

Influence of environmental variables on the feeding and diet of European hake (*Merluccius merluccius*) on the Mediterranean Iberian coasts

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The feeding intensity and the diet of *Merluccius merluccius* were studied along a 1000 km latitudinal scale on the coasts of the Iberian Peninsula (western Mediterranean) in spring 2000. *Merluccius merluccius* was distributed along two bathymetric bands corresponding to the deep continental shelf (between 36 to 148 m), and the upper slope (between 215 to 310 m). At the shelf small crustaceans (mainly euphausiids and mysids) were dominant in the diet while fish (mainly Myctophidae) were the preferred prey on the slope. Feeding intensity of hake was significantly higher in areas with higher hake density suggesting feeding aggregations. Also, feeding intensity was significantly correlated with phytoplankton pigment concentrations (ppc), though only with ppc recorded one month before on the hake sampling stations. This delay between ppc and feeding intensity of hake may be a response to higher prey availability, because most hake prey were pelagic in origin (euphausiids, Clupeiformes) and they may reach high densities after exploiting local phytoplankton blooms. This delayed response seems to have more a local or *spotted* pattern. During three 8-h sampling cycles food consumed by hake ranged between 1.01 to 5.51% body wet weight (BWW), on average within the range of food consumption rates of other benthopelagic, active swimmer, fish.

INTRODUCTION

The diet of the European hake *Merluccius merluccius* has been widely studied because of its economic interest (e.g. Frogliani, 1973; Velasco & Olaso, 1998). Prey comprises benthopelagic organisms with ontogenic changes in the diet. Small juveniles prey on small crustaceans (euphausiids, natantian decapods and mysids), while fish assume an increasing importance in the diet with increasing size of hake. The smallest juveniles, seem to move up the water column at night (Orsi-Rellini et al., 1997) probably to feed. Food intake peaks at sunset and morning in the Adriatic Sea (Frogliani, 1973).

Studies on hake feeding have mainly been focused on the description of ontogenic, seasonal and bathymetric changes in the diet at a local scale, with little attention to variables affecting the feeding and food at narrow temporal (e.g. daily variations) and wide spatial scales. Recent studies have related changes in the diversity of fish communities to environmental variables such as temperature (Jacob et al., 1998) and surface phytoplankton concentrations (McClatchie et al., 1997). Such variables, however, have been rarely considered to autoecological levels. One of the aims of this study, rather than the description of hake diet, is to relate possible changes in the diet and feeding intensity of hake with changes in environmental variables (e.g. temperature and phytoplankton pigment concentration), along a north–south 1000 km spatial range covering the Mediterranean Iberian coast.

MATERIALS AND METHODS

Fish were collected between 27 to 790 m depth along the coasts of the Iberian Peninsula (western Mediterranean) from Cape of Gata (36°38'N) to Cape of Creus (41°11'N) during the cruise MEDITS-ES2001 (19 May–12 June 2001). *Merluccius merluccius* were collected from trawl hauls between 36 to 325 m. Fish were sampled with a bottom trawl, with an horizontal aperture of ~18 m, vertical opening of 2 m, and codend mesh size of 20 mm.

The trawl catches were used to estimate density (ind/h) of *M. merluccius*. A total of 660 hakes, collected in 48 hauls, were dissected on-board immediately after capture. Everted stomachs (16.4%) were excluded from the analyses. Individuals were measured in mm (total length [TL]) and weighed to the nearest 0.1 g. Stomach contents were identified on-board to the lowest possible taxonomic level and weighed to the nearest 0.1 g.

Specimens ranged between 9.8 to 68.9 cm TL. We excluded sizes below 10 cm TL due to methodological difficulties on-board. The following indices to measure feeding intensity and diet were calculated:

1. percentage vacuity (empty stomachs/total stomachs × 100);
2. stomach fullness (stomach weight/fish weight × 100);
3. stomach fullness calculated after excluding empty stomachs;
4. stomach fullness for fresh prey (fresh prey weight on stomachs/fish weight × 100);

5. frequency of occurrence (%F) of prey;
6. percentage numeric abundance of prey (%N); and
7. percentage wet weight of prey (%W).

