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Predation by Benguela hake (*Merluccius polli*) on commercially exploited shrimps (*Parapenaeus longirostris* and *Aristeus varidens*) in Angolan waters.

By

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Abstract

In order to evaluate the impact of *Merluccius polli* on the commercially exploited shrimps (*P. longirostris* and *A. varidens*), the seasonal consumption of these species by hake was estimated. A total of 1138 stomachs of fish over range of 10 to 59 cm and representing five age groups were examined. 28% of the stomachs collected were empty, with higher incidence in the size groups 20-29 and 30-39 cm. The relative importance and the total consumption in tonnes shows that this hake feeds mainly on fish, shrimps and cephalopods, with some preference for Myctophidae. The changes in prey species and its length size increase with increasing length of the predator and prey availability. The consumption of shrimps was higher than fish during summer (47.1%), and decreased to 32.2% during winter, related to the decrease in consumption of *P. longirostris*. The presence of this prey species in the stomachs sampled between 400-800 m during both seasons apparently justifies the vertical migration of hake. 41.6 % of the variance was between individuals caught in the same haul.

Keywords: Consumption, Hake, shrimps.

1. Introduction

Benguela hake (*Merluccius polli*) is part of the by-catch in the important fishery for deep sea shrimp on the coast of Angola. Commercial trawling for shrimps takes place between 05° S and 12° S, a region which also comprises part of the area of distribution for Benguela hake. This is the most important commercial fish in the by-catch and is mainly caught along the slope area (Pshenichnyi, Abramov and Pupyshev, 1987). Oleachea and Formoso (1980) considered that it is not very abundant, but could represent a profitable industry.

A study based on the research surveys sponsored by the Europeen Community and conducted by commercial Spanish vessels in the period 1989 to 1991 showed that the relative importance of striped shrimp (*A. varidens*) and *M. polli* in average weight of the catch is 11 % and 9 % between 500-600 m depth, and 8 % and 9 % between 600-700 m of depth respectively. Between 200-300 m, the relative importance in average weight of *M. polli* is 11 %. Rose shrimp (*P. longirostris*) was the dominant shrimp species with 2 % of the catch weight in average (Vaz Velho 1995).
The observed co-occurrence of hake, rose shrimp (*P. longirostris*) and striped red shrimp (*A. varidens*) seems to support the hypothesis that hake is one of the possible shrimp predators (Anon., 1994).

Many studies on Benguela hake have been carried out in Angolan waters, but the emphasis has been placed on its population dynamics (Oleachea and Formoso, 1980; Macpherson and Roel, 1988; Pshenichnyi, Abramov and Puryshev, 1987). However, little is known about food and feeding habits of this species.

2. Objectives

Research conducted in the 1970's has provided the evidence that piscivorous fish may not only have a major impact on year class success of species taken as prey, but that these predators may consume larger quantities of species of commercial interest than are harvested by the fisheries (Bowman, R.E. 1986).

The purpose of this study is to investigate the effect (impact) of Benguela hake predation on shrimp stocks of *A. varidens* and *P. longistris*. Emphasis was put on analysing the stomach contents and variations in diet by area, season and length group. In addition, the hake consumption of shrimps was quantified and the impact on the shrimp stocks was evaluated. Also due to potencial importance of Benguela hake as source of protein, sustained supply of this resource could benefit from future management advices.

3. Material and methods

3.1. Area and surveys

Stomach samples were collected during surveys with R/V "Dr. Fridtjof Nansen" along the Angolan coast, from Cabinda to Benguela (Fig.1). The first set was collected from 11 March to 2 April 1995 (summer season), and the second in August 1995 (winter season). The sampling gear was a "Gisund super bottom trawl", with a head line of 31 m, footrope 47 m and 20 mm meshsize in the codend with an innernett of 10 mm meshsize (Anon., 1994). The continental slope was covered with swept-area hauls and stations were randomly spread within each stratum. Strata were organized in following depth intervals: 100-400 m and 400-800 m.

Table 1 presents the number of stomachs sampled by season,day/night, depth zone and predator size group.

3.2. Sampling strategy

The aim was to collect up to 10 stomachs of Benguela hake for each 5 cm lengthgroup on each station. Fish showing evidence of regurgitation was, if possible, replaced with non-regurgitating feeding fish. Stomachs were removed carefully by a longitudinal incision along the mid ventral line, put in small labelled polyethylene bags, and frozen separatly as soon as possible after sampling. Data on each individual predator (length, weight, sex, maturity stage and number caught of the same length per trawl) were recorded together with the station data. The stomach contents were visually classified according to their degree of fullness, from empty to total full (i.e., 0= empty, 1= quarter full, 3= three quarter full, and 4 completly full). The state of digestion was classified from fresh to completly digested (i.e., 0= fresh, 1= one-third digested, 2= two-third digested, 3= completly digested).

3.3. Laboratory procedures

In the laboratory the stomachs were opened and formalin washed out. Fishprey and shrimps were identified to species level when possible. Each recognizable prey species, genus, family or higher order were split into size-classes and damp dried on bibulos paper. Numbers and total wet weight, measured to the nearest milligram, were recorded for each size-class and prey category separately. In many instances, the fish are partially digested, but their head and other skeletal parts remain clearly identifiable. These parts and other external characters may be used to identify the fish species (Godssii, 1954; Munro, 1955; Watanabe, 1964; Fisher and Bianchi, 1984; Smith and Heemstra, 1986), cited by Maldeniya (1992). The weight of partly unidentified prey at different taxonomic levels was redistributed

