–	–
hmm	0.110	0.172	–	–	–	–	–
hom	**0.000**	**0.004**	0.962	–	–	–	–
jaa	0.177	0.270	1.000	0.995	–	–	–
mac	1.000	1.000	0.222	0.067	0.338	–	–
mas	0.884	0.833	0.040	**0.000**	0.065	0.967	–
pil	**0.000**	**0.003**	**0.003**	**0.000**	**0.004**	0.127	0.089

The contribution of different prey sizes to total dietary carbon regardless of the fish species revealed no significant trend with fish length (Fig. 8). All fish size classes depended mostly on prey ranging from 1000–2000 µm, except for fish <13 cm, represented by ane, which also showed a significant contribution of larger prey (2000–5000 µm) to dietary carbon (mostly mysids and euphausiids), and fish of size classes 20–25 cm, represented by adult mas, bog and hom had prey larger than 10000 µm in their stomachs, corresponding to large decapods.

Cannibalism and intraguild predation

Fish eggs were present in the stomachs of all PF species except for jaa (Table 4, Table S1 in the Supplement), although results from the latter (and also those of hmm) must be considered with caution given the low number of stomachs analysed (Table 1). Most abundant fish eggs in the stomachs were from sardine, followed by unidentified fish eggs and those of anchovy.

Sardine eggs were particularly abundant for fish captured off southern coast compared to the western coast (Table 4, Table S1) and were more frequent and abundant in the stomachs of pil, mas and bog. FO of sardine eggs in pil stomach pools was 42.8% for all sardines samples, with (mean ± SD) 50.3 ± 81.2 eggs stomach^{-1}. In the case of mas, sardine eggs were mostly predated by juveniles, occurring in 78% of the stomach pools, whereas for adults, sardine eggs occurred in 50% of the stomach pools. For bog, sardine eggs occurred in a large number of the stomach pools (>80%). Sardine eggs were present in lower numbers (FO < 24% with <5 eggs stomach^{-1}) in the diet of adult ane and hom, and were absent in the diet of juvenile ane.

