

Diets of deep-sea macrourid fishes in the western Mediterranean

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ABSTRACT: The feeding habits of the 4 most abundant macrourids that occur on the deep slope of the Catalan Sea (western Mediterranean) were examined for the first time for the Mediterranean at depths between 1000 and 2250 m. Diets of *Chalinura mediterranea*, *Coryphaenoides guentheri*, *Coelorhynchus labiatus* and *Trachyrhynchus trachyrhynchus* were analysed for 2 seasons (summer and autumn) and/or 3 different bathymetric strata. *Coryphaenoides guentheri* was the most euryphagous and *T. trachyrhynchus* the least. *Chalinura mediterranea*, *Coelorhynchus labiatus* and *T. trachyrhynchus* has a benthopelagic diet, whilst *Coryphaenoides guentheri* has a benthic diet. *Coelorhynchus labiatus* has a slight preference for bathybenthic prey (polychaetes, gammaridean amphipods) whereas *Chalinura mediterranea* and *T. trachyrhynchus* display a preference for bathypelagic prey (calanoid copepods, mysids). *Chalinura mediterranea* and *Coryphaenoides guentheri* have bathymetric differences in diet marked by the capture of different prey-items and also by a greater vacuity, a greater consumption of prey and a greater diversity at 1800 to 2250 m. A greater diversity in the diet is found in the Mediterranean populations of *Chalinura mediterranea*, *Coryphaenoides guentheri* and *Coelorhynchus labiatus* than in the Atlantic populations; this is probably an adaptation to the faunal paucity of the Mediterranean deep sea. General affinities among the diets of all macrourids are also analysed. The apparent coincidence between the diets of *Chalinura mediterranea* and *T. trachyrhynchus* could explain the bathymetric segregation of their respective niches. *Coelorhynchus labiatus*, whose habitat width lies within those of the other 3 macrourids, has a dietary overlap intermediate to those of the other 3 macrourids. Ecological separation is maintained by a combination of differential depth distribution and feeding habits.

KEY WORDS: *Chalinura mediterranea* · *Coryphaenoides guentheri* · Macrouridae · Feeding ecology · Western Mediterranean · Deep-sea ecology

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INTRODUCTION

The family Macrouridae is present in all oceans from subarctic to antarctic regions (Marshall & Iwamoto 1973) and constitutes one of the most important deep-water demersal fish families. Of the approximately 300 species, 90% inhabit the continental slope areas between depths of 200 and 2000 m (Marshall 1965). Eight species of macrourids occur in the northwestern Mediterranean Sea and only 5 of them are present in the lower slope, below 1000 m depth. The Macrouridae are the best represented family (of the total 19 families)

in terms of number of species, the third in number of individuals and the fifth in terms of biomass in the Catalan deep sea between depths of 1000 and 2250 m (Stefanescu et al. 1992a).

Information about the distribution and biology of macrourids in the Atlantic is plentiful (e.g. McLellan 1977, Geistdoerfer 1978, 1978–1979, Mauchline & Gordon 1984a, 1985, 1986, Gordon & Duncan 1987, Merrett 1987, Gordon & Mauchline 1990). In the Mediterranean, the bathymetric distribution has been studied by Macpherson (1979), Stefanescu et al. (1992a, 1994) and Massutí et al. (1995). Information on Mediterranean macrourids biology is limited. Data regarding growth, depth-size trends and morphometrics of the

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alimentary canal have been given by Morales-Nin (1990), Stefanescu et al. (1992b), Carrassón & Matallanas (1994) and Massutí et al. (1995). Diets of macrourids for depth ranges of 200 to 800 m have been studied by Macpherson (1979, 1981), and some generic data on the diet of 1 specimen of *Coryphaenoides guentheri* and 1 *Chalinura mediterranea* from a depth of more than 2400 m have been reported by Geistdoerfer (1978). Apart from these 2 observations, no studies have been carried out on the diet of macrourids below a depth of 1000 m in the Mediterranean. In demersal deep-sea fishes in the western Mediterranean, a different behaviour in depth-size trends has been found compared to that in Atlantic waters; at the same time, a significant size reduction in Mediterranean populations of many species (among them the macrourids) has been observed compared to Atlantic populations (Stefanescu et al. 1992b). Stefanescu et al. (1993) demonstrated the existence of 2 distinct assemblages at depths between 1000 and 2250 m in the northwestern Mediterranean, one at 1000 to 1425 m and the other at 1425 to 2250 m, where the ichthyofauna is of a largely homogeneous nature, and they also observed a transition group on the lower slope between approximately 1425 and 1800 m. The existence of assemblages generally corresponds to important changes in the available trophic energy in the demersal ecosystem, and therefore to changes in the trophic habits of the species, such as has been observed in some species of fishes in the zone (Carrassón et al. 1997, Carrassón & Matallanas 1998, 2001).

The object of this paper is to present and compare new and detailed information on the feeding ecology of a group of species constituting one of the main components of the deep-sea megafauna. We present a study on the trophic habits of the 4 most abundant macrourids inhabiting the lower slope (below 1000 m depth) of the northwestern Mediterranean: *Chalinura mediterranea* Giglioli, 1893, *Coryphaenoides guentheri* (Vaillant, 1888), *Coelorhynchus labiatus* (Koehler, 1896) and *Trachyrhynchus trachyrhynchus* (Risso, 1810). The feeding habits of *Chalinura mediterranea* and *Coryphaenoides guentheri* are analysed for different bathymetric strata, sizes of specimens and seasons. Preliminary data on the feeding habits of *Coelorhynchus labiatus* and *T. trachyrhynchus* (below 1000 m) are also presented. How the factors of bathymetric strata or sizes or seasons influence the diet and patterns of dietary overlap is also discussed.

MATERIALS AND METHODS

All material was collected from the continental slope of the Catalan Sea (Western Mediterranean), during

6 cruises (BATHOS II-V, SPERMA, RETRO), on board the RV 'García del Cid' (Table 1). Samples were obtained with 2 different semi-balloon otter-trawls towed from a single warp, OTSB-14 (Merrett & Marshall 1981) on the BATHOS and SPERMA cruises, and OTMS-27.5 (Sardà et al. 1994) on the RETRO cruise, as described in previously published papers (Stefanescu et al. 1992a, Cartes & Sardà 1993, Stefanescu et al. 1994). The vertical opening of the trawls was 1.5 m and 1.8 to 2 m for OTSB-14 and OTMS-27.5 respectively; the horizontal opening was 7 and 14 m respectively. Deployment of this sort of gear is standard practice in deep-sea demersal sampling; it can be therefore assumed that results drawn from such surveys in different areas are comparable (cf. Haedrich & Merrett 1988).

