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Feeding - Morphology and histology of the digestive system
The place of Macrouridae in the deep-sea food chain

by P. Geistdoerfer

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INTRODUCTION

MACROURIDAE

Macrouridae constitute the largest family of deep-sea, bottom-dwelling fishes. In general, they are fairly large; some species, such as *Coryphaenoides rupestris* or *Macrourus berglax*, may attain a metre in length, while other species, such as *Hymenocephalus italicus*, are rarely longer than 20 cm. The maximum size of most Macrouridae is about 30 to 50 cm.

More than 300 benthopelagic species live on the continental slope (90% of them) and on the abyssal plain, where the most common genera are *Chalinura*, *Lionurus*, and *Nematonurus*. Two genera, *Cynomacrurus* and *Odontomacrurus*, are bathypelagic (Marshall 1964). According to Hubbs (1954), most species have a fairly limited geographical distribution, mainly because of characteristics of the surface waters where the larvae live.

Some members of the Macrouridae family have been known since the time of Ström (1762) and Fabricius (1780). The genus name *Macrourus*, from which the family name is derived, we owe to Bloch (1786), although Gunnerus (1765) had previously made up the name *Coryphaenoides*--failing, however, to follow the rules of nomenclature. The species *Coryphaenoides rupestris* was, as a matter of fact, the first one to be described (Gunnerus 1765). Fabricius (1780) used the same root for the name *Coryphaena rupestris*. However, in 1786 Bloch replaced

Coryphaenoides with Macrourus, in naming Macrourus rupestris. Finally, this species was redefined by Lacépède in 1801, who created the species Macrourus berglax; he said that the name was chosen because of the relationship the fish seemed to bear with the salmon, called lachs or lax in several Northern languages, and because of the rocks among which the fish frequently dwells (Lacépède 1802). The two species names, Coryphaenoides rupestris and Macrourus berglax, have subsisted.

In his "Table générale des poissons", Lacépède (1802) classifies the genus Macrourus, and the species Macrourus berglax, among the "osseux" (those whose dorsal spine is composed of boney vertebrae) with an operculum and a branchial membrane. Macroura were classified as "thoracin" (those with one or two fins on the underside) and constitute the 19th order in the fish classification.

Today the Macrouridae are classified in the order Gadiformes, of which they are the most primitive family.

Macrouridae are commonly called grenadiers. According to Risso (1810), this name, which Cuvier had previously employed, arose from the supposed resemblance between a soldier's helmet and the snout of Coelorhynchus coelorhynchus. The fishermen of Boulogne expressed their contempt for these "false fishes" by calling them rats.

After the voyages of HMS Challenger and Günther's resultant work (1887), and the work of Vaillant (1888), who studied fish caught in the deep-sea fishing excursions of the Travailleur and the Talisman in the years 1880 to 1883, and the publication of Goode and Bean's "Oceanic Ichthyology" (1896), Macrouride, like other deep-sea fishes, became better known. They have been the subject of many systematic studies since the beginning of this century. We might mention those of Gilbert and Hubbs (1916, 1920), Okada and Matsubara (1938), Parr (1946), and Okamura (1970a). Marshall's recent study of the family (Marshall 1973b), while it is not strictly speaking revisionary, does go well beyond an examination of the northwest Altantic species, which are its main subject. We have referred to this study and to his section on Macrouridae (Marshall 1973a) in the Catalogue of Fishes of the North Atlantic and the Mediterranean. Marshall does not discuss Trachyrhynchus, trachyrhynchus, Coryphaenoides zaniophorus, and Macrourus holotrachys as they are not native to the regions he studied.

Our taxonomic study of species was conducted in the traditional manner. In addition, for certain species we used electrophoretic analysis of the proteins of the crystalline lens, which reveals new criteria of discrimination among species.

Provenance of the Macrouridae studied

Our fish were caught during benthic trawling expeditions done in deep waters by three oceanographic ships: the Jean Charcot, of the Centre national pour l'exploitation des océans, in the North Atlantic and the Mediterranean (Roux and Hureau 1969; Geistdoerfer, Hureau, and Rannou 1970 (1971), 1971; Geistdoerfer and Rannou, 1970 (1971), 1972); the Thalassa, of the Institut scientifique et technique des pèches maritimes, on the northwest African slope and the Barents Sea; and the Marion Dufresne, of the Territoire des terres australes et antarctiques françaises, in the southern Indian Ocean (see table, figure 1).

1. EXAMINATION OF STOMACH CONTENTS

All of the fishes were caught by trawls along the bottom. Once on board ship they were fixed by 10% neutralized formol, after the visceral cavity of large and medium-sized specimens had been opened to allow rapid fixation of the stomach contents.

Each fish was measured (standard length) and weighed in the laboratory, and all the food in the esophagus and stomach was removed and weighed. The prey were then identified and counted under a binocular magnifying glass. For the eight species we studied, 388 fishes containing 3,059 prey were examined.

When the trawl is coming up, many fish evaginate their stomachs to some degree. Regardless of the depth of the draught, almost all _Trachyrynchus trachyrynchus_ exhibit this phenomenon, but it is less frequent in other species. Any specimen showing the slightest sign of evagination was rejected.

Prey at various stages of digestion and in various states of conservation were found side by side in the stomachs. For example, often only the byssa or some tiny body fragments of polychaete annelids, and on rare occasions the anterior extremity, were found (unless there was evidence to the contrary, all of the polychaete remains were considered to be those of a single specimen); the chitinous carapace of crustaceans had been more resistant to digestive juices.

Since it would have been far too inaccurate to weigh isolated prey specimens, considering their small sizes and numbers, and since no reference collection exists, the total weight of each prey group (blotted dry beforehand) was determined instead. Then the average individual weight was calculated for each prey group. This estimate was made on fixed material, so all in all it cannot be considered to give the weight; rather it assigns a weight coefficient to each prey group. Given the conditions of our study, this approach was the only possible one, and it takes into account the relative importance of various prey and allows our method of analysis and presentation of results to be applied.

To complement the examination of stomach contents, we did a qualitative examination of intestine contents, which proved useful in some instances.

2. PRESENTATION OF RESULTS

There are many methods of analysis of stomach contents. Hynes (1950) and Pillay (1952) have done some critical revisions. The main methods are: the occurrence method; the number method; the weight method and its variant, the volume method; the points method; and the fullness method.

The occurrence method shows food preferences: the number of times a particular prey is present is computed and expressed as a percentage of the total number of fishes examined.

The number method, in which the total number of each prey is given as a percentage of the total number of all prey, introduces a source of error, since the size of the prey is not taken into account; it also gives an inaccurate picture of the fish's diet.

The weight method (or the volume method), in which the weight (or volume) of each prey is determined and expressed as a percentage of the total weight (or volume) of all prey.

The points method is an attempt to combine the last two methods: the importance of each prey in the stomach contents is estimated visually and a certain number of points is assigned accordingly.

The fullness method also involves the assignment of points, this time based on the degree to which the observer considers the stomach to be full, compared with a stomach considered to be totally full. The main purpose of this method is to study seasonal variations in diet.

Hynes considers the points method the most satisfactory, since with this method a smaller number of points can be assigned to smaller prey. However, it is obvious that this method, as well as the fullness method, is subjective, and must be rejected for that reason. Furthermore, it makes it difficult--if not impossible--to compare results in different publications, even if the same method was used to obtain the two. Jones (1952) finds the number method best for comparisons between importance of a prey in a fish's diet and its importance in the environment.

Reys (1960), Arnaud and Hureau (1966), and Hureau (1970) have continued the evaluation of various methods of analysis. They reject all methods of visual estimation, retaining three method types: number methods, weight methods, and Blegvad's (1928) combined methods, which combine counting and weighing, applied by Hureau to a study of the diet of Nototheniidae. The volume method is merely a variant of the weight method, with the observer determining volume rather than weight (Sorbe 1972).

Following Hureau (1970), we will use the combined method. Both qualitative and quantitative, it puts into play a number of coefficents, defined by Hureau, and allows the observer to make fine distinctions among various diets and their variations.

Here are Hureau's coefficients:

-coefficient of emptiness (V), the percentage of empty stomachs in the total number of stomachs examined;

-fullness index (Ir), the percentage of the weight of the stomach contents in total weight of fish;

-prey frequency index(f), the ratio between the number of fish whose stomachs contain this prey(n), and the total number of stomachs examined;

-percentage by number*(Cn), the ratio between the number of individuals of a specific prey (N) and the total number of all prey, expressed as a percentage;

-percentage by weight*(Cp), the ratio between the total weight of individuals of a specific prey (P), and the total weight of all prey ingested by a single species;

-average number of prey per stomach; the total number of all prey divided by the number of stomachs examined;

-average weight of prey, the total weight of all prey divided by the total number of all prey;

-food coefficient of a prey (Q), the product of the percentage in number of a given prey and its percentage in weight.

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* When Cn percentages were above 1%, we computed confidence limits at 95% (column i of tables 4 to 17), based on the following formula for standard deviation: $\sigma = \sqrt{\frac{Cn\ (1-Cn)}{N}}$ (Lamotte 1962). The tables also show the percentages by number that are less than 1%, to which this formula is not applicable (Lamotte 1962). They are meant simply to show that a prey group is present in the food. We did

not do similar computations for the percentages by weight (Cp), as they are based on an unquantifiable approximation of weight, for which this kind of computation would make no sense.

According to Hureau, the food coefficient, which he introduced in 1970, makes it possible to evaluate the relative importance and the value of different prey in a fish's food, taking into account both the weight and the number of prey. It also allows Hureau to classify prey as preferential (for which $Q>200$), secondary (Q between 20 and 200), and incidental ($Q<20$).

The food coefficient has been used by Sorbe (1972) and Vivien (1972), although Sorbe classifies prey as preferential, secondary, and incidental on the basis of frequency, rather than the food coefficient.

The percentages by weight, and thus the food coefficient, are based on the average individual weight of each prey. For tiny bathybenthic and bathpelagic crustaceans, the percentages by weight are a good representation of their relative importance. However, in certain cases, this method of calculation minimizes the importance of some prey groups (for example, that of big shrimp and fishes eaten by Ventrifossa occidentalis, which eat large prey) and it exaggerates X the importance of these same prey groups when eaten by fishes that feed mainly on small organisms. Aside from this point, the use of an average individual weight has proven to be a satisfactory method of describing diets. Of course, the average weight must be determined from actual weights, obtained when stomach contents are weighed. No weight value was computed for cephalopods, since in general nothing was left of them but their crystalline lenses and beaks.

In this study, prey groups were divided into three categories, and each category was divided into two sub-categories, using the food coefficient (Q) and the frequency index (f):

1. *primary prey*, for which $Q>100$, comprising *preferential primary prey*, for which $f>0.30$ and *occasional primary prey*, for which $f<0.30$;

2. *secondary prey*, for which Q is between 10 and 100, comprising *frequent secondary prey*, for which $f>0.10$ and *accessory secondary prey*, for which $f<0.10$.

3. *complementary prey*, for which $Q<10$, comprising *first-rank complementary prey*, for which f 0.10 and *second-rank complementary prey*, for which f 0.10.

The categories primary, secondary, and complementary do not refer to a selection or a choice made by the fish, but rather represent the importance a given prey group has in its food. A secondary prey, such as copepods for *Hymenocephalus italicus*, has a high frequency index ($f = 0.88$), which means that it is present in almost all stomachs, either because of deliberate selection by the fish or because it is abundant in the environment. However, the food value of a copepod is still less than that of a fish or a shrimp. It was for the express purpose of accounting for "selection" that we divided each category into two sub-categories, expressing the frequency of consumption of a given prey. This division affords a better appreciation of the importance of each prey group and a better understanding of the feeding habits of each species of fish.

In our opinion, the term "selection" does not necessariy imply a subjective, voluntary choice on the part of the fish; but rather simply expresses the fact that all prey groups are not utilized by a fish species with the same degree of frequency.

In studying fishes' selection of prey, Ivlev (1961) developed a selectivity index;

$$-1 \leq \frac{r_i - p_i}{r_i + p_i} \leq -1$$

where r_i is the proportion of prey i in the diet and p_i is the proportion of prey in the environment, or within the subset of available prey. Thus -1 represents a prey that is never eaten and +1 represents a prey that is chosen preferentially despite its scarcity in the environment. (Thomas (1961) also used an index based on the same principle, in researching the correlation between fish diet and benthic fauna.)

It is obviously impossible for us to adopt this kind of index, since we have no samples of micronektonic, planktonic, and benthic fauna from our fishing expeditions, and since a qualitative assessment of the faunal environment of Macrouridae is already quite difficult. This kind of index can really be used easily only in a breeding ground where all parameters are perfectly known.

If we establish the average diet of Macrouridae (based on the sum of all prey in the same group for the eight species), we can define a new index E, the <u>index of relative selectivity.</u> The importance of each prey group is then compared with its importance in the average diet.

In this way, we can determine to what extent a fish selects a given prey group. We set the following equation:

$$E = \frac{r_{i_j} - r_{i_J}}{r_{i_j} \times r_{i_J}}$$

where r_{i_j} is the portion of a prey group (in percentage by number) in in the fish's food j, and r_{i_J} is the average proportion of prey in in the average diet, based on the diest of the eight species.

Methods of studying the food of marine fish are of necessity based on the examination of the organisms present in their digestive tract when they are caught. A general idea of their eating habits can be gained in this way, but it is also desirable (although usually impossible, especially for deep-water fishes) to evaluate the digestion time of various types of prey. There is a greater probability of finding an echinoderm or a mollusk, which must be digested slowly, than of finding an annelid. This can lead to an overestimation of the importance of some groups. Abraham, Hiyama, and Yasuda (1962), using radioactive 32_p phosphorus, concluded that the prey absorbed most rapidly are fishes, and the speed of absorption increases in proportion to the degree of relation between predator and victim.

7. Macrourus berglax

(Figure 11, table 15)

Macrourus berglax is found in the Arctic Ocean and the North Atlantic. It lives at relatively shallow depths: 200 to 600 m. It can reach more tha a metre in length. The 26 specimens whose stomachs we examined were caught at depths between 465 and 818 m, at the three stations (A 169, A 171, A 179) in the Barents Sea, on the muddy bottom of the continental slope, off the western shores of Spitzbergen and Bear Island. Their length varied from 164 to 727 mm.

The coefficient of emptiness was zero, as all of the stomachs contained some food (a total of 193 prey belonging to 10 zoological groups). The fullness index was always low: between 0.10 and 1.78. The average weight of the prey was 0.552 g.

As in Coelorhynchus coelorhynchus, the percentage by number of crustaceans was low (70.4%), while that of amphipods (from 2 to 8 mm long) was high (38.9%, of which 34.7% were gammarids and three were Caprella). Natantia, which were found in the digestive tract of onlt the largest M. berglax (longer than 484 mm), are large prey of at least 30-40 mm, sometimes 60-80 mm. Sometimes several were found in a single stomach (for example, in one M. berglax of 727 mm standard length there were five shrimp 60 to 70 mm long, two shrimp 30 mm long, one 15 mm long, and a head; in another M. berglax 517 mm long, there were four shrimp from 60 to 70 mm long.) Natantia represented 15.5% of the prey. Echinoderms (Ophiurides) were particularly abundant here (Cn = 13.0%), much more so than in Nezumia sclerorhynchus (Cn = 0.6%), as were Lamellibranchia (Cn = 3.6%, and 1.6% in Nezumia sclerorhynchus). There were few polychaetes (Cn = 9.3%). The crustaceans classified as "indterminate crustaceans" were probably Nebaliacea. Six ctenophores should be added to the list of invertebrates; possibly they are Beroë, abundant among the plankton of this area.)

Table 15. Macrourus berglax

(See photocopy of original.)

Legend

1. Polychaeta
2. Lamellibranchia
3. Amphipoda
4. Gammarids
5. Other and indeterminate
6. Isopoda
7. Cumacea
8. Natantia
9. Caridea
10. Peneidea
11. Indeterminate
12. Other and indeterminate crustaceans
13. Ctenophora
14. Echinodermata
15. Fishes

M. berglax does not demonstrate any marked preference in its choice of prey. The most frequent prey are Polychaeta (f = 0.62), Amphipoda (f = 0.58), and Natantia (f = 0.42). Lamellibranchia were found only in the fish caught at Station A 179, but Ophiurida were found in those caught at Stations A 171 and 179 (only one fish from Station A 169 was examined)--in unequal proportions, however: in three of eight stomachs at A 171 and in only four of 17 stomachs at 17 179.

