

## Feeding preferences of *Scomber japonicus* in the Canary Islands area\*

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**SUMMARY:** Analysis of the stomach contents of 721 specimens of *Scomber japonicus* shows a feeding preference for three different items: copepods, mysids and fish. This feeding preference is influenced by habitat, seasonal fluctuations of the available food and the behavioural pattern of the prey species. The importance of mysids in the diet of immature and adult fish, in comparison with their importance to juveniles, show differences caused by habitat. On the other hand, fish are eaten, almost exclusively, during the first two quarters of the year. *Scomber japonicus* shows a predation on this item conditioned by the period of maximal abundance of fry in the area. Fish may feed on swarms of mysids taking advantage of their positive phototactic response to weak light sources, just as purse seiners use light to lure mackerel at night. This would explain the differences in the abundance of mysids between the stomach contents of chub mackerel and data from sampling programs of zooplankton in the area. There are some aspects, however, that still remain unsolved.

*Key words:* *Scomber japonicus*, feeding, trophic preferences, Canary Islands.

**RESUMEN:** PREFERENCIAS TRÓFICAS DE *SCOMBER JAPONICUS* EN AGUAS DE CANARIAS. – El estudio de los contenidos estomacales de 721 individuos de *Scomber japonicus* indica una posible afinidad trófica hacia determinadas presas. Esta afinidad está influenciada por el hábitat, la componente estacional del alimento y el patrón de comportamiento de las presas. La importancia de los misidáceos para los individuos inmaduros y adultos, en comparación con los juveniles, reflejan una diferencia establecida por el hábitat. Por otro lado, la presencia de los peces, de forma casi exclusiva, durante los dos primeros trimestres del año, indican una predación sobre estos relacionada con los períodos de máxima abundancia en el área. La formación de densos enjambres y la respuesta fototáctica positiva de los misidáceos hacia las fuentes de luz, como la utilizada por los barcos cerqueros de pesca nocturna, puede facilitar la predación de las caballas sobre los mismos. Esto explicaría las diferencias en abundancia relativa entre los contenidos estomacales y los datos procedentes de los programas de muestreo de la comunidad zooplanctónica del área. Pero, aún quedan algunos aspectos por resolver.

*Palabras clave:* *Scomber japonicus*, alimentación, preferencias tróficas, Islas Canarias.

### INTRODUCTION

A species is more or less opportunistic depending on its own biology and the characteristics of its ecosystem, as well as the characteristics of food resources (colour, mobility, size, prey accessibility, etc.) (MAGNHAGEN and WIEDERHOLM, 1982; BROWMAN and MARCOTTE, 1986, 1987a, 1987b; MARCOTTE and BROWMAN, 1986). Selectivity increa-

ses with the available food, but this occurs even with those species classified as opportunistic (IVLEV, 1961).

The quantitative description of food selection by fish is generally based on comparisons between the relative abundance (by number, weight, or volume) of prey in the stomach and abundance of the same item in the habitat. The first problem that we can find is the slant in information obtained: samples of the stomach contents can not suitably represent the relative abundance of prey that has been consumed,

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and samples of potential prey types do not accurately reflect the potential available food for predators. The second source of error is that the quantitative measure of selection is in itself biased, or, its usefulness is limited. Mathematical variations of the selective indices diet-habitat have been developed to remedy inadequate observations. They almost always consist of great theoretical treatments, but have little application in field studies (KOHLER and NEY, 1982).

Diet changes as a function of the location and the abundance of each specific prey, reflecting the availability of prey when it exists in important quantities. However, when prey is scarce, and due to the fact that fish can turn to other potential prey types that normally are not abundant in the habitat, the real abundance may be masked (COWEN, 1986).

The aim of this paper is to try to give an insight to the feeding preferences of *Scomber japonicus* toward some food items, always bearing in mind the opportunistic and non selective character of this fish species. "Trophic selection" is not considered suitable for use in this paper. The method used in this study does not give actual information about prey selection by fish, due to the lack of basic data for studies of trophic selection, as quantity of available food at sea. Therefore, it is more correct to speak of "feeding preferences".

## MATERIAL AND METHODS

Specimens of *Scomber japonicus* were obtained from commercial catches taken from the fishing grounds around Gran Canaria (Fig.1) between March 1988 and May 1989. Most samples were obtained from purse-seine nets, except for juveniles which were caught in beach-seine nets. Total body length (TL), wet mass, sex and maturity stage (by macroscopic examination of gonads) were recorded. Stomachs were removed and preserved in 70% ethanol. A total of 721 stomachs were analysed.