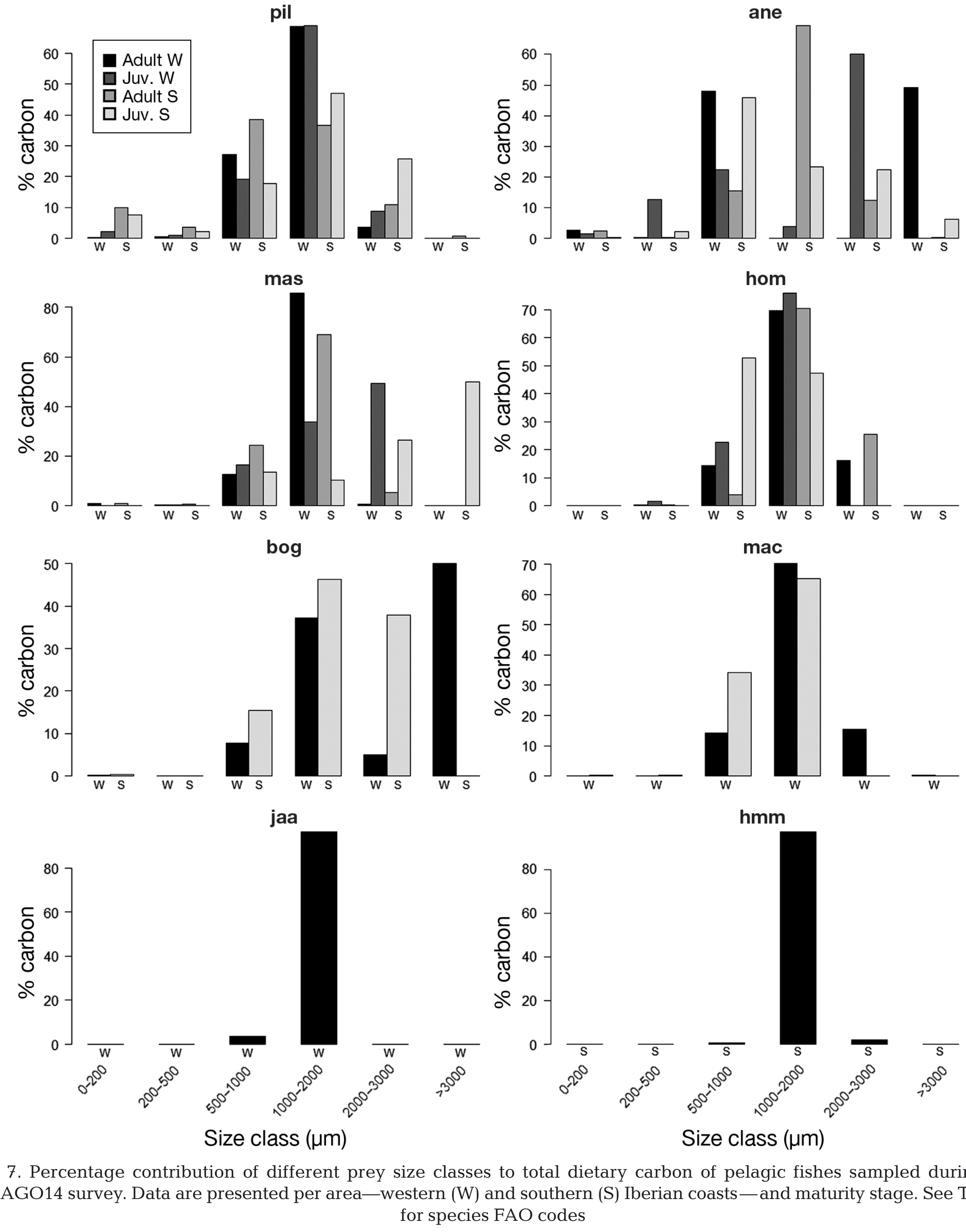

Fig. 7. Percentage contribution of different prey size classes to total dietary carbon of pelagic fishes sampled during the PELAGO14 survey. Data are presented per area—western (W) and southern (S) Iberian coasts—and maturity stage. See Table 1 for species FAO codes

Unidentified fish eggs were spherical with 807.1 ± 152.07 µm (mean ± SD) diameter and can be eggs of all the sampled PF (including unfertilized sardine eggs) except for ane, but no further identification was possible due to digestion. Unidentified fish eggs were particularly important in the diet of pil, mas and ane, followed by bog and mac (Table 4). No unidentified fish eggs were found in the diet of ane, hom, mac and hmm.

Anchovy eggs were found in the stomachs of juvenile and adult pil, mas, bog and hmm, although FO or the mean number of anchovy eggs per stomach was

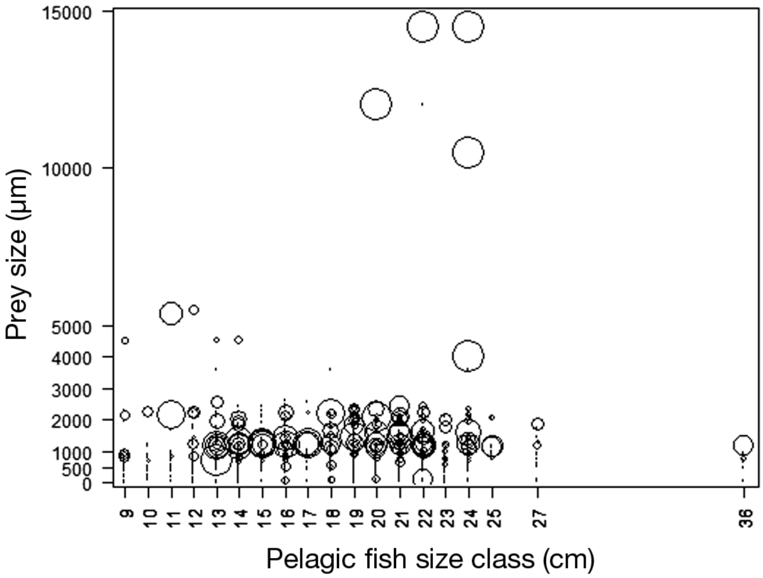

Fig. 8. Relationship between pelagic fish length and prey size contribution to dietary carbon. Symbol size represents the relative contribution to dietary carbon of each of the prey items identified in each of the stomach pools of a given fish species, length class and trawl (see Table 1)

very low for the latter 3 species (FO < 6% for mas and bog, <0.5 eggs stomach^{-1} for hmm). Anchovy eggs were especially frequent and abundant in the stomachs of juvenile pil captured off the southern Iberian coast. For adult pil captured from both areas and juveniles off the western Iberian coast, anchovy eggs were less frequent and abundant (Table 4).

DISCUSSION

This work is the first comparative study of the diet composition of juveniles and adults of the most abundant PF species inhabiting the WIUE. It describes, for the first time, the diet of Atlantic chub mackerel, jack mackerel, bogue and Mediterranean horse mackerel in this area.

