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Ontogenetic and spatial variation in the diet of hake (*Merluccius merluccius*) in the Bay of Biscay and the Celtic Sea

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Abstract:

Analysis of the diet of trawl-caught hake (*Merluccius merluccius*) from three locations in the Bay of Biscay and the Celtic Sea in autumn 2001 showed that small hake fed almost exclusively on crustaceans (mainly euphausiids), but that there was a significant shift towards a fully piscivorous diet in hake >23 cm. A change in fish prey was also size-dependent, because smaller hake (<30 cm) preyed on small pelagic fish (3–12 cm), such as horse mackerel, anchovy, and pilchard, and larger hake on larger demersal prey (12–23 cm), such as blue whiting. There was a significant positive relationship between hake and fish prey length. In terms of fish prey selectivity, hake exhibited particular preference for small pelagic prey (anchovy, pilchard, and argentine) and for other hake. The diet did not generally reflect fish prey availability. Although horse mackerel and blue whiting were the two most abundant fish prey species in the environment, they were not positively selected by hake. Cannibalism accounted for a non-negligible part of the diet and was observed mainly in large hake (>30 cm). For all sizes analysed, conspecifics constituted 19.2%W of the diet and the frequency of occurrence of hake in the stomachs was 10.53%. Most hake prey were 0-group juveniles (<20 cm). Hake cannibalism appeared to be influenced mainly by the abundance of juveniles and the overlap between distribution patterns of juveniles and adults.

Keywords: cannibalism, diet, European hake, northeast Atlantic, prey selectivity, spatial variations

1. Introduction

Fisheries management and stock-assessment science have historically taken a single-stock approach to evaluating and predicting the population dynamics of exploited species. Because fisheries operate within a complex array of species interactions, scientists increasingly recommend multispecies approaches to fisheries management (Botsford *et al.*, 1997). Biological interactions among species can play a dominant role in structuring marine fish communities, and can significantly affect the dynamics of marine fish populations (Rothschild, 1991). Specifically, predation by piscivorous fish has a dramatic influence on population and community level dynamics (Bax, 1998; Juanes *et al.*, 2002). In many fish species, predation and cannibalism have been suggested as a source of mortality that can regulate recruitment and hence population size (Neuenfeldt and Köster, 2000, Wespestad *et al.*, 2000; Tsou and Collie, 2001). Therefore, management may benefit greatly from an increased understanding of the role that biological interactions, such as trophic relationships, play in resource dynamics. In the North Sea, for example, decreasing the fishing mortality on cod (*Gadus morhua*), haddock (*Melanogrammus aeglefinus*), whiting (*Merlangius merlangus*), and saithe (*Pollachius virens*) would have the counter-intuitive result of reducing overall yield because of increased predation (Pope, 1991).

The European hake (*Merluccius merluccius*) is commercially valuable and the subject of targeted fisheries. It is an abundant demersal gadid fish of medium to large size, widely distributed in the northeast Atlantic Ocean and the Mediterranean Sea (Casey and Pereiro, 1995). It is nectobenthic and usually found between 70 and 400 m deep, but is also found as shallow as 30 m and as deep as 1 000 m. It lives close to the seabed bottom by day but moves up into the water column by night. Bozzano *et al.* (2005) showed that feeding was one of the possible regulators of vertical migration of juvenile hake. Hake spawn on the shelf edge, with eggs present throughout the first half of the year in the proximity of the slope from the Bay of Biscay north to west of Ireland (Alvarez *et al.*, 2001). During late summer and early autumn, juvenile hake begin to enter their demersal phase (at lengths of 6–10 cm). The northern Bay of Biscay (the Grande Vasière) and the northwestern Celtic Sea are important nursery grounds of hake (Kacher and Amara, 2005).

Although a comprehensive study on the role of European hake in its ecosystem has not yet been carried out, previous studies of hake diet in European areas (Gonzales *et al.*, 1985; Guichet, 1995; Du Buit, 1996; Velasco and Olaso, 1998; Carpentieri *et al.*, 2005) categorize hake as large piscivorous predators of many commercial species, placing them at the top of the foodweb. As they are an abundant predator, hake predation probably plays an important role in the dynamics of other economically important fish species, as well as of forage species. The ecological position of European hake together with its importance to the fishery makes a study of its diet particularly necessary.

Here, we assess spatial and ontogenetic trends in hake diet in the Bay of Biscay and Celtic Sea. The objective of the study was to increase our knowledge of the diet of European hake and to explore whether the species selects fish prey in accordance with availability in the environment, as indicated by trawl catches. Finally, we describe the incidence of cannibalism and discuss some of its implications on the population dynamics of the species.

2. Material and methods

Sampling

Sampling was carried out in the Bay of Biscay and the Celtic Sea in autumn 2001 with the RV “Thalassa” during the EVHOE survey (Figure 1). During each cruise, a grid of 150 stations distributed according to a random design located between 30 and 200 m deep, was occupied. Fish were caught with a GOV 36/47 bottom trawl (net length 36 m, with a codend liner of 20 mm mesh) during daylight, from 06:30 to 18:30. Trawls lasted 30 min (time on the seabed), and the towing speed was 4 knots. All hake caught were counted, sexed, weighed, and measured on board (see Kacher and Amara, 2005). In addition, other fish species were identified and counted on board for comparison of prey abundance with hake diet. The study area was divided into three geographic sectors: the Celtic Sea (ICES division VIIIh, j and g), the northern part of the Bay of Biscay (VIIIa), and the southern part of the Bay of Biscay (VIIIb) (Figure 1).

Stomach content analysis

Immediately after being brought aboard, stomachs were examined and only non-empty stomachs were preserved in 10% formalin following dissection from the fish. Empty stomachs and those with partially regurgitated contents (i.e. hake with everted stomachs or with partially digested food in the mouth) were excluded. The stomachs were dissected later in the laboratory and, using identification keys (Tattershall and Tattershall, 1951, Mauchline, 1984), items were identified and sorted to the lowest possible taxonomic group, weighed, and measured when possible. When the state of digestion did not permit identification of the prey directly, the otolith and the vertebrae of fish or the chelae of decapod crustaceans were frequently used to identify and estimate the length of the prey organisms. Relationships between fish prey otolith size and fish size or weight were established.