Attending to morphometric, biological, ecological and fishery characteristics, juveniles were defined as those fish ranging in size from 1.5 to 13.5 cm TL, immature fish as those ranging between 13.6 and 22.5 cm TL and adults as fish longer than 22.6 cm TL (CASTRO, 1993). These size-classes are similar to those used by WATANABE (1970) and ANGELESCU (1979) for *S. japonicus* from Japanese and Argentinian waters.

All food items from the stomach were placed on filter paper to remove excess moisture and weighed.

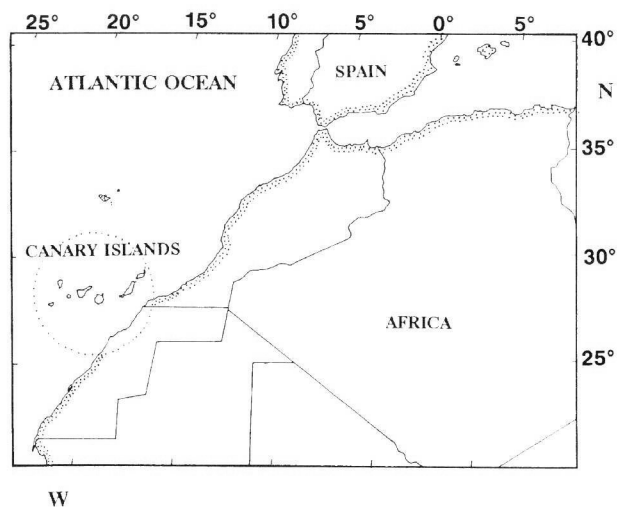


FIG. 1. – Geographic location of Gran Canaria Island.

Stomach fullness (SF) was calculated as

$$SF = (\text{Wet mass of the gut contents} / \text{Wet mass of fish}) \cdot 100.$$

Prey items were identified to the lowest taxa possible. For each stomach examined, counts were made of the number of prey items in each prey category. An index of importance by number (IN) for each stomach was calculated as the mean for each prey category, where  $IN = ((\% \text{ composition by number}) \cdot (\% \text{ occurrence}))$  (WINDELL 1971, VESIN *et al.* 1981), with reference to a scale of 100. The percentage occurrence was the frequency of occurrence of a prey item in the stomach.

Wet masses were determined for each prey category for juvenile, immature and adult fish, and an index of the importance of each prey category by wet mass (IM) was calculated, where  $IM = ((\% \text{ wet mass}) \cdot (\% \text{ occurrence}))$  (CASTRO, 1993), and also with reference to a scale of 100.

The small and numerous prey items were magnified with the index of importance by number, while the index of importance by wet mass magnified those prey items with low number but which were heavy. An index of total importance (TI) of each prey category was calculated as the mean value between IN and IM ( $TI = (IN + IM) / 2$ ), always with reference to a scale of 100. Each index of importance was calculated by fish size-class and by year quarter.

Bearing in mind the advantages of the frequential method for stomach content analysis (simplicity and ability to illustrate seasonal changes in diet and competition between fish groups of the same species of different species) (HYSLOP 1980, BOWEN 1985), a matrix of data was made, where each row represen-