- Tableau 15 -

Macrourus berglax

	N	n	f	Cn	i	P	Cp	Q
1 Polychètes	18	16	0,62	9,3	13,5-5,1	0,567	1,3	11,65
2 Lamellibranches	7	4	0,15	3,6	6,3-0,9	0,139	0,3	1,11
3 Amphipodes								
4 (Gammariens	67	I4	0,54	34,7	6,4-1,0	(0,131 (	0,3	11,22
5 (Autres et ind.	8	6	0,23	4,1	7,0-1,3			
6 Isopodes	17	4	0,15	8,8	12,9-4,7	0,057	0,1	1,11
7 Cumacés	1	I	0,04	0,5	-	0,0005	0,001	0,0006
8 Natantia								
9 Caridea	8	3	0,12	4,I	7,0-1,3	((27,630 (	60,9	944,51
10 Peneidea	4	3	0,12	2,I	4,1-0			
11 Indet.	18	7	0,27	9,3	13,5-5,1			
12 Crustacés autres et indét.	13	2	0,08	6,7	10,3-3,1	-	-	-
13 Cténaires	6	6	0,23	3,1	5,6-0,6	-	-	-
14 Echinodermes	25	7	0,26	13,0	17,8-8,1	14,608	32,2	416,93
15 Poissons	1	1	0,04	0,5	-	2,239	4,9	2,52

M. berglax ne manifeste pas de préférence bien marquée et les seules proies fréquemment rencontrées sont les Polychètes (f = 0,62), les Amphipodes (f = 0,58) et les Natantia (f = 0,42). Si les Lamellibranches ne sont présents que chez les poissons pêchés à la station A 179, les Ophiures le sont aux deux stations A 171 et A 179 (un seul poisson de la station A 169 a été examiné), mais de façon fort inégale puisque dans trois estomacs sur 8 à A 171 et seulement dans quatre sur

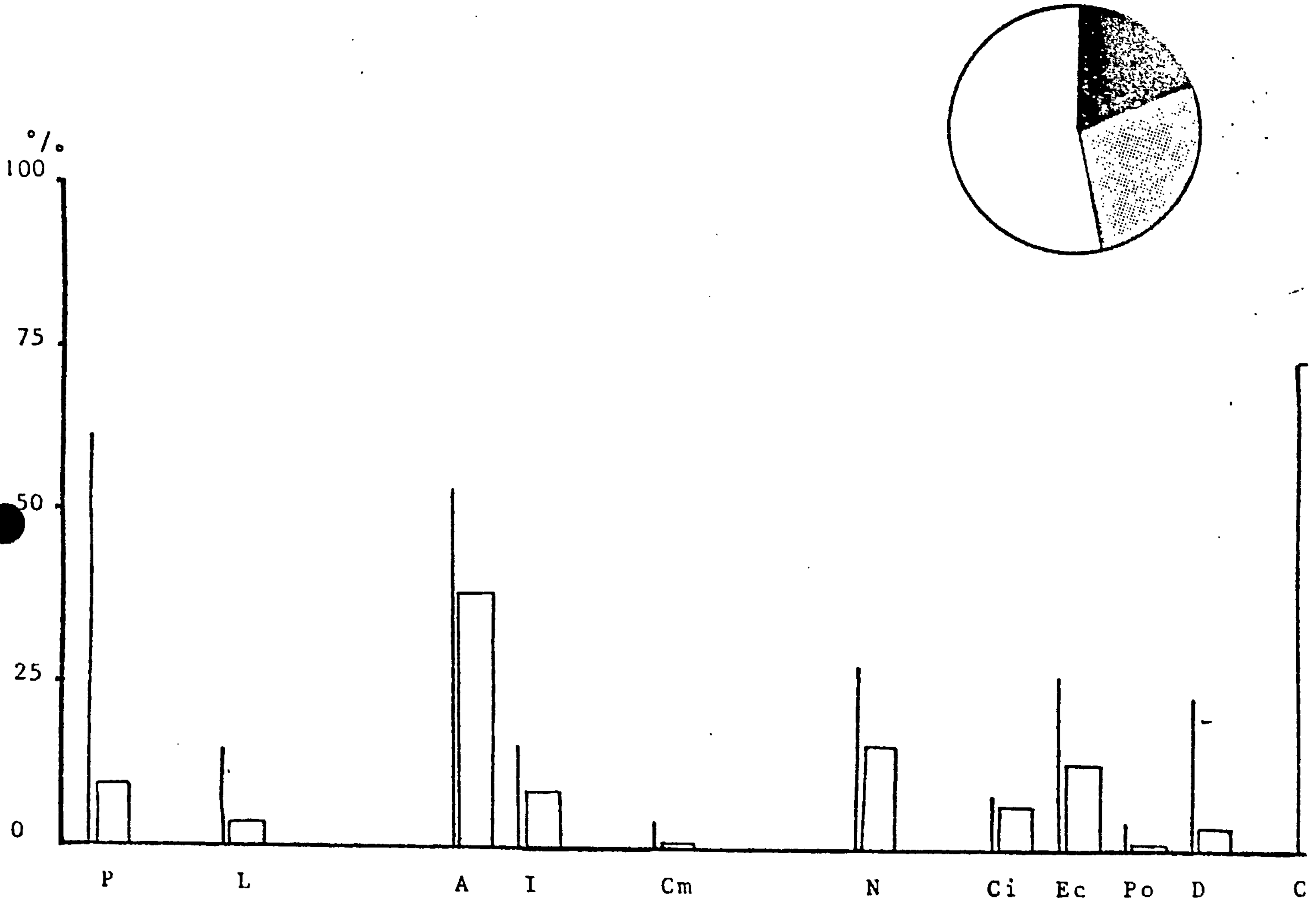

FIG.11 _ MACROURUS BERGLAX

Legend and list of abbreviations p 39

Ophiurida are found much more frequently in *M. berglax* than in *N. sclerorhynchus* (f = 0.26 vs f = 0.04), as are Lamellibranchia (f = 0.15 vs f = 0.06).

Although we caught some large *M. berglax*, bnly one fish was found in the stomach contents, and it was unidentifiable.

The high food coefficients of Natantia (Q = 944.51) and Echinodermata (Q = 416.93) point up their importance in the diet of *M. berglax*, although it must be noted that the energy value of Ophiurida is overestimated, since the weight of the skeleton is much greater than that of the edible matter. The rest of the diet consists of Polychaeta and Amphipoda.

The prey are classified as follows:

-primary prey	
preferential	Nantatia
occasional	Ophiurida
-frequent secondary prey	Polychaeta Amphipoda
-complementary prey	
first-rank	Lamellibranchia Isopoda (Ctenophora)
second rank	Cumacea Fishes

Of the prey, 19.1% belonged to pelagic groups, 26.4% to benthic groups, and 54.4% to pelagic and benthic groups.

Macrourus berglax is basically benthophagous, despite the importance of Natantia in its diet.

Our examination of the stomach contents confirms our previous knowledge of the diet of M. berglax. and contributes more detailed information. Frieb, Ekström, and Sundevall (1895) hypothesized from the appearance of M. berglax's teeth that it must feed on small fishes (capelins) and hard-shelled crustaceans. Collett (1904) reported finding a capelin in one stomach, and Andriyashev (1964) stated that the digestive tubes contained shrimp (Pandalus borealis, Hymenodora glacialis), benthic organisms (Ophiacantha abyssicola), mollusks (Buccinum, Fusus) and amphipods, a description that conforms to our observations. Joensen and Vedel Taning (1970) say only that M. berglax feeds on crustaceans, mollusks, and fishes, while Konstantinov and Podrazhanskaya (1972) describe a diet made up of benthic animals and fishes. Although fishes are often reported to be a part of M. berglax's diet, we found only one, although in the same trawls that caught our M. berglax specimens we found small fish that they might have caught, such as Boreogadus saïda.

Variations in diet (Table 16)

The eight Macrourus berglax caught at Station A 171 varied in length from 430 to 687 mm; at Station A 179, they were from 164 to 727 mm. Thus, although we had few individuals, there was a wide range in size. We divided the fish into three size groups, combining the catches of both stations, since their food did not differ from one to the other.

Lot 1. from 160 to 280 mm-5 specimens--63 prey
Lot 2. from 300 to 500 mm--9 specimens--68 prey
Lot 3. from 520 to 727 mm--10 specimens--51 prey

Table 16

(See photocopy of original.)

Legend

1. Polychaeta
2. Lamellibranchia
3. Amphipoda
4. Isopoda
5. Cumacea
6. Natantia
7. Indeterminate crustaceans
8. Echinodermata
9. Ctenophora
10. Fishes
11. Number of prey groups

The diet of the smallest fish is composed entirely of benthic organisms; that of the second lot is 87.7% benthic; and that of the third lot is 56.8% benthic.

The change in diet with increasing size seems to involve a decrease in benthic organisms. Large M. berglax are able to catch quicker, bigger prey, eg Natantia. Small benthic crustaceans disappear from their diet, whereas they are the staple prey for young M. berglax. The nutrition of larger individuals is almost exclusively dependent on big shrimp from the continental slope as, fishes are rarely captured and Ophiurida, despite their number, have little nutritional value.

- Tableau 16 -

	Lot 1	Lot 2	Lot 3
1 Polychètes	7,9 %	10,3 %	7,8 %
2 Lamellibranches	-	7,3 %	1,9 %
3 Amphipodes	63,0 %	42,7 %	11,8 %
4 Isopodes	26,9 %	-	-
5 Cumacés	1,6 %	-	-
6 Natantia	-	11,7 %	35,3 %
7 Crustacés indéterminés ..	-	17,6 %	-
8 Echinodermes ..	-	5,8 %	35,3 %
9 Cténaires	-	4,4 %	5,9 %
10 Poissons	-	-	1,9 %
11 Nombre de groupes proies	4	7	7

L'alimentation des poissons les plus petits est à 100 % d'origine benthique ; celle du deuxième lot à 83,7 % benthique ; celle du troisième, à 56,8 % benthique.

L'évolution de l'alimentation avec les tailles croissantes paraît se faire ici au détriment de la contribution benthique, les grands *M. berglax* étant capables d'attraper des proies rapides et de tailles élevées, les Natantia. Les petits Crustacés benthiques disparaissent rapidement de la nourriture, alors que chez les *M. berglax* les plus jeunes, ils fournissent l'essentiel des proies. Pour les grands *M. berglax* la nutrition dépend donc presque exclusivement des grosses crevettes du talus continental, les poissons semblant n'être guère capturés et les Ophiures, malgré leur nombre, étant de très faible valeur nutritive..

Chapter III

GENERAL CHARACTERISTICS OF THE FOOD OF MACROURIDAE

1. General description

1. All of the Macrouridae we studied were caught by trawls on the bottom. This means that they live either on the bottom itself, or in the immediate vicinity. They feed on invertebrates and fishes that they hunt in the epibenthic layer of water, on the bottom, and perhaps in the first few centimetres of sediment. Unlike many benthic fishes of the continental slope, Macrouridae are able to leave the bottom to hunt their prey in open water. They are all euryphagous carnivores.

2. They all eat pelagic and benthic organisms, although in varying proportions.

3. The prey are always vagile; no fixed or pivoting form is included in the diet, except Lamellibranchia.

4. Crustaceans are always dominant in the diet, both in number and in variety. Most are small species.

It should be mentioned that the preponderance of crustaceans in the diet, very widespread in marine fishes, especially those of the continental slope, may simply be due to the abundance of crustaceans in the environment. However, it may also result from the fact that crustacians' carapaces are resistant to enzymes and thus their digestion is slower. The apparent absence of invertebrates such as Chaetognatha and Salpa may be a result of their rapid digestion. For example, were it not for the beaks and crysalline lenses of the cephalopods, there would be no trace of this group in the stomach contents.

The importance of crustaceans in the diet has been pointed out many times: by Longhurst (1957) for the Rockel River estuary in West Africa, by Collignon and Aloncle (1960) for the Moroccan Atlantic continental shelf, by Steven (1930) for the "Corner Fishing Ground, by Blegvad (1917) for the Danish coast, by Reys (1960) for the Golfe du Lion, and by Sorbe (1972) for the south Biscay continental shelf.

5. Consistently low coefficients of emptiness and the presence of animals at various stages of digestion in a single stomach seem to indicate that feeding is more or less continuous.

The predators Trachyrynchus trachyrhynchus and Ventrifossa occidentalis have the highest coefficients of emptiness. Trachyrhynchus trachyrhynchus also has the lowest average number of prey per stomach.

6. The average weight of prey is very low for Hymenocephalus italicus, but it is higher for microphagous species whose food is basically benthic, especially the predators Ventrifossa occidentalis, Trachyrhynchus trachyrhynchis, and Macrourus berglax.

7. As the fish grow in size, the number of prey groups increases, as

does the number of nektonic animals. Fishes with a predominatly pelagic diet tend to turn to the benthos, and those with a benthopelagic or benthic diet, despite their discovery of the nekton, still find most of their food among benthic animals. This, however, is not true for the larger M. berglax.

Ventrifossa occidentialsi, like the other species, utilizes the same type of food throughout its adult growth, but it preys increasingly on large, highly vagile animals--much more so than even the Macrourus, which grow to a larger size.

Thus the diet of Macrouridae is established very early: its main characteristics are often present in the early adult stages. Later changes in feeding habits are superimposed on a well-defined base.

Similar variations in food have been observed in other fish--for example, Gadus morhua, throughly studied in the Gulf of St Lawrence by Corbeil (1953, 1954b) and Powles (1958). These authors studied the food of cods of various sizes (from 11 to 100 cm). The prey found in the stomachs of cod 11-20 cm long were (percentages by number): Teleosts (6.5%), Mysidacea (15.4%), Euphausiacea (30.8%), Amphipoda (7.4%), Decapoda (3.9%), Chaetognatha (3%), Caprella (2.5%), and Cumacea (1%); prey found in the stomachs of cod 21-30 cm long were: Teleosts (10%), Mysidacea (15.4%), Euphausiacea (22%), Amphipoda (3.6%), Decapoda (19.5%), Chaetognatha (12.7%), Capprella (traces), Cumacea (traces), Annelida (9.6%), and Mollusca (1.8%).

Thus, the main element in the food of the smallest cod, like that of small Macrouridae, is little crustaceans (Mysidacea, Euphausiacea, Amphipoda); with age, the tendency to consume fishes appears, along with a diversification in diet (appearance of annelids and mollusks) and a quantitative and qualitative change in the crustaceans consumed. Crustaceans drop from 90% in volume of total food consumed to 60%; Mysidacea still have an important place in the diet but the volume of Euphausiacea increases, as do the number and volume of decapods--big shrimp and Pagura. The number of amphipods is halved. These tendencies are confirmed in larger cod, 30 cm in length: there is a decrease in the number of benthic and pelagic crustaceans consumed; and a decrease in the volume of Mysidacea and Euphausicea, although their numbers remain high; and an increase in the number of decapods (mainly Pagura). The consumption of mollusks, annelids, and echinoderms remains steady (echinoderms especially are very frequently consumed by the larger cod), and there is an increasing preponderance of fishes (25% of the volume of prey in cod from 31 to 50 cm; 32% in those 51-70 cm, and 69% in those 71-100 cm). Finally it is interesting to note that large cod catch jellyfishes and Ctenophora, which we also observed in large <u>Macroura berglax</u>.

A final characteristic of the evolution in the cod's diet: cod eat mainly pelagic animals, and the food is always partly pelagic even in the largest fishes, although some benthic prey are present. These pelagic prey and their nychthemeral migrations are perhaps the cause of the cod's daily vertical migration (Corbeil 1954b; Powles 1958; Brunel 1965, 1968).

Such a lengthy development of this example is justified because of its similarity to the feeding habits of Macrouridae: an increase in the number of prey groups as the fish grows bigger, an increase in the consumption of nekton, utilization after a certain size of benthic organisms (but within a diet that remains essentially pelagic), and a decrease in the importance of small crustaceans--which, however, are not eliminated from the diet. It should also be emphasized that of all the fish of the continental shelf, these cod perhaps have the diet closest to that of Macrouridae, especially *Ventrifossa occidentalis*, although it is not identical to any one we studied.

8. In general, there is an *increase in the number of prey groups, especially complementary prey, when the transition is made from mainly pelagic food to benthopelagic food or mainly benthic food*.

For all eight species, Natantia are the main source of food (present in seven cases as primary or secondary prey). Next are Mysidacea and Amphipoda, because of their numbers (present five times), and fishes and polychaetes because of their weight (present four times).

9. *Macrouridae are not "sediment eaters"*, or more accurately eaters of sand microfauna. Sediment (grains of sand or mud) was found in their digestive tracts only when polychaetes were part of the stomach contents and had sediment in their own digestive tracts. (Of the 388 fish examined, there were only two exceptions: one *Trachyrhynchus trachyrhynchus* and one *Nezumia sclerorhynchus*.) This fact does

not necessarily imply that Macrouridae do not burrow in the sediment with their "shovel-shaped" snouts, at least in cases where the mouth is not terminal, or that they cannot in this way unearth and seize tiny animals living in the sediment. However, we have not been able to directly observe or photograph instances of Macrouridae feeding (Pérès 1958; Marshall and Bourne 1964, 1967).

