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Allometric relations and consequences for feeding in small pelagic fish in the Bay of Biscay

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The body size of fish is an important factor in determining their biology and ecology, as predators eat prey smaller than themselves. Predator mouth size restricts the availability of possible prey. In this paper we provide the allometric relationships of eight common, small pelagic fish species in the Bay of Biscay. In addition, we describe the predator-prey size ratios for different species, and we determine changes in their ratio-based trophic-niche breadth with increasing body size. Results suggest that gape size does not totally determine the predator-prey size ratio distribution, but predators use the entire available prey size range, including the smallest. As they grow they simply incorporate larger prey as their increased gape size permits. Accordingly, a large degree of overlap was found in the diet composition in terms of size and predator-prey ratios, even between fish of different sizes. Of the species studied, only horse mackerels seem to be clearly specialized in relatively large prey.

Keywords: allometric relationships, Bay of Biscay, predator-prey size ratio, small pelagic fish, stomach weight, trophic-niche breadth.

Introduction

Body size has an important influence on the biology and ecology of any animal (Peters, 1986; Brown *et al.*, 2004; Barnes *et al.*, 2010). Similarly, prey size can affect the predator's feeding success (Eggers, 1982; Luo *et al.*, 1996; Pepin and Penney, 1997) and prey selection (Eggers, 1977, 1982; Schmitt, 1986; Pepin and Penney, 1997; Barnes *et al.*, 2010), although the variability in prey selection could be related to interspecific morphological differences depending on the species (Sabatés and Saiz, 2000).

Many studies have shown a general trend for the food spectrum of fish to widen as they grow (Peterson and Ausubel, 1984; Mahé *et al.*, 2007; Bacha and Amara, 2009). Due to allometric relationships small increases in prey length can result in large increases in the energy intake (Conway *et al.*, 1999). According to the prey size spectrum of small pelagic fish, relatively large prey that are only caught occasionally by the fish, but which make an important contribution to their diet, are difficult to quantify. For example, several studies have shown that krill is important in terms of ingested biomass for pelagic fish such as anchovy (Plounevez and Champalbert, 1999; Espinoza and Bertrand, 2008), mackerel (Olaso *et al.*, 2005) and horse mackerel (Olaso *et al.*, 1999).

Other pelagic fish species overlap in size during growth and share the same environment. Little is known about the relative influence of the size of different species on their diet composition or interspecies competition. In the Bay of Biscay several small pelagic fish species share the environment (sardines, anchovies, mackerels, horse mackerels, sprats and bogues). It has been suggested that intraguild predation (Polis *et al.*, 1989) could be an important factor regulating the population dynamics of these populations (Irigoien *et al.*, 2008; Irigoien and De Roos, 2011). Intraguild predation can be divided into two aspects: competition for food and predation on each other (Polis *et al.* 1989). In this paper we focus on the competition aspect of this mechanism by determining predator-prey sizes and their contribution to the diet of the different small pelagic species present in the Bay of Biscay.

Therefore, the objective of this study is to contribute allometric information about pelagic fish, prey sizes, and predator-prey ratios in the Bay of Biscay.

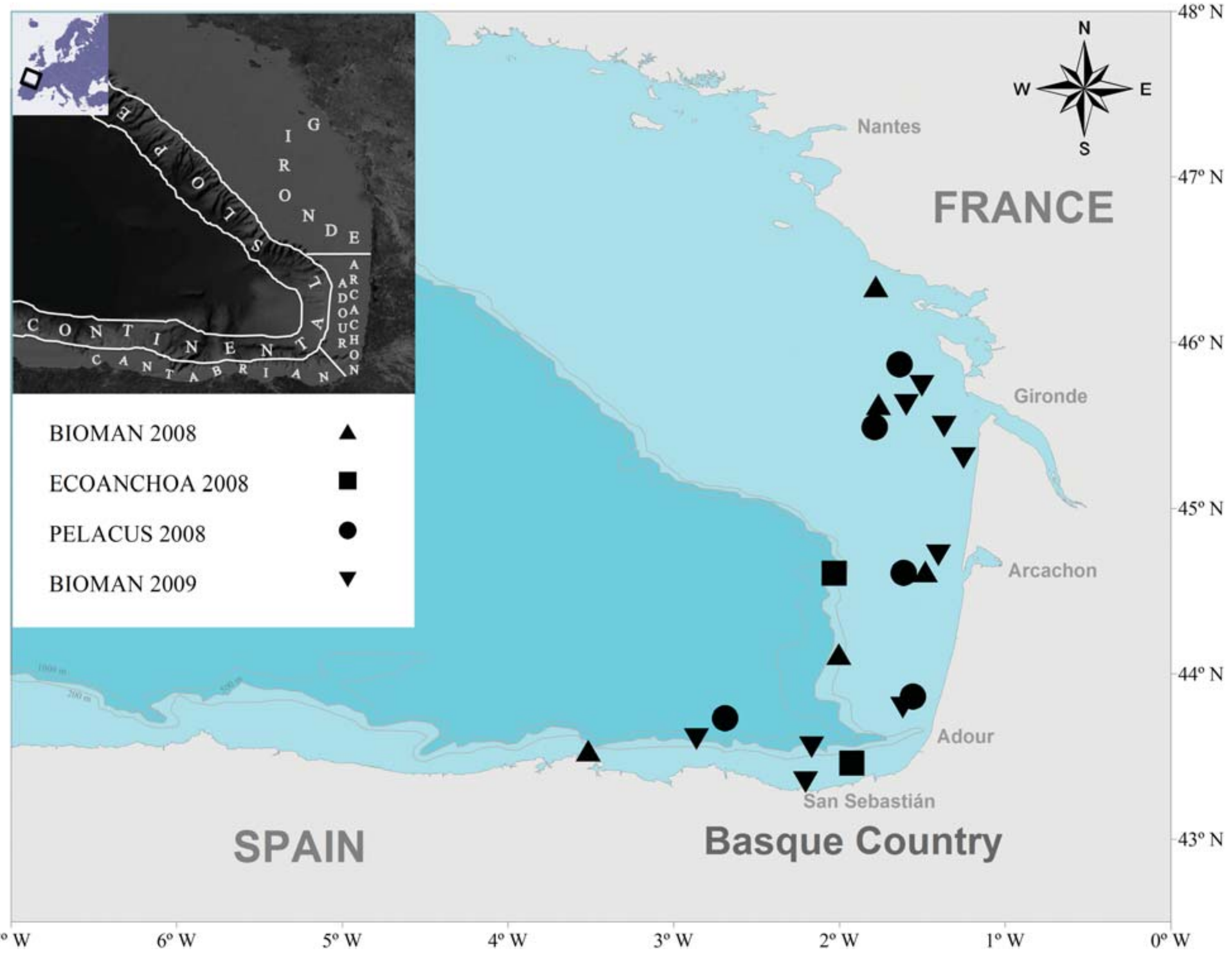

Figure 1. Study area and location of samples used in the study in relation to the survey. Predefined geographical areas (Cotano *et al.*, 2008) are shown in the small map in the top left of the figure. Pelagic trawl was used to catch fish samples during BIOMAN 2008 (May 6–May 26) and BIOMAN 2009 (May 5–May 25) surveys aboard the R/V *Emma Bardán* (Vigo) and aboard the R/V *Thalassa* (IFREMER) during the PELACUS 2008 survey (Sept 17–Oct 16). Purse seine was used to catch samples during ECOANCHOA 2008 survey (June 27–July 13) aboard the F/V *Ama Antiguakoa* (Ondarroa).