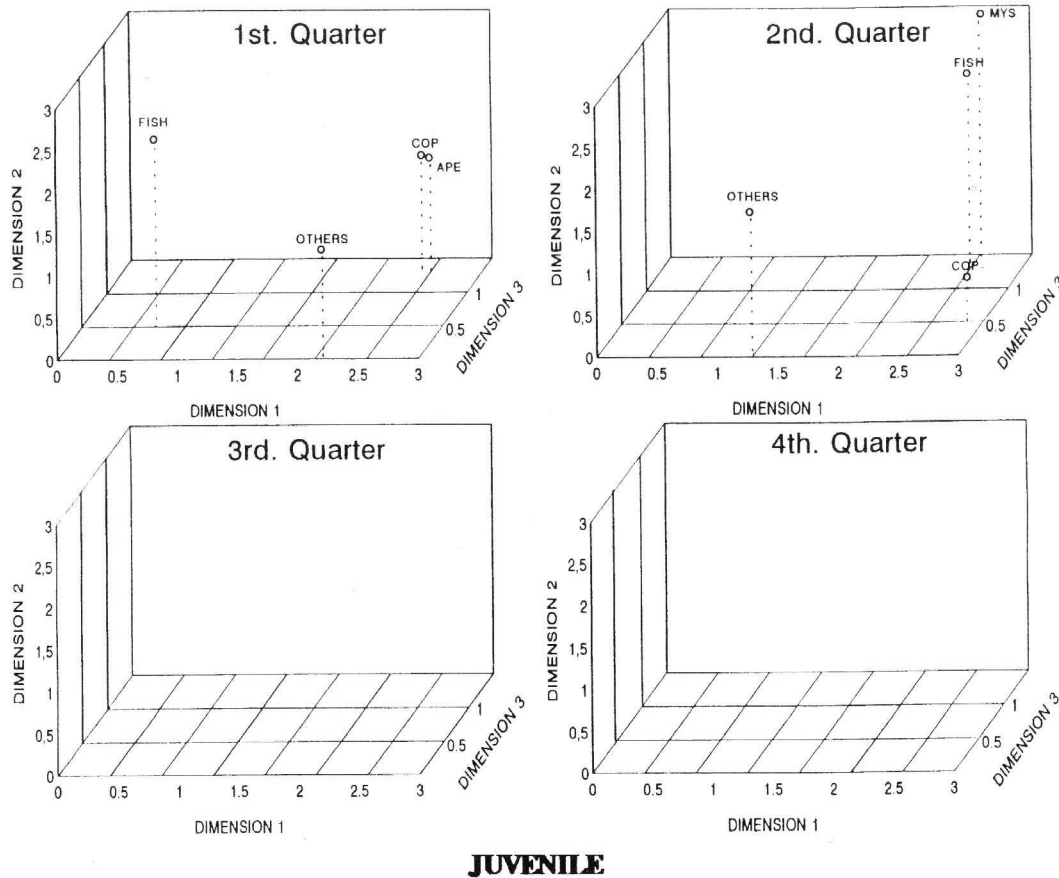


FIG. 2. - Three dimensional figure obtained from the multidimensional scaling results of the diet of juvenile specimens of *Scomber japonicus*, during the 1st and 2nd quarters. The figure represents only the most important food items: (FISH, COP (copepods); APE (appendicularians); and, MYS (mysids). Included under the term OTHERS all those food items that showed close distances between them.

ted a chub mackerel sampled, and each column represented a food type. The data of this matrix was codified as 0 (when the food type was absent) or 1 (when the food type was present). With the objective of measuring the similarity between the predation on different preys, the Euclidean distances between couples of food types were calculated. Using the statistical software CSS:Statistica (1991), a multidimensional scaling analysis was done (FIELD *et al.* 1982, DAVISON 1983, CUACHES 1991). Each prey type was represented in a three dimensional space, in such a way that in this space the distances between points corresponded, in a high degree, to the original distances between prey types. The interpretation of figures 2, 3 and 4 is simple: the feeding preferences of the predator toward different prey types are much more similar when their representation points are closer.

The ordinal association degree between two

points is given by the coefficient of monotony ( $\mu$ ).