Results of this study show that PF species captured off the western and southern Iber-

Table 4. Frequency of occurrence (FO) and mean number of fish eggs in the stomach contents of pelagic fish species captured during the PELAGO14 cruise off the western and southern coast of the Iberian peninsula. See Table 1 for species FAO codes. Unid.: unidentified. Zero values: no fish eggs were found in the stomachs of that species and maturity stage; blank spaces: no fish from that species, area and maturity stage was sampled

Species	Prey	West coast				South coast			
		Juvenile		Adult		Juvenile		Adult	
		FO (%)	Fish eggs (no.)	FO (%)	Fish eggs (no.)	FO (%)	Fish eggs (no.)	FO (%)	Fish eggs (no.)
pil	Unid. fish eggs	51	10.7	71	57.3	75	8.1	75	35.7
	Anchovy eggs	0	0	29	11.7	50	728.6	13	2.2
	Sardine eggs	86	35.5	29	30.1	50	10.2	75	92.1
ane	Unid. fish eggs	0	0	23	4.1	33	1.0	57	101.4
	Anchovy eggs	0	0	0	0	0	0	0	0
	Sardine eggs	0	0	15	4.8	0	0	14	2.2
mas	Unid. fish eggs	20	6.7	43	23.3	75	16.1	50	34.0
	Anchovy eggs	0	0	0	0	0	0	50	2.0
	Sardine eggs	60	58.2	43	15.2	100	46.9	50	8.0
hom	Unid. fish eggs	0	0	28	0.3	100	0.5	0	0
	Anchovy eggs	0	0	0	0	0	0	0	0
	Sardine eggs	0	0	28	0.3	100	1.0	0	0
bog	Unid. fish eggs			33	19.2			100	24.0
	Anchovy eggs			16	36.0			0	0
	Sardine eggs			16	8.9			80	51.6
mac	Unid. fish eggs	0	0	100	38.5				
	Anchovy eggs	0	0	0	0				
	Sardine eggs	0	0	0	0				
jaa	Unid. fish eggs			0	0				
	Anchovy eggs			0	0				
	Sardine eggs			0	0				
hmm	Unid. fish eggs					0	0		
	Anchovy eggs					100	0.2		
	Sardine eggs					0	0		

ian coasts during spring had highly diversified diets, with mesozooplankton prey ranging in size from 1000–2000 µm being the most important contributors to dietary carbon for juvenile and adult sardines, anchovies, chub mackerel, horse mackerel and mackerel, adult bogue and Mediterranean horse mackerel and juvenile jack mackerel. A recent study comparing the diet composition of PF species in the Bay of Biscay found similar results, with a high degree of trophic overlap between PF species and a predominance of calanoid copepods (Bachiller & Irigoien 2015).

Stomach fullness was similar between all species analysed, except for anchovies, which had a slightly higher ratio of stomach weight to fish total weight. Stomach fullness values are in accordance to those reported for sardines (Garrido et al. 2008a) and horse mackerel (Garrido et al. 2008b) in the same region. Stomach fullness was significantly higher for fish captured off the western Iberian coast when compared to the southern coast, in accordance to a previous work on Iberian sardine diet composition (Garrido et al. 2008a). This is explained by the fact that the western coast is more productive than the southern coast because of the occurrence of higher river discharge and also stronger and more frequent upwelling events. Juvenile fish had slightly higher stomach fullness when compared to the adults, which was also observed in previous studies on horse mackerel (Garrido et al. 2008c) but is contrary to results described for sardines (Garrido et al. 2008a). This is probably due to the fact that juveniles have higher metabolic needs related to growth than adults (Rosenfeld et al. 2015), and/or are not engaged in reproduction. At the same time, prey diversity was similar for juvenile and adult fish. There were significant ontogenetic changes in diet composition for all PF species for which both maturity stages were sampled, particularly for sardines, anchovies, chub mackerel, horse mackerel and bogue. This shows that, in order to properly describe PF feeding ecology, the diet overlaps between species and the different stages of fish life-cycle must be taken into account. Moreover, for most feeding studies, including the present study, not all size-classes of juveniles and adults are represented, and one can assume that smaller juveniles and larger adults might have significant differences of diet composition, as shown in studies covering a larger part of the fish ontogeny (e.g. Borme et al. 2009, Nikolioudakis et al. 2012).

