FOOD WEB OF THE AZOREAN SHALLOW WATER MARINE ICHTHYOLOGICAL COMMUNITIES: A GUILD APPROACH

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With 1 figure and 1 table

ABSTRACT. A list of the most common shallow water fishes of the Azores, containing 66 species, is compiled. Information gathered about their diets and spatial distribution is presented, based on studies made on the Azores and elsewhere. An allocation of fish species into trophic guilds is proposed, as follows: herbivores (3 spp.), macro and microomnivores (9 and 1 spp., respectively), and micro, meso and macrocarnivores (22, 20 and 11 spp., respectively). These guilds are further subdivided according to the benthic or pelagic provenance of the diet items. It is concluded that most species are dependent on benthic primary production, the invertebrates playing an important role in the transfer of energy from the algae to the higher trophic levels. Some of the mechanisms linking the benthic and pelagic food webs are outlined.

INTRODUCTION

It was only recently that ichthyological research in the Azores as begun to focus on synecology, with studies made on the distribution and abundance of fish species in various habitats: intertidal (ARRUDA, 1979, 1980; SANTOS *et al.*, 1994), rocky subtidal (PATZNER & SANTOS, 1993) and sandy beaches (NASH *et al.*, 1994a, 1994b). These studies, as well as most of the more recent research in the field of marine ecology in the Azores (v. ANON., 1974; HAWKINS *et al.*, 1990; MARTINS *et al.*, 1992), have been conducted on shallow water, from the intertidal zone to the 30m bathymetric, for the simple reason that this is the most accessible area, notably with SCUBA diving gear. The present analysis will therefore also be limited to those boundaries.

The analysis of food web patterns is one of the most productive areas of recent research into community structure (PUTMAN, 1994). One such analysis involves the establishment of trophic guilds (*sensu* ROOT, 1967), as a form of reducing the number of

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components in a community and thus allowing a better study of its organization (KREBS, 1985). The present paper brings together information about the diet and spatial distribution of the most common fish species found in the shallow waters around the Azores. Attention is given to the benthic or pelagic provenance of the diet items. Based on this information, a trophic guild arrangement of the species is proposed, and a preliminary analysis of the ichthyological food web is carried out.

MATERIAL AND METHODS

A list of the shallow water fishes of the Azores was compiled from recent faunistic surveys (WOOD & WILLIAMS, 1974; ARRUDA *et al.*, 1992; AZEVEDO *et al.*, 1992; PATZNER *et al.*, 1992). This list contains 66 species, most of which are referred to by at least two of the papers searched. Some species that were recorded by only one of the papers, with indications such as "bought from local fisherman", "rare, only one specimen found" or "deeper water (30 m +)" were not included in the present analysis. These are: *Galeorhinus galeus* (LINNAEUS, 1758), *Myliobatis aquila* (LINNAEUS, 1758) and *Sarda sarda* (BLOCH, 1793), recorded by PATZNER *et al.* (1992) and *Belone belone gracilis* LOWE, 1839, *Labrus mixtus* LINNAEUS (= *L. bimaculatus* LINNAEUS, 1758), *Lepidopus caudatus* (EUPHRASEN, 1788) and *Scorpaena scrofa* LINNAEUS, 1758, from WOOD & WILIAMS (1974).

The diet of each species was assessed from local studies, whenever possible, or from studies conducted elsewhere. A bibliographic survey was performed using the Aquatic Sciences and Fisheries Abstracts database (1978-1993), with genus or species names as search words. From the papers thus obtained, additional references were selected. WHITEHEAD *et al.* (1984) and FISCHER *et al.* (1987) proved invaluable as a source of information, specially when original papers could not be found. When no data could be found regarding the diet of a particular species, general inferences could still be made from that of related species with similar ecological preferences. Bibliographic information was in a few cases complemented with the author's unpublished data and personal observations.