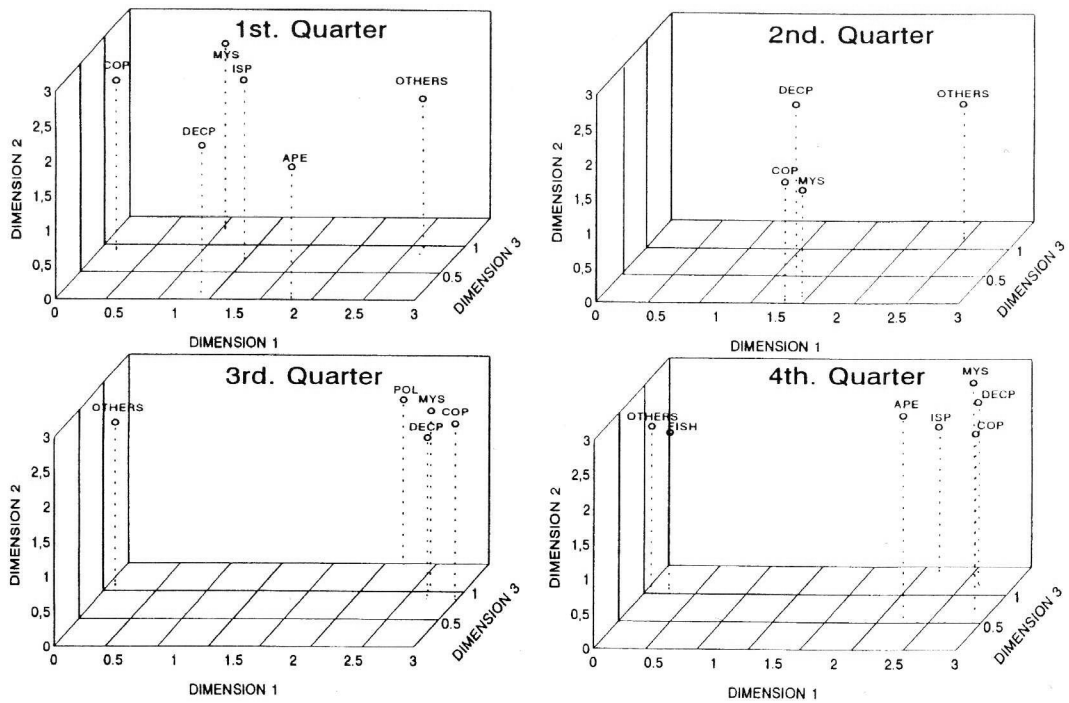
$$\mu = (\sum_{ij} \delta_{ij} d_{ij})^2 / ((\sum_{ij} \delta_{ij}^2) \cdot (\sum_{ij} d_{ij}^2))^{1/2}$$

where  $d_{ij}$  is the distance in the original space (721x17 dimensions) and  $\delta_{ij}$  is the distance in the new space (3 dimensions). The fitting is better when  $\mu$  is low, or when the coefficient of alienation is closer to zero, being

$$K = (1 - \mu^2)^{1/2}$$

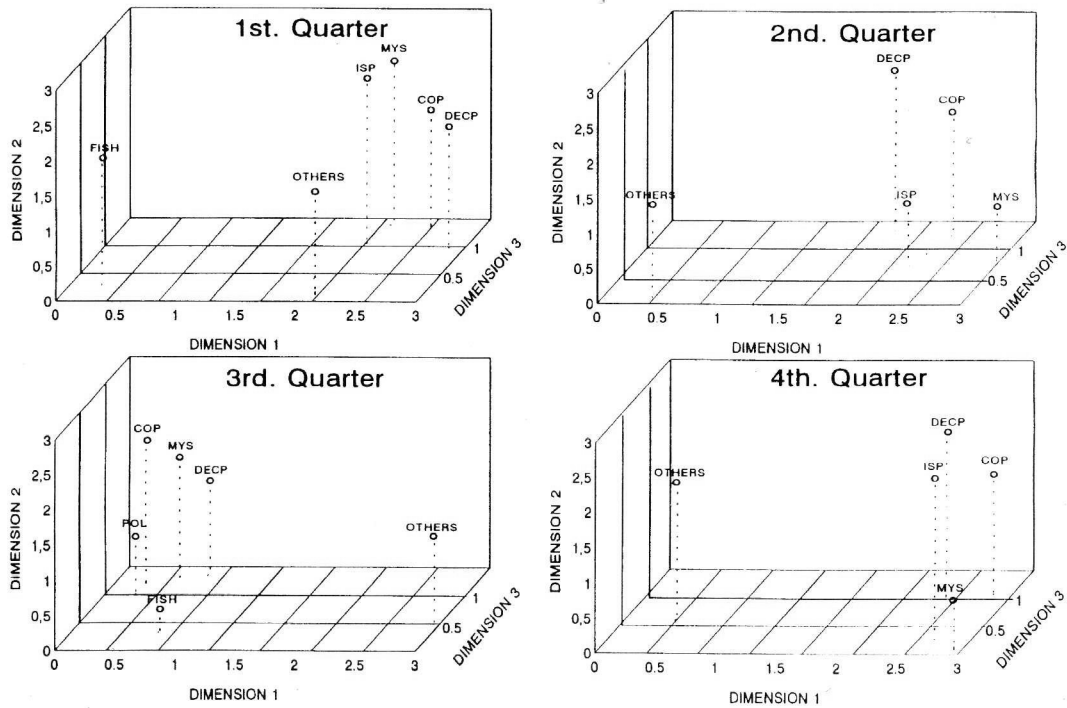
where K is the coefficient of alienation.