Sardine had the highest mean number of prey taxa inside the stomachs, followed by chub mackerel, and the species richness for these species was significantly higher than for the other PF. This was due to the high prevalence of different species of small prey (<500 µm) in the diet of sardine and juvenile chub mackerel. These small prey size classes were only found in high numbers in the diets of sardine and chub mackerel, followed by anchovy and bogue, and were absent or negligible in the diet of the other fish species. This type of diet constitutes an important advantage for fish around the productive Iberian coasts, where upwelling events and river run-off are responsible for high biomasses of small plankton (Sobrinho-Gonçalves et al. 2013). In fact, a previous study has shown that for sardine, the relative contribution of phytoplankton to dietary carbon can be as high as 90%, and is higher during the warmer months (Garrido et al. 2008a). Moreover, the present study shows that the contribution of small plankton (phytoplankton, crustacean eggs and nauplii) was higher for adult sardines than for juvenile sardines collected off the southern Iberian coast. The higher importance of small prey, particularly phytoplankton, as sardines grow older agrees with the fact that the filtering apparatus develops throughout the ontogeny; particularly gill-rakers increase in length and number with age (Andreu 1969, Costalago et al. 2012). The higher prevalence of small prey in older sardines was also observed in previous studies analysing stomach contents of adults captured in the Mediterranean Sea (Nikolioudakis et al. 2012) and using stable isotopes for fish captured off Atlanto–Iberian waters (Bode et al. 2003). However, the ontogenetic difference of diet composition of sardine was not significant in a more recent study using stable isotopes in a larger dataset (Bode et al. 2007). The higher contribution of small prey to sardine diet as fish grows older is the opposite to the results found for chub mackerel, since for this species, adults ingested significantly larger prey (>2000 µm) than juveniles. Therefore, the competition for food between chub mackerel and sardine is more relevant among sardine (adults and juveniles) and chub mackerel juveniles, which was reflected in the results of the Schoener's diet overlap index estimated between these 2 species. This result is consistent with the spatial overlap of the species/maturity stages: sardine adults and juveniles and chub mackerel juveniles distribute in the inner part of the shelf while chub mackerel adults distribute in the outer shelf and slope areas (Martins et al. 2013).

Another similarity in chub mackerel and sardine diet composition which was even stronger than high relative importance of small phyto- and microzooplanktonic prey when compared to the other species was the high contribution of sardine eggs to total dietary carbon, both in the diet of juveniles and adults. Off the southern coast, juvenile sardines depended mostly on fish eggs (unidentified, anchovy and sardine eggs) and copepods (calanoids, harpacticoids and poecilostomatoids), whereas chub mackerel depended mostly on calanoid copepods (>70% of dietary carbon), followed by sardine eggs, phytoplankton, cirripeds, decapods and unidentified fish eggs. Although we have no information on plankton availability during this cruise and therefore cannot attest whether resources were limited, all prey taxa that were identified as the most important for chub mackerel diet were also identified in the present work and in a previous study (Garrido et al. 2008a) as the major prey groups for adult sardines off Iberia, making chub mackerel a potentially strong competitor against sardines in this region. This is particularly relevant since there has been an increase in the abundance and a northward expansion of chub mackerel (Martins et al. 2013) that has reached the main spawning grounds of sardines off the Iberian coast. Acoustic surveys indicate that chub mackerel have become the second most abundant PF in the WIUE, with biomass levels approaching those of sardine (maximum and minimum abundance during the period of 2007 to 2009 being 150 000–250 000 t and 250 000–500 000 t for chub mackerel and sardine, respectively). This potential for competition should be further investigated to ascertain if competition and intraguild predation can, at least partially, explain the recent decline in sardine abundance in southern and western Iberian coastal waters (ICES 2013).

The diet composition of bogue was different between the fish from the western and southern coasts—for west coast bogue, decapod larvae, calanoid copepods and fish eggs (including those of anchovies and sardines) were the main contributors to dietary carbon, wheras south coast bogue mostly depended on calanoid copepods and sardine eggs. To our knowledge, there are no other studies on bogue diet in western and southern Iberian waters. In the Bay of Biscay, adult bogue mostly depended on euphausiids and appendicularians, followed by fish larvae and copepods (Bachiller & Irigoien 2015). Other studies conducted in the Mediterranean and Adriatic Seas showed that larvae and small juveniles (≤6 cm) preferentially consume copepod nauplii (Sánchez-Velasco & Norbis 1997) and calanoid copepodites (Dobroslavić et al. 2013), whereas the diet of larger juveniles and adults (9.6–26.6 cm) was gravimetrically dominated by small fish, siphonophores and crustaceans (decapods, amphipods and isopods), regardless of fish size (Derbal & Kara 2008). This is contrary to our results since adult bogue captured in the present study in Atlanto–Iberian waters had no small fish prey and siphonophores in the stomachs, revealing the adaptability of these forage fish to plankton availability.

