

# Partitioning of space and food resources by three fish of the genus *Diplodus* (Sparidae) in a Mediterranean rocky infralittoral ecosystem

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**ABSTRACT:** White sea bream *Diplodus sargus*, two-banded sea bream *D. vulgaris* and sharpnose sea bream *D. puntazzo* coexist in Mediterranean infralittoral rocky habitats. Diets of the 3 species were quantitatively analysed, and the relative abundance of algae found in stomach contents was compared with the abundance of algae in the different habitats. These results were compared with observational studies on distribution and feeding use of the habitats. The results suggest that there was marked resource partitioning between the 3 species of *Diplodus* in the rocky infralittoral. *D. sargus* mainly exploited the surge zone, while *D. puntazzo* and *D. vulgaris* preferentially exploited deeper waters. Diet analysis suggested a strong feeding niche overlap between *D. sargus* and *D. vulgaris*, although they fed in different habitats, except small individuals (total length <13 cm) of both species, which shared the same resources. *D. vulgaris* and *D. puntazzo* showed strong habitat overlap, although they exploited different food resources. *D. sargus* and *D. puntazzo* showed low spatial and feeding-niche overlap. Habitat partitioning appeared to be as important as food partitioning in structuring *Diplodus* assemblages.

**KEY WORDS:** Resource partitioning · Littoral fish · Infralittoral habitats · *Diplodus* · Mediterranean

## INTRODUCTION

The coexistence of similar species within the same ecosystem may occur owing to different resource use. Resource partitioning includes food, habitat and/or time segregation (e.g. Pianka 1973, Schoener 1974), and has been extensively documented among fishes in temperate rocky reefs (e.g. Love & Ebeling 1978, Hixon 1980, Larson 1980, Yoshiyama 1980, Hallacher & Roberts 1985, Ebeling & Laur 1986, Holbrook & Schmitt 1986). Food segregation seems to play a more important role than habitat or temporal separations within many fish assemblages (Ross 1986). Resource partitioning in fish has received little attention in the Mediterranean (Macpherson 1981, Rosecchi 1985, Harmelin-Vivien et al. 1989), and few studies have

been carried out in the rocky infralittoral dealing exclusively with small-sized fishes (Zander 1982, Macpherson 1994).

In NW Mediterranean waters, several species of Sparidae, mainly of the genus *Diplodus*, dominate fish assemblages in shallow rocky infralittoral habitats. The fishes *Diplodus sargus* (L.), *Diplodus vulgaris* E.G. Saint-Hilaire and *Diplodus puntazzo* (Cetti) are found in the rocky infralittoral. Both *D. sargus* and *D. vulgaris* contribute greatly to the total fish abundance (up to 56%; García-Rubies 1997). Because the 3 species of *Diplodus* are (1) taxonomically related, (2) necto-benthic species (sensu Harmelin 1987), (3) markedly benthophagous (Rosecchi 1985, Bell & Harmelin-Vivien 1983, Sala 1996), and (4) usually found within a small bathymetric range (García-Rubies 1997), one might presume they are potential competitors for space and food resources.

Fish of the genus *Diplodus* are omnivorous (Joubert & Hanekom 1980, Coetzee 1986, Mann & Buxton 1992),

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and the amount of algae found in the stomachs of fishes from the 3 species may be considerable (Sala 1996). Regardless of whether algal consumption is voluntary or the digestion of plant material is low (Joubert & Hanekom 1980), *Diplodus* species ingest a considerable amount of algae when foraging on benthic communities (Sala 1996). Algal communities show marked zonation patterns in the Mediterranean (Feldmann 1937, Ballesteros 1992), and each community is found within a relatively narrow range of environmental conditions (chiefly light and water motion). Since some algal species are restricted to or grow preferentially in certain communities, they may be good indicators of the habitat in which fish species feed.

In this study we examined patterns of habitat and food utilization shown by the 3 species of Sparidae mentioned above, which are common inhabitants of rocky infralittoral bottoms of the Medes Islands Marine Reserve (NW Mediterranean). We analysed the diets of the 3 species, and compared the abundance of algae in stomach contents with the abundance of algae in the field. We also recorded the distribution and habitat use of these fishes, and compared the results obtained from the assessment of resource partitioning made by stomach content analysis.

#### STUDY SITE AND SPECIES

The study was carried out in the Medes Islands Marine Reserve, in NE Spain. The Marine Reserve, where fishing is prohibited, is located 1 km offshore opposite the town of L'Estartit (42° 16' N, 03° 13' E), has an area of 93 ha, and encompasses a group of a few small islands (surface area less than 20 ha).

Sampling sites were characterized by bottoms of large limestone boulders, with a profusion of holes and crevices that provide refuge for fishes. At these sites, rocky substrata are covered by numerous species of

alga and high densities of small invertebrates (both sessile and mobile; Ros et al. 1984).

The white sea bream *Diplodus sargus* is abundant in the Mediterranean (Tortonese 1975), occurring also along all the coast of Africa. It inhabits rocky bottoms and *Posidonia oceanica* beds, from the surface to a depth of 50 m (Corbera et al. 1996). In common with most Sparidae, *D. sargus* is very active, and frequents the surge zone, primarily at dawn. The two-banded sea bream *Diplodus vulgaris* is present throughout the Mediterranean basin (Tortonese 1975), on the Atlantic coast of the Iberian Peninsula, and on the West African coast down to Angola (De La Paz 1975). *D. vulgaris* is abundant over infralittoral rocky bottoms (from the surface to 30 m) but often forms schools of up to 100 individuals which remain at a fixed position in the water column (Corbera et al. 1996). The sharpnose sea bream *Diplodus puntazzo* is frequent throughout the Mediterranean, occurring also in the tropical Atlantic and off the north coast of Spain (Bauchot & Pras 1980). Generally a solitary fish, *D. puntazzo* frequents rocky bottoms down to 50 m.