Material and methods

Small pelagic fish were caught with pelagic trawls in 2008 and 2009 during four different oceanographic surveys and in different sampling areas around the Bay of Biscay (Figure 1). Samples of European anchovy (*Engraulis encrasicolus*), sardine (*Sardina pilchardus*), Atlantic horse mackerel (*Trachurus trachurus*), Mediterranean horse mackerel (*Trachurus mediterraneus*), Atlantic mackerel (*Scomber scombrus*), Atlantic Chub mackerel (*Scomber colias*), bogue (*Boops boops*) and sprat (*Sprattus sprattus*) were caught and immediately frozen on board for later biological sampling in the laboratory.

Morphological measurements of gape height (*GH*) and gape width (*GW*) were obtained with a calliper; according to Scharf *et al.* (2000), gape height was defined as the maximum linear distance between the upper and lower jaws with the mouth stretched open, and gape width as the linear distance between the left and right corners of the open mouth. Total length (using an ichtyometer model SCANTROL FishMeter 100) and weight (using an electronic balance model SCANVAEGT Marine Scale 8400 Series) were measured on board, and stomach weight was measured later in the laboratory (with a balance model METTLER TOLEDO PB1502). Collected stomachs (Figure 1) were preserved in ph7 buffered formaldehyde (4%), according to Harris *et al.* (2000).

Diet characterization

Prey size

Stomach contents preserved in formaldehyde were used to characterize the diets of the fish. Zooplankton found in gut contents were identified under the microscope (model NIKON SMZ 645) to the lowest identifiable taxonomic level. All stomachs were opened with claws and tweezers and analysed individually in the laboratory. Subsampling was only used with small prey and in order to identify no more than 500 individuals per stomach. In this case, after separating manually the largest prey (e.g. Euphausiid and Decapoda) the rest of the stomach content was spilled out with distilled water in a 50 ml bottle. After stirring the bottle in order to homogenize the content, a 2 or 5 ml subsample (depending on the stomach content concentration) was taken with a Hensen sampling pipette (www.hydrobios.de). The subsample was then spilled out in a petri plate for the taxonomic identification and measurement of prey items. Small prey abundance ABD_{Total} (in numbers) was extrapolated according to the sub-sampling ratio for each of the prey items found:

$$ABD_{Total} = VAbd_{Subsample}/Vol_{Subsample} \tag{1}$$

where V is the volume in ml of the sample, $Abd_{Subsample}$ is the number of items counted in the subsample and $Vol_{Subsample}$ is the volume of the subsample (2ml or 5ml). In each case, previously separated large prey numbers were added to this calculation.

The total length of the first whole 50 individuals was measured in each stomach with an upper limit of 30 measurements per prey species and stomach; i.e. when the first 30 individuals corresponded to the same species, we continued measuring the rest of the prey species in order to obtain a total of 50 prey length measurements per stomach. Broken zooplankton was not measured.

Prey length (TL_{Prey}) was determined by the average length obtained from measurements in each of the prey species and predator species (i.e. one TL_{Prey} mean value per prey species or taxonomic group and fish species).

We tested whether prey lengths varied significantly depending on survey, area or predator species. Areas were defined according to Figure 1 (Cotano *et al.*, 2008): the "Cantabrian area" is the area within the Cantabrian continental shelf, the "Adour-Arcachon area" is the area within the French continental shelf under the influence of the Adour River and the Arcachon estuary, the "Gironde area" is the area within the French continental shelf that is under the influence of the Gironde River input, and the "Continental Slope area" is the area that delimitates the shelf break ($>$250 m depth).

Since the data on prey length averages were not normally distributed (Shapiro-Wilkinson normality test, p values $>$0.05), multiple range (homogeneous groups) and Kruskal-Wallis tests were performed in order to test differences in prey lengths.

Predator-prey ratio

Patterns of relative prey size use among predators were examined by generating relative frequency histograms of predator/prey size ratios (*PPSRs*) for the prey consumed by each predator species, according to the following equation:

$$PPSR = TL_{Predator}/TL_{Prey} \tag{2}$$

where $TL_{Predator}$ is the total length of the predator and TL_{Prey} the total length of the prey. One *PPSR* value for each prey item in the stomach was obtained. The relative frequency distributions (%) of *PPSRs* and cumulative frequencies were plotted as in Scharf *et al.* (2000). A high *PPSR* value indicates relatively smaller prey items ingested, whereas low *PPSR* values correspond to relatively larger items in stomach contents.

Trophic-niche breadth

Trophic-niche breadth was examined on a ratio scale by determining changes in the range of relative prey sizes with increasing predator size (Scharf *et al.*, 2000). *PPSR*s versus predator size regression quantiles (90th and 10th) were generated to estimate the extremes of the ratio scale data for each predator species. Slope comparisons were made between upper and lower bounds, with significant differences indicating an increase (divergent slopes) or decrease (convergent slopes) in *PPSR*-based trophic-niche breadth with increasing predator size. The difference between predicted values of upper and lower bound regressions at any given predator size represented the trophic-niche breadth (Scharf *et al.*, 2000).

Results

Allometric relationships

Total length and weight

In order to simplify comparisons between predator fish species, we established 130 and 230 mm as the limits for separating small, medium and large individuals. Therefore, all species would be represented in at least two of the three size ranges and a balanced n would be obtained for all ranges. All sampled species showed a significant length–weight relationship. Descriptive statistics, the sample size and the length–weight relationship parameters are presented in Table 1. The length–weight relationships of the different species were significantly different (F-tests for both the slopes and intercepts, $p < 0.0001$). Anchovy and sprat had the highest slopes, and the difference remained significant when the other fish data used were restricted to the maximum length of anchovy and sprat.

Gape size vs. total length

The gape height and width were found to be related to the total length; however, this relationship differed significantly (F-tests for slopes, $p < 0.0005$ for gape height and $p < 0.0001$ for gape width; F-tests for intercepts, $p < 0.0001$ both for gape height

Table 1. Sample size (ranged by size), descriptive statistics and weight-length relationship parameters for the eight small pelagic fish species sampled.