The number of prey identified in the stomach contents of PF was similar between species, except for in horse mackerel for which the number of prey inside the stomachs was slightly lower. This was due to the absence of small prey (<200 µm) and low numbers of prey from 200–500 µm in the stomachs of adult and juvenile horse mackerel. The absence of small zooplankton and microzooplankton prey inside horse mackerel stomachs is in accordance with previous studies (e.g. Cabral & Murta 2002, Garrido & Murta 2011), showing that this species is not able to take advantage of the high concentrations of phytoplankton and microzooplankton that occur in this productive upwelling area and that it relies on capturing larger prey, even at the juvenile stage. Horse mackerel depended mostly on calanoid copepods in both areas, followed by decapods off the western coast and euphausiids and sardine eggs off the southern coast. The prevalence of copepods, decapods and euphausiids agrees with the findings of Cabral & Murta (2002), but the presence of sardine eggs is significantly higher in the present study, as no fish eggs in horse mackerel stomachs were identified in the former study. This can be explained by the fact that stomachs analysed in Cabral & Murta (2002) were collected during summer and early autumn months, when sardine spawning off western Iberia is at its lowest. In our work no fish prey (besides fish eggs) were identified in the stomachs of juvenile and adult horse mackerel (ranging from 13–24 cm total length). This is similar to what was observed in the Bay of Biscay (Bachiller & Irigoien 2015) and contrary to the findings of Garrido & Murta (2011), showing that juvenile fish (including sardines) and euphausiids were the main contributors in the diet of horse mackerel fish captured off the southern and western Iberian coasts during one year. However, this latter study focused on fish >20 cm, which seems to be threshold size at which horse mackerel change their diet composition (Cabral & Murta 2002) to include fish (juveniles and adult) in their diet. Large horse mackerel (>20 cm) are generally found in a more offshore distribution, near the shelf break (Murta et al. 2008), and the smallest horse mackerel analysed in the present work are those living in the same areas and often sharing the same shoals as sardines, the main target species of the present study.

The diet of mackerel captured off the western Iberian coast was dominated by calanoid copepods, similar to the diet of horse mackerel and anchovy, but this prey group represented on average 93.7 and 94.4% of total dietary carbon for mackerel juveniles and adults, respectively. Most of the calanoid copepods found in mackerel stomachs in the present study, as well as for all the other fish species captured off the western coast were *Centropages chierchiae*, a very abundant copepod species in this region during all year except for in colder months (Sobrinho-Gonçalves et al. 2013). The dominance of calanoid copepods in the diet of mackerel agrees with the diet of mackerel collected in the Bay of Biscay (Bachiller & Irigoien 2015) and is in contrast to previous findings of Cabral & Murta (2002) and Olaso et al. (2005) studying the diet of similarly sized mackerel off Atlanto–Iberian waters, showing a high importance of fish in the diet, particularly blue whiting, and also euphausiids, which were absent from mackerel's diet in the present study. Moreover, whereas the mean number of prey per stomach in the diet of mackerel captured in northern Iberian waters (Olaso et al. 2005) was only 180, in the present study mean number of prey was 2070 and 13312 for juveniles and adults, respectively (Table S1 in the Supplement). This shows, as mentioned for bogues, the high plasticity of the diet of foraging PF, taking advantage of small and abundant prey when found in high concentrations.

This work represents the first description of the diet of jack mackerel and Mediterranean horse mackerel in this region, although a low number of stomachs were analysed. Decapods were the dominant prey in jack mackerel juvenile stomachs in terms of the relative contribution to dietary carbon, followed by large copepods (*Calanus helgolandicus* and *Candacia* spp.). Calanoid copepods dominated the diet (particularly unidentified species and *Calanus helgolandicus*) of adult Mediterranean horse mackerel. These results agree with the diet description for these species in the Mediterranean sea (Deudero & Morales-Nin 2001, Bayhan et al. 2013).