10. Each of the eight species studied has a separate, well-defined diet; thus it is possible to recognize different ecological food types.

2. Choice of prey

The contents of a single stomach may include prey of greatly varying sizes and nutritional value. Often prey are quite tiny in relation to the length of the fish. The prey are of varied types and shapes: long and short, hard and soft. Except for polychaetes they do not appear to have been selected during the passage through the buccal and pharyngeal cavities.

The most abundant groups are little bathybenthic and bathypelagic crustaceans, whose nutritional value is low compared with that of the shrimp, fishes, and cephalopods swallowed at the same time.

The question of accessibility and choice of prey has been discussed by many researchers. Elton (1927) described the upper and lower size limits of food a fish can seize, and Stevens (1930) established that, in addition to size, the accessibility of an animal depends on its habits and activity and those of its predator. Allen (1941), studying the biology of young Salmo salar, lists size, appearance, habits, and taste among the important characteristics of prey; all of these factors intervene in determining the accessibility of a given prey. Both Allen and Neill (1938) consider that accessibility is probably a more important factor than choice for fishes that hunt by sight.

In attempts to elucidate this question, comparisons have been made between fishes' faunal environment and the prey they consume (Larsen 1936; Jones 1952; Steven 1930). Numerous indices (Ivlev 1961; Thomas 1966) have been defined.

In their study of _Sternoptyx diaphana_, a bathypelagic species, in five different regions,(one in the Pacific and four in the Atlantic), Hopkins and Baird (1973) establish the importance of the faunal environment in determining the diet of this planktonophagous species. Differences in the abundance and species of potential prey from one region to another are reflected in the size and composition of the dominant food of _S. diaphana_.

Hopkins and Baird observe that not only are there great differences from one region to another, but there are also substantial variations within a single region, from one catch to another, even in fish caught in the same draught. They conclude that S. diaphana is a solitary hunter, one that sees its prey (apparently because of their bioluminescence) but, with its limited capacity for chase, makes no selection, taking merely those in the immediate vicinity that it can consume.

Other authors are also of the opinion that differences among the stomach contents of benthic fish do not necessarily indicate a selection by the fishes, but rather represent variations in the biotope. Kitamori (1962), for example, reports that Pseudorhombus pentophtalmus eats shrimp on sandy bottoms and polychaetes on muddy bottoms.

Geogrpahical variations, such as those we observed for Nezumia sclerorhynchus, have been described for many other species (for example, Hertling 1928; Blegvad 1930). They do not imply the absence of a species-specific diet, nor the absence of selection.

Jones (1952), while he observes that the composition of flatfishes' diet varies with the bottom type, also shows that there is active selection: on fine sand Pleuronectes platessa and Limanda limanda eat mainly the Lamellibranchia Cultellus and Ensis; on muddy sand, the preferred food of Pleuronectes platessa is still Cultellus, and it will eat the Ophiura Amphiura only if Cultellus is scarce; Limanda limanda, on the other hand, eats more Amphiura than Cultellus, even if the latter are abundant. De Groot (1971) describes highly individualized diets in the various Pleuronectiforme families.

Corbeil (1954a) and Powles (1958) have established that small Canadian cod practice prey selection. A single prey--Mysis mixta--was prominent in their stomachs contents, while it was only the third most abundant in the environment; shrimp, although abundant in the environment, were not consumed as much as their density on the bottom would indicate; there were practically no euphausiids and amphipods available as prey on the bottom, but the latter, being pelagic forms (Hyperidae), could not be caught; some forms, such as annelids, were found in the stomachs but not on the bottom, while echinoderms were found on the bottom but not in the stomachs, even when they were of a size easily accessible to the fishes.

To the extent that the concept of a diet applies, as it does to Macrouridae, the concept of selection is necessarily present. In a single draught we caught species whose diets were clearly distinct (different preferential and secondary prey, and differences in the frequency and abundance of prey groups): Ventrifossa occidentalis and Coeloryhnchus coelorynchus are often grouped together, as are Bathygadus melanobranchus, Nezumia sclerorhynchus, and Coelorhynchus coelorhynchus, and Trachyrhynchyus trachyrhynchus, Hymenocephalus italicus, and Nezumia sclerorhynchus.

We saw that the food ecology of Nezumia sclerorhynchus of the Mediterranean and of the Atlantic was the same.

This example and the study of the stomach contents of all eight Macrouridae species show that, while selection is practiced, there is also a certain amount of eclecticism in the "choice" of prey, which shows up in various ways: none of the Macrouridae feeds exclusively on pelagic or benthic animals; the diet is never composed of only one prey group; there is always a variety of prey types and sizes in the stomach; there are geographical variations; the composition of the diet changes with age, but while the largest fish do catch large prey, this does not mean that smaller prey are abandoned, although the energy contribution the smaller prey make is reduced.

Dragging and plankton sampling were not done along with the trawling, so we were unable to make comparisons between the biotope's potential and the use made of it by Macrouridae, in order to see if the apparent selection we deduced from the study of the stomach contents is evidence of actual selection.

To offset this shortcoming, we did a study of some specific cases, concluding that there is indeed selection, since the Macrouridae do not utilize all the animal groups that are available and accessible on the bottom.

a. At four stations our trawls (Blake and beam trawls) brought up groups that were not found in the Macouridae's diet.

Coelorhynchus coelorhynchus at the Muséum station (214-235 m) had no Ophiura, Branchipoda, or sponges in the digestive tract. Nezumia aequalis at the Muséum station (1120-900 m) had no echinoderms, mollusks, or Branchiopoda in the digestive tract.

At the two southern Indian Ocean stations where Macrourus holotrachys were caught, the following were found in the trawl but not in the stomach contents: Spongiae, Hydroida, Madreporaria, Alcyonaria, Nemertia, Mollusca (other than Cephalopoda), Pycnogonides, Cirripedia, Echinodermata, Bryozoa, Tenaidacea, Ascidia, and Euphausiacea. The absence of this last group in the food of M. holotrachys is worthy of note.

B. The prey found in Macrouridae and the prey found in other fishes caught at the same time were compared for two draughts.

At the northwest Africa continental slope station Z 239, Capros aper, Scorpaenidae (Helicolenus dactylopterus and Trachiscorpia cristulata), Triglidae, Chlorophtalmus atlanticus, and Synagrops microlepsis were found in the trawl along with Coelorgynchus coeloryhnchus and Ventrifossa occidentalis. The presence or absence of various prey groups is shown in table 18: Galathea, Pagura, and Ophiura are totally absent from the food of the two Macrouridae, and fewer Euphausiacea and Mysidacea are found in them than in the *Capros aper* or the Triglidae.

Table 18

(See photocopy of original.)

Legend

1. Polychaeta
2. Mollusca (benthic)
3. Cephalopoda
4. Ostracoda
5. Copepoda
6. Gammarids
7. Isopoda
8. Mysidacea
9. Cumacea
10. Galathea
11. Pagura
12. Euphausiacea
13. Ophiura
14. Fishes

At station 179, on the western continental slope of the Barents Sea off Bear Island, the following fish were caught at the same time as *Macrourus berglax*: *Raja radiata*, which had eaten Mysidacea, Euphausiacea, Natantia, Gammarids, and fishes (of which remains of the vertebral columns were found); Newfoundland turbot (*Reinhardtius hippoglossoides*), whose stomachs were empty; *Anarhichas lupus*, which had eaten *Micromesistius poutassou*; and *Micromesistius potassou*, whose stomachs were full of Euphausiacea. No Euphausiacea were found in the *Macrourus berglax* (or in the *Macrourus holotrachys*), nor were Mysidacea.

C. The use of an index of relative selectivity makes it possible to evaluate the choice of a prey group by various species in comparison with the average diet of Macrouridae (table 19).

Hymenocephalus italicus and *Trachyrhynchus trachyrhynchus* have a clear preference for zooplankters, especially copepods; however, the index of relative selectivity of copepods is negative for all other

- Tableau 18 -

	Coelor. coelor.	*V.occid.*	*Capros aper*	Scorp.	Trigl.	*Chlor. atlan.*	*Synag. micr*
1 Polychètes	+	+	−	+	+	+	−
2 Mollusques (benthiques)	+	−	−	−	−	−	−
3 Céphalopodes	+	+	−	−	−	−	−
4 Ostracodes	−	+	−	−	−	−	−
5 Copépodes	+	+	+	−	−	−	+
6 Gammariens	++	++	+	+	−	−	−
7 Isopodes	+	+	−	+	+	−	−
8 Mysidacés	−	+	++	−	−	−	+
9 Cumacés	+	+	−	−	+	−	−
Natantia	+	++	−	−	−	−	+
10 Galathées	−	−	−	+	−	−	−
11 Pagures	−	−	−	+	−	−	−
12 Euphausiacés	−	+	−	+	−	++	−
13 Ophiures	−	−	−	+	−	−	−
4 Poissons	+	+	−	+	−	+	+

A la station A 179, sur le talus continental occidental de la mer de Barents au large de l'île de l'Ours, ont été pêchés en même temps que *Macrourus berglax*, des *Raja radiata* qui avaient mangé des Mysidacés, des Euphausiacés, des Natantia, des Gammariens et des poissons (restes de colonnes vertébrales), des flétans noirs *Reinhardtius hippoglossoides* dont les estomacs étaient vides, des *Anarhichas lupus* qui avaient capturé des *Micromesistius poutassou*, et des *Micromesistius poutassou* dont tous les estomacs étaient remplis d'Euphausiacés . Les Euphausiacés manquent totalement chez *Macrourus berglax* (comme chez *Macrourus holotrachys)* et les Mysidacés également .

C - Enfin *l'utilisation de l'indice de sélectivité relative* permet d'apprécier, par rapport au régime alimentaire moyen des Macrouridae, le choix de tel ou tel groupe proie par les différentes espèces (tableau 19) .

Les préférences pour les zooplanctontes, en particulier pour les Copépodes, apparaît clairement pour *Hymenocephalus italicus* et species (except Nezumia sclerorhynchus). Cephalopods and fishes are selectively chosen by two predatory species, Trachyrhynchus trachyrhynchus and Ventrifossa occidentalis; their indices are at same level--an especially high one. Ventrifossa occidentalis and Macrourus berglax show more of a preferance for Natantia than do other species. Only the Macrouridae with a benthic diet--Coelorhynchus coelorhynchus, Macrourus berglax, and Macrourus holotrachys--show a preference for amphipods, although they are present regularly. The preference of Nezumia aequalis and Macrourus holotrachys for Mysidacea is clearly apparent, as is the preference for Reptantia of Ventrifossa occidentalis.

On the whole, the index of relative selectivity brings out characteristics of each diet and allows for comparison among diets. It shows the preference for planktonic animals of some species, and the preference of others for nektonic or benthic animals.

Table 19

(See photocopy of original.)

Legend

1. Polychaeta
2. Gasteropoda
3. Lamellibranchia
4. Cephalopoda
5. Ostracoda
6. Copepoda
7. Amphipoda
8. Isopoda
9. Tanaidacea
10. Cumacea
11. Mysidacea
12. Euphausiacea
13. Echinodermata
14. Fishes

- Tableau 19 -

	Trachy. trachy.	*Hym. ital.*	*Nez. aeq.*	*Nez. sclero.*	*Vent. occid.*	*Coelo. coelo.*	*Macr. berglax*	*Macr. holo.*
1 Polychètes	- 0,60	-	- 0,24	- 0,04	- 0,37	+ 0,40	- 0,01	- 0,56
2 Gastéropodes	+ 0,33	-	-	+ 0,03	-	+ 0,42	-	-
3 Lamellibranches	-	-	-	+ 0,37	-	-	+ 0,67	-
4 Céphalopodes	+ 0,68	-	-	- 0,82	+ 0,77	- 0,20	-	- 0,27
5 Ostracodes	-	- 0,59	+ 0,77	+ 0,20	0	- 0,33	-	-
6 Copépodes	+ 0,28	+ 0,38	- 0,36	+ 0,26	- 0,83	- 0,63	-	- 0,81
7 Amphipodes	-	- 0,78	+ 0,09	- 0,32	- 0,07	+ 0,31	+ 0,23	+ 0,23
8 Isopodes	-	-	+ 0,24	+ 0,05	- 0,28	+ 0,11	+ 0,55	- 0,79
9 Tanaidacés	-	-	-	+ 0,53	-	-	-	-
10 Cumacés	-	- 0,28	- 0,24	+ 0,21	+ 0,43	- 0,09	- 0,45	- 0,63
11 Mysidacés	+ 0,24	-	+ 0,60	- 0,48	+ 0,08	- 0,96	-	+ 0,68
12 Euphausiacés	-	+ 0,53	-	- 0,83	- 0,55	+ 0,39	-	-
Natantia	+ 0,13	- 0,53	- 0,71	- 0,62	+ 0,69	+ 0,01	+ 0,52	- 0,69
Reptantia	-	-	- 0,13	- 0,83	+ 0,79	+ 0,22		
13 Echinodermes	-	-	-	- 0,24	-	-	+ 0,86	-
14 Poissons	+ 0,72	- 0,64	-	- 0,84	+ 0,71	- 0,35	- 0,38	+ 0,14

3. The Food of Macrouridae--ecological types

Rauther (1940) classifies fishes as carnivorous, herbivorous, iliophagous [?], and omnivorous; he divides the carnivores into those that eat small animals and those that eat large animals (the true predators). Al-Hussaini (1947) classifies fishes as plankton-eaters, carnivores, omnivores, and herbivores; carnivores are divided into three types: a) those that choose their prey, including mollusk-eaters, fish-eaters, and crustacean-eaters; b) those that feed on several groups, including sand-eaters and "others", and c) omnivores, including detritus-feeders and coral-eaters. Bertin (1958) distinguishes among plankton-eaters, open-water predators that feed on crustaceans, mollusks, and fishes, madrepore-eaters, mud-burrowers, and herbivores. Nikolsky (1963) proposes only three categories: herbivores and detritus-feeders; carnivores that eat invertebrates; and fish-eating predators. However, he emphasizes the subjectivity of such a categorization, since most fishes eat a variety of prey, and carnivores often behave like predators, and vice versa. For greater accuracy, he classifies fishes as euryphagous, those that eat a variety of prey; stenophagous, those that confine themselves to a few types; and monophagous, those that feed on only one type. Randall (1967) distinguishes the vegetation-and detritus-feeders, the zooplanktonophages, the eaters of sessile animals, the eaters of invertebrates with carapaces, general carnivores, piscivores, and ectoparasites. In her study of the ichthyofauna of coral reefs, Vivien (1972) makes three primary distinctions--herbivores, omnivores, and carnivores--with further subdivisions that take into account the fish's behaviour, prey quality, and the ethology of both fish and prey. In this way, by successive divisions, she is able to include all species in her classification--at the risk, however, of obscuring the main categories. The problem of the limits of a classification and its purpose is raised. A similar problem exists with Vegas-Velez's classification (1972); it contains no fewer than 24 categories of food (to which there is a possibility of further additions), and although the classification is intended to be both general and synthetic, it is practically impossible to tell where Macrouridae might fit in.

Sorbe (1972) has the distinction of proposing only two categories of carnivorous fishes: the stenophages, with quite specialized diets (plankton-eaters, fish-eaters, and shellfish-eaters), and the euryphages, whose diet is made up of 10 to 20 zoological groups, with crustaceans dominating. Hureau (in press) confines himself to three categories of nektonic animals: planktivores, predators, and benthivores.

As mentioned earlier, Macrouridae are carnivorous euryphagous fishes (according to Sorbe's classification).

In our study by species, it became apparent that not all Macrouridae have the same diet. Using as criteria the trophic relationships a species has with its environment, we can define three distinct ecological types of food.

Although up until now we have classified certain prey groups, (eg amphipods and isopods) among the pelagic or benthic animals, henceforth we shall adopt a more realistic (with a few exceptions) classification, as follows: Cephalopoda, Natantia, fishes, Copepoda, Mysidacea, and Euphausiacea are pelagic, and Ostracoda, Amphipoda, Isopoda, Tanaidacea, Cumacea, Reptantia, Polychaeta, Gasteropoda, Lamellibranchia, and Echinoderatma are benthic. Thus for each species we can establish what proportion of its food comes from the open sea and what proportion from the bottom, as shown in table 20. (Pelegic food coefficients are underestimated because Cephalopoda were not evaluated.)

Table 20

(See photocopy of original.)