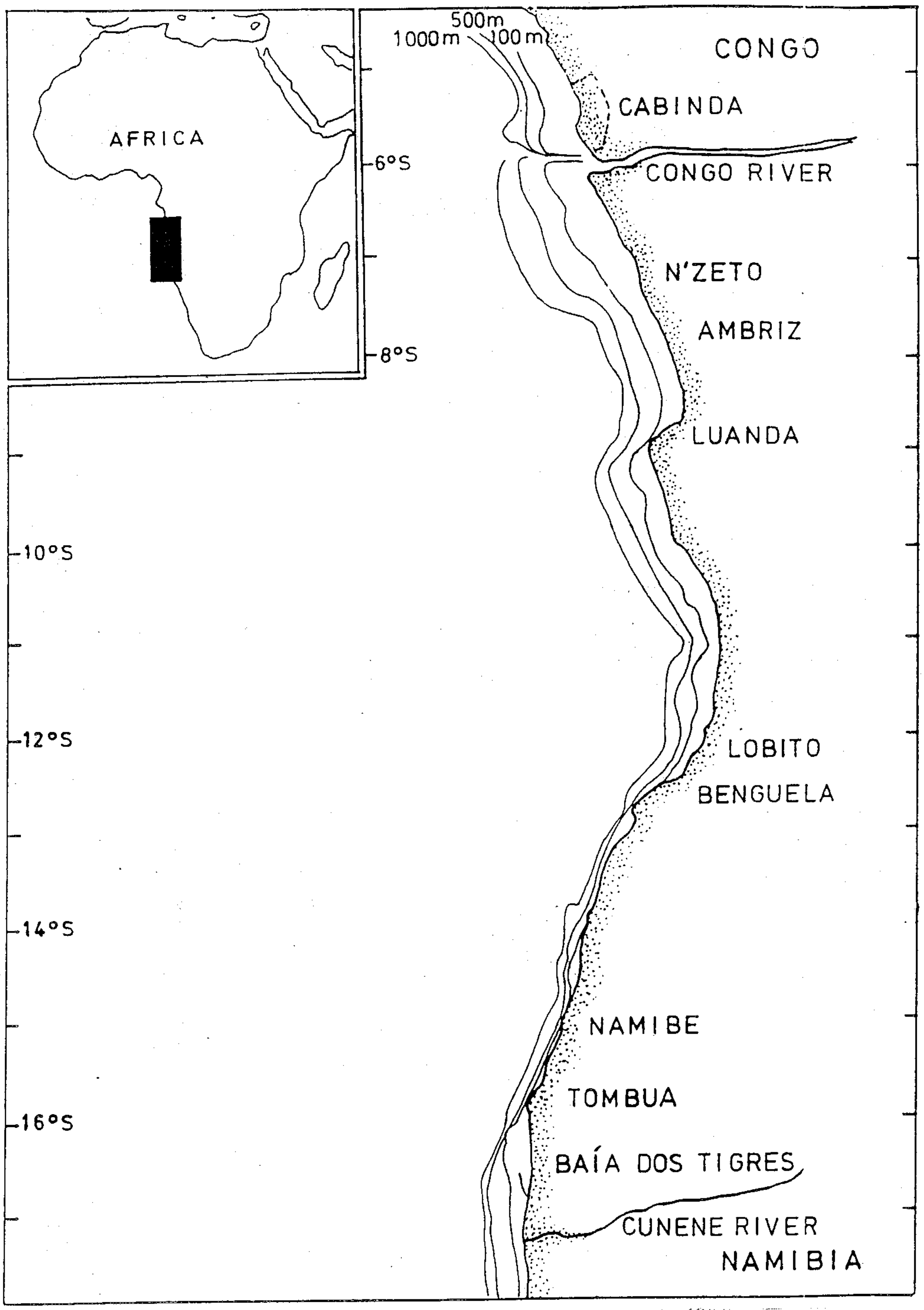


Figure 1. Location of the Angolan coast. (Redrawn from Dias and Machado, 1973).

proportionally among the various identified components. The totally unrecognizable components were apportioned among the identified taxonomic groups.

Table 1: Number of hake stomachs sampled by season, day/night, depth and predator size group. 1=10-19 cm, 2=20-29 cm, 3=30-39 cm, 4=40-49 cm, 5=50-60 cm.

Warm season							Cold season						
a. All stations													
Pradator size group							Predator size group						
	1	2	3	4	5	Tot		1	2	3	4	5	Tot
Nr	10	19	19	23	2	73	Nr	1	28	31	24	7	91
Ns	31	157	220	126	2	535	Ns	2	277	240	77	7	603
Ne	6	58	82	39	1	186	Ne	0	62	54	20	1	137
b.Days													
	1	2	3	4	5	Tot		1	2	3	4	5	Tot
Nr	9	13	9	7	2	40	Nr	1	27	27	14	2	71
Ns	26	104	65	16	2	213	Ns	2	261	230	42	2	537
Ne	5	40	18	4	1	68	Ne	0	59	52	9	0	120
c.Nights													
	1	2	3	4	5	Tot		1	2	3	4	5	Tot
Nr	1	6	10	16	-	33	Nr	-	1	4	10	5	20
Ns	5	53	155	110	-	322	Ns	-	16	10	36	5	66
Ne	1	18	64	35	-	118	Ne	-	3	2	11	1	17
d.0-399 m													
	1	2	3	4	5	Tot		1	2	3	4	5	Tot
Nr	10	17	12	6	2	47	Nr	1	22	22	12	3	60
Ns	31	151	164	46	2	394	Ns	2	215	191	34	3	445
Ne	6	55	56	15	1	133	Ne	-	43	47	9	-	99
d.400-800 m													
	1	2	3	4	5	Tot		1	2	3	4	5	Tot
Nr	-	2	7	17	-	26	Nr	-	6	9	12	4	31
Ns	-	6	56	79	-	141	Ns	-	62	49	43	4	158
Ne	-	3	26	24	-	53	Ne	-	19	7	11	1	38

Ns; number of stomachs, Ne; number of empty stomachs, Nr; number of stations.

3.4. Analysis

To estimate the contribution of various factors to the total variability in stomach content weight, The coefficient of variaton (CV) was used as a mesure of variability since it appeared to be nearly independent of size class(Jiang, W. and Jorgensen, T.1995). If two or more fish in the same size class were caught in the same haul, the sample CV was calculated. The average of all such values over all length classes was used to estimate the variability between sample. In a similar proccedure, variability between hauls and seasons were also calculated. From these values the percentage contribution of each factor to the total variance in stomach content weight was estimated.

The contribution of prey types was assed by estimating the Index of Relative Importance (IRI) (Pinkas *at al.*, 1971). The IRI was calculated as follows:

$$IRI = (\%N + \%W) * \%F$$

Where: %N= Percentage by number, %W= Percentage by weight, %F= Percentage frequency of occurrence.

The percentage of the number of a given prey item to the total number of individuals in all prey items found is defined as the "percentage by number".

The average wet weight (grams) of each prey item per size class of hake was estimated as follows;

$$Wij = \sum_{k=1}^{ni} Xijk/Ni$$

Where Wij= average total wet weight (g) of prey category j in predator size class i, Xijk= the weight of each individual prey item in the category j found in each stomach (k), ni= the number of stomachs with food in size class i, Ni= the total number of stomachs in size class i (including empty).

The 95% confidence intervals for the estimated average weight were calculated using the normal approximation (point estimate + or - 1.96 standar error), (Bhattacharyya and Johnson, 1977).

