

Role of prey abundance and geographical variables in a demersal top predator's feeding habits (*Merluccius merluccius*)

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ABSTRACT: Demersal predators can take advantage of a large pool of potential prey including benthic, demersal and pelagic species; therefore disentangling the variables that influence their diet is of key relevance for food web ecologists. To this aim, we analysed a large dataset of the stomach contents of European hake *Merluccius merluccius*, a top predator in the demersal food web of the Cantabrian Sea. We combined 2 modelling approaches: a zero-truncated generalised additive model targeting fullness variability, and a multinomial model on the probability of consumption for each prey. Predator size, geographical variables (i.e. longitude and depth), and abundance of prey were considered as independent variables, and had significant effects on predator stomach fullness. We also documented a positive effect of continental shelf width on predator stomach fullness. The hake's main prey, blue whiting *Micromesistius poutassou*, had the strongest effect on predator feeding success. However, in the absence of this prey species, consumption of all other prey items increased. Consumption was highly influenced by prey abundance, but predator density dependence was only evident in instances of cannibalism. Both the full/empty ratio and stomach fullness decreased during ontogeny, and a change from low-energy demersal to high-energy pelagic prey was documented, matching the onset of maturity. While the abundance of prey significantly affected feeding success, a large diet breadth rather than prey surrogates seemed to act as an effective buffer, ensuring feeding at low abundance of specific prey.

KEY WORDS: European hake · Prey abundance · Diet · Multinomial regression · Generalised additive models · Cannibalism

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INTRODUCTION

The direction and strength of trophic connections in natural food webs are conditioned by a number of interconnected factors. Among them, the effect of prey abundance on predator response is a paradigm in ecology. While predator–prey overlap is a necessary condition for predation to occur, prey selection is often proportional to prey availability in the environment (Link & Garrison 2002, Pinnegar et al. 2003), and feeding intensity can dramatically increase with high prey densities (Wellenreuther & Connell 2002);

yet the occurrence of cannibalism has been attributed to overlapping high densities of juveniles and adults of the same species (Parker Stetter et al. 2007, Preciado et al. 2015). At low prey abundance however, a predator's functional feeding response is expected to decrease following a Holling type III sigmoidal curve (Kempf et al. 2008). Large demersal predators can potentially feed from a large prey pool containing species of differing energy content and size-dependent capturability. The combination of the characteristics and abundance of prey species produces a complex matrix of optimal foraging opportu-

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nities. In addition to prey-dependent variables, several other factors are known to influence fish diet, such as environmental variables and predator length (Stefansson & Palsson 1997, Velasco & Olaso 1998, Trenkel et al. 2005) as well as predator abundance (Cartes et al. 2009). Food web links are typically characterised by different connection strengths, which adapt throughout ontogeny to varying environmental conditions (Link & Garrison 2002). Disentangling these interacting factors is a key aspect of trophic ecology.

European hake *Merluccius merluccius* becomes an apical demersal predator after recruitment (Velasco & Olaso 1998, Sanchez & Olaso 2004). Studies on the feeding habits of European hake have been carried out throughout its distribution from the Celtic Sea to the central Mediterranean Sea, and have shown a marked change from a crustacean-based to a piscivorous diet at lengths of 15 to 23 cm, when juvenile hake leave their nursery areas. Although the diet of hake varies regionally and most studies have focused on the crustacean-based diet of hake juveniles (Ferraton et al. 2007, Carpentieri et al. 2008, Cartes et al. 2009, Modica et al. 2011), the importance of pelagic forage fish and demersal fish such as blue whiting *Micromesistius poutassou* or silvery pout *Gadiculus argenteus*, as well as the occurrence of cannibalism in the pre-adult and adult stages have also been widely described for this species (Bozzano et al. 1997, Velasco & Olaso 1998, Carpentieri et al. 2005, Mahe et al. 2007, Stagioni et al. 2011, Rodriguez-Cabello et al. 2014, Preciado et al. 2015). In our study area, adult hake have a main trophic link with blue whiting, which constitutes as much as 63% of all fish ingested by adult hake (Velasco & Olaso 1998, Velasco 2007). These species share demersal dwelling habits on

the shelf and a circadian vertical migration pattern (Johnsen & Godø 2006).

In this study, we used adult hake as a model species to analyse the possible dependence of the diet of an apical demersal predator on geographical variables, predator density-dependence, ontogeny, and the distribution of its main prey. To this end, we used a large dataset of adult hake diet comprising 24 yr and nearly 17 000 stomachs. With this dataset, we comprehensively assessed feeding ecology of hake during its piscivorous phase, which is commonly under-represented in food web studies due to the sparser distribution of pre-adults and adults. We hypothesized that hake diet would mirror prey availability, and thus at low prey abundance a decrease in feeding intensity and a change in diet would be expected.

MATERIALS AND METHODS

Data source

Pre-adult and adult hake were sampled every autumn (mid-September to the end of October) between 1990 and 2013 from the soft bottom of the Cantabrian Sea continental shelf (Fig. 1) using bottom trawl surveys designed to assess demersal and benthic stocks (the 'DEMERSALES' survey) in ICES area VIIIc (for detailed survey information see Sanchez & Serrano 2003). The survey design followed a randomly stratified sampling scheme covering a depth range of 70 to 500 m. Additional tows were performed annually at deeper and shallower depths (>500 and <70 m) following the same sampling protocol, and are also considered in this

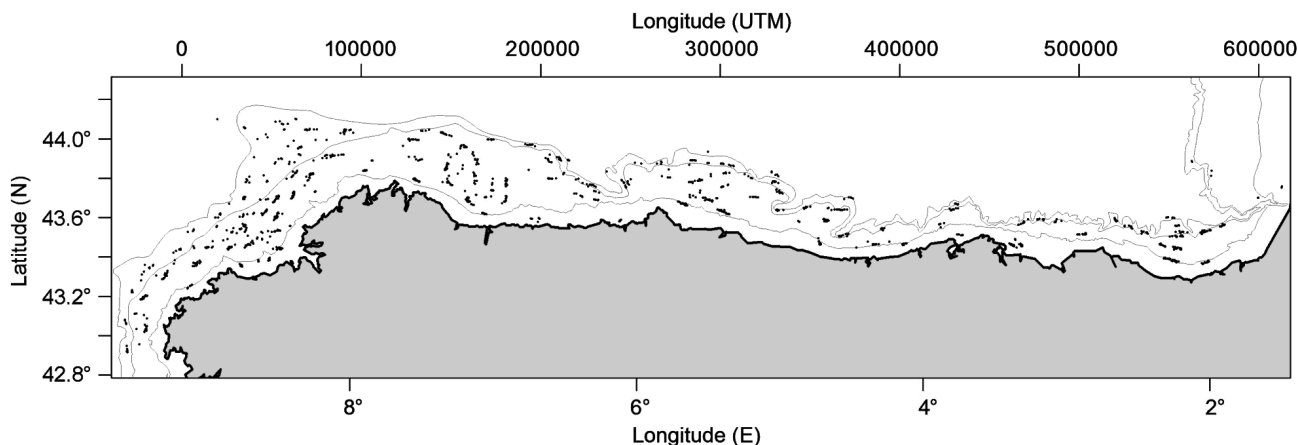


Fig. 1. Study area showing location of the sampling hauls along the time series. Isobaths (light grey lines) indicate 100, 200 and 500 m depth