	Sample size (*n*)			**Length (mm)**		**Weight (g)**		**Regression parameters**			
Species	**<130mm**	**130–230mm**	**>230mm**	**Min**	**Max**	**Min**	**Max**	***a***	***b***	**s.e. (*b*)**	**r^2**
E. encrasicolus	246	359	–	65	194	1.22	68.7	8.47 (10^{-7})	3.42	18 (10^{-3})	0.98
S. pilchardus	48	450	28	100	247	5.9	119.6	3.97 (10^{-6})	3.13	22 (10^{-3})	0.98
T. trachurus	343	176	179	45	370	0.77	376.2	5.74 (10^{-6})	3.06	8 (10^{-3})	0.99
T. mediterraneus	137	85	62	69	391	2.37	420	6.22 (10^{-6})	3.04	13 (10^{-3})	0.99
S. scombrus	8	241	150	108	420	7.9	551.1	4.80 (10^{-6})	3.07	15 (10^{-3})	0.99
S. colias	–	33	64	137	405	16.58	660.7	1.49 (10^{-6})	3.30	27 (10^{-3})	0.99
B. boops	2	58	69	122	360	17	453.4	7.25 (10^{-6})	3.05	26 (10^{-3})	0.99
S. sprattus	161	4	–	50	143	0.56	23.6	2.71 (10^{-7})	3.75	43 (10^{-3})	0.98

n = sample size corresponding to each of the predefined length ranges, Min and Max = minimum and maximum length (mm) and weight (g) recorded, a and b = parameters of the weight–length relationship $TW = a\ TL^b$, s.e. (b) = standard error of b, r^2 = coefficient of determination.

and width) depending on the predator species (Table 2): all sampled predator species showed a similar polynomial increase in gape size with total length, except anchovies and bogues. Anchovies had the largest gape size compared with the other species at the same size. Bogues had the smallest gape height and width (Table 2).

Stomach contents

Stomach weight

Stomach weights (SW) were related to the total weight (TW) of fish (Table 3); however, slopes and intercepts of that relationship differed significantly between predator species (F-tests, $p < 0.0001$). For the small sizes, the data from different species overlapped. However, Atlantic and Atlantic Chub mackerels, which are larger fish, had heavier stomach weights than Atlantic and Mediterranean horse mackerels of the same size.

Prey size

In the case of ingested Euphausiids, an eye size–body length relationship model was used to estimate the length of those for which only eyes were found in the stomach contents. In a preliminary study, we used whole Euphausiids found in stomach contents to measure both the total length and the eye diameter. The total length (TL) of Euphausiids showed a significant linear relationship

$$TL = 22.86ED - 3.35 (n = 190; p < 0.001; r^2 = 0.95) \quad (3)$$

with eye diameter (ED).

The median prey size (i.e. total length) was not significantly different between surveys (Kruskal-Wallis test, $p = 0.75$) or geographical areas (Kruskal-Wallis test, $p = 0.52$). In contrast, significant differences were found between predator species (Kruskal-Wallis test, $p = 0.0002$).

Since the lack of enough detail for prey is often cited as a problem (e.g. Barnes *et al.*, 2008, 2010), the average and extreme prey-size values for the different predator species ranged by size (i.e. $TL < 130$ mm, TL 130–230 mm, $TL > 230$ mm) are presented as supplementary data (Table A1).

While large predators (e.g. Atlantic mackerels) were able to predate on the largest prey, they also used small zooplankton as a resource. Likewise, small predators (e.g. anchovies) could also prey on many large particles as they had a relatively wide prey size spectrum. These results were also observed when predator size was compared with the maximum and minimum prey sizes. For example, the prey size range of anchovies was nearly as wide as that of Atlantic and Atlantic Chub mackerels, in spite of being much smaller predators, whereas predators like sardines and bogues showed a narrow prey-size range. Atlantic and Atlantic Chub mackerels of all sizes were also able to predate on large prey. Descriptive statistics are presented in Table 4.

The maximum prey length increased with predator body size. In addition, the maximum prey size measurements were found in predators with large gape size in relation to body size. However, Atlantic and Mediterranean horse mackerels and some small Atlantic and Atlantic Chub mackerels with small mouth apertures were also able to ingest prey with lengths larger than

Table 2. Allometric relationships between the gape size (mm) and total length of fish (mm) for the eight small pelagic fish species sampled.

		Gape width (*GW*)					**Gape height (*GH*)**				
Species	***n***	***a***	***b***	***c***	**s.e. (*c*)**	**r^2**	***a***	***b***	***c***	**s.e. (*c*)**	**r^2**
E. encrasicolus	118	$-1.25\ (10^{-3})$	0.57	−29.77	4.81	0.94	$-8.90\ (10^{-4})$	0.43	−16.84	4.72	0.93
S. pilchardus	98	$-2.66\ (10^{-4})$	0.20	−6.42	4.50	0.85	$-1.61\ (10^{-4})$	0.17	−3.34	2.37	0.96
T. trachurus	129	$-3.36\ (10^{-4})$	0.27	−12.17	1.67	0.98	$-3.01\ (10^{-4})$	0.25	−9.56	1.88	0.97
T. mediterraneus	32	$-3.22\ (10^{-4})$	0.20	−2.43	5.28	0.91	$-3.90\ (10^{-4})$	0.22	−3.66	4.84	0.92
S. scombrus	70	$-3.43\ (10^{-4})$	0.31	−24.43	5.41	0.94	$-2.59\ (10^{-4})$	0.26	−16.33	5.29	0.94
S. colias	9	$-1.12\ (10^{-4})$	0.18	−4.73	77.48	0.93	$-9.26\ (10^{-4})$	0.70	−81.77	41.62	0.95
B. boops	22	$-9.35\ (10^{-5})$	0.08	−0.99	7.48	0.87	$-2.12\ (10^{-4})$	0.13	−4.87	7.90	0.90
S. sprattus	9	$-3.3\ (10^{-3})$	0.75	−32.01	38.90	0.74	$-1.05\ (10^{-3})$	0.31	−10.14	11.15	0.86

n = sample size, a and b = parameters of the TL–*gape size* relationship GH *or* $GW = aTL^2 + bTL + c$; s.e. (c) = standard error of constant c; r^2 = coefficient of determination.

Table 3. Descriptive statistics and the total weight (TW)–stomach weight (SW) relationship parameters for the eight small pelagic fish species sampled.