#### METHODS

Five distinct habitats, which together occupy almost all the substrate from the surface to -15 m, and where fishes have always been seen foraging, were investigated (Fig. 1). These were: (1) surge zone (hereafter referred to as SZ), (2) shallow vertical walls (SW), (3) photophilic plain (PP), (4) hemisciaphilic plain (HP), and (5) sciaphilic walls (ScW); their characteristics are summarized in Table 1.

Fish distribution was determined by visual census using the stationary point method (Harmelin-Vivien et al. 1985). The observer remained stationary on the bottom at a random location and recorded the number and sizes of all fishes of the 3 species in a radius of 7 m,

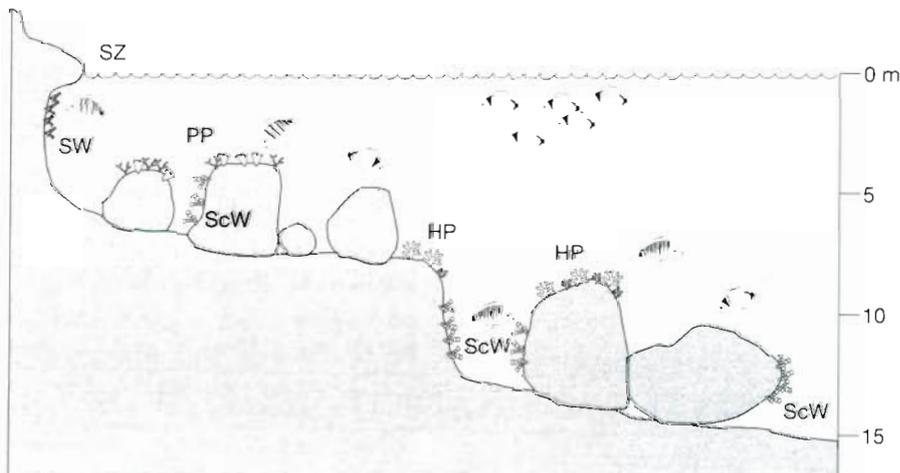


Fig. 1. Schematic representation of the Medes Islands rocky infralittoral habitats. SZ: surge zone; SW: shallow walls; PP: photophilic plain; HP: hemisciaphilic plain; ScW: sciaphilic walls. See Table 1 for a description of habitat characteristics

Table 1. Characteristics of habitats investigated in this study

Habitat	Depth interval (m)	Habitat characteristics
Surge zone (SZ)	+0.5, -0.5	Wave-splashed zone; mussel <i>Mytilus galloprovinciale</i> beds, belt of brown alga <i>Cystoseira mediterranea</i> , and rim of the Corallinaceae <i>Lithophyllum lichenoides</i> , with high microspatial complexity
Shallow walls (SW)	-0.5, -2.0	Vertical walls with dominance of small red algae (community of <i>Plocamium cartilagineum</i> ) and barnacles ( <i>Balanus perforatus</i> ); low spatial complexity
Photophilic plain (PP)	-3.0, -7.0	Plain or upper side of big boulders with dominance of photophilic algae ( <i>Dictyota fasciola</i> , <i>Padina pavonica</i> , <i>Halopteris scoparia</i> , <i>Corallina elongata</i> )
Hemisciaphilic plain (HP)	-9.0, -12.0	Plain or upper side of deeper big boulders with dominance of hemisciaphilic algae ( <i>Codium vermilara</i> , <i>Dictyota dichotoma</i> , <i>Rhodymenia ardissoni</i> , <i>Peyssonnelia</i> spp.)
Sciaphilic walls (ScW)	Below -6.0	Vertical walls, deep or in the north-oriented sides of shallow big boulders, with dominance of sciaphilic algae ( <i>Flabellia petiolata</i> , <i>Halimeda tuna</i> , <i>Peyssonnelia</i> sp. plur.) and suspension-feeders (sponges and soft corals)

within the first minute. Twenty stationary point replicates were carried out for each of 3 depth-defined zones: surge zone (between +0.5 m and -0.5 m), shallow zone (between -2 m and -7 m; including SW and PP), and deep zone (between -9 m and -15 m; including HP and ScW) in summer 1996. Individual sizes were recorded in 3 discrete classes. These classes encompassed one-third of the maximum total length of each species recorded in the literature (Corbera et al. 1996). Therefore, size classes were (total length): small (<13 cm), medium (13–26 cm), and large (>26 cm). The determination of fish size near the limits of size classes implied a certain degree of subjectivity, especially when fish were several meters away from the observers. Thus, the inclusion of individuals into size classes was subjected to unknown error. To test differences in density between habitats, individual 1-way ANOVAs were performed for each fish species. When the analysis of variance showed significant differences, a Tukey HSD test was used.

In order to determine habitat use, feeding was observed in summer 1996 by SCUBA diving. Square (2 m × 2 m) quadrats (for SW, PP, HP and ScW), and 1 m × 4 m rectangles (for SZ) were placed on the substrate. Feeding use was recorded as individual bites within the quadrats. Bites and size of each individual of the 3 species were recorded over 15 min intervals. We counted 3 quadrats per habitat, and 3 replicates per quadrat. To test differences in feeding rate between habitats, individual 1-way ANOVA were performed for each fish species. When the analysis of variance showed significant differences, a Tukey HSD test was used.