study. Fish species including hake, blue whiting, silvery pout and horse mackerel were measured (total length rounded down to the nearest cm) and their total catch weight was recorded. From each haul, a maximum of 10 hake individuals in each size category were set aside for extended biological sampling (categories comprised size ranges of 5 cm). Only pre-adult and adult hake (individuals >18 cm) were used as predators in the analysis, and will be referred to as adult hake throughout the text.

Quantitative diet estimates were obtained by measuring the stomach content volume (cm³) using a trophometer (Olaso 1990), a device consisting of a series of graduated semi-cylinders. Individuals that had regurgitated were identified by inspecting their gall bladder (Robb 1992) and examining their fish gape for food residues. In each stomach, prey were separated, identified to the lowest taxonomic level, and measured whenever possible. All dissections and identification of stomach contents were carried out onboard. Fresh prey or any items presumably consumed in the net were excluded from the analysis. Ingestion of discards were incidental and thus not considered in the analysis.

The energy content of each prey category was obtained from Spitz et al. (2010). For the benthic-demersal and unidentified fish categories, energy content was calculated by standardising the energy content of each species to the volume contribution of that species, to the total volume of the prey category to which it belonged. Invertebrates were excluded from this part of the analysis due to lack of information regarding their energetic content at a species-specific level.

Statistical analyses

To characterise the feeding habits of hake, 2 modelling approaches were applied. We first analysed the standardised stomach fullness (the volume of the stomach as a percentage of the predator's weight, V%BW; hereafter referred to as stomach fullness) using a zero-truncated model (Stefansson & Palsen 1997). This metric standardises prey volume by predator weight, while avoiding attributing more weight to the prey of larger hake individuals, as would be the case if using stomach volume alone. With this modelling approach, we considered the zeros (empty stomachs) separately from the positive values of the stomach fullness distribution. Secondly,

the probability of ingestion of different prey categories was modelled using a multinomial regression approach. Prey species that contributed more than 1% to hake diet (considering percentage of this prey from the total prey volume) were considered at a species taxonomic level, while other prey items were grouped based on a combination of taxonomical and ecological criteria, generating a total of 15 prey categories (Table 1).

Model selection was performed following a stepwise procedure in which a new variable was added and retained if it resulted in a decrease of the model's Akaike's information criterion (AIC) value. To test if the stepwise procedure we followed had any effect on the variables being selected, we conducted a backwards stepwise elimination, dropping variables from the full model in a stepwise procedure, which provided the same results. The initial pool of explanatory variables was the same across all models, including geographical variables (longitude and depth), predator abundance and size (total length) and prey abundance (juvenile hake, blue whiting, silvery pout and horse mackerel) computed for each haul and year, thus preserving inter-annual variability. While prey size is known to be a key factor in determining diet, it was not included in the analysis since this variable could only be measured in freshly digested prey (approximately one-third of the prey in our database). In addition, considering prey size would bias the analysis towards prey with longer digestion times. Other fish prey species such as mackerel, anchovy or sardine are not adequately sampled by bottom trawling and their abundances could not be estimated for inclusion in the zero-truncated model. Longitude (UTM) is minimum at our westernmost location and increases toward the inner Bay of Biscay (east). This variable, along with depth, sufficed to characterise spatial distribution since the coastline configuration follows a west-east axis; the effect of its interaction was disregarded as it was not significant. Correlation between covariates was low in all cases (Pearson's correlation < 0.5) and thus accepted in generalised models.

Sediment size was not included in the analysis as it was regarded as a poor proxy for habitat information due to the patchy distribution of bottom types (Serrano et al. 2006) and the vertical mobility of adult hake. In the Northern Bay of Biscay, juvenile hake are associated with muddy bottoms (Wuillez et al. 2007). In our study area, nursery areas were identified east of the main capes (Sanchez & Gil 2000, Preciado et al. 2015) regardless of bottom type. These nursery areas can be identified in our study using

Table 1. Prey categories of species and taxa identified in the stomach sample prior to analyses (listed alphabetically), N: number of observations available for each category. Unid. = unidentified