These values give an idea of the comparative importance of benthic and pelagic food, and allow us to define the following ecological types:

a. the pelagic type (more than 70% pelagic prey), with one planktophagous species (*Hymenocephalus italicus*) and one predacious species (*Trachyrhynchus trachyrhynchus*).

b. mixed or benthopelagic type (from 30% to 70% pelagic prey), with one

Alors que nous avons placé jusqu'ici un certain nombre de groupes proies (Amphipodes, Isopodes, ...) parmi les animaux pélagiques ou benthiques, nous allons considérer désormais, ce qui est plus conforme à la réalité malgré quelques exceptions, que sont pélagiques les Céphalopodes, Natantia et Poissons, les Copépodes, Mysidacés et Euphausiacés, et que sont benthiques les Ostracodes, Amphipodes, Isopodes, Tanaïdacés, Cumacés et Reptantia, les Polychètes, Gastéropodes, Lamellibranches et Echinodermes . Nous avons alors précisément pour chaque espèce la part de son alimentation qui provient du pélagos et du benthos, comme le montre le tableau 20 (où les coefficients alimentaires pélagiques sont sous-estimés par l'absence d'évaluation pour les Céphalopodes) .

- Tableau 20 -

	Cn (in %)		Q (in %)	
	Pel.	Benth.	Pel.	Benth.
Trachyrhynchus trachyrhynchus	94,5	3,1	99,9	0,1
Hymenocephalus italicus	94,9	4,3	99,6	0,4
Nezumia aequalis	43,0	55,3	96,6	3,4
Nezumia sclerorhynchus	66,4	32,3	45,8	54,2
Ventrifossa occidentalis	52,4	41,8	96,7	3,3
Coelorhynchus coelorhynchus	22,2	76,5	83,2	16,8
Macrourus berglax	19,1	76,1	62,2	31,8
Macrourus holotrachys	41,0	41,0	98,5	1,5

A partir de ces valeurs qui permettent d'apprécier les rôles comparés du benthos et du pélagos, nous pouvons définir les types écologiques d'alimentation suivant :

a- pourcentage des proies pélagiques supérieur à 70 % : *type pélagique* avec une espèce planctonophage, *Hymenocephalus italicus* et une espèce prédatrice, *Trachyrhynchus trachyrhynchus* .

b- pourcentage des proies pélagiques compris entre 30 et 70 % : *type mixte ou benthopélagique* avec une espèce prédatrice

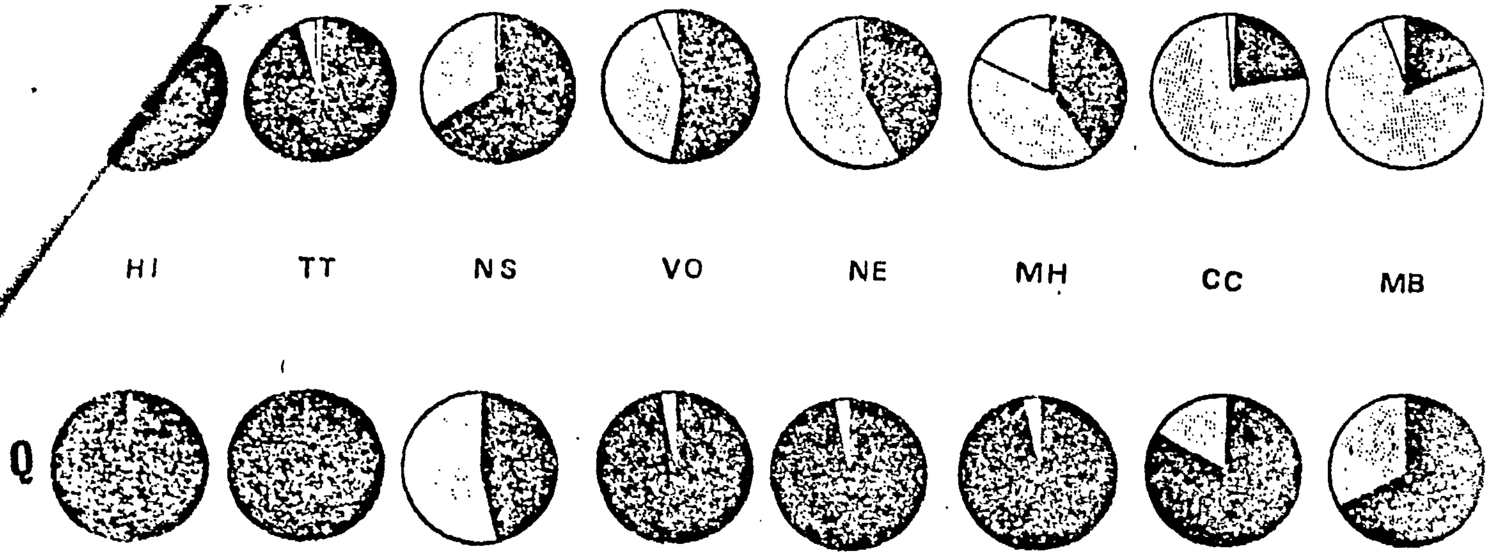

FIG.13C *Part des proies pélagiques (secteur noir), benthiques (secteur tramé), pélagiques ou benthiques (secteur blanc) exprimée en pourcentage en nombre (Cn) pour les cercles de la ligne supérieure, en coefficient alimentaire (Q) pour les cercles de la ligne inférieure.*

ABREVIATIONS: H.I. *Hymenocephalus italicus* ; T.T.*Trachyrhynchus trachyrhynchus* ; N S a , *Nezumia sclerorhynchus* atlantiques; N S m, *Nezumia sclerorhynchus* méditerranéens; N S , *Nezumia sclerorhynchus* (ensemble des individus); V O ,*Ventrifossa occidentalis*; N E , *Nezumia aequalis*; M H , *Macrourus holotrachys* ; C C ,*Coelorhynchus coelorhynchus*; M B , *Macrourus berglax* .

Ventrifossa occidentalis et trois espèces microphages *Nezumia sclerorhynchus*, *Nezumia aequalis* et *Macrourus holotrachys* .

c - pourcentage des proies pélagiques inférieur à 30% : type benthique avec l'espèce microphage *Coelorhynchus coelorhynchus* et l'espèce à tendance prédatrice *Macrourus berglax* .

Bien que l'environnement faunistique de chaque espèce puisse, comme on l'a vu, faire subir des modifications à l'alimentation, celle-ci ne varie qu'entre des limites précises, correspondant à ces différents types écologiques .

Ces trois types, qui découlent de la sélection de la nourriture par chaque espèce, apparaissent notamment lors de l'examen de l'indice de sélectivité relative . En effet, ont des indices positifs et élevés pour les animaux du plancton, les espèces du premier type, pour les animaux du necton, les prédateurs (avec l'opposition entre *V. occidentalis* et *T. trachyrhynchus*); pour les espèces microphages à régime benthopélagique ou benthique, les indices ne sont jamais très élevés en général, car ces animaux capturent beaucoup de groupes proies.

Fig 13 ECOLOGICAL TYPES OF FOOD

(See photocopy of original.)

Figure 13A The proportion of various prey groups in the diet of each species

Legend

1. Fishes Cephalopoda
2. Miscellaneous prey
3. Natantia
4. Benthic crustaceans (excluding Amphipoda)
5. Benthic prey (excluding crustaceans)
6. Amphipoda
7. Planktonic crustaceans

Figure 13B The utilization of various prey groups in an average diet, expressed as percentage by numbers (Cn).

Fig 13C (See photocopy of original.)

The proportion of pelagic (black section), benthic (shaded section), and pelagic/benthic (white section) prey, expressed as the percentage by numbers (Cn) for the circles in the top row, and as food coefficient (Q) for those in the bottom row.

ABBREVIATIONS: HI Hymenocephalius italicus; TT Trachyrhynchus trachyrhynchus; NSa Nezumia sclerohynchus (Atlantic); NSm Nezumia sclerorhynchus (Mediterranean): NS Nezumia sclerorhynchus (all individuals); VO Ventrifossa occidentialis; NE Nezumia aequalis; MH Macrourus holotrachys; CC Coelorhynchus coelorhynchus; MB Macrourus berglax.

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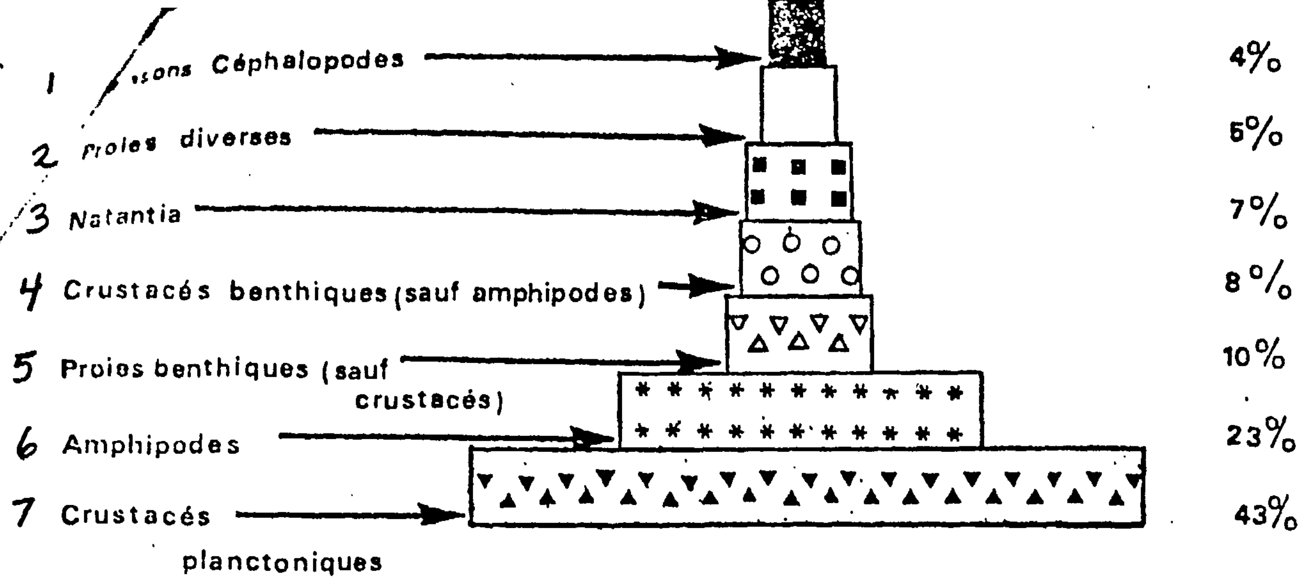
predacious species (Ventrifossa occidentalis) and three microphagous species (Nezumia sclerorhynchus, Nezumia aequalis, and Macrourus hototrachys).

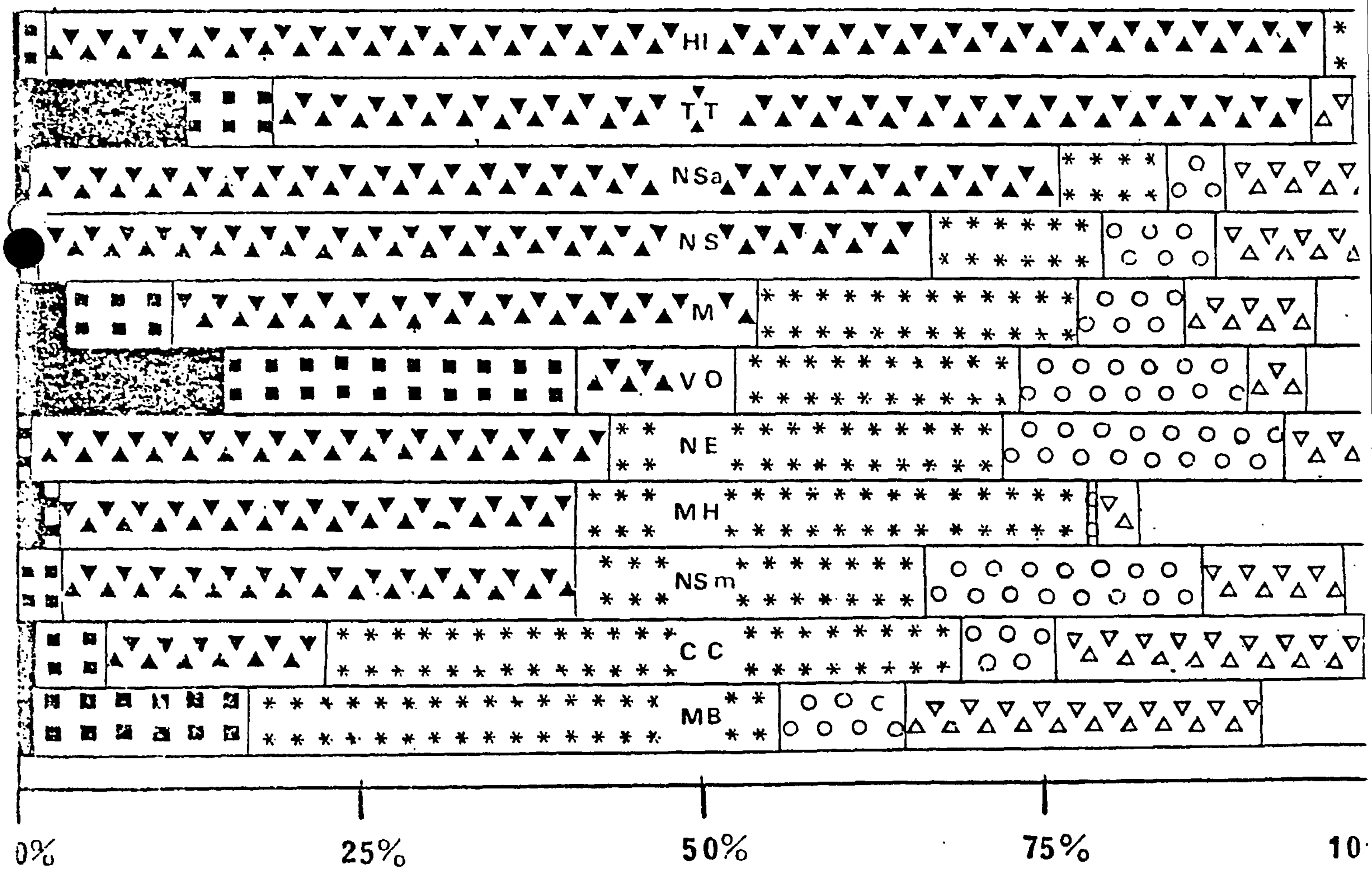
c. benthic type (less than 30% pelagic prey prey), with one microphagous species (Coelorhynchus coelorhynchus) and one species tending to predation (Macrourus berglax).

Although the faunal environment may cause changes in diet, variations will be within precise limits, which correspond to these three ecological types.

The three types, based mainly on each species's selection of food, are especially apparent in the index of relative selectivity.



13 A *Part des différents groupes proies dans l'alimentation de chaque espèce.*



13 B *Utilisation des différents groupes proies, exprimée en pourcentage en nombre (Cn), dans le cas d'un régime alimentaire moyen.*

FIG.13 MAS DES TYPES ECOLOGIQUES D'ALIMENTATION

X The pelagic type has a high positive index for planktonic animals; the predators have a high positive index for nektonic animals (with the contrast between V. occidentalis and T. trachyrhynchus); for the microphagous species of the benthic or benthopelagic type, the indices are in general not very high, since these animals feed on many prey groups.

A closer look at the food reveals that the pelagic type is basically planktophagous (or planktivorous), since the majority of prey are planktonic crustaceans (Copepoda, Mysidacea, Euphausiacea): 93.2% in Hymenocephalus italicus 75.8% in Trachyrhynchus trachyrhnchus. H. italicus is a strict planktonophage, and T. trachyrhynchus is a predator, obtaining its food by actively hunting Natantia, Cephalopoda, and fishes, which make up most of its diet.

Within the mixed type, there is a clear contrast between, on the one hand, Ventrifossa occidentalis, another active predator whose diet consists of up to 40% Natantia, Cephalopoda, and fishes, and, on the other, the two Nezumia species and Macrourus holotrachys, which feed on plankton and tiny animals that live on the surface and perhaps in the first few centimetres of the sediment. Zooplankters make up 65.1% of Nezumia sclerorhynchus's prey, 421% of Nezumia aequalis's, and 36.7% of Macrourus berglax's.

As for the benthic type, the pelagic portion of Coelorhynchus coelorhynchus's prey consists of planktonic animals (Cn = 16.0%) and that of Macrourus berglax's consists of Natantia decapods (Cn = 15.5%)

However, considering the food value of the two areas (benthic and pelagic) by examining the food coefficients, the situation appears quite different. In general, nektonic animals are usually bigger than benthic animals. Therefore, pelagic animals are much more important in the diet of the eight species we studied. The open sea is a basic food source for Macrouridae, but it is not the only one.

