HAKE FOOD CONSUMPTION IN THE SOUTHERN BAY OF BISCAY ESTIMATED FROM A GASTRIC EVACUATION MODEL

by

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Abstract

Hake, *Merluccius merluccius* (L. 1758) food consumption per quarter and age class is estimated using the results of the analysis of 11504 hake stomach contents. Samples were collected and analysed on board in two quarterly samplings carried out in the Cantabrian Sea and off the Galician north coast during 1994 and 1997. Food consumption is estimated through a general gastric evacuation model for gadoids including as variables: water temperature, predator size, stomach content weight and prey energy density. According to our results, hake quarterly food consumption varies from 29 g for an age 0 class hake to 1513 g for an age 6+ class hake. Compared with the other quarters, consumption in quarter 2 is lower for hake of age classes 1 and 2, and generally higher for older hake. Quarterly rations are allocated into the main commercial species and other prey groups using hake diet composition in volume by age class and quarter. Results show that blue whiting is the most important prey for hake and makes up more than half of the consumption from age class 2-3 upwards. In its lifetime from age class 0 to age class 5 one hake consumes 11.6 kg, and almost 8 kg of them are of blue whiting. Crustaceans are only important for younger hake but are almost negligible from age class 2 upwards. The importance of the rest of the fish species varies among ages and quarters. Using blue whiting, horse mackerel and hake length distributions in stomachs, the number of blue whiting, horse mackerel and hake of each length range consumed per quarter by one hake of each age class and quarter is estimated.

Key words: Ration estimate; Gastric evacuation; Consumption rates; *Merluccius merluccius*

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Introduction

Trophic dynamics of fish populations are becoming increasingly important for multispecies assessment, and also for the study of the effect of food consumption on variation in fish growth. Food ration is one of the uncertainties in multispecies modelling and is directly translated into uncertainties in estimates of natural mortality rates used by both single species and multispecies modelling. The study of the effect of food consumption on variation in fish growth is usually carried out through bioenergetic models that combine data on growth, costs of living of a predator and its food conversion efficiency. But given the uncertainties in some of the variables included in these models, it is useful to have independent estimates of food consumption to contrast results. A method to estimate food consumption of fish in the field consists of combining field data on stomach contents with information about gastric evacuation rates (Bajkov, 1935; Daan, 1973; Pennington, 1985).

European hake (*Merluccius merluccius*) is a major predator in the demersal ecosystem of the Bay of Biscay and its diet composition and feeding intensity (variations in emptiness percentage and in stomach content in relation to body size) have been studied by several authors (González *et al.* 1985; Olaso, 1990; Olaso, 1993; Guichet, 1995; Velasco and Olaso, 1998). Nevertheless, no studies on its food consumption have been carried out until now, although there are some works dealing with food consumption of other hake species (Cohen & Grosslein, 1981; Durbin *et al.*, 1983; Francis, 1983; Pillar & Barange, 1995). Hake was included in the EC Contract No. FAIR-CT 95-0604 "Consumption Rates on Predatory Fish Relevant for Multispecies assessment in the North Sea and the Atlantic off Spain and Portugal" (CORMA). This paper is a preliminary report on the results concerning hake food consumption in the Bay of Biscay estimated from a gastric evacuation model, including estimates of hake predation by length range of commercial species such as blue whiting (*Micromesistius poutassou*), horse mackerel (*Trachurus trachurus*) and hake-on-hake predation.

Material and Methods

The model

According to Bajkov (1935), at steady state, consumption rate will equal gastric evacuation rate. If, following Jones (1974) and Temming & Andersen (1994), evacuation rate is expressed as:

$$\mathrm{d}S/\mathrm{d}t = -\rho S^{\alpha},$$
(g/h)   Eq. (1)

where S is the total stomach content (g wet weight) and ρ and α parameters of the model, then:

$$\mathrm{d}C/\mathrm{d}t = \rho S^{\alpha},$$
(g/h)   Eq. (2)

where $\mathrm{d}C/\mathrm{d}t$ is the food consumption rate. To estimate hake consumption the gastric evacuation model proposed by Andersen (1998, 1999) for whiting (*Merlangius merlangus*) is used, modified as:

$$\mathrm{d}S/\mathrm{d}t = -0.00132 L^{1.44} e^{0.078T} E^{-0.875} S^{0.5},$$
(g/h)   Eq. (3)

(N.G. Andersen, pers. comm.) where S is the total stomach content (g wet weight), L is the length of the hake (cm total length), T is the temperature (ºC), and E is the prey energy density (kJ/g wet weight). This modification of the model is more robust to extensive extrapolations to preys with high energy densities and describes gastric evacuation in other gadoid species (N.G. Andersen, pers. comm.).

Over time, the average consumption rate of a fish population may be described by:

$$C_{\mathrm{avg}} = \rho \, \mathrm{avg}\big[S^{\alpha}\big],$$
(g/h)   Eq. (4)

(Pennington, 1985). In the present study average consumption per age class and quarter is calculated as

$$C_Q = \frac{(F+R)}{F \times (F+R+E)} \times 2190 \times \sum dC_i/dt$$, (g) Eq (5)

where F is the number of full stomachs in the appropriate age class and quarter, E the number of empty stomachs, R the number of regurgitated stomachs, dC_i/dt the estimated consumption rate by application of the gastric evacuation model on the ith full stomach, and 2190 the number of hours in one quarter, used because the consumption rate is expressed in g/h. Daily rations were obtained by multiplying by 24 h instead of 2190. This expression corrects for the effect of regurgitated stomachs (Hislop *et al.* 1991), which are very common in hake (Velasco and Olaso, 1998).