The main items of the diet of each species were recorded and, according to them, each species was allocated to one of the following trophic guilds (sensu ROOT, 1967): herbivores, omnivores or carnivores. Subdivisions of these guilds were made. Omnivores were divided into macroomnivores (who graze on the algae or vegetation, ingesting it together with its associated invertebrates) and microomnivores (who feed mainly by sucking or scrapping the diatom film in the sediment or the air/water interface). Given that the relative size of the potential preys is an important element determining a predator's diet (PETERS, 1983), the size of the prey items is a logical way of grouping the carnivorous fishes. The categories (a) micro, (b) meso and (c) macrocarnivores were used (as in, e.g., EBLING & HIXON, 1991) to group those fishes according to their specific prey: (a) the smallest invertebrates (amphipods, isopods, microgastropods), (b) the medium sized invertebrates

(decapoda, echinoderms, polychaetes) and small fishes (either small-sized species or juveniles of larger ones) and (c) the larger invertebrates (cephalopods, majid crabs, lobsters) and medium to large fishes. Since diet varies ontogenetically (HELFMAN, 1978; LIVINGSTON, 1982), only the data concerning the adult stages of each species were recorded, the only exceptions being those species that are found on shallow water only in the juvenile phase of their life cycle.

The benthic or pelagic provenance of the diet items was noted. The meso and macro carnivores were found to be difficult to classify as to the benthic/pelagic provenance of their prey, specially as the degree of ichthyophagy increased. In those cases, the spatial distribution (see below) of the predator species was used as an indication: species in categories 1-3 were considered to feed mainly on pelagic preys, species in categories 4-6 on benthic preys.

The spatial distribution of each species was taken from HARMELIN (1987) and SANTOS (1992). The 6 categories scheme of HARMELIN (1987) was used: category 1 - water column fishes, usually in highly mobile shoals; category 2 - water column fishes, sedentary; category 3 - nectobenthic fishes, vertical movements of only a few meters and lateral movements of variable importance; category 4 - nectobenthic fishes, very small vertical movements, important lateral ones; category 5 - nectobenthic fishes, sedentary; category 6 - nectobenthic fishes, highly sedentary. For the few species not listed by the above mentioned authors, the classification was made according to the available published information.

RESULTS

The number of the more common fish species on the Azorean shallow waters added up to a total of 66. Table 1 contains the information gathered about each species diet, provenance of the diet items, and spatial distribution.

Three species can be considered true herbivores: the sparid Sarpa salpa and the blennids Parablennius sanguinolentus and Ophioblennius atlanticus atlanticus.

Of the 10 omnivorous species, 9 are macroomnivores. Examples are the blenniid Parablennius incognitus, the pomacentrid Abudefduf luridus and the scarid Sparisoma cretense. The mugilid Chelon labrosus is the only microomnivore present.

The majority of the species (53) are carnivores. Microcarnivores represent 22 species. Most of them (13) feed mainly on benthic invertebrates, like the labrids Coris julis and Thalassoma pavo. Six other species, such as the juveniles of Trachurus picturatus and of Pagellus spp., feed mainly on pelagic invertebrates and are therefore planktivores. Three others, including the pomacentrid Chromis limbata, are able to capture prey in both realms. A total of 20 species were considered mesocarnivores, 3 of them preying mainly on pelagic items. Macrocarnivores totaled 11 species, of which 4 are also pelagic predators.

Overall (Fig. 1), the more diverse trophic guild is that of the benthic feeding carnivores, about three quarters of which are micro or meso carnivores. It is followed by the

pelagic feeding carnivores. Fish species that include algal material in their diets are a clear minority.

DISCUSSION

The faunistic surveys on which the present species list was based have included different sampling strategies (from ichthyocide collections to visual or photographic identifications) in both the intertidal and subtidal areas. It is believed that they provide a fairly complete inventory of the most common shallow water fishes of the Azores.