		Total weight (g)		**Stomach weight (g)**		**Regression parameters**			
Species	***n***	**Min**	**Max**	**Min**	**Max**	***a***	***b***	**s.e. (*b*)**	**r^2**
E. encrasicolus	533	1.22	68.70	0.10	4.70	$24\ (10^{-3})$	$-41\ (10^{-3})$	$2\ (10^{-3})$	0.64
S. pilchardus	497	5.90	119.60	0.01	4.30	$19\ (10^{-3})$	$113\ (10^{-3})$	$1\ (10^{-3})$	0.58
T. trachurus	659	0.77	376.20	0.10	5.20	$9\ (10^{-3})$	$117\ (10^{-3})$	$2\ (10^{-4})$	0.78
T. mediterraneus	267	2.37	420.00	0.02	5.90	$9\ (10^{-3})$	$79\ (10^{-3})$	$2\ (10^{-4})$	0.84
S. scombrus	342	7.90	551.10	0.30	13.60	$14\ (10^{-3})$	$662\ (10^{-3})$	$1\ (10^{-3})$	0.71
S. colias	80	16.58	660.70	0.40	16.80	$15\ (10^{-3})$	$531\ (10^{-3})$	$2\ (10^{-3})$	0.65
B. boops	108	17.00	453.40	0.10	16.20	$26\ (10^{-3})$	$-333\ (10^{-3})$	$2\ (10^{-3})$	0.81
S. sprattus	155	0.56	23.60	0.01	0.80	$17\ (10^{-3})$	$13\ (10^{-3})$	$2\ (10^{-3})$	0.50

n = sample size, Min and Max = minimum and maximum total weight and stomach weight (g) recorded, a and b = parameters of the TW–SW relationship $SW = aTW + b$, s.e. (b) = standard error of b, r^2 is the coefficient of determination. Note that the linear regression parameters are for the log-transformed data.

Table 4. Average minimum, mean and maximum prey lengths (*TL*) obtained in stomach contents of different predators according to size, as well as for the entire size range ("ALL").

	$n_{predators}$				n_{prey}				Prey Average Min. *TL* (mm)				Prey Average *TL* (mm)				Prey Average Max. *TL* (mm)			
Predator species	**<130**	**130–230**	**>230**	**ALL**	**<130**	**130–230**	**>230**	**ALL**	**<130**	**130–230**	**>230**	**ALL**	**<130**	**130–230**	**>230**	**ALL**	**<130**	**130–230**	**>230**	**ALL**
E. encrasicolus	49	101	0	**150**	5257	27 774	0	**33 031**	0.89	0.55		**0.63**	1.17	1.89		**1.73**	2.25	7.61		**6.41**
S. pilchardus	6	114	10	**130**	1916	77 071	11216	**90 203**	0.35	0.37	0.41	**0.38**	0.92	0.99	1.29	**1.02**	1.55	2.54	5.05	**2.75**
T. trachurus	64	65	43	**172**	2108	14 233	919	**17 260**	0.88	0.89	1.48	**1.01**	1.60	1.99	4.34	**2.34**	3.49	4.26	11.18	**5.43**
T. mediterraneus	26	0	25	**51**	4163	0	72	**4235**	0.96		0.91	**0.94**	1.87		1.35	**1.71**	14.36		1.56	**10.43**
S. scombrus	3	41	101	**145**	20	1107	449 988	**451 115**	1.00	2.37	9.05	**7.29**	8.66	4.71	13.41	**11.18**	33.12	13.65	22.89	**20.69**
S. colias	0	15	14	**29**	0	1818	325	**2143**		0.36	0.61	**0.47**		1.82	5.24	**3.32**		6.94	34.26	**18.96**
B. boops	0	21	32	**53**	0	164	2456	**2620**		0.80	0.62	**0.64**		1.08	1.46	**1.42**		2.55	7.05	**6.60**
S. sprattus	56	4	0	**60**	18468	719	0	**19 187**	0.52	0.44		**0.50**	1.42	1.02		**1.33**	3.02	1.86		**2.78**

n = sample size. The prey number (n_{prey}) has been extrapolated to the total number estimated according to the subsampling ratio.

their gape size. This was also observed for anchovies, given that they had a relatively larger gape size than the other predators in relation to their total length (Figure 2; Tables 2 and 4).

Predator-prey size ratios

Predator-prey size ratio frequencies (i.e. frequency of occurrence) were analysed in terms of abundance in the stomach contents of different sized predators. Relative frequency distributions (%) of *PPSR*, and cumulative frequencies corresponding to different predator species ranged by size (i.e. $TL < 130$ mm, TL 130–230 mm, $TL > 230$ mm) are presented as supplementary material (Figure A1).

Atlantic and Atlantic Chub mackerels had the widest prey size range in their diet (1–33.12 mm and 0.36–34.26 mm, respectively) (Table 4). Atlantic mackerels had the widest *PPSR* range, showing the lowest minimum and the highest maximum *PPSR* values (*PPSR* 2–1197); however, they also showed the highest mode, Q_1 and Q_2, compared to the other predators. Atlantic Chub mackerels had a similar range in ratios (*PPSR* 4–826), but in general values were lower in relation to the other predators (the minimum mode) as they ingested large prey more frequently (Tables 5 and 6).

Bogues had relatively high ratio values, showing that they prey more frequently on small prey relative to their size. In fact, after Atlantic mackerels, they showed the highest relative ratios, and 25% of the total prey abundance was composed of relatively large plankton (Tables 5 and 6).

Atlantic and Mediterranean horse mackerels preyed frequently on relatively large prey, and had the lowest mode after Atlantic Chub mackerels. Moreover, Mediterranean horse mackerels showed lower values for the median and the third quartile, which indicates that they ingested larger prey relative to their size more frequently than the rest of the predators. This was also observed in sprats, which showed the lowest maximum *PPSR* (Tables 5 and 6).

Anchovies and sardines had diets based on relatively small prey and, compared to the other species, they did not show any extreme values except the minimum *PPSR* value, which was highest for sardines (Tables 5 and 6). However, although both predator species ingested relatively small prey at any size (i.e. relatively high *PPSR* values were frequently obtained), larger prey were also often found in the gut contents of both predators, especially in fish smaller than 230 mm (Tables 5 and 6).

The cumulated size-frequency curves in Figure 3 show the differences between species in terms of the prey size ratios that made up their diets (in numbers). Sprat and Atlantic and Mediterranean horse mackerels obtained 100% of their diet at predator–prey size ratios below 200. The rest of the species showed a wider food range. However, with the exception of Atlantic mackerels, all of them obtained > 60% of their diet at predator-prey size ratios < 200. Moreover, 75% of the diet of fish < 130 mm, except for anchovies and sardines, consisted of relatively larger prey, i.e. *PPSR* < 100 (Tables 5 and 6).