Category	Species	Category	Species		
Benthic crustaceans (N = 179)	<i>Alpheus dentipes</i>	Benthic-pelagic shrimp (cont.)	<i>Plesionika heterocarpus</i>		
	<i>Alpheus glaber</i>		<i>Processa canaliculata</i>		
	Amphipoda unid.		<i>Processa</i> spp.		
	<i>Atelecyclus undecimdentatus</i>		<i>Solenocera membranacea</i>		
	Brachyura unid.		Cephalopods (N = 108)	<i>Alloteuthis media</i>	
	Crangonidae unid.			<i>Alloteuthis</i> spp.	
	<i>Dichelopandalus bonnierii</i>			<i>Alloteuthis subulata</i>	
	<i>Galathea</i> spp.			Cephalopoda unid.	
	<i>Gnatophausia zoea</i>			<i>Illex coindetii</i>	
	<i>Goneplax rhomboides</i>			<i>Loligo forbesi</i>	
	Isopoda unid.			<i>Loligo</i> spp.	
	<i>Lophogaster typicus</i>			<i>Sepia elegans</i>	
	<i>Munida</i> spp.			<i>Sepia officinalis</i>	
	Mysidacea unid.			Sepiolidae unid.	
	Paguridae unid.			Engraulis encrasicolus (N = 291)	<i>Engraulis encrasicolus</i>
	Alpheidae chelipeds				Gadidulus argenteus (N = 208)
	Brachyura chelipeds			Merluccius merluccius (N = 380)	
	<i>Pontophilus spinosus</i>				Micromesistius poutassou (N = 2864)
	<i>Scyllarus arctus</i>		Other fish (N = 1825)	<i>Argentina sphyraena</i>	
	Benthic-demersal fish (N = 351)			<i>Acantholabrus palloni</i>	<i>Capros aper</i>
<i>Arnoglossus imperialis</i>		Clupeidae unid.			
<i>Arnoglossus laterna</i>		<i>Maurolicus muelleri</i>			
<i>Arnoglossus</i> spp.		Teleostea unid.			
<i>Boops boops</i>		<i>Scomber japonicus</i>			
<i>Callionymus maculatus</i>		<i>Scomberesox saurus</i>			
<i>Callionymus</i> spp.		Others (N = 18)		Algae	
<i>Cepola rubescens</i>				<i>Aporrhais pespelicani</i>	
<i>Chelidonichthys cuculus</i>				Bivalvia unid.	
<i>Conger conger</i>			<i>Holothuria forskali</i>		
<i>Deltentosteus quadrimaculatus</i>			Fish larvae		
<i>Echiodon dentatus</i>			Unidentified prey		
Gadidae unid.			Polychaeta unid.		
<i>Gaidropsarus macrophthalmus</i>			Salpidae		
Gobidae unid.			Tunicata unid.		
Labridae unid.			Pelagic crustaceans (N = 311)	Euphausiacea unid.	
<i>Lepidotrigla cavillone</i>		Hyperperiidae unid.			
<i>Lesueurigobius friesii</i>		<i>Meganctyfares norvergica</i>			
<i>Microchirus variegatus</i>		Sardina pilchardus (N = 191)		<i>Sardina pilchardus</i>	
<i>Mullus surmuletus</i>				Scomber scombrus (N = 263)	<i>Scomber scombrus</i>
<i>Pagellus acarne</i>	Trachurus trachurus (N = 375)	<i>Trachurus trachurus</i>			
<i>Phycis blennoides</i>		Unidentified crustaceans (N = 38)		Crustacea unid.	
Pleuronectoidei unid.	Decapoda unid.				
<i>Pomatochistus</i> spp.					
<i>Serranus cabrilla</i>					
<i>Trisopterus luscus</i>					
<i>Trisopterus minutus</i>					
<i>Trisopterus</i> spp.					
<i>Zeus faber</i>					
Benthic-pelagic shrimp (N = 509)	<i>Chlorotocus crassicornis</i>				
	Natantia unid.				
	<i>Pasiphaea multidentata</i>				
	<i>Pasiphaea sivado</i>				
	<i>Pasiphaea</i> spp.				

juvenile hake abundances, which are in the range of 1000 to 3000 ind. km⁻² (Sanchez & Gil 2000). The other 3 prey species considered here are not known to have any habitat associations on the shelf.

Prior to the analysis, net catch abundance data for predator and prey (ind. km⁻²) were interpolated by means of generalized additive models (GAMs) using Poisson distributions and a log link (N = 2895), in

which abundance was annually regressed using longitude, latitude, and depth as covariates. The output of these species distribution models (SDMs) are considered to be more representative of the actual availability of prey at the time of predation than raw local observations, since they partly compensate for the space–time mismatch between feeding and sampling, and partly filter the noise inherent in species distribution data. The SDMs were not constrained by degrees of freedom, thus preserving the high degree of variability in the distribution of species abundances while smoothing abrupt changes between adjacent points. Results from these models were very accurate, with explained deviance ranging from 80.40 to 92.70%; these data are hereafter referred to as abundance data. Abundance data were log transformed before inclusion in the models in order to correct for high skewness in the distributions.

The zero-truncated model consisted of a binomial GAM on the probability of a predator having ingested any food (full and regurgitated stomachs vs. empty stomachs) and a GAM with a Gaussian distribution and identity link for modelling the positive side of the fullness distribution, previously cubic root transformed to satisfy the normality criteria. Cubic root transformation is a common tool for obtaining normal distributions from gamma-like distributed data (Cox 2011). The maximum number of degrees of freedom allowed for each term was constrained to 4, based on ecological criteria with exception of longitude. The probability of finding a specific prey category in the predator's diet was explored using a multinomial regression model. Categories with a small number of observations such as unidentified crustaceans ($n = 38$) and others ($n = 18$) were not included to avoid model instability. This log-linear model was fitted via neural networks using the function 'multinom()' in the R library 'nnet' (Venables & Ripley 2002). We assessed the goodness-of-fit comparing the input data with the model output using a chi-squared test. To ease the results interpretation, we used effect displays (Fox & Andersen 2006) with the aim of finding fitted probabilities for selected combinations of values of the predictor variables. According to Fox & Andersen (2006), standard errors were calculated by approximation using the delta method which, in its essence, expands a function of a random variable about its mean with a 1-step Taylor approximation. The log odds of a given category for an observation are computed relative to the log odds of membership in all other categories. Confidence intervals calculated in the logit scale can be later translated to the probability scale.

RESULTS

In total, 16 878 pre-adult and adult hake were analysed during the study period, 45% of which had empty stomachs, with the remainder being either full or regurgitated. Among the full individuals, stomach fullness reached maximum values of 80%, with median and mean values of 7.6 and 10.3%, respectively. The binomial GAM ($n = 16\,878$; explained deviance 2.29%) identified 6 covariates that significantly affected the full/empty ratio (Fig. 2, Table 2). Increasing depth strongly decreased the ratio of full/empty individuals on the continental shelf (<250 m) but its effect was weaker over the slope (250 to 650 m) (Fig. 2a). The effect of longitude was highly variable, but a general decrease toward the east was evident (Fig. 2b). A negative effect on the full/empty ratio was found for predator size over approx. 35 cm total length (Fig. 2c). The effect of prey abundance on the full/empty ratio was variable; abundances of blue whiting over 1000 ind. km⁻² had a positive effect on the full/empty ratio (Fig. 2d); a positive association was also noted between the full/empty ratio and silver pout abundance (Fig. 2e). However, juvenile hake abundance had the opposite effect on the full/empty ratio, as the probability of finding a full stomach decreased for juvenile abundances in the range of 30 to 3000 ind. km⁻² (Fig. 2f). The second half of the zero-truncated model, the GAM on the positive values of the stomach fullness distribution ($n = 6044$; deviance explained = 5.69%), complemented this insight into hake foraging habits. This analysis identified 6 covariates as drivers of the stomach fullness distribution (Fig. 3; Table 2), 5 of which matched the results of the binomial GAM. Longitude, predator size, and blue whiting abundance were significant explanatory variables, following similar patterns as in the binomial GAM (Fig. 3a–c, respectively). Depth, however, displayed an opposite trend to the binomial model, showing a linear and positive relation to stomach fullness (Fig. 3d). Stomach fullness also showed a significant response to juvenile hake and horse mackerel abundance; the effect of hake abundance on stomach fullness was negative up to intermediate abundances of juvenile hake in the range of 1000 to 3000 ind. km⁻², decreasing by ca. 1% (Fig. 3e). A negative effect was only evident for horse mackerel from an abundance threshold of 100 ind. km⁻² (Fig. 3f), showing a smooth decline of 0.34% in stomach volume for every unit of increased horse mackerel abundance in the logarithmic scale.