The contribution of each prey category to the diet of hake was examined through frequency of occurrence (%O), and by percentage composition by number (%N) and weight (%W) of each prey. Each of these three measurements provides a different insight into the feeding habits of fish (Hyslop, 1980). To integrate the three parameters, an index of relative importance (IRI; Pinkas *et al.*, 1971, modified by Hacunda, 1981) was used, where $IRI_i = (\%N_i + \%W_i) \times \%O_i$, where i is a specific prey.

Food niche width (B), which characterizes the food resource spectrum used by a fish species, was calculated following Piélou (1969), using the antilogarithm of the Shannon–Wiener index of diversity:

$$B = e^{H'}, \quad H' = -\sum_{i=1}^S p_i \log_2 p_i,$$

where p_i is the proportion by number represented by each prey category i .

Hake were divided into three age classes (Kacher and Amara, 2005): age group 0 (0–17 cm), group 1 (18–31 cm), and group 2+ (>32 cm). Diet composition and the percentage of empty stomachs were compared between age classes and geographical area (Celtic Sea (CS); northern Bay of Biscay (NBB), and southern Bay of Biscay (SSB)). The computer program SYSTAT version 10 was used to carry out the statistical analyses. The percentage of empty stomachs relative to hake age groups and sampling areas was tested using a χ^2 non-parametric test with a level of significance of 0.05.

Feeding selectivity was determined from the relative abundance of the main fish prey in hake stomachs and their relative abundance in the GOV bottom trawl. Chesson's selectivity index (α_i ; Chesson, 1978) was used to compare hake selectivity by age group and geographical area.

$$\alpha_i = \frac{r_i/p_i}{\sum_{i=1}^m r_i/p_i}, \quad i = 1, \dots, m$$

where α_i is the selectivity for prey type i , r_i the relative abundance of prey type i in hake stomachs, p_i the relative abundance of prey type i in the environment, and m is the number of prey types available. α_i was calculated for six ($m = 7$) fish prey species (horse mackerel [*Trachurus trachurus*], blue whiting [*Micromesistius poutassou*], anchovy [*Engraulis encrasicolus*], pilchard [*Sardina pilchardus*], argentine [*Gadiculus argenteus*], and pout [*Trisopterus* sp.]), as well as for hake. Random feeding occurs when $\alpha_i = m^{-1}$; in our study, values of $\alpha_i > 0.14$ or $\alpha_i < 0.14$ were taken to represent selection and avoidance of prey, respectively.

Cannibalism was inferred from the percentage contribution of hake to the total stomach content weight and by the frequency of occurrence of hake in non-empty stomachs. Hake prey species were aged using a relationship between otolith size and hake size (Kacher, 2004).

3. Results

Diet composition

In all, 1995 stomachs of hake measuring between 7 and 53 cm total length (mean length \pm s.d. = 18.73 \pm 8.52 cm) were examined. Of these, just 405 stomachs were not empty or without evidence of regurgitation. Empty hake stomachs represented 79.6% of the total, and there was no difference between the three geographical sectors investigated ($p > 0.05$). Fish and crustaceans were the major prey components identified (Table 1). In all, 35 prey taxa were identified in the stomachs of hake: 14 fish, 20 crustaceans, and 1 mollusc. Fish were the most important prey, accounting for 89.5% by weight of the total prey items consumed and found in 65.4% of the hake examined. Fish taken as prey were generally actively swimming fish such as horse mackerel, anchovy, pilchard, and blue whiting. Two fish species were particularly well represented in the diet: horse mackerel (44.8%W) and small hake (cannibalism) (19.20%W). Crustaceans showed the broadest species diversity, with euphausiids as the main prey, constituting 71.4% by number of the prey taken, though just 10.5% by weight.

Ontogenetic changes in diet

The composition of the diet changed with increasing predator size (Figure 2). Crustaceans, mainly represented by euphausiids (*Euphausia krohni*, IRI = 55.5%) dominated the diet of 0-group hake (TL <20 cm). A piscivorous diet commences at ~11 cm TL, but becomes significant only in hake >20 cm TL. The fish prey of 0-group hake are small pelagic fish such as horse mackerel (IRI = 15.6%) of length 3.5–9.5 cm (Figure 3, Table 1), and other small species such as argentines and gobies. As hake grow, fish become more prevalent in their diet. Blue whiting, horse mackerel, anchovy, pilchard, and small hake (cannibalism) are particularly important prey for hake. Hake between 21 and 31 cm TL (1-group hake) feed mainly on small pelagic fish (3–12 cm) such as horse mackerel (IRI = 46.3%) and sardine or anchovy (Figure 3). The importance of fish increases in further in hake > 32cm TL (Group 2+), where they account for almost the total diet (IRI = 99.3%). In that group, that is a shift towards larger demersal prey (>12 cm) such as blue whiting and hake (cannibalism), and a simultaneous decline in consumption of horse mackerel.

Both prey diversity (H) and niche breadth (B) decrease during ontogenesis (Table 2), indicating a tendency for less generalized feeding as hake grow. The number of prey taxa identified in 0-group, 1-group and 2+ group were 28, 22, and 9, respectively.

Relationship between prey size and predator size

Figure 3 shows the length distribution of the main fish prey in hake stomachs. The size of the fish prey ranged from 3 to 24 cm TL, most (76%) falling between 5 and 11 cm. The smallest were essentially horse mackerel of mean size 7.33 cm, followed by anchovy of mean length 8.6 cm. The largest fish prey were hake and blue whiting, with mean lengths of 12.8 and 15 cm, respectively. Although the prey <11 cm consumed by hake were mainly horse mackerel and anchovy, blue whiting and hake dominated prey items >11 cm. For the three study areas, there were significant positive relationships between hake predator length and the length of the main fish preyed upon. When the data of the three areas are combined the correlation was very significant ($n = 194$; $r^2 = 0.55$; $p < 0.01$) (Figure 4). Hake tended to eat fish that were about half their size. 0-group juveniles ate fish <10 cm and larger hake consumed large fish. The range of fish prey sizes eaten expanded with increasing size of hake. For all hake sizes examined, other hake taken as prey were generally larger than other fish prey, although there were also differences between areas (Figure 4). In the Celtic Sea, hake ate larger fish than in the other two areas.

