



# Seasonal and spatial variability of Atlanto-Iberian pelagic fish diet with estimates of intraguild predation

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**ABSTRACT:** The diets of 3 of the most abundant coastal pelagic fish species in the eastern Atlantic (sardine, anchovy and Atlantic chub mackerel) were investigated, including seasonal, geographical and ontogenetic variability of the diets. We also estimated the impact of cannibalism and intraguild predation on egg mortality, and a different method to evaluate egg mortality is proposed taking the spatial overlap of predators and eggs into account. Diet overlap occurred between the 3 pelagic species, which derive most of their dietary carbon from mesozooplankton prey. However, calanoid copepods were mostly important for anchovy and sardine, whereas the diet of the Atlantic chub mackerel also included crustacean eggs, nauplii, small copepodites and larger prey such as decapods. Sardine was the main predator of fish eggs (90% of all identified eggs), followed by Atlantic chub mackerel (8%) and anchovy (2%). Cannibalism by anchovies and sardines on their eggs was low (<10% of spawned eggs) for all areas and seasons. The impact of sardine predation on anchovy egg mortality was high (71% of the anchovy eggs spawned per day during the spring off northwestern Iberia) and may explain why anchovy abundance has only peaked in recent years, when sardine abundance was at its lowest level, highlighting the importance of taking an ecosystem approach to fisheries management into account. However, species-specific data of gastric evacuation rates and feeding durations are needed to obtain more accurate estimates of the impact of cannibalism and intraguild predation on egg mortality.

**KEY WORDS:** Trophic ecology · Small pelagics · Stomach contents · Egg mortality · Cannibalism

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## 1. INTRODUCTION

Small pelagic fish are key components of the pelagic food web, particularly in coastal upwelling regions, where they occupy an intermediate trophic level (Bakun 2006). These species directly consume plankton, exerting a top-down control over planktonic communities and at the same time a bottom-up control over top predators (Cury et al. 2000). A comparison of diet composition of co-occurring small pelagic fish species has been studied in different ecosystems (van der Lingen et al. 2009, Garrido & van der Lingen 2014, Bachiller & Irigoien 2015), and a trophically mediated alternation of abundance has

been proposed for anchovy and sardine (van der Lingen et al. 2006). However, other coastal pelagic species are frequently found in the same area and in mixed shoals with small pelagics, such as species of the genera *Scomber* and *Trachurus*, which are planktivorous at least during part of their ontogeny and whose trophic niche can overlap that of small pelagic species (Garrido et al. 2015).

In the Canary Current upwelling system, the European sardine *Sardina pilchardus* is the dominant pelagic fish species, followed by other coastal pelagics such as the Atlantic chub mackerel *Scomber colias* and horse mackerel *Trachurus trachurus*. The anchovy *Engraulis encrasicolus* is particularly abun-

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dant in the northern part of the Canary Current upwelling system, off the Iberian Peninsula, with their abundance increasing in recent years (maximum historical values in 2018 and 2020), following years of minimum historical values for sardine (ICES 2020). The abundance of Atlantic chub mackerel has also increased in recent years off Atlanto-Iberian waters, and recruitment for this species was shown to be negatively correlated with that of sardine (Martins et al. 2013). In Atlanto-Iberian waters, sardine is widely distributed, anchovy is mainly present in the Gulf of Cadiz and the northwestern Iberian coast and almost absent in southwestern Iberia, while chub mackerel populations are particularly abundant in the southern Iberian coast. The 3 species are often found in mixed shoals, are present in the studied area all year, and no clear latitudinal seasonal migration has been described for any of them.

European sardine, European anchovy and Atlantic chub mackerel are important socio-economic resources, representing the main targets of a purse-seine fishery based in both Portugal and Spain (Feijó et al. 2018, ICES 2020). These species are difficult to manage due to their high inter-annual variability in distribution and abundance (ICES 2020). Food availability has been shown to be the main driver of growth, reproduction and migration (Alheit et al. 2009, Nikolioudakis et al. 2014), and for this reason, information on their trophic ecology is necessary to understand the dynamics of these resources.

Small pelagic species have highly diversified diets, resulting from their feeding behaviour of alternating between particulate feeding (selective) and filtration (non-selective), which allows efficient exploitation of a wide range of planktonic prey (James & Findlay 1989, Garrido et al. 2007a). Diet composition changes with ontogeny, particularly for sardines whose feeding apparatus evolves over time, allowing them to retain smaller particles (Costalago et al. 2014), and also for Atlantic chub mackerel, which is a planktivore during the juvenile stage (Garrido et al. 2015) but includes piscivory in the adult stage (Castro 1993, Bachiller & Irigoien 2015, Garrido et al. 2015, Romero et al. 2021). Diet composition of planktivorous fish is strongly dependent on food availability, varying seasonally and spatially (Garrido et al. 2008). Regional differences in productivity of Iberian waters were shown to have a significant effect on sardine trophic ecology (Garrido et al. 2007a), subsequently affecting their lipid and fatty acid reserves that transfer to their progeny (Garrido et al. 2007b). The knowledge of spatial and seasonal variability of adult fish feeding is valuable, since it can impact fish

recruitment through maternal effects (Brosset et al. 2020).

Top-down control of planktivorous fish (Checkley et al. 2009) suggests that changes in plankton availability may result in competition for resources (Irigoien & de Roos 2011). Competition can play an important role in population dynamics when resources are limiting and may favour one species over another (Bachiller et al. 2015). Resource partitioning between co-occurring sardine and anchovy species is well described, with sardines more adapted to filtering small prey while anchovies are more adapted to particulate feeding on larger mesozooplanktonic prey (van der Lingen 2006, Garrido & van der Lingen 2014). The diet of Atlantic chub mackerel is less studied, but this species seems to have higher trophic overlap with small pelagics than other coastal pelagics that share the same habitat and is also one of the main predators of sardine eggs (Garrido et al. 2015). Horse mackerel, on the other hand, is very abundant in the studied area, but previous studies have shown that its diet has a significantly lower overlap with small pelagics, and fish eggs are rarely found in the stomachs (Garrido & Murta 2011, Garrido et al. 2015).

Most sardine and anchovy species, and also chub mackerel, are known to feed on their own eggs and larvae, as well as those of other clupeiformes that share the same trophic niche, through intraguild predation and cannibalism (Bachiller 2012, Garrido & van der Lingen 2014, Garrido et al. 2015). Cannibalism has been proposed as a density-dependent, self-regulatory mechanism (Valdés-Szeinfeld 1991), used as a way to compensate for reduced food availability (Valdés-Szeinfeld 1993, Pájaro et al. 2007, Garrido et al. 2008). Time series of stomach data could help elucidate if egg consumption increases with decreasing alternative prey availability and/or with higher population density. Estimates of egg mortality due to cannibalism or intraguild predation vary greatly with species and area, but accurate assessment of their impact is important because they have the potential to be a significant source of mortality, sufficient to cause fluctuations in year-class strength (Smith & Reay, 1991).

In Iberian waters and in the Bay of Biscay, fish eggs are an important prey for pelagic fish (Garrido et al. 2008, Bachiller et al. 2015, Garrido et al. 2015), contrasting with other areas where egg predation by the same species is reduced, such as the Mediterranean Sea (Costalago et al. 2012, Nikolioudakis et al. 2012). Off Argentina and South Africa, high levels of anchovy egg cannibalism were also estimated (Valdés et al. 1987, Pájaro 1998, Pájaro et al. 2007; Table 1). There is a high discrepancy in the estimates of egg

consumption rates between studies, which may be derived from spatial and seasonal differences in diet composition but is also a consequence of assumptions made when estimating egg mortality. When calculating egg consumption rates, it is necessary to take the following into account: (1) the method used in defining the weight of the predator, (2) the gastric evacuation rate, (3) the duration of feeding, and (4) the total biomass of the predator (Bachiller et al. 2015). For most species, there are no species-specific data of feeding duration and gastric evacuation times, and values derived for other species/prey are generally utilized. Also, it is generally assumed that all predators occurring in a given area are potential predators of fish eggs. However, the distributions of predators and eggs rarely are completely coincident. For example, anchovy eggs off western Iberia are mainly concentrated near the estuaries located off northern Portugal, while sardine adults have a broad distribution over the Iberian continental shelf. Knowing the spatial overlap of predators and fish eggs could significantly improve estimates of egg mortality.