To determine feeding habits of the 3 species, fish were speared at several sites within the Marine Reserve in April, May, August and November 1992, and in February 1993. All collections were made between 7:00 and 11:00 h. This time period yielded the

maximum amount of identifiable gut contents, since fish start feeding after sunrise. Fish were conserved in a portable fridge and then transported to the laboratory. Total and gutted mass (g) and total length (mm) were measured for each fish sampled. Stomachs, removed by severing the oesophagus near the buccal cavity and the intestine just anterior to the pyloric caecae, were preserved in a neutral 10% formalin solution within 4 h of spearing.

Stomach contents were carefully sorted and their contents were quantified following the method described by Harmelin-Vivien (1979). Food items were identified to the lowest possible taxon and then weighed. For each stomach, the cover of each algal taxon (in cm<sup>2</sup>) was determined on a reticulated field, and the relative cover of each algal species calculated. The rate of feeding activity was measured by an activity index (AC), which is the percentage of stomachs containing food with respect to the total number of stomachs examined. The AC varies from 0 (no feeding activity) to 100 (all individuals with food). Several coefficients were calculated to determine the importance of prey in the diet. The occurrence index (*F*) is the percentage of non-empty stomachs that contained a particular prey item. Percentages by weight of prey (*W*) were calculated as the ratio of the weight of a prey category (*W<sub>i</sub>*) to the total weight of the stomach content (*W<sub>T</sub>*):  $W = W_i / W_T \times 100$ . In order not to overemphasize the importance of occasional large prey, a ranking index (*K*), modified from Hobson (1974), was computed by multiplying the occurrence index (*F*) by weight of a prey ( $K = F \times W / 100$ ).

To test whether algal species were similarly present in the diets of the 3 species of *Diplodus*, individual ANOVAs were used. Some species of algae were rare, or of marginal importance, in the diet. Therefore we analysed those algal species that represented a mean cover >1% for at least one fish species. When the

analysis of variance showed significant differences, a Tukey HSD for unequal  $N$  (Spjøtvoll/Stoline) test was used.

Resource use overlaps between the 3 species were calculated on the basis of prey types, habitat distribution and habitat use (feeding use). To assess the degree of overlap in use of food between the 3 species the Schoener's index ( $T$ ) was used as follows:

$$T = 1 - 0.5 \sum |px_{fi} - py_{fi}|$$

where  $px_{fi}$  and  $py_{fi}$  are the proportions by weight in stomachs of the resource  $fi$  (prey category) for all fish species pairs  $x, y$ . Habitat overlaps from (1) species distribution and (2) habitat (feeding) use were determined as:

$$\alpha_H = 1 - 0.5 \sum |px_{hi} - py_{hi}|$$

where  $px_{hi}$  and  $py_{hi}$  are (1) the proportions of abundance (from visual census) in the habitat  $hi$  for all fish species pairs  $x, y$ ; or (2) the proportions of habitat use (from feeding observations) of the microhabitat  $hi$  for all species (or size) pairs  $x, y$ . These overlap indexes vary from 0, when the 2 species use totally different resources, to 1, when they use the same prey categories in the same proportions. An overlap equal to or above 0.6 was considered significant, following Keast (1978).

The distribution of algal species over the 5 habitats was quantitatively studied by means of 25 cm × 25 cm quadrats, divided in 25 subquadrats of 5 cm × 5 cm. Six quadrats were positioned within each of the 5 habitats. The percentage of subquadrats in which a species appeared was recorded and used as the unit of measure. A highly abundant species that appeared in all 25 subquadrats would produce a presence of 100%, whereas the total lack of a species would produce a presence of 0%. Presence of a species in each habitat was then calculated as the mean of the percentage presence values of the 6 quadrats sampled in the habitat. Field visual methods did not allow identification of the smallest algal species in the Medes Islands, which exhibit a very intricate complex formed by several species of small filamentous algae. Hence, these species were pooled in a single group, called 'turf algae complex', during visual estimations. Subsequently, a semi-quantitative sampling of this complex was carried out for each of the 6 quadrats in each habitat. Each sample was carefully sorted in the laboratory, and all algal species were determined. The presence of a species in a habitat was then calculated as the percentage of quadrats in which this species was present.

In order to correlate the abundance of algae in fish stomach contents with the distribution of algae among the 5 habitats, individual non-parametric correlations on untransformed data were carried out between the

abundance (percentage presence) of algae for each habitat and the relative cover of algae found in stomach contents for each fish species. We assume that highest correlation coefficients will indicate the habitat in which fish are eating most.

## RESULTS

All fish species were found within all depth zones, except *Diplodus vulgaris*, which was not found in the surge zone (Fig. 2). *D. sargus* was found at higher abundance in the surge zone (average of 389 ind. 150 m<sup>-2</sup>), and its density significantly decreased with depth (1-way ANOVA,  $F = 50.97$ ,  $df = 2$ ,  $p < 0.001$ ; Tukey HSD test,  $p < 0.001$ ). The density of *D. vulgaris* significantly increased with depth (1-way ANOVA,  $F = 4.05$ ,  $df = 2$ ,  $p < 0.05$ ), reaching maximum average densities of 18.7 ind. 150 m<sup>-2</sup> in the deep zone (Tukey HSD test,  $p < 0.05$ ). Although more abundant in deep waters (4.1 ind. 150 m<sup>-2</sup>), *D. puntazzo* did not show significant differences in density between zones (1-way ANOVA,  $F = 1.97$ ,  $df = 2$ ,  $p = 0.12$ ). Habitat (spatial distribution) overlap ( $\alpha_H$ ) was high and significant only between *D. vulgaris* and *D. puntazzo* ( $\alpha_H = 0.82$ ), the other combinations of species pairs returned values  $< 0.6$ .