Spatial variation and prey selectivity

Table 1 shows the importance of the main prey of hake in the three geographical areas studied. In the Celtic Sea (CS) and northern Bay of Biscay (NBB), horse mackerel (51.4 and 28.3%W, respectively) and small hake were the main fish prey. Blue whiting and clupeids were of moderate importance in those two areas, but in the southern Bay of Biscay (SBB) they were the most important species (blue whiting,

28.9%W, clupeids, 23.3%W). Prey diversity also showed spatial variation. In hake of all size, fish prey species were more varied in the NBB (12 fish species) than in the CS or SBB (8 and 7, respectively).

A more detailed study by age group indicated marked differences in the feeding of hake in the three areas (Figure 5). Whatever the area, crustaceans were the main food of 0-group hake and comprised >50% of the diet (%IRI: 65.4, 90, and 51.5 in SBB, NBB, and CS, respectively). The proportion of teleosts in the diet of 0-group hake was higher in the Celtic Sea than in either area of the Bay of Biscay. Horse mackerel (IRI = 40%, 54.8%W) represented a large part of the diet of 0-group hake in the Celtic Sea. The importance of this species in the diet of hake in the Celtic Sea was also observed for 1-group hake (IRI = 88%, 53.8%W). In the southern Bay of Biscay, blue whiting, horse mackerel, and anchovy were important prey of 1-group hake, whereas in the northern Bay of Biscay, 1-group hake were characterized by a high occurrence of euphausiids (IRI= 51%). For hake >32 cm TL, blue whiting (IRI = 58.6%) dominated the diet in the southern Bay of Biscay, whereas small hake (cannibalism) dominated the diet in the northern Bay of Biscay and the Celtic Sea (IRI= 83.5% and 92.9%, respectively).

According to Chesson's selectivity index, hake exhibited some preference for conspecifics and small pelagic fish (anchovy, pilchard, and argentine) (Table 3). Although horse mackerel and blue whiting were apparently the two most abundant fish species in the areas analysed (Table 4), they were not positively selected by hake. The geographic differences in fish prey species in the hake stomachs did not generally correspond to the abundance of the prey in the three areas (Table 4). For example, the high abundance of horse mackerel in the southern and northern Bay of Biscay (respectively, 84.19% and 45.43% of the abundance of the main fish prey in these areas) was not reflected in hake diet. In the southern Bay of Biscay, hake consumed more blue whiting and clupeids, whereas in the northern Bay of Biscay, euphausiids dominated the diet of 0- and 1-group hake.

Cannibalism

Cannibalism of hake accounted for a non-negligible part of the diet. It was observed mainly in large hake (>30 cm), being rare in smaller hake (<20 cm). For all hake sizes analysed, conspecifics constituted 19.2%W of the diet, and the frequency of occurrence of hake in stomach was 10.53%O. Most hake prey were 0-group juveniles (TL <20 cm), and there were differences in predation patterns on hake between areas (Table 1, Figure 5). Cannibalism was important in the northern Bay of Biscay and the Celtic Sea, but rare in the southern Bay of Biscay. For hake >20 cm TL, the frequency of occurrence of hake in stomachs was 26.25% and 32.26% in the northern Bay of Biscay and the Celtic Sea, respectively, reaching highest values in hake >32 cm (51.8 and 66.7%O). In those two areas, conspecifics accounted for most of the diet of group 2+ hake (83.54 and 92.89%IRI, respectively, in the northern Bay of Biscay and the Celtic Sea). There was a significant positive relationship between hake predator length and the length of the hake prey (Figure 6).

4. Discussion

Hake are top predators that occupy different trophic levels during development. Ontogenetic diet shifts are typical of hake species (Velasco and Olaso, 1998; Garrison and Link, 2000). This study has shown that during the first year of life, hake feed almost exclusively on crustaceans (mainly euphausiids), but that there is a significant shift towards a fully piscivorous diet in hake >23 cm TL. Change in feeding behaviour during ontogeny, with fish becoming more prevalent in the diet, is common in non-specialist fish, and is an advantage because fish contain a greater energy content than crustaceans (Juanes *et al.*, 2002). Such an ontogenetic shift from crustaceans to fish probably occurs because crustaceans are more difficult to handle and ingest than fish, resulting in less capture success, longer handling times, and, as a consequence, lower profitability (Juanes *et al.*, 2001). The increase in visual acuity (Mas-Riera, 1991) and hearing (Lombarte and Popper, 1994) with *M. merluccius* growth is an advantage that allows the predator to detect mobile prey such as fish at greater distance. However, ontogenetic development, particularly an increase in mouth size and mobility, also influences shifts in diet.

Both prey diversity (H') and niche breadth (B) decrease during ontogenesis, indicating a tendency towards less generalized feeding as hake grow. According to Alheit and Pitcher (1995), hake species worldwide typically feed on fast-moving pelagic prey which they ambush in the water column, despite their primarily demersal daytime life, and this was confirmed in this study of European hake, in which the fish prey were

mainly actively swimming species such as horse mackerel, anchovy, pilchard, and blue whiting. There is evidence already that juvenile European hake move into midwater at night to feed in response to similar migrations of their prey (Bozzano *et al.*, 2005). Two fish species particularly well represented in hake diet were horse mackerel (44.8%W), dominant prey of smaller hake, and other hake (19.20%W), the main prey of larger hake. Comparing the results of the present diet study with those of other studies, there are some differences. According to Guichet (1995), hake in the Bay of Biscay feed mainly on horse mackerel, and there is little cannibalism, and according to Du Buit (1996) and Velasco and Olaso (1998), hake >20 cm in the Celtic Sea and the Cantabrian Sea feed primarily on blue whiting and horse mackerel. Further, Carpentieri *et al.* (2005) recorded the main prey of hake 16–36 cm TL in the Mediterranean Sea to be anchovy and pilchard. Although European hake have always been considered opportunistic, generalist feeders (Guichet, 1995; Velasco and Olaso, 1998), our results suggest that some prey may be preferred to other. According to Chesson's selectivity index, the hake we analysed exhibited some preference for feeding on small pelagic fish (anchovy, pilchard, and argentine) and a marked preference for small hake. In their study on the closely related shallow-water Cape hake off Namibia (*M. capensis*), Macpherson and Gordo (1994) found that cannibalism is neither related to the density of small conspecifics nor to the density of alternative prey, but is more a consequence of large hake having a dietary preference for small hake. Although horse mackerel and blue whiting were the two most abundant fish prey species in the environment we studied here, they were not positively selected by hake.