It can be concluded that most of the Azorean fish species are dependent on the benthic primary production. This is not surprising giving that the algae-covered rocky substrate is by far the most common habitat in the Azores littoral (CHAPMAN, 1954). Rocky bottom is mostly igneous in origin, with a complex topography in a large range of scales. Predominant algal growth is in the form of a generally short, plurispecific turf (NETO, 1992; NETO & TITLEY, 1995). This kind of algal cover further adds to the habitat's structural complexity (HICKS, 1985; DEAN & CONNEL, 1987), providing shelter for an abundant invertebrate fauna of minute polichaets, gastropods and crustaceans (CHAPMAN, 1955; CASTRO & VIEGAS, 1983; BULLOCK *et al.*, 1990; AZEVEDO, 1992; HAWKINS *et al.*, 1990; MORTON, 1990; see also FRETTER & MANLY, 1977 as to the protective role of the algal turf). These animals directly support most of the species on the two more diverse trophic groups, the micro and mesocarnivores, and are also important elements on the diet of omnivore species. Coupled to the reduced number of herbivorous species of fish, this fact suggests that the bulk of the benthic primary production reaches the higher trophic levels via the benthic invertebrate community.

Rocky reef communities have another source of energy, besides the primary production of attached plants: organic matter of pelagic origin (EBLING & HIXON, 1991). This pelagic-based food web is less diverse, since there are few holopelagic species. However, it is specially important for the young stages of most species. With few exceptions, all the littoral fishes have planktonic larval stages. Most settle at metamorphosis, but several sparid and carangid species maintain a pelagic juvenile phase. Abundant schools of juvenile Trachurus picturatus and Pagellus spp. are common around the Azorean shores. As they grow, they become increasingly dependent on benthic food, migrating into deeper waters and assuming a demersal way of life (ISIDRO, 1990; BAUCHOT, 1987b). There are several other links between the benthic and the pelagic food webs besides those derived from ontogenic diet changes. Species like Chromis limbata, for instance, who feed alternately on plankton and benthic microinvertebrates, transfer energy from the pelagic food web to the benthic one. Nictimeral migration of zooplanktonts also accomplishes this. Settling juveniles are important prey for benthic/demersal mesocarnivores and therefore constitute another mechanism for the downward transfer of energy. Predatory incursions of the pelagic carnivores

and all the planktonic spawning products do the reverse, i.e., are channels for the upward transfer of organic matter.

The number of species (as used here) is just one of the possible indicators of the ecological importance of each of the above defined trophic guilds and energy pathways. An ecologically more meaningful picture of the azorean shallow water ichthyological communities will require quantitative data on the abundance of each species, as well as on their local diets and feeding strategies.