The index of relative importance (IRI) ($IRI = \%F + \%N + \%W$) was calculated. Multivariate analyses were performed on %W data to identify trends in food and feeding.

Diet was described in two bathymetric bands (shelf: between 36 to 148 m; slope: between 215 to 310 m), based on 196 (on the shelf) and 45 (on the slope) specimens with food in their guts. In addition, we related food and feeding to some intrinsic and/or environmental variables which may influence them. Diet composition and feeding intensity indices (e.g. stomach fullness and vacuity %) were the dependent variables, and potentially explanatory factors were predator size (mean wet weight), mean size of prey (wet weight/number of prey in stomachs), hake density (individuals h^{-1}), time of day (Greenwich Mean Time [GMT]), depth (m), latitude, temperature ($^{\circ}C$) and phytoplankton pigment concentration ($mg\ Chla \cdot m^{-3}$) as an indication of surface primary production.

All samplings were performed at day at time intervals comprising 8 h between 0646 to 1540 h (GMT). We also calculated food consumption in this sampling interval based on three sampling cycles conducted on 2, 3, and 5 June 2001 at depths between 48 to 145 m. Duration of trawlings was 0.5 h, while the time between trawl hauls did not exceed 1.5 h.

These cycles allow the calculation of food consumption for hake using two different estimates: (1) the actual daily ration (DR) proposed by Maynou & Cartes (1997) consisting of the calculation of mean fullness of non-

digested prey along a sampling cycle; and (2) the food consumption based on the model by Eggers (1977), where the food consumed (C) during 24 h time interval is:

$$C_{(24E)} = F_{24}R_{24} \quad (1)$$

F_{24} is the mean stomach fullness index over 24 h (8 h in this study) and R is a coefficient of gastric evacuation. R is basically dependent on temperature and it can be obtained from temperature-based models (Maynou & Cartes, 1977). R was also deduced from the state of digestion shown by an *indicator* prey, the shrimp *Chlorotocus crassicornis*, which showed a rhythm of occurrence in the diet of hake (see Discussion).

Temperature (at surface) and phytoplankton pigment concentration (ppc) were respectively obtained from www.ieo.es and from seawifs.gsfc.nasa.gov, which provide daily to weekly, and monthly average values. Map of temperature corresponded to 30 May 2001. Maps of ppc were obtained from May 2001 (monthly average), and weekly from mid March to early June. Satellite images were read and the scale of ppc values was superimposed on each image (Photoshop 6.0) on the position of trawls to obtain the corresponding *lectures* of ppc. We wanted to test the hypothesis that feeding intensity by hake may be affected by local changes in temperature and water productivity within the study area. Different periods, simultaneously and before (2 weeks, 1 month, 2 months) the sampling of stomachs, were considered to test possible relationships between feeding intensity and ppc.

Feeding intensity (e.g. mean stomach fullness, and % vacuity) were calculated based on 32 samplings attaining at least ten individuals per haul. After this, we searched

Table 1. *Main prey in the diet of Merluccius merluccius. (*) less than 0.1. Minor prey (not exceeding 5% of %F, %N, %W):* Lampanyctus crocodilus, Notolepis rissoi, Argentina sphyraena, Micromesistius poutassou, Gaidropsarus megalokynodon, Gadidulus argenteus, Aphia minuta, Spicara sp., Cepola rubescens, Solenocera membranacea, Pasiphaea sivado, Sergestes arcticus, Plesionika gigliolii, Processa sp., Pontocaris lacazei, Liocarcinus depurator, Lophogaster typicus, Alloteuthis media, Sepiolidae.