Many factors can influence the size and the type of prey chosen by a predator (Juanes *et al.*, 2002). These include the effort required to find, pursue, and handle prey, the morphology or visual acuity of the predator, and the behaviour and habitat use of the prey (which in turn affect the encounter rate) (Pinnegar *et al.*, 2003). Clupeiform prey such as anchovy display short reaction distances, allowing predators to approach closely before attempting an escape response (Scharf *et al.*, 2003). In balancing the cost and the benefits, predators foraging optimally can adjust their preferences to take into account prey quality (Juanes *et al.*, 2002). Interestingly, smaller pelagic species (e.g. anchovy and pilchard), tend to be more lipid-rich than larger pelagic species (e.g. horse mackerel) or gadoids (e.g. pout and blue whiting) (Van Pelt *et al.*, 1997). The consequence of this would be that hake would exhibit greater preference for small pelagics, as suggested by Pinnegar *et al.* (2003).

Hake appear to show feeding plasticity between areas as described for other hake species (Payne *et al.*, 1987; Roel and Mcpherson, 1988). These authors showed that the relative importance of each item in the diet of Cape hake (*Merluccius paradoxus* and *M. capensis*) of the South African west coast, varies both geographically and seasonally according to availability of the prey, thus illustrating the opportunistic nature of hake feeding. Differences in hake diet were observed between the three geographic sectors studied. Geographic differences in the fish prey of hake do not generally reflect their abundance in the three areas we studied. In the southern Bay of Biscay (SBB), despite horse mackerel being abundant, scarcer and larger blue whiting were preferred. Carrera *et al.* (2001) showed that blue whiting distribution tends to be related to the position of the shelf-break, so the importance of blue whiting as food to hake may be explained by the abrupt bathymetry of the SBB continental shelf, on which hake might be distributed at greater depth than in the north. Thus, as suggested by Velasco and Olaso (1998) for hake in the Cantabrian Sea, the coincidence of hake habitat with that of species favouring shallower water (e.g. horse mackerel) would be less, and predation on such species would be less too, therefore favouring predation on blue whiting.

Many studies have demonstrated that fish have an optimal prey size, which is selected if the predator is given a choice (Hart and Connellan, 1984). Clearly, size is an important determinant of fish diet, and many authors (e.g. Scharf *et al.*, 2000) have attempted to relate the physical attributes of a predator (e.g. gape size and length) with that of the prey in its stomach. We confirm the positive relationship between European hake and fish prey length suggested already by, among others, Gonzalez *et al.* (1985) and Velasco and Olaso (1998). As in other piscivorous species (Juanes, 2003), hake of like size prey on conspecifics that are generally larger than the other fish they prey upon. Therefore, the increased dominance of blue whiting and hake in the diet of the largest hake is concluded to be due to the species' preference for larger prey than alternative prey that may be equally or more available.

Cannibalism is a widespread phenomenon that can have strong population and community effects (Elgar and Crespi, 1992). It is common among piscivorous marine fish and can make a significant contribution to the diet (Smith and Reay, 1991). For example, conspecifics can contribute up to 40% of the diet of silver hake (*M. bilinearis*), >70% of the diet of Cape hake (*M. capensis*) off Namibia (Macpherson and Gordo, 1994), and >50% of the diet of Chilean hake (*M. gayi*; Stobberup, 1992). In the present study, hake positively selected other hake. The cost and the benefits of cannibalism have been debated already

(Juanes, 2003). One potential benefit of cannibalism may be an increased availability and perhaps encounter rate with relatively large prey that otherwise might be fairly scarce. Smith and Reay (1991) suggested that the likelihood of cannibalism is enhanced by factors such as low food availability, high density, size disparity, and lack of refuge. Most gadoids are demersal and live in large aggregations which, if composed of different ages and size classes, could make smaller hake readily accessible and/or available (Juanes, 2003).

The cannibalistic habit of hake generally has often been reported in the literature, but in the North Atlantic and Mediterranean, the phenomenon is of less importance in some areas (Du Buit, 1996; Bozzano *et al.*, 1997; Velasco and Olaso, 1998; Cabral and Murtat, 2002). However, high levels of cannibalism have been reported in areas with a broad continental shelf, where hake of different lengths probably coexist (Hickling, 1927; Carpentieri *et al.*, 2005). This does not happen on steep continental shelves such as that off Portugal or the Cantabrian Sea, where different length groups of hake tend to live at different depths. In our study, cannibalism accounted for a non-negligible part of European hake diet and was observed mainly in large hake (>30 cm). Most hake prey were 0-group juveniles (TL <20 cm).

In certain cases, a high incidence of spatial overlap of hake and their progeny may lead to *de facto* selection of the small hake as prey (Garrison and Link, 2000). The northern Bay of Biscay (the Grande Vasière) and the northwestern Celtic Sea are important nursery grounds of hake (Kacher and Amara, 2005). On the basis of hake distribution, overlapping distributions of large and small fish (a requirement for cannibalism to take place) would be most likely in the northern Bay of Biscay (NBB) and Celtic Sea (CS). Indeed, cannibalism was much more prevalent in those two areas, which are characterized by a broad continental shelf. On the contrary, cannibalism was low in the SBB probably because of both low spatial overlap between juveniles and adults and the scarcity of juveniles (Kacher and Amara, 2005). The latter authors showed that 0-group hake are mainly found between 70 and 200 m deep, with peak density at 100 m.

Because they are numerically dominant in their ecosystems and consume a high proportion of fish prey, hake generally occupy an important position in the trophodynamics of continental shelf fish-communities, and they can compete with fisheries for exploitable biomass (Du Buit, 1996; Garrison and Link, 2000). Hake cannibalism in the Bay of Biscay and Celtic Sea appears to be controlled mainly by the abundance of juveniles and by the overlap between the distributions of juveniles and adults. As abundant predators of commercially exploited juvenile fish and pelagic species, the dynamics of hake on the dynamics of some currently overexploited stocks currently targeted for recovery are closely linked. As fishing pressure is reduced in an effort to rebuild European hake stocks (recovery plan, EC 811/2004), it is important to evaluate even more precisely the role of hake predation on the population dynamics of exploited species, particularly through the impacts on juvenile survivorship and recruitment success, as suggested for other species of hake (Garrison and Link, 2000; Jurado-Molina *et al.*, 2006).