Fish eggs were mainly predated by juvenile and adult sardines, juvenile chub mackerel and adult bogue (no juvenile bogue were sampled). These species had the highest FO and number of sardine eggs and unidentified fish eggs in their stomachs and eggs represented a major contributor to total dietary carbon for the 3 species. Anchovy eggs were rare or absent in the stomachs of PF species except for juvenile sardines captured off the southern Iberian coast. Predation of fish eggs is expected to be even higher during the spawning peaks of these species, namely in winter months for sardine and during summer months for anchovy, as confirmed by a former study of sardine feeding seasonality (Garrido et al. 2008a). Our results suggest that the major predators of PF eggs in the Atlanto–Iberian region are sardine, chub mackerel and bogue. Given the frequent and abundant consumption of fish eggs by several PF species, the predation of eggs by all PF combined must be further explored because it can be a major source of mortality and consequently may have a negative impact on recruitment (Irigoien & de Roos 2011). Some of these PF species have strong diel variations of feeding intensity (e.g. horse mackerel, Garrido et al. 2008a), related, at least in part, to the diel vertical migrations of fish schools (e.g. Cardinale et al. 2003). Diel cycles of fish vertical positioning can strongly affect food quantity and composition. In fact, the absence of sardine eggs in the stomachs of sardines at the Mediterranean, in contrast to the prevalence of this prey type found in the WIUE, was proposed to be related to the opposite trends in the diel vertical migration of sardine schools (Costalago et al. 2015). A diel study of the vertical positioning and diet composition and intensity of PF (particularly sardines, chub mackerel and bogue) carried out in the main spawning areas and seasons, and combined with a correct estimation of fish evacuation rates and with estimates of abundance of the different pelagic species, should be performed in order to correctly estimate the impact of egg cannibalism and intraguild predation on egg mortality, and consequently, on the recruitment of pelagic species. Eggs of PF species other than the conspicuous ones from sardines and anchovies are very difficult to visually identify in the stomachs. Alternative molecular techniques (e.g. Albaina et al. 2015) could be explored to correctly identify these eggs and discriminate the impact of cannibalism and intraguild predation on PF.

The present work allows the identification of the main potential competitors among the most abundant PF species in the WIUE during spring. This study shows that there is a high trophic overlap between all the PF species in terms of preferred prey size class (1000–2000 µm) and type (calanoid copepods as a major prey group). However, some differences, such as the prevalence of phytoplankton and microzooplankton prey for sardines, chub mackerel and anchovies might confer an advantage to these species in the productive western Iberian waters. This study identified sardines, chub mackerel and bogues as the main predators of fish eggs, particularly those of sardines, and identified juvenile chub mackerel as a potential competitor for sardine. Given the northward expansion of several PF species such as chub mackerel, associated with a warming trend that is being registered in the northeast Atlantic (Relvas et al. 2009), these trophic relationships should be further investigated. Forage fish are known to have a high plasticity of feeding ecology, with diets varying according to different areas, seasons and year (e.g. Garrido & Murta 2011). Further studies are required to study the potential competition during other seasons of the year, and should include an evaluation of food availability to ascertain the potential feeding selectivity. Analysing the trophic ecology of co-habiting PF species comparatively, such as in the present study, is a fundamental step towards more detailed knowledge of coastal foodwebs, towards improving the understanding of PF population dynamics, and informs models for an ecosystem approach to fisheries management.

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LITERATURE CITED

Abaunza P, Gordo L, Karlou-Riga C, Murta A and others (2003) Growth and reproduction of horse mackerel, *Trachurus trachurus* (Carangidae). Rev Fish Biol Fish 13: 27–61

Afonso-Dias I, Amorim P, Silva A (2008) Problems with assigning the ovaries of sardine (*Sardina pilchardus*) to the appropriate macroscopic maturity stage. Mar Biodivers Rec 1:e20

Albaina A, Irigoien X, Aldalura U, Cotano U, Santos M, Boyra G, Estonba A (2015) A real-time PCR assay to estimate invertebrate and fish predation on anchovy eggs in the Bay of Biscay. Prog Oceanogr 131:82–99

Andreu B (1969) Las branquispinas en la caracterización de las poblaciones de *Sardina pilchardus* (Walb.). Investig Pesq 33:425–607

Bachiller E, Irigoien X (2015) Trophodynamics and diet overlap of small pelagic fish species in the Bay of Biscay. Mar Ecol Prog Ser 534:179–198

Bakun A (2006) Wasp-waist populations and marine ecosystem dynamics: navigating the 'predator pit' topographies. Prog Oceanogr 68:271–288

Bayhan B, Sever TM, Kara A (2013) Diet composition of the Mediterranean horse mackerel, *Trachurus mediterraneus* (Steindachner, 1868) (Osteichthyes: Carangidae), from the Aegean Sea. Belg J Zool 143:15–22

Bernal M, Stratoudakis Y, Coombs S, Angelico M and others (2007) Sardine spawning off the European Atlantic coast: characterization of and spatio-temporal variability in spawning habitat. Prog Oceanogr 74:210–227

Bode A, Carrera P, Lens S (2003) The pelagic foodweb in the upwelling ecosystem of Galicia (NW Spain) during spring: natural abundance of stable carbon and nitrogen isotopes. ICES J Mar Sci 60:11–22

Bode A, Alvarez-Ossorio MT, Cunha ME, Garrido S and others (2007) Stable isotope studies of the pelagic food web on the northern and north western shelf of the Iberian Peninsula. Prog Oceanogr 74:115–131