Stomach contents

Stomach contents were collected in two quarterly samplings carried out during 1994 and 1997. The first sampling, including 5828 stomach contents of hake, was studied in Velasco & Olaso (1998), but only covered the eastern area of ICES Division VIIIc (VIIIc1). In order to study the whole ICES division, another sampling was carried out in 1997, covering both ICES Divisions VIIIc1 and VIIIc2 (Figure 1). In this sampling 5676 additional stomach contents were analysed.

Stomach contents were analysed volumetrically on board sampling vessels following the methodology explained in Velasco & Olaso (1998). Available data for these samplings are: length, sex and sexual maturity of the predator, together with its state, classified as empty, full or regurgitated. Regurgitated stomachs were identified according to Robb's (1992) criteria on the gall bladder state. From every full stomach the data collected are total content in volume (cc) and number and type of preys. Furthermore, for each prey type the partial volume of the total stomach volume is recorded, and for fish, cephalopods and decapod crustaceans, length and/or otolith size. Total length was estimated from otolith length using the regression formulae from Robles (1970) for blue whiting, Piñeiro & Hunt (1989) for hake, and $Lf = -2.993 + 3.5366 \times Lot$ ($r^2 = 0.94$, P. Abaunza from Instituto Español de Oceanografía, Santander, Pers. comm.) for horse mackerel. Length distribution of these species in the stomachs were transformed into weight using length-weight regressions of those preys taken from the literature and used to estimate the number of blue whiting, horse mackerel and hake of each length range consumed by one hake of each age class and quarter.

Stomach content data in volume are transformed into weight terms using the regression $W = 0.933 \times V^{0.993}$ ($r^2 = 0.995$; $n = 115$), W and V being the weight (g) and volume (cc) of the stomach content respectively.

An age was attributed to each predator using deterministic age-length keys (Hilborn & Walters, 1992) to calculate quarterly food consumption and diet composition in volume percentage by age class. The deterministic age-length key was calculated with the von Bertalanffy model from ICES Division VIIIc ($k = 0.076$; $L_\infty = 120.5$; $t_0 = -1.24$) supplied by C. Piñeiro (pers. comm.), from project BIOSDEF (EU Study Contract DG: XIV 95/038). C. Piñeiro also supplied quarterly hake length-weight relationships from the same project (Qt. 1 $W = 0.0052 \times L^{3.06}$; Qt. 2 $W = 0.0042 \times L^{3.13}$; Qt. 3 $W = 0.0048 \times L^{3.10}$; Qt. 4 $W = 0.0045 \times L^{3.11}$; where W is the wet weight g), which were used to convert estimated food rations in percentage of body weight by dividing each value by the weight corresponding to the mean length of the age class and quarter sample.

Temperatures

Distribution of hake by age and season in ICES Division VIIIc is not well enough known to allow the calculation of a representative temperature regime. Therefore data on mean temperatures by quarter and depth stratum were calculated from results found in the literature on the area.

Temperature data from 1994 and 1995 in three different sampling radials carried out in different oceanographic projects (Anon, 1998; Lavín *et al.*, 1998) have been collected. Two sampling areas were located in ICES Division VIIIc1 (one off Santander and the other off Gijón, see Figure 1) and the third was in VIIIc2 (off A Coruña). Radials were carried out every month and covered a depth range from 25 m to 855 m.

These data were used in the gastric evacuation model (Equation 3) assigning a temperature to each individual stomach according to the season and depth in which it had been sampled. To this end, a depth range between 25 m and 800 m was selected in accordance with hake distribution, and only bottom temperatures were used, since hake lives mainly close to the bottom. Comparing available temperature data and according to hake depth changes in abundance, it was decided to use a modification of the depth strata given by Sánchez (1993) to calculate quarterly mean temperatures. Geographical variation was not considered as differences were only pronounced in the shallower points where hake is scarce. Final temperature data used to estimate hake consumption are summarised in Table 1.

Energy density of the preys

The main fish prey species for hake in ICES Division VIIIc were sampled quarterly during routine research surveys. Samples were frozen on board sampling vessels and brought to the laboratory, where the fish were thawed. They were then weighed and measured for length individually before being homogenised, after which the energy density was measured by bomb calorimetry. Samples of blue whiting, anchovy, hake, sardine, mackerel, horse mackerel and silvery pout were collected mainly in ICES Division IXa and also in ICES Division VIIIc. Energy density was determined by size class (only for fish prey) at IPIMAR (Instituto Portugues de Investigaçao das Pescas e do Mar). Figures for size classes not sampled were extrapolated from the energy values for that species. Stomach contents were divided into the main prey species and other fish, crustaceans, cephalopods and polychaetes. Fish species in the "other fish" category were attributed to one of three groups, fatty, medium or lean fish according to its characteristics. Energy densities for the fatty fish were derived from the average of those for sardine, anchovy and Spanish mackerel. For medium and lean fish the energy densities of horse mackerel and hake were used respectively. Crustaceans were classified as large and small depending on the nature of the exoskeleton. Crustaceans with thin, and therefore easily digestible exoskeletons were classified as small, and crustaceans with thick exoskeletons classified as large. Energy values and their sources are shown in Table 2.

These values were used to estimate consumption rate through equation (3). In the case of stomachs with more than one prey, overall energy density (*E*) was calculated as:

$$E = \sum E_i p_i \text{ ,} \qquad \text{(kJ/g wet weight)} \qquad \text{Eq. (6)}$$

where E_i is the energy density of prey i, n the number of preys in the stomach, and p_i the relative share of prey i in the stomach. Energy densities of the preys were also used to convert quarterly food ration estimates by age class into energy units (kJ) using a weighted average of the energy density of the different preys in the appropriate quarter and age class.