The 3 species exhibited different uses of the habitats (Fig. 3). *Diplodus sargus* fed more intensely in the surge zone (~147 bites 15 min<sup>-1</sup> 4 m<sup>-2</sup>), and its feeding rate decreased from photophilic to hemisciaphilic to sciaphilic habitats (1-way ANOVA,  $F = 10.66$ ,  $df = 4$ ,  $p < 0.001$ ; Tukey HSD test,  $p < 0.001$ ). *D. vulgaris* was not found feeding in the surge zone, and its maximum feeding rate (79.4 bites 15 min<sup>-1</sup> 4 m<sup>-2</sup>), in the hemisciaphilic plain, was significantly higher than its feeding rate in the other habitats (1-way ANOVA,  $F = 4.31$ ,  $df = 4$ ,  $p < 0.01$ ; Tukey HSD test,  $p < 0.05$ ). *D. puntazzo*

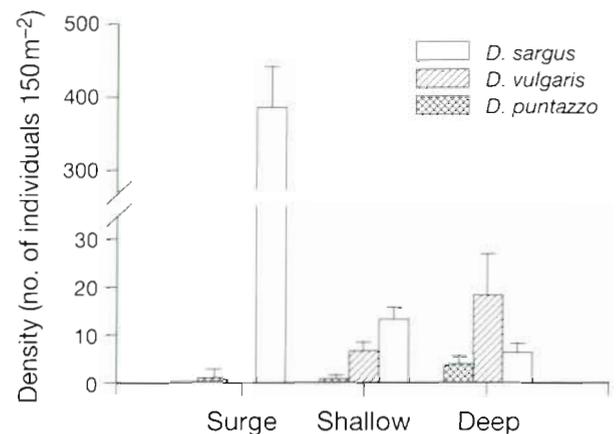


Fig. 2. *Diplodus* spp. Densities (mean ± SE) of the 3 species at each of the 3 depth-defined zones considered

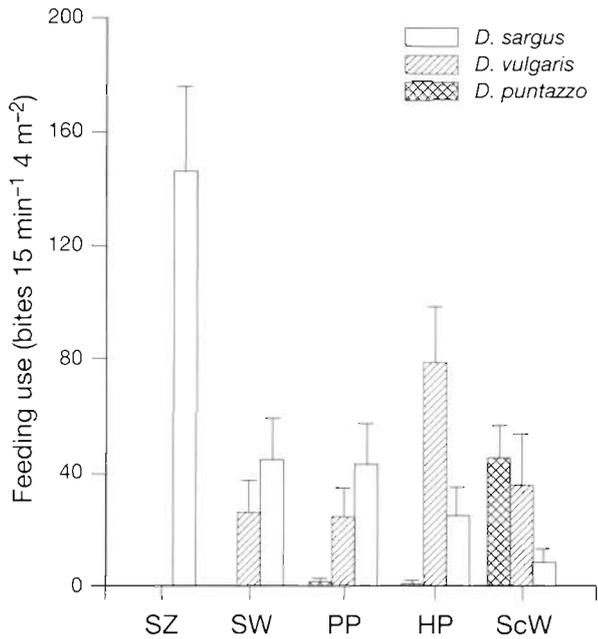


Fig. 3. *Diplodus* spp. Habitat use (feeding rate; mean  $\pm$  SE) for the 3 species in the Medes Islands rocky infralittoral. SZ: surge zone; SW: shallow walls; PP: photophilic plain; HP: hemisciaphilic plain; ScW: sciaphilic walls

was the species with the most restricted feeding: it used only 3 of the 5 habitats investigated in this study (PP, HP and ScW), and its maximum feeding rate was on the sciaphilic walls (45.7 bites  $15 \text{ min}^{-1} 4 \text{ m}^{-2}$ ), which was significantly higher than its feeding rates in the other habitats (1-way ANOVA,  $F = 15.54$ ,  $df = 4$ ,  $p < 0.001$ ; Tukey HSD test,  $p < 0.001$ ). The use of habitats as a function of size is shown in Fig. 4. *D. sargus* exhibited an increase in feeding rate for medium and large individuals in SZ, whereas small individuals fed more intensely in SW and PP. Small and medium *D. vulgaris* fed mostly in HP, whereas large individuals fed only in ScW. Medium and large *D. puntazzo* fed mostly in ScW. We did not find any small *D. puntazzo*.

There was no intraspecific habitat (feeding use) overlap ( $\alpha_H$ ) for size classes within any species, and there was strong interspecific overlap in only 2 cases: (1) between small *Diplodus sargus* and *D. vulgaris* ( $\alpha_H = 0.80$ ), and (2) between medium *D. puntazzo* and large *D. vulgaris* ( $\alpha_H = 0.99$ ).