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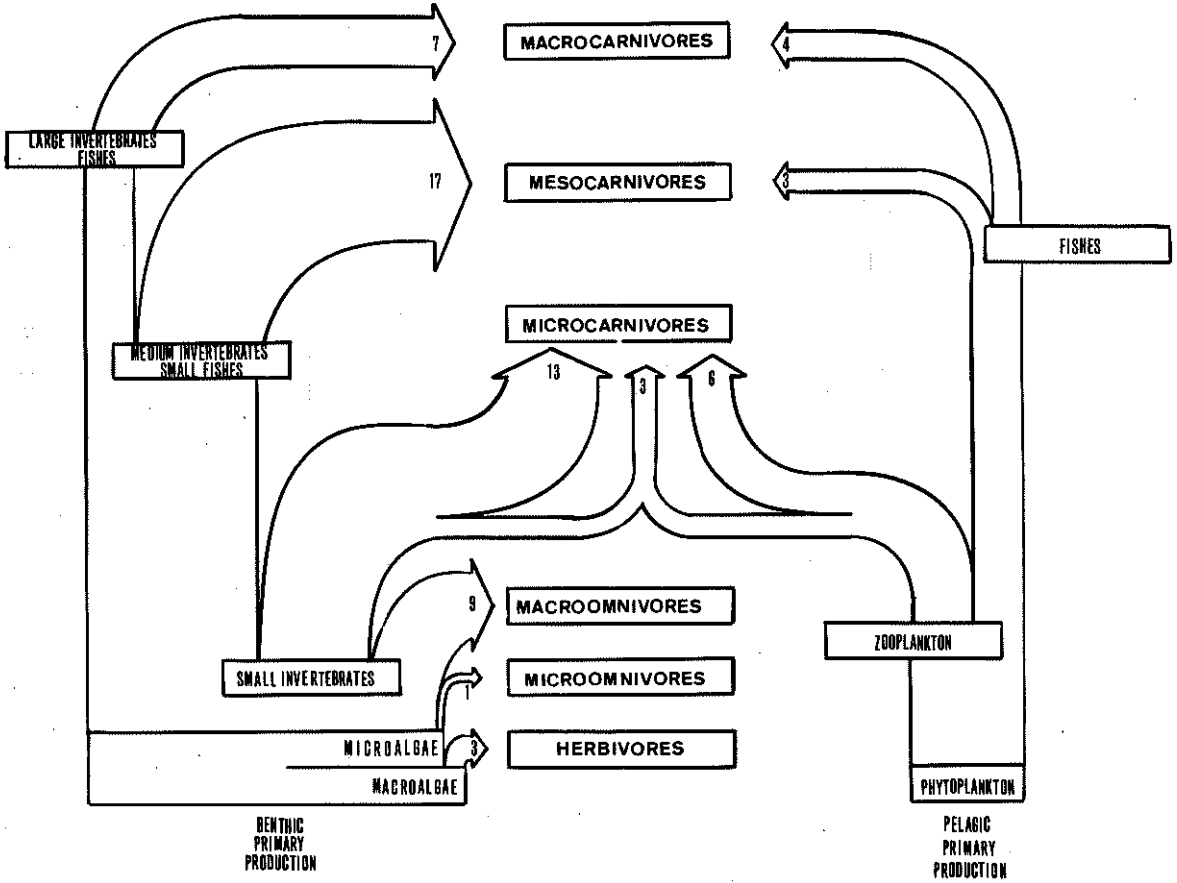

Figure 1 - Simplified food web of the main trophic guilds of azorean shallow water fishes. Guilds are grouped according to their dependence on the benthic and/or pelagic primary production. The number of species in each guild is indicated by the width of the arrow and by the number printed on it.

TABLE 1 - Main items on the diet of the azorean shallow water fishes. Also noted is the spatial distribution category of each fish species (Dist.) and the provenance of the majority of the food items (Prey: B- benthic; P- pelagic). See text for explanation of terms. Numbers following the species name refer to the faunistic lists were they are recorded: (1) WOOD & WILLIAMS, 1974; (2) ARRUDA *et al.*, 1992; (3) AZEVEDO *et al.*,1992; (4) PATZNER *et al.*,1992.