A total of 994 specimens (191 *Chalinura mediterranea*, 611 *Coryphaenoides guentheri*, 43 *Coelorhynchus labiatus*, 149 *Trachyrhynchus trachyrhynchus*) were collected between depths of 1000 and 2250 m to examine feeding activity (Table 1). These 4 species are found in the North Atlantic as well as in the Mediterranean (Geistdoerfer 1986). In the western Mediterranean, the bathymetric distribution of *Chalinura mediterranea* and *Coryphaenoides guentheri* is restricted to depths greater than 1300 m, but down to 1500 to 1600 m they appear only occasionally (Stefanescu et al. 1992a). *Coelorhynchus labiatus* occurs between 1200 and 1600 m, and its occurrence outside this range is rare (Stefanescu et al. 1992a). *T. trachyrhynchus* occurs down to 1589 m, but its maximum abundance and biomass lie outside this depth range, between 900 and 1000 m (Massutí et al. 1995), and below 1300 m it is rare (Stefanescu et al. 1992a).

All specimens were fixed in 10% formalin immediately after capture. Once in the laboratory, they were measured (total length, TL, to the nearest millimeter) and dissected to analyse stomach contents.

Food items were identified to the lowest taxonomic level possible. Numbers and weights were recorded to the nearest 0.1 mg after drying with blotting paper to remove surface moisture.

The quantitative importance of each prey group in the diet was determined by the index of relative importance (IRI, Pinkas et al. 1971), defined as:

$$IRI = \%F(\%N + \%V)$$

where %F = frequency of occurrence of a food item in the stomachs of a whole sample; %N = numerical percentage of a food item in the stomachs, and %V = percentage by volume of a food item in the stomachs (Hureau 1970). In the present study, weight (%W) was used instead of volume (%V). This modified index is expressed as %IRI = (IRI/ΣIRI) × 100 (Rosecchi & Nouaze 1987). Prey were sorted in decreasing order of

Table 1. *Chalinura mediterranea* (C. m.), *Coryphaenoides guentheri* (C. g.), *Coelorhynchus labiatus* (C. l.) and *Trachyrhynchus trachyrhynchus* (T. t.) sampling data. L(N): Latitude North; L(E): Longitude East; B: BATHOS cruises; SP: SPERMA cruise; R: RETRO cruise

Station	Date (dd/mm/yy)	Depth (m) (initial-final)	Final position		C. m.	No. of specimens		
			L(N)	L(E)		C. g.	C. l.	T. t.
BII-5	30/07/87	1715-1753	40° 25.4'	1° 56.9'	16	29		
BIII-3	25/06/88	1774-1783	40° 18.5'	1° 57.2'	12	136		
BIII-4	26/06/88	2163-2039	40° 37.7'	3° 06.2'	34	110		
BIII-5	26/06/88	2256-2239	40° 32.3'	3° 44.7'	8			
BIII-6	27/06/88	1857-1855	40° 32.9'	2° 51.4'	1	26		
BIII-7	27/06/88	1539-1621	40° 09.2'	3° 01.0'	1	30	14	
BIII-8	28/06/88	1737-1729	40° 16.7'	2° 54.8'	1	32		
BIII-9	30/06/88	2193-2198	40° 38.7'	3° 23.1'		25		
BIII-11	02/07/88	1520-1429	40° 57.6'	2° 23.3'	6	6		
BIII-12	02/07/88	1617-1635	40° 57.3'	2° 32.3'	8	28	1	
BIII-15	03/07/88	1015-996	40° 55.3'	1° 44.4'				4
BIII-16	04/07/88	1235-1214	40° 45.2'	1° 38.8'			6	
BIII-17	04/07/88	1393-1434	40° 45.8'	1° 55.4'		6		
BIII-28	11/07/88	1820-1927	40° 26.4'	2° 37.7'	4	4		
BIV-1	26/07/88	1002-970	41° 21.5'	3° 18.6'				25
BIV-2	26/07/88	2017-2083	41° 17.5'	3° 27.4'	3	9		
BIV-3	27/07/88	2158-2188	41° 08.5'	3° 32.1'	31	30		
BIV-4	28/07/88	2071-1880	41° 05.0'	3° 06.7'	12	41		
BIV-6	28/07/88	1837-1880	41° 14.2'	3° 17.3'	3	59		
BIV-7	29/07/88	2198-2221	41° 05.1'	3° 29.4'	42			
BIV-8	29/07/88	1784-1765	41° 07.1'	2° 46.6'	9	9		
BIV-9	30/07/88	1823-1796	41° 44.0'	2° 28.6'		6		
BIV-10	30/07/88	1284-1286	40° 58.8'	2° 18.6'			3	3
BIV-11	31/07/88	1531-1471	41° 03.5'	2° 37.2'			2	
BIV-12	31/07/88	1317-1329	41° 02.6'	2° 23.1'			3	2
BV-10	27/10/88	1014-1004	40° 53.9'	1° 45.0'				19
BV-11	28/10/88	1036-1026	40° 55.4'	1° 52.6'				36
BV-13	28/10/88	1085-961	40° 57.4'	2° 07.5'				25
BV-14	28/10/88	1158-1165	41° 00.3'	2° 11.3'				10
BV-16	29/10/88	1008-1089	41° 06.9'	2° 22.9'				11
SP-3	17/10/89	1772-1808	40° 20.9'	2° 01.2'		40		
SP-5	18/10/89	1478-1547	40° 04.5'	1° 38.4'			1	
SP-6	19/10/89	1289-1301	38° 15.4'	1° 05.9'			1	
R1-9	25/04/91	1267-1167	41° 93.1'	2° 20.3'			12	14

their %IRI contribution, and the cumulative %IRI was calculated (the sum of the IRI of 1 prey with all the preceding in the list). Prey were classified into 3 categories, according to their contribution to the cumulative %IRI (Rosecchi & Nouaze 1987): preferential prey (the first prey on the list whose contribution increased the accumulative %IRI to at least 50% of the total %IRI); secondary prey (the next prey on the list whose cumulative %IRI, when added to that of the preferential prey, increased the accumulative IRI to approximately 75% of the total %IRI); and accidental prey (the remaining prey).

The diet of *Chalinura mediterranea* was studied for 2 bathymetric strata: 1425 to 1800 m and 1800 to 2250 m.

To analyse the diet of *Coryphaenoides guentheri*, individuals from all trawls were grouped according to capture depth (2 bathymetric strata: 1425 to 1800 m and 1800 to 2250 m), season (summer and autumn) and

size of individuals (2 categories: Size 1, total length < 173.5 mm; Size 2, total length ≥ 173.5 mm). There are no studies in the literature on the size at maturity of *C. guentheri* in the Mediterranean, so we attempted to calculate this using our specimens in order to be able to analyse possible variations in diet between the juveniles and adults. Our *C. guentheri* were not in their reproductive season, but small atresic eggs were found in the gonads with a weight of >0.03 g. From this, we calculated a possible size at maturity of 173.5 mm, the TL which separates our 2 size classes. The %IRI of the main prey items was determined for each of the 5 combinations (see Table 2) of depth, season and size by pooling diet data from the individuals included in each combination. The affinity of these 5 combinations was computed using hierarchical analysis (unweighted pair-group method using arithmetic averages, UPGMA, as the aggregation algorithm, with Euclidean distance as a measure of similarity).