Results

Diet composition

Quarterly distribution by age class of the 11504 stomach contents of hake analysed is summarised in Table 3. Figure 2 shows the diet of hake by quarter and age class in volume percentage. These results coincide with those presented in Velasco & Olaso (1998), although the latter were studied on a length basis and therefore will not be explained in depth. Crustaceans, and also cephalopods to a lesser extent, are important only in age classes 0 and 1, but almost negligible from age 2 upwards. Fish are the most important prey in every age class and quarter except for age 0 in the first and

second quarters. Among them, blue whiting stands out clearly from age 2, and even from age 1 in the third and fourth quarters. The rest of the fish preys vary in their importance among quarters and age classes.

Table 4 presents length distribution found in hake stomachs of blue whiting, horse mackerel and hake prey per predator age class. Predation on other important commercial species such as anchovy, sardine or mackerel have a seasonal pattern and probably change from year to year depending on the abundance of species in the area (Olaso *et al.*, 1994). The sample of lengths in stomachs is not large enough to obtain a significant distribution. Furthermore, in the case of sardine and mackerel, hake prey on large fish which make an important contribution in weight, but smaller in number. A clear relationship between blue whiting prey length and predator length is observed, as stated by Velasco & Olaso (1998). This relationship is not so clear in the case of the other two species, especially in older age classes of hake, since predation on these species is less important in these age classes.

Food consumption

Daily rations by age class and quarter are shown in Figure 3. According to these results, the quarterly consumption of hake (shown in Table 6) ranges from 29 g for a 0 age class hake to 1513 g for 6+ age class hake. Compared with the other quarters, consumption in quarter 2 is higher for older hake, age class 3 upwards. For age class 1 consumption is higher in quarters 3 and 4, more than the double the consumption in quarters 1 and 2, which may be related to the higher percentage of blue whiting in the diet composition of those quarters (see Figure 2).

To compare our results with those from other studies, daily rations by age and quarter have been converted into percentage of body weight (Table 5). With the exception of age class 0 and age class 1 in some quarters, there is a clear decreasing trend in food consumption as a percentage of body weight as age increases.

Quarterly rations by age class were allocated into the main commercial species and other prey groups using hake diet composition in volume by age class and quarter (see Figure 2), and the results are summarised in Table 6. As stated above, blue whiting is the most important prey for hake, making up more than half of the consumption from age class 2-3 upwards. In its lifetime from age class 0 to age class 5 (both inclusive), one hake consumes almost 8 kg of blue whiting, making up more than 75% of the total 11.6 kg consumed.

Quarterly food ration in energy units per age class and quarter, also summarised in Table 6, once more reflect the higher consumption of older hakes in quarter 2.

An estimate of the number of blue whiting, horse mackerel and hake in 5 cm length ranges consumed by quarter per hake of each age class is summarised in Tables 7-9. Blue whiting (Table 7) is consumed by hake of all age classes but its importance is negligible in age class 0 and it is restricted to quarters 3 and 4 in age classes 1-2. The main length range of blue whiting consumed by hake is 10-30 cm, larger specimens being scarce. Consumption of horse mackerel (Table 8) varies seasonally. Small horse mackerel (under 10 cm) are preyed on by hake up to age class 2. For the older ages of hake the main length range of horse mackerel consumed is 10-20 cm. As for cannibalism, hake prey (Table 9) is mainly consumed by age classes from 0 up to 3 (results in older age classes being omitted given the small sample size, see Table 4) and consumption is concentrated in a 5-20 cm length range, which limits hake prey to age class 0.

Discussion

Quarterly food consumption results follow the seasonal pattern stated for feeding intensity (percentage of empty stomachs and variation in stomach contents as a percentage of body weight) in Velasco & Olaso (1998). This pattern may be related to recovery from the spawning season

(Velasco & Olaso, 1998) which, in the southern Bay of Biscay, takes place mainly from December to April.

The twelve species of the genus *Merluccius* are distributed in coastal areas in all latitudes from 60ºN to 60ºS, between 4º C - 20º C (Alheit and Pitcher, 1995). Studies on food consumption have been carried out only on four species of the genus *Merluccius*. Durbin *et al.* (1983) used the Elliot & Persson (1978) model to estimate food consumption of silver hake (*Merluccius bilinearis*) in the Northwest Atlantic, and calculated that food ration ranged between 1.8 %BW in spring and 4.65 %BW in the fall for the small hake (<20 cm), and 2.4 and 1.9%BW for large hake in these seasons respectively. Cohen & Grosslein (1981) also used the same method to study silver hake among other species, and found a daily ration ranging from 0.6 %BW to 2.2 %BW which increased with age except for age class 0. Edwards and Bowman (1979) estimated the daily ration of silver hake to be 3.1 %BW. Francis (1983) used a bioenergetic approach and estimated a extremely low daily ration of 0.4 %BW for Pacific hake (*Merluccius productus*). Daily ration in Cape hake (*Merluccius capensis*) was calculated by Pillar & Barange (1995) as 5.51 %BW applying the Elliot & Pearson model, and 4.15 %BW using the Eggers (1977) method.

Our estimates of daily ration (Table 5) are within the range of most of the estimates mentioned above. Differences with the Cohen & Grosslein (1981) estimates may be due to the fact that average weight of the stomach contents in body weight percentage was lower than that found in European hake in this study, which ranges from 5.19 %BW to 1.51 %BW in our samples (calculated using the correction factor for regurgitated stomachs used in equation 5), in contrast to the 0.5-1.7%BW range found by these authors. The higher temperatures in the area studied compared with those found in the Durbin *et al.* (1983) study would also affect consumption rates, making estimates higher than at lower temperatures.