Acknowledgements

We thank our IFREMER colleagues in Lorient (R. Bellail and J. C. Mahe) for their contribution to sampling and for making available the data on fish abundance, and Ana Gordo and an anonymous reviewer for their helpful remarks on an early draft of this paper.

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Figures

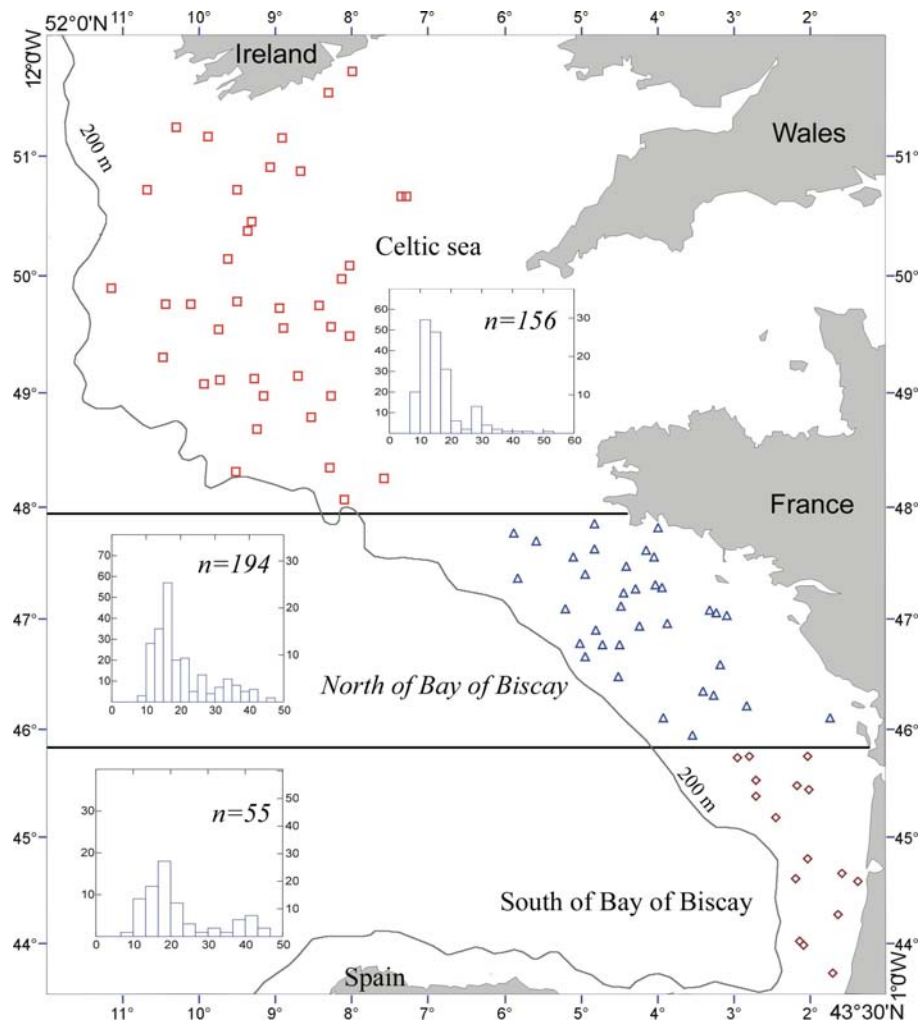


Fig. 1

Figure 1. Map of the study area showing the location of the sampling stations within the three study areas: Celtic Sea, northern Bay of Biscay, and southern Bay of Biscay. For each area, the number and the length frequency distribution of hake analysed for stomach contents is shown. The horizontal lines indicate the geographical limit of each area.

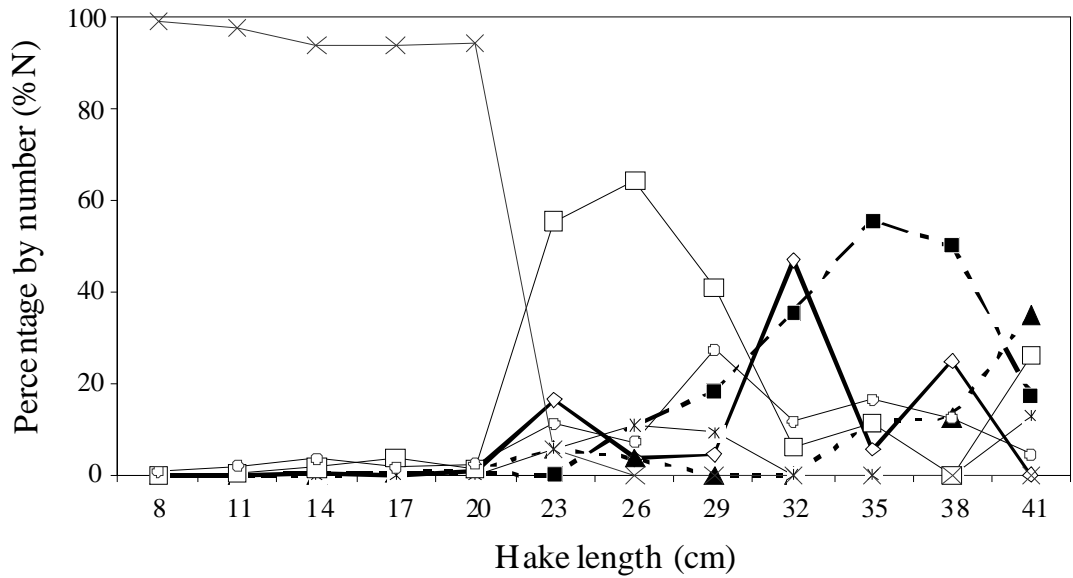


Fig. 2

Figure 2. Ontogenetic change in diet, expressed as percentage composition by number (%N) of major prey items in the diet of hake by 3-cm size class: crosses and thin line, crustaceans; diamonds and thick line, anchovy; stars and thin line, pilchard; filled squares and dot-dash thick line, hake; open squares and thin line, horse mackerel; filled triangles and dotted thick line, blue whiting; open circles and thin line, other fish.