Trophic-niche breadth

All examined predators demonstrated a significant change in *PPSR*-based trophic-niche breadth with increasing body size (Table 7). In case of Clupeids, anchovies and sardines tended to show a decrease in *PPSR*-based trophic-niche breadth with increasing body size, whereas sprats showed an increase. Regarding

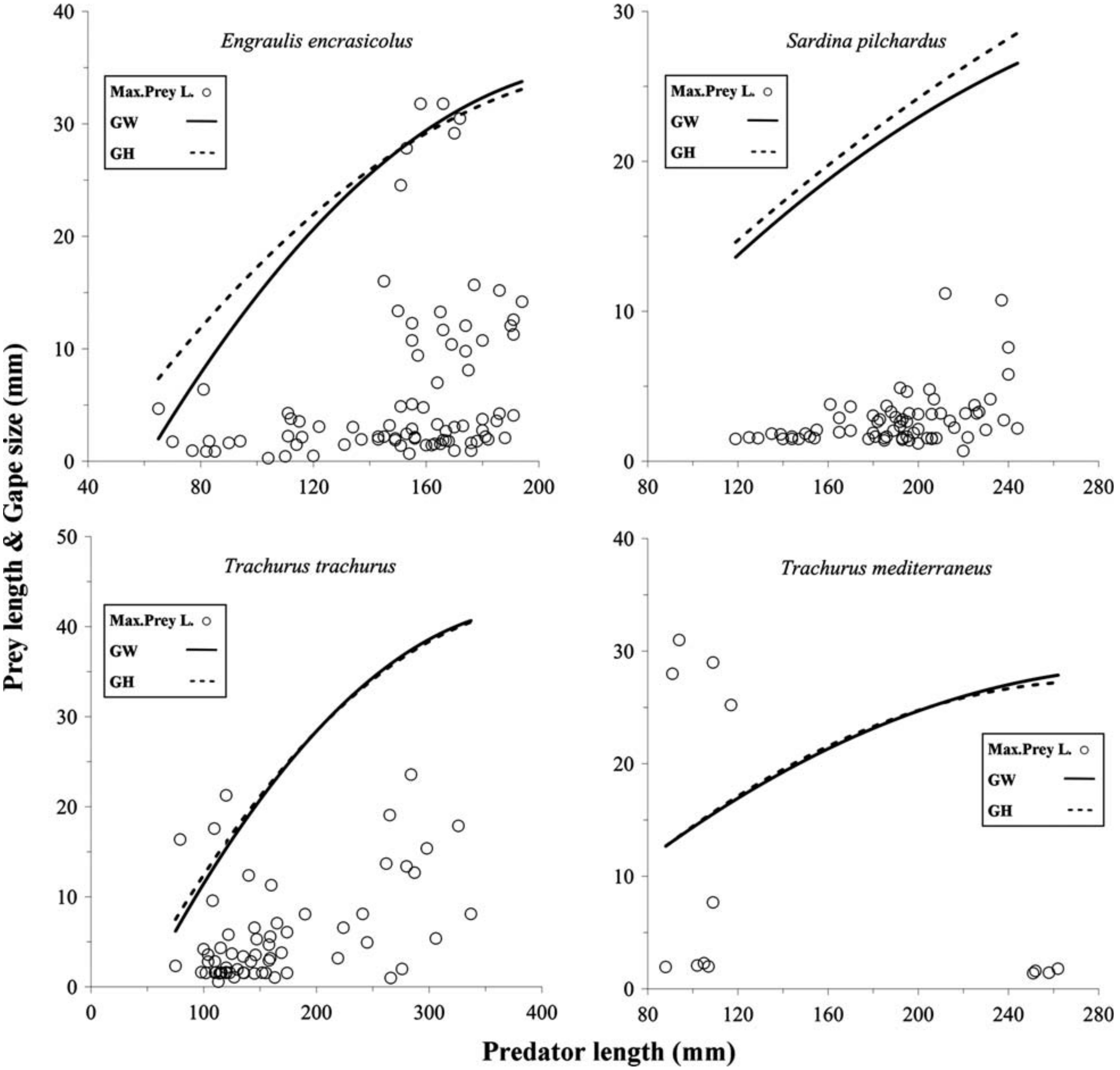

Figure 2. Predator length – maximum length of prey scatter diagrams for eight small pelagic fish predators. Each open circle represents the maximum value of the average prey sizes consumed by a predator. For each scatter diagram, thick continuous lines represent gape width vs. predator size regressions, and thick dashed lines represent gape height vs. predator size regressions. Regression equations are presented in Table 2.

larger predators, a decrease in the trophic-niche breadth with increasing body size was detected in bogues and Atlantic horse mackerels; in contrast, Mediterranean horse mackerels, as well as Atlantic and Atlantic Chub mackerels, tended to show an increase in the trophic-niche breadth with increasing body size (Table 7). Average *PPSR*-based trophic-niche breadth demonstrated an increasing trend with increasing average predator size across the range of predators examined (Figure 4). However, the regression equation was significant only when excluding Atlantic Chub mackerels (with much higher average trophic-niche breadth than the rest) from the analysis ($Trophic\text{-}niche\ breadth = 0.9627^{*}\ Predator\ length + 48.961$; $r^2 = 0.56$; $p = 0.055$).

Discussion

All sampled species showed a length-weight relationship in accordance with the general allometric pattern of small pelagic species (Lucio and Martin, 1989; Lucio, 1997; Mendes *et al.*, 2004; Cicek *et al.*, 2006; Ozaydin and Taskavak, 2006).

Also in accordance with the gravimetric results (Hyslop, 1980), the stomach weight of all sampled predators was strongly related to the total weight of the fish—e.g. Lucio (1997)—although the stomach weights of large Atlantic and Mediterranean horse mackerels were lighter.

Previous literature shows that in general the average prey size increases with the size of the predator (Peterson and Ausubel,