In any case, it has to be taken into account that different methods have been used to estimate all these food consumption rations from different hake species, and this must affect the results, making them not directly comparable. Wheter our approach is appropriate depends on the applicability to hake of the whiting model used in this study; given the difficulties in obtaining European hake alive to test its evacuation rates in the laboratory, it's difficult to discuss their suitability. Especially bearing in mind that the present study is the first one to estimate food consumption of European hake. Nevertheless, this model gives a good description of gastric evacuation in other gadoids, appart from whiting, such as saithe (*Pollachius virens*) (N.G. Andersen, pers. comm.), and can therefore be used as a sound and available approach to the study of hake food consumption from stomach contents collected in the field.

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Tables and Figures

Table 1.- Mean temperature (ºC) by depth stratum and quarter used to estimate hake consumption (n: number of items used to obtain means)[*]

Depth strata	<35 m		36-90 m		91-250 m		251-800 m	
	Mean temp.	n	Mean temp.	n	Mean temp.	n	Mean temp.	n
1st Quarter	13.0 (±0.25)	3	12.3 (±0.22)	3	12.6 (±0.41)	8	10.6 (±0.28)	6
2nd Quarter	12.9 (±1.45)	3	12.9 (±0.79)	4	12.1 (±0.20)	9	10.6 (±0.19)	8
3rd Quarter	18.8 (±3.25)	2	14.8 (±1.58)	6	12.0 (±0.15)	10	10.6 (±0.23)	8
4th Quarter	14.5 (±1.64)	2	15.0 (±0.80)	6	12.9 (±0.65)	10	10.7 (±0.30)	7

([*]) Original data collected from Lavín *et al.* (1998) and Anon. (1998).

Table 2.- Energy densities of major hake prey species. Samples processed by L. Hill at IPIMAR during the CORMA project

Prey species	Length range (cm)	1st Quarter	2nd Quarter (kJ / g Wet weight)	3rd Quarter	4th Quarter
Engraulis encrasicholus	8-10	5.8	5.8	5.8	5.8
Engraulis encrasicholus	10-12	6.0	6.0	6.0	6.0
Engraulis encrasicholus	12-15	7.1	7.1	7.1	7.1
Engraulis encrasicholus	15-20	8.1	8.1	8.1	8.1
Gadiculus argenteus	6-8	4.8	4.8	4.8	4.8
Gadiculus argenteus	8-10	5.1	5.1	5.1	5.1
Merluccius merluccius	8-10	4.1	4.1	4.1	4.1
Merluccius merluccius	10-12	4.0	4.0	4.0	4.0
Merluccius merluccius	12-15	4.2	4.1	4.2	4.2
Merluccius merluccius	15-20	4.0	4.0	4.0	4.1
Merluccius merluccius	20-25	3.9	3.9	3.9	3.9
Merluccius merluccius	25-28	4.2	4.2	4.2	4.2
Merluccius merluccius	28-30	4.1	4.1	4.1	4.1
Micromesistius poutasou	8-12	4.2	4.2	4.2	4.2
Micromesistius poutasou	12-15	4.2	4.2[*]	4.2	4.2[*]
Micromesistius poutasou	15-20	5.1	4.3	4.8	5.0[*]
Micromesistius poutasou	20-25	5.6	5.6[*]	5.5	5.3[*]
Micromesistius poutasou	25-35	6.3	7.6	6.3	5.0[*]
Sardina pilchardus	8-10	6.6	6.6	6.6	6.6
Sardina pilchardus	10-12	6.8	6.8	6.8	6.8
Sardina pilchardus	12-15	5.7	5.7	5.7	5.7
Sardina pilchardus	15-20	8.2	9.2	8.5	12.7
Sardina pilchardus	20-25	7.0	8.6	8.3	10.7
Scomber scombrus	20-25	4.4[*]	4.4	4.4	4.4
Trachurus trachurus	4-6				15.5
Trachurus trachurus	6-8	6.0	6.5	6.5	7.0
Trachurus trachurus	8-10	6.2	6.0	6.0	5.8
Trachurus trachurus	10-12	6.4	6.4	6.4	6.4
Trachurus trachurus	12-15	6.5	6.6	6.6	6.7
Trachurus trachurus	15-20	5.8	6.9	6.9	8.0
Trachurus trachurus	20-25	4.2	6.1	6.1	8.0
Small crustaceans		4.0	4.0	4.0	4.0
Large crustaceans		5.4	5.4	5.4	5.4
Cephalopods		3.5	3.5	3.5	3.5
Polychaetes		4.5	4.5	4.5	4.5

Source of data:

White squares	Samples collected in ICES division IXa
#.#[*]	Samples collected in ICES division VIIIc
Shaded squares	Extrapolated figures
Small crustaceans	Values from the North Sea
Cephalopods and Polychaetes	Values from the North Sea

Table 3.- Number of stomachs and percentage of empty stomachs by age class and quarter. In brackets: length ranges (cm) of each age class of hake

Length range (cm)	Age 0 (9-18)	Age 1 (19- 25)	Age 2 (26- 32)	Age 3 (33- 39)	Age 4 (40- 44)	Age 5 (45- 50)	Age 6+ (51-90)
1st QUARTER							
Number of stomachs	468	316	217	359	388	193	228
% Empty	32.3	41.1	42.4	46.5	47.7	51.3	50.0
2nd QUARTER							
Number of stomachs	716	591	147	249	350	402	622
% Empty	42.9	57.0	48.3	38.2	38.0	40.5	44.2
3rd QUARTER							
Number of stomachs	662	424	451	349	360	158	213
% Empty	44.0	38.0	46.1	46.4	56.9	51.3	56.8
4th QUARTER							
Number of stomachs	952	367	474	646	826	244	132
% Empty	53.0	42.0	41.6	47.2	47.0	48.4	43.2