A food-intensity index (K) was determined using the average index of the amount of food eaten per fish (weight of the stomach contents \times 100/weight eviscerated fish: Yasuda 1960). Trophic diversity (H') was calculated, in terms of mean % weight of prey-items using the Shannon index. In *Chalinura mediterranea* and *Coryphaenoides guentheri*, degree of overlap of different bathymetric strata and seasons was determined also, based on mean % weight results, using the quantitative Schoener index (Schoener 1974).

RESULTS

Chalinura mediterranea

Of the 191 specimens analysed, 28 had the stomach everted, and of the remaining 163, 40 were empty. From the 123 stomachs containing food, 43 categories of prey items were identified (Table 2).

The diet was dominated by Mysidacea (%IRI = 32.70) and Copepoda (%IRI = 26.13). Gammarid Amphipoda (%IRI = 22.87) were secondary prey. Polychaete and decapod Natantia were the main accidental groups.

Individuals from 1425 to 1800 m: The diet of 40 specimens collected indicated that copepods (mainly calanoids) and mysids were the most consumed prey groups. Copepods were abundant (% N = 31.36) and

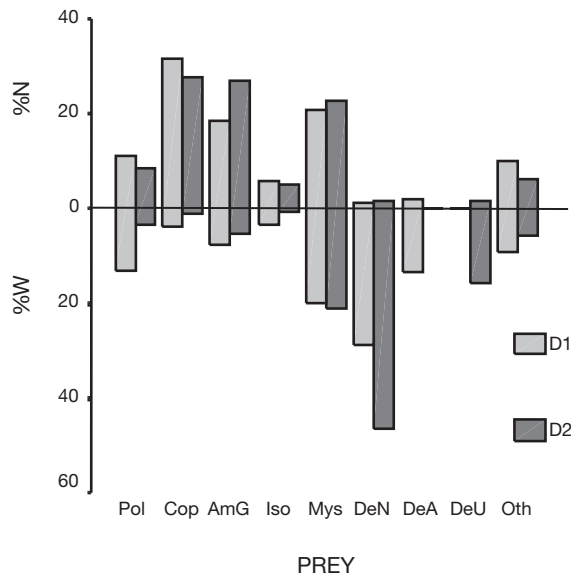


Fig. 1. *Chalinura mediterranea*. Percentage by number (% N) and by weight (% W) of prey species in the diet of individuals from 1425 to 1800 m depth (D1) and individuals from 1800 to 2250 m depth (D2). Pol: Polychaeta; Cop: Copepoda; AmG: amphipod Gammaridea; Iso: Isopoda; Mys: Mysidacea; DeN: decapod Natantia; DeA: decapod Anomura; DeU: unidentified decapod; Oth: others

the importance of mysids was related to their high weight (% W = 20.00: Fig. 1). *Boreomysis arctica* was the mysid most frequently captured. Gammaridean amphipods and polychaetes were secondary prey (%IRI = 19.41 and 16.30 respectively: Table 2) and the rest accidental prey.

Individuals from 1800 to 2250 m: Of the 83 specimens analysed the mysids and copepods were the dominant prey, the gammaridean amphipods the secondary prey, and polychaetes and natantian decapods the major accidental prey. Copepods were the most abundant (% N = 27.70) and natantian decapods the heaviest prey (% W = 46.4) (Fig. 1), but due to their low frequency and abundance the latter had a low %IRI (5.3%). *Boreomysis arctica* was the more abundant mysid captured and *Rhachotropis* sp. the most abundant amphipod in the diet.

In terms of the different depth ranges, the ratio of full foreguts at 1425 to 1800 m was lower than at 1800 to 2250 m (Table 3), but not significantly ($p > 0.05$, χ^2 criterion).

K reached its statistically significant maximum in specimens caught between 1800 and 2250m (Table 3; Student's t -test, $p < 0.01$). The average number of prey per stomach (N_p) and the average weight of prey per stomach (W_p) showed a similar trend to K (Table 3); the largest and most numerous prey were consumed at 1800 to 2250 m, but the differences were not significant (both t -test, $p > 0.05$).

Trophic diversity values (H' : Table 3) were higher at the maximum depth. Dietary overlap (Schoener index) was 0.629 between groups from 1425 to 1800 m and 1800 to 2250 m.

Coryphaenoides guentheri

Of the 626 specimens analysed, 132 had everted stomachs and 76 had empty stomachs. From the 418 stomachs containing food, 94 categories of prey items were identified (Table 2).

Gammarid amphipods were the preferred prey (%IRI = 46.90), being the most abundant the most frequently captured, and the heaviest prey. Cumaceans were secondary prey (%IRI = 22.25), and polychaetes accidental (%IRI = 14.91).

The cluster analysis of the size, season and depth combinations identified 3 groups (Fig. 2). The specimens collected at depths of 1425 to 1800 m in autumn (Group A) were clearly separated in the dendrogram from all the summer individuals. Size 1 and Size 2 in all categories were clustered together, being grouped together with individuals collected at 1425 to 1800 m in summer (Group B), and the 1800 to 2250 m specimens (Group C).

Table 2. Composition of the diet of macrourids in the bathymetric and seasonal groups established (numbers in parentheses show total no. of specimens/number containing food). IRI: index of relative importance; %IRI: percentage of IRI; -: absent