Regarding the different prey types in the diet, results from the multinomial model draw a clear picture

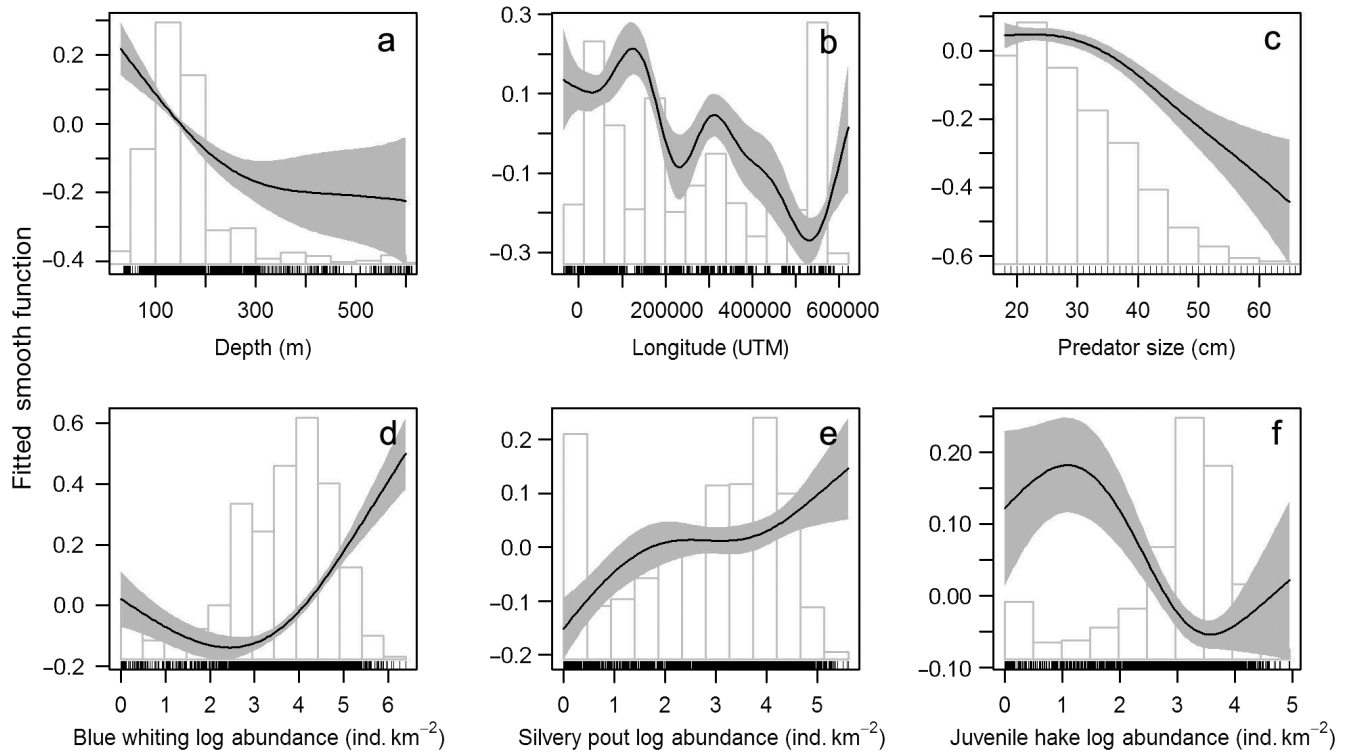


Fig. 2. Cubic spline smoother fits (black solid lines) of the binomial generalised additive model based on adult European hake *Merluccius merluccius* full/empty ratio as a function of longitude, depth, predator size and the abundance of 3 of its prey species (blue whiting, juvenile hake, and horse mackerel). Grey area: 95% confidence limits; grey bars: relative frequency of observations along the x-axis

of how the probability of ingesting a particular prey category varied along the set of covariates considered. Blue whiting clearly dominated the prey species pool, regardless of the covariate configuration. The probability of predation for any given prey species increased with prey abundance values (Fig. 4). However, the density-dependent effect of predator abundance differed depending on the prey considered. The probability of predation on blue whiting was not affected by predator abundance (Fig. 4a), while silvery pout and horse mackerel displayed a slight decrease (ca. 2%) in the probability of being depredated at high predator and prey abundances (10 000 and 100 000 ind. km⁻², respectively) (Fig. 4b,c). On the contrary, in the case of juvenile hake this probability increased dramatically (10 to 25% increase) at high predator and prey abundances (predator abundances of 10 000 ind. km⁻² with prey abundances ranging from 1000 to >10 000 ind. km⁻²) (Fig. 4d), and was the most affected by predator density-dependence.

The multinomial model allowed us to explore how predation on all prey groups varied along the hake's main prey abundance gradient (Fig. 5a). We found an

evident decrease in the probability of consumption of all other prey categories as blue whiting abundance increased. Although the unidentified fish category was the most likely replacement for blue whiting, benthic–pelagic shrimp and benthic invertebrates achieved consumptions up to 15 and 12%, respectively, in the post-recruits. Anchovy represented up to 7% of the diet of 20 to 25 cm hake, juvenile hake up to 20% in the diet of 30 to 35 cm hake, and horse mackerel and mackerel between 16 and 25% of the diet of the largest individuals (Fig. 5b). In fact, consumption of invertebrates, small fish, large pelagic fish, and large demersal fish displayed distinct trends along hake's ontogeny. The probability of consuming an invertebrate group progressively decreased throughout ontogeny (Fig. 6a). Small fish such as anchovy (mainly juveniles <11 cm) and silvery pout decreased in adult hake diet along ontogeny (Figs. 6b & 7). The probability of predation showed a dome shape for blue whiting and juvenile hake (Fig. 6c). Larger pelagic fish such as mackerel, horse mackerel and sardine, which occur predominantly over the shelf, showed an increasing probability of being consumed along the predator's ontogeny (Fig. 6d).