The diets of 78 individuals of *Diplodus sargus* were examined, and 69 of these, ranging from 70 to 400 mm length (mean = 246 mm), contained food (Table 2). *D. sargus* was clearly omnivorous, with bivalves (mainly *Mytilus galloprovincialis*) representing the most important prey type (following ranking index), followed by algae, sea urchins, and barnacles. However, benthic algae were the most frequently found item in the stomachs of *D. sargus* ( $F = 44\%$ ). Polychaetes, deca-

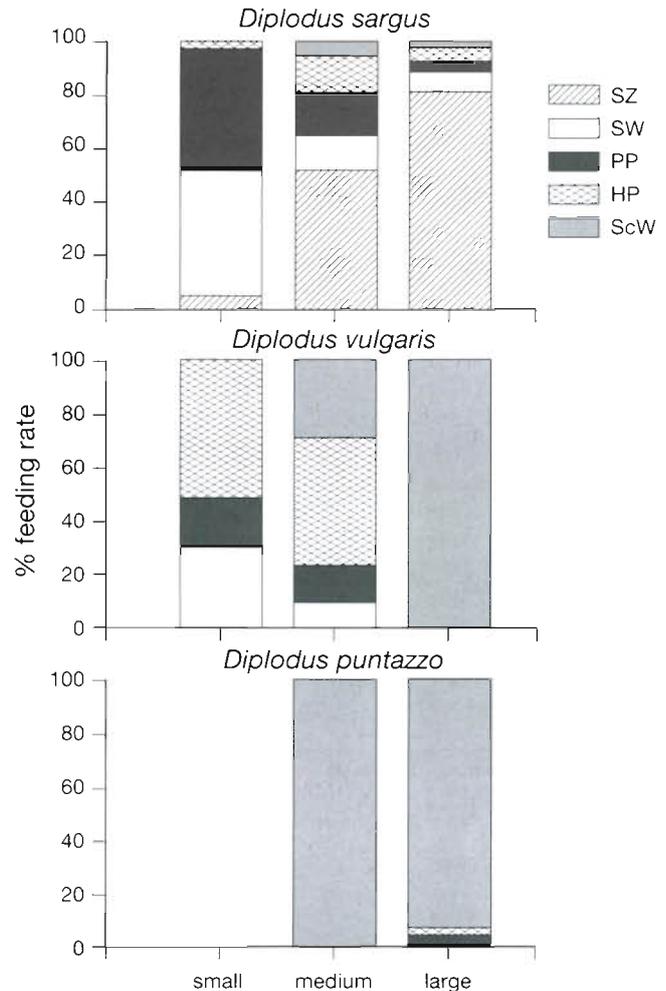


Fig. 4. *Diplodus* spp. Habitat use as a function of size, expressed as percentage of feeding rate performed by each fish size class at each habitat, for the 3 species. SZ: surge zone; SW: shallow walls; PP: photophilic plain; HP: hemisciaphilic plain; ScW: sciaphilic walls. Small, <13 cm (total length); medium, 13–26 cm; large, >26 cm

pods and amphipods were also well represented. The ingestion of algae was diverse, with 55 species of algae found in the stomachs. Other organisms were ingested less frequently.

The diets of 47 individuals of *Diplodus vulgaris* were examined, and 44, ranging from 100 to 240 mm (mean = 183 mm), contained food (Table 2). *D. vulgaris* may be considered as omnivorous, bivalves representing the most important prey type, followed by ophiuroids and polychaetes. However, amphipods and benthic algae were frequently found in the stomachs of *D. vulgaris* ( $F = 59\%$  and  $57\%$  respectively), in spite of the low amount in stomachs. Other groups like hydroids and sea urchins were also abundant, but low by ranking index, relative to percentage total biomass. Stolons from hydroids were also frequently found in stomach contents.

Table 2. Overall food and feeding habits of 3 *Diplodus* species inhabiting rocky infralittoral bottoms in the Medes Islands. AC: % stomachs containing food; F: % occurrence frequency of prey; W: % prey weight; K: ranking index; +: <0.1

	<i>Diplodus sargus</i>			<i>Diplodus vulgaris</i>			<i>Diplodus puntazzo</i>		
	F	W	K	F	W	K	F	W	K
No. of ind. examined	78			47			16		
No. of ind. with full stomachs	69			44			16		
AC	88.5			93.6			100		
Length range (mm)	70–400			100–240			285–365		
Algae	43.5	10.4	4.5	56.8	3.8	2.2	100	21.9	21.9
Seagrasses	8.7	0.9	0.1	5.0	0.1	+	–	–	–
Sponges	–	–	–	–	–	–	81.2	23.1	18.8
Hydroids	14.5	0.1	+	34.1	0.8	0.3	81.2	7.7	6.3
Anthozoans	–	–	–	2.3	0.1	+	37.5	19.7	7.4
Sipunculids	–	–	–	2.3	0.4	+	–	–	–
Polyplocophores	1.4	0.2	+	9.1	0.7	0.1	–	–	–
Gastropods	4.3	0.5	+	6.8	0.2	+	–	–	–
Opisthobranchs	–	–	–	2.3	+	+	18.7	+	+
Bivalves	37.7	57.5	21.7	40.9	51.8	21.2	62.5	4.0	2.5
Polychaetes	18.8	0.9	0.2	38.6	8.2	3.2	43.8	2.7	1.2
Harpacticoid copepods	1.4	+	+	11.4	0.2	+	6.2	+	+
Barnacles	27.5	5.0	1.4	–	–	–	25.0	0.8	0.2
Decapods	17.4	1.3	0.2	13.6	1.8	0.2	6.2	+	+
Cumaceans	1.4	+	+	–	–	–	–	–	–
Tanaids	1.4	+	+	2.3	+	+	6.2	+	+
Isopods	2.9	+	+	36.4	0.1	+	–	–	–
Amphipods	36.2	0.6	0.2	59.1	3.6	2.1	62.5	0.3	0.2
Pycnogonids	1.4	+	+	4.5	0.1	+	18.8	+	+
Bryozoans	4.3	+	+	4.5	0.1	+	50.0	0.1	+
Holothurians	1.4	+	+	–	–	–	–	–	–
Echinids	13.0	19.4	2.5	34.1	1.7	0.6	–	–	–
Asteroids	–	–	–	2.3	0.2	+	–	–	–
Ophiures	2.9	+	+	36.4	14.1	5.1	56.2	0.3	0.2
Ascidians	2.9	0.5	+	2.3	+	+	18.8	0.2	+
Rock fragments	–	–	–	6.8	0.4	+	–	–	–
Unidentified fragments	39.1	2.5	1.0	79.6	11.3	9.0	100	19.0	19.0

Sixteen individuals of *Diplodus puntazzo* were examined and all individuals, ranging from 285 to 365 mm length (mean = 336 mm), were found to contain food (Table 2). *D. puntazzo* was markedly omnivorous, algae representing the most important prey type, followed by sponges (18 species) and cnidarians. These groups accounted for 72% of the weight of total stomach contents. Algae were found in all stomachs examined, and sponges in 81% of stomachs.