	N=196 36–148 m				N=45 215–310 m			
	%F	%N	%W	%IRI	%F	%N	%W	%IRI
<i>Sardinella aurita</i>	1.0	0.5	9.3	0.7	0	0	0	0
<i>Sardina pilchardus</i>	5.1	2.4	18.4	6.9	0	0	0	0
<i>Trachurus trachurus</i>	0.5	0.2	0.3	*	2.2	1.4	9.5	1.0
<i>Boops boops</i>	1.5	0.7	16.4	1.7	0	0	0	0
Myctophidae	1.0	0.5	0.1	*	22.2	24.6	15.8	36.2
<i>Lepidopus caudatus</i>	0.5	0.2	0.3	*	4.4	2.9	35.4	6.9
<i>Merluccius merluccius</i>	3.1	1.5	40.1	8.3	0	0	0	0
<i>Phycis blennoides</i>	0	0	0	0	8.9	5.8	4.2	3.6
Osteichthyes unident.	10.7	5.6	2.1	5.4	31.1	15.9	9.1	31.4
Euphausiacea	24.5	28.2	1.2	47.1	8.9	27.5	0.6	10.1
Mysids	11.7	22.3	0.4	17.4	0	0	0	0
Gammaridean Amphipods	6.6	5.3	0.1	2.3	0	0	0	0
Decapoda Natantia unident.	6.1	2.9	0.9	1.5	0	0	0	0
<i>Chlorotocus crassicornis</i>	3.6	2.0	0.9	0.7	0	0	0	0
<i>Plesionika heterocarpus</i>	0	0	0	0	11.1	7.2	10.9	8.1
<i>Alpheus glaber</i>	6.1	2.9	0.2	1.3	2.2	1.4	0.5	0.2
Crustacea unident.	8.2	4.6	0.1	2.5	4.4	2.9	0.1	0.5

%F, frequency of occurrence; %N, percentage numeric abundance; %W, percentage weight; IRI, index of relative importance.

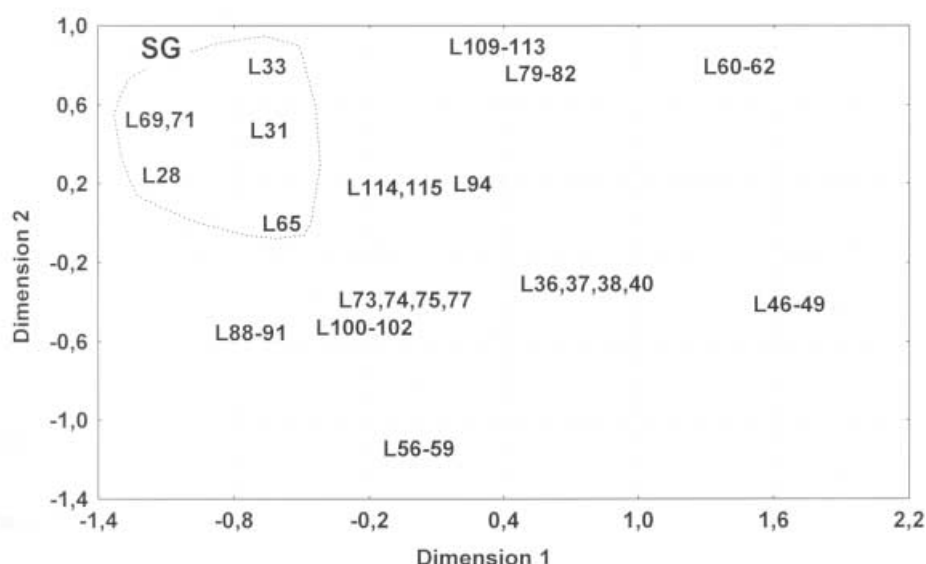


Figure 1. Results of multidimensional scaling analysis performed on the diet of *Merluccius merluccius* (Stress, 0.159; SG, slope group). L, trawl sample.

correlations (non-parametric Spearman) between feeding intensity variables and size of predators (body wet weight [BWW]), mean size of prey, density of hake, time of day, depth, latitude, temperature and ppc.

Diet was submitted to a similar analysis. Cluster analysis using UPGMA as algorithm of aggregation and $1-r$ (Pearson's correlation) as distance were used to classify samples. In base to the similarity matrix generated, multidimensional scaling (MDS) techniques were applied for the ordination of samples (as a function of their prey composition) along two dimensional axes. To attain a minimum number of individuals analysed, we pooled trawls performed during the same day. This reduces the number of data to 16 (between 10 to 36 stomachs analysed per day). We also searched correlations (Spearman r) between the projections of hauls along Dimensions 1 and 2 of MDS and the variables size of hake, mean size of prey, hake density, depth, latitude, temperature and ppc as possible explanatory variables of diet patterns.