Dietary items	<i>Chalinura mediterranea</i>		<i>Coryphaenoides guentheri</i>		<i>Coelorhynchus labiatus</i>		<i>Trachyrhynchus trachyrhynchus</i>					
	1425–1800 m Summer (49/40) IRI %IRI	1800–2250 m Summer (114/83) IRI %IRI	1425–1800 m Autumn (14/10) IRI %IRI	Summer (216/189) IRI %IRI	1800–2250 m Summer (264/219) IRI %IRI	1000–1800 m (15/11) IRI %IRI	1000–1425 m (8/5) IRI %IRI					
FORAMINIFERA												
Unidentified	2.9	0.04	1.5	0.02	1333.2	17.85	48.0	0.56	210.6	2.26	–	–
Mud Foraminifera	–	–	27.0	0.68	–	–	–	–	2.5	0.06	–	–
<i>Globigerinoides ruber</i>	2.9	0.07	1.5	0.04	638.2	16.02	48.0	1.15	120.3	3.01	–	–
<i>Globorotalia truncatulinoides</i>	–	–	–	–	–	–	–	–	0.4	0.01	–	–
	–	–	–	–	27.0	0.68	–	–	1.1	0.03	–	–
SIPHONOPHORA												
Unidentified	–	–	–	–	–	–	–	–	0.1	0.00	–	70.7
<i>Chelophyes appendiculata</i>	–	–	–	–	–	–	–	–	0.1	0.00	–	–
	–	–	–	–	–	–	–	–	–	–	–	70.7
PRIAPULIDA												
SIPUNCULIDA												
Unidentified	–	–	–	–	121.7	3.05	–	–	1.4	0.04	–	–
	–	–	–	–	–	–	–	–	0.1	0.00	–	–
MOLLUSCA												
Gastropoda												
Unidentified	–	–	–	–	236.9	3.17	0.2	0.00	8.7	0.09	22.4	0.19
<i>Benthonella tenera</i>	–	–	–	–	–	–	–	–	2.4	0.06	22.4	0.42
<i>Roxania utriculus</i>	–	–	–	–	236.9	5.95	–	–	2.4	0.06	–	–
Bivalvia												
Unidentified	–	–	–	–	–	–	13.5	0.16	–	–	–	–
<i>Yoldiella philippiana</i>	–	–	–	–	–	–	0.1	0.00	117.7	1.27	–	–
<i>Batharca grenophia</i>	–	–	–	–	–	–	0.1	0.00	0.1	0.00	–	–
<i>Batharca philippiana</i>	–	–	–	–	–	–	0.1	0.00	0.1	0.00	–	–
<i>Ledella messanensis</i>	–	–	–	–	–	–	–	–	15.1	0.38	–	–
<i>Nuculoma aegensis</i>	–	–	–	–	–	–	0.1	0.00	0.1	0.00	–	–
<i>Thyasira</i> sp.	–	–	–	–	–	–	–	–	0.4	0.01	–	–
<i>Katadesmia cuneata</i>	–	–	–	–	–	–	0.3	0.01	0.2	0.01	–	–
<i>Malletia cuneata</i>	–	–	–	–	–	–	0.1	0.00	–	–	–	–
Malletidae	–	–	–	–	–	–	0.1	0.00	2.8	0.07	–	–
Bivalve Protobranchia	–	–	–	–	–	–	2.3	0.06	0.7	0.02	–	–
ANNELIDA												
Unidentified	–	–	–	–	–	–	–	–	2.1	0.05	–	–
Polychaeta												
Unidentified	1088.0	16.30	455.9	6.99	1680.9	22.51	1140.8	13.41	1413.4	15.19	4380.3	36.35
	365.9	8.73	44.6	1.14	749.6	18.82	445.2	10.67	761.6	19.09	1151.7	21.51
Aphroditomorpha	190.8	4.55	192.1	4.90	–	–	7.6	0.18	3.5	0.09	–	–
<i>Aglaophanius</i> sp.	–	–	–	–	–	–	–	–	–	–	370.0	6.91
Eunicidae	–	–	–	–	–	–	0.2	0.00	–	–	–	–
Flabelligeridae	–	–	–	–	–	–	0.6	0.01	6.0	0.15	–	210.6
<i>Notomastus</i> sp.	–	–	–	–	–	–	10.4	0.25	2.7	0.07	–	–
Capitellidae	–	–	–	–	–	–	–	–	1.9	0.05	–	–

Table continued on next page

Table 2 (continued)

Dietary items	Chalinura mediterranea		Coryphaenoides guentheri		Coelorthynchus labiatus		Trachyrhynchus trachyrhynchus	
	1425–1800 m Summer (49/40) IRI %IRI	1800–2250 m Summer (114/83) IRI %IRI	Autumn (14/10) IRI %IRI	1425–1800 m Summer (216/189) IRI %IRI	1800–2250 m Summer (264/219) IRI %IRI	1000–1800 m (15/11) IRI %IRI	1000–1425 m (8/5) IRI %IRI	
Polychaeta (continued)								
Pectinariidae	–	–	–	–	–	–	–	–
Terebellidae	–	–	–	–	–	–	–	–
Glycera sp.	–	–	–	–	–	25.4	0.47	–
Hirudinea								
Pontobdellidae	–	–	–	–	–	–	–	–
CRUSTACEA								
Unidentified	411.4	9.81	–	1.5	0.04	–	–	–
Copepoda	1927.6	28.87	242.6	405.7	4.77	2486.1	20.63	3012.7
Unidentified	3.1	0.07	–	0.1	0.00	205.0	3.83	–
Copepod Calanoida	1775.3	42.33	242.6	357.2	8.56	1262.1	23.57	3012.7
Copepod Harpacticoida	–	–	–	1.7	0.04	–	–	–
Ostracoda								
Unidentified	–	–	–	6.4	0.08	–	–	–
Cytheridae	–	–	–	0.1	0.00	–	–	–
Amphipoda	1295.8	1587.3	4149.6	5.2	0.13	–	–	–
Unidentified	–	–	–	1214.6	–	–	–	–
Amph. Gammaridea	1295.8	19.41	1954.7	4175.6	49.08	3327.6	27.61	50.5
Unidentified	138.5	3.30	–	568.8	13.63	508.8	9.50	759.3
<i>Orchomene humilis</i>	–	–	–	–	–	53.6	1.00	53.2
<i>Tryphosites longipes</i>	–	–	–	–	–	–	–	52.3
Lysianassidae	17.6	0.42	25.7	4.2	0.10	–	–	–
<i>Ampelisca</i> sp.	–	–	–	0.1	0.00	–	–	–
<i>Harpinia</i> sp.	1.9	0.04	–	9.0	0.22	–	–	–
<i>Bruzelia typica</i>	–	–	28.2	22.1	0.53	18.1	0.34	–
<i>Pseudotiron bouvieri</i>	8.8	0.21	146.2	828.4	19.85	–	–	–
<i>Nicippe tumida</i>	–	–	319.4	–	–	–	–	–
<i>Idunella pirata</i>	–	–	–	0.3	0.01	–	–	–
<i>Rhachotropis caeca</i>	9.7	0.23	–	–	–	13.0	0.24	–
<i>Rhachotropis</i> sp.	183.0	4.36	92.3	188.9	4.53	593.6	11.09	–
<i>Eusirus longipes</i>	–	–	–	0.6	0.01	16.8	0.31	–
<i>Monoculodes</i> sp.	1.9	0.05	–	0.4	0.01	64.2	1.20	–
<i>Oediceropsis brevicornis</i>	–	–	–	0.2	0.00	–	–	–
<i>Bathymedon</i> sp.	–	–	–	0.5	0.01	–	–	–
Oediceridae	–	–	–	1.7	0.04	–	–	–
<i>Epimeria cornigera</i>	–	–	–	–	–	–	–	–
Amph. Hyperideia	–	–	–	0.1	0.00	–	–	–
Unidentified	–	–	–	0.1	0.00	–	–	–

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Table 2 (continued)