Groupings of food types, by fish size-classes and by year quarters, were made from the three dimensional figures of the multidimensional scaling (Figures 2, 3 and 4). Subsequently, an index of importance by food group (IG), was calculated as the sum of the index of total importance (IT) of each



**IMMATURE**

FIG. 3. – Three dimensional figure obtained from the multidimensional scaling results of the diet of immature specimens of *Scomber japonicus*, by year quarters. The figure represents the most important food items: (FISH, COP (copepods); APE (appendicularians); MYS (mysids); CRD (decapod larvae); ISP (isopods); and, POL (polychaetes) Included under the term OTHERS all those food items that showed close distances between them.



**ADULT**

FIG. 4. – Three dimensional figure obtained from the multidimensional scaling results of the diet of adult specimens of *Scomber japonicus*, by year quarters. The figure represents only the most important food items: FISH, COP (copepods); MYS (mysids); CRD (decapod larvae); ISP (isopods); and, POL (polychaetes). Included under the term OTHERS all those food items that showed close distances between them.

component of the food group. The IG values allowed us to classify the food groups in principal, secondary and circumstantial, in function of the contribution to the diet. The food group was considered as principal when its contribution to the diet was over 50% or more, whereas a secondary food group represented over 20% of contribution alone.

## RESULTS

Off the Canary Islands, the diet of *Scomber japonicus* consisted of 17 taxonomic groups (Table 1). All size-groups have mixed diets. Copepods and mysids were the dominant prey. Fish were less frequent in the diet but their importance was moderately high.

TABLE 1. – The food taxa and dominant species found in the stomach contents of *Scomber japonicus*.

1. CHAETOGNATHA	10. STOMATOPODA
2. POLYCHAETA	11. EUPHAUSIACEA
3. CLADOCERA	<i>Euphausia</i> spp.
4. OSTRACODA	12. DECAPODA
5. COPEPODA	13. GASTROPODA
<i>Oncaea</i> sp.	14. LAMELLIBRANCHIATA
6. AMPHIPODA	15. CEPHALOPODA
<i>Dexamine</i> sp.	<i>Ommastrephes bartrami</i>
7. ISOPODA	16. APPENDICULARIA
<i>Idotea</i> sp.	17. PISCES
8. CUMACEA	<i>Sardina pilchardus</i>
9. MYSIDACEA	<i>Macroramphosus scolopax</i>
<i>Gastrosaccus normani</i>	
<i>Anchialina agilis</i>	

Despite its low numerical abundance in the diet, the wet mass of fish consumed was highest in juveniles, compared with mysids, copepods, amphipods and appendicularians. However, appendicularians and copepods ranked first and second in terms of numerical contribution to the total prey consumed. The diet of juveniles was dominated by fry and small prey. Copepods and appendicularians were the main components of the diet, decreasing in importance with fish size.

Wet mass of mysids and copepods consumed was high in the diet of immature fish. On the other hand, appendicularians ranked second by number of prey consumed, but their contribution in wet mass was low. Fish contribution in the diet of immature chub mackerel was not significant in terms of number and wet mass.

Mysids and fish were the most important prey in the diet of adult chub mackerel. The importance of

copepods and appendicularians, by number and wet mass, was the lowest of the three size-groups.

Chub mackerel exhibit a seasonal variation in feeding intensity. A high percentage of individuals caught from December to May showed SF higher than 1. At the beginning of this period the frequency of small fish (smaller than 5 cm TL) was high in the stomach contents. However, during the last part of this period fish of middle size (8-10 cm TL), were dominant in the diet, including juveniles of *Scomber japonicus*, and specially juveniles of sardine (*Sardina pilchardus*).

The frequency of stomachs with SF higher than 1 was in the range 5.7-56.4% ( $x=34.7\%$ ,  $SD=25.97$ ) and 22.7-82.1% ( $x=47.5\%$ ,  $SD=27.68$ ) during the last and first quarters of the year respectively, while during the second and third quarters this frequency decreased to 4.8-43.5% ( $x=26.4\%$ ,  $SD=15.58$ ) and 11.4-34.0% ( $x=20.0\%$ ,  $SD=12.23$ ) respectively. Feeding intensity of juveniles was the highest with SF variable from 0 to 13%. On the other hand, feeding intensities of immature and adult fish were similar, and lower than that of juveniles, with SF variable from 0 to 8.04% and from 0 to 7.39% respectively.