Table 2. Zero-truncated generalised additive model results with statistics resulting from including each new variable added to the model formula. The final model is highlighted in **bold**; edf (estimated degrees of freedom) and p-values for each predictor variable are specified in square brackets. AIC: Akaike's information criterion; ***p ≤ 0.01; *p < 0.05. (a) Full/empty ratio model (binomial; no. of observations = 16878). (b) Stomach fullness model (Gaussian; no. of observations = 6044)

Estimate	AIC	Deviance explained (%)	R ² (adj)
(a) Full/empty ratio model			
Longitude			
Longitude + Blue whiting abund.	23016.35	0.891	0.012
Longitude + Blue whiting abund. + Predator size	22843.44	1.66	0.022
Longitude + Blue whiting abund. + Predator size + Silvery pout abund.	22780.74	1.95	0.026
Longitude + Blue whiting abund. + Predator size + Silvery pout abund. + Depth	22770.52	2.02	0.026
Longitude + Blue whiting abund. + Predator size + Silvery pout abund. + Depth + Juvenile hake abund.	22743.62	2.15	0.028
Longitude + Blue whiting abund. + Predator size + Silvery pout abund. + Depth + Juvenile hake abund.	22720.07	2.29	0.03
[8.344 ***] [2.681 ***] [2.111 ***] [2.331 ***] [2.759 ***] [2.918 ***]			
(b) Stomach fullness model			
Blue whiting abund.			
Blue whiting abund. + Predator size	13388.35	3.58	0.035
Blue whiting abund. + Predator size + Depth	13344.23	4.34	0.043
Blue whiting abund. + Predator size + Depth + Longitude	13322.33	4.73	0.046
Blue whiting abund. + Predator size + Depth + Longitude + Juv. hake abund.	13291.58	5.45	0.052
Blue whiting abund. + Predator size + Depth + Longitude + Juv. hake abund. + Horse mackerel abund.	13290.09	5.55	0.053
Blue whiting abund. + Predator size + Depth + Longitude + Juv. hake abund. + Horse mackerel abund.	13285.21	5.69	0.054
[2.721 ***] [1.704 ***] [1.000*] [7.784 ***] [2.634] [1.762*]			

DISCUSSION

Our results demonstrate that the diet of the demersal top predator European hake *Merluccius merluccius* depends on several factors, including geographical variables, predator size and prey distribution. However, only the abundance of its main prey had a strong effect on both the probability of feeding and stomach fullness. Despite these results, the vast majority of stomach fullness variability remained unexplained by our zero-truncated model. Similar modelling approaches have been successfully applied to other large datasets of stomach content data for determining spatio-temporal patterns (Stefansson & Palsson 1997, Trenkel et al. 2005, Espinoza & Bertrand 2008). Stefansson & Palsson (1997) reported explained deviances of 11 to 31% for the binomial model and 20 to 63% for the gamma model using predator length, depth, and other spatial variables as covariates when modelling Icelandic cod stomach fullness. These high values contrast with the low explanatory power of our analyses. The difference could originate from the greater diet breadth of adult hake in the Bay of Biscay compared with that of Icelandic cod, which could allow adult hake to achieve high stomach fullness even in absence of its main prey. In addition, we constrained the predictor variables in our models to 4 degrees of freedom in order to obtain ecologically relevant trends (with the exception of longitude). Constraining the degrees of freedom slightly decreased the explained variance of the model.

The existence of predation hotspots (Temming et al. 2007, Methratta & Link 2012) could also contribute to the low amount of explained variance in our models, since feeding could be patchy on prey aggregations and sampling could have occurred after the prey aggregation had been depleted. Predation hotspots, while relevant at the ecosystem level, are almost invisible at the coarse scale at which assessment surveys operate (Temming et al. 2007). Nevertheless, the temporal and spatial extent of our dataset and the fact that blue whiting (adult hake's main prey) does not aggregate speak against considering predation hotspots as a main driver of unexplained variance. In addition, as Fig. 4 indicates, the probability of predation for a given prey type approaches zero when prey abundance is zero or very low, which would not be the case if strong prey depletion was occurring in feeding hotspots.

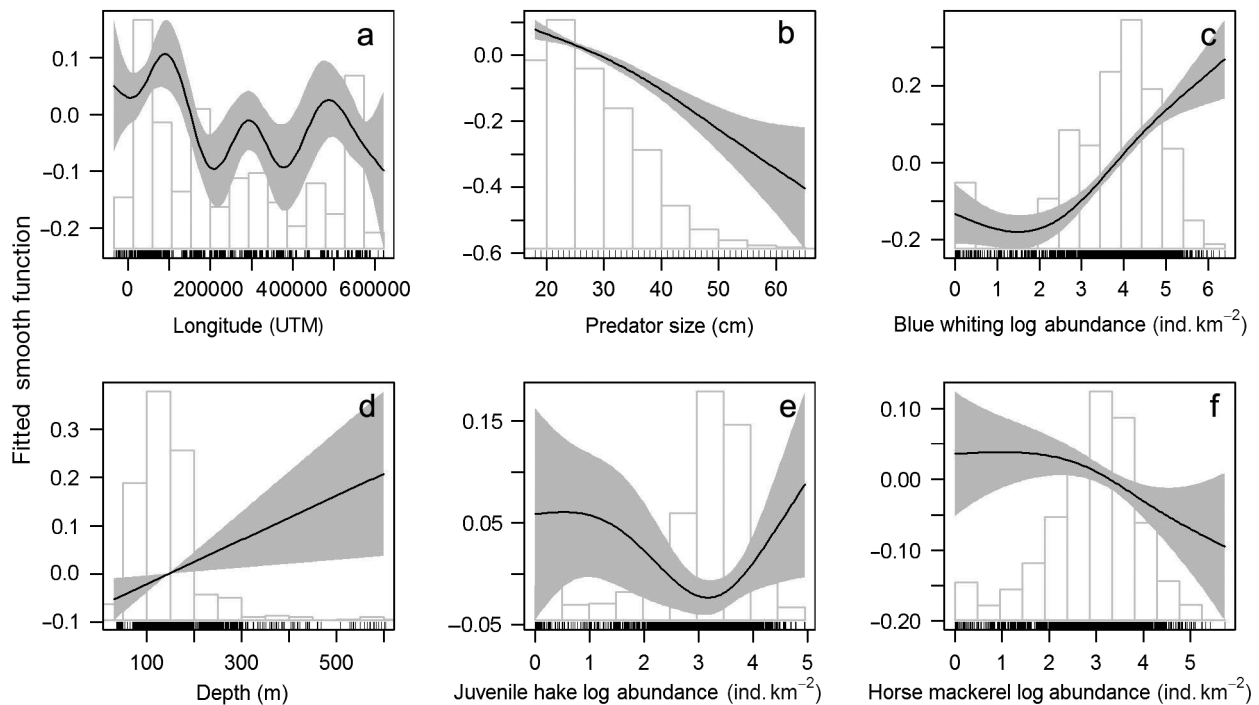


Fig. 3. Cubic spline smoother fits (black solid lines) of the Gaussian generalised additive model based on European hake *Merluccius merluccius* adult stomach fullness as a function of longitude, depth, predator size and the abundance of 3 of its prey species (blue whiting, juvenile hake, and silvery pout). Grey area: 95% confidence limits; grey bars: relative frequency of observations along the x-axis