This study aims to increase the knowledge of the seasonal and geographical variability of trophic overlap and egg predation of 3 abundant coastal pelagic fish species of high importance for Iberian fisheries, namely sardine *Sardina pilchardus*, anchovy *Engraulis encrasicolus* and Atlantic chub mackerel *Scomber colias*. These 3 species were selected as they are very abundant in the northern Canary Upwelling System and not only have the potential to compete for food, but they also include fish eggs and larvae in their diets. This study specifically intends to: (1) describe

the diet of sardine, anchovy and Atlantic chub mackerel in Atlanto-Iberian waters, evaluating the diet overlap for adults and juveniles in different areas (west and south Iberian coasts), and during 2 seasons (spring and fall) and (2) estimate sardine and anchovy egg mortality due to cannibalism and intraguild predation, by using a novel method that takes into account the spatial overlap of eggs and fish at the time of collection, which has not been considered in previous approaches.

## 2. MATERIALS AND METHODS

Pelagic fish were collected during the spring and fall of 2018, during 3 annual acoustic surveys aiming to estimate the abundance of pelagic fish species off the western and southern Atlantic Iberian waters (ICES 2018): (1) the PELAGO18 survey, which took place during spring (April and May), and covered the area from Galicia to the Gulf of Cadiz, (2) the ECO-CADIZ-Reclutas18 survey, which occurred during fall (October) and covered the Gulf of Cadiz from Cape S. Vicente (Portugal) to Cape Trafalgar (Spain) and (3) the IBERAS18 survey, which took place during fall (November) along the western Iberian coast (Fig. 1).

All fish samples were collected during the day, mostly by pelagic trawling and to a lesser extent by bottom trawls. Samples were also obtained from purse seiners operating in collaboration with the research vessel, to capture fish corresponding to shoals identified acoustically. In total, 653 pelagic fishes were collected, including 272 sardine (*S. pilchardus*,

Table 1. Summary of studies on the percentage of predation of sardine and anchovy eggs by sardine and anchovy. Results presented as percentage of total egg mortality resulting from cannibalism or intraguild predation with the exception of Ward et al. (2008), where the values are presented as % of eggs in the diet. -: absence of information in the respective study. *S. pilchardus*: *Sardina pilchardus*; *S. sagax*: *Sardinops sagax*; *S. ocellatus*: *Sardinops ocellatus*; *E. encrasicolus*: *Engraulis encrasicolus*; *E. anchoita*: *Engraulis anchoita*; *E. capensis*: *Engraulis capensis*; *E. ringens*: *Engraulis ringens*; *E. mordax*: *Engraulis mordax*

Reference	Geographical region	Study species	Egg species	Predation by sardine (%)	Predation by anchovy (%)	Feeding duration (h)
Bachiller et al. (2015)	Bay of Biscay	<i>E. encrasicolus</i> / <i>S. pilchardus</i>	<i>E. encrasicolus</i>	33	4	12
Bachiller (2012)	Bay of Biscay	<i>E. encrasicolus</i> / <i>S. pilchardus</i>	<i>E. encrasicolus</i>	14–48	2	24
Garrido et al. (2008)	Portugal	<i>S. pilchardus</i>	<i>S. pilchardus</i>	30	–	9
Ward et al. (2008)	Australia	<i>S. sagax</i>	<i>S. sagax</i>	3.7 (of diet)	0.1 (of diet)	–
Pájaro et al. (2007)	Argentina	<i>E. anchoita</i>	<i>E. anchoita</i>	–	33.4	12
Pájaro (1998)	Argentina	<i>E. anchoita</i>	<i>E. anchoita</i>	–	27	12
Valdés Szeinfeld (1991)	South Africa	<i>E. capensis</i> / <i>S. ocellatus</i>	<i>E. capensis</i>	56	6	24
Valdés (1987)	South Africa	<i>E. capensis</i>	<i>E. capensis</i>	–	70	24
Alheit (1987)	Peru	<i>E. ringens</i> / <i>S. sagax</i>	<i>E. ringens</i>	–	22	24
Santander et al. (1983)	Peru	<i>E. ringens</i> / <i>S. sagax</i>	<i>E. ringens</i>	–	10	24
Hunter & Kimbrell (1980)	California	<i>E. mordax</i>	<i>E. mordax</i>	–	32	24
MacCall (1981)						

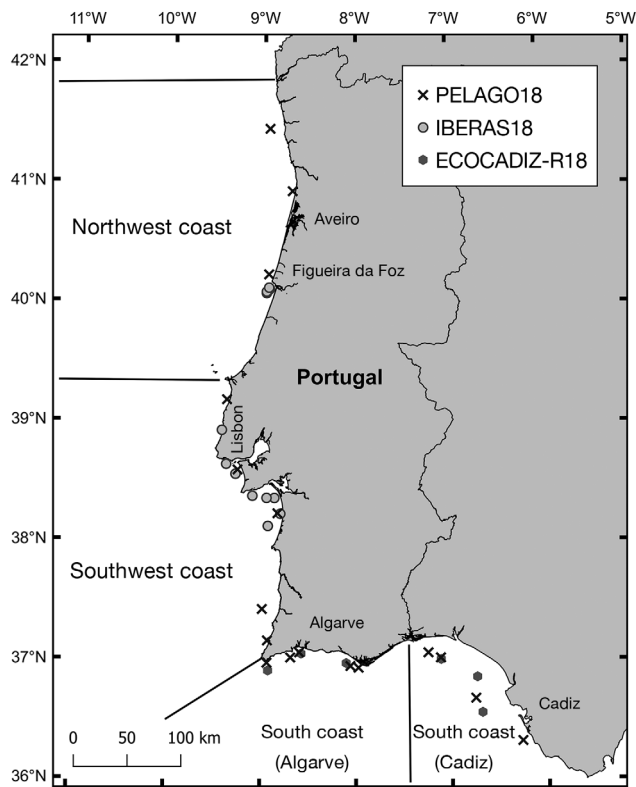


Fig. 1. Portuguese continental coast and Gulf of Cadiz, with the capture sites of Atlantic chub mackerel, anchovy and sardine, during the cruises of PELAGO18, IBERAS18 and ECOCADIZ-Reclutas18

Table 2. Average total length (cm), respective SD and total number (n) of sardines (PIL), anchovies (ANE) and Atlantic chub mackerels (VMA) analyzed. Data aggregated by season (spring and fall, with research cruise in parentheses), maturity (adult and juvenile) and study area (west coast and south coast). --: absence of samples

Species	Maturity	West coast			South coast		
		Mean	SD	n	Mean	SD	n
<b>Spring (PELAGO18)</b>							
PIL	Adult	18.7	0.8	49	16.7	0.3	7
	Juvenile	12.0	0.5	20	9.8	2.2	46
ANE	Adult	12.4	0.2	15	12.5	0.3	27
	Juvenile	10.2	0.2	21	10.7	0.5	32
VMA	Adult	--	--	--	25.4	1.7	28
	Juvenile	20.2	0.3	12	18.5	1.7	81
<b>Fall (IBERAS18/ECOCADIZ-Reclutas18)</b>							
PIL	Adult	19.2	1.3	79	16.6	0.5	13
	Juvenile	14.2	0.7	41	15.1	0.7	17
ANE	Adult	13.4	0.7	25	14.7	1.4	28
	Juvenile	11.5	0.2	5	11.7	0.1	2
VMA	Adult	26.4	2.1	19	26.0	3.1	27
	Juvenile	20.2	1.0	56	21.2	1.0	3

PIL), 155 anchovy (*E. encrasicolus*, ANE) and 226 Atlantic chub mackerel (*S. colias*, VMA) (Table 2). Juvenile and adult fish were classified by the mean size (length, cm) at first maturity (L50) taken from the literature. For anchovy, this is defined as 12 cm (Millán 1999), for Atlantic chub mackerel 22 cm (Vasconcelos et al. 2012) and for sardine 16 cm (Garrido et al. 2015).

In order to characterize the diet composition of pelagic fish by area (western and southern Iberia), species (anchovy, sardine and chub mackerel) and maturity stage (juvenile and adult), we aimed to collect 15 individuals per grouping. We defined this number based on expected availability of samples taken for on board routine biological sampling per maturity stage and the number used in previous studies (Tudela & Palomera 1997, Plounevez & Champalbert 2000, van der Lingen 2002, Garrido et al. 2008, 2015, Espinoza et al. 2009). While this number was achieved for most of the groups, 4 groups had a very low number of individuals: anchovy juveniles collected in the fall from both areas (5 and 3 individuals each), chub mackerel juveniles in the south during the fall (3 individuals) and sardine adults collected from south Iberia during the spring (7 individuals). While unequal sample size can affect the power of the statistical tests, most groups had sufficient numbers of stomachs available, and in all cases we tested for homogeneity of variances when comparing means among the different groupings.