During the first quarter of the year the diet of juveniles was composed of three groups of food. The principal food was copepods and appendicularians (IG= 47.68), while fish formed the secondary food resource (IG=24.37). The other food items formed a single circumstantial food group (IG=27.93). During the second quarter two food groups, composed of three prey, were identified. Fish and mysids (IG=36.88) and also copepods (IG=37.68), composed the principal food resource. The other prey items together constituted the circumstantial food group (IG=26.64) (Table 2).

The composition of the diet of immature chub mackerel could be classified into two food categories, principal and circumstantial, except during the first quarter where appendicularians formed a third food category, as secondary food resource. The principal food group was dominated, in total importance, by copepods and mysids. These two food items have associated several prey types, with significant seasonal variation, and with larvae of decapods dominant. The total importance of the principal food group was in the range 49.3-83.1% ( $x=67.4$ ,  $SD=14.9$ ), where the copepod and mysid contribution was normally in the range 71.7-87.8% ( $x=81\%$ ,  $SD=7.4$ ). In the circumstantial food group, the average of importance of its components was 1.8% ( $SD=2.5$ ) (Table 2).

TABLE 2. – Food categories in the diet of *Scomber japonicus*, size-classes by year quarters. The total importance of each prey item is between brackets. On the top of each box is expressed the importance of the food group.

FOOD TYPE	JUVENILE				IMMATURE				ADULT			
	1st Quarter	2nd Quarter	1st Quarter	2nd Quarter	3rd Quarter	4th Quarter	1st Quarter	2nd Quarter	3rd Quarter	4th Quarter		
PRINCIPAL	IG=47.7	IG=74.6	IG=49.3	IG=61.8	IG=75.3	IG=83.1	IG=47.0	IG=45.6	IG=44.8	IG=87.9		
	APE (32.1) COP (15.6)	COP (37.7) FISH (25.0) MYS (11.9)	COP (37.4) MYS (5.0) ISP (3.9)	COP (31.0) MYS (23.3) DECP (4.9) EGGS (1.8) CHA (0.8)	COP (36.2) MYS (23.0) DECP (8.4) POL (4.2) CHA (1.7) EGGS (1.8)	MYS (32.3) COP (27.3) APE (11.3) DECP (7.4) ISP (2.4) EGGS (2.4)	COP (32.1) DECP (10.3) MYS (3.1) ISP (1.5)	COP (18.4) MYS (17.0) ISP (5.5) DECP (4.7)	MYS (25.0) COP (11.2) ISP (2.2) CUM (2.3) OSP (3.1) CHA (1.0)	MYS (64.6) COP (10.3) ISP (6.1) DECP (5.2) CHA (1.7)		
SECONDARY	IG=24.4		IG=35.2				IG=19.3	IG=21.9				
	FISH (24.4)		APE (20.2) DECP (8.4) EGGS (4.3) HYP (2.0) MOLL (2.2)				FISH (19.3)	FISH (21.9)				
CIRCUMSTANTIAL	IG=27.9	IG=25.4	IG=15.2	IG=38.3	IG=24.5	IG=16.7	IG=33.7	IG=29.8	IG=55.2	IG=12.0		
	MYS (12.7) GAMM (8.5) DECP (2.3) EGGS (1.2) ISP (0.9) OSC (0.8) MOLL (0.6) POL (0.4) CEPH (0.2) EUP (0.1) CUM (0.1) CHA (0.04) CAP (0.01) HYP (0.01)	ISP (6.4) DECP (5.2) GAMM (3.6) APE (3.0) EGGS (1.5) POL (1.2) CEPH (0.9) HYP (0.9) MOLL (0.9) OSP (0.6) CHA (0.5) OSC (0.4) CUM (0.2)	FISH (3.9) EUP (3.2) MOLL (2.3) CEPH (1.7) POL (1.4) OSC (1.0) GAMM (0.9) CAP (0.3) OSP (0.2) CUM (0.2) CLA (0.1)	APE (13.5) GAMM (6.3) ISP (3.3) MOLL (3.2) EUP (2.3) FISH (2.0) EGGS (1.7) OSC (1.3) OSP (1.2) CLA (1.5) OSP (1.0) POL (0.6) HYP (0.5) CUM (0.5) CEPH (0.2) CAP (0.03)	APE (10.6) EUP (2.9) GAMM (2.1) EGGS (1.8) ISP (1.7) MOLL (1.6) OSC (1.3) OSP (0.9) HYP (0.6) FISH (0.3) CUM (0.2) CAP (0.1) CLA (0.1)	EUP (4.5) POL (3.6) FISH (2.0) CHA (1.9) OSC (1.3) GAMM (1.1) MOLL (0.9) OSP (0.9) CAP (0.2) CLA (0.1) CUM (0.1) HYP (0.1)	EUP (9.0) APE (7.6) MOLL (3.9) EGGS (3.5) HYP (2.6) GAMM (1.8) CEPH (1.6) OSC (1.4) POL (1.1) CHA (1.0) CLA (0.2)	APE (12.2) EUP (4.4) GAMM (4.3) EGGS (2.3) OSB (1.9) MOLL (1.5) CEPH (1.5) OSC (0.9) POL (0.8) HYP (0.7) CHA (0.6) CLA (0.5) CUM (0.4) CAP (0.1)	EGGS (12.7) POL (11.2) FISH (7.6) DECP (7.3) GAMM (7.1) EUP (3.3) MOLL (2.5) OSC (1.2) APE (1.0) CAP (0.7) HYP (0.6) CLA (0.5) CUM (0.4) CAP (0.1)	FISH (4.2) POL (1.8) OSP (1.5) EUP (1.4) GAMM (0.9) OSC (0.5) MOLL (0.5) CUM (0.4) EGGS (0.3) CEPH (0.2) HYP (0.2) CAP (0.1)		
APE: Appendicularias; COP: Copepods; FISH: Fish;	MYS: Mysids; GAMM: Amphipods Gammaridae; DECP: Decapods larvae;	EGGS: Eggs; ISP: Isopods; OSC: Ostracods (CONCHOECIA);	EGGS: Eggs; ISP: Isopods; OSC: Ostracods (CONCHOECIA);	OSP: Ostracods (POLICOPIIDAE); MOLL: Mollusca larvae; POL: Polichaetes;	OSP: Ostracods (POLICOPIIDAE); MOLL: Mollusca larvae; POL: Polichaetes;	CEPH: Cephalopods; EUP: Euphausiids; CUM: Cumaceans;	CEPH: Cephalopods; EUP: Euphausiids; CUM: Cumaceans;	CHA: Chaetognats CAP: Amphipods caprellidae HYP: Amphipods hyperidae				