Large amounts of unexplained variance are common when modelling feeding habits of marine fishes in continental shelf systems (Methratta & Link 2012). The circadian feeding rhythm of piscivorous predators is commonly weakened due to the long digestion times required for large prey (often over 24 h), impairing the identification of daily feeding cycles. Fish have a physiological capacity for feeding at a rate 2 to 3 times higher than they actually do on average (Armstrong & Schindler 2011), which is an evolutionary adaptation to highly heterogeneous foraging opportunities; this may explain the high variability observed in the stomach fullness of hake and why it is difficult to capture in a model.

Our results show that a number of factors influence both the full/empty ratio and the stomach fullness of hake, pointing to the prevalence of depth, longitude, predator size, and blue whiting abundance over other prey in the feeding habits of adult hake. In agreement with Velasco & Olaso (1998), we found a negative trend in the full/empty ratio along a depth gradient (especially over the continental shelf), but a positive effect of depth on stomach fullness, which should be considered with caution given its marginal statistical significance. Our model detected and disentangled the effect of both depth and predator

length on stomach fullness. We noted an unprecedented longitudinal effect, which could be related to the continental shelf width. An exploratory analysis of this post hoc hypothesis provided a significant correlation between continental shelf width between 0 and 200 m and the longitudinal effect on the full/empty ratio (Pearson's correlation = 0.65) as well as on stomach fullness (Pearson's correlation = 0.43). Continental shelf width could be related to the availability of suitable habitat for both predators living on the shelf and their prey resources, but to our knowledge, this is the first time that fish foraging success has been linked to this variable. Our finding suggests that continental shelf width could be a relevant variable affecting the abundance and composition of the demersal species assemblage, especially in southern European seas that are characterised by highly variable shelf widths.

Predator size also significantly affected both full/empty ratio and stomach fullness; we found a decrease in both indices along predator ontogeny. Nevertheless, the long digestion times needed for larger prey and the fact that prey with higher lipid content (such as pelagic fish) are evacuated more slowly (Bromley 1994) might be misleading, and this result must be considered with caution.

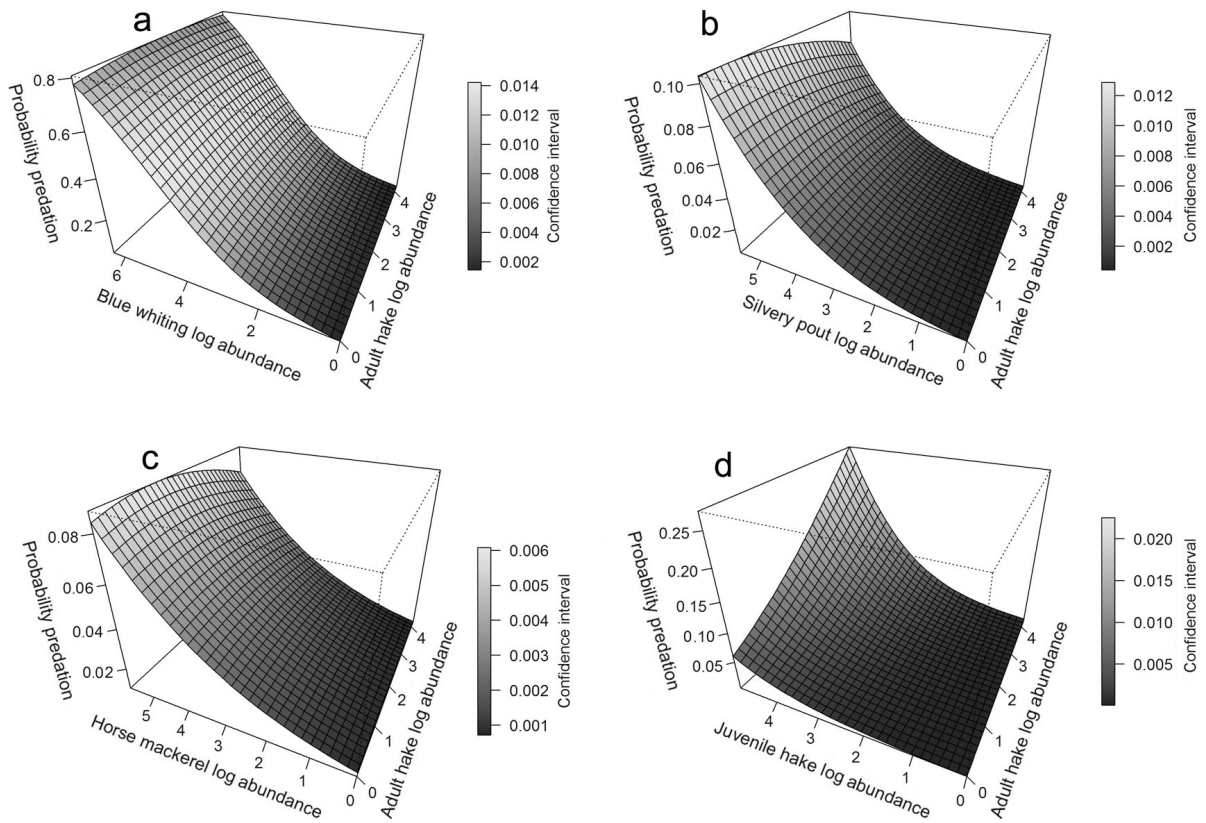


Fig. 4. Probability of European hake *Merluccius merluccius* consuming species from the main demersal prey categories along the predator and prey abundance axes, as estimated by the multinomial model. Grey shading: confidence limits around the estimated probability value

Among the prey species, blue whiting abundance was most affected by adult hake foraging. Since this interaction features the strongest food web link between hake and its prey pool, a positive effect of blue whiting abundance on feeding was certainly expected. However, we found that this positive relationship was triggered by a feeding threshold: a minimum blue whiting abundance of 100 to 1000 ind. km⁻², suggesting a Holling type III response of the predator to its main prey. The existence of prey refuges at low prey abundances has also been observed in other gadoid species (Kempf et al. 2008).