The percentage average wet weight of each prey item (j) in predator size class i, to the total weight of all prey items in that class was used as the weight percentage. The %W was calcuated as follows:

$$\%W = (Wij \;/\; \sum_{j=i}^{ni} Wi) * 100$$

The biomass of hake was calculated using the equations :

$$Bs=\overline{ds} * A$$

$$\overline{ds}= 1/Nq*(\sum_{I\in S} Ysi/ai)$$

Where: $\overline{ds}$ is an estimate of the mean density per unit area in the sea area , A is the area covered by the survey, ai is the area swept by the trawl , N is the number of trawl stations, Ysi is the weight of species s caught per hour in trawl station i, and q is the catchability coefficient (proportion of the fish in the path of the gear that were caught, normally set to 1).

The number of individuals was `calculated as follow:

$$N= \sum_{j} \overline{A}j(\sum_{I(j)}(nl,i,j\ Xij) / (Zi,j\ Ai,j)) / \sum_{I(j)} l)$$

Where N is an estimte of the number of fish in length-class l;

$\sum_{j}$ indicates summation over all depth strata j;

$\sum_{i(j)}$ is summation over all station i in stratum j;

Ai,j is the total area swept by the trawl at the *ith* station in stratum j - calculated taking the trawl time, vessel speed and net opening into account;

$\overline{A}j$ is the area of depth stratum j;

nl,i,j the number of fish from the trawl at the *ith* station in stratum j which were measured to be in length-class l;

Xij is the total mass of hake caught by the trawl at the *ith* station in stratum j;

Zij is the mass of hake caught by the trawl at the *ith* station in station j which was measured.

Then, the hake stock's food consumption was estimated using mainly the same method of calculation as Mehl and Westgard (1983). The consumption in tonnes of prey species i, by predator size group j in season k, Cijk is given by:

Cijk= 2 *(Wijn * Xjk * days of season)/D(i)

Where

D(i) = digestion time in days for prey species i

For the evacuation time the values used by Payne *et al* (1987) were used for Cape hake (i.e., fish 3 days, cephalopods 1.5 days and crustaceans 1 days).

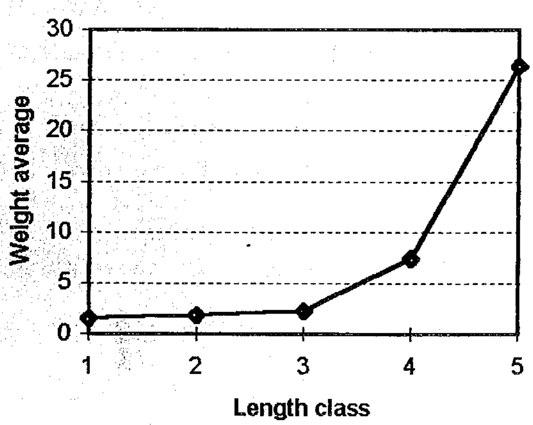
Wijk = mean stomach content in grams of prey species i in season k for predator length group j.

Xjk = number of individuals of predator length group j in season k.

4. Results

4.1. Variability in the weight of stomach content

Figure 2a and b shows the coefficient of variation versus fish size and average weight versus fish size respectively. The CV was



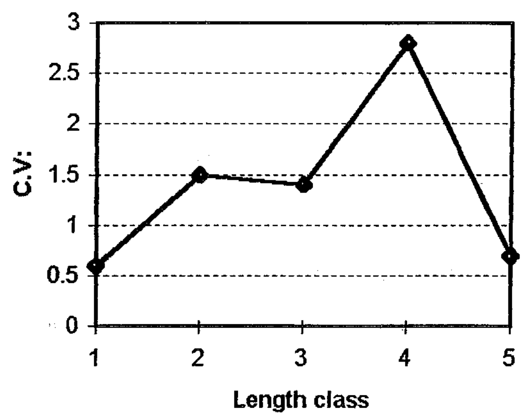


Figure 2 a-b. Mean stomach content weight versus length class (a) and coefficient of variation versus length class (b). 1=10-19cms, 2=20-29 cms, 3=30-39 cms, 4=40-49 cms and 5=50-59cms.

found to be independent of fish size (Kruskal-Wallis test, Batthacharyya and Johnson, 1977). The calculation of the percentage contribution of each source of variability showed that 41.6% of the variance in stomach content weight was between individuals caught in the same haul, while the remaining variance was quite equally distributed between the factors area, season and year (Table 2).

Table 2.Average over size classes of coefficient of variation for various levels and sources of variability of stomach content for fish of the same length.

Level	Average C.V.	Source of variability	Percentage of the total
Within a sample	0.92	Between individuals	41.6
Within a haul	1.22	Between hauls	18.8
Within a season	1.49	Seasonal	18.4
Total	1.58	Yearly	21.2

4.2. Food and feeding habits

Only 323 (28%) of the 1138 fish examined had empty stomachs. The number of hake stomachs sampled in each season are given in the Table 1. Within a year, the proportion of empty stomachs within a predator length class was significantly different between both seasons (warm and cold) in 7 of 8 cases tested (Chi-square test, Battacharyya and Johnson,1977). The proportion ranged from 19 to 50% for the warm season, and from 0 to 31% for the cold season. This difference was partly caused by the lack of fish <20 cm during the cold season. The adult fish >50 cm were poorly represented during both seasons. Within a season, a significant difference was found within a length class between days, nights and strata (0-399, 400-800 for all the cases tested(Chi-square test).The comparison between days and nights shows that the percentage of empty stomachs is higher for fish between 30-50 cm during the night in the warm season, and lower for fish between 20-40 cm during the nights in the cold season. The comparison between strata (0-399 m and 400-800 m) shows highest percentage of empty stomachs between 400-800 m during warm season in the size groups 20-29 cm and 30-39 cm. The strata between 0-399 m shows a slight increase in empty stomachs through size groups during winter.The highest percentage of empty stomachs between 0-399 m was found in the size group 50 - 59 cm during summer.

4.2 Diet composition

Table 3 presents the prey species found in the stomachs. Considering its insignificant contribution, data of Euphausiacea are not analysed further in this work.
Due to the opportunistic feeding habits of hake (Payne et al. 1987; Roel *et al.*, 1988), the main constituents of hake diet are fish, particulary Myctophidae, crustaceans and cephalopods (Table 6-7). Values of the index of relative importance show that fish are the main food components of hake stomachs, shrimps constitute

the next important food item, and cephalopods are of minor importance in the diet of hake.