	Main food items	Dist	Prey	References
Herbivorous				
Ophioblennius atlanticus atlanticus (Valenciennes, 1836) [1, 2, 3, 4]	Algae	6	B	Nursall, 1977; Labelle & Nursall, 1985
Parablennius sanguinolentus (Pallas, 1811) [2, 3, 4]	96% (weight) herbivorous	6	B	Azores: Santos & Barreiros, 1993. Elsewhere: Gibson, 1968; Mayer, 1971, 1972; Taborsky & Limberger, 1980; Zander, 1984; Goldschmid *et al.*, 1984
Sarpa salpa (Linnaeus, 1758) [1, 2, 3, 4]	Algae	3	B	Azores: Pereira, 1995. Elsewhere: Christensen, 1978; Joubert & Hanekom, 1980; Anato & Ktari, 1983; Gerking, 1984; Bennett, 1989; Verlaque, 1990
Omnivorous				
Microomnivores: microalgae and associated invertebrates				
Chelon labrosus (Risso, 1826) [1, 2, 3, 4]	Filamentous algae, diatoms, copepods, mud	3	B	Drake & Arias, 1984
Macroomnivores: macroalgae and associated invertebrates				
Abudefduf luridus (Cuvier, 1830) [1, 2, 3, 4]	Filamentous algae and attached animals	5	B	Azores: Mapstone & Wood, 1974. Elsewhere: Quignard & Pras, 1984c
Boops boops (Linnaeus, 1758) [1, 2, 4]	Diploblastica, polychaeta, crustacea and vegetables	1	B	Anato & Ktari, 1983
Coryphoblennius galerita (Linnaeus, 1758) [1, 2, 4]	Algae (73% weight) and cirripeds	6	B	Gibson, 1968, 1972; Zander, 1972; Fives, 1980; Carvalho, 1982; Milton, 1983; Goldschmid *et al.*, 1980,1984
Diplodus sargus (Linnaeus, 1758) [1, 2, 3, 4]	4-50% algae, fish, amphipods, polychaetes, bivalves, decapods, echinoderms	3	B	Christensen, 1978; Joubert & Hanekom, 1980; Coetzee, 1986; Rosecchi, 1987
Kyphosus sectator (Linnaeus, 1766) [2, 4]	Algae, small crabs and molluscs	3	B	Tortonese, 1984c; Bauchot, 1987b
Lypophris pholis (Linnaeus, 1758) [2, 4]	Gastropods and bivalves (52 and 22% weight)	6	B	Qasim, 1957; Gibson, 1972; Dunne, 1977; Carvalho, 1982; Milton, 1983
Parablennius incognitus (Bath, 1968) [1, 2, 3, 4]	Algae and associated small benthic animals and detritus (30% herbivorous)	6	B	Goldschmid & Kotrschal, 1981; Goldscmidt *et al.*, 1984
Sparisoma cretense (Linnaeus, 1758) [1, 2, 4]	Algae (*Corallina*) and small invertebrates	5	B	Quignard & Pras, 1984d; Bauchot, 1987b
Sphoeroides marmoratus (Lowe, 1839) [1, 2, 3, 4]	Crustaceans, echinoderms, molluscs, polychaets and plants (less than 10% of diet)	4	B	*Sphoeroides spengleri*: Shipp, 1974; Targett, 1978; Tortonese, 1984e

	Main food items		Hab	References
Carnivorous				
Microcarnivores				
Atherina sp. [1]	Plankton and small bottom-living animals	1	P	Quignard & Pras, 1984a
Capros aper (Linnaeus, 1758) [2]	Copepods, euphasids	1	P	MacPherson, 1979
Centrolabrus trutta (Lowe, 1833) [1, 2, 4]	Small algae-associated invertebrates	5	B	Azores: Rodrigues, 1991; Rodrigues, 1995
Chromis limbata (Valenciennes in Cuv.& Val., 1833) [1, 2, 3, 4]	Small planktonic or benthic animals (copepods, larvaceans, bivalves)	2	B/P	Azores: Mapstone & Wood, 1974. Elsewhere (*C. chromis*): Quignard & Pras, 1984c; Bauchot, 1987b
Coris julis (Linnaeus, 1758) [1, 2, 3, 4]	Small benthic invertebrates	5	B	Azores: Rodrigues, 1991; Rodrigues, 1995. Elsewhere: Quignard, 1966; Vos, 1974; Michel *et al.*, 1987; Duka *et al.*, 1981
Diplecogaster bimaculata pectoralis Briggs, 1955 [2, 3, 4]	Amphipods and caridean decapods	6	B	Gibson & Ezzi, 1987
Hippocampus ramulosus Leach, 1814 [2, 4]	No data	6	B	Dawson, 1984
Lypophris trigloides (Valenciennes, 1836) [2, 4]	Gastropods, isopods and amphipods	6	B	Carvalho, 1982; Goldschmidt *et al.*, 1984
Macroramphosus scolopax (Linnaeus, 1758) [1]	Pelagic invertebrates, mainly copepods; also bottom invertebrates for the adults	1	B/P	Ehrich, 1975; Brethes, 1979; Matallanas, 1982
Pagellus acarne (Risso, 1826) (juv.) [4]	Benthic invertebrates and fish larvae	1	P	Bauchot & Hureau, 1984; Bauchot, 1987b
Pagellus bogaraveo (Brünnich, 1768) (juv.) [3]	Pelagic invertebrates, fish eggs, larvae and juveniles	1	P	Bauchot & Hureau, 1984; Bauchot, 1987b
Pagrus pagrus (Linnaeus, 1758) (juv.) [3, 4]	Amphipods, copepods, stomatopods and annelids.	3	B/P	Collignon & Aloncle, 1960; Manooch, 1977; Chakroun-Marzouk & Kartas, 1987
Parablennius ruber (Valenciennes, 1836) [2, 3, 4]	Small benthic animals (amphipods, polichaetes, bryozoans, etc.) and small fragments of *Corallina*	6	B	Azores: Santos, 1987
Pomatoschistus pictus (Malm, 1865) [2, 3, 4]	Small crustaceans (copepods, amphipods)	2	B	Azores: Patzner & Santos, 1990. Elsewhere: Miller, 1984
Sardina pilchardus (Walbaum, 1792) [4]	Crustaceans and other planktonic animals	1	P	Whitehead, 1984; Bauchot, 1987b
Symphodus mediterraneus (Linnaeus, 1758) [1, 2, 3, 4]	Small benthic invertebrates	5	B	Quignard, 1966; Michel *et al.*, 1987
Symphurus nigrescens Rafinesque, 1810 [4]	Polychaetes, ophiuroid, molluscs	4	B	MacPherson, 1978; Munroe, 1990
Syngnathus acus Linnaeus, 1758 [1]	Small benthic invertebrates	1	B	Bennett, 1989
Thalassoma pavo (Linnaeus, 1758) [1, 2, 3, 4]	Small benthic invertebrates	5	B	Azores: Rodrigues, 1991; Rodrigues, 1995. Elsewhere: Quignard, 1966; Vos, 1974; Michel *et al.*, 1987
Thorogobius ephippiatus (Lowe, 1839) [4]	Crustaceans (copepods, amphipods, decapods), polychaetes, gastropods, algae	6	B	Miller, 1984
Trachurus picturatus (Bowdich, 1825) (juv.) [1, 2]	Zooplankton	1	P	Dahl & Kirkegaard, 1986, 1987; Goberna, 1987; Ben Salem, 1988
Tripterigion delaisi Cadenat & Blache, 1971 [1, 2, 3, 4]	Small invertebrates	6	B	Zander, 1982; Zander & Berg, 1984; Zander & Hagemann, 1989