Table 4.- Length range of main hake prey species by age class of their predator

Blue whiting	Predator hake age						
Length range (cm)	0	1	2	3	4	5	6+
<5	0	5	0	0	1	0	0
5-9	4	8	7	2	1	1	1
10-14	6	131	149	99	33	12	5
15-19	2	25	58	120	86	38	28
20-24	0	0	25	118	174	148	120
25-29	0	0	2	14	55	63	58
30-34	0	0	0	0	0	5	5
Total number	12	169	241	353	350	267	217
Mean Length	10.8	12.4	14.4	17.7	20.5	22.1	22.3
Horse mackerel	Predator hake age						
Length range (cm)	0	1	2	3	4	5	6+
5-9	3	10	12	6	0	2	0
10-14	0	5	34	25	3	2	1
15-19	0	0	3	3	3	4	2
20-24	0	0	0	0	0	0	6
25-28	0	0	0	1	0	1	6
Total number	3	15	49	35	6	9	15
Mean Length	8.3	9.1	11.1	11.6	14.2	14.8	22.3
Prey hake	Predator hake age						
Length range (cm)	0	1	2	3	4	5	6+
<5	5	0	0	0	0	0	0
5-9	9	8	0	0	0	0	0
10-14	5	18	6	7	0	0	1
15-19	2	6	3	2	0	0	0
20-24	0	0	5	3	1	1	0
25-28	0	0	0	0	1	0	1
Total number	21	32	14	12	2	1	2
Mean Length	8.4	11.9	16.4	15.2	23.0	20.0	29.5

Table 5.- Daily ration in percentage of body weight of hake by quarter and age class

	Age 0	Age 1	Age 2	Age 3	Age 4	Age 5	Age 6+
1st Quarter	4.42	2.14	2.48	1.94	1.69	1.34	1.19
2nd Quarter	2.53	1.50	2.47	2.58	1.98	1.67	1.32
3rd Quarter	2.83	4.02	2.83	2.26	1.35	1.24	1.21
4th Quarter	1.89	3.75	2.43	1.74	1.55	1.25	1.18

Table 6.- Hake quarterly consumption, g ww, of each major prey group and quarterly energy consumption, kJ (continues)

QUARTER 1							
PREY	Age 0	Age 1	Age 2	Age 3	Age 4	Age 5	Age 6+
Antonogadus macrophtalmus	6.0	3.2	1.7	0.0	0.0	0.0	0.0
Gadiculus argenteus	7.4	5.8	3.9	15.7	2.4	26.4	15.9
Micromesistius poutassou	0.0	4.5	108.9	390.1	602.4	593.4	887.7
Merluccius merluccius	2.5	6.6	13.5	0.0	0.0	0.0	3.6
Trachurus trachurus	2.6	32.0	153.2	26.3	11.9	23.3	27.2
Clupeoids	0.0	0.0	0.0	0.0	33.6	0.0	0.0
Other fishes	10.7	29.8	61.8	82.3	86.7	176.7	335.2
Shrimps	24.8	24.8	4.6	3.2	0.9	9.0	12.2
Krill	13.2	7.2	0.3	0.8	0.0	0.0	0.0
Other crustaceans	0.0	0.4	0.0	0.0	0.4	6.0	0.0
Cephalopods	8.0	1.7	0.0	0.0	0.0	1.3	0.0
Total food, g ww	**75.2**	**116.0**	**347.8**	**518.3**	**738.4**	**836.1**	**1281.7**
Mean energy density, kJ/g ww	4.9	5.8	6.1	5.3	5.3	5.2	5.3
Total energy consumption, kJ	**370**	**670**	**2127**	**2737**	**3934**	**4360**	**6794**

QUARTER 2							
PREY	Age 0	Age 1	Age 2	Age 3	Age 4	Age 5	Age 6+
Gadiculus argenteus	3.1	1.4	5.9	2.8	4.4	0.3	13.3
Micromesistius poutassou	4.9	11.3	190.5	587.4	778.6	993.2	1005.3
Merluccius merluccius	4.2	0.0	2.5	16.5	2.7	6.0	13.8
Sardina pilchardus	1.9	8.4	3.9	0.0	0.0	0.0	0.0
Engraulis encrasicholus	0.3	11.3	0.0	2.6	8.5	7.2	8.3
Trachurus trachurus	0.0	2.7	42.9	24.6	24.0	8.0	147.2
Scomber scombrus	0.0	0.0	0.0	0.0	0.0	4.8	70.5
Other fishes	10.0	19.5	74.5	113.3	121.7	98.9	248.9
Shrimps	8.9	20.9	11.6	2.8	5.4	6.1	4.7
Krill	7.2	0.7	0.3	0.3	1.0	1.5	0.6
Other crustaceans	0.6	0.4	1.1	0.6	2.7	0.0	0.0
Cephalopods	4.7	6.1	0.0	0.0	0.0	0.2	0.5
Gastropods	0.1	0.0	0.0	0.0	0.0	1.2	0.0
Polychaets	0.0	0.0	0.4	0.2	0.0	0.0	0.0
Total food, g ww	**45.9**	**82.8**	**333.6**	**751.0**	**948.9**	**1127.4**	**1513.1**
Mean energy density, kJ/g ww	5.1	5.9	5.8	5.4	5.4	5.3	5.6
Total energy consumption, kJ	**235**	**490**	**1938**	**4084**	**5162**	**6000**	**8468**

Table 6.- (Continued) Quarterly consumption, g ww, of each major prey group and quarterly energy consumption, kJ, by hake from ICES division VIIIc, as estimated by the gastric evacuation method.