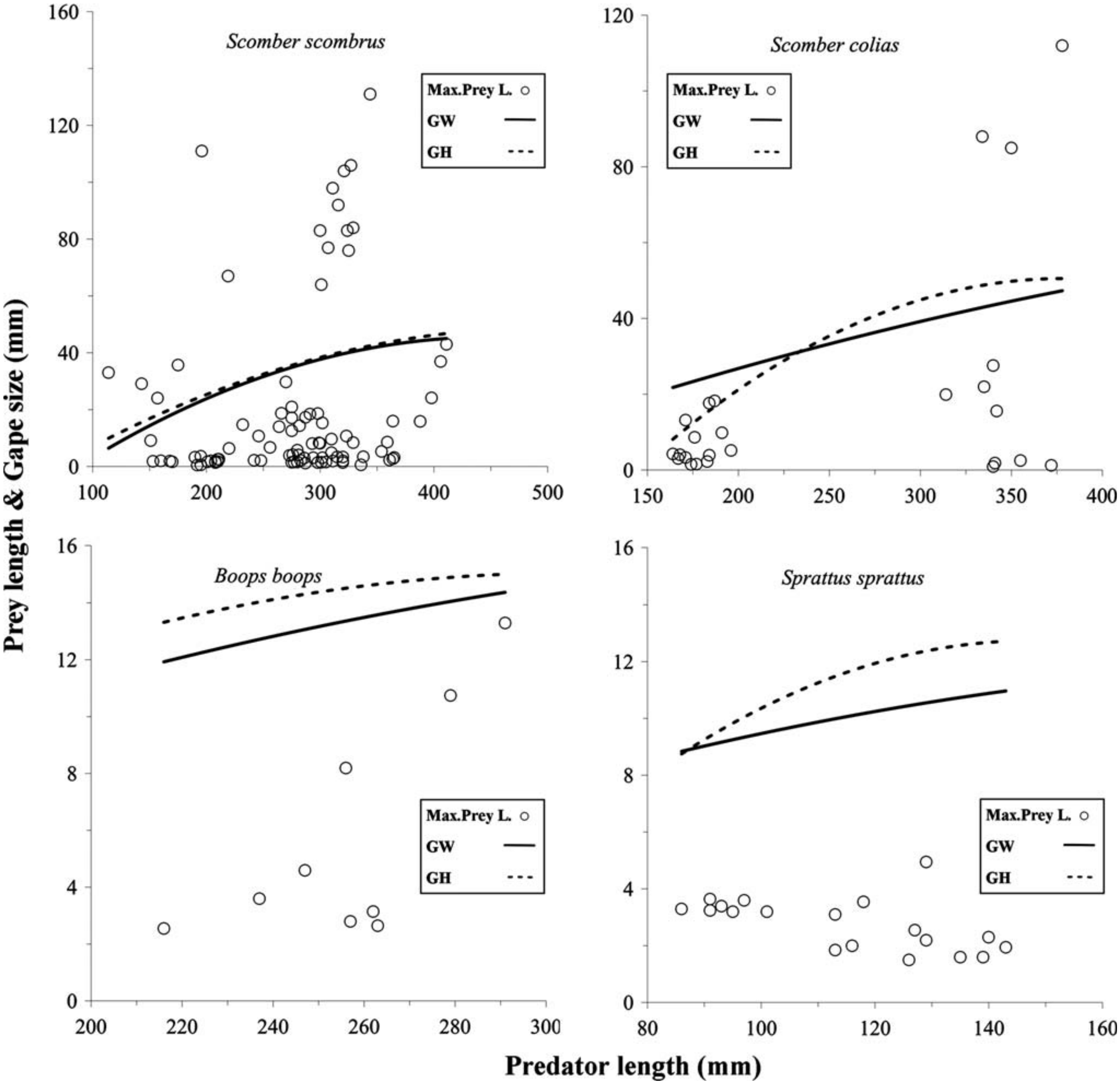

Figure 2 *Continued*

1984; Dahl and Kirkegaard, 1986; Hansen *et al.*, 1994; Olaso *et al.*, 1998; Velasco and Olaso, 1998a, b; Scharf *et al.*, 2000; Dörner and Wagner, 2003; Barnes *et al.*, 2008, 2010). In this study, a clear positive relationship was also found between the average and maximum prey sizes and the predator size. According to the trophic-niche breadth changes in the range of *PPSR* with increasing predator size (Scharf *et al.*, 2000; this study), differences are observed between species. However, predators showing rapid ontogenetic increases in maximum prey size do not necessarily increase the minimum prey size rapidly; for example, Atlantic Chub mackerels were able to predate on relatively larger prey with increasing body size but they also ingested the smallest prey, showing an increase in trophic-niche breadth. In addition, the observed increasing trend for average trophic-niche breadths with ontogeny (Figure 4) was also observed in the Northwest Atlantic by Pepin and Penney (1997) for many larval fish species, but not by Scharf *et al.* (2000) for adults, and may indicate that small prey could also be bulked in with larger prey items when selective feeding occurs. This suggests the ability of large competitors to eat a wider range of prey sizes than small ones, large fish being able to use essentially all of the prey size spectrum available to small ones, plus particles too large for the small ones (Brooks and Dodson, 1965; Pearre, 1986). Thus, expansion with length of absolute prey size range for most predators could indicate increases in behavioural and morphological capabilities for capturing and swallowing large prey, combined with high encounter rates and susceptibility of small prey (Scharf *et al.*, 2000).

Table 5. Descriptive statistics of the predator-prey size ratio (*PPSR*) percentages in terms of prey abundances found in the stomach contents of the sampled predators according to size (i.e. small-medium-large).

Predator species	$PPSR_{max}$			$PPSR_{min}$			Mode			Q_1			Q_2			Q_3		
	<130	130–230	>230	<130	130–230	>230	<130	130–230	>230	<130	130–230	>230	<130	130–230	>230	<130	130–230	>230
E. encrasicolus	375	547		12	48		245	108		101	105		201	113		245	229	
S. pilchardus	304	687	773	78	37	23	225	85	178	91	88	175	222	145	182	280	187	370
T. trachurus	245	518	488	9	16	26	80	64	55	76	67	38	84	98	59	98	129	94
T. mediterraneus	173		437	3		146	66		184	62		181	68		185	76		188
S. scombrus	63	592	1197	4	2	3	64	175	265	8	79	198	53	139	258	64	177	266
S. colias		742	826		10	4		48	225		51	123		87	226		125	327
B. boops		275	525		62	19		114	111		86	107		112	118		184	273
S. sprattus	367	330		4	61		67	105		63	107		70	139			82	223

$PPSR_{max}$ and $PPSR_{min}$ = maximum and minimum *PPSR*s. For the *PPSR* frequencies in terms of abundance (%), mode and the 1st (Q_1), 2nd (Q_2) and 3rd (Q_3) quartiles of the ratios are presented. The sample size is the same as described in Table 4. A *PPSR* value of 800 has been used as the cut-off point in the calculations, which covers ≥99.7% of the accumulated frequency.