4. A comparison of the food of the Macrouridae we studied and that of other fishes

a. Comparison with other Macrouridae species

Coryphaenoides rupestris is the only species of Macrouridae whose diet is well known. Frieb, Ekström, and Sundevall (1895) considered that crustaceans were the basis of its diet, since Hyperidae and shrimp were found in the stomach contents. Collett (1903), using bottom wetlines at 200 m in the Norwegian fiords, caught this species and found large shrimp in its digestive tract. Andriyashev (1964), taking up the work of Crieg (1898) and Collett (1903), states that C. rupestris's diet consists mainly of Pandalus borealis, and also of P. annulicornis, P. propinquus, Pasiphae, Hemimysis abyssicola, Themisto, and "others". According to Podrazhanskaya (1967), Pasiphaea shrimp seem to be the main food in the summer of C. rupestris 40 to 170 cm long off Iceland; Themisto and Euphausiacea are much less frequent. Other foodstuffs are much rarer: (fishes, Calanus spp., Cephalopoda, Limacina, Ctenophora). Later works (Pechenik and Troyanovskii 1969; Konstantinov and Podrazhanskaya 1972; Joensen and Vedel Taning 1970; Nobel, Orias, and Rodella 1972) confirm this diet based almost entirely on invertebrates (shrimp, Amphipoda, Cumacea, and in smaller amounts Cephalopoda and fishes--Pechenik and Troyanovskii 1969.)

Okamura (1970 a, b) describes the food of 25 species and 12 genera of Macrouridae in the Japanese seas; unfortunately, however, he only examined a few stomachs of each species, except for three specimens: Hymenocephalus striatissimus (20 specimens), Coelorhynchus multispinulosus (24 specimens), and Coelorhynchus hubbsi (21 species). Okamura's results give an idea of the entire family's diet that differs on several points from what we found: 1. mud is regularly present in the stomach (24 species), although in infinitesimal quantity; 2. there is a total absence of amphipods and copepods, which is quite astonishing; 3. euphausiids are nearly always present, and often make up a large proportion, or even the totality, of prey; 4. polychaetes are less important; 5. there is only a small number of prey groups; 6. the benthos is weakly represented (mainly by polychaetes). Okamura concludes that the group euphausiids shrimp-fishes (which he estimates at 86%) is the basic food of Macrouridae, and that other prey, except perhaps cephalopods for a few species, are purely incidental (crabs, isopods, squill, polychaetes).

Using the data available in the literature, we can attempt to summarize the diets of the different genera and species in the Macrouridae family.

The genus Bathygadus seems to be planktonophagous, as we observed for B. melanobranchus. This opinion is shared by Marshall (1973b). B. antrodes (Okamura 1970b) eats little shrimp and a lot of euphausiids. Marshall (1973b) and Okamura (1970b) report an analogous diet for the neighbouring genus Gadomus: and remains of copepods and small decapods were found in the intestine of two G. longifilis and one G. dispar (Marshall 1973b); Euphausiids and shrimp were found in G. colletti (Okamura 1970b).

Hymenocephalus, a genus of smaller-sized fishes, is also planktonophagous. We saw earlier that the species H. italicus, very widespread, eats mainly copepods and euphausiids. The only species whose diet Okamura could really study was H. striatissimus; it eats only fishes and euphausiids (Okamura 1970b). The species H. lethonemus eats only euphausiids.

Okamura (1970b) also examined a few stomachs of Nezumia condylura, and found that they had caught mainly euphausiids (48%) and polychaetes (45%). There were also a few shrimp (7%).

Two neighbouring genera, Malococephalus and Ventrifossa, are active predators, as we saw for *V. occidentalis*. Gilbert (1905) found the remains of squid and shrimp in the stomach contents of *M hawaiensis*, *V. atherodon*, and *V. ctenomelas*. *M. leavis* eats *Cirolana borealis*, *Nephrops*, Pasiphae, *Pandalus*, Crangonidae, Amphipoda, *Geryon*, and *Gonoplax* (Hickling 1925), and squid and euphausiids (Okamura 1970b). In one individual 45 cm long, Koefoed (1927) found a 10-cm *Chlorotocus*, a few 5-cm Schizopoda, and several Isopoda and Copepoda. *V. garmani* and *V. misakis* apparently eat euphausiids, shrimp, and isopods (Okamura 1970b). Myctophidae, euphausiids, and shrimp were found in *Coelorhynchus macrochir*

(Marshall 1973). Coelorhynchus occa seems to eat mainly little fishes (Myctophidae) and benthic crustaceans (Pagura and other decapods) (Marshall 1973b), though Koefoed (1927) reports finding a fragment of Ascidia, a Sergestes, an ostracod, and some copepod remains. Rattray (1947) concludes that Coelorhynchus fasciatus lives on or near the bottom, as he found in its food many polychaetes, squill, crabs, Pagura, shrimp, many Mysidacea, many Copepoda (Calanidae), remains of Cephalopoda, and some fishes (eg Paracellionymus maurolicus, Myctophum). Davies (1949) confirms this diet. A Myctophidae was found in C. quicunciatus (Gilbert and Hubbs 1920); squid and fishes were found in C. smithi and C. asteroides (Okamura 1963). The importance that fishes seem to have in the diets of this genus--much greater than what we observed for C. coelorhynchus, a clearly benthic species--seems to be confirmed in Okamura's study of ten Japanese species. However, sufficient numbers were examined for only two species: C. multispinulosus and C. hubbsi. (The other species are C. kishinoyei, C. jordani, C. kamoharai, C. longissimus, C. smithi, C. anatirostris, C. japonicus, and C tokiensis.) All of these species eat euphausiids and polychaetes, five of them eat fishes, some also eat shrimp, isopods, and squills, except C. kishinoyei, which had mainly polychaetes in its digestive tube. Five of these species have a diet that is made up of more than 70% pelagic animals, and it is more than 40% for nine of them. Thus Japanese Coelorhynchus seem to feed from the open sea more than the bottom, unlike C. coelorhynchus. This is because of the absence of amphipods and the importance of euphausiids.

While Coryphaenoides pectoralis (Okamura 1970, four specimens) seems to have a pelagic diet like C. rupestris and also C. acrolepsis (Okamura 1970a), C zaniophorus is, on the contrary, benthophagous, as are two Japanese species, C. marginatus and C. nasutus, which feed mostly on polychaetes but also on squid, euphausiids, shrimp, and isopods. Finally, Marshall (1973b) concludes that C. macrocephalus must be a predator, given its morphology and strong teeth. This is confirmed by the numerous squid beaks found in the stomach of one specimen.

Marshall (1973b) also reports finding fish remains in the stomachs of Trachonurus sulcatus, Sphagemacrurus grenadae, and Odontomacrurus murrayi; copepods and fishes in Cetonurus globiceps; and copepods, amphipods, isopods, Tanaidacea, and Polychaeta in two Echinomacrurus mollis.

b. Comparison with other deep-sea families

Among the bathybenthic families, Eretmophoridae, like Macrouridae, seem to depend on animals that live on and near the bottom, particularly crustaceans and polychaetes. Templeman (1970) made a list of the prey found in the stomachs of 13 Lepidion eques of the northwest Atlantic: 94.3% were crustaceans (Copepoda, Mysidacea, Cumacea, Isopoda, Amphipoda, Euphausiacea, Natantia), 4.8% were polychaetes, and there were some cephalopod remains. The species Lepidion lepidion of the Mediterranean and Lepidion guentheri in the Madeira region have the same type of diet.

The diet of the Gadidae Micromesistius poutassou, studied by Zilanov (1966-68) and by Tournier (1968) in the Mediterranean, is also similar, but has a larger proportion of fishes: it includes Euphausiacea, Hyperidae, Natantia, Cyclothone, Paralepsis, Myctophum, Gadiculus argenteus larvae, Coelorhynchus larvae, Trachypterus larvae, Cephalopoda, Polychaeta, and Ophiura.

The diet of other deep-sea families is practically unkown. However, we are familiar with the diet of <u>Benthocometes robustus</u> (Brotulidae), through the work of Bougis and Ruivo (1954), who studied Mediterranean specimens caught at a depth of 330 to 500 m. This species, whose digestive tract is characteristic of fishes that eat sedimentary microfauna, feeds mainly on crustaceans, in particular ostracods. It seems to be more dependent on the bottom than Macrouridae.

The diet of Hymenocephalus italicus is similar to that of mesopelagic and bathypelagic planktophagous fishes, which, according to Maurin (1966), because of their small size cannot consume nektonic prey and must resort to plankton, the only nutritional element available to them, with a heavy concentration of copepods and euphausiids (Maurin 1966). The food biology of Myctophidae, a prey of Macrouridae, is the best known. Collard (1970), in a study of 42 mesopelagic fish species of the eastern Pacific (including 18 Myctophidae), states that 95% of the prey are crustaceans, mostly copepods and euphausiids. According to Collard, the fishes do not select their prey; an apparent preference for a particular prey is merely the consequence of its preponderance in the feeding ground, or a consequence of size. Anderson (1967) and Paxton (1967) give prey percentages similar to those of Collard; Paxton, however, thinks that selection is involved. Samyshev and Schetinkin (1973) also believe that there is selection in the feeding habits of three Myctophidae species and one Gonostomidae species of the northwest African continental slope: the only food they consume are euphausiids (sometimes alone but always dominant), Reptanita decapod larvae, and in lesser numbers copepods; no other plankton groups are consumed (Chaetognatha, Siphonophora, Tunicata, etc). From the point of view of Paxton, Samyshev, and Schetinkin, selection is also practiced not only by Hymenocephalus italicus but also by other Macrouridae that eat planktonic animals.

Other authors have confirmed that importance of copepods and euphausiids in the diet of mesopelagic and bathypelagic species. The diet of some species is quite varied, as it the case for Hymenocephalus italicus. One particularly abundant Gonostomidae, Cyclothone, eats mainly copepods but also some other crustaceans (euphausiids in particular), and some Chaetognatha (Gunther and Deckert 1952; Marshall 1960; Fitch and Lavenburg 1968; Legand et al 1972). The diet of the deep-sea species Cyclothone acclinidens is made up of 10.7% Copepoda, 3.6% Chaetognatha, 2.4% Ostracoda, 1.2% Amphipoda (De Witt and Cailliet 1972). The only fish found in the stomach of Hymenocephalus italicus was, in fact, a Cyclothone, and it is clear that its diet is no different from that of its predator (except for its own presence): it does not eat euphausiids--undoubtedly because of its small size--but catches Chaetognatha instead. This example points up the small size of Macrouridae's prey in relation to their own size.

The diet of large deep-sea pelagic predators (Stomiatoidei, Alepisauroidei, Lyomeri) is in no wise similar to that of any of the Macrouridae. They hunt nektonic animals almost exclusively, far from the bottom, and eat no benthic prey; whereas Macrouridae live near the bottom and, in our opinion find some proportion--however small--of their prey, on or in the sediment.

c. Comparison with demersal and littoral species

As a general rule, there are no demersal fishes with a diet similar to that of Macrouridae--that is, with a large proportion of both benthic and pelagic animals. Diet types seem to be less eclectic, which can perhaps be explained by the wealth of prey at the bottom of the continental shelf and in the surface waters.

Many fishes of the continental shelf eat planktonic crustacean larvae when they come to the bottom: we might mention Trachurus trachurus, Gadus luscus, Trigla obscura, Trigla pini, Trigla lucerna, Cepola rubescens, Mullus surmuletus, and Arnoglossus imperialis on the south Biscay continental shelf (Sorbe 1972). Nothing similar has been observed in Macrouridae; larvae must be considerably scarcer near the bottom of the slope than on the shelf.

As we saw above, one fish with a diet similar to that of Macrouridae, especially the predacious species, is Gadus morhua, or at least those between 11 and 20 cm. Rae (1966, 1967, 1968), working in the North Atlantic and the North Sea, describes the same changes in the diet of large cod as does Powles (1958); and Lefranc, working in the eastern part of the English Channel and southern part of the North Sea, makes similar reports.

The whiting (Merlanguis merlangus), an active predator, also eats fishes, crustaceans, annelids, mollusks, and sometimes echinoderms. The haddock (Melanogrammus aeglefinus) is a benthophagous fish that consumes echinoderms, annelids, mollusks, and crustaceans (Ritchie 1937; Jones 1954), but the proportions of the various groups are not the same as in the diet of Macouridae and there is no evidence of the same nearly consistent balance between the benthic and the pelagic food.

Among the demersal fishes, the sediment burrowers that eat fauna found in the first few layers of the sediment differ from Macrouridae by the absence of plankton and nekton in their diet.

Considering, finally, the small fishes of the littoral zone, that live in ecological conditions as nearly opposite as can be imagined to those of the continental slope and the abyssal plain, we see there is little possibility of similarity to Macrouridae. However, one of those studied by Gibson (1968, 1971) at Banyuls and Roscoff, on the Catalan coast and the Brittany coast, has a diet similar to that of Macrouridae. This is *Gaidropsarus mediterraneus* (Gadidae). It feeds exclusively on vagile animals, mainly amphipods and polychaetes, with some Gasteropoda, Ostracods, Isopoda, Mysidacea, Macrura and Brachyura. The Roscoff specimens also ate fishes and a few of them ate some algae. (The Gadidae *Ciliata mustela* at Roscoff also has a similar diet.) Mention should also be made of the Cottidae *Acanthocottus bubalis*, which lives near the coast and has a diet similar to that of Macrouridae: amphipods, crabs, shrimp, isopods, Mysidacea, polychaetes, teleosts, and in smaller numbers, mollusks, copepods, and Pycnogonides (Rice 1962).

5. Conclusion

Few data are available on the behaviour of bathybenthic fishes. The available data are the result of direct or photographic observations from bathyscaphs or with automatic cameras (Pérès 1958; Marshall and Bourne 1964, 1967). Macrourinae, benthopelagic fishes, swim above the bottom, slightly inclined toward it, a result of their body and fin shape (Marshall 1965). According to Marshall, this position must make it easier to seize prey on the bottom and to burrow. In the subfamily Bathygadinae, on the other hand, fin movement inclines the body upward; this may be an adaptation for catching planktonic prey. Their well-developed air bladder certainly makes vertical movement easier.

While the diet of Bathygadinae is certainly based on zooplankton, Marshall's statement must be qualified for Macrourinae, since they combine benthic and planktonic food. Like Bathygadinae, species such as *Hymenocephalus italicus*, *Ventrifossa occidentalis*, and *Coryphaenoides rupestris* have a terminal mouth; therefore they are probably unable to burrow in the sediment like genera with a more inferior mouth, such as *Coelorhynchus*, *Nezumia*, *Macrurus*.

Macrouridae most certainly have normal vision: their eyes are well developed, even huge, and the optic lobes are large. Thus Macrouridae living on the upper edge of the continental slope can hunt by sight, especially if their prey are luminescent, like Myctophidae and many other pelagic animals, such as euphausiids and cephalopods.

According to Uchihashi (1953), the combination of highly developed olfactory bulbs and complex olfactory lobes in Macrouridae (Okamura 1966, 1970b) indicates that the fishes have a keen sense of smell. Marshall (1969) states that the olfactory surface of bathypelagic Macrouridae such as *Squalogadus* is smaller than that of benthopelagic forms such as *Coelorhynchus*.

As early as 1914, Pfüller had pointed out the development of cephalic sensory canals in Macrouridae. Marshall (1967) emphasizes the importance of the lateral system, in particular the head canals, writing: "Macrouridae certainly feed on a wide range of benthic and free-swimming organisms. The former organisms may be most readily detected by touch and taste, unless, like crabs, pagurids, etc..., they produce respiratory currents and could stimulate the neuromasts. Free-swimming organisms, such as euphausiids, decapods, squids, and fishes should be detected by the head neuromasts at considerable distances."

Tuge and Shimamura (1959), in their study of the cephalic canals-nerve V- cerebellum crest structure, showed that Macrouridae have a well-developed somatic sensory system. Fänge, Larsson, and Lidman (1972) analysed the composition of the endolymph of the lateral line-canal on Coryphaenoides rupestris. These canals are closed, covered by the flexible membrane, which prevents sediment particles from entering. Alexander (1967) considers this to be an adaptation for mud-burrowing fish.

As Marshall (1964) has pointed out, the lateral line in bathypelagic Macrouridae is more developed than in the benthopelagic species.

The taste organs--superficial, labial, and buccal--and the chin barbel with its abundant taste buds and nerves, are also involved in the search for food.

In conclusion, Macrouridae are perfectly adapted to seeking out vagile prey both on and in the sediment and in the epibenthic layer of water. Although distinct ecological types of diet can be discerned, the diets of the various species (all euryphagous carnivores) have a number of points in common, specific to Macrouridae. Other fishes, living in different conditions--especially on the continental shelf where food is abundant and varied--do not have the same characteristics.

Basically, all the Macrouridae use the available food resources to the fullest; they are all benthophagous, planktonophagous, and predacious, though to varying degrees.

Chapter IV

THE DIGESTIVE SYSTEM AND FOOD OF MACROURIDAE

Fishes in the Macrouridae family are those caught most often in trawls on the abyssal plain and especially on the continental slope. An explanation for their "success" in the deep sea is their ability to make use of several sources of food, which is to a great extent controlled by the structure of their digestive system, and their ability to catch and retain a variety of prey.