Dietary items	Chalinura mediterranea		Coryphaenoides guentheri		Coelorhynchus labiatus		Trachyrhynchus trachyrhynchus	
	1425–1800 m Summer (49/40) IRI %IRI	1800–2250 m Summer (114/83) IRI %IRI	1425–1800 m Autumn (14/10) IRI %IRI	1800–2250 m Summer (264/219) IRI %IRI	1000–1800 m (15/11) IRI %IRI	1000–1425 m (8/5) IRI %IRI	IRI	%IRI
Isopoda								
Unidentified	187.6	110.7	300.2	415.5	455.0	203.9	2.46	
<i>Gnathia</i> sp.	75.5	19.9	120.6	12.4	14.3	—	—	
Anthuridae	—	0.3	—	0.4	—	52.7	0.76	
<i>Cirolana borealis</i>	—	8.7	—	1.0	—	49.2	0.71	
Cirolanidae	—	—	—	—	63.7	1.19	—	
Arcturidae	—	—	—	—	—	—	—	
<i>Munna</i> sp.	—	—	—	5.5	—	—	—	
<i>Munnopsurus atlanticus</i>	2.4	0.03	—	0.1	—	—	—	
Eurycopidae	—	2.6	—	6.4	—	—	—	
<i>Ilyarachna</i> sp.	—	0.5	—	46.3	—	—	—	
<i>Janirella</i> sp.	18.0	0.43	39.8	0.3	22.8	0.43	—	
Tanaidacea								
Unidentified	7.9	1.2	234.9	22.4	67.3	0.56	—	
Apeudes sp.	1.5	0.04	234.9	0.1	67.3	1.26	—	
<i>Sphyrapus anomalus</i>	—	—	—	0.1	—	—	—	
Apeudidae	2.4	0.06	—	0.3	—	—	—	
Tanaidae	—	—	—	9.9	—	—	—	
<i>Leptognathia</i> sp.	—	1.2	—	2.6	—	—	—	
Cumacea								
Unidentified	—	7.5	346.5	2490.7	59.6	0.49	61.1	0.74
<i>Cyclaspis longicaudata</i>	—	4.8	4.64	948.0	59.6	1.11	—	
<i>Leucon longirostris</i>	—	—	4.44	229.7	—	—	—	
<i>Leucon</i> sp.	—	—	177.1	3.8	—	—	—	
<i>Campylaspis</i> sp.	—	—	—	0.8	—	—	—	
<i>Platysympus typicus</i>	—	0.3	—	0.0	—	—	—	
<i>Platysympus</i> sp.	—	—	27.0	3.9	—	—	—	
<i>Diastylis</i> sp.	—	—	—	9.3	—	—	—	
<i>Makrokylindrus longipes</i>	—	—	—	0.1	—	—	—	
<i>Makrokylindrus</i> sp.	—	—	—	0.1	—	—	—	
Mysidacea								
Unidentified	1526.8	22.87	1016.1	26.5	1047.6	8.69	61.1	0.88
<i>Boreomysis arctica</i>	484.7	11.56	458.0	63.0	425.8	7.95	1175.2	14.18
<i>Boreomysis</i> sp.	265.7	6.34	—	42.9	—	—	208.3	3.02
<i>Erythrops</i> sp.	1.9	0.04	101.3	—	—	—	575.2	8.33
<i>Parapseudomma</i> sp.	2.7	0.06	—	0.3	—	—	—	—
Decapoda								
Unidentified	341.9	1065.9	123.7	0.8	178.9	3.34	—	—
	—	124.6	22.3	0.2	—	—	—	—
	—	3.18	—	0.01	—	—	—	—
	—	—	—	2.6	—	—	—	—
	—	—	—	0.07	—	—	—	—

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Table 2 (continued)

Dietary items	<i>Chalinura mediterranea</i> 1425–1800 m		1800–2250 m		Autumn (14/10)		Summer (216/189)		1800–2250 m Summer (264/219)		<i>Coelothynchus labiatus</i> 1000–1800 m (15/11)		<i>Trachyrhynchus trachyrhynchus</i> 1000–1425 m (8/5)	
	IRI	%IRI	IRI	%IRI	IRI	%IRI	IRI	%IRI	IRI	%IRI	IRI	%IRI	IRI	%IRI
Decapoda (continued)														
Dec. Macrura Natantia	150.8	2.26	345.3	5.30	–	–	39.2	0.46	9.5	0.10	–	–	224.5	2.71
Unidentified	–	–	3.5	0.09	–	–	–	–	–	–	–	–	–	–
Sergestidae	–	–	–	–	–	–	–	–	–	–	–	–	–	–
<i>Pasiphaea multidentata</i>	–	–	–	–	–	–	0.5	0.01	–	–	–	–	–	–
<i>Acanthephyra eximia</i>	–	–	206.9	5.27	–	–	–	–	–	–	–	–	–	–
<i>Acanthephyra</i> sp.	–	–	2.4	0.06	–	–	–	–	–	–	–	–	–	–
<i>Pontophilus norvegicus</i>	150.8	3.60	–	–	–	–	29.3	0.70	9.5	0.24	–	–	–	–
Dec. Macrura Reptantia	–	–	3.7	0.06	–	–	–	–	–	–	–	–	–	–
Unidentified	–	–	3.7	0.09	–	–	–	–	–	–	–	–	–	–
<i>Calocaris macandreae</i>	–	–	–	–	–	–	–	–	–	–	–	–	–	–
Dec. Anomura	77.1	1.16	–	–	–	–	19.0	0.22	–	–	–	–	1109.1	13.38
Unidentified	–	–	–	–	–	–	–	–	–	–	–	–	–	–
Paguridae	–	–	–	–	–	–	–	–	–	–	–	–	–	–
<i>Munida</i> sp.	77.1	1.84	–	–	–	–	19.0	0.45	–	–	–	–	159.7	2.31
ECHINODERMATA														
Ophiuroidea	–	–	–	–	–	–	0.2	0.00	–	–	–	–	–	–
Unidentified	–	–	–	–	–	–	0.2	0.00	–	–	–	–	–	–
TUNICATA														
Ascidiacea	–	–	–	–	–	–	–	–	0.3	0.00	–	–	–	–
Pyrosomida	–	–	–	–	–	–	–	–	0.3	0.01	–	–	–	–
OSTEICHTHYES														
Unidentified	–	–	1.6	0.02	–	–	–	–	–	–	–	–	–	–
Osteich. Crystalline lens	–	–	0.5	0.01	–	–	–	–	–	–	–	–	–	–
Unidentified	–	–	0.3	0.01	–	–	–	–	–	–	–	–	–	–
FISH SCALES														
Unidentified	–	–	–	–	–	–	–	–	0.4	0.01	–	–	–	–
MUD														
Unidentified	–	–	1.5	0.04	–	–	1.4	0.03	–	–	–	–	–	–
UNIDENTIFIED														
Unidentified	–	–	–	–	–	–	0.1	0.00	1.8	0.04	147.3	2.75	227.6	3.30

Table 3. *Chalinura mediterranea*, *Coryphaenoides guentheri*, *Coelorhynchus labiatus* and *Trachyrhynchus trachyrhynchus*. Vacuity percentage, food intensity index, trophic diversity (Shannon index), mean number of prey and mean weight of prey in each bathymetric (D1: 1425 to 1800 m, D2: 1800 to 2250 m) and seasonal group established