	QUARTER 3						
PREY	Age 0	Age 1	Age 2	Age 3	Age 4	Age 5	Age 6+
Gadiculus argenteus	14.4	12.2	4.9	5.7	0.2	22.2	6.8
Micromesistius poutassou	7.1	188.2	321.6	547.7	610.2	826.8	1143.9
Merluccius merluccius	3.2	20.5	3.6	15.8	0.0	0.0	0.0
Trachurus trachurus	0.2	0.0	0.0	5.7	6.2	0.0	0.0
Scomber scombrus	0.0	0.0	46.4	35.9	4.9	0.0	78.3
Other fishes	8.9	24.5	41.3	47.3	23.1	17.1	43.1
Shrimps	5.1	7.0	5.4	1.6	0.3	6.1	12.0
Krill	2.6	0.0	0.0	0.0	0.0	0.0	0.0
Other crustaceans	0.4	0.3	1.2	0.3	0.0	3.2	0.0
Cephalopods	2.2	0.0	0.0	0.7	5.1	0.0	49.8
Total food, g ww	**44.3**	**252.7**	**424.3**	**660.7**	**649.9**	**875.5**	**1333.9**
Mean energy density, kJ/g ww	5.1	5.1	5.1	5.1	5.1	5.0	4.9
Total energy consumption, kJ	**227**	**1280**	**2148**	**3344**	**3285**	**4400**	**6602**

	QUARTER 4						
	Age 0	Age 1	Age 2	Age 3	Age 4	Age 5	Age 6+
Gadiculus argenteus	2.4	1.2	2.7	3.1	3.1	7.9	6.8
Micromesistius poutassou	3.1	162.0	244.5	397.2	621.2	624.5	969.4
Merluccius merluccius	1.8	11.2	43.1	14.8	10.6	0.0	0.0
Sardina pilchardus	0.0	0.0	7.2	18.1	27.7	100.8	149.8
Engraulis encrasicholus	0.7	33.3	34.1	2.1	1.8	0.0	0.0
Trachurus trachurus	0.0	3.2	39.9	38.1	19.6	71.9	171.0
Other fishes	8.5	27.9	35.9	52.7	42.5	33.8	121.9
Shrimps	7.1	5.1	0.7	1.2	1.4	2.0	0.0
Krill	1.9	0.0	0.4	0.0	0.2	0.0	0.0
Other crustaceans	1.2	0.1	0.0	0.0	0.7	4.7	0.0
Cephalopods	2.1	0.2	0.0	0.1	0.4	0.6	0.0
Total food, g ww	**28.8**	**244.3**	**408.5**	**527.2**	**729.3**	**845.9**	**1418.9**
Mean energy density, kJ/g ww	5.5	5.3	5.4	5.3	5.1	5.5	5.7
Total energy consumption, kJ	**158**	**1293**	**2220**	**2811**	**3704**	**4653**	**8149**

Table 7.- Number of blue whiting prey of each length class (cm) consumed by a hake by quarter and age class[1]. Empty columns correspond to quarters without blue whiting consumption

Length (cm)	Age 0				Age 1				Age 2				Age 3				Age 4				Age 5				Age 6+			
Quarter	1	2	3	4	1	2	3	4	1	2	3	4	1	2	3	4	1	2	3	4	1	2	3	4	1	2	3	4
<5		0	0	0	0	0.78	0.19	0	0	0	0	0	0	0	0	0	0	0.19	0	0	0	0	0	0		0	0	0
5-9		0	0.48	0	0	1.17	0.38	0	0	0	0.88	0	0	0	0.16	0	0	0	0.07	0	0	0	0.14	0		0.10	0	0
10-14		0.98	0.48	0.10	0.72	15.93	8.38	0	0.58	17.23	7.83	0.16	0.38	8.79	4.34	0.19	0.00	1.50	1.70	0.30	0.21	0.92	0.86	0		0.10	1.83	0.50
15-19		0	0.12	0.10	0.14	1.36	3.24	1.25	0.58	3.65	3.91	6.58	2.50	6.07	3.06	6.27	1.39	1.88	2.48	3.64	1.27	1.84	1.14	2.24		1.74	2.44	1.51
20-24		0	0	0	0	0	0	0.89	2.31	0.81	1.01	2.96	7.50	3.35	3.62	4.18	6.59	5.08	6.16	4.85	6.44	8.58	6.13	5.98		7.94	10.97	6.05
25-29		0	0	0	0	0	0	0.18	0.29	0	0	0	0.58	0.84	0.56	1.52	3.12	1.88	1.34	1.21	4.43	2.14	1.43	4.49		3.49	3.05	5.54
30-34		0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0.32	0	0.29	0		0.48	0	0
Total		0.98	1.08	0.20	0.86	19.24	12.19	2.32	3.76	21.69	13.63	9.70	10.96	19.05	11.74	12.16	11.10	10.53	11.75	10.00	12.67	13.48	9.99	12.71		13.85	18.29	13.60

[1] Blue whiting length-weight relationship: $W = 0.0032 \cdot L^{3.1933}$ M. Meixide Instituto Español de Oceanografía, Vigo (Comm. Pers.)