In order to study egg mortality, sardine and anchovy eggs were counted in the stomachs for individual fish and compared between predator species, maturity stages and zones corresponding to the ICES sub-divisions within the studied area: sub-division 9a.CN, corresponding to the northwestern Iberian coast (NWC); sub-division 9aCS, corresponding to the southwestern Iberian coast (SWC); 9aS-alg, corresponding to the southern Portuguese coast (ALG) and 9aS-Cad, representing the Gulf of Cadiz (CAD).

In the laboratory, biological data of 653 specimens were analyzed, including total length (cm), total and gutted weight (g), gonad weight (g), sex, maturity stage and indices of fat content (Pinto & Barraca 1958). Stomachs were removed and frozen at  $-20^{\circ}\text{C}$  for later analysis. This analysis consisted of weighing each stomach, removing stomach contents and weighing the contents and the empty stomach linings separately. Only the contents of the cardiac stomach and the fundulus of the stomach were 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 cod end feeding. All weight measurements were

made to the nearest 0.01 mg (572-37 Kern Balance). Stomach contents were filtered through a 200 µm sieve, resulting in 2 samples; items <200 µm were identified using an inverted microscope (magnification 200×), and those >200 µm were identified using a stereomicroscope (Olympus SZX10 magnification 90×). Stomach analysis started by the identification of ichthyoplankton in the entire stomach contents individually, using a stereomicroscope (magnification 90×). Eggs were identified as *S. pilchardus* eggs (Russell 1976), *E. encrasicolus* eggs (Russell 1976) and unidentified fish eggs (all other eggs with spherical shapes and average diameters of 900 µm). The mean number of eggs per stomach and the frequency of occurrence (FO) were calculated.

After identifying fish eggs in the stomach contents, microscopic analysis of prey items was conducted by pooling stomachs of the same trawl, species and maturity stage. Differences in prey number and composition are expected to be minimal in species caught in the same haul (Garrido 2003), as observed in several previous studies (van der Lingen 2002, Garrido et al. 2008, Nikolioudakis et al. 2012, Costalago et al. 2015, Garrido et al. 2015).

All prey were identified to the lowest possible taxon and all different genus/species identified are shown in Tables S1, S2 & S3 in the Supplement at [www.int-res.com/articles/suppl/m687p095\\_supp.pdf](http://www.int-res.com/articles/suppl/m687p095_supp.pdf). To determine the relative importance of prey, the carbon content was estimated using equations in the literature (Garrido et al. 2008, Garrido & van der Lingen 2014), and the percentage contribution to dietary carbon of each prey was estimated. Carbon content of phytoplankton was estimated for individual cells.

Feeding intensity (FI) was standardized to account for differences in the size of the stomach in relation to fish size using the following equation:

$$FI = \frac{\text{stomach content weight}}{(\text{total weight} - \text{gonad weight})} \times 100\% \quad (1)$$

Mean number of prey per stomach was estimated by dividing the number of prey identified in each stomach pool by the number of stomachs in that respective pool. Species richness was obtained with the mean number of prey species found in each stomach pool analysed. Shannon-Wiener ( $H'$ ) diversity index was calculated using the following expression:

$$H' = \sum_i^R p_i \ln(p_i) \quad (2)$$

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  $i$ . Prey types used in the calculation of

the diversity and richness indexes correspond to the lowest taxonomic level at which prey were identified. Diet overlap of the different pelagic fish ( $S$ ) was estimated using the Schoener's index, defined as:

$$S = 1 - 0.5 \sum_{i=1}^n |P_{xi} - P_{yi}| \quad (3)$$

where  $P_{xi}$  and  $P_{yi}$  are the relative contribution to total carbon content of prey type  $i$  in the diet of fish species  $x$  and  $y$ , respectively. Values of diet overlap index vary between 0 and 1, and values >0.6 are considered biologically significant (Wallace & Ramsey 1983).

To examine whether the contribution of fish eggs to dietary carbon was higher during periods of reduced food availability, a linear regression analysis was used to study the relationship between the carbon content of fish eggs in the stomachs and the carbon content of the other prey. An analysis of variance (ANOVA) was used to test for differences in diet diversity (Shannon-Wiener index) and richness between species, maturity stages, seasons and areas. *A posteriori* Tukey tests were used to identify the differences between each group. The assumptions of ANOVA were checked with Shapiro-Wilk test for normality and Levene test for homogeneity of variances. The mean prey per stomach did not follow a normal distribution; therefore, a nonparametric Kruskal-Wallis test was used to assess differences of prey number between species, seasons, areas, and maturity stage. *An a posteriori* Mann-Whitney test was used to identify groups with significant differences. All the tests described above were performed with SPSS v.25 statistical software (released 2017). A significance level of  $p < 0.05$  was used for all tests.

A generalized linear model (GLM) was used to compare feeding intensity between species, maturity stages, areas and seasons, using the R software version 4.0.2 (R Development Core Team 2020). Since our data were strictly positive, a Gamma distribution model was chosen. For feeding intensity and diet composition analyses, data were log-transformed. The differences in diet composition between species and areas were investigated using permutational ANOVA (PERMANOVA) (Adonis routine; Anderson et al. 2008), using the Bray-Curtis distance matrix and 999 permutations, implemented in R package 'vegan' (Oksanen et al. 2019). Data dispersion of prey communities among groups were analysed using the Betadisper test (PERMANOVA dispersions) in R package 'vegan' (Oksanen et al. 2019) and performed multiple comparisons using the 'pairwise.adonis' function (Martinez Arbizu 2019) to identify the differences between each species pair. To

analyse the average dissimilarity between species/maturity stages and to identify which prey had the highest contribution to the observed differences in diet composition, a SIMPER analysis was used, implemented in PRIMER v6 (Clarke & Gorley 2006).

To estimate egg mortality due to cannibalism and intraguild predation, the method described in Garrido et al. (2008) was first used. The average number of eggs found per stomach was divided by the mean weight of the fish to obtain the mean number of eggs  $\text{kg}^{-1}$  fish. The average number of eggs eaten was estimated by the equation of Hunter & Kimbrell (1980):

$$C = EE g t \quad (4)$$

where  $C$  is the mean number of eggs eaten  $\text{kg}^{-1}$  fish during feeding time  $t$ ,  $EE$  is the mean number of eggs observed  $\text{kg}^{-1}$  fish mass and  $g$  is the gastric evacuation rate for eggs.

The gastric evacuation rates of eggs for sardines, anchovies and chub mackerel were assumed to be equal to that of northern anchovy *Engraulis mordax* feeding on their own eggs ( $-0.701 \text{ h}^{-1}$ ; Hunter & Kimbrell 1980), which corresponds to an egg digestion time of approximately 2 h. The time per day used to particulate-feed on fish eggs (visual feeding mode; Garrido et al. 2007a) was estimated as the light hours available during the spawning season, which in the case of sardine occurs between October and November (winter and fall) and in the case of the anchovy is between April and May (spring and summer). Assuming a digestion time of 2 and 10 h of daylight in fall would mean that fish would be able to ingest 5 times the average amount of eggs  $\text{d}^{-1}$  estimated from stomach contents during the spawning season of sardine. In late spring, with an average of 13 h of daylight, fish would be able to ingest up to 7 times the average amount of eggs  $\text{d}^{-1}$  during anchovy spawning season.

To evaluate the impact of predation on egg mortality, the reproductive parameters obtained for fish collected off the Iberian coast in recent years were used. Daily fecundity of sardines and anchovies was obtained from literature values of specific daily fecundity of 12.60 eggs  $\text{g}^{-1}$  per female for sardine and 70 eggs  $\text{g}^{-1}$  per female for anchovy (ICES 2017, 2018). Sardine and anchovy abundances of juvenile and adult populations per area were obtained from the estimates of the acoustic surveys (Carrera et al. 2018, Moreno et al. 2018, ICES 2019). The spawning fraction was obtained using a sex ratio of 62 and 53% for sardines and anchovies, respectively (ICES 2018).