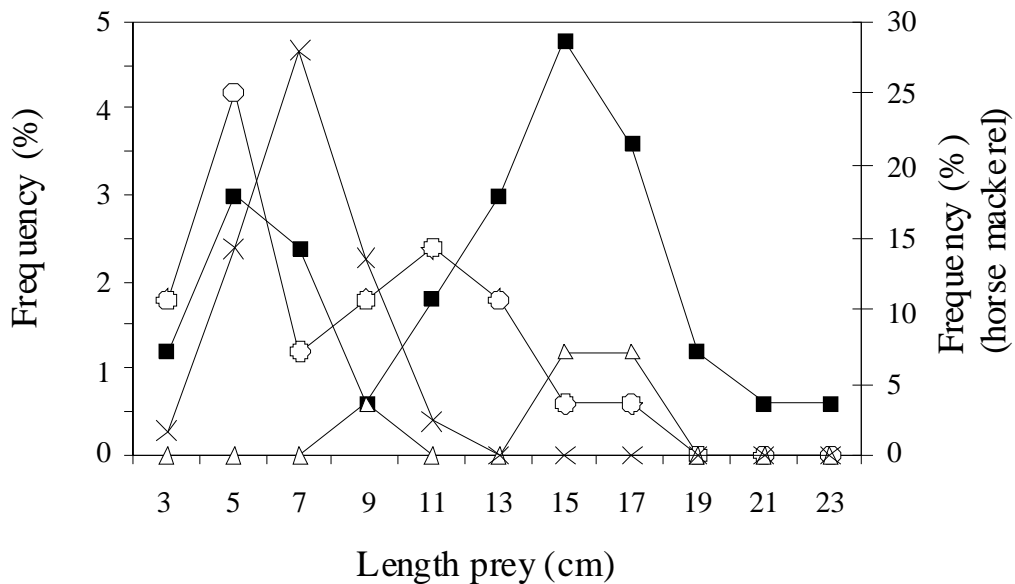


Fig. 3

Figure 3. Size frequency distribution of the major fish prey found in hake stomachs: circles, anchovy; filled squares, hake; triangles, blue whiting; crosses, horse mackerel.

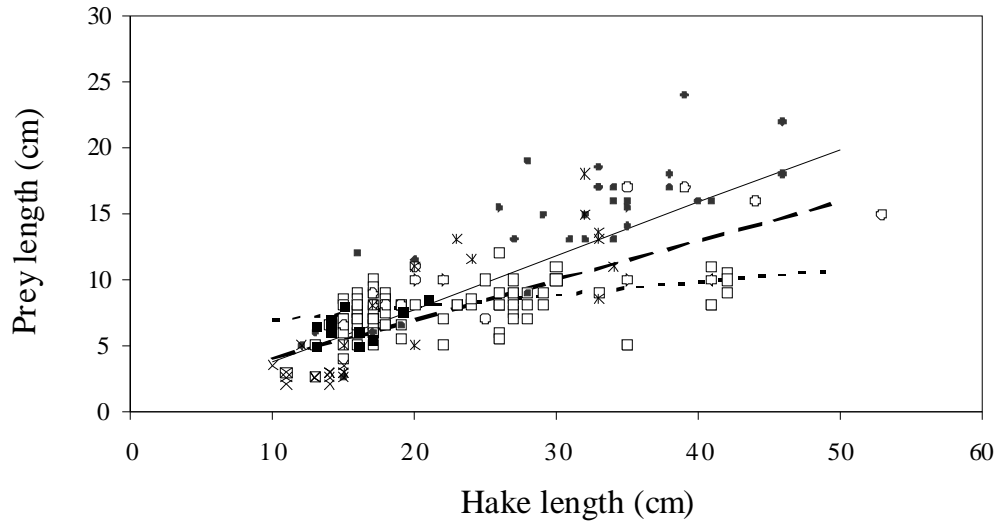


Fig. 4

Figure 4. Relationship between the length of major fish prey taxa and hake predator length by geographical area. For the Celtic Sea (thin line), $y = 0.40x - 0.34$ ($r^2 = 0.57$, $n = 89$); for the northern Bay of Biscay (long-dashed line), $y = 0.29x + 1.02$ ($r^2 = 0.43$, $n = 99$); and for the southern Bay of Biscay (short-dashed line), $y = 0.097x + 5.91$ ($r^2 = 0.03$, $n = 6$). When all data are combined, $y = 0.34x + 0.89$ ($r^2 = 0.55$, $n = 194$, $p < 0.001$). Open squares, horse mackerel; filled circles, hake; open circles, blue whiting; crosses, gobies; stars, anchovy; filled squares, argentine.