TABLE 3. – Comparison of percentages of the components of the diet of *Scomber japonicus* in the sea (HERNÁNDEZ-LEÓN, 1988) and in the stomach contents of chub mackerel. The last column does not take into account those taxa not found by HERNÁNDEZ-LEÓN (1988).

PREY TYPE	HERNÁNDEZ-LEÓN, 1988 (%)	<i>Scomber japonicus</i> STOMACH CONTENTS (%)	<i>Scomber japonicus</i> STOMACH CONTENTS (%)*
Fish	-	17.2	-
Mysids	-	32.0	-
Copepods	85.2	18.9	81.3
Ostracods	03.7	02.3	03.1
Appendicularians	04.3	03.8	06.2
Chaetognaths	03.7	01.2	03.7
Others	03.1	24.6	05.7

(\*) Percentages of fish, Mysids, cephalopods, amphipods and cumaceans have not been taken into account.

On the other hand, the prey components of the diet of adults could be classified into the three food categories described before, except during the third and fourth quarter, when there was no secondary food category. As was observed in the diet of immature fish, copepods and mysids were the main contributors to the principal food category. Isopods were associated with copepods and mysids in this group, although with a much lower importance. During the two first quarters of the year copepods were the most important item, being significantly replaced by mysids in the other two quarters. Also, in this food category the larvae of decapods stood out, as a satellite item in the food category. The secondary food category was exclusively composed of fish during the first half of the year, with a contribution to the diet around 20% in total importance (Table 2).

## DISCUSSION

Many authors classify *Scomber japonicus* as a non selective species (ANGELESCU 1979, BAIRD 1978, HABASHI and WOJCIECHOWSKI 1973, HATANAKA and TAKAHASHI 1960, KONCHINA 1983, TAKAHASHI 1966, SCHAEFER 1980), feeding on any available item (dead or alive). This conclusion can also be drawn from data shown in this paper, although a predation tendency towards certain prey items is observed, almost in a preferential way.

When the prey contribution to the diet by number and by wet mass is removed, with the objective of calculating the Euclidean distances between couples of prey types, the frequency of appearance along time is powered as a measure of abundance.