The method of estimating total egg consumption for a given population using estimates of total biomass, daily egg production and daily egg consumption ac-

ording to Hunter & Kimbrell (1980), as used in the past (Alheit 1987, Valdés et al. 1987, Valdés-Szeinfeld 1991, Pájaro et al. 2007, Bachiller et al. 2015) can overestimate the impact of predation on egg mortality, given that it assumes that eggs are available to the entire biomass of predators inhabiting the stock area, when in fact there is seldom complete overlap between the adult population distribution and spawning area. We developed a new method that takes the spatial overlap of fish eggs and predator species observed during collection into account. Distributions of juvenile and adult fish off Atlanto-Iberian waters were obtained from the results of 3 acoustic surveys carried out during sardine and anchovy spawning seasons (fall and spring, respectively), whereas the distribution of fish eggs was obtained by the regular sampling with the continuous underway fish egg sampler (CUFES) (Checkley et al. 1997) operating during PELAGO18 and IBERAS18 surveys. A grid of 21.6 km squares was constructed, assuming it represents the area an adult small pelagic fish can swim during the period of 1 d (Garrido et al. 2007a). The number of squares with eggs and predators was counted as well as the number of squares with eggs but no predators. The overall percentage overlap between predator and eggs was then estimated for each for each of ICES sub-divisions. The method assumes that when fish eggs overlapped with predators, they are available to be consumed at a quantity defined by the number of fish in that area and the daily ration of eggs for that species/area.

To estimate egg mortality, several parameters had to be assumed from those obtained for other species (e.g. gastric evacuation rate), or inferred from fish behaviour (e.g. time per day used for feeding), see above. To evaluate the impact of assuming different values for such parameters on the estimation of egg mortality, estimates of anchovy egg mortality by sardine predation during spring obtained in the present work were repeated, using other values available in the literature for different species/prey or used in similar studies. Specifically, we have analysed the impact on the variability of egg mortality rate estimates resulting from varying gastric evacuation rates, feeding periods and the percentage overlap of eggs and predators.

### 3. RESULTS

#### 3.1. Feeding intensity

Stomach content weight varied from 0.02 to 13.52 g for *Scomber colias*, 0.01 to 1.59 g for *Sardina pil-*

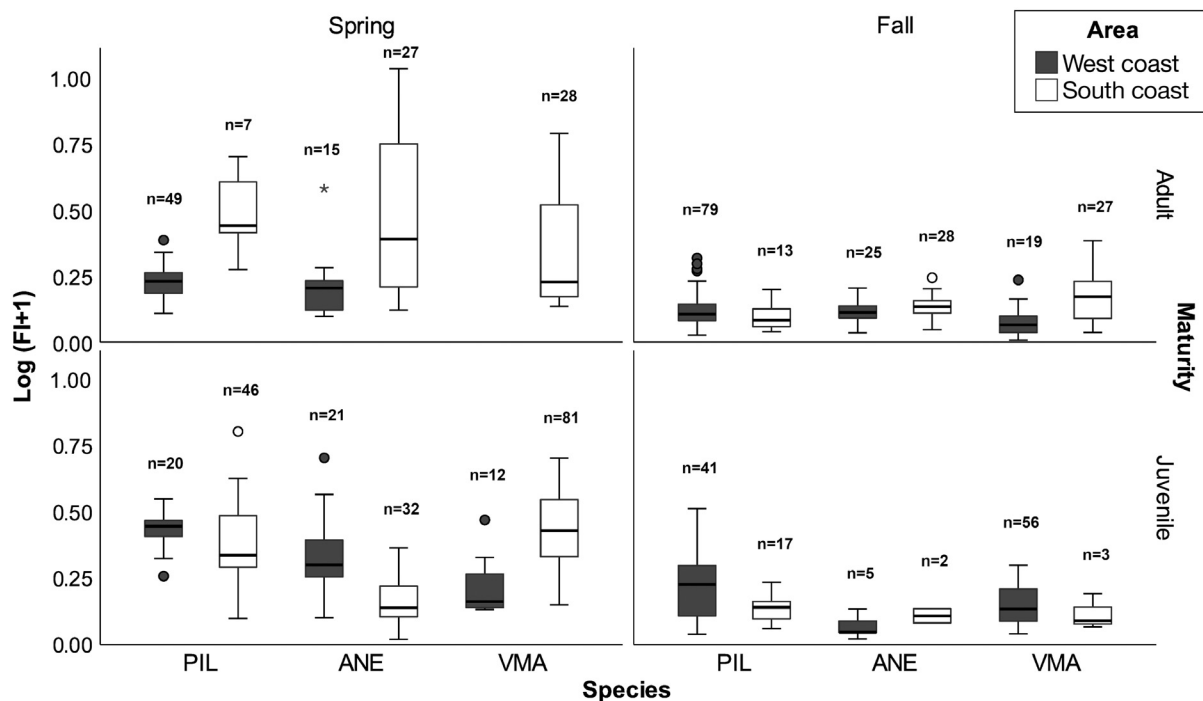


Fig. 2. Standardized feeding intensity of sardine (PIL), anchovy (ANE) and Atlantic chub mackerel (VMA). Data grouped by season (spring and fall), maturity (adult and juvenile) and study area (west coast and south coast). Boxes show 1st and 3rd quartile and median with 95% confidence interval. Points represent outliers and the asterisks extreme values. FI: feeding intensity

*chardus* and 0.002 to 0.88 g for *Engraulis encrasicolus*. FI of these pelagic fish varied from 0.02 to 9.78%, with a maximum of 9.78% for anchovy, 5.38% for sardine and 5.32% for Atlantic chub mackerel (Fig. 2). FI of anchovy was significantly higher than those of sardine ( $p = 0.018$ ) and chub mackerel ( $p = 0.02$ ). The FI of juveniles was higher than that of adults ( $p = 0.02$ ), higher in the west coast compared to the south ( $p < 0.001$ ) and was significantly higher during the spring than during the fall ( $p < 0.0001$ ).

### 3.2. Diet diversity

No empty stomachs were found in this study. The mean number of prey identified per stomach (mean  $\pm$  SD) varied widely, with sardines having a higher average number of prey per stomach ( $8272 \pm 2345$ ), followed by Atlantic chub mackerel ( $3871 \pm 2774$ ) and anchovy ( $1320 \pm 1204$ ; Table S4). Significant differences in the number of prey in the stomachs were found between anchovy and sardine (Mann-Whitney,  $p = 0.013$ ) and between anchovy and Atlantic chub mackerel ( $p = 0.007$ ). Prey number in the stomachs was not significantly different between seasons, areas and maturity stages. Species richness in stomach contents varied between 4 and 24 prey taxa, and the maximum number of prey taxa was registered for

juvenile sardines during spring, while the minimum occurred for adult anchovy in fall. There were no significant differences in species richness in the diets of the 3 pelagic fish ( $F_{2,30} = 1.728$ ,  $p = 0.195$ ) and between seasons ( $F_{1,30} = 2.187$ ,  $p = 0.150$ ), adults and juveniles ( $F_{1,30} = 0.024$ ,  $p = 0.878$ ) and areas ( $F_{1,30} = 0.805$ ,  $p = 0.377$ ).

The Shannon-Wiener ( $H'$ ) diversity index varied between 0.13 and 2.44 (Fig. 3), mean values being  $1.70 \pm 0.39$ ,  $1.36 \pm 0.62$  and  $1.24 \pm 0.53$  for anchovy, sardine and Atlantic chub mackerel. There were no significant differences in dietary diversity between species ( $F_{2,30} = 1.099$ ,  $p = 0.346$ ), adults and juveniles ( $F_{1,30} = 0.311$ ,  $p = 0.581$ ) and areas ( $F_{1,30} = 0.059$ ,  $p = 0.809$ ). On the other hand, significant differences of diet diversity were found between seasons ( $F_{1,30} = 6.762$ ,  $p = 0.014$ ), with higher diversity occurring in spring (Fig. 3).