Table 3: List of prey items found in hake stomachs in Angolan waters in 1995.

Main taxon	Family	Especies
Crustacea	Euphausiacea	*Euphausia spp.*
	Nematocarcinidae	*Nematocarcinus africanus*
	Aristeidae	*Aristeus varidens*
		Plesiopenaeus edwardsianus
	Penaeidae	*Parapenaeus longirostris*
Cephalopoda	Octopodidae	*Octopus spp.*
	Ommastrephidae	*Todaropsis eblanae*
		Illex coindetii
Pisces	Merluccidae	*Merluccius polli*
	Gonostomatidae	*Gonostoma denudatum*
		Triplophos hemingi
	Trichiuridae	*Trichiurus lepturus*
		Benthodesmus tenui
	Myctophidae	(Myctophidae)
	Acropomatidae	*Synagrops microlepis*
	Macrouridae	*Coelorinchus coelorinchus*
		Hymenocephalus italicus
	Apogonidae	*Epigonus telescopus*
	oOphidiidae	*Brotula barbata*
		Nemicthtys curvirostris

4.3. Feeding in relation to predator length groups

The five length groups ranged from 10 to 60 cm. Tables 4 - 5 summarize the composition of food in the length groups, by average weight, standard deviation, confidence limits, weight percentage, number percentage, frequency of occurrence, and index of relative importance. Within a season, the average weight consumed by hake was significantly different trough size class in all the cases tested (Chi-square test, Battacharyya and Johnson, 1977).The data show that in the first group (juveniles), diet consists of shrimps and myctophidae during the warm season, and only Myctophidae during the cold season. The diet of adult hake is variable and its relative importance of each item varies according to its local abundance in the fauna. The most important prey were fish, and Myctophidae was the most commonly occurring in hake between 10 and 40 cm, while *P. longirostris* and *A. varidens* were more important for hake between 40 and 60 cm.

Cannibalism occurred in individuals > 30 cm. No significant difference was observed in average weight between seasons and length class in 6 of 10 cases tested (Kruskal-Wallis test).

4.4. Feeding in relation to depth

The distribution of preys by strata (0-400 m, 400-800 m) is given in the Table 6. Most of the preys occurred in both strata, except *S. microlepis, E. telescopus, C. coelorinchus, B. tenui and P. edwardsianus* which did not occure in the depth between 400 and 800 m. Myctophidae occured predominantly in both strata, with a significant increase during the cold season (58.4% between 0-400 m, 46.6% between 400-800 m). *P.longirostris* was the second most impotant prey, showing a decrease during the cold season (8.8% between 0-400, 10.1% between 400-800 m). The occurrence of this species in stomachs sampled between 400-800 m during the warm and cold seasons apparently justify the vertical migration of hake, since *P. longirostris* mainly is found between 0-400 m.

4.5 Seasonal variations

Seasonal variation of prey composition is given in Tables 4-5. Fish, principally Myctophidae, are most frequent in the stomach of hake during both seasons. It constitutes 70.4% of all prey for the small hake (10-20 cm) during the warm season, and 90% for fish of the 20-30 cm during the cold season. The proportional representation of this group varies from 29.1% to 70.4% in the diet of hake between 10-30 cm, and from 7.6% to 13.9% for the hake > 30 during the warm season. During the cold season Myctophidae varies from 2.2% to 42.7 % for the hake > 30 cm.
The shrimps *P. longirostris* and *A. varidens* were the second most important in the diet of hake, but their contribution decreased during the cold season. The contribution of the cephalopod *Octopus* in weight percentage increased signficantly during the cold season. There is some seasonal variation in hake as prey, and cannibalism was only observed in hake between 40-49 cm during the warm season.

4.6. Size distribution of the diet of hake

Intact or sightly digested prey was measured to study the variation in the prey size, data of the two seasons were pooled, and lenght data of the most elongated prey species were simply discarded, in order to prevent distortion during computation.
Figure 3 shows the distribution of the prey size by size-groups of hake. The minimum size of the prey did not vary so much, the minimum and the maximum size of the prey were between 2-39 cm, (excluding the most elongated prey as *Trichiurus sp*), and the average were between 4.5-18 cm. Myctophidae, the most common prey, showed highest average size in the predator length group

of 20-30 cm.

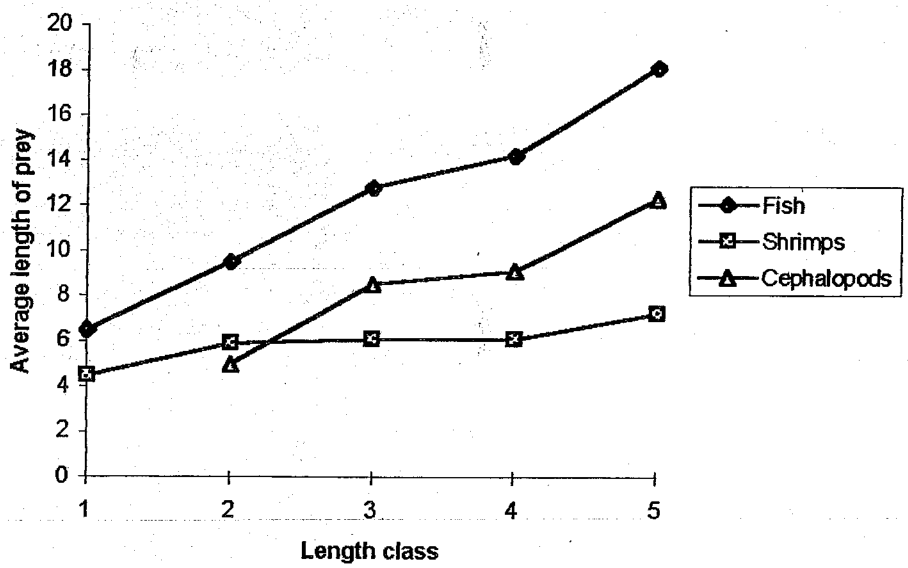


Fig 3. Distribuition of prey size by size-groups of hake.

5. Consumption of hake

5.1. Consumption of major prey groups

Table 7 summarize the hake stock's consumption by season and length groups. The annual consumption shows that fish were the most important prey (42.0), followed by shrimps (37.0%) , and cephalopods the last with 22.2%. Shrimps were the most important prey during the warm season, and the less important during the cold season.