The overall feeding niche overlap ( $T$ ) was high and significant only between *Diplodus sargus* and *D. vulgaris* ( $T = 0.69$ ), but was low between the other species pairs.

Although the 3 fish species consumed large numbers of common species of algae, there were differences in the amounts of the species consumed (Table 3). The most abundant algae ingested by *Diplodus sargus* were, in decreasing order of abundance, *Gelidium pusillum*, *Corallina elongata*, *Ulva rigida*, and *Osmundea truncata*. For *D. vulgaris*, algal species were *Falkenbergia rufolanosa*, undetermined Bryopsidales, *Plocamium cartilagineum*, and *Cladophora* spp. *D. puntazzo* ingested preferentially *Flabellia petiolata*, *P.*

*cartilagineum*, *Rhodymenia ardissoni*, and undetermined Bryopsidales.

The 3 fish species showed distinct algal feeding habits (Table 3). The Tukey HSD test showed that the algae *Ulva rigida*, *Gelidium pusillum*, and *Osmundea truncata* were primarily consumed by *Diplodus sargus*. *Flabellia petiolata*, *Lomentaria ercegovicii*, *Rhodymenia ardissoni*, and *Peyssonnelia* spp. were primarily consumed by *D. puntazzo*. However, *D. vulgaris* did not exhibit a clear pattern of algal ingestion. The Tukey test showed no significant differences between *D. vulgaris* and *D. puntazzo* for *Plocamium cartilagineum*, *Falkenbergia rufolanosa*, *Halopteris filicina*, *Dictyota dichotoma*, undetermined Bryopsidales, and *Rhodophyllis divaricata*. The overall niche overlap in algal feeding was low ( $T < 0.6$ ) and thus we might conclude that there was no overlap between *Diplodus* species.

The distribution of algae in the 5 habitats is shown in Table 4. Several macroalgal species were common to all habitats, but certain characteristic species were found only in one particular habitat. The turf algae

Table 3. Relative cover ( $\pm$  SE) of algae found in stomachs of 3 *Diplodus* species in the Medes Islands. Algal taxa with an average abundance <1% for all fish species were not included in the analysis. Significance level from individual ANOVA. NS: non significant, \* $p < 0.05$ , \*\* $p < 0.01$ , \*\*\* $p < 0.001$