	Main food items		Hab	References
Carnivorous				
Mesocarnivores				
Anguilla anguilla (Linnaeus, 1758) [2, 3]	Polychaetes, bivalves, shrimp	6	B	Costa *et al.*, 1992
Anthias anthias (Linnaeus, 1758) [2, 4]	Small crustaceans and fish	2	P	Tortonese, 1984d; Bauchot, 1987b
Apogon imberbis (Linnaeus, 1758) [1, 2, 3, 4]	Small invertebrates and fish	6	B	Tortonese, 1984a
Apterichthus caecus (Linnaeus, 1758) [2, 3, 4]	No data	6	B	Bauchot, 1984b; 1987b
Balistes carolinensis Gmelin, 1789 [1, 2, 4]	Benthic molluscs and crustaceans	1	B	Tortonese, 1984b; Bauchot, 1987b
Bothus podas maderensis (Lowe, 1834) [1, 2, 3, 4]	Polychaetes, molluscs, crustaceans, fish	4	B	Azores: Nash *et al.*, 1991. Elsewhere: Weber, 1965; De Groot, 1971
Dasyatis pastinaca (Linnaeus, 1758) [1, 2, 3, 4]	Bottom-living invertebrates (crustaceans, cephalopods and bivalves) and fishes	4	B	McEachran & Capapé, 1984; Bauchot, 1987a; Capapé & Zaouali, 1992
Echiichthys vipera (Cuvier, 1829) [4]	Small fish (47-85% number); macrobenthic fauna especially crustacean amphipods; polychaetes and bivalves are only secondary preys	4	B	Sorbe, 1981; Creutzberg & Duineveld, 1986; Dauvin, 1988; Creutzberg & Witte, 1989
Gaidropsaurus guttatus (Collett, 1890) [1, 2, 3, 4]	Small fish, mainly blennies	6	B	Azores: Santos, 1987
Gobius paganellus Linnaeus, 1758 [1, 2, 3, 4]	Polichates, amphipods (52 and 25% number), small fishes	6	B	Costa, 1988
Labrus bergylta Ascanius, 1767 [1, 2, 3, 4]	Decapod crustaceans, isopods, molluscs	5	B	Quignard, 1966; Vos, 1975; Dipper *et al.*, 1977; Michel *et al.*, 1987
Mullus surmulettus Linnaeus, 1758 [1, 3, 4]	Polychaetes, crustacea (amphipoda, decapoda): 41,8 and 45,1% number	4	B	Gharbi & Ktari, 1981; Dauvin, 1988; Ben-Elihau & Golani, 1990
Phycis phycis (Linnaeus, 1766) [1, 2, 3, 4]	Invertebrates and small fishes	6	B	Svetovidov, 1984; Bauchot, 1987b
Pseudolepidaplois scrofa (Valenciennes, 1839) [1, 2, 4]	No data	6	B	Quignard & Pras, 1984b
Scorpaena maderensis Valenciennes, 1833 [1, 2, 3, 4]	Crustaceans and small fishes	6	B	Azores: pers. obs. Elsewhere: Hureau & Litvinenko, 1984; Bauchot, 1987b
Scorpaena notata Rafinesque, 1810 [2, 3, 4]	Crustaceans and small fishes	6	B	Azores: pers. obs. Elsewhere: Hureau & Litvinenko, 1984; Bauchot, 1987b
Serranus atricauda Günther, 1874 [1, 2, 3, 4]	Invertebrates and fish	5	B	Tortonese, 1984d
Synodus saurus (Linnaeus, 1758) [2, 4]	Shrimps and fish	4	B	Bauchot, 1987b
Trachinotus ovatus (Linnaeus, 1758) [1, 2, 3, 4]	Invertebrates, primarily small crustaceans and molluscs, and small fishes, mainly Clupeidae	1	P	Smith-Vaniz, 1984; Bauchot, 1987b
Zeus faber Linnaeus, 1758 [1]	Mysids and fish	1	P	Gibson & Ezzi, 1987; Stergiou & Fourtouni, 1991