Borme D, Tirelli V, Brandt SB, Fonda Umani S, Arneri E (2009) Diet of *Engraulis encrasicolus* in the northern Adriatic Sea (Mediterranean): ontogenetic changes and feeding selectivity. Mar Ecol Prog Ser 392:193–209

Cabral HN, Murta A (2002) The diet of blue whiting, hake, horse mackerel and mackerel off Portugal. J Appl Ichthyol 18:14–23

Cardinale M, Casini M, Arrhenius F, Håkansson N (2003) Diel spatial distribution and feeding activity of herring *Clupea harengus* and sprat *Sprattus sprattus* in the Baltic Sea. Aquat Living Resour 16:283–292

Costalago D, Navarro J, Alvarez-Calleja I, Palomera I (2012) Ontogenetic and seasonal changes in the feeding habits and trophic levels of two small pelagic fish species. Mar Ecol Prog Ser 460:169–181

Costalago D, Garrido S, Palomera I (2015) Comparison of the feeding apparatus and diet of European sardines of Atlantic and Mediterranean waters: ecological implications. J Fish Biol 86:1348–1362

De'ath G (2001) Multivariate regression trees: a new technique for modelling species environment relationships. Ecology 83:1105–1117

Derbal F, Kara MH (2008) Composition du régime alimentaire du bogue *Boops boops* (Sparidae) dans le golfe d'Annaba (Algérie). Cybium 32:325–333

Deudero S, Morales-Nin B (2001) Prey selectivity in planktivorous juvenile fishes associated with floating objects in the western Mediterranean. Aquacult Res 32:481–490

Dobroslavić T, Zlatović A, Bartulović V, Lućić D, Glamuzina B (2013) Diet overlap of juvenile salema (*Sarpa salpa*), bogue (*Boops boops*) and common two-banded sea bream (*Diplodus vulgaris*) in the south-eastern Adriatic. J Appl Ichthyol 29:181–185

Dorel D (1986) Poissons de l'Atlantique nord-est relations taille-poids. Institut Français de Recherche pour l'Exploitation de la Mer, Nantes

Garrido S (2002) Alimentaçao de *Sardina pilchardus* (Walbaum, 1792) ao largo da costa continental portuguesa e implicaçoes da condiçao nitricional das fêmeas na qualidade dos oócitos. MSc thesis, Universidade do Porto

Garrido S, Murta A (2011) Horse mackerel (*Trachurus trachurus*) feeding off Portugal: inter-decadal and spatial variations of diet composition. J Fish Biol 79:2034–2042

Garrido S, van der Lingen CD (2014) Feeding biology and ecology. In: Ganias K (ed) Biology and ecology of sardines and anchovies. CRC Press, Boca Raton, FL

Garrido S, Marçalo A, Zwolinski J, van der Lingen CD (2007a) Laboratory investigations on the effect of prey size and concentration on the feeding behaviour of *Sardina pilchardus*. Mar Ecol Prog Ser 330:189–199

Garrido S, Rosa R, Ben-Hamadou R, Cunha ME, Chícharo MA, van der Lingen CD (2007b) Effect of maternal fat reserves on the fatty acid composition of sardine (*Sardina pilchardus*) oocytes. Comp Biochem Physiol B 148: 398–409

Garrido S, Ben-Hamadou R, Oliveira PB, Cunha ME, Chícharo MA, van der Lingen CD (2008a) Diet and feeding intensity of sardine *Sardina pilchardus*: correlation with satellite-derived chlorophyll data. Mar Ecol Prog Ser 354: 245–256

➤ Garrido S, Rosa R, Ben-Hamadou R, Cunha ME, Chícharo MA, van der Lingen CD (2008b) Spatio-temporal variability in fatty acid trophic biomarkers in stomach contents and muscle of Iberian sardine (*Sardina pilchardus*) and its relationship with spawning. Mar Biol 154: 1053–1065

➤ Garrido S, Murta A, Moreira A, Ferreira MJ, Angélico MM (2008c) Horse mackerel (*Trachurus trachurus*) stomach fullness off Portugal: index calibration and spatio-temporal variations of feeding intensity. ICES J Mar Sci 65: 1662–1669

Gordo L (1995) On the sexual maturity of the bogue *Boops boops* (Teleostei, Sparidae). Sci Mar 59:279–286

ICES (2008) Report of the International Bottom Trawl Survey Working Group (IBTSWG). Vigo, Spain, 31 March–4 April 2008. ICES CM 2008/RMC:02