In our morphological study, we saw that the relationship between the digestive system and the diet of Macrouridae was relatively easy to establish, specifically in terms of the shape and position of the mouth, the teeth, and the gill rakers.

In attempting to define, on the basis of what is known of the digestive system and food of teleosts, a fish type corresponding to a given food type, the task is relatively simple if we confine ourselves to extreme food types: that of predators (macrophages planktophages, herbivores, and limivores. If we consider fishes with less specialized diets, the task is not so simple.

Therefore a correlation can be established, for the Macrouridae studied here, between certain morphological, histological, and mechanical characteristics and the various food types. However, only for those fishes whose planktonophagous (including *Bathygadus melanobranchus*, which can also eat benthic animals such as Anomura, and *Hymenocephalus italicus*), predacious (including *Ventrifossa occidentalis* and perhaps *Nematonurus armatus*), or benthic microphagous (including Coelorhynchus coelorhynchus) tendencies are well-established do we find digestive systems that tend to resemble those of typically planktonophagous, predacious, and benthic macrophagous teleosts.

For Macrouridae species with a benthopelagic diet, such as the Nezumia, the relationship is less clear. As we mentioned above, the correlation exists between an "average" euryphagous food type and the digestive system of an unspecialized carnivorous fish.

While it is clear that there is some relationship between diet and digestive system, caution is advisable when establishing an association between a particular diet with a particular digestive system--an adaptation. This is especially true for Macrouridae. For example, Trachyrhynchus trachyrhynchus, with its long snout, its small, extremely inferior mouth, and its barbel, is the fish that looks most like a mud-burrower.

It should also be pointed out that the size limits of prey restrict maximal size more than minimal size. While it is true that it would hardly be possible for Coelorhynchus coelorhynchus, with its tiny, extremely inferior mouth, little teeth, and relatively weak jaw muscles, to seize and retain a Myctophidae, it is also true that Ventrifossa occidentalis does not feed exclusively on Natantia and bathypelagic fishes. A similar example is that of bathypelagic and abyssopelagic fishes such as Chauliodus, which have large jaw fangs but eat micronektonic and planktonic animals.

Structures for gripping and holding prey are not the only factors that determine prey size: the relationship between predator size and prey size also comes into play. Species that grow to a large size, such as Trachyrhynchus trachyrhyhnchus (50 cm) and Macrourus berglax (1 m), despite their small teeth and greatly inferior mouth, may manifest predacious tendencies as they age, similar to those a species such as Ventrifossa occidentalis, with its strong teeth, can show to smaller species.

From this study of their digestive systems, we can conclude that Macrouridae, except bathypelagic species, have the characteristics of carnivorous fishes: pointed teeth, usually numerous; a well-developed set of throat teeth, with many teeth similar to the jaw teeth; few gill rakers, usually in the form of jagged tubercules; a simple, short digestive tube, a well-differentiated caecal stomach; taste organs in the lips and in the bucco-pharyngeal cavity but never in any great quantity; well-developed musculature of the stomach wall, especially in the pyloric region, "in the gizzard".

Building on this average digestive system, which can be associated with an euryphagous benthypelagic diet, some species show certain tendencies:

- a predacious type, such as Ventrifossa occidentalis, which devotes a part of its diet to micronektonic fishes and shrimp, and cephalopods: a large sub-terminal, mouth, capable of little protraction; jaw teeth not numerous but strong; highly-developed stomach muscles; very efficient jaw muscles; a relatively short digestive tube.

- a benthic microphagous type, such as Coelorhynchus coelorhynchus: an inferior, highly protractile, and small mouth; numerous tiny teeth; a small set of gill rakers; jaw muscles less efficient than in the predacious type; a relatively long digestive tube.

The majority of Macrouridae studied here have a digestive system similar to that of the benthic microphagous type.

The structure of the digestive system is not the only factor that determines diet. The faunal environment also plays a role.

Finally, it must not be forgotten that the digestive system is but one element of a living organism that must at all times be viewed as the result of many complex material interactions--not always harmonious--between parts, each with its own material composition and development.

CONCLUSION

MACROURIDAE IN THE OCEAN:

DEEP-SEA FOOD CHAIN AND BIOGEOGRAPHY

In 1933 Joubin, during a lecture to the Institut océanographique in Paris, summarized (albeit with some inaccuracies) Macrouridae's place at the depths of the seas

> These fishes are well-adapted to abyssal life. A few year ago, they were still believed to be rare. Now we know that they are present in abundance on the slope of the continental shelf, and down to 6000 metres, becoming rarer and rarer. They are of an average size, of very dark colour; they burrow in the mud with their shovel-shaped snout and swallow through their protractile, toothless mouth.. They have enormous eyes, and a long, whip-like tail. They are among the most typical of the abyssal fauna, eating vegetable particles and tiny animals found in the mud. (Translation of quotation).

Their diet is certainly one of the most remarkable adaptations of the Macrouridae, enabling them to use available food resources to the fullest.

There are at least three consequences of this diet, which we shall discuss in the conclusion to this work:

The first is technical, and we shall not dwell long on it. Macrouridae, we have seen, are far from being confined to the bottom. They can travel several metres--perhaps much more--from the bottom. The most appropriate device for catching Macrouridae is a trawl with a large vertical opening--a semipelagic trawl.

The second consequence has to do with the place of Macrouridae in the deep-sea food chain. The analysis of trophic relationships among prey groups and between Macrouridae and prey groups shows that Macrouridae are at the top of the food pyramid of the continental slope and the abyssal plain, and that they are a transition point between, on the one hand, the pelagic level and the benthic level, and on the other, the deep-sea food chain and the continental shelf food chain, despite the nycthemeral migration which transfers energy to the deeper levels. This last point is of economic interest, since predators of Macrouridae seem to be mainly large fishes that are fished commercially.

Lastly, a study of the food of several species of Macrouridae can be one approach to the study of their distribution in the oceans, which in turn can help us refine our analysis of their adaptation to deep-sea life.

1. The place of Macrouridae in the deep-sea food chain

Deep-sea animals eat other species, organic detritus (especially feces, whose importance was established by Moore 1958), and dead organisms from lower levels. Organic matter in the deep sea is constantly renewed from the euphotic zone (Jrgensen 1966).

The diet of micronektonic and nektonic organisms of the deep-sea is closely connected with the amount of plankton present. The amount decreases with depth, but this relationship can not bequantitatively evaluated at present.

Some members of the zooplankton and the micronekton may migrate vertically, thereby transferring energy from the surface layers to the deep layers. The importance of this active transfer has been emphasized by, in particular, Vinogradov (1962, and a comprehensive work 1968-(1970)). Because of this migration, it is important to know what time of day the trawlings that brought in Macrouridae were carried out. Those of the Thalassa, which brought in the the largest number of specimens, were all done during the daytime.

In order to understand the position of benthopeleagic Macrouridae in the deep-sea food chain, it is first necessary to define the role of each prey-group in the diet of the entire family, and to identify the nutritional sources of each prey group.

A. The trophic role of various prey-groups

In order to define the trophic role of each prey group, we used the percentage by numbers for the previously defined average diet, and a cumulative frequency F, which represents the total observations of the eight Macrouridae species whose food was studied in detail.

a. Polychaeta (Cn = 9.5%; F = 0.39)

Polychaeta, although their number is underestimated, are an important source of food for Macrouridae: they are one of the three most frequent groups ($F > 0.20$). They were not found in the planktonophagous Hymenocephalus italicus, and rarely found in Trachyrhynchus trachyrhynchus (f = 0.09); however, they were frequent in species with a benthopelagic diet, especially those with a microphagous tendency--Ventrifossa occidentalis (f = 0.16), Nezumia aequalis and Macrourus holotrachys (f = 0.33), Nezumia sclerorhynchus (f = 0.45)--and very frequent in the two benthophagous species--Macrourus berglax (f = 0.62) and Coelorhynchus coelorhynchus (f = 0.93, the highest frequency index of all the prey groups). Polychaeta are thus a indicator of benthophagy.

It is difficult to identify the Polychaeta families, because the worms are never whole and sometimes the only sign of their presence is the byssa. They all seem to belong to free-moving families: Aphroditidae, Nereidae, Nephtyidae were recognized, although they are most certainly not the only families to have been caught:

The regular presence of sediment in the digestive tubes of polychaetes found in the stomachs indicates that we are indeed dealing with benthic groups. This is, to a certain extent, confirmed by the absence of polychaetes in the diet of Hymenocephalus italicus, a species with a pelagic tendency.

Although it is usually impossible to determine the length of the polychaetes that were ingested, their diameter indicates that they are small.

The food coefficient of Polychaeta is often relatively high. However, in Coeloryhnchus coelorhynchus, where they are the most abundant prey group (Cn = 22.31%), their food coefficient is only 21.40, because of the presence of Natantia. It reaches 100.90 in Nezumia sclerorhynchus, since Natantia have a low food coefficient for this species. This prey group is a preferential prey only for Nezumia sclerorhynchus; it is a complementary prey for Coelorhynchus coelorhynchus, Nezumia aequalis, and Macrourus berglax.

The importance of Polychaeta in fishes' diet has been pointed out by several authors (Fauvel 1923; Trégouboff and Rose 1957; Sorbe 1972). Sorbe (1972) states that Polychaeta, whether sedentaria or errantia, are sometimes an important source of food for burrowing benthic (Soleidae, Callionymus lyra) and nektobenthic (Mullus surmuletus and Gadus luscus) fishes. Jones (1954), on the other hand, in his study of the whiting in the North Sea, found only a few Polychaeta in their stomachs (average frequency: 9%) and only in individuals shorter than 40 cm, (for the most part, free-moving species). The cumulative frequency given by Sorbe (1972) for all demersal species of fish in the Bay of Biscay is only 13.1.

Polychaetes are a transition food between the remains of small animals of the sediment and fishes.* It is possible that some free-moving polychaetes may also eat suspended matter, as Hartley (1950) has observed in Nereis diversiocolor.

b. Gasteropoda (Cn = 0.39%; F = 0.03)

Although Gasteropoda are not consumed in quantity by Macrouridae, they are sometimes an important part of the diet, as in some Nototheniidae (Hureau 1970). No Gasteropoda were found in five species; their cumulative index is very low; and the percentages by number are always less than 1% (which was obtained for Coelorhynchus coelorhynchus). Gasteropods are tiny (less than 10 mm) and are only a second-rank complementary prey, of only minor importance in the diet. On several occasions we found intact shells in the intestinal contents, apparently with the animal still inside.

c. Lamellibranchia (Cn = 0.72%; F = 0.03)

Lamellibranchia have the same cumulative frequency index as Gasteropoda. They are present only in the diet of Nezumia sclerorhynchus and Macrourus berglax. Like Gasteropoda their food value is low.

Often the shell has not been attacked, or hardly, by gastric juices. The animals pass into the intestine and are expelled, without having contributed to nutrition. The presence of a great number of intact bivalves in the stomach of Nezumia sclerorhynchus (table 26) is evidence of this, and also shows that, despite its small contribution to nutrition, this group is consumed more frequently than might be imagined from an examination of the stomach contents.

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[*] A part of the sentence seems to be missing in the original. This is my interpretation of the rest -Tr.

Table 26

	STOMACH CONTENTS	INTESTINAL CONTENTS
First individual	-1 gasteropod (Natice) 3 mm -8 Lamellibranchia (Leda) from 1 to 3 mm	-1 gasteropod of 3.5 mm -44 Lamellibranchia, 3.5 and 5 mm -indeterminate material
Second individual	-1 polychaete -1 gasteropod of 2 mm -1 Lamellibranch (Leda) of 3 mm -2 gammarids -1 isopod -sediment	-39 Lamellibranchia, several with attacked shells -1 gasteropod of 2 mm -indeterminate material
Third individual	-4 copepods -2 polychaetes -1 ostracod -3 gammarids -2 isopods -sediment	-4 Lamellibranchia from 3 to 5 mm -indeterminate material -15 Lamellibranchia from 2 to 6 mm -sediment -indeterminate materials

Although Lamellibranchia were never found in the stomach of *Macrourus berglax*, on several occasions we found their remains in the intestine.

We never found one with an intact shell. The Macrourus berglax seem to crush the shells before they pass into the stomach.

All of the Lamellibranchia found in the stomach contents were small--a few millimetres.

Most Lamellibranchia feed on matter suspended in the water and organic deposits in the sediment (Jørgensen 1966).

d. Cephalopoda (Cn = 1.04%; F = 0.08)

The only traces of Cephalopoda found in the stomachs of Macrouridae were their crystalline lenses and horny beaks.

Cephalopoda are abundant in the deep sea (Pérès and Devèze 1963). They are often the prey of species of a predacious tendency, such as Trachyrhynchus trachyrhynchus (f = 0.21) and Ventrifossa occidentalis (f = 0.28), which also eat fishes and the larger Natantia. Nematonurus armatus also consume cephalopods (Waite 1916).

In Trachyrhynchus trachyrhynchus and Ventrifossa occidentalis there is a clear parallelism between the amount of fishes consumed and the amount of cephalopods consumed, and the diets of these two Macrouridae are analogous (table 27).

Table 27

	Cn		f	
	Cephalopoda	Fishes	Cephalopoda	Fishes
V. occidentalis	8.2	6.7	0.3	0.2
T. trachyrhycnhus	5.5	7.0	0.2	0.2

Similar proportions are found in the less predacious Macrouridae (table 28).

Table 28

	Cn		f	
	Cephalopoda	Fishes	Cephalopoda	Fishes
C. coelorhynchus	5.5	7.0	0.1	0.1
N. sclerorhynchus	0.1	0.1	0.01	0.01
M. holotrachys	0.6	1.5	0.1	0.1

In *Trachyrhynchus trachyrhynchus*, *Nezumia sclerorhynchus* (Atlantic), *Coelorhynchus coelorhynchus*, and *Macrourus holotrachys* there is also parallelism among the amount of Natantia consumed, the amount of Cephalopoda consumed, and the amount of fishes consumed.

Although we were unable to evaluate their importance, Cephalopoda must have great nutritional value and constitute an occasional primary prey for *Ventrifossa occidentalis* and *Trachyrhynchus trachyrhynchus*.

Sorbe (1972) indicates that on the continental shelf cephalopods are primarily prey for ichthyophagous species (for example, Merluccius merluccius) and, to a lesser degree, for small euryphagous carnivores (Trachinus draco and Arnoglossus imperialis). Clarke and Merret (1972) found cephalopod remains from which species could be determined in the stomachs of fishes (mostly Selachians) caught on fishing lines between 1000 and 2000 m.

Cephalopods are predators.

e. Ostracoda (Cn = 1.92%; F = 0.10)

Ostracoda are benthic; they live in the sediment or at its surface. Although one family is pelagic (the Halocypridae) and some benthic forms can be caught among the plankton, especially in deep waters (Trégouboff and Rose 1957), Ostracoda as a group can be considered a benthic food source. As food, their contribution to Macrouridae is low, except for Nezumia sclerorhynchus (Cn = 14.9%; Q = 7.88).

They were not found in Trachyrhynchus trachyrhynchus or the two Macrourus species. However, they were a first-rank complementary prey for Macrouridae with a benthic or benthopelagic diet (Coelorhynchus coelorhynchus, Nezumia aequalis, the Mediterranean Nezumia sclerorhynchyus, and N. sclerorhynchus). They were a second-rank complementary prey for Hymenocephalus italicus and Ventrifossa occidentalis, and for the Atlantic Nezumia sclerorhynchus, whose diet is more pelagic than that of its Mediterranean counterpart.

Ostracods eat suspended organic particles or deposits, detritus, and micro-organisms.

e. *Copepoda* (Cn = 36.77%; F = 0.45)

This group, one of those with the most deep-sea species according to Russell (1935), is the one most frequently found in the diet of Macrouridae, although it is absent from the diet of *Macrourus berglax*.

Copepods are almost the only food of *Hymenocephalus italicus* (Cn = 82.5%). Is this because *H. italicus* prefers copepods, or is it rather a reflection of its faunal environment? The same question can be asked for other planktonophagous fishes, such as Myctophidae, which eat mainly copepods and euphausiids, and a variety of answers have been given (Paxton 1967; Anderson 1967; Collard 1970; Samyshev and Schetinkin 1973).

Although copepods constitute 65.6% of *Trachyrhynchus trachyrhynchus*'s prey, their nutritional contribution is poor. This situation is even more clearcut for *Ventrifossa occidentalis*. Only for microphagous Macrouridae do copepods have no significant nutritional value: for *Nezumia aequalis* and *Nezumia sclerorhynchus* (especially Atlantic individuals), and *Coelorhynchus coelorhynchus*, their numbers (if not their weights) are important. This does not hold for *Macrourus holotrachys* (Cn = 3.9%).