### 3.3. Diet composition and diet overlap

Overall, the diets of sardine, anchovy and Atlantic chub mackerel were mostly dependent on zooplankton (mean contribution to dietary carbon,  $87 \pm 15$ ,  $98 \pm 2$  and  $98 \pm 4\%$ , respectively; Fig. 4, Tables S1, S2 & S3). Copepods were the main prey, corresponding to  $40 \pm 19$ ,  $43 \pm 25$  and  $16 \pm 16\%$  of the diet of

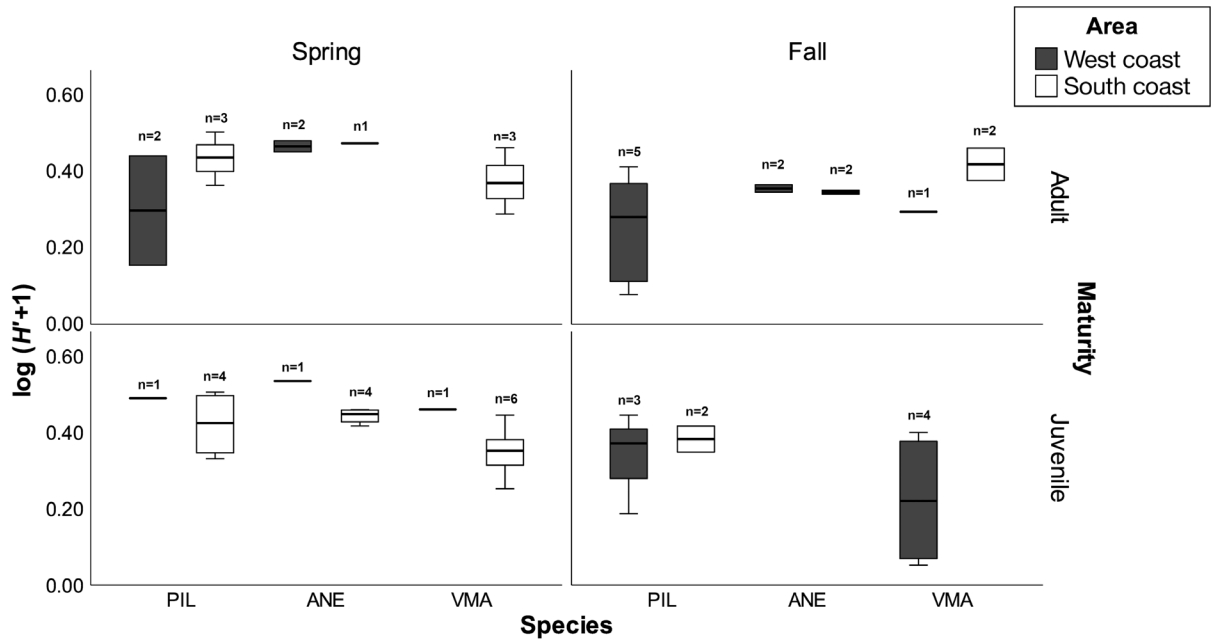


Fig. 3. Shannon-Wiener diversity index ( $H'$ ) standardized, of prey identified in sardine (PIL), anchovy (ANE) and Atlantic chub mackerel (VMA) stomachs. Data grouped by season (spring and fall), maturity (adult and juvenile) and study area (west coast and south coast). Boxes show 1st and 3rd quartile and median with 95 % confidence interval

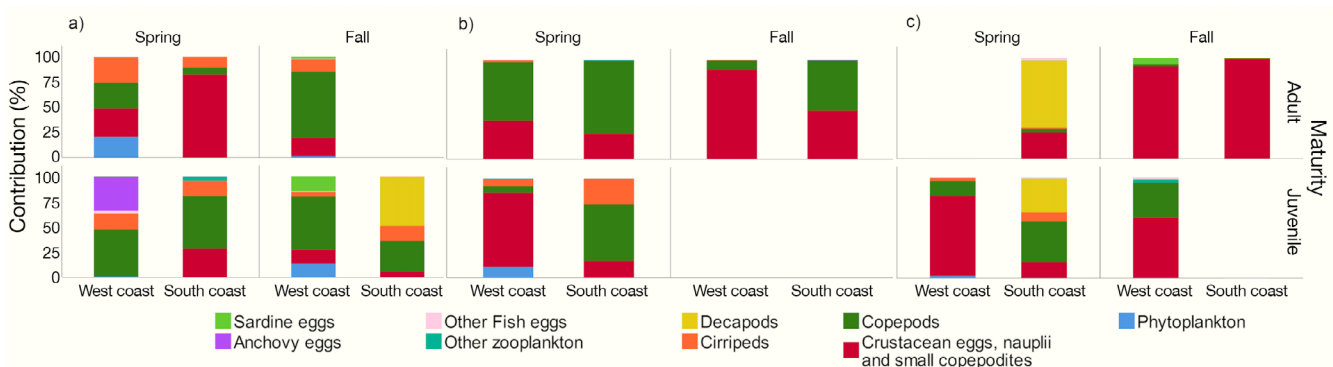


Fig. 4. Percentage of the relative contribution of the main prey to the carbon content of (a) sardine, (b) anchovy and (c) Atlantic chub mackerel diets. Data grouped according to maturity (adult and juvenile), season (spring and fall) and study area (west coast and south coast)

sardine, anchovy and Atlantic chub mackerel, respectively (Fig. 4). Sardine generally had a higher number of prey and higher number of different prey groups/species, which is related to a higher contribution of phytoplankton and ichthyoplankton than the other 2 fish species. The contribution of phytoplankton was almost negligible for the Atlantic chub mackerel diet ( $<0.5 \pm 1\%$ ), compared to  $2 \pm 4\%$  for the anchovy, while fish eggs were more important in the diet of Atlantic chub mackerel ( $2 \pm 2\%$ ) than that of anchovy ( $<0.5 \pm 0.1\%$ ).

There was a high dietary overlap ( $S$ ) of sardine and anchovy, particularly for anchovy collected during spring and sardine from both seasons (Table 3). Sardine and Atlantic chub mackerel had a low diet overlap ( $S < 0.6$ ), which was also the case for anchovy and

Atlantic chub mackerel (Table 3). There was a significant dietary overlap between juvenile and adult sardines collected during both seasons (Table 3).

Diet composition changed significantly with season (Fig. 5). During the spring, significant differences in diet composition were found between areas ( $F_{1,17} = 3.7173$ ,  $p = 0.003$ ) and species ( $F_{2,17} = 2.8260$ ,  $p = 0.003$ ), while no significant differences were found between adult and juvenile fish ( $F_{1,17} = 1.0745$ ,  $p = 0.396$ ). Pairwise comparisons revealed that the diet composition of sardine and Atlantic chub mackerel was significantly different ( $p = 0.003$ ), in contrast to the more similar diets of sardine and anchovy ( $p = 0.666$ ) and of anchovy and Atlantic chub mackerel ( $p > 0.05$ ). During the fall, no significant differences were found in the diet composition between areas



Table 3. Schoener's index diet overlaps from sardine (PIL), anchovy (ANE) and Atlantic chub mackerel (VMA) on the west coast (Wc) and south coast (Sc). Condensed matrix, only showed comparisons values >0.6, which were classified as a significant overlap. Dashes represent values <0.6 (not significant)

Species	Season	Maturity		PIL						ANE		VMA
				Spring			Fall			Fall		Spring
				Adult	Sc	Juvenile	Adult	Juvenile	Adult	Sc	Juvenile	
Wc	Sc	Sc	Wc	Sc	Wc	Sc	Wc					
PIL	Spring	Juvenile	Sc	0.6	–							
		Adult	Wc	0.6	–	0.7						
	Fall	Juvenile	Wc	0.6	–	–	–					
ANE	Spring	Adult	Sc	–	–	0.6	0.6	–				
		Juvenile	Sc	0.6	–	0.7	0.7	–				
VMA	Spring	Adult	Sc	–	–	–	–	0.6	–	–		
		Juvenile	Sc	–	–	–	–	–	–	–	–	
	Fall	Adult	Wc	–	–	–	–	–	0.8	–	–	
		Sc	–	0.6	–	–	–	–	–	–	0.8	
		Juvenile	Wc	–	0.6	–	–	–	–	0.6	–	