Cephalopods' consumption increased significantly during the cold season. The inter-size difference shows that shrimps were most consumed by length groups II and III during summer, and by length group III during winter, while cephalopods were more consumed by length group IV during winter. Probably most of the difference in the consumption estimate is a consequence of differences in estimates of hake biomass (Punt, Lislie and Plessis, 1992). The biomass of hake was highest during winter.Table 8 shows the biomass and number of individuals by season and strata.

5.2. Consumption of the main prey species

Table 9 summarizes the hake stock's consumption of main prey species by season, depth strata and size-group.

Merluccius polli: The consumption of this prey was observed in hake length group 30-39 cm during summer, and distributed between both strata. However, it was mainly consumed by hake of the length 30-39 cm with a significant increase during the cold season, though only in the strata between 0-399 m. The total consumption was higher between 0-399 m (4.4%) and with only 0.69% between 400-800 m. Cannibalism did not occur in the deepest stratum during winter.

Gonostoma denudatum: This prey is of minor importance according to the frequency of occurrence. But the consumption was high between 400-800 m during both seasons (26.1% and 21.9% respectivelly). During summer this prey was prefered by size-group II, and by size-group III and IV during winter.

Myctophidae: This group constitutes the most important prey in the diet of hake. It was slightly more consumed between 400-800 m, showing its highest consumption during winter (49.1%). It was consumed by the size-group I to IV between 0-399 m, and by size group II to IV between 400-800 m. No clear trends were observed in the percentage of the total between the seasons in the depth stratum 0-399 m (27.6 and 26.6 respectively).

Synagrops microlepis: This is also one of the important prey species of hake. It was consumed in the depth zone 0-399 m during both seasons, showing highest percentage during winter (15.4%), due to the increase of fish consumption by hake and its availability throughout the distributional area of hake. It was consumed by the size-group II and III during summer, and by size group III and V during winter.

Nematocarcinus africanus: This species is one of the preferred shrimps in the diet of hake, and was found during all seasons and strata. In the cold season it was most heavily consumed between 400-800 m, showing its highest contribution (9.4%) during this period, with a significant decrease (3.1%) during the warm season in the same stratum. This specie was not eaten by the length groups I and V during both seasons,and heavily eaten by the length group II during summer between 0-399 m, and by the length group III during winter between 400-800 m of depth.

Parapenaeus longirostris: This commercially important shrimp also belong to the prey preferred by hake. In the warm season it was mainly consumed between 0-399 m, showing its highest contribution (29.3%) during warm season. A significant decrease was observed between 400-800 m during the warm season (12.4%). Its presence in this interval during winter is apparently due to the vertical migration of hake during this season, because of the relatively shallow distribution of this prey (0-400 m). The species was more consumed during summer by the length groups II and III.

Aristeus varidens: The consumption of this important commercial shrimp was also highest between 0-300 m (29.2%) during winter, and lower between 400-800 m during the warm season (17.3%). It was not found between 400-800 m during the cold season. This shrimp was not consumed by hake < 20 cm, due to the deep distribution of this shrimp species.

6. DISCUSSION

Sources of error

The sampling area included the whole area of the distribution for hake during summer (from Benguela to Cabinda), while the whole area was not covered during the winter cruise, covering only the area from Benguela to around Luanda. Moreover, the sampling intensity was higher during the winter and a lower percentage of empty stomachs was observed. Even considering the low varibility in the type of prey of hake, this fact may lead to a certain distortion of the diet.

According to Bromley (1989), the main sources of bias are likely to be regurgitation and feeding during capture. In cases where expansion of the swimblader has caused eversion of the stomach through the mouth, regurgitation is obvious, as it is if there is past-digested food in the bucal cavity, or the stomach is distended, thin walled and flacicid but is empty or only part-full. In this point there is possibility of regurgitated stomachs beeing classified as empty, causing the overstimation of the percentage of empty stomachs, and the average weight of the stomach content is understimated. For fish >40 cm, there is higher evidence of detectable regurgitation, but even for those fish showing no evidence of regurgitation there was a lower measurable stomach content in deep water.

Another source of error, (Jiang 1992), is post-capture digestion which might lead to understimation of the total amount of stomach contents. Contrary, feeding in the trawl may cause overstimation of the stomach content. Due to the procedure of the sampling during this work, those sources were not considered as major sources of error.

The evacuation times used differ between the three groups of prey species, they were assumed to be constant within each group and independent of prey length, ambient temperature and meal size. This will certainly lead to some further bias in estimates of annual consumption and daily ration. Also, the survey biomass estimates of the predator are known to be negatively biased because of net avoidance (De Alteris *et al.* 1989), the consumption estimates wil also be negatively biased (Punt *et al*, 1992).

The total consumption and daily ration can be calculated by a number of methods. Macpherson and Roel (1988) and Jobling (1986) pointed out that few of the parameters have been satisfactory estimated (rate of gastric evacuation, influence of prey and predator sizes, frequency of feeding, etc.). In this study hake was assumed not to feed continously, and remain trophically inactive between one periode of ingestion and the next, when the stomach has virtually emptied. According to Elliot and Person, cited by Macpherson and Roel(1988), this fact would not necessarily affect the model's results, when provided stomach samples are collected at intervals of 3 hours or less.

The composition of food in *M. polli* confirms the opportunistic nature of hake feeding. The diet consisted of a small number of item per stomach (i.e. 1-3prey species), with the highest percentage of single prey. The data show that hake feed mainly on fish, shrimp and cephalopods. Although, the relative importance of each item in different areas varies according to its local abundance in the fauna (Payne *et al*,1987). The higher percentage of empty stomachs, particularly for big fish (>40 cm) hauled at greater depth is supposed to be caused by regurgitation during trawling .

The data in the Tables 4 and 5 show that the small hake (10-19 cm) feed mainly on Myctophidae and small shrimps, most of these food items also occured in the stomachs of fish > 20 cm. The relative importance of each prey species changed with the size of the predator, but Myctophidae were dominant in all length groups, except for the group > 50 cm. This fact is related to the availability of this prey species and its homogeneous distribution through the distributional area of hake.The number of prey species was low for individuals > 50 cm, showing a slight index of cannibalism. As the metabolic activities decrease with age or size (Zeuthen, 1953), it becomes more beneficial for the larger fish to obtain more food at a lower rate of energy expenditures (Wahbeh *et al.*, 1985). The reduced number of prey species in the diet of large hake may also be related to the small number of fish sampled in this length group.

Most of the prey species occured in both strata. Some of the shallow waters prey species, as *P. longirostris,* occured in both strata, and cannibalism also occured in both strata during the cold season. Al these facts are probably related to the prey species availability, vertical migrations of hake for feeding or occasional changes in the environment, exemplifying the opportunistic feeding habits of hake.