Cannibalism also followed a characteristic pattern; feeding intensity, described by both the full/empty ratio and the stomach fullness index, had a marked negative relationship with juvenile hake abundance from values of 30 to approximately 3000 ind. km⁻², the latter of which corresponds to abundance levels characteristic of nursery areas (Sanchez & Gil 2000). This pattern suggests feeding inhibition of adult hake in the nursery areas manifested both in the full/empty ratio and stomach fullness. Preciado et al. (2015) recently identified several foci of cannibalism in the Cantabrian Sea associated with nursery

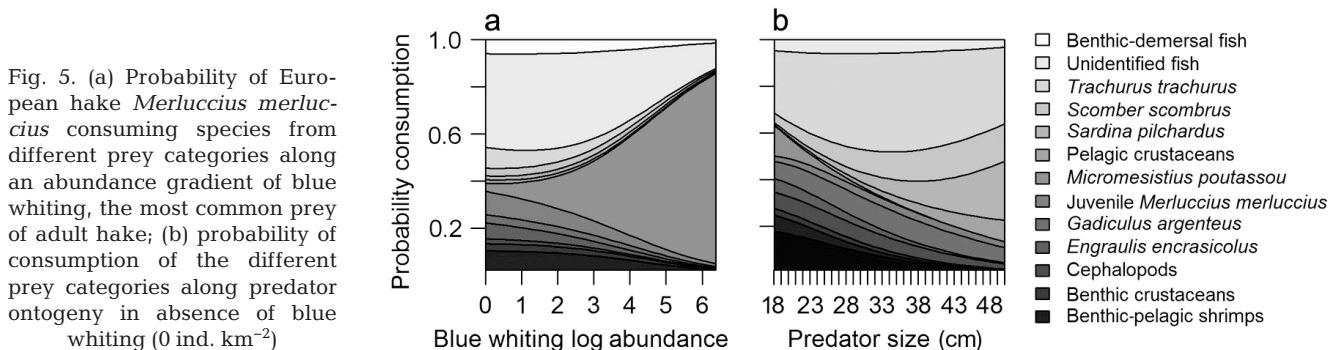


Fig. 5. (a) Probability of European hake *Merluccius merluccius* consuming species from different prey categories along an abundance gradient of blue whiting, the most common prey of adult hake; (b) probability of consumption of the different prey categories along predator ontogeny in absence of blue whiting (0 ind. km⁻²)

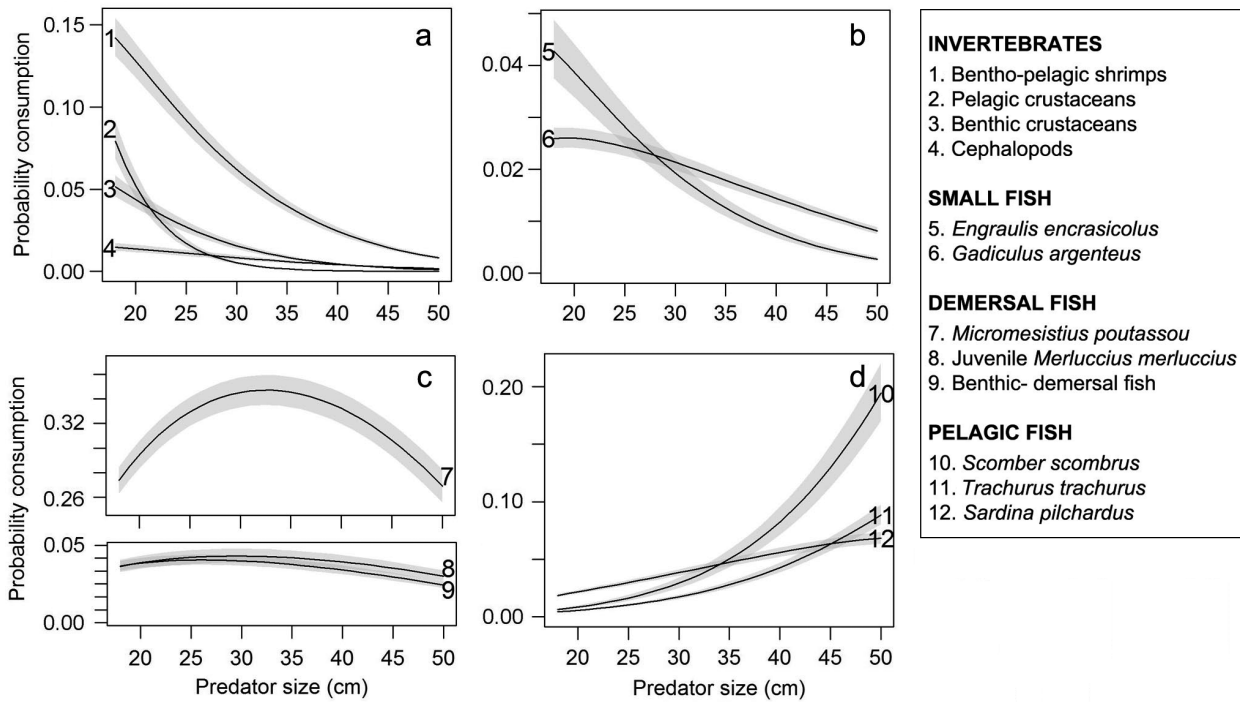


Fig. 6. Probability of European hake *Merluccius merluccius* consuming species from the different prey categories throughout the predator's ontogeny as estimated by the multinomial model. Grey shading: confidence limits around the estimated probability value

areas, notwithstanding the lower full/empty ratio and fullness index we found in these areas. Although the annual recruitment index correlates with cannibalism levels in the area (Preciado et al. 2015), cannibalism is limited to areas where extremely high concentrations of both predator and prey occur as the results of the multinomial model suggest. Cannibalism is a

common feeding behaviour among hake species (Garrison & Link 2000) but it is generally low in European hake; annual values range between 0.11 and 21.33% by volume in the Southern Bay of Biscay (Preciado et al. 2015).