Only two of the predator species have a gape size in relation to their body size that is significantly different from the other species: anchovies have the largest and bogues have the smallest. However, while bogues prey on smaller prey, the diet of anchovies does not reflect this relation in prey size or in predator–prey size ratios. In fact, although they have the largest gape size in relation to their body size, anchovies show high predator-prey size ratios, and thus ingest relatively small prey, especially when they are < 130 mm in length. These results suggest that relatively large gape size (in relation to body size), while making it possible to capture large prey that make a high biomass contribution, does not determine the *PPSR* distribution. Accordingly, in contrast with what Pepin and Penney (1997) and Sabatés and Saiz (2000) observed for fish larvae, in small pelagic fish in the Bay of Biscay, large gape sizes are not always related to a diet dominated by larger prey; on the other hand, relatively small gape size, observed for example in sprats, does not prevent an increase in trophic-niche breadth with increasing body size. In addition, if the largest predators swallow other large prey (e.g. smaller fish) longitudinally (extreme cases), the limiting size of prey would be more determined by width rather than by total length, and in this case the gape size would not be a good limiting factor of the maximum prey size consumed (Scharf *et al.*, 2000). That could explain larger maximum prey lengths than the estimated gape size of predator observed in some cases (e.g. Atlantic and Atlantic Chub mackerel) in which prey dorsoventral body depth measurements (Scharf *et al.*, 2000) could be more appropriate. Moreover, studies with other species have shown that prey-evasive behaviours and differences in prey availability can also limit the consumption of large prey (Hambright, 1991; Keeley and Grant, 1997; Scharf *et al.*, 2000).

If food is in sufficient amount, one might expect a filtering feeding, by which the smaller fraction would be over-represented (the larger prey would escape when the predator is seen). If food is scarce, one would expect the predator to select larger prey as it shifts to biting behaviour. For example, the plastic feeding behaviour of the anchovy allows them to shift from filtering to biting feeding, and hence they might not necessarily shift to larger prey, even if they are present, if capturing this large prey is energetically too demanding. Hence, the presence of relatively large organisms in stomach contents would indicate active opportunistic predation, which only occurs under favourable conditions, as previously described for various species such as anchovies (Tudela and Palomera, 1997; Plounevez and Champalbert, 1999, 2000; Bacha and Amara, 2009; Borme *et al.*, 2009) and, less frequently, sardines (Van der Lingen, 1994; Garrido *et al.*, 2007). Similarly, bogues also obtained 60% of the total ingested abundance from relatively large prey ($PPSR < 150$). Surprisingly, sprats mainly eat large prey in relation to their body size (they obtained 100% of their diet in numbers from a $PPSR < 200$). More than 80% of the diet of Atlantic and Mediterranean horse mackerels was comprised of relatively large prey ($PPSR < 150$), which is in accordance with previous observations (Olaso *et al.*, 1999). More than 40% of the diet in numbers of Atlantic Chub mackerels was comprised of large plankton, and it had lower *PPSR* values than the other predators (i.e. large prey). In contrast, Atlantic mackerels, with both maximum and minimum *PPSR* modes, showed the widest prey size spectrum. The diet of Atlantic mackerel is known to be limited mainly by the composition of zooplankton in the area (Castro, 1993; Cabral and Murta, 2002; Olaso *et al.*, 2005) as well as ontogeny (Conway

Table 6. Comparison of gape height (*GH*) and width (*GW*) as a percentage of the total length and descriptive statistics of the *PPSR* percentages in terms of prey abundances found in the stomach contents for all size ranges.

					Freq. Distrib. of *PPSR*			
Species	*GW* (% of *TL*)	*GH* (% of *TL*)	$PPSR_{max}$	$PPSR_{min}$	Mode	Q_1	Q_2	Q_3
E. encrasicolus	17	19	547	12	108	105	115	232
S. colias	13	14	826	4	48	52	112	144
T. mediterraneus	13	14	437	3	66	63	68	77
T. trachurus	13	13	518	9	65	67	94	126
S. scombrus	12	13	1197	2	265	198	258	266
S. pilchardus	12	12	773	23	85	91	163	212
S. sprattus	10	10	367	4	67	63	70	85
B. boops	6	6	525	19	111	17	117	264

The sample size is the same as that described in Table 4. A *PPSR* value of 800 has been used as the cut-off point in the calculations, which covers ≥99.7% of the accumulated frequency. Predators are ordered by relative buccal apertures, from the widest to the smallest.