Myctophidae were highly dominant during both seasons, apparently as a result of the high availability of this prey during the year 1995. The percentages by weight, number and frequency of occurrence were highest in the length group 10-19 cm during both seasons, and decreased with increasing length. This phenomenon is caused by the increase of prey availability with the increase of predator length size. Shrimps and cephalopods were more consumed during the warm season. Seasonal variation may occur when availability of important prey species seems to be at its

lowest level (Roel *et al*, 1988).
Cannibalism is slightly more common during the cold season. There is higher concentration of hake between 200-400 m during the cold season (Anon. 1994), and probably that cause the overlap of young and adult hake, increasing the rate of cannibalism.

The increasing average size of the prey eaten by hake (Fig.3) through length groups show that this predator selects the size of the prey according to its own size. The minimum and maximum size of the prey species were situated between 2-39 cm, however, the minimum size of the prey did not vary so much. This is apparently because small prey can be caught by either large or small predators. There is an apparent limit, determined by the size of the mouth of the predator, to the size of the prey (*Roel et al*, 1988).

In summer, the total consumption was somewhat higher than the hake's total biomass during this period (38.5%). On the contrary, in winter the total consumption was highest than the hake's biomass (58.8%). This fact is apparently related to the difference of temperature during both seasons (i. e., during the warm season the temprature is higher than during the cold season, and the digestion occur in shorter interval of time than during the cold season). Also, the biomass estimates of hakes may be affected by the vertical migration. This may also change according to season. According to the total consumption values, fish was the most important prey of hake, and shrimp the second most important. Cephalopods were of the minor importance in the diet. However, this prey was more important than shrimp during the cold season in the size group 50-59 cm. This fact may be related to the size of cephalopods specimens (big ones) consumed by hake, and also the reduced availability of shrimps during this period.

The small hake (10-19 cm) and the big hake (> 50 cm) showed low values of consumption. The gear evoidence by the small hake and the high percentage of regurgitation for hake > 50 cm are supposed to be the reason of this probable underestimation.

Hake was more consumed by the hake of the length group between 30-39 cm with a significant increase during the cold season, even reduced to the strata between 0-399. The main reason for this is the overlaping between small and big hake in that interval of depth, due to the vertical migrations and also the decrease in shrimp availability during this period.

Also the highest consumption of Myctophidae was observed during the cold season (49.1 %). Fisher *et* al. (1981) classified this prey species as abundant and widespread. As stated before, the decrease in shrimp availability dealed to the increased consumption of Myctophidae and other prey species by hake.

The shrimp *P. longirostris* was highly consumed between 0-399 m of depth during the warm season (Table 6), and the stratum covers the main distribution of this prey. One of the reason may be that this shrimp is not commercially exploited during February, and this break justifies the highest availability of this prey during this period.On the contrary, its consumption decreased to 1/4 in the same stratum during the cold season. This apparently explains the possible competition between hake and man (mortality from fishing and predation).It is also the reason of highest consumption of the *shrimp N.africanus* during this period.

7. Conclusions.

1. The lack of literature about the diet of hake (*M. polli*) in Angolan waters underlines the importance of this first attempt of studying the diet and estimating the consumption of this hake. Also the comparison (from literature) of this predator habits with the Namibian and South African *M. capensis* and *M: paradoxus* showed that there is something in common with these species, although *M. capensis* is a more water dweller.

2. The results of this study show that *M. polli* feed mainly on fish, shrimps and cephalopods according to the availability, and there is some preference for Myctophidae, *P. longirostris* and *A. varidens*.

3. The analysis of the diet showed that small hake (10-19 cm) feeds mainly on small Myctophydae and shrimps. The changes in prey species and its length size increase with increasing of length of the predator and prey availability.

4. The resuts suggested that there is significant seasonal changes in the consumption of the commercially exploited shrimps (*P. longirostris* and *A. varidens*). The consumption of shrimps decreased significantly during the cold season, apparently due to the competition between fishing mortality and predation by hake. Annual comparison of this diet *must* be *undertaken in order* to define the level of predation and fishing mortality.

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Table 4: Summary of food composition for *Merluccius polli* in the warm season expressed in average weight, standard deviation, confidence limites, weight percentage per predator (W) , numerical percentage per predator (N) and frequency of occurrence (Fo) by length class. The index of relative importance (IRI) is also shown.

L.gro.	Food item	Av	Sd.	Conf. Limit.	W (%)	N (%)	Fo	IRI
10-19 N=31	Myctophidae	1.1	0.98	0.63-1.57	47.0	67.65	54.8	0.7569
	Pisces	0.79	1.73	0-2.1	33.8	26.47	22.6	0.1188
	P.longirostris	0.45	0.07	0.35-0.55	19.2	5.88	6.5	0.0060
20-29 N=157	Myctophidae	0.86	0.77	0.64-1.08	2.213	38.73	29.9	0.2030
	S.microlepis	11.9	4.95	5.02-18.8	30.6	1.41	1.3	0.0024
	Pisces	0.93	1.26	0.38-1.48	2.39	23.24	13.4	0.0503
	B.tenui	17.2	0.28	16.8-17.6	44.2	0.70	0.6	0.0009
	N.africanus	0.6	0.24	0.27-0.93	1.54	1.41	1.3	0.0003
	P.longirostris	0.76	0.35	0.61-0.91	1.95	18.31	12.7	0.0375
	A.varidens	0.93	0.55	0.49-1.37	2.39	4.93	3.8	0.0035
	Caridea	0.6	0.24	0.39-0.81	1.54	7.75	3.8	0.0035
	I.coindetii	3.6	0.57	2.81-4.39	9.26	2.11	1.3	0.0009
	T.eblanae	1.5	0	-	3.86	1.41	1.3	0.0005
30-39 N=220	*G.denudatum*	37	0	-	45.6	0.43	0.5	0.0007
	T.lepturus	9.4	0	-	11.6	0.43	0.5	0.0002
	Myctophidae	1.04	1.38	0.62-1.46	1.28	22.84	19.5	0.0717
	S.microlepis	15.2	0	-	18.7	0.43	0.5	0.0003
	N.curvirostris	6.53	5.8	0.0-13.1	8.04	1.72	1.4	0.0013
	Pisce	1.71	2.63	0.38-3.04	2.10	9.48	6.8	0.0131
	T.hemingi	5.6	2.12	1.44-9.76	6.90	1.29	1.4	0.0011
	N.africanus	1.21	0.27	1.03-1.39	1.49	4.74	4.1	0.0029
	P.longirostris	0.75	0.4	0.63-0.87	0.92	25.43	19.5	0.0740
	A.varidens	1.47	1.21	1.04-1.90	1.81	19.40	15.5	0.0564
	Caridea	0.72	0.72	0.55-0.89	0.89	11.64	9.1	0.0155
	S.africanus	0.52	0.13	0.40-0.64	0.64	2.16	2.3	0.0007
40-49 N=126	*M.polli*	0.7	0.36	0.35-1.05	0.70	1.65	2.4	0.0052
	T.lepturus	7.8	0	-	7.78	0.55	0.8	0.0002
	Myctophidae	0.99	0.63	0.76-1.22	0.99	21.43	24.6	0.0713
	Pisce	2.64	3.14	0.47-4.81	2.63	9.89	5.6	0.0083
	B.barbata	5.3	0.28	4.91-5.69	5.29	1.10	1.6	0.0006
	N.africanus					3.30	3.2	0.0013
	P.longirostris	0.84	0.47	0.68-1.0	0.84	23.08	15.1	0.0349
	A.varidens	2.42	1.86	1.56-3.28	2.41	12.09	15.1	0.0349
	Caridea	1.76	1.35	1.05-2.47	1.76	23.8	11.1	0.0323
	P.edwardsianus					1.10	0.8	0.0001
	Octopus sp.	54.3	2.97	50.8-58.4	54.2	1.10	1.6	0.0044
	I.coindetii	2.2	0	-	2.20	0.55	0.8	0.0001
	T.eblanae	21.9	0.28	21.5-22.3	21.9	1.10	1.6	0.0019
50-60 N=3	*A.varidens*	1.85	0.07	1.75-1.95	100	100	33.3	0.6667