RESULTS

Density of hake along its depth range distribution marked two non-related peaks of abundance at the shelf and at the upper slope separated by a lag between 150 to 215 m where the species was hardly captured. The diet of *Merluccius merluccius* was quite different at the shelf (between 36 to 148 m) and at the slope (between 215 to 310 m). Once small recruits (e.g. TL < 10 cm) were excluded from analyses, size of hakes with food in their stomachs was between 9.8–68.5 cm on the shelf (mean size 17.1 ± 0.9 confidence interval [CI] 95%) and between 9.9–44 cm on the slope (mean size 21.5 ± 1.9 CI 95%). At the shelf, small crustaceans were dominant in the diet with euphausiids and mysids accumulating 47.1% and 17.4% of IRI (Table 1). Fish (epipelagic species: *Sardina pilchardus* and *Boops boops*, and *Merluccius merluccius*) were secondary prey in terms of IRI, though dominant in terms of weight. At the slope the dominant prey were fish (Myctophidae with 36.5% of IRI, and unidentified osteichthyes with

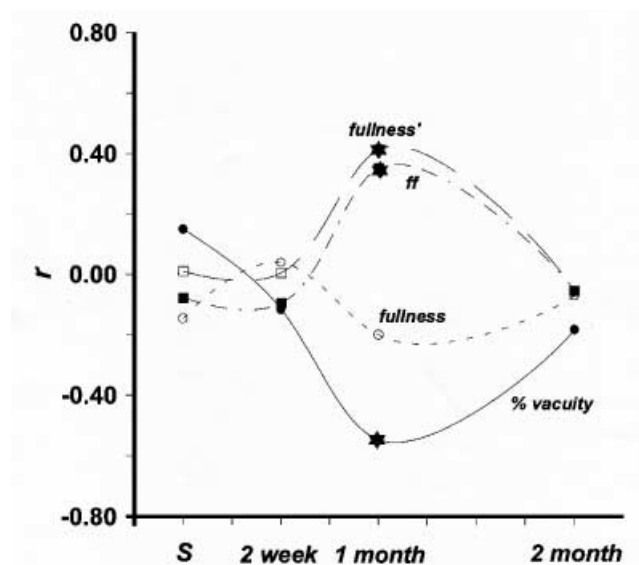


Figure 2. Spearman correlation between feeding intensity indices by hake and phytoplankton pigment concentration (ppc) at time of sampling and at different times before the actual sampling date. ff, fresh fullness. (★) significant r ($P < 0.05$).

31.4%), while euphausiids, *Plesionika heterocarpus* and *Lepidopus caudatus* were secondary prey.

The MDS separated groups of samples mainly as a function of depth (Figure 1; stress=0.159). Samples L28, L31, L33, L65, L69, and L71 (SG: slope group) were grouped in the left part of axis (Dimension) 1. These samples ranged between 215 to 310 m depth.

Correlations with the projections of samples on dimensions 1 and 2 ($N=16$) showed how D1 was only significantly correlated with depth (Spearman r : 0.548). No significant correlations were found with latitude, mean weight of hake and mean weight of prey, temperature, and ppc. Dimension 2 was not significantly correlated with any variable.

Table 2. Food consumption (*F*) by *Merluccius merluccius* during three cycles of 8 h performed on 2, 3 and 5 June 2001. *R*: coefficient of gastric evacuation. Fullness for *Chlorotoccus crassicornis* only calculated with stomachs containing this prey. *N*=number of prey (fresh prey in parantheses).