	<i>D. sargus</i>	<i>D. vulgaris</i>	<i>D. puntazzo</i>	p-level
Length range (mm) of ind. with stomachs containing algae	180 – 365	170 – 240	285 – 365	
<i>Acrosorium venulosum</i>	0.00 $\pm$ 0.00	0.00 $\pm$ 0.00	1.32 $\pm$ 1.32	NS
<i>Aphanocladia stichidiosa</i>	0.53 $\pm$ 0.31	4.54 $\pm$ 3.14	0.94 $\pm$ 0.64	NS
Bryopsidales undetermined	0.00 $\pm$ 0.00	13.94 $\pm$ 6.02	7.73 $\pm$ 4.15	·
<i>Bryopsis duplex</i>	1.01 $\pm$ 0.60	0.00 $\pm$ 0.00	0.62 $\pm$ 0.62	NS
<i>Bryopsis</i> sp. plur.	0.69 $\pm$ 0.69	3.49 $\pm$ 3.49	0.06 $\pm$ 0.06	NS
<i>Ceramium rubrum</i>	0.00 $\pm$ 0.00	1.82 $\pm$ 1.82	0.00 $\pm$ 0.00	NS
<i>Champia parvula</i>	2.87 $\pm$ 2.87	1.51 $\pm$ 1.51	0.00 $\pm$ 0.00	NS
<i>Cladophora pellucida</i>	2.10 $\pm$ 1.55	0.00 $\pm$ 0.00	0.00 $\pm$ 0.00	NS
<i>Cladophora prolifera</i>	0.00 $\pm$ 0.00	0.00 $\pm$ 0.00	2.06 $\pm$ 2.06	NS
<i>Cladophora</i> sp. plur.	1.24 $\pm$ 0.87	9.79 $\pm$ 6.26	0.06 $\pm$ 0.06	NS
<i>Codium vermilara</i>	7.80 $\pm$ 4.22	0.00 $\pm$ 0.00	0.11 $\pm$ 0.11	NS
<i>Corallina elongata</i>	10.40 $\pm$ 4.74	4.54 $\pm$ 4.54	2.78 $\pm$ 1.89	NS
<i>Cryptonemia lomation</i>	0.00 $\pm$ 0.00	0.00 $\pm$ 0.00	2.41 $\pm$ 2.41	NS
Delesseriaceae undetermined	0.00 $\pm$ 0.00	3.57 $\pm$ 2.56	0.00 $\pm$ 0.00	NS
<i>Dictyota dichotoma</i>	0.00 $\pm$ 0.00	2.27 $\pm$ 2.27	0.90 $\pm$ 0.42	·
<i>Falkenbergia rufolanosa</i> stadium	1.27 $\pm$ 0.94	21.90 $\pm$ 7.90	1.82 $\pm$ 1.09	·
<i>Flabellia petiolata</i>	0.00 $\pm$ 0.00	0.00 $\pm$ 0.00	20.83 $\pm$ 8.06	***
<i>Gelidium pusillum</i>	11.63 $\pm$ 4.89	0.00 $\pm$ 0.00	0.58 $\pm$ 0.58	·
<i>Halimeda tuna</i>	2.41 $\pm$ 2.16	0.00 $\pm$ 0.00	0.00 $\pm$ 0.00	NS
<i>Halopteris filicina</i>	0.00 $\pm$ 0.00	2.27 $\pm$ 2.27	4.81 $\pm$ 2.99	·
<i>Jania rubens</i>	0.80 $\pm$ 0.59	0.00 $\pm$ 0.00	2.53 $\pm$ 2.53	NS
<i>Osmundea truncata</i>	8.17 $\pm$ 4.18	0.00 $\pm$ 0.00	0.00 $\pm$ 0.00	·
<i>Lomentaria clavellosa</i>	0.90 $\pm$ 0.52	0.00 $\pm$ 0.00	2.02 $\pm$ 1.16	NS
<i>Lomentaria ercegovicii</i>	0.00 $\pm$ 0.00	0.00 $\pm$ 0.00	2.02 $\pm$ 1.24	·
<i>Peyssonnelia</i> sp.	0.00 $\pm$ 0.00	1.52 $\pm$ 1.52	2.03 $\pm$ 1.31	·
<i>Plocamium cartilagineum</i>	2.17 $\pm$ 1.74	12.00 $\pm$ 5.20	19.17 $\pm$ 5.16	***
<i>Polysiphonia</i> spp.	5.24 $\pm$ 3.67	1.14 $\pm$ 0.83	1.00 $\pm$ 0.68	NS
<i>Porphyra leucosticta</i>	1.61 $\pm$ 1.41	0.00 $\pm$ 0.00	0.00 $\pm$ 0.00	NS
<i>Porphyra umbilicalis</i>	1.69 $\pm$ 1.28	0.00 $\pm$ 0.00	0.00 $\pm$ 0.00	NS
<i>Rhodophyllis divaricata</i>	0.04 $\pm$ 0.04	2.27 $\pm$ 2.27	5.61 $\pm$ 4.14	·
<i>Rhodymenia ardissoni</i>	1.81 $\pm$ 1.34	1.51 $\pm$ 1.51	8.43 $\pm$ 3.71	·
<i>Schottera nicaeensis</i>	4.90 $\pm$ 3.54	0.00 $\pm$ 0.00	0.00 $\pm$ 0.00	NS
<i>Sphacelaria cirrosa</i>	0.09 $\pm$ 0.09	6.81 $\pm$ 4.98	1.07 $\pm$ 0.64	NS
<i>Sphaerococcus coronopifolius</i>	0.00 $\pm$ 0.00	1.52 $\pm$ 1.52	0.99 $\pm$ 0.99	NS
<i>Ulva rigida</i>	9.56 $\pm$ 4.15	0.00 $\pm$ 0.00	0.00 $\pm$ 0.00	·
<i>Valonia utricularis</i>	1.36 $\pm$ 1.36	0.00 $\pm$ 0.00	0.00 $\pm$ 0.00	NS

complex was abundant in all habitats. Likewise, some turf algae species were frequently found in all habitats, but some species exhibited differential distributions among habitats. If we consider the algae that indicated trophic segregation between the 3 species of *Diplodus* (Table 3), the patterns of distribution were the following. Some species exhibited wide distribution patterns. *Falkenbergia rufolanosa* was highly abundant in the turf algae complex within all habitats, though large plants were only found in the shallow habitats (SZ, SW and PP). *Plocamium cartilagineum* was also found in the turf algae complex of all habitats—principally in HP and ScW—although large plants were only found in the SW. *Halopteris filicina* was present in HP and ScW. The undetermined Bryopsidales and *Rhodophyllis divaricata* were present in the turf algae complex of

all habitats. The *Peyssonnelia* species were found in most habitats, but only 2 species were present in shallow habitats, whereas 5 species were found in ScW. *Dictyota dichotoma* was found in 4 habitats, but mainly in PP and HP. Some other algal species exhibited narrow patterns of distribution. *Flabellia petiolata* was only found in the deep habitats, and chiefly in ScW. *Lomentaria ercegovicii* was present in the turf algae complex of PP and ScW. *Rhodymenia ardissoni* was most abundant in ScW. *Gelidium pusillum* was only found in the SZ and SW habitats. *Ulva rigida* and *Osmundea truncata* were only found in the SZ habitat.

Correlations between fish stomach contents and habitats are shown in Table 5. The algae found in *Diplodus sargus* were significantly and positively correlated with algae of SZ. *D. vulgaris* algal diet was

Table 4. Percentage presence of algae ( $\pm$  SE) in the 5 habitats investigated in the rocky infralittoral in the Medes Islands. SZ: surge zone; SW: shallow walls; PP: photophilic plain; ScW: sciaphilic walls; HP: hemisciaphilic plain