Table 5: Summary of food composition for *Merluccius polli* in the cold season expressed in average weight, standard deviation, confidence limits, weight percentage per predator (W) , numerical percentage per predator (N) and frequency of occurrence (Fo) by length class. The index of relative importance (IRI) is also shown.

L.gro.	Food item	Av	Sd.	Conf.lim.	W	N	FO	IRI
10-19 N=2	Mictophydae	2	0.14	1.81-2.19	100	100.0	100.0	2.0000
20-29 N=277	*T.lepturus*	4.3	0	-	27.6	0.19	0.4	0.0000
	Myctophydae	2.67	2.36	2.33-3.01	17.1	90.0	75.8	1.3647
	H.italicus	2.1	0	-	13.5	0.19	0.4	0.0000
	Pisce	1.02	0.81	0.66-1.38	6.54	3.71	6.9	0.0049
	N.africanus	0.67	0.3	0.45-0.89	4.30	1.48	2.5	0.0006
	P.longirostris	1.86	1.62	0.74-2.98	11.9	2.41	3.6	0.0019
	A.varidens	0.30	0	-	1.92	0.19	0.4	0.0000
	Caridea	0.87	0.5	0.43-1.30	5.58	1.48	1.8	0.0005
	S.africana	1.8	1.56	0.00-3.97	11.5	0.37	0.7	0.0001
30-39 N=240	*M.polli*	14.7	0	-	19.4	0.44	0.8	0.0003
	G.denudatum	12.6	2.75	9.92-15.3	16.7	0.89	1.7	0.0014
	T.lepturus	1.55	0.21	0.99-2.15	2.05	0.44	0.8	0.0001
	Myctophidae	3.30	2.57	2.78-3.82	4.36	53.1	45.8	0.4398
	S.microlepis	13.6	6.73	9.22-18.0	17.9	2.22	4.2	0.0086
	H.italicus	3.0	1.24	1.91-4.09	3.96	1.33	2.1	0.0007
	Pisce	3.58	3.69	1.58-5.58	4.73	4.89	5.4	0.0052
	E.lelescopus	10.9	0	-	14.4	0.22	0.4	0.0001
	N.africanus	1.4	0.97	0.83-1.97	1.85	4.00	4.2	0.0025
	P.longirostris	1.57	1.47	0.99-2.15	2.07	7.78	11.3	0.0150
	A.varidens	1.18	1.05	0.82-1.54	1.56	13.3	15.0	0.0282
	Caridea	1.16	0.87	0.80-1.52	1.53	7.78	9.2	0.0104
	S.africana	2.06	1.53	1.00-3.12	2.72	13.33	3.8	0.0021
	I.coindetii	5.10	2.55	1.56-8.64	6.73	0.22	0.4	0.0000
40-49 N=77	*G.denudatum*	27.0	16.0	15.2-38.8	11.8	4.73	9.1	0.0232
	T.lepturus	38.0	19.9	15.4-60.6	16.7	2.03	3.9	0.0057
	Myctophydae	2.19	1.12	1.46-2.92	0.96	10.1	15.6	0.0192
	S.microlepis	14.5	0	-	6.36	1.35	2.6	0.0011
	N.curvirostris	4.40	0	-	1.93	0.68	1.3	0.0003
	H.italicus	0.70	0.42	8.12-9.28	3.81	2.03	3.9	0.0015
	Pisce	4.73	3.75	2.40-7.06	2.07	10.1	14.3	0.0241
	E.telescopus	18.5	0	-	8.11	0.68	1.3	0.0004
	N.africanus	1.58	0.91	0.95-2.21	0.69	9.46	11.7	0.0128
	P.longirostris	2.53	3.76	0.49-4.57	1.11	26.4	22.1	0.0662
	A.varidens	2.75	1.23	1.77-3.73	1.21	18.24	10.4	0.0208
	Caridea	1.26	1.16	0.40-2.12	0.55	8.11	9.1	0.0083
	S.africana	1.58	0.91	0.95-2.21	0.69	2.03	2.6	0.0006
	Octopus sp.	92.7	70.3	23.8-162.	40.7	2.70	5.2	0.0226
	I.coindetii	8.1	0	-	5.55	1.35	2.6	0.0008
50-60 N=7	*M.polli*	*18.8*	0	-	9.18	12.5	14.3	0.0254
	C.coelorinchus	21.6	0	-	10.5	12.5	14.3	0.0265
	N.curvirostris	3.50	0	-	1.71	12.5	14.3	0.0193
	H.italicus	4.20	0	-	2.05	12.5	14.3	0.0195
	P.longirostris	3.0	0	-	1.85	12.5	14.3	0.0194
	Octopus	153.	15.6	131.-174.	74.7	37.5	42.9	0.5271

Table 6 : Prey species found in hake stomachs between 0-399 m and 400-800 m expressed in: percentage of weight per predator (W), percentage of number per predator (N), frequency of occurrence (Fo).