Copepods are also eaten by *Bathygadus melanobranchus*, *Coryphaenoides zaniophorus*, *Nematonurus armatus*, *Chalinura mediterranea*, and *Lionurus carapinus* (11 Copepoda out of 27 prey).

All families that we were able to identify were pelagic: Calanidae, Aetideidae, and Metridiidae, with the genus *Pleuromamma*.

Most of the larger deep-sea planktonic animals (bigger than 2 mm)--in particular, the Copepoda--are, according to Chindonova (1959) carnivorous. However, there are some herbivorous copepods that make vertical migrations between the surface and a depth of about 1000 m (Chindonova 1959; Wicstead 1962). Gueredrat and Friess (1971) observed vertical migrations of several hundred metres by bathypelagic copepods in the central equatorial Pacific. Harding (1974) is of the opinion that deep-sea copepods feed on detritus from lower layers, especially remains of organisms, and dissolved organic matter and particles, bacterial flora that grow on this organic matter, and zooplankters that make vertical migrations. These deep-sea copepods may filter suspended matter (although Jørgensen (1966) believes that they are not filter-feeders in the strict sense of the term), or they may be carnivores or omnivores.

a. Amphipoda (Cn = 24.22%; F = 0.43)

Almost all the Amphipoda found in the stomachs of Macrouridae were benthic gammarids. In fishes with a plankton-based diet (such as Hymenocephalus italicus) amphipods were neither frequent nor abundant, and made little contribution to their nutrition. For Ventrifossa occidentalis, the food coefficent of amphipods was very low (Q = 1.65), and none were found in Trachyrhynchus trachyrhynchus.

On the other hand, amphipods are found frequently and abundantly in microphagous Macrouridae with benthic or benthopelagic diets; even in Macrourus berglax, their contribution to nutrition is relatively important. They are frequent secondary prey for Nezumia sclerorhynchus (Q = 11.21--5.90 for Atlantic individuals and 26.24 for Mediterranean individuals), Macrourus berglax (Q = 11.22), Nezumia aequalis (Q = 27.39), and Coelorhynchus coelorhynchus (Q = 51.40). They are also present in the diet of Bathygadus melanobranchus, Coryphaenoides zaniophorus, Nematonurus armatus, Chalinura brevibarbis, and Lionurus carapinus.

Like polychaetes, amphipods can be considered an indicator of benthophagy. Amphipods are carnivores and detritus feeders.

h. Isopoda (Cn = 2.54% F = 0.11)

Isopoda are not found in Macrouridae with a pelagic diet, and they have little importance for Ventrifossa occidentalis and Macrourus holotrachys. For the other Macrouridae, their frequency indices are at about the same level (from 0.10 to 0.20); they are not abundant (Cn from 2.8% for Nezumia sclerorhynchus to 8.8% for Macrourus berglax), and thus make little contribution to nutrition.

i. Tanaidacea (Cn = 0.16%, F = 0.11)

These benthic crustaceans, which live in burrows or tubes, are present only in the diet of the Mediterranean Nezumia sclerorhynchus. One Tanaidacea was also found in the stomach of a Nematonurus armatus.

j. <u>Cumacea</u> (Cn = 1.34%; F = 0.07)

Cumacea spend most of their life on the bottom, in contact with the sediment, where they burrow, sometime disappearing almost entirely (Page 1951). According to Trégouboff and Rose (1957), however, they can sometimes be caught near the bottom, and some species (Page 1951) have a nocturnal pelagic phase, during which they swim actively.

These tiny crustaceans make little contribution to the diet of Macrouridae, although they are found regularly in the stomach contents (with frequency indices from 0.04 to 0.25). Mediterranean Nezumia sclerorhynchus consume the most Cumacea (Cn = 7.7% and f = 0.25). Thus the two burrowers, Tanaidacea and Cumacea, are characteristic of the diet of Mediterranean Nezumia sclerorhynchus.

Sorbe (1972) states that Cumacea are common prey of benthic sediment-burrowing fishes, and they make a greater contribution to the diet of these fishes than to that of Macrouridae (for Mullus surmulatus f =0.15, Cn = 4.5%; for Trigla obscura f = 0.14, Cn = 2.4%; for Pegusa lascaris f = 0.46, Cn = 4.6%).

All Cumacea eat organic detritus and micro-organisms that they find in the mud.

k. Mysidacea (Cn = 6.16%; F = 0.11)

These tiny shrimp, like many other animals of the plankton, swim in schools and are hunted by numerous fishes. There are many deep-sea genera of Mysidacea, and some species are largely eurybathic, making a major vertical migration daily. Although some live at great depths, their maximum concentration is between 100 and 400 m.

Their cumulative frequency index is low. Their presence in the stomach contents was very irregular--not only across all the Macrourdae species, but also within a single species.

None were found in *Hymenocephalus italicus* and *Macrourus berglax*; there were a few in Nezumia *sclerorhynchus* and especially *Coelorhynchus coelorhynchus*; and they are a part of the food of *Ventrifossa occidentalis* (Q = 19.76) and *Trachyrhynchus trachyrhynchus*. For two species with diets tending toward the microphagous and benthopelagic (*Nezumia aequalis* and *Macrourus holotrachys*), Mysidacea are a preferential primary prey (Q = 1884 and 1811 respectively).

Despite these two exceptions, Mysidacea are not a basic element of the food chain that ends with the Macrouridae. This situation is quite different from the one observed by Sorbe (1972) on the continental shelf of the Bay of Biscay, where Mysidacea are the zoological group with the highest average frequency, for a very small number of individuals.

Some Mysidacea eat suspended organic debris or micro-organisms, but most of them are carnivorous, and catch zooplankters.

1. Euphausiacea (Cn = 3.26%; F = 0.05)

These little pelagic crustaceans make vertical migrations (Lacroix 1961; Roger 1974). Along with copepods, they constitute a major food source for deep-sea pelagic planktonophagous fishes. However, they are not very frequent in Macrouridae, except for Hymenocephalus italicus, for which copepods and euphausiids make up 93.2% of the prey. They are absent from the diet of both the benthopelagic-feeding fish Nezumia aequalis and the pelagic predator Trachyrhynchus trachyrhynchus.

Euphausiacea are essentially carnivorous animals (Roger 1974), feeding from the zooplankton. However, some species in the surface layer also eat phytoplankters.

m. Natantia (Cn = 4.85% F = 0.17)

This is the only group that was present in the food of all eight Macrouridae species whose diet was studied in detail. These decapod crustaceans play an important role in the diet of Macrouridae, although they are abundant only in Macrourus berglax and Ventrifossa occidentalis. They are found in the stomachs, the abdomen folded up under the cephalothorax and the head toward the esophagus; they usually occupy the dilated esophagus-stomach area. Their partially digested carapaces and broken appendices are usually insufficient evidence to determine their species.

Even when infrequent, Natantia are a good source of energy because they are usually quite large. They are a preferred prey for predacious Macrouridae (for Trachyrhynchus trachyrhynchus Q = 154; for Ventrifossa occidentalis Q = 1443; for Macrourus berglax Q = 945), and as we saw in the section on cephalopods, they are fairly characteristic of these fishes' diets. In the case of microphagous Macrouridae species with a more or less benthic diet, such as Coelorhynchus coelorhynchus or the Mediterranean Nezumia sclerorhynchus, the preponderance of Natantia in the diet is the consequence of the smallness of the other prey caught by these fishes. In the two species for which Mysidacea hold a dominant position, Nezumia aequalis and Macrourus holotrachys, they make little nutritional contribution.

Deep-sea shrimp are either benthic or pelagic, but there is a temporary transition from one environment to the other (Crosnier and Forest 1973).

In 1912, Hjort proposed the hypothesis, which has since been confirmed, that there exists a "shrimp belt" associated with the "mud-line" described by Murray (Murray and Renard 1891; Murray 1895; Murray and Hjort 1912). There is only a single shrimp belt in the Boreal-Arctic regions where Hjort worked, but passing from the north to the south, in conjunction with changes in the sediment, it goes deeper (100 m in the north, compared with 500 m off Mauritania) and doubles back over itself in the Bay of Biscay--at 200 to 400 m and at 900 to 1000 m (Lagardère 1969-(1970); 1971-(1972)) and in the Iberian, Moroccan, and Mauritanian regions and the western Mediterranean (Maurin 1962a and b, 1963). Shrimp in these shrimp belts may make vertical migrations of several hundreds of metres, bringing them closer to the surface--100 to 150 m in depth (Maurin 1962); Lagardère 1971-(1972)).

The vertical distribution of Macrouridae with a predacious tendency corresponds to that of the belts of large shrimp, on the upper part of the continental slope. *Macrourus berglax* in the Boreal-Arctic regions go up to 100 m in depth and *Ventrifossa occidentalis* off the Mauritanian coasts stay within 150-600 m.

The diet of deep-sea shrimp has been studied thoroughly (Maurin and Carries 1968; Lagardère 1971 (1972), 1973). They are euryphagous carnivores that make extensive use of the resources of the continental slope, with a diet similar to that of Macrouridae: copepods, amphipods, isopods, Mysidacea, Cumacea, Euphausiacea, Reptantia, echinoderms, polychaetes, mollusks, cephalopods, and fish corpses. Lagardère (1971-(1972)) found scales from a Macrouridae corpse in the stomachs of *Parapenaeus longirostris*). Euphausiids are particularly important in the diet of deep-sea shrimp.

n. *Reptantia* (Cn = 1.07; F = 0.05)

These decapod crustaceans are Anamura and Brachyura. They were not found in the stomach contents of many individuals, and are never very frequent, except in *Ventrifossa occidentalis* (f = 0.24; Cn = 9.1; Q = 56.24).

In *Coelorhynchus coelorhynchus* the majority of Reptantia found were Brachyura, with cephalothoraxes from 3 to 10 mm wide, and small Thalassinides (4 mm). Small Brachyura were found in the two *Nezumia* species as well. In *Ventrifossa occidentalis*, apart from a few Brachyura, most of the Reptantia found were Galathea, some of which were several centimetres in length.

Reptantia are detrivorous and necrophagous.

o. *Echinodermata* (Cn = 1.01; F = 0.03)

With one exception, the only echinoderms found were Ophiura. In spite of their weight, these animals have a low energy value, because organic matter makes up only a small part of their weight. Although there are swarms of them on some parts of the sea bottom, Ophiura were found infrequently and were characteristic of the diet of only two Macrouridae: *Nezumia sclerorhynchus* (in both the Mediterranean and the Atlantic) and especially *Macrourus berglax*. In this latter species, arm fragments were found on several occasions in the intestine, although there were no Ophiura in the corresponding stomachs. Arms found in the stomach are always broken; in many cases only the disk, always tiny, is found.

Ophiura are carnivorus, but some many feed mainly on suspended particles--for example, *Ophiotrix fragilis* or *Ophropholis aculeata* (Wintzell 1918; Roushdy and Hansen 1960).

p. *Teleosts* (Cn = 1.14; F = 0.07)

Of all the prey consumed by Macrouridae, fishes definitely have the highest nutritional value. Hertling (1938), in his study of the diet of whiting in the North Sea, calculated that weight for weight the energy value of fishes is approximately twice that of crustaceans.

The importance of fishes in the diet of predcaious~~-tending~~ species and the link between the prey groups of Cephalopoda, Natantia, and fishes were already pointed out in the study of Cephalopoda. Fishes make little contribution to the food of microphagous species, which are poorly equipped to catch them. Sometimes their diets contain no fishes at all.

The fishes caught belong to bathypelagic families; there were many Myctophidae (eg *Notoscopelus*, *Myctophum*) and Gonostomaridae (eg *Cyclothone*, *Maurolicus*), which are planktonophagous, and members of families of the continental shelf that go down the upper part of the slope, wuch as *Synagrops microlepsis* (planktonophagous and predacious) and *Capros aper* (planktonophagous).

B. The deep-sea food chain (Figure 32)

Following Bougis (1974), we can define several levels of production within secondary production: "level 2 for herbivores, level 3 for carnivores, level 4 for predatory carnivores. To avoid any ambiguity, level 1 is reserved for primary production (in these conditions, level 0 represents precursers of organic matter, still in the mineral state)." [Translation of quotation.] In this way we can specify the level occupied by Macrouridae.

Micronektonic food is made up of cephalopods (levels 3 and 4), Natantia (levels 3 and 4, and detritivores), and bathypelagic fishes that are essentially planktonophagous (levels 3 and 4). Thus Macrouridae are always at level 4.

Planktonic food is made up of zooplankters, sometimes herbivores (level 2), usually carnivores (levels 3 and 4), and filter-feeders.

Benthic prey, whether epigeal or hypogeal (the latter can be captured when they temporarily leave the sediment, so the fish does not have to burrow for them) may be either filter-feeders (sometimes corresponding to level 2), or consumers of the superficial organic film on the sediment, or consumers of microfauna in the sand, or carnivores that eat the preceding groups. Often these animals are also necrophagous.

Autotrophic bacteria that live on deposited or suspended organic matter are classified as deep-sea primary production that can be used by benthic and planktonic animals.

Figure 32.The place of Macrouridae in the deep-sea food chain

(See photocopy of original.).

Legend

1. solar energy
2. fishing
3. nutritional salts
4. primary production
5. predators of Macrouridae
6. herbivorous zooplankton
7. organic tripton
8. carnivorous zooplankton
9. micronekton
10. bacteria
11. benthic animals
12. sediment
13. Figures show trophic level.

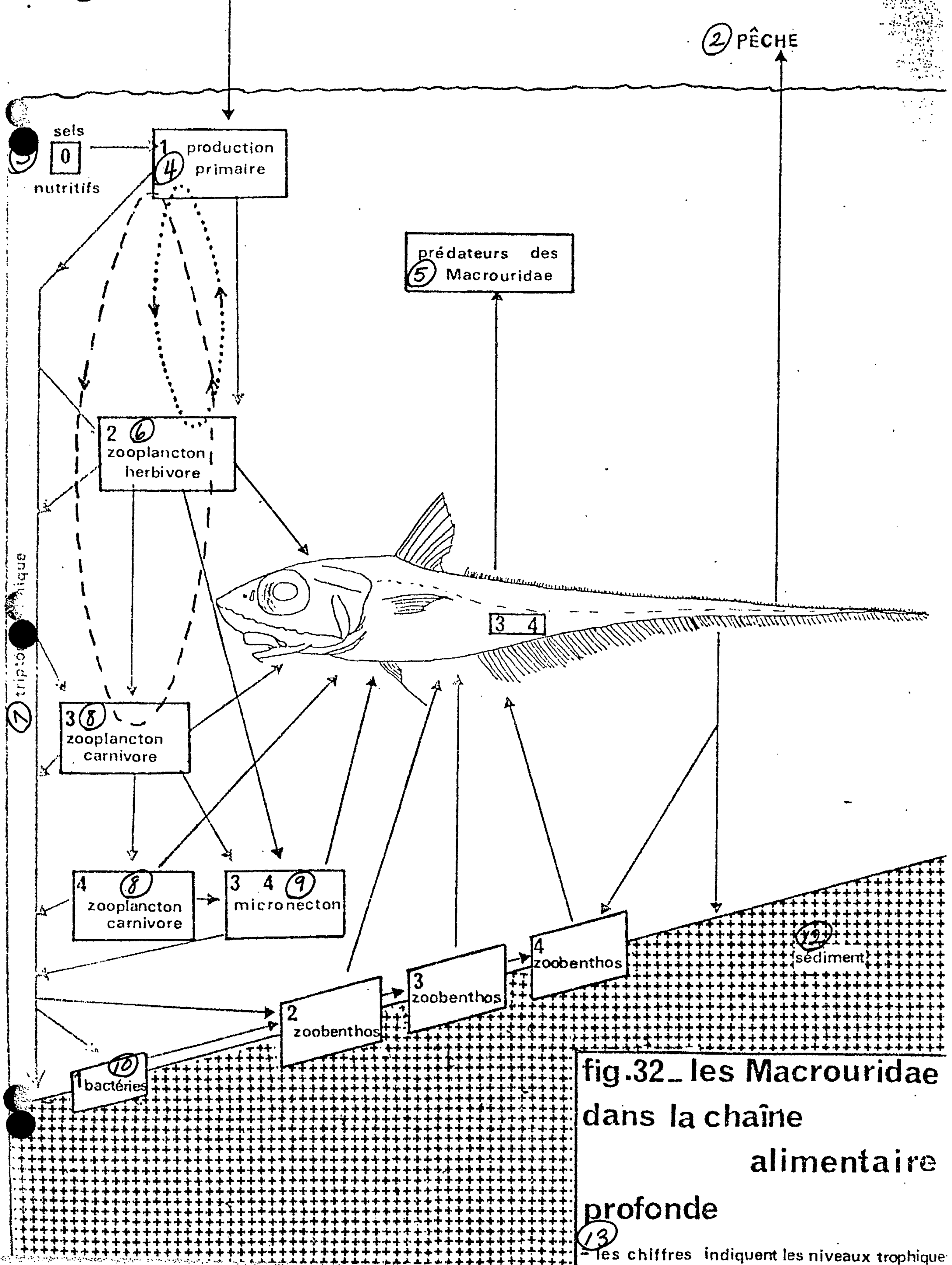

fig.32_ les Macrouridae dans la chaîne alimentaire profonde

⑬ - les chiffres indiquent les niveaux trophique

On the continental slope and the abyssal plain, then, Macrouridae are at the top of the food chain. However, their predation is exercised at various levels of the chain and at varying degrees of intensity, depending on the type of diet: predators live mainly off level 4 pelagians; pelagic microphages off level 2 and especially level 3 and level 4 pelagians; and benthic or benthopelagic microphages off level 2 and especially level 3 and level 4 pelagians and bottom-dwellers.