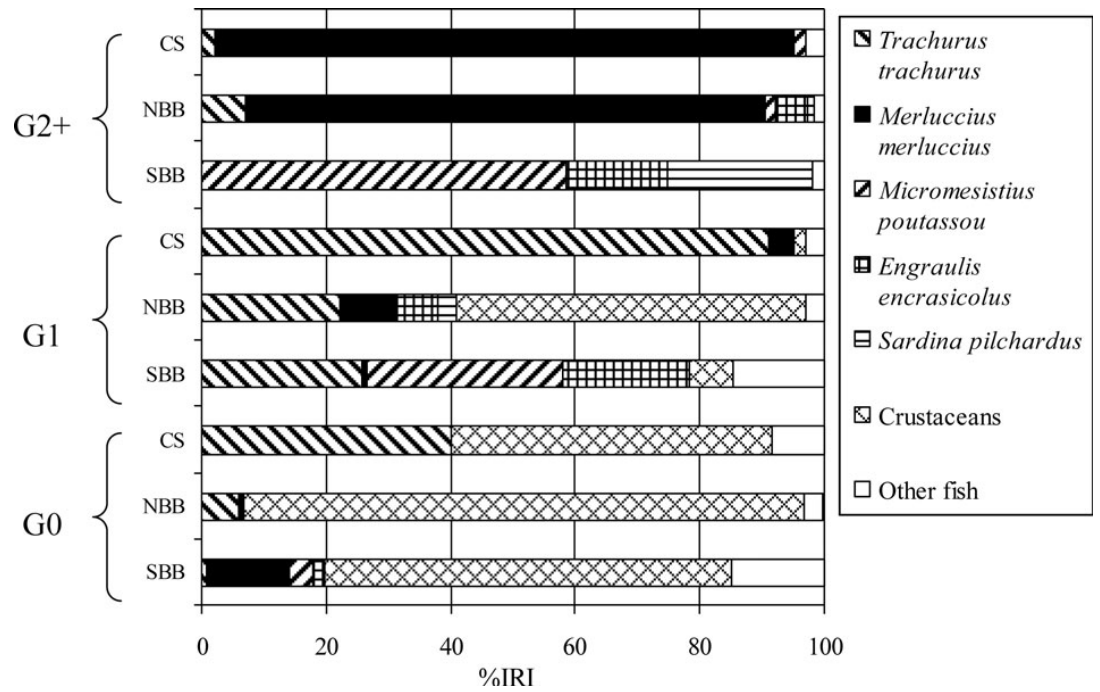


Fig. 5

Figure 5. Composition of the diet (major prey taxa) of hake (%IRI) by age group and area (CS, Celtic Sea; NBB, northern Bay of Biscay; SBB, southern Bay of Biscay)

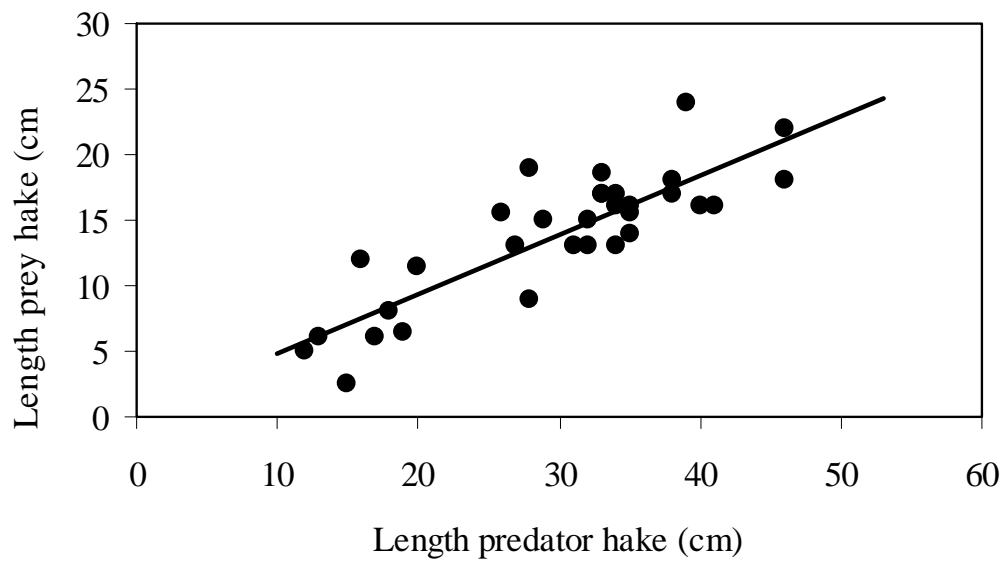


Fig. 6

Figure 6. Relationship between the length of hake as prey and length of hake as predator: $y = 0.45x + 0.39$; $n = 32$; $r^2 = 0.71$; $p = 0.006$.

Tables

Table 1. Percentage number (%N) and percentage weight (%W) of prey taxa in European hake diet by age group of hake (G0, G1, and G2+, see text) and geographical area.