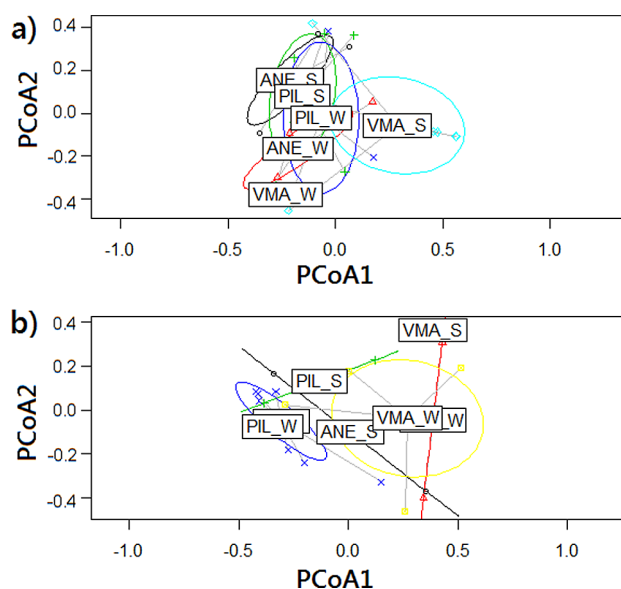


Fig. 5. Dispersion of sardine (PIL), anchovy (ANE) and Atlantic chub mackerel (VMA) diets, in function of the 2 areas: west coast (W) and south coast (S). Diets of species were divided into (a) spring and (b) fall. PcoA1: Principal Coordinates Analysis 1; PcoA2: Principal Coordinates Analysis 2

( $F_{1,13} = 2.0889$ ,  $p = 0.103$ ) and maturity stages ( $F_{1,13} = 1.0640$ ,  $p = 0.387$ ). Diet composition was significantly different between species ( $F_{2,13} = 3.9830$ ,  $p = 0.002$ ), particularly between sardine and Atlantic chub mackerel ( $p = 0.003$ ) and sardine and anchovy ( $p = 0.027$ ). No significant differences were found between the diet of anchovy and Atlantic chub mackerel ( $p > 0.05$ ).

SIMPER analysis revealed that the average dissimilarity between diets was high between sardines and Atlantic chub mackerel during the spring, and the prey groups that mostly contributed to that dissimilarity were decapods (19%), crustacean eggs and nauplii (13.3%) and calanoid copepods (11%). Decapods were only present in the stomachs of individuals collected along the south coast (both for sardine and Atlantic chub mackerel). Crustacean eggs and nauplii were present in the diet of the 2 species collected along the west and south coast, being more important for Atlantic chub mackerel, while calanoid copepods were more important in the diet of fish collected from the west coast.

During the fall, crustacean eggs and nauplii contributed to more than 19% of the dissimilarity in the diet of sardine and anchovy (more important for the anchovy), followed by calanoid copepods, cirriped larvae and sardine eggs. Cirriped larvae and sardine eggs were both more important prey for sardine diet than for the anchovy. During the fall, the prey groups that mostly contributed to the dissimilarity in the diet of sardine and chub mackerel were crustacean eggs and nauplii (20.7%), followed by calanoid copepods, cirriped larvae, poecilostomatoid copepods and sardine eggs (Table S5). Crustacean eggs and nauplii were more important for Atlantic chub mackerel whereas cirriped larvae, calanoid and poecilostomatoid copepods were more important for sardine.

The prey groups that had the highest contribution for the dissimilarity of the diet of fish collected from western and southern Iberia were crustacean eggs and nauplii (17%), followed by calanoid copepods

(11.1%), phytoplankton (10.95%) and decapods (10.3%). Phytoplankton was more important for the diet of sardines on the west coast, while decapods were more important for Atlantic chub mackerel on the south coast. Calanoid copepods and crustacean eggs and nauplii were more important for fish collected on the west coast than on the south coast.

### 3.4. Egg predation

Of the stomachs analysed, anchovy eggs were present in 16%, sardine eggs were present in 13% and unidentified fish eggs (of different sizes/species) were present in 33% (Table 4). Sardine was the main consumer of sardine and anchovy eggs, with a higher incidence of eggs in juvenile sardines. Anchovy eggs were mainly found in the stomachs during the spring,

particularly of juvenile sardines collected from the northwestern coast of Portugal (maximum of 488.9 eggs per stomach in this group, with a total of 9778 eggs identified). Sardine eggs were mostly abundant in sardine stomachs during the fall, with the highest incidence occurring in juvenile sardines collected from the southwest coast of Portugal (maximum of 28.3 eggs per stomach). Unidentified fish eggs were less abundant in sardine stomachs and were mainly present in spring, particularly for juveniles collected from both areas (Table 4).

Anchovy eggs were rare in anchovy stomachs and were found mainly in adult anchovies collected during fall along the southern Portuguese coast. Sardine eggs were absent from anchovy stomachs, and unidentified fish eggs were also rare, and mostly present in individuals collected during the spring on the northwest coast (Table 4). Anchovy eggs were rare in the stom-

Table 4. Mean number of eggs per stomach of sardine (PIL), anchovy (ANE) and Atlantic chub mackerel (VMA), respective SD and frequency of occurrence (FO). Data divided into anchovy eggs (*Engraulis encrasicolus*), sardine eggs (*Sardina pilchardus*) and other fish eggs (not identified). The stomachs of sardines, anchovies and Atlantic chub mackerel are grouped by season (spring and fall), maturity (adult and juvenile) and study area (NWC: northwest coast; SWC: southwest coast; ALG: Algarve; CAD: Cadiz)

Species	Season	Maturity	Area	Anchovy eggs			Sardine eggs			Other fish eggs		
				Mean	SD	FO (%)	Mean	SD	FO (%)	Mean	SD	FO (%)
PIL	Spring	Adult	NWC	0.0	0.0	0	0.0	0.0	0	0.8	0.8	53
			SWC	0.1	0.2	6	0.0	0.0	0	1.0	2.4	32
			ALG	0.0	0.0	0	0.3	0.5	29	0.6	1.1	29
	Juvenile	NWC	488.9	214.2	100	0.2	0.4	20	8.0	4.6	95	
		ALG	7.2	6.6	100	0.0	0.0	0	3.2	4.8	70	
		CAD	2.8	4.7	61	0.0	0.0	0	0.8	1.1	47	
PIL	Fall	Adult	NWC	0.0	0.0	0	1.0	1.4	47	0.1	0.3	7
			SWC	0.0	0.0	0	0.6	1.2	25	0.3	0.6	20
			ALG	0.0	0.0	0	0.0	0.0	0	0.4	0.9	20
	Juvenile	NWC	0.0	0.0	0	1.0	1.7	33	0.7	1.7	20	
		SWC	0.0	0.0	0	28.3	35.7	87	0.0	0.0	0	
		ALG	0.0	0.0	0	0.0	0.0	0	0.4	0.9	20	
ANE	Spring	Adult	NWC	0.2	0.4	20	0.0	0.0	0	0.4	0.9	24
			CAD	0.0	0.0	0	0.0	0.0	0	0.0	0.0	0
			ALG	0.0	0.0	0	0.0	0.0	0	0.0	0.0	0
	Juvenile	NWC	1.0	1.2	57	0.0	0.0	0	1.1	1.3	52	
		CAD	0.1	0.2	6	0.0	0.0	0	0.0	0.0	0	
		ALG	0.0	0.0	0	0.0	0.0	0	0.0	0.0	0	
ANE	Fall	Adult	NWC	0.0	0.0	0	0.0	0.0	0	<0.1	0.2	3
			ALG	8.3	30.1	27	0.0	0.0	0	0.0	0.0	0
			CAD	0.0	0.0	0	0.0	0.0	0	0.0	0.0	0
VMA	Spring	Adult	ALG	0.2	0.4	17	0.2	0.4	17	7.9	4.1	100
			CAD	0.0	0.0	0	0.0	0.0	0	1.5	1.1	81
	Juvenile	SWC	0.0	0.0	0	0.1	0.3	8	0.2	0.6	8	
		ALG	1.1	2.6	26	0.2	0.7	14	4.4	5.2	85	
VMA	Fall	Adult	SWC	0.0	0.0	0	10.1	14.8	60	0.1	0.4	13
			ALG	0.0	0.0	0	0.0	0.0	0	0.1	0.3	7
			CAD	0.0	0.0	0	10.7	13.4	87	1.7	2.1	53
		Juvenile	SWC	0.0	0.0	0	<0.1	0.1	2	0.4	1.6	12

achs of the Atlantic chub mackerel, and only found in fish collected during spring along the south Iberian coast. Atlantic chub mackerel was the main consumer of sardine eggs following sardines, particularly adult fish collected during the fall from southwestern Iberia and in the Gulf of Cadiz. Atlantic chub mackerel was the main predator of unidentified fish eggs, particularly during spring off the south Portuguese coast (Table 4).

No significant relationship was found between the total carbon content of prey in the stomachs and the contribution of fish eggs to dietary carbon content ( $p > 0.05$ ).