Therefore, those close prey types in the multidimensional scaling analysis have a similar frequency of presence and absence in the stomach contents. In a first approximation, it can be said that those prey types that are close in the three-dimensional figures (2, 3 and 4) of Euclidean distances between preys, generate a similar attraction to the predator, although this does not mean that they have the same importance in the fish diet. The abundance of such prey in the environment might be very different, in which case the predator would have found the prey to differ in attractiveness. The closeness of two prey types in the analysis could be due to a coupling between the biological cycles of both and not an indicator of similar abundance or similar selection by the predator. But, as can be seen from the analysis of diet by size-classes, this last option is not totally clear. There are important differences between the diet of adults and immature fish caught at the same area in the same time period (Table 2).

If the analysis is limited to a simple comparison between the relative abundance (by number or wet mass) of prey in the stomach contents and in the habitat (according to the plankton bibliography of the area), one finds a notable difference between both sources of information (Table 3). The predation on copepods could be a consequence of the fact that this prey type is the most abundant in the area (HERNÁNDEZ-LEÓN, 1988) (Table 3). The predation on fish reflects a seasonal pattern (during the first and second quarters as a consequence of the presence of juveniles of many fish species in the area of chub mackerel distribution). However samples from the habitat do not always reliably reflect the potential available food for the predator, the presence of mysids in the diet poses several questions which are

difficult to resolve. This can be explained as a function of the feeding preference toward certain prey, possibly favoured by prey behaviour, and their interactions with the predator.

Obviously, mysids play a more important trophic role than initially expected from data of the zooplankton communities around the Island. Oddly, they have been overlooked by sampling programmes investigating zooplankton communities around the Archipelago (CORRAL and GENICIO 1970, BAKER 1970, FOXTON 1970, HERNÁNDEZ and LOZANO 1984, HERNÁNDEZ-LEÓN 1988, FERNÁNDEZ de PUELLES and BRAUN 1989, SANTAMARIA *et al.* 1989, among others). Use of inappropriate sampling methodology for catching species that undergo extensive vertical and horizontal migration and exhibit highly specific behavioural patterns (many species are associated with the sea bed) (MAUCLINE 1980; FOSSA 1985; KAARTVEDT 1985) is probably responsible for this situation. The possibility that fish may feed on swarms of mysids taking advantage of their positive phototactic response to weak light sources (MAUCLINE 1980), just as purse seiners use light to lure mackerel at night, cannot be ruled out. During December 1988 several stomach full of mysids were found (average of mysids per stomach = 4071 ( $\sigma = 1007.8$ ); average of SF = 4.17 ( $\sigma = 1.52$ );  $n=4$ ), in adult fish caught to the north of Gran Canaria (area with the narrowest shelf of the Island) and using a beach-seine in the morning. This indicates the existence of another strategy of predation on mysids different from their concentration around light.

Therefore, it is very difficult to affirm that there is a selection toward specific prey types, although a feeding preference toward three food items was observed. This preference is influenced by the habitat of each size-class of *Scomber japonicus*, as well as the seasonal component of food items. The importance of mysids in immature and adult diets, in comparison with juvenile ones, reflects differences caused by the habitat. Juveniles of coastal habits (SÁNCHEZ 1982, CASTRO 1993), have less access to mysids, crustaceans of habitats related with deep waters. Mysids are more accessible to immature and adult fish, that share the same habitat during the spawning season (BAIRD 1978), and have a spatial distribution related to the presence of the slope. On the other hand, the presence of fish, almost exclusively during the first two quarters of the year, indicates a predation on fish related to the period of maximal abundance. As a consequence of spawning of many fish species at the end of winter and early spring, it is common to find fry and juveniles in the

coastal area during the spring and beginning of summer. These fry and juveniles, especially of *Sardina pilchardus* and *Atherina presbyter*, are very accessible to the voracious juveniles of chub mackerel (HUNTER and KIMBRELL 1980). Juveniles of *Macroramphosus scolopax*, distributed offshore, are also very accessible to adults *S. japonicus*.

It can be concluded that the diet of *Scomber japonicus* is influenced by the available food in the habitat, its seasonal variability and the behaviour of the prey. A feeding preference induced by the prey size cannot be ruled out, as is indicated by the high importance of fish in the diet of juveniles and the low importance of copepods in the trophic habits of adults.

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