	Main food items		Hab	References
Carnivorous				
Macrocarnivores				
Conger conger ([Artedi, 1738] Linnaeus, 1758) [4]	Fish, crustaceans and cephalopods	6	B	Bauchot & Saldanha, 1984; Bauchot, 1987b
Enchelycore anatina (Lowe, 1841) [4]	No data	6	B	Bauchot, 1984a
Epinephelus marginatus (Lowe, 1834) [1, 2, 3, 4]	Fish, crabs and octopods	5	B	Cadenat, 1954; Joubert & Hanekom, 1980; Bruslé, 1985; Smale, 1986
Gymnothorax unicolor (Delaroche, 1809) [2, 3]	Crabs, gasteropods and cephalopods	6	B	Bauchot, 1984a
Muraena augusti Kaup, 1860 [3, 4]	Similar to *M. helena*	6	B	Azores: pers. obs.
Muraena helena Linnaeus, 1758 [1, 2, 3, 4]	Mainly cephalopods and fish	6	B	Bauchot, 1984a
Mycteroperca fusca (Lowe, 1836) [1, 2, 4]	No data	5	B	Tortonese, 1984d
Pomatomus saltator (Linnaeus, 1766) [4]	Fish, cephalopods, shrimp	1	P	van der Elst, 1976; Bennett, 1989
Pseudocaranx dentex (Bloch & Schneider in Schneider, 1801) [1, 2, 3, 4]	Benthic invertebrates	1	P	Smith-Vaniz, 1984; Bauchot, 1987b
Seriola spp. [1, 2, 4]	Feeding primarily on other fishes	1	P	Smith-Vaniz, 1984; Bauchot, 1987b
Sphyraena sp. [1, 2, 3, 4]	Mostly fish	1	P	Ben-Tuvia, 1984; Bauchot, 1987b