### 3.5. Egg mortality due to predation

During spring (anchovy spawning season and end of sardine spawning season in the region), intraguild predation by sardines off northwestern Iberia was responsible for a large percentage of anchovy egg mortality  $d^{-1}$  (71%). Sardine was also responsible for 10% of anchovy egg mortality in southern Iberia. In terms of egg cannibalism, anchovy was responsible for ingesting 1 and  $>0.05\%$  of anchovy eggs  $d^{-1}$  in northwestern Iberia and in southern Iberia, respectively (Table 5). Anchovy were not found to ingest sardine eggs.

During the fall (beginning of sardine spawning season and transition from end of spawning to resting season for anchovies), there was lower egg predation, and increased cannibalism for sardine. Sardine was responsible for consuming 6% of its own eggs  $d^{-1}$  off southwestern Iberia, and 1% anchovy eggs  $d^{-1}$  in southern Iberia. Similar to spring, there was no anchovy predation on sardine eggs. Anchovy was responsible for consuming 11% of its eggs  $d^{-1}$  in the Algarve and Cadiz regions (Table 5).

Varying the parameters used in the estimation of egg mortality rates according to those used in other

studies revealed that the spatial overlap, gastric evacuation rates and feeding duration values used significantly impacted the resulting estimates of egg mortality. In particular, incorporating the instantaneous spatial overlap resulted in a 71% anchovy egg mortality resulting from sardine consumption. If spatial overlap was assumed to be greater than 30%, it would lead to unrealistic mortality rates (i.e.  $>100\%$ ). As an example, if we utilized 100% overlap for fish inhabiting a large area as has been done in previous studies (Alheit 1987, Valdés et al. 1987, 1991, Pájaro 1998, 2007, Bachiller et al. 2015), it would lead to 337% anchovy egg mortality. We tested for 2 alternatives of the gastric evacuation rate assumed in this study, one estimated for sardines in the Mediterranean Sea (Nikolioudakis et al. 2011) and another estimated for sprat (Bernreuther et al. 2009), both lower than that used here and derived from *E. mordax* consuming fish eggs. These would result in estimates of egg mortality significantly lower than those obtained in this work (21 and 3%). Finally, in this study we have assumed that sardine prey on fish eggs using particulate feeding during daylight hours. If we assumed egg predation can occur throughout the day, the egg mortality rate would be 131%. On the other hand, if we assumed eggs are mostly ingested during a particular time of the day due to diel vertical migration, egg consumption estimates would decrease significantly (Table S6).

## 4. DISCUSSION

Our work compares the diet composition of 3 coastal pelagic fish species—*Sardina pilchardus*, *Engraulis encrasicolus* and *Scomber colias*—contrasting 2 areas and 2 different seasons that coincide with sardine and anchovy spawning seasons. Although several studies have described the diet of co-occurring

Table 5. Percentage of sardine eggs (PIL) and anchovy eggs (ANE) consumed per day by the total sardine or anchovy in the northwest coast, southwest coast and Algarve and Cadiz regions, during spring and fall. Values in brackets are equivalent to the traditional methodology without taking the spatial overlap of fish eggs and predator species into account. Due to absence of information, some values (%) of eggs consumed were not estimated, represented by dashes. *S. pilchardus*: *Sardina pilchardus*; *E. encrasicolus*: *Engraulis encrasicolus*

Species	Northwest coast		Southwest coast		Algarve and Cadiz	
	PIL eggs	ANE eggs	PIL eggs	ANE eggs	PIL eggs	ANE eggs
<b>Spring (13 h daylight period)</b>						
<i>S. pilchardus</i>	$>0.05$ (0.2)	71 (337)	–	–	$>0.05$ (0.1)	13 (29)
<i>E. encrasicolus</i>	0	1 (3)	–	–	0	$>0.05$ (0.1)
<b>Fall (10 h daylight period)</b>						
<i>S. pilchardus</i>	1 (1)	0	6 (8)	0	0	1
<i>E. encrasicolus</i>	0	0	–	–	0	11

coastal pelagic fish, few have done so with a comparative approach.

To describe diet composition, we intended to analyse a minimum of 15 stomachs per species, maturity stage and area. This was not possible for some groups, particularly anchovy juveniles collected in the fall from both areas and juvenile Atlantic chub mackerel collected from the southern Iberia, whose groups had a low number of stomachs (<6). While previous works have shown that the variability of prey composition for fish of the same species captured in the same haul is low (Bogstad et al. 1995, Garrido et al. 2012), results from these groups should be interpreted with caution.

Feeding intensity was higher for juveniles compared to adults for the 3 fish species, which is in accordance with results from Nikolioudakis et al. (2014) and Garrido et al. (2015) and could reflect the higher metabolic requirement of juveniles for growth and the fact that they are not yet engaged in reproduction. On the other hand, diet composition was similar for juveniles and adults of the 3 species. Anchovy feeding apparatus is fully developed by the late larval stage (Costalago et al. 2012), which may account for the lack of difference in the diet composition in these 2 groups. Conversely, the feeding apparatus of sardines continues to develop during the adult stage (Andreu 1969), and as a consequence, the filtering efficiency increases with ontogeny (Costalago & Palomera 2014). Several studies have found a difference in the diet composition between juveniles and adults of sardines (e.g. Bode et al. 2003, Costalago & Palomera 2014, Garrido et al. 2015) while that difference was not discernible in others (Bode et al. 2007) such as the present one. The Atlantic chub mackerel is planktivorous as juvenile but includes piscivory in the adult stage, beginning at around 22.5 cm total length (Castro 1993, Castro & Santana del Pino 1995). However, the majority of the Iberian population is composed of juveniles and young adults, which probably explains the lack of difference in the diet with maturity stage.

Feeding intensity varied significantly with season, being particularly high during spring for the 3 species, and the number and diversity of prey in stomachs was also higher in spring. Feeding intensity was also significantly higher on the west coast. These results are likely the result of increased productivity related to spring–summer plankton blooms triggered by increasing sunlight and intensification of upwelling events in the region (Santos et al. 2007). The west Iberian coast has stronger and more frequent upwelling episodes compared to the southern coast and is usually more productive (Fiúza 1983).

The number of prey per stomach was significantly higher in sardine when compared with the anchovy but more similar to that of Atlantic chub mackerel. In fact, on average, sardine had 6 times more prey per stomach than anchovy, and 2 times more prey than the Atlantic chub mackerel. This can be explained by the morphology of the sardine filtering apparatus, which allows it to retain particles as small as 12 µm, and by the high plasticity/flexibility of *S. pilchardus* feeding behaviour, with the ability to alternate between selective and non-selective feeding over a wide range of prey sizes, with great efficiency (Garrido et al. 2007a). The ability of sardines to feed on smaller prey, compared to the other 2 species can be advantageous, especially on the west coast where productivity is higher.

Mesozooplankton was the prey group with the highest contribution to dietary carbon for the 3 species. Both sardine and anchovy derived most of the carbon content of the diet by consuming copepod taxa such as Poecilostomatoid (*Oncaea* spp.) and Calanoida (*Centropages chierchiae*), agreeing with previous studies such as Garrido et al. (2015) and Bode et al. (2003) for the Iberian Peninsula and Nikolioudakis et al. (2012) for the Mediterranean Sea. While adult copepods were also important prey in the diet of the Atlantic chub mackerel, this species derived most of its dietary carbon from crustacean eggs, crustacean nauplii and small copepodites. The dominance of microzooplankton and small mesozooplankton in the diet of this species during the juvenile and young adult stage agrees with the results of Garrido et al. (2015). Despite the observed differences in the diet of the pelagic species under study, there was a high degree of overlap in their diet, suggesting a high potential to compete in seasons/areas of reduced food availability. Unfortunately, we have no plankton samples to identify potential areas of increased competition between the species.

In this study, no euphausiids were found in the diet of the 3 coastal pelagic species. This is in accordance with other studies conducted in the same region in which euphausiids were absent from the diet of sardine (Garrido et al. 2008, 2015) and were absent (Castro et al. 2013) or rare (Garrido et al. 2015) in the stomachs of anchovy. This contrasts with other areas such as the Bay of Biscay, where a positive selection of euphausiids during the night was found for anchovy >130 mm (Bachiller 2012). The inner part of the northwestern Iberian shelf is dominated by mysids and amphipods, and euphausiids are only dominant in the middle part of the shelf, concentrated in near bottom layers during the day, migrating upwards during the night (Cunha et al. 1997). The largest pro-

portion of the pelagic species under study are found in the inner part of the shelf (<100 m bathymetric), which can explain why euphausiids are rare in the stomachs. Moreover, sardines off Iberia show an opposite diel vertical migration to euphausiids (Zwolinski et al. 2010), which may justify why these prey are seldom found in the stomachs.