As a family, Macrouridae exploit to the fullest the food potential of the deep-sea zones, of which they, along with the Selachians, are the largest inhabitants.

It should be recalled that substances dissolved in the water can be absorbed through the gills (Love 1970), as is the case, for example, with glucose in Salvelinus fontinalis (Phillips et al 1953).

Macrouridae do not seem to fall prey to other bathyal and abyssal fishes, except perhaps the Selachians. As far as we know, deep-sea teleosts are most often euryphagous and microphagous: examples are Benthocometes robustus (Bougis and Ruivo 1954), Lepidion eques (Templeman 1970), and Bathypterois longipes (Marshall 1971). The largest of these teleosts are usually about the same size as Macrouridae.

Macrouridae must fall prey mainly to large Gadidae that make temporary forays to the top of the continental slope. Frieb et al (1895) report that a Coelorhynchus coelorhynchus was found in the stomach of a cod; Rattray (1947), in his study of the food of the Cape hake (*Merluccius capensis*), states that *Coelorhynchus coelorhynchus* is regularly, but rarely, present (along with Myctophidae, Gonostomatidae, Cephalopoda, and so forth) in the stomach contents of fishes caught at 300 to 400 m depth. This partially confirms the observation of Gilchrist (1922), who, remarking that the Cape hake was often found at 600 or even 1000 m depth, wrote: "Its presence in deeper water is explained by the fact that it seems to feed almost exclusively on *Macrurus fasciatus*, which is so abundant in these regions."

Farran (1924) found a Coelorhynchus coelorhynchus in the stomach of a Molva dypterygia dypterygia.

A small species such as Hymenocephalus italicus can fall victim to both large and medium size predators. This species was found in the stomach of Centrolophus niger and Chlorophtalmus agassizi (Bombace and Li Greci 1970).

Both the feces and corpses of Macrouridae make an important contribution to deep-sea organic matter.

Since they are not confined to the bottom, they are an important factor in the transfer of energy from the slope toward the bottom through their predators, from the open sea to the bottom through their remains and excretions, and from one depth to another through their vertical movements above the continental slope and the abyssal plain.

Finally, Macrouridae can be fished. Their delicate flesh is suitable for human consumption. According to Frieb et al (1895), the Eskimos have had a long-standing appreciation of Macrourus berglax. And Farran (1924) writes: "With suitable cooking, as experiments on board the Helga have shown, they are just as palatable as many other fishes commonly exposed for sale." At present, only Coryphaenoides rupestris, in the North Atlantic, is fished commercially, by Soviet trawlers (and to a small extent by Polish and East German ones).

According to the FAO's Yearbook of Fisheries Statistics (vol 32, 1972), the amount of Coryphaenoides rupestris caught in 1967 was 18,000 tonnes, in 1968 33,000 tons, in 1969 15,000 tonnes, in 1970 29,000 tonnes, and in 1971 84,000 tonnes. Macrouridae are thus involved both indirectly--as prey to commercial species--and directly in human food.

2. Macrouridae in the ocean

a. Geographical distribution of Macrouridae

Essentially bathypelagic Macrouroidinae have a vast distribution (Marshall 1965, 1973b): *Macruroides inflaticeps* lives off the Phillipines, in the Indian Ocean, and the South Atlantic; *Squalogadus modificatus* lives off Japan, in the equatorial Atlantic, and the Gulf of Mexico. The same is true for the two mesopelagic or bathypelagic Macrourinae: *Cynomacrurus piriei* probably has a circumantarctic distribution; *Odonotomacrurus murrayi* is found in the northeast Atlantic, the East Atlantic (from the Azores to the African coast and the Gulf of Guinea), in the western Indian Ocean, and the China Sea. Similarly broad distribution is also observed for other families, for deep-sea pelagic species such as *Lampadena luminosa* (the northwest and equatorial Atlantic, the Antilles Sea, the Indian Ocean, the equatorial Pacific--Nafpaktitis and Paxton 1968) or *Argyropelecus hemigymnus* (throughout the Pacific, from the Arctic to Antarctic, Indonesia, the Indian Ocean, throughout the Atlantic from subantarctic regions to the Arctic, and the Mediterranean--Baird 1971).

Thus we have some reason to suppose that a relation exists between a species's geographical distribution and its behaviour--benthic or pelagic. Here we use the ecological food type of each species to express its lifestyle.

All the Macrouridae studied here have a benthopelagic diet to some degree, and neither those that live at the top of the continental slope nor those that live on the abyssal plain have as vast a distribution as the pelagic species. Brauer (1906), Hubbs (1954), and Marshall (1965, 1973b) have already pointed out the limited geographical distribution of the benthopelagic species.

In order to understand a species's distribution in the ocean, the study of its behaviour and its relationship to the bottom are not sufficient. Other factors must be considered, such as a characteristics of the water layers in which the larval and post-larval stages live (probably at 200 to 300 m in depth, before they go down to the bottom--Marshall 1965) and those in which the adult stages live, submarine topography, and so forth.

Hymenocephalus italicus, an essentially planktonophagous species, is found in the Atlantic, the Mediterranean, and the Indian Ocean (figure 33), but Bathygadus melanobranchus (figure 33) and Coryphaenoides rupestris (figure 39), which feeds mainly on Natantia, is found only in certain parts of the Atlantic.

Macrourus berglax, a benthophage, lives off Newfoundland and Labrador, but farther east it is confined to the Denmark Strait, the Norwegian Sea, and the Barents Sea (figure 39). Coryphaenoides rupestris has more pelagic habits, judging from its diet; it is also found in the West Atlantic, in the same regions as Macrourus berglax (the two species can even be fished at the same time), but goes not much farther north than the latitude of Iceland, extending to Ireland and the Bay of Biscay, beyond the Mid-Atlantic Ridge.

Macrourus berglax's range to the south and east seems to be limited, then, by the Faeroe-Iceland ridge and the Wyville-Thomson ridge--and also the abyssal plains, since it lives near the bottom on the top of the slope. Coryphaenoides rupestris is found beyond the Faeroe-Iceland ridge, which reaches its highest point at 300 m depth, and even as far as the southern coast of Norway. However, movements by adult fishes are not in themselves sufficient to explain the horizontal distribution of these two species; the eggs, larvae, and post-larval stages may be moved by currents. The distribution of *Macrourus berglax* seems to be connected with the Greenland and Labrador current system, and the distribution of *Coryphaenoides rupestris* with the North Atlantic Current and its two branches, one leading to the Norwegian coast and one leading to the western European coast and the Bay of Biscay.

The distribution of *Trachyrhynchus trachyrhynchus*, a species with an essentially pelagic (nektonic and planktonic) diet, is more or less analogous to that of the benthophagous species *Coelorhynchus coelorhynchus*, with Cape Verde as its southern limit. However, all of the _Coelorhynchus coelorhynchus_ subspecies (Marshall and Iwamoto 1973) occupy the continental slopes on both sides of the Atlantic (figure 35).

Ventrifossa occidentalis, a benthopelagic predator, is found only in the tropical zone of the northeast Atlantic basin; but in the western Atlantic, it is caught from Argentina to Newfoundland (figure 38). Adult behaviour alone is not sufficient explanation of this distribution; dispersion of the eggs and larvae by the equatorial current system is another factor. In the eastern Atlantic, _Ventrifossa occidentalis_ seems to be confined to the tropical zone; its benthopelagic habits seem to limit its latitudinal movement. In the western Atlantic, there is a correlation between _Ventrifossa occidentalis's_ distribution and the extension of the Brazil current, which disappears off Argentina. In the northwestern Atlantic, there is a similar correlation between the Guyana current-Antilles current-Gulf Stream and the distribution of _Ventrifossa occidentalis_. Water temperature and duration of the larval and post-larval stages are probably pertinent factors.

Macrourus holotrachys seems to have an antarctic circumpolar distribution (figure 39). It lives near the bottom, south of the Atlantic-Indian Ridge system. The lack of topographical obstacles might explain why this species extends as far as the Argentine Basin. On the other hand, the fact that the Ridge goes (and for the larvae the Agulhas current) around southern Africa prevents it from passing from the Crozet Basin to the Agulhas and Cape Basins.

The relatively limited distribution of *Nezumia sclerorhynchus* and *Nezumia aequalis* (figure 34), *Coryphaenoides guentheri* and *Coryphaenoides zaniophorus* (figure 36), *Chalinura brevibarbis*, *Chalinura mediterranea*, and *Lionurus carapinus* (figure 37) can be explained by their benthopelagic habits and microphagous diet. However, the geographical distribution of the last two genera is still largely unknown, because they live at great depths, even on the abyssal plain (*Lionurus*), and thus have not been caught frequently.

This board geographical distribution of Nematonurus armatus (figure 38), probably partially microphagous and benthic and partially predacious and pelagic like Ventrifossa occidentalis (but on the abyssal plains), is perhaps due to the fact that it leads a more active life than do microphagous species.

b. Vertical distribution of Macouridae

It appears that the upper portion of the slope is inhabited by the benthophagous species Macrourus berglax and Coelorhynchus coelorhynchus, the planktonophagous species Hymenocephalus italicus, and the benthopelagic predator Ventrifossa occidentalis. The vertical range of each of these species is limited (table 29). As we saw in the study of diet and digestive system, these four species have relatively specialized diets.

Trachyrhynchus trachyrhynchus lives between 400 and 1500 m; as a planktomphagous predator, it has a less specialized diet.

Coryphaenoides rupestris, a pelagic predator, also lives in the upper part of the slope but appears to make vertical migrations to search for food (Natantia, Copepoda, Mysidacea, and so forth). Pechenik and Troyanovskii (1970), basing their conclusions on the catches of Soviet trawlers, believe that at the end of the summer the Coryphaenoides rupestris population off the coast of Labrador moves up along the continental slope to a depth of about 600 m, and in the middle of winter goes back down to about 1200 m or even deeper.

It is possible that other Macrouridae species make similar migrations.

Bathygadus melanobranchus, a species with planktonophagous tendencies, is an exception: it has an immense vertical distribution. It is probably a better swimmer (its second dorsal fin is well developed) and is thus more pelagic than Macrouridae.

Microphagous species, on the other hand, some of them probably benthopelagic, live at the foot of the slope and in the abyssal plain. Their vertical distribution is vast: more than 400 m for *Nematonurus armatus* and *Lionurus carapinus*.

Table 29: Correlation between diet and distribution of Macrouridae

(See photocopy of original.)

Legend

1. species
2. range of vertical distribution
3. zones where the species lives
4. geographical distribution
5. number of oceans where the species lives
6. diet
7. microphagous (M) or predacious (P)
8. microphagous (M) or predacious (P)
9. pelagic (P) or benthic (B)
10. high slope--abyssal plain, 300-4700 m
11. foot of the slope--abyssal plain, 1440-5610 m
12. slope, 400-3200 m
13. foot of the slope--beginning of the plain, 1500-3700 m
14. slope, 450 - 2600 m
15. slope, 200 - 2300 m
16. foot of the slope--plain (Mediterranean), 1200-2800 m
17. 1200 - 2600 m, foot of the slope, 800 - 2200 m
18. Northwest Atlantic--Indian Ocean and Pacific Ocean
19. Northwest and northeast Atlantic
20. Northeast Atlantic--Mediterranean
21. Northeast Atlantic
22. East and West Atlantic
23. Northeast and northwest Atlantic
24. East Atlantic--Mediterranean

25. East Atlantic
26. few data
27. upper slope, 400 - 1500 m
28. upper slope, 140 - 1250 m
29. upper slope, 400 - 1200 m
30. upper slope, 100-820 m
31. upper slope, 300-800 m
32. upper slope, 150-600 m
33. upper slope 350 (?)-600 (?) m
34. East Atlantic
35. Atlantic
36. North Atlantic
37. North Atlantic--Norwegian Sea-Barents Sea
38. Atlantic--Indian Ocean
39. Atlantic
40. Atlantic--Indian Ocean

1 ESPECES	2 Amplitude de la distribution verticale	3 zones où vit l'espèce	4 répartition géographique de l'espèce	5 nombre d'océans où vit l'espèce	6 Alimentation 7, 8 microphage (M) ou prédatrice (P)	9 pélagique (P) ou benthique (B)
Nematonurus armatus	4400 m	10 haut talus - plaine abyssale 3000 à 4700 m	18 Atlantique NW - Océans Indien et Pacifique	3	MP	P B
Lionurus carapinus	4170 m	11 pied talus - plaine abyssale 1440 à 5610 m	19 Atlantique NW et NE	1	M	P B
Nezumia sclerorhynchus	2800 m	12 talus 400 à 3200 m	20 Atlantique NE Méditerranée	1	M	P B
Chalinura brevibarbis	2200 m	13 pied talus - début plaine 1500 à 3700 m	21 Atlantique NE	1	M	P B
Bathygadus melanobranchus	2150 m	14 talus 450 à 2600 m	22 Atlantique E et W	1	M	P
Nezumia aequalis	2100 m	15 talus 200 à 2300 m	23 Atlantique NE et NW	1	M	P B
Chalinura mediterranea	1600 m	16 pied talus - plaine (Méditerranée) 1200 à 2800 m	24 Atlantique E Méditerranée	1	M	P B
Coryphaenoides guentheri	1400 m	17 1200 à 2600 m pied talus 800 à 2200 m	25 Atlantique E	1	M	P B
Coryphaenoides zaniophorus						

Trachyrhynchus trachyrhynchus	1100 m	27 haut talus 400 à 1500 m	34 Atlantique E	1	MP	P
Coelorhynchus coelorhynchus	1100 m	28 haut talus 140 à 1250 m	35 Atlantique	1	M	B
Coryphaenoides rupestris	800 m	29 haut talus 400 à 1200 m	36 Atlantique N	1	P	P
Macrourus berglax	720 m	30 haut talus 100 à 820 m	37 Atlantique N mers de Norvège et de Barents	1	P	B
Hymenocephalus italicus	500 m	31 haut talus 300 à 800 m	38 Atlantique océan Indien	2	M	P
Ventrifossa occidentalis	450 m	32 haut talus 150 à 600 m	39 Atlantique	1	P	P B
Macrourus holotrachys (peu de données) 26	250 m ?	33 haut talus 350 m ? à 600 m ?	40 Atlantique océan Indien	2	M	P B

- Tableau 29 -

Correspondance entre l'alimentation et la répartition des Macrouridae

c. Conclusion

An unspecialized, euryphagous diet, based primarily on benthic and pelagic prey, and a microphagous tendency can be considered to be adaptations to deep-sea conditions.

This kind of diet cannot help but have a favourable effect on animals that live in an environment that is poor in planktonic food. With increasing depth, the decrease in the benthic biomass is less marked than the decrease in the pelagic biomass.

At the end of the post-larval stage, when it goes down to the bottom, a young Macrouridae will die if it does not reach a zone where it can find food. This may explain the longitudinal distribution of Macrouridae.

However, it must be emphasized that, since we were able to do a detailed study of the diet of only those Macrouridae of the continental slope, we cannot exclude the possibility that at great depths there are not only differences in diet for a single species (between individuals living at 1500 m and those living at 5000 or 6000 m), but also utilization of new prey groups. A fish like *Nematonurus armatus* might very well eat Holothuria, for example, which are abundant on the abyssal plains.

The ecological food type--pelagic, benthic, or benthopelagic; predacious or microphagous--seems to be more fundamental than the consumption of any given prey group.

The distribution in the oceans of Macrouridae and perhaps all deep-sea benthic and benthopelagic fishes is the consequence of a number of factors, some of them imperfectly understood or even unknown: species phylogeny, physical-chemical conditions of the different water layers in which the fishes spend the various stages of their life, the history of the ocean basins, the topography of the bottom, which may restrict the latitudinal distribution of some species, and so on.

Diet, in particular, helps determine the distribution of deep-sea species, especially their vertical distribution, which seems to be directly related to food ecology.