The effect of silvery pout and horse mackerel was restricted to only 1 index; silvery pout had a positive effect on the full/empty ratio while horse mackerel had a negative effect on stomach fullness. A positive effect of prey abundance on the full/empty ratio falls within our expectations; the negative effect of horse mackerel abundance on stomach fullness is unexpected and remains unexplained. The multinomial results show a higher consumption of each of the 4 prey species considered (blue whiting, juvenile hake, silvery pout, and horse mackerel) at larger prey abundances. This analysis also shows that density-dependent effects differed among prey, with cannibalism being the only food web link affected by predator abundance; only at high densities of both juvenile and adult hake did cannibalism show a steep increase. However, the predator density-dependent effect

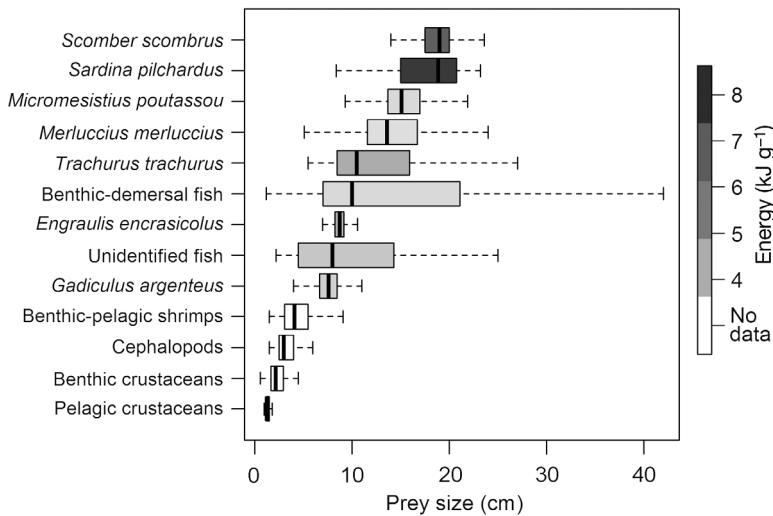


Fig. 7. European hake *Merluccius merluccius* prey size distribution for species in different prey categories. Grey scale: energy content for each prey category based on data from the literature (Spitz et al. 2010)

was generally not relevant; we included hake abundance in the analysis of foraging indices but it was not selected by the model. Cartes et al. (2004) found a higher full/empty ratio and stomach fullness related to hake density in the western Mediterranean. One potential reason why our analysis did not reproduce this result is that we focused on pre-adult and adult hake, which have a sparser distribution than juvenile hake, which commonly aggregate in nursery areas (Sanchez & Gil 2000, Bartolino et al. 2011) and possibly constitutes the bulk of the data analysed by these authors (their sampled individuals ranged between 10 and 69 cm).

Based on results from the multinomial model, we could investigate changes in prey preferences associated with variation in the abundance of blue whiting, the hake's main prey in the area. As blue whiting abundance decreased, a homogeneous increase of all other prey occurred for a given predator size. Thus, the diet diversity of adult hake could compensate for the lack of its main prey. Considering ontogenetic changes in diet in the absence of blue whiting, invertebrates constituted almost half of the diet of early pre-adults, and pelagic fish in the largest individuals. Ontogenetic diet shifts of hake are well described in the literature (Bozzano et al. 1997, Velasco & Olaso 1998, Cartes et al. 2004, Carpentieri et al. 2005, Stagioni et al. 2011, Sinopoli et al. 2012). Our study focused on the piscivorous phase of hake, after the main ontogenetic shift occurred; nevertheless, we found a strong effect of predator size on prey selection. Interestingly, we found that the probability of hake feeding on large demersal fish (i.e. blue whiting) peaked around 30 to 35 cm, which identifies an optimal predator size window in which consumption of these prey generally occur, while predation on small fish (i.e. silvery pout and anchovy) rapidly decreases during ontogeny. On the contrary, the probability of consuming large pelagic fish (i.e. mackerel, horse mackerel, and sardine) increases at larger hake size. This increase of pelagic fish consumption and the decrease in stomach fullness along ontogeny cause a dome-shape relationship in the prey volume of pelagic fish in hake diet, which achieves a maximum in the size range 20 to 29 cm (over 4.5 V%BW consisted of pelagic prey) and decreases thereafter (Preciado et al. 2008).

Diet shifts commonly occur during fish ontogeny, and European hake undergoes 2 well-documented ontogenetic shifts. However, its reflection in the energy budget has not been quantitatively assessed. Demersal fish prey such as silvery pout, juvenile hake or blue whiting have similar energy values

(around 4 to 5 kJ g⁻¹) but generally larger size (Fig. 7) than the invertebrate prey which juvenile hake consume (Spitz et al. 2010) before the first ontogenetic diet shift. Only juvenile anchovy stands out from the fish prey after this first diet shift for its higher energetic value (Fig. 7), but consumption of this species shows strong inter-annual variability due to extreme changes in anchovy recruitment (Lopez-Lopez et al. 2012). The second main shift in hake's diet occurs around 35 cm in our study area (Velasco 2007), which is about the size of first maturity (37.9 cm as estimated by Piñeiro & Sainza 2003). After this shift, consumption of demersal fish decreases and the consumption of larger fish such as mackerel and horse mackerel increases. The increased consumption of larger and highly energetic prey (Fig. 7) matches the energy needs for oocyte development, with energy bursts possibly followed by periods of food depletion, as suggested by the trends of full/empty ratio at large predator size. Indeed, European hake directly utilise the energy surplus from food intake rather than energy reserves for oocyte development during its protracted spawning season (Domínguez-Petit et al. 2010) and the batch spawning interval lasts between 5 and 12 d (Murua & Motos 2006). While adult hake sex ratio is strongly biased towards females in the largest size classes (reviewed by Murua 2010), no significant differences in feeding habits were found among sexes in previous studies (Velasco 2007). Increasing consumption of larger prey is expected during ontogeny in predatory fish (Scharf et al. 2000, Costa 2009), but these ontogenetic changes are commonly related to overcoming physical limitations rather than the onset of new physiological needs. Our results advocate considering reproduction needs as a possible trigger for this later diet shift in adult hake.

Alternation in the use of pelagic and benthic resources (fast and slow food web energy channels respectively) by top demersal predators has been proposed as a mechanism to buffer the effect of environmental variability, potentially acting as a safeguard for ecosystem stability (Rooney & McCann 2012, Woodland & Secor 2013). During its piscivorous phase, however, hake rely mostly on pelagic and demersal prey, the latter comprised mainly of juvenile blue whiting and hake (based on their size distribution; Fig. 7). Since juvenile fish abundance is strongly dependent on environmental variability, these demersal juveniles should be considered within the fast energy channel. Therefore, in the case of adult European hake, reliance on a wide set of prey rather than benthic–pelagic coupling could represent a key adaptation for maintaining population sta-

bility. Nevertheless, the contrasting energy contribution of pelagic and demersal prey and their alteration depending on prey availability could have an effect on adult fecundity that currently remains unexplored. The results of our work constitute a stepping stone for studying the effects of intra-guild predation and diet variability in hake population dynamics.

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