Table 8.- Number of horse mackerel prey of each length class (cm) consumed by a hake by quarter and age class[2]. Empty columns correspond to quarters without horse mackerel consumption

| Length (cm)	Age 0				Age 1				Age 2				Age 3				Age 4				Age 5				Age 6+			
Quarter	1	2	3	4	1	2	3	4	1	2	3	4	1	2	3	4	1	2	3	4	1	2	3	4	1	2	3	4
5-9	0.38	0.06	2.20	0	1.62	1.06	0		2.48	0	0			0.55	0	0		0	0	0	0.65	0	0					0
10-14	0	0	1.26	0.17	0	8.80	1.81		1.38	0.69	1.40			1.56	0	1.09		0.38	0.45	0.10	0	0	0.11					0
15-19	0	0	0	0	0	0.35	0.45		0.28	0.46	0			0.09	0.36	0		0.38	0.45	0.20	0.32	0.92	0					0.84
20-24	0	0	0	0	0	0	0		0	0	0			0	0	0		0	0	0	0	0	0.44					1.67
25-28	0	0	0	0	0	0	0		0	0	0			0.09	0	0		0	0	0	0.32	0	0.67					0
Total	0.38	0.06	3.46	0.17	1.62	10.21	2.26		4.14	1.15	1.40		*	2.29	0.36	1.09	**	0.76	0.90	0.30	1.29	0.92	1.22					2.51

[2] Horse mackerel length-weight relationship: $W = 0.013 \cdot L^{3.1933}$ (Fariña, 1983)

(*) One hake from age class 3 consumes 5.7 g of horse mackerel, but there are no data on length distribution

(**) One hake from age class 4 consumes 6.2 g of horse mackerel, but there are no data on length distribution

Table 9.- Number of hake prey of each length class (cm) consumed by a hake by quarter and age class. Empty columns correspond to quarters without hake consumption. Older ages of hake are omitted given the small importance of hake canibalism and the small sample size on length distibution