	<i>C. mediterranea</i>		<i>C. guentheri</i>			<i>C. labiatus</i>	<i>T. trachyrhynchus</i>
	D1	D2	D1 Autumn	D1 Summer	D2 Summer		
Vacuity percentage (<i>V</i>)	18.37	27.19	28.57	12.50	17.05	26.67	37.50
Food intensity index (<i>K</i>)	0.0728	0.2468	0.0806	0.0926	0.0988	0.1786	0.1491
Trophic diversity (<i>H'</i>)	3.79	4.01	3.43	4.48	4.87	3.88	3.05
Mean number of prey (<i>Np</i>)	4.22	5.17	4.10	5.13	5.82	6.82	8.20
Mean weight (g) of prey (<i>Wp</i>)	0.0100	0.0246	0.0078	0.0069	0.0067	0.0193	0.0913

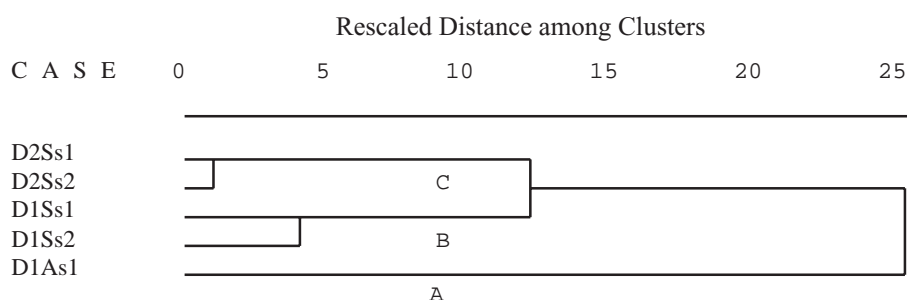


Fig. 2. *Coryphaenoides guentheri*. Dendrogram of dissimilarity between diets of different groups (bathymetric, seasonal and ontogenic). D2Ss1: immature (Size 1) summer individuals from 1800 to 2250 m depth; D2Ss2: mature (Size 2) summer individuals from 1800 to 2250 m depth. D1Ss1: immature (Size 1) summer individuals from 1425 to 1800 m depth; D1Ss2: mature (Size 2) summer individuals from 1425 to 1800 m depth; D1As1: immature (Size 1) autumn individuals from 1425 to 1800 m depth; groups identified: A = D1As1; B = D1Ss1 and D1Ss2, C = D2Ss1 and D2Ss2

Group A, 1425 to 1800 m in autumn: The high percentage of everted stomachs (65 %) and vacuity ($V = 28.57\%$) precludes conclusions. In 10 specimens with food, gammarid amphipods (%IRI = 26.18) and polychaetes (%IRI = 22.51) were the dominant prey (Table 2), the polychaetes being the heaviest (% $W = 32.30$; Fig. 3). The importance of amphipods was due to the combination of frequency and abundance of species such as *Pseudotiron bouvieri*, *Bruzelia typica* and *Rhachotropis* sp. Foraminifera and mysids were secondary groups, and the rest were accidental items.

Group B, 1425 to 1800 m in summer: In 189 specimens analysed the most important prey-group was gammarid amphipods. Their high frequency (% $F = 74.60$) and abundance (% $N = 30.30$; Fig. 3) resulted in a %IRI of 49.08, the amphipod *Pseudotiron bouvieri* being the first preferred prey-item (%IRI = 19.85; Table 2). Cumaceans and polychaetes were secondary prey, while mysids were the major accidental prey (%IRI = 9.24).

Group C, 1800 to 2250 m: Similar to Group B, gammarid amphipods predominated in the 219 specimens analysed (%IRI = 44.11), but the primary amphipod species was *Rhachotropis* sp. (%IRI = 12.81), while cumaceans were secondary (%IRI = 26.77). Poly-

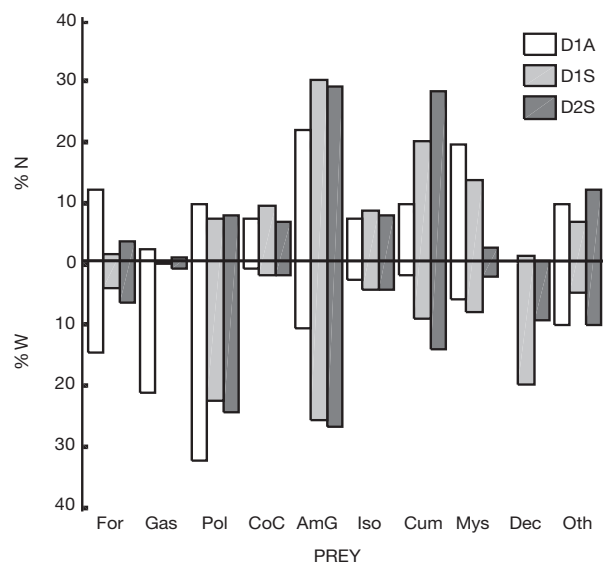


Fig. 3. *Coryphaenoides guentheri*. Percentage by number (% N) and by weight (% W) of prey species in the diet of autumn individuals from 1425 to 1800 m depth (D1A) summer individuals from 1425 to 1800 m depth (D1S), and summer individuals from 1800 to 2250 m depth (D2S). For: Foraminifera; Gas: Gastropoda; Pol: Polychaeta; CoC: copepod Calanoida; AmG: amphipod Gammaridea; Iso: Isopoda; Cum: Cumacea; Mys: Mysidacea; Dec: Decapoda; Oth: others

chaetes were the major accidental prey (%IRI = 15.19) because of their high weight (Fig. 3).

In terms of different seasons and depths, no significant differences were found in any of the indices analysed: vacuity coefficient ($p > 0.05$, χ^2 criterion), food intensity index K (ANOVA, $p > 0.05$), average number of prey per stomach (N_p) and average weight of prey per stomach (W_p) (both ANOVA with $p > 0.05$) (Table 3).

Trophic diversity (H' : Table 3) was lowest at depths of 1425 to 1800 m in autumn and higher at 1800 to 2250 m in summer. Dietary overlap was high (overlap, Schoener index = 0.708) among groups from 1425 to 1800 m and 1800 to 2250 m in summer. Affinity between the diets of summer and autumn specimens at all depths was low (Schoener_{autumn 1425–1800 m with summer 1425–1800 m} = 0.469; Schoener_{autumn 1425–1800 m with summer 1800–2250 m} = 0.425).

Coelorhynchus labiatus

Only 11 stomachs of *Coelorhynchus labiatus* with food were analysed, due to the high number of everted and empty stomachs (32 of 43 specimens). Polychaetes and gammarid amphipods were the dominant prey, while copepods were secondary prey. Polychaetes were the most weighted prey-group (% W = 59.5), and, in spite of their low abundance (% N = 9.33), they were the primary preferred prey-group (%IRI = 36.35) (Table 2). Gammarid amphipods were the most abundant prey-group (% N = 30.67). The contribution of the remaining prey was accidental (%IRI < 9). *C. labiatus* contained a large number of prey items per stomach (N_p = 6.82), with an average weight per stomach of 0.0193 g (Table 3).