Fish eggs were frequently found in the stomach contents of the 3 pelagic species examined, as opposed to fish larvae, which were not identified in any stomach. This may be due to the difficulty in identifying larvae due to their rapid digestion or to their lower number and concentration in the water column and agrees with previous studies (reviewed in Garrido & van der Lingen 2014). Fish eggs were an important prey for sardine and Atlantic chub mackerel. Sardines mainly ingested sardine and anchovy eggs, while Atlantic chub mackerel mainly ingested sardine and unidentified fish eggs. Egg consumption by the anchovy was residual. These results are in accordance with Garrido et al. (2015), who identified sardines and Atlantic chub mackerel as the major egg predators of the coastal pelagic fishes inhabiting Atlanto-Iberian waters. Sardines selectively prey on fish eggs, preferentially ingesting fish eggs rather than other prey such as copepods and decapods, as shown in laboratory experiments (Garrido et al. 2007a). Individual eggs of marine animals have extremely high concentrations of essential fatty acids, and egg patches create rich nutritional resources for egg predators (Fuiman et al. 2015).

No significant relationship was found between the total carbon content of fish eggs and that of other prey in the stomachs, which appears to contradict the hypothesis that fish eggs are mainly consumed in periods/areas of lower food availability. However, more data are needed to test this hypothesis because the biomass of prey in the stomachs depends on factors other than prey availability, such as diel variability of feeding intensity, selective feeding behaviour, prey evasiveness and satiation level.

In this study, egg mortality was mainly due to intraguild predation rather than to cannibalism. Sardine, followed by chub mackerel, were the main predators of anchovy eggs during the spring, particularly for juveniles of both species. This agrees with previous studies showing that sardines are an important predator of anchovy eggs (Alheit, 1987, Bachiller et al. 2015). Spring corresponds to the main anchovy spawning season, which extends from March to October with a peak between April and August (Milán 1999). Anchovy egg consumption was higher on the northwestern Iberian coast. During 2018, when

this study was conducted, the maximum historical abundances of anchovies and anchovy eggs in the western Iberia were recorded (ICES 2019), and northwestern Iberia is identified as a main spawning area of the Iberian anchovy stock. This can explain the high prevalence of anchovy eggs in the stomachs. During the following year, sardine recruitment peaked, contrasting with the previous decade of historically low recruitments. Anchovy egg availability can positively influence sardine recruitment by being an important contributor to sardine diet during the season when the species is accumulating fat that will be invested in the spawning season (Ganias et al. 2007, Nunes et al. 2011). In fact, sardines generally dominate in this region, and only in recent years when sardine abundance declined sharply did anchovy abundance increase to historically high levels (ICES 2019). Given the importance of fish eggs for sardine diet, it is hypothesized that anchovy egg availability might have benefited sardines. This strengthens the importance of conducting multi-species assessment to manage co-habiting small pelagic species.

The group of unidentified fish eggs, which could be eggs of horse mackerel *Trachurus trachurus*, Atlantic chub mackerel *S. colias*, bogue *Boops boops* and other teleosts inhabiting the same area, were particularly abundant in the stomachs of Atlantic chub mackerel. Unlike sardine and anchovy eggs, whose seasonality reflects the timing of their spawning season, unidentified fish eggs were abundant in both spring and fall, with a homogenous distribution throughout the study area. Identifying the species corresponding to these unidentified eggs that are more prevalent in coastal pelagic fish stomachs may require molecular identification of these eggs due to their similar size and morphology for many species.

Estimating egg mortality implies the knowledge of different variables that may be generally unknown for most species, such as gastric evacuation rates and feeding durations. Different assumptions lead to very different estimates (Garrido & van der Lingen 2014). For example, the feeding duration varies among studies, being estimated from 9 h (Garrido et al. 2008) to 24 h (Alheit 1987, Valdés et al. 1987, Valdés-Szeinfeld 1991; Table 1). In this study, we assumed a feeding duration dependent on the daylight hours (given that fish eggs are mainly consumed by using a visual particulate-feeding mode, Garrido et al. 2007a), which would be greater during spring than during fall. With 13 h of feeding duration for spring and 10 h of feeding duration for fall, the average anchovy egg consumption was 307 943 eggs kg<sup>-1</sup> fish (during the spring) and 70 eggs kg<sup>-1</sup> (during fall) for sardine, 1250 eggs

kg<sup>-1</sup> (spring) and 5223 eggs kg<sup>-1</sup> (fall) for anchovy and 3358 eggs kg<sup>-1</sup> (spring) for Atlantic chub mackerel. Compared with similar studies in other regions (Valdés-Szeinfeld 1991, Pájaro et al. 2007, Bachiller et al. 2015), these values are among the highest estimated. In a nearby area, the Bay of Biscay, with a 12 h feeding duration, anchovy daily ration was estimated as 218 eggs kg<sup>-1</sup> fish for anchovy, 853 eggs kg<sup>-1</sup> for sardine and 27 eggs kg<sup>-1</sup> for Atlantic chub mackerel (Bachiller et al. 2015).

In terms of cannibalism, both sardine and anchovy were responsible for a small percentage of egg mortality. Egg mortality due to cannibalism for Engraulidae species shows high variability, with values ranging from 3 to 70% (Alheit 1987, Valdés et al. 1987, Valdés-Szeinfeld 1991, Pájaro 1998, Gennotte et al. 2007; Table 1). This discrepancy is probably linked to species and population differences but also to prey availability at the time the studies were carried out. Sardine cannibalism observed in the present study was lower than that observed in the same area in previous studies (Garrido et al. 2008). In our study, the maximum value of egg mortality by sardine cannibalism was 6% (during the fall), whereas Garrido et al. (2008) obtained values around 30% during the winter, which may be due to the fact that overall egg availability was lower at that time of the year.

Previous estimates of egg mortality due to cannibalism and intraguild predation (reviewed in Garrido & van der Lingen 2014) assumed that, for a given area where populations of fish and eggs are known to occur, there is a complete spatial overlap between both or that all predators can potentially prey on eggs found in that area. This is not likely to be true since, at a given time, the spatial distribution of eggs and predators may not be exactly the same. For example, anchovy eggs are mainly concentrated in a small area of the northwestern Iberia coast between Aveiro and Figueira da Foz (Fig. 1), whereas sardine adults (main predators) have a broad shelf distribution. To take the spatial overlap at the time of sampling into account, we used a different method of estimating egg mortality than that used formerly for small pelagics; our method takes into consideration the instantaneous distribution of fish and eggs in the studied area, registered during the acoustic surveys. Egg mortality estimated by using the alternative methodology described in Garrido et al. (2008) would lead to unrealistically high values for the present study, far above 100% for anchovy eggs consumed by sardines in spring (Table 5). Our analysis of the impact of varying assumed parameters used in the calculation of egg mortality rates suggests that

experimentally derived species-specific rates of gastric evacuation of fish eggs by pelagic fish are needed, since variations of rates within published data for other planktivorous predators and prey can lead to huge variations in the estimated egg mortality rates (from 3 to 71% using rates estimated for sprat and for sardine feeding on zooplankton, respectively; Table S6). Finally, the feeding time used by predators per day to capture fish eggs has an equally large relevance for the resulting egg mortality estimate. These parameters should be determined by studying the species-specific diel variability in feeding intensity and egg predation, to increase understanding of the impact of cannibalism and intraguild predation on egg mortality.

The present study increases the available knowledge related to the diet overlap of the 3 main target species of purse-seine fisheries in Atlanto-Iberian waters and also provides improved estimates of egg mortality due to cannibalism and intraguild predation. There were significant differences in the diet composition of the 3 species under study, particularly between sardine and Atlantic chub mackerel, while there were no differences between maturity stages for any of the species. Diet varied spatially and temporally, reflecting the flexibility to adapt to the prevailing food availability. This study demonstrates that sardines are the main predators of fish eggs on the western and southern Iberian coasts and thus can have a large impact on sardine and anchovy egg mortality. Further studies combining molecular analyses with detailed visual analysis of stomach contents will allow identification of fish eggs, larvae and plankton to the lowest taxonomic level, providing valuable information for operational ecosystem-based approaches to stock management.

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