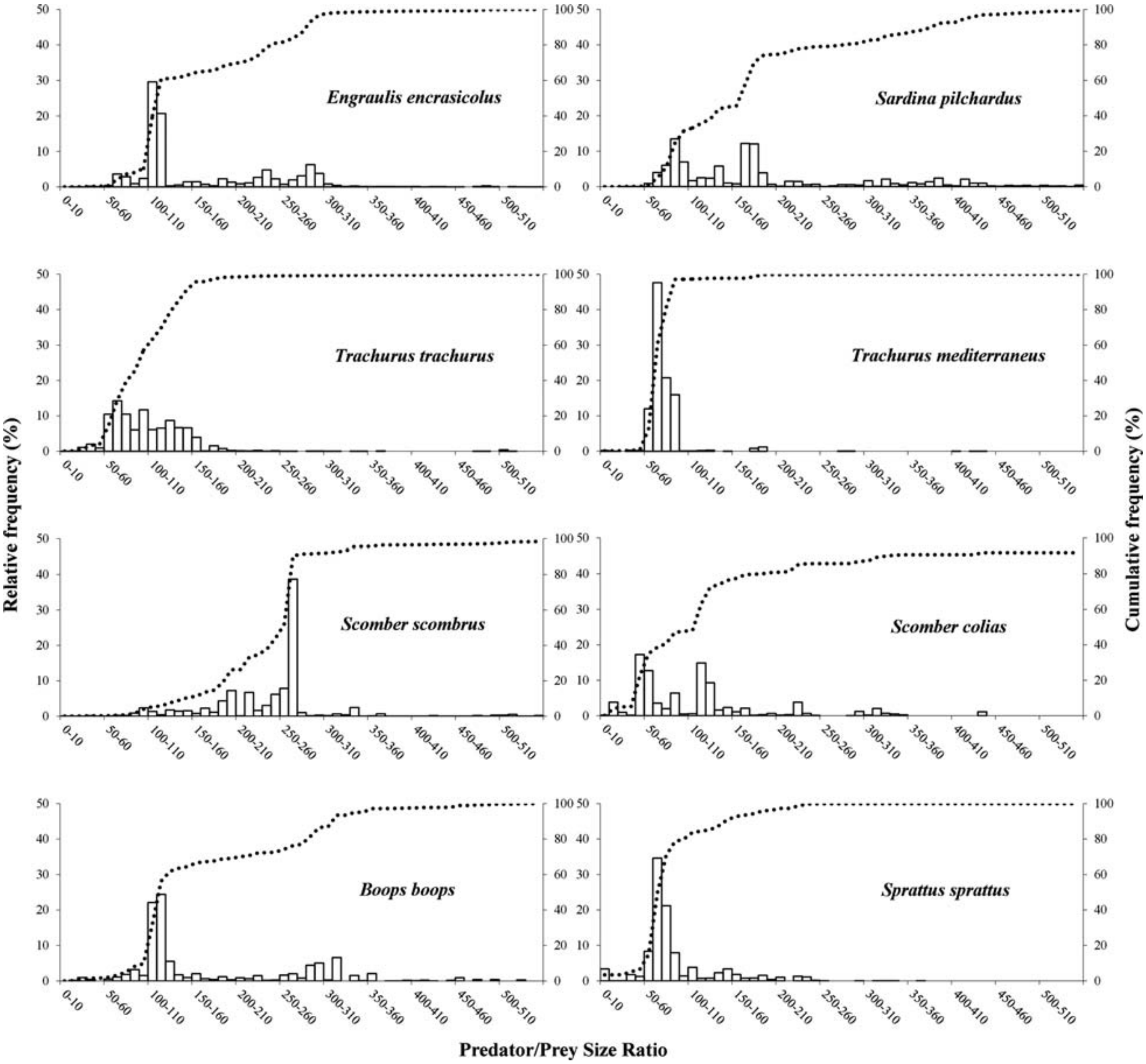

Figure 3. Relative frequency distribution of abundances of prey consumed by small pelagic predators. Cumulative *PPSR* frequencies are indicated by discontinuous lines. A *PPSR* value of 550 has been used as the cut-off point in graphs, which covers ≥91.93% of the accumulated frequency.

Table 7. Change in ratio-based trophic-niche breadth with increasing predator size for the eight small pelagic species.

	Predator-prey size ratio vs. Predator size		
Predator species	**Upper bound slope (± s.e.)**	**Lower bound slope (± s.e.)**	**Change in trophic-niche breadth**
E. encrasicolus	−0.0782 (±0.0417)′	0.0476 (±0.0068)***	decrease
S. pilchardus	−0.0825 (±0.0328)*	0.1256 (±0.0036)***	decrease
T. trachurus	−0.3616 (±0.0571)***	−0.0442 (±0.0045)***	decrease
T. mediterraneus	0.4905 (±0.0499)***	−0.8756 (±0.0545)***	increase
S. scombrus	1.0083 (±0.0216)***	0.0377 (±0.0021)***	increase
S. colias	0.3881 (±0.1202)**	−0.0871 (±0.0094)***	increase
B. boops	−0.992 (±0.1447)***	−0.1722 (±0.0251)***	decrease
S. sprattus	1.7836 (±0.0358)***	0.4675 (±0.0063)***	increase

Upper- and lower-bound slopes are quantile regressions estimating 90th (upper) and 10th (lower) quantiles of *PPSR* vs. predator length comparisons (***$p < 0.0001$, **$p < 0.001$, *$p < 0.01$, ′$p < 0.1$). s.e. is the standard error of each quantile regression. Decreases or increases in trophic-niche width are based on statistically significant differences between upper- and lower-bound slopes ($p < 0.001$ in all species).

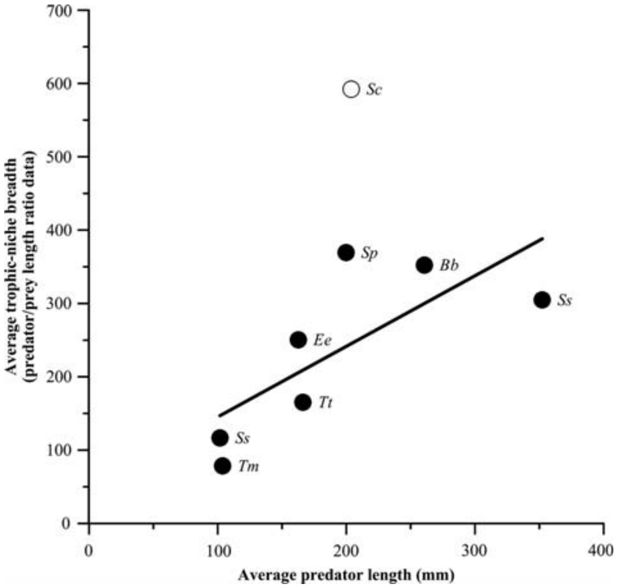

Figure 4. Average trophic-niche breadth plotted against average predator size for trophic-niche breadths calculated using *PPSRs*. Error bars (± 1 s.e.) are not visible since they are all <1. *Ee* = *E. encrasicolus*, *Sp* = *S. pilchardus*, *Tt* = *T. trachurus*, *Tm* = *T. mediterraneus*, *Ss* = *S. scombrus*, *Sc* = *S. colias*, *Bb* = *B. boops*, *Ss* = *S. sprattus*. Open circle indicates that it has been excluded from the regression fit (*Sc*).

et al., 1999). However, the incorporation of a considerable number of intermediate-sized prey in the diet of large predators, while they continue to feed on small vulnerable prey, has also been observed in previous studies with other species, and the interspecific variability has been attributed to several morphological and behavioural characteristics (Scharf *et al.*, 2000). The differences between Atlantic and Atlantic Chub mackerels may actually be due to the differences in the number of sampling stations where they were found as well as in the number of individuals analysed. In the same way, the stomach contents are a snapshot in time of the diet, and we cannot determine where the prey was captured in the vertical range, or even the horizontal. This limits the value of the comparison with zooplankton samples at the same time of fishing.

All the results suggest that the contribution made by the different prey sizes to fish diets is determined more by the available plankton sizes in relation to predator size (with sprats and mackerels being the extremes in predator size) than the behaviour or morphology of the fish. The minimum ingested prey size shows more similarity between species than the maximum size, which increases with predator size. This indicates that predators use the entire available size range, including the smallest sizes, and as they grow, simply incorporate larger prey as they become capable of catching it. As a result the *PPSRs* and trophic-niche breadth are dependent on changes in predator size. In addition, most species have similar stomach weights in relation to size, and the percentage of stomachs containing prey is similar. The exception seems to be Atlantic and Mediterranean horse mackerels, which show intra-specific differences when the general trends of their trophic-niche breadth with increasing body size are observed (i.e. opposite trends, Table 7). However, the minimum prey size of both horse mackerel species is larger than that of the other species, and, although they are as large as Atlantic and Atlantic Chub mackerels, most of their diet has low *PPSR* values, their stomach weight in relation to size is lighter than that of the other species, and the percentage of empty stomachs is much higher (Olaso *et al.*, 1999; this study). All these observations agree with a real specialization in large prey, and therefore ingestion will be less frequent (leading to a lower average stomach weight and a higher frequency of empty stomachs). Nevertheless, it could also be a consequence of higher regurgitation rates during capture and differences in regurgitation depending on the stomach contents. In any case, Atlantic and Mediterranean horse mackerels offer an interesting model for making comparisons with the diets of other small pelagic fish.

In conclusion, our data indicate that, except for horse mackerels, the diets of the different species show a large degree of overlap in terms of prey size, even between fish of different sizes.

Supplementary data

Supplementary data are available at *ICES Journal of Marine Science* online.

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