Length (cm)	Age 0				Age 1				Age 2				Age 3			
Quarter	1	2	3	4	1	2	3	4	1	2	3	4	1	2	3	4
<5	0	0.61	0	0.09	0	0	0	0	0	0	0		0	0	0	
5-9	0	0.61	0.17	0.09	0	0.39	0.29	0	0	0	0		0	0	0	
10-14	0.24	0.31	0	0.17	0.56	0.70	0.68	0	0	0.06	0.73		0	0.50	0.37	
15-19	0	0	0.09	0	0	0.39	0.10	0.32	0	0	0.29		0	0.33	0	
20-24	0	0	0	0	0	0	0	0	0.05	0.06	0.44		0.34	0	0.18	
25-26	0	0	0	0	0	0	0	0	0	0	0		0	0	0	
Total	0.24	1.53	0.26	0.35	0.56	1.48	1.07	0.32	0.05	0.12	1.46		0.34	0.83	0.55	
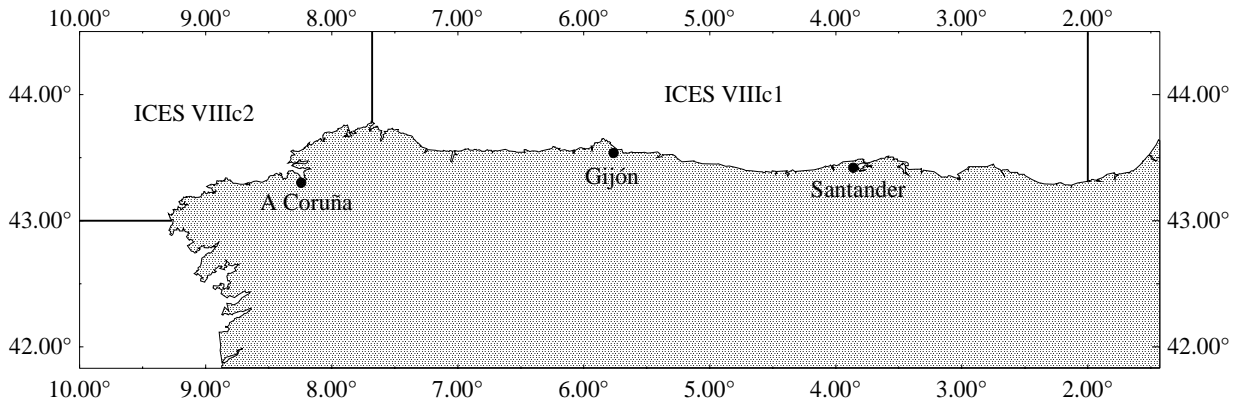
Figure 1.- ICES Division VIIIc with Subdivisions VIIIc1 and VIIIc2 and temperature sampling areas (off A Coruña, Gijon and Santander)
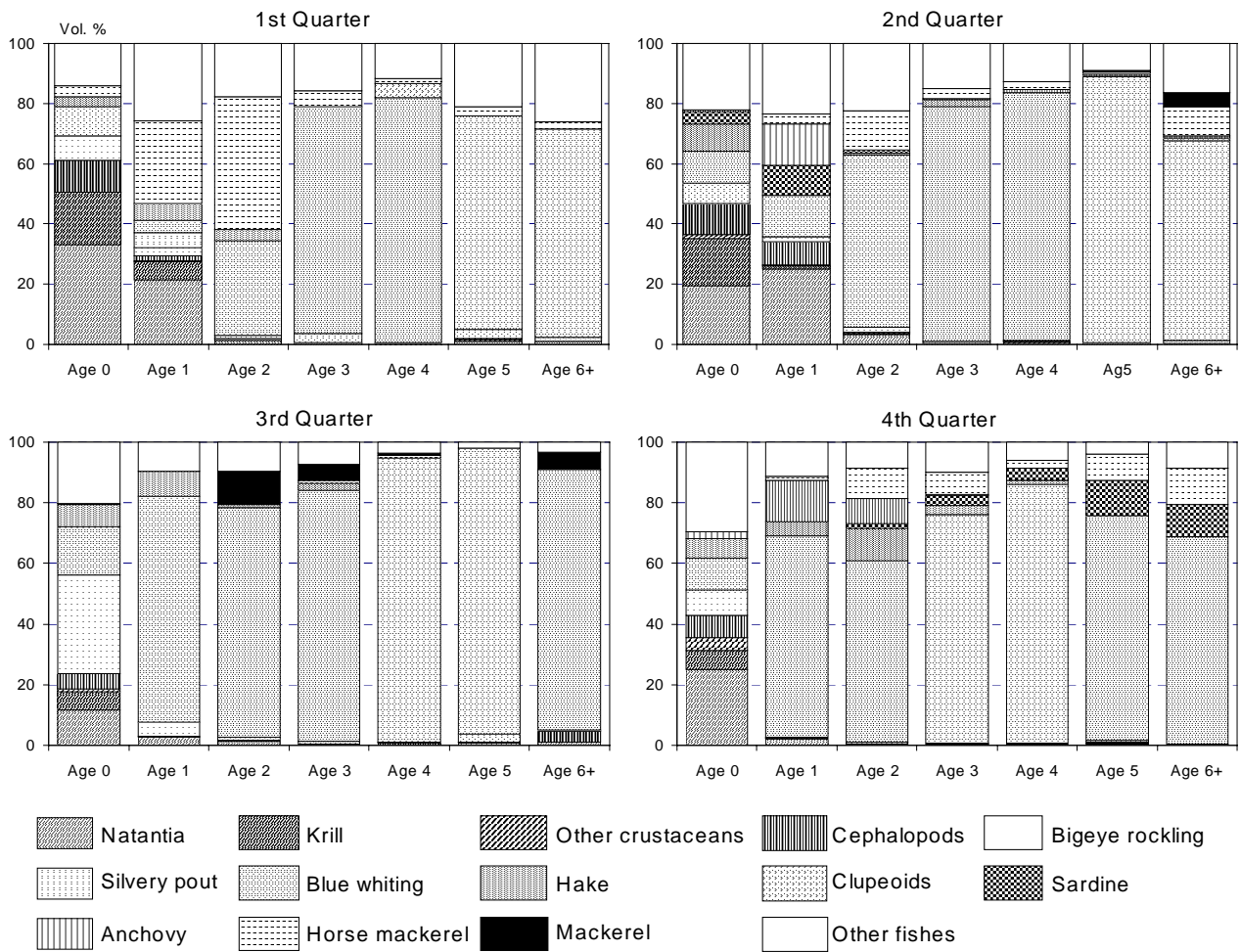
Figure 2.- Diet composition (volume %) of hake by age class and quarter
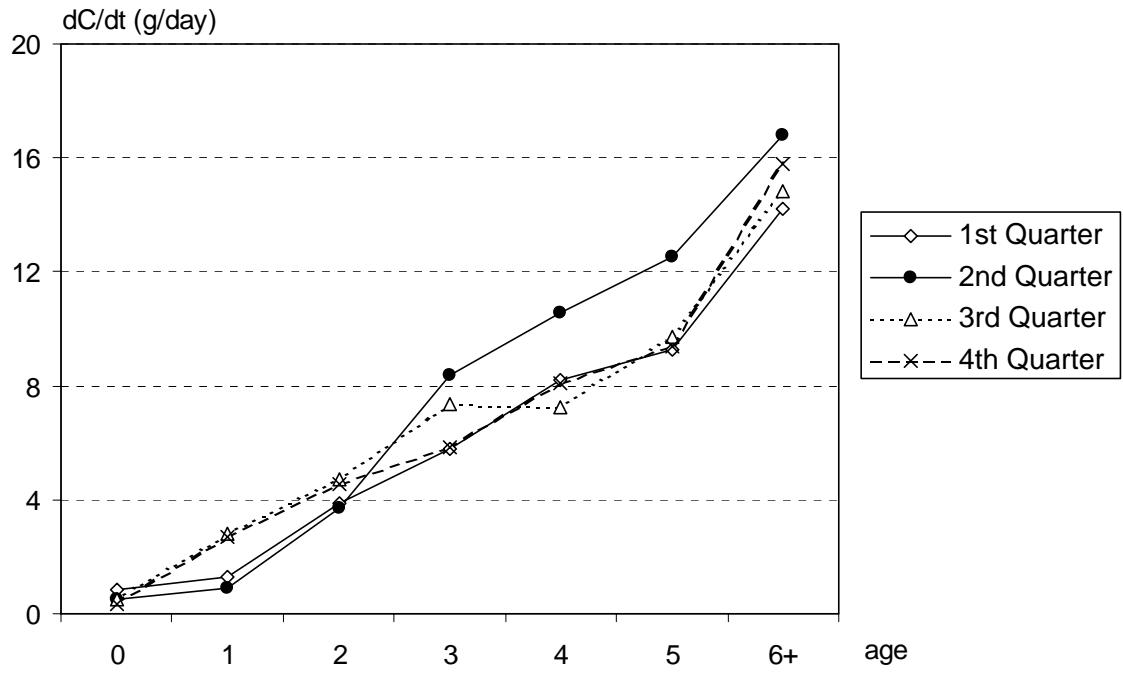
Figure 3.- Hake daily ration by age class and quarter