Trachyrhynchus trachyrhynchus

The diet of *Trachyrhynchus trachyrhynchus* at depths between 1000 and 1425 m in the Mediterranean are analysed here for the first time. The high number of everted stomachs, caused by the expansion of the swimbladder during ascent to the surface (141 of the 149 specimens analysed) hinders conclusions regarding the food and feeding habits of this species on the middle slope (under 1000 m depth). Of the 8 stomachs not everted and analysed, only 5 contained food; a total of 41 prey items was found, corresponding to 19 categories of prey items (Table 2). Calanoid copepods were the most abundant (15 individuals) and frequently captured (in 4 stomachs) item, and *Calocaris macandreae* was the heaviest prey (% W = 53.01). Other relatively abundant prey were mysids (4 *Bore-*

omysis arctica), gammarid amphipods (3 Lyssianasidae and 1 *Orchomene humilis*) and polychaetes (2 Flabelligeridae). The mean number of prey per stomach was very high (N_p = 8.2: Table 3).

DISCUSSION

The macrourids analysed had a relatively broad diet ($H' = 3.05$ to 4.90), the most euryphagous being *Coryphaenoides guentheri* and the least being *Trachyrhynchus trachyrhynchus*.

Chalinura mediterranea, *Coelorhynchus labiatus* and *Trachyrhynchus trachyrhynchus* in the Mediterranean have a benthopelagic diet, whilst *Coryphaenoides guentheri* has a benthic diet. In this study, the diet of *Coelorhynchus labiatus* (which, according to Cohen et al. 1990, replaces *Coelorhynchus occa* in the eastern Atlantic) has been analysed for the first time in the Mediterranean. Although the number of specimens was not very large, it is clear that *C. labiatus* feed on benthopelagic prey, with a slight preference for bathybenthic prey (polychaetes, gammaridean amphipods). *Chalinura mediterranea* and *T. trachyrhynchus*, also benthopelagic, have a slight preference for bathypelagic prey (calanoid copepods and mysids in both species and natantian decapods in *C. mediterranea*) over benthic prey (amphipods, polychaetes). In 1 specimen of *C. mediterranea*, Geistdoerfer (1978) in the Mediterranean also observed that it consumes copepods, isopods and decapods. On the other hand, *Coryphaenoides guentheri* in the NW Mediterranean is primarily a benthic feeder, consuming mainly gammaridean amphipods and cumaceans, supplemented by polychaetes and a wide variety of other organisms such as isopods, copepods and mysids. The only specimen analysed in the Mediterranean contained an isopod and a mysid (Geistdoerfer 1978).

The different diets of 1425 to 1800 m and 1800 to 2250 m specimens of *Chalinura mediterranea* and of summer and autumn specimens of *Coryphaenoides guentheri* may be the consequence of a change in available resources. This is the case for *Boreomysis arctica* (Cartes & Sorbe 1995), *Acanthephira eximia* (Cartes & Sardà 1992) and *Platysympus typicus* (Cartes & Sorbe 1997), which are most abundant at great depths (1800 to 2250 m), and for *Pontophilus norvegicus*, which is most abundant at 1000 to 1700 m (Cartes & Sardà 1992), coinciding with that observed in the diet of *Chalinura mediterranea*. Our preliminary observations of the diet of autumn specimens of *Coryphaenoides guentheri* are not conclusive because of the limited number of specimens that could be analysed. Nevertheless, our data suggest a difference

in the prey consumed in autumn and summer (Schoener index = 0.42 to 0.47), with polychaetes, which are secondary prey in summer, becoming the principal prey in autumn and the mysids undergoing an important recruitment in late autumn (Cartes 1998). This seasonal fluctuation in the feeding pattern of *Coryphaenoides guentheri* offers a plausible hypothesis to explain growth seasonality, which is well documented by the periodicity of otolith ring formation (Morales-Nin 1990, Massutí et al. 1995) in fish species of the deep Mediterranean, where temperature and salinity cannot be causative factors because they are fairly constant below 150 to 200 m. The bathymetric differences in the diet of summer specimens of *Coryphaenoides guentheri* and in the diet of *Chalinura mediterranea* are also marked by greater vacuity, a greater consumption of prey, and a greater diversity at 1800 to 2250 m than at 1425 to 1800 m. The scarcity of resources, which decrease steadily below 1200 to 1400 m (Cartes & Sorbe 1993, Cartes 1998), may force these species to diversify their diet at 1800 to 2250 m, extending it to include other prey such as ostracods, cumaceans or decapod macrurans. Decreasing specialization with increasing depth, as observed in the macrourids analysed, enables deep-sea predators to be more adaptable (Dayton & Hessler 1972).

Trachyrhynchus trachyrhynchus, which occurs in this region at depths of 200 to 1589 m (Macpherson 1979, Stefanescu et al. 1992a, Massutí et al. 1995), also seems to exhibit bathymetric changes in its diet. At 200 to 800 m depth *T. trachyrhynchus* is stenophagous, tending to feed on infauna (Macpherson 1979); however, below a depth of 1000 m, despite the few specimens examined, a benthopelagic diet emerged with a slight preference for bathypelagic (copepods and mysids) over benthic prey.

The differences in the feeding habits of the Mediterranean and Atlantic fish populations, which have already been observed in other species in the same zone, such as *Centroscymnus coelolepis* (Carrassón et al. 1992) and *Alepocephalus rostratus* (Carrassón & Matallanas 1998), were also observed in the 4 macrourids analysed in the present study. These differences are as apparent in the prey-species consumed as in the type of prey-species or in the feeding intensity and alimentary diversity. Thus, Atlantic *Chalinura mediterranea*, which also has a benthopelagic diet (Mauchline & Gordon 1984a), consumes copepods with greater frequency (%N between 45.4 and 61.2) than Mediterranean individuals (maximum %N 31.6 at 1425 to 1800 m depth). The co-dominance of copepods, amphipods and mysids on a weight basis observed in the diet of Atlantic specimens, is not observed in Mediterranean specimens, for which amphipods constitute the secondary prey. However, certain prey

(euphausiids, cephalopods and chaetognaths) occur in Atlantic specimens (Marshall & Merrett 1977, Mauchline & Gordon 1984a, Gordon & Duncan 1987) but not in Mediterranean specimens, and vice versa, e.g. foraminiferans, ostracods and tanaidaceans, are found in Mediterranean but not in Atlantic specimens.