F	Depth		Time	Mean fullness	CI 95%	Fresh fullness	n'	Fresh fullness <i>Chlorotoccus crassicornis</i>		
	(m)							weight	(%)	N
2 June 2001	L73	96	6.32	1.998	1.109	0.679	15	5.86	76.2	3(2)
	L74	145	8.10	5.658	5.545	0	8	0.64	42.7	2(1)
	L75	91	10.16	3.234	3.768	0.329	7			
	L77	90	12.50	2.660	2.364	0	13	0	0	1(0)
	L78	80	14.30	0.281	0.551	0	4			
3 June 2001	L79	138	6.14	5.545	4.099	5.157	23	<i>t</i> evacuation=6 h 20'		
	L80	95	7.53	2.511	3.997	0	10			
	L82	78	11.15	2.003	1.916	0.358	15			
	L83	112	13.44	2.119	2.343	0	10			
5 June 2001	L88	48	6.11	1.252	0.957	0.502	12			
	L89	70	7.15	1.636	1.262	0.589	14			
	L90	143	10.14	4.320	3.820	0.057	19			
	L91	105	11.42	2.278	2.317	0	10			
	L92	72	13.33	0.500	0.100	0	20			
	2 Jun	3 Jun	5 Jun 2001							
<i>FEggers</i>	4.084	4.745								
<i>Factual</i>	1.008	5.515	1,148							
<i>RWorobec</i> (<i>t</i> =11.9°C)	0.164									

The %vacuity was negatively correlated with depth ($r: -0.448$; $P < 0.01$), and positively correlated with time of day ($r: 0.606$; $P < 10^{-4}$). In other words, % of empty stomachs were higher at shallower depths, and they were lower in the early time of day (morning). Consistently, mean fullness was positively correlated ($r: 0.482$; $P < 10^{-3}$) with depth (increased deeper), while it was negatively correlated ($r: -0.386$; $P < 0.03$) with time (higher in the morning, lower in the afternoon).

The %vacuity was also negatively correlated with hake density ($r: -0.408$; $P < 0.02$; $N=32$) and, consistently, fullness was positively correlated ($r: 0.389$; $P < 0.03$) with hake density. No significant correlations were obtained relating to feeding intensity and temperature. Concerning ppc, significant negative r was obtained between ppc measured one month before the stomach sampling and % of vacuity, with significant positive r with fullness (zeros excluded) and fullness on fresh prey. No significant relations with other temporal measures of ppc (contemporaneous, ppc_{2 weeks} or ppc_{2 months} before) were obtained (Figure 2).

Concerning food consumption, no significant feeding peaks (one-way analysis of variance) were detected in stomach fullness in our sampling interval during 2, 3 June, but there was a significant peak during 5 June ($P < 0.0053$) between L90 and L92 (post-hoc Scheffé test). We only applied here the Eggers model to the first two sampling cycles, accomplishing the assumption of continuous feeding.

Temperature at depths between 48 to 145 m averaged around 11.9°C (from conductivity-temperature-depth measures) and the *t*-model by Worobec gives a $R=0.164$. R was also deduced from the state of digestion showed by the indicator prey *Chlorotoccus crassicornis* which was digested

in hake stomachs in 6 h 20 min. This gut residence time gave an estimation of $R=0.158$. Estimations of food consumed in the period sampled in our study ranged between 1.01 to 5.51% BWW (actual daily ration) and 4.08 to 4.74% BWW (Eggers model) (Table 2).

DISCUSSION

Merluccius merluccius was distributed over two bathymetric bands corresponding to the continental shelf and the upper slope. Diet was quite different at these two depth ranges with small crustaceans (euphausiids, mysids and small natantian decapods) being dominant at the shelf, and fish (mainly Myctophidae) being the main prey on the slope. Though this trend seems consistent with the depth-size distribution of hake, because juveniles mainly inhabit the shelf region (Maynou et al., 2002) in the Catalan coasts, no significant correlations were found between depth and the size of hake (and its own prey) in our dietary analysis. This could be because hake <10 cm TL were excluded from these analyses.

Cannibalism (mainly directed to sizes between 8.4 and 10 cm) occurred in the present study with %IRI on the shelf of 8.3%, higher than that reported in other areas (Froggia, 1973; Velasco & Olaso, 1998). A possible explanation would be that our sampling was restricted to spring, comprising a period of high recruitment in the Iberian Mediterranean coasts.

Feeding intensity of hake was higher in areas with higher hake density, suggesting shoal aggregations to feed, and higher food consumption by hake in those areas with best ecological conditions for the species.