	SZ	SW	PP	ScW	HP
<i>Bryopsis muscosa</i>	2.0 $\pm$ 2.0				
<i>Callithamnion granulatum</i>	7.1 $\pm$ 1.1				
<i>Callithamnion tetragonum</i>	6.2 $\pm$ 2.2				
<i>Ceramium ciliatum</i>	22.4 $\pm$ 7.1				
<i>Ceramium diaphanum</i>	16.7 $\pm$ 5.1				
<i>Ceramium rubrum</i>	44.3 $\pm$ 9.0				
<i>Cladophora laetevirens</i>	35.5 $\pm$ 15.2				
<i>Cystoseira mediterranea</i>	7.0 $\pm$ 3.5				
<i>Enteromorpha compressa</i>	3.3 $\pm$ 3.3				
<i>Grateloupia filicina</i>	2.0 $\pm$ 2.0				
<i>Osmundea truncata</i>	11.2 $\pm$ 3.6				
<i>Porphyra leucosticta</i>	2.0 $\pm$ 2.0				
<i>Scytosiphon lomentaria</i>	4.4 $\pm$ 4.4				
<i>Ulva rigida</i>	33.3 $\pm$ 13.0				
<i>Aglaozonia melanoidea</i> stadium		14.0 $\pm$ 8.1			
<i>Amphiroa rigida</i>		0.7 $\pm$ 0.7	1.3 $\pm$ 1.3		6.7 $\pm$ 3.8
<i>Asparagopsis armata</i>	4.3 $\pm$ 2.3	6.7 $\pm$ 6.7			
Bryopsidales undetermined		8.0 $\pm$ 8.0	2.7 $\pm$ 2.7	8.0 $\pm$ 4.5	
<i>Cladophora pellucida</i>		38.7 $\pm$ 8.9			
<i>Coilomenia sinuosa</i>		5.3 $\pm$ 3.2	1.3 $\pm$ 1.3		
<i>Corallina elongata</i>	95.0 $\pm$ 4.4	29.3 $\pm$ 15.7	72.7 $\pm$ 12.8		38.7 $\pm$ 12.4
<i>Dictyota dichotoma</i>	2.5 $\pm$ 2.5	2.7 $\pm$ 2.0	32.0 $\pm$ 9.8		33.3 $\pm$ 7.3
<i>Dictyota fasciola</i>		6.0 $\pm$ 1.7	6.7 $\pm$ 2.7		
<i>Falkenbergia rufolanosa</i> stadium	2.5 $\pm$ 2.5	51.3 $\pm$ 14.4	16.7 $\pm$ 8.9		
<i>Gastroclonium clavatum</i>	7.5 $\pm$ 2.5	2.7 $\pm$ 2.0	1.3 $\pm$ 1.3		
<i>Gelidium pusillum</i>	10.0 $\pm$ 3.3	38.7 $\pm$ 12.0			
<i>Gigartina acicularis</i>	6.0 $\pm$ 3.0	3.3 $\pm$ 2.2	1.3 $\pm$ 1.3		1.3 $\pm$ 1.3
<i>Lomentaria clavellosa</i>		2.0 $\pm$ 2.0			
<i>Lygbya</i> sp.		6.7 $\pm$ 2.2			
Melobesiae unidentified		80.0 $\pm$ 10.0			
<i>Peyssonnelia dubyi</i>		17.3 $\pm$ 6.7			
<i>Plocamium cartilagineum</i>		4.7 $\pm$ 3.3			
<i>Pseudochlorodesmis furcellata</i>		8.7 $\pm$ 5.5			1.3 $\pm$ 1.3
Turf Algae Complex		57.3 $\pm$ 10.6	88.7 $\pm$ 3.3	72.0 $\pm$ 8.7	91.3 $\pm$ 4.4
<i>Valonia utricularis</i>		1.3 $\pm$ 1.3	2.7 $\pm$ 2.7		
<i>Aglaozonia</i> sp.			18.7 $\pm$ 8.0		
<i>Cladophora hutchinsiae</i>			0.7 $\pm$ 0.7		
<i>Codium vermilara</i>			2.7 $\pm$ 1.7		9.3 $\pm$ 4.2
<i>Corallina granifera</i>			10.7 $\pm$ 5.4		13.3 $\pm$ 13.3
<i>Cystoseira compressa</i>			1.3 $\pm$ 1.3		
<i>Halopteris scoparia</i>			8.0 $\pm$ 6.5		26.7 $\pm$ 10.1
<i>Laurencia</i> cf. <i>obtusata</i>			20.7 $\pm$ 11.2		
<i>Lithophyllum incrustans</i>			43.2 $\pm$ 12.4		53.2 $\pm$ 6.5
<i>Mesophyllum lichenoides</i>			36.7 $\pm$ 14.2	82.0 $\pm$ 5.1	27.3 $\pm$ 7.9
<i>Padina pavonica</i>			13.3 $\pm$ 9.1		17.3 $\pm$ 8.8
<i>Peyssonnelia squamaria</i>			20.7 $\pm$ 8.5	0.7 $\pm$ 0.7	18.0 $\pm$ 10.2
<i>Acrosorium venulosum</i>				8.7 $\pm$ 5.5	
<i>Botryocladia boergesenii</i>				1.3 $\pm$ 1.3	
<i>Cryptonemia lomation</i>				3.3 $\pm$ 2.2	1.3 $\pm$ 1.3
<i>Flabellia petolata</i>				63.3 $\pm$ 8.9	12.0 $\pm$ 7.9
<i>Gloiocladia furcata</i>				2.0 $\pm$ 2.0	
<i>Halimeda tuna</i>				4.7 $\pm$ 3.9	0.7 $\pm$ 0.7
<i>Halopteris filicina</i>				6.0 $\pm$ 2.9	18.7 $\pm$ 7.1
<i>Lithophyllum expansum</i>				4.7 $\pm$ 2.2	
<i>Peyssonnelia bornetii</i>				4.7 $\pm$ 3.0	
<i>Peyssonnelia harveyana</i>				2.0 $\pm$ 2.0	
<i>Peyssonnelia rosa-marina</i