In the case of *Coryphaenoides guentheri*, differences between the Mediterranean and Atlantic populations, are clearer, since in Atlantic waters it is a benthopelagic feeder (Mauchline & Gordon 1984a, Gordon & Duncan 1987), including epibenthic components in its diet and also sediment (Mauchline & Gordon 1984b), whereas in Mediterranean waters it is primarily a benthic feeder. The copepods and amphipods that dominate the diet of specimens from the 1000 to 2500 m depth range (Mauchline & Gordon 1984a) and from the 2200 to 2900 m depth range (Gordon & Duncan 1987) in the Atlantic are totally accidental in the diet of specimens in the Mediterranean. On the other hand, in spite of a slight increase in the size of the prey with increasing predator size, in the Mediterranean specimens of *Coryphaenoides guentheri* the bathymetric dietary differences found were clearer than ontogenic differences (Fig. 2). Thus, a relative increase in the importance of cumaceans occurred in specimens at 1800 to 2250 m (D2) compared to specimens at 1425 to 1800 m (D1). The overlap in the Schoener index among the prey-species consumed indicates that these differences are greater among the autumn D1 and D2 individuals than among D1 and D2 individuals at summer. In Atlantic specimens of *Coryphaenoides guentheri*, Mauchline & Gordon (1984a) found important ontogenic differences in small-sized individuals, which live only between 1000 and 1250 m, compared with the remaining size-groups. The lack of differences between small and large Mediterranean species (Fig. 2) could indicate that the Atlantic results are related to the bigger-deeper trend displayed by *Coryphaenoides guentheri* (as by *Coelorhynchus labiatus* and *Chalinura mediterranea*) in North Atlantic waters (Mauchline & Gordon 1984a, Gordon & Duncan 1987, Merrett et al. 1991), which does not occur in Mediterranean specimens. Thus, in addition to (as indicated by Mauchline & Gordon 1984a) being a direct result of the smaller size of the fish and their selection of smaller sized prey organisms, these ontogenic differences would be the result of bathymetric differences in the prey availability in relation to the predator. None of the exclusively lower-slope species in the Western Mediterranean (among them, *Coryphaenoides guentheri* and *Chalinura mediterranea*) showed any significant size-depth variation or trend (Stefanescu et al. 1992b), and in Mediterranean waters the bathymetric differences in diet of these 2 macrourids may mainly reflect a change in prey availability.

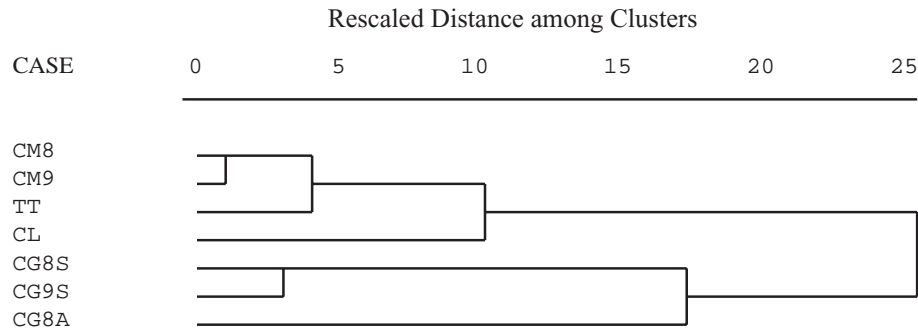


Fig. 4. Dendrogram of dissimilarity between diets of different groups (bathymetric, seasonal and ontogenic) of macrourids analysed. CM8: *Chalinura mediterranea* from 1425 to 1800 m depth; CM9: *Chalinura mediterranea* from 1800 to 2250 m depth; TT: *Trachyrhynchus trachyrhynchus*; CL: *Coelorhynchus labiatus*; CG8S: summer individuals of *Coryphaenoides guentheri* from 1425 to 1800 m depth; CG9S: summer individuals of *Coryphaenoides guentheri* from 1800 to 2250 m depth; CG8A: autumn individuals of *Coryphaenoides guentheri* from 1425 to 1800 m depth

Coelorhynchus labiatus in the Atlantic consumes copepods, decapods, polychaetes, amphipods, isopods and fishes (Marshall & Iwamoto 1973, Marshall & Merrett 1977, du Buit 1978), preferring bathypelagic prey such as copepods (Mauchline & Gordon 1984a), with bathybenthic prey being only occasional (polychaetes: %N = 6%; amphipods: %N = 8%). However, in the Mediterranean populations, bathybenthic prey are the main prey.

The feeding habits of *Trachyrhynchus trachyrhynchus* in the Atlantic vary regionally and, as with the Mediterranean population, in the SE Atlantic large individuals also feed mainly on bathypelagic prey, with small individuals feeding more on bathybenthic organisms (Macpherson 1983), whilst those in the NE Atlantic have a mixed diet, pelagic and benthic (Marshall & Merrett 1977, McLellan 1977, Geistdoerfer 1978, Hureau et al. 1979, Merrett & Marshall 1981).

The significantly smaller size of Mediterranean populations of *Chalinura mediterranea* and *Coryphaenoides guentheri* compared to Atlantic populations (Geistdoerfer 1986) (340 and 730 mm TL for *Chalinura mediterranea*, and 220 and 480 mm TL for *Coryphaenoides guentheri*) and of *Coelorhynchus labiatus* (244 mm TL in Mediterranean specimens, 380 mm TL in Atlantic specimens: Mauchline & Gordon 1984a) provides further proof of the adaptation of the Mediterranean populations to a poorer environment. The Mediterranean is an environment which, below 1000 m depth, becomes progressively more trophically restrictive; increasing oligotrophy with increasing depth is reflected by an important drop in macrofaunal and megafaunal biomass between 1000 and 2250 m (Stefanescu et al. 1992b, Sardà & Cartes 1993, Cartes 1998).

Macpherson (1979) showed that rates of competitive exclusion were low among 4 species of macrourids on the upper-middle slope (200 to 800 m) of the Mediterranean, and stated that macrourids, in general, have

narrow diets, exhibiting some specialisation. The present study makes it clear that in the middle-lower slope (below 1000 m) this strategy changes with the macrourids becoming euryphagic predators, with a wide variety of prey.

Dendrogram of dissimilarity between diets of all macrourids analysed below 1000 m depth are shown in Fig. 4. The apparent similarity between the diets of *Chalinura mediterranea* and *Trachyrhynchus trachyrhynchus* could explain the bathymetric segregation of their respective niches. Their habitat widths do not overlap in this depth zone (Stefanescu et al. 1992a). On the other hand, *Coryphaenoides guentheri* and *Chalinura mediterranea*, which coexist from 1308 to 2250 m, showing an almost total overlap of their respective space niches (Stefanescu et al. 1992a), have marked differences in their diets, one feeding on benthic prey and the other preferentially on bathypelagic prey. Finally, *Coelorhynchus labiatus* has a dietary overlap intermediate to those of the other 3 species of macrourids, as visible from Fig. 4, which shows that its diet is different from that of the bathypelagic feeders associated with it. Their habitat width is 1200 to 1700 m in the Western Mediterranean (Stefanescu et al. 1992a), i.e. in the depth zone where the dominant medium-sized macrourid species *T. trachyrhynchus* is replaced by smaller species (*Chalinura mediterranea* and *Coryphaenoides guentheri*). Similar to macrourids of the NE Atlantic (Mauchline & Gordon 1984a), all Mediterranean macrourids are generalist feeders, and ecological separation is maintained by a combination of differential depth distribution and feeding habits.

A detailed examination of resources among macrourids has been described in this paper; however, this is of limited value unless considered within the context of the fish associations of the region as a whole. This will be attempted for the Catalan Sea (Western Mediterranean) in a later paper.

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