The study of correlations between feeding intensity and ppc gave a delay around one month between maximum primary production and peaks of feeding intensity of hake, probably a response to higher prey availability. Most hake prey in this study were pelagic in origin (euphausiids, clupeiforms, myctophids) and their higher concentrations probably may depend (with a logic time delay of ~1 month) on local increases in primary production. Euphausiids and *Sardina pilchardus* can directly eat phytoplankton, and small euphausiids showed a peak of abundance in April in the Ligurian Sea (Sardou et al., 1996), situated in the north-east of the study area. Relationships between some parameters of fish communities such as the diversity and regional surface phytoplankton concentrations has previously been reported (McClatchie et al., 1996), with striking correspondence between hot spots of diversity and regions of high productivity probably associated with areas of geostrophic current intensification. Our results would suggest a (delayed) trophic link in these relationships. Our feeding intensity data did not give any correlation with latitude, therefore a possible relation between food intake and primary production would follow more of a *spotted* model.

Feeding activity was higher during the morning in our sampling period, as can be deduced, for instance, from the importance of undigested prey in stomachs during sampling cycles. In the same way, % fresh fullness was significantly correlated ($P < 0.003$) with time of day ($r = 0.577$; $N = 32$), % of empty stomachs was lower in the morning, and mean fullness was higher at the beginning of our sampling period. As deduced from the study of rhythms of capture in the western Mediterranean, hake probably leaves the bottom at night (Orsi-Relini et al., 1997). Also, the species probably feed in the water column at night, though this activity has also been reported to continue in the morning (Frogliola, 1973). This general pattern seems common to that described for other Merlucciidae. Thus, most feeding in *Macruronus novaezelandiae* takes place in the water column at night off south-eastern Australian waters (Bulman & Blaber, 1986).

Detailed analysis of the undigested prey captured by hake in this study indicated predation in the morning (the first haul of the sampling cycle) towards species not collected together with hake in the same haul, and this may be presumably explained by behavioural rhythms of prey. This was the case of the pandalid *Chlorotocus crassicornis* or the gadoid *Micromesistius poutassou*. *Chlorotocus crassicornis* seems to emerge from sediment at night (P. Abelló, personal communication), though nocturnal oblique displacements by this shrimp upwards (or by hake to deep waters to feed) must also be considered. Thus, *C. crassicornis* was only preyed on the shelf (between 36–148 m) by hake, while this shrimp was captured during the day by bottom trawls exclusively below 176 m in our sampling, reaching peaks of density between 200–300 m. On the shelf, hake mainly preyed on small crustaceans (euphausiids, mysids) though both zooplankton and suprabenthos in the water–sediment interface (Sabatés et al., 1989; Maynou et al., 2002) attained maximum biomass (daytime) offshore, over 200–250 m in the Catalan Sea off Barcelona. In the case of zooplankton these peaks are associated with the existence of permanent frontal systems (Sabatés et al.,

1989), offshore to the shelf area occupied by hake. As a conclusion, the daytime distribution of trophic resources (macrozooplankton, suprabenthos) exploited by hake are controversial with their own hake distribution, suggesting day–night oblique displacements by demersal fauna.

Food consumed by hake ranged between 1.01 to 5.51% BWW in our 8-h cycle, which represents a high daily food consumption in the range to those of other macroplankton-active swimmer predators (e.g. *Hoplostethus atlanticus* with DR between 0.9 to 1.15; bathypelagic fish, with DR between 0.8 to 8.1; mesopelagic Myctophidae with DR between 4.3 to 6.5), and higher than those of dispersed benthic predators such as Macrourids, *Lophius upsicephalus* or *Helicolenus dactylopterus* (DR between 0.55 to 1.6 summarized by Maynou & Cartes, 1997). In conclusion, *Merluccius merluccius* seems a species of high metabolic requirements, its feeding, and probably also its distribution, may probably be: (i) linked to coupling between planktonic and demersal systems via trophic processes (with a delayed response of one month) after peaks of primary production; and (ii) probably determined by the proximity to productive areas (e.g. oceanic fronts or eddies at a local scale; upwelling areas at a global scale).

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