Prey	%N									%W								
	Celtic Sea			Northern Bay of Biscay			Southern Bay of Biscay			Celtic Sea			Northern Bay of Biscay			Southern Bay of Biscay		
	G0	G1	G2+	G0	G1	G2+	G0	G1	G2+	G0	G1	G2+	G0	G1	G2+	G0	G1	G2+
	(101)	(46)	(9)	(90)	(77)	(27)	(17)	(28)	(10)	101	46	9	90	77	27	17	28	10
Fish	11.7	81.0	100	2.3	7.4	97.1	7.5	41.7	100	80.6	97.3	100	59.5	98.4	99.9	88.6	99.1	100
<i>Trachurus trachurus</i>	5.6	55.6	18.2	0.4	2.7	20.6	0.6	8.3	-	54.8	53.8	1.2	35.1	27.7	7.8	3.5	27.8	-
<i>Gadiculus argenteus</i>	0.2	3.2	-	-	-	-	-	-	-	0.6	3.5	-	-	-	-	-	-	-
<i>Merlangius merlangus</i>	-	-	-	-	0.2	2.9	-	-	-	-	-	-	-	9.6	4.5	-	-	-
<i>Merluccius merluccius</i>	0.5	6.4	54.6	0.2	1.0	44.1	0.6	1.4	-	1.5	29.1	82.5	9.5	20.0	51.6	56.6	6.6	-
<i>Micromesistius poutassou</i>	-	-	9.1	-	0.6	5.9	0.6	8.3	57.1	-	-	7.2	-	2.6	6.5	16.8	35.9	30.2
<i>Trisopterus</i> sp.	0.2	4.8	18.2	-	0.7	2.9	-	1.4	7.1	0.2	7.9	9.0	-	4.1	0.7	-	3.7	3.8
<i>Alosa alosa</i>	-	-	-	-	0.2	-	-	-	-	-	-	-	-	3.2	-	-	-	-
<i>Engraulis encrasicolus</i>	0.2	-	-	-	0.8	11.8	0.6	11.1	21.4	1.3	-	-	-	18.0	9.0	7.3	17.4	11.0
<i>Sardina pilchardus</i>	-	-	-	-	0.6	2.9	-	-	14.3	-	-	-	-	11.1	12.7	-	-	55.0
<i>Argentina</i> sp.	2.7	6.4	-	-	-	2.9	-	-	-	19.5	2.6	-	-	-	2.1	-	-	-
<i>Arnoglossus imperialis</i>	-	-	-	-	-	-	-	1.4	-	-	-	-	-	-	-	-	0.9	-
<i>Atherina presbyter</i>	-	-	-	0.1	-	-	-	-	-	-	-	-	2.6	-	-	-	-	-
<i>Callionymus reticulatus</i>	-	-	-	-	0.1	-	-	-	-	-	-	-	-	0.1	-	-	-	-
<i>Pomatochistus</i> sp.	1.2	-	-	0.7	-	-	-	-	-	1.1	-	-	5.7	-	-	-	-	-
Unidentified fish	1.0	4.8	-	0.8	0.6	2.9	5.0	9.7	-	1.7	0.5	-	6.6	2.2	5.2	4.3	6.8	-
Crustaceans	88.3	19.0	0.0	97.6	92.5	2.9	92.5	58.3	0.0	19.4	2.7	0.0	36.4	1.5	0.2	11.5	0.9	0.0
<i>Alpheus glaber</i>	0.2	-	-	-	-	-	-	-	-	1.1	-	-	-	-	-	-	-	-
<i>Crangon allmanni</i>	5.1	11.1	-	-	-	-	-	-	-	4.4	2.5	-	-	-	-	-	-	-
<i>Eualus gaimardii</i>	-	-	-	-	-	-	1.9	-	-	-	-	-	-	-	-	0.5	-	-
<i>Eualus</i> sp.	0.5	-	-	-	-	-	1.9	-	-	0.2	-	-	-	-	-	1.1	-	-
Palaemonidae	-	-	-	-	-	-	-	1.4	-	-	-	-	-	-	-	-	0.7	-
<i>Pandalus montagui</i>	-	-	-	0.1	-	-	-	-	-	-	-	-	0.4	-	-	-	-	-
<i>Processa canaliculata</i>	6.1	3.2	-	0.1	-	2.9	-	-	-	9.0	0.2	-	2.8	-	0.2	-	-	-
<i>Euphausia krohni</i>	67.1	-	-	90.2	91.6	-	83.8	55.6	-	1.6	-	-	16.0	1.3	-	6.0	0.3	-
Euphausiidae	0.2	-	-	-	-	-	1.3	-	-	0.0	-	-	-	-	-	1.3	-	-
<i>Meganctyphanes norvegica</i>	2.0	-	-	-	-	-	1.9	-	-	0.6	-	-	-	-	-	1.8	-	-
<i>Thysanopoda</i> sp.	0.5	1.6	-	0.1	-	-	-	-	-	0.2	0.0	-	0.1	-	-	-	-	-
<i>Lophogaster typicus</i>	5.1	-	-	6.2	0.3	-	0.6	-	-	2.4	-	-	15.7	0.0	-	0.7	-	-
<i>Gastrosaccus sanctus</i>	0.2	3.2	-	-	-	-	-	-	-	0.0	0.0	-	-	-	-	-	-	-
<i>Gastrosaccus spinifer</i>	-	-	-	-	0.2	-	-	-	-	-	-	-	-	-	-	-	-	-
<i>Leptomysis lingvura</i>	-	-	-	0.4	-	-	-	-	-	-	-	-	0.0	-	-	-	-	-
<i>Schistomysis ornata</i>	-	-	-	0.2	-	-	-	-	-	-	-	-	0.1	-	-	-	-	-
Mysidae	-	-	-	-	0.1	-	-	-	-	-	-	-	-	0.0	-	-	-	-
<i>Hyperia galba</i>	0.2	-	-	-	-	-	-	-	-	0.0	-	-	-	-	-	-	-	-
Amphipoda	0.5	-	-	-	-	-	-	1.4	-	0.0	-	-	-	-	-	-	0.0	-
Copepoda	0.2	-	-	-	-	-	-	-	-	0.0	-	-	-	-	-	-	-	-
Unidentified crustaceans	0.2	-	-	0.3	0.4	-	1.3	-	-	0.0	-	-	1.3	0.2	-	0.0	-	-

Molluscs	0.0	0.0	0.0	0.2	0.1	0.0	0.0	0.0	0.0	0.0	0.0	0.0	4.3	0.1	0.0	0.0	0.0	0.0
<i>Sepiolo atlantica</i>	-	-	-	0.1	-	-	-	-	-	-	-	-	4.1	-	-	-	-	-
Unidentified molluscs	-	-	-	0.1	0.1	-	-	-	-	-	-	-	0.2	0.1	-	-	-	-

The numbers of hake analysed are shown in parentheses.

Table 2. Shannon–Wiener diversity index (H') and niche breadth (B) by age group (see text for definition of age group) of hake.

Paramete r	G0	G1	G2+
H'	0.75	0.81	1.83
B	2.11	2.24	6.24

Table 3. Chesson's selectivity index (α_i) of hake by age group and area on their main fish prey.

Species	Celtic Sea			Northern Bay of Biscay			Southern Bay of Biscay		
	G0	G1	G2+	G0	G1	G2+	G0	G1	G2+
Horse mackerel	0.00	0.08	0.01	0.05	0.02	0.01	0.00	0.00	0.00
Blue whiting	0.00	0.00	0.02	0.00	0.01	0.00	0.01	0.02	0.08
Anchovy	0.98	0.00	0.00	0.00	0.09	0.08	0.14	0.53	0.60
Pilchard	0.00	0.00	0.00	0.00	0.49	0.01	0.00	0.00	0.19
Argentine	0.01	0.47	0.00	0.00	0.00	0.05	0.00	0.00	0.00
Pout	0.00	0.05	0.06	0.00	0.03	0.01	0.00	0.04	0.13
Hake	0.00	0.40	0.92	0.95	0.35	0.85	0.86	0.40	0.00

Values of $\alpha_i > 0.14$ represent positive selection, and values < 0.14 represent negative selection.

Table 4. Mean trawl catch (number caught per 30 min) and percentage of the dominant prey species in the three areas studied.

Species	Catch by number and (percentage)		
	Celtic Sea (CS)	Northern Bay of Biscay (NBB)	Southern Bay of Biscay (SBB)
Horse mackerel	5 183.8 (70.98)	2 312.6 (45.43)	17 891 (84.19)
Blue whiting	1 214 (16.63)	1 739.1 (34.16)	2 311.1 (10.88)
Anchovy	0.1 (0.001)	176.7 (3.47)	117 (0.55)
Pilchard	0.3 (0.004)	264.4 (5.19)	699.9 (3.29)
Argentine	104.7 (1.43)	61.8 (1.21)	34.9 (0.16)
Pout	678 (9.28)	477.3 (9.38)	177.5 (0.84)
Hake G0 (0–17 cm)	118.9 (1.63)	50.4 (0.99)	17.0 (0.08)
Hake G1 (18–31 cm)	3.0 (0.04)	8.5 (0.17)	2.8 (0.01)