ICES (2013) Working Group on Acoustic and Egg Surveys for Sardine and Anchovy in ICES Areas VIII and IX (WGACEGG), 25–29 November 2013, Lisbon, Portugal. ICES CM 2013/SSGESST:20

ICES (2014) Report of the Working Group on Southern Horse Mackerel, Anchovy and Sardine (WGHANSA). 20–25 June 2014, Copenhagen, Denmark. ICES CM 2014/ACOM:16

➤ Irigoien X, de Roos A (2011) The role of intraguild predation in the population dynamics of small pelagic fish. Mar Biol 158:1683–1690

➤ Jurado-Ruzafa A, García Santamaría MT (2013) Reproductive biology of the blue jack mackerel, *Trachurus picturatus* (Bowdich,1825), off the Canary Islands. J Appl Ichthyol 29:526–531

➤ Linton R, Davies RW, Wrona FJ (1981) Resource utilization indices: an assessment. J Anim Ecol 50:283–292

➤ Martins MM, Skagen D, Marques V, Zwolinski J, Silva A (2013) Changes in the abundance and spatial distribution of the Atlantic chub mackerel (*Scomber colias*) in the pelagic ecosystem and fisheries off Portugal. Sci Mar 77: 551–563

➤ Millán M (1999) Reproductive characteristics and condition status of anchovy *Engraulis encrasicolus* L. from the Bay of Cadiz (SW Spain). Fish Res 41:73–86

➤ Murta AG, Abaunza P, Cardador F, Sánchez F (2008) Ontogenic migrations of horse mackerel along the Iberian coast. Fish Res 89:186–195

➤ Nikolioudakis N, Isari S, Pitta P, Somarakis S (2012) Diet of sardine *Sardina pilchardus*: an 'end-to-end' field study. Mar Ecol Prog Ser 453:173–188

➤ Olaso I, Gutiérrez JL, Villamor B, Carrera P, Valdés L, Abaunza P (2005) Seasonal changes in the north-eastern Atlantic mackerel diet (*Scomber scombrus*) in the north of Spain (ICES DivisionVIIIc). J Mar Biol Assoc UK 85: 415–418

➤ Relvas P, Luis J, Santos AMP (2009) The importance of the mesoscale in the decadal changes observed in the Northern Canary upwelling system. Geophys Res Lett 36: L22601, doi:10.1029/2009GL040504

➤ Rosenfeld J, van Leeuwen T, Richards J, Allen D (2015) Relationship between growth and standard metabolic rate: measurement artefacts and implications for habitat use and life-history adaptation in salmonids. J Anim Ecol 84:4–20

Sánchez-Velasco L, Norbis W (1997) Comparative diets and feeding habits of *Boops boops* and *Diplodus sargus* larvae, two sparid fishes co-occurring in the northwestern Mediterranean. Bull Mar Sci 61:821–835

➤ Silva A, Santos MB, Caneco B, Pestana G, Porteiro C, Carrera P, Stratoudakis Y (2006) Temporal and geographic variability of sardine maturity at length in the northeastern Atlantic and the western Mediterranean. ICES J Mar Sci 63:663–676

➤ Smith C, Reay P (1991) Cannibalism in teleost fish. Rev Fish Biol Fish 1:41–64

➤ Sobrinho-Gonçalves L, Moita MT, Garrido S, Cunha ME (2013) Environmental forcing on the interactions of plankton communities across a continental shelf in the Eastern Atlantic upwelling system. Hydrobiologia 713: 167–182

Valdés E, Shelton PA, Armstrong MJ, Field JG (1987) Cannibalism in South African anchovy:egg mortality and egg consumption rates. S Afr J Mar Sci 5:613–622

van der Lingen CD (2002) Diet of sardine *Sardinops sagax* in the Southern Benguela upwelling ecosystem. S Afr J Mar Sci 24:301–316

Vasconcelos J, Afonso-Dias M, Faria G (2012) Atlantic chub mackerel (*Scomber colias*) spawning season, size and age at first maturity in Madeira waters. Arquipelago. Life Mar Sci 29:43–51

Viette M, Giulianini PG, Ferrero EA (1997) Reproductive biology of scad, *Trachurus mediterraneus* (Teleostei, Carangidae), from the Gulf of Trieste ICES. J Mar Sci 54: 267–272

➤ Wallace H, Ramsay JS (1983) Reliability in measuring diet overlap. Can J Fish Aquat Sci 40:347–351

Walsh M, Hopkins P, Witthames P, Greer-Walker P, Watson NJ (1990) Estimation of total potential fecundity and atresia in the western mackerel stock, 1989. ICES CM 1990/H:31, Aberdeen

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