0-399 m	Warm season			Cold season		
	W	N	F	W	N	F
M.polli	9.95	0.51	0.6	3.57	0.37	0.7
G.denudatum	4.42	0.17	0.2	1.78	0.24	0.4
T.lepturus	2.05	0.32	0.4	0.64	0.37	0.7
Myctophydae	15.0	28.8	25.7	52.5	63.4	58.4
S.microlepis	4.66	0.51	0.6	13.5	1.47	2.2
C.coelorinchus				1.87	0.12	0.2
N.curvirostris	2.34	0.68	0.6			
H.italicus				1.98	0.98	1.6
B.barbata	1.27	0.34	0.4			
E.telescopus				2.55	0.24	0.4
T.hemingi	2.19	0.51	0.6			
B.tenui	2.08	0.17	0.2			
N.africanus	1.23	3.21	2.8	1.33	3.30	3.4
P.longirostris	9.34	21.8	18.6	5.02	7.94	8.8
A.varidens	11.8	12.7	11.2	4.81	10.7	10.1
S.africana	0.29	0.85	0.9	1.64	1.95	2.2
P.edwardsianus	0.11	0.34	0.2			
Octopus sp.	12.9	0.34	0.4			
I.coindetii	1.12	0.68	0.6	0.29	0.12	0.2
T.eblanae	5.59	0.68	0.7			
400-800 m						
M.polli	7.18	0.62	0.7			
G.denudatum	9.80	0.62	0.7	16.0	2.74	5.7
T.lepturus				8.31	0.91	1.9
Myctophydae	8.08	24.7	23.1	15.6	67.8	46.8
S.microlepis						
C.coelorinchus						
N.curvirostris				0.58	0.61	1.3
H.italicus						
B.barbata	2.81	1.23	1.4	1.15	0.91	1.9
E.telescopus						
T.hemingi	3.76	1.23	1.4			
B.tenui						
N.africanus	0.93	4.32	2.8	1.29	3.95	10.1
P.longirostris	6.41	22.2	23.1	2.40	7.0	10.1
A.varidens	10.2	11.7	12.6			
S.africana	0.16	0.62	0.7	0.25	1.22	1.9
P.edwardsianus						
Octopus sp.	28.8	1.23	1.4	49.3	2.1	4.4
I.coindetii	0.58	0.62	0.7	1.09	0.61	1.3
T.eblanae	11.6	1.23	1.4			

Table 7: Total consumption of hake in tonnes by season and size group

a. Warm season							
Prey	Hake size group						
	I	II	III	IV	V	Tot.	%
Fish	749.0	4093.1	1554.3	267.2	-	6663.6	45.5
Shrimp	83.2	3313.5	2938.3	525.6	34.7	6895.2	47.1
Cephalopods	-	682.2	-	407.3	-	1089.5	7.4
Total	832.2	8088.8	4492.6	1200.1	34.7	14648.3	
b. Cold season							
Fish	4.4	1308.3	4775.1	6522.7	15.1	12625.5	40.4
Shrimp	-	190.5	6648.8	3216.7	3.5	10059.6	32.2
Cephalopods	-	-	30.2	8393.5	143.6	8567.3	27.4
Total	4.4	1498.8	11454.1	18133	162.2	31252.4	
c.Annual consumption							
Fish						19289.1	42.0
Shrimp						16954.1	37.0
Cephalopods						9656.8	21.0

Table 8 : Biomass (tonnes) and number (millions) of Benguela hake by season, depth and size group in Angolan waters in 1995.

a.Warm season						
0-399 m	Predator size					
M. polli	I	II	III	IV	V	Tot
Number	7.6	41.1	7.7	0.5	0.01	56.0
Biomass	1696	4862	1087	116	0.0	7661
400-800						
Number	0.0	12.3	9.8	1.3	0.1	23.6
Biomass	13	635	2351	1287	-	4286
b.Cold season						
0-399						
Number	0.018	0.9	9.54	7.2	0.018	17.7
Biomass	335	2533	1767	187	0.0	4822
400-800						
Number	0.0	4.32	6.84	1.98	0.0	3.93
Biomass	7	884	718	187	2	1798

Table 9 : Hake stock's consumption in tonnes of the main preys by predator by predator size groups, depht and season.

a. Warm season							
0-399 m	Size group					Total	%
	I	II	III	IV	V		
M.polli	-	-	-	74.2	-	74.2	1.0
G.denudatum	-	600.1	-	-	-	600.1	8.4
Myctophidae	545.6	1250.1	178.0	9.1	-	1982.8	27.8
S.microlepis	-	800.1	84.3	-	-	884.4	12.4
N.africanus	-	150.0	84.3	5.5	-	239.8	3.4
P.longirostris	83.2	1500.2	449.7	43.8	-	2076.9	29.1
A.varidens	-	600.1	646.4	27.4	3.5	1277.3	17.9
400-800 m							
M.polli	-	-	-	53.8	-	53.8	1.4
G.denudatum	-	987.7	-	-	-	987.7	26.2
Myctophidae	-	404.1	1049.5	47.5	-	1500.8	39.7
S.microlepis	-	-	-	-	-	-	-
N.africanus	-	-	107.3	9.5	-	116.8	3.1
P.longirostris	-	-	357.7	109.1	-	466.8	12.4
A.varidens	-	-	465.0	185.1	-	650.1	17.2
a. Cold season							
0-399 m	Size group					Total	%
	I	II	III	IV	V		
M.polli	-	-	742.8	-	13.7	756.6	11.1
G.denudatum	-	-	-	-	-	-	-
Myctophidae	4.4	200.4	1160.7	464.3	-	1829.7	26.8
S.microlepis	-	-	429.5	630.7	-	1060.2	15.5
N.africanus	-	6.6	-	289.1	-	295.7	4.3
P.longirostris	-	16.4	-	893.5	-	909.9	13.3
A.varidens	-	-	696.4	1287.7	-	1984.1	29.0
400-800 m							
M.polli	-	-	-	-	-	-	-
G.denudatum	-	-	516.1	1060.1	-	1575.9	29.6
Myctophidae	-	841.1	1905.7	9,64	-	2756.33	51.9
S.microlepis	-	-	-	-	-	-	-
N.africanus	-	31.5	324.6	166.2	-	522.3	9.8
P.longirostris	-	94.6	199.7	166.2	-	460.6	8.7
A.varidens	-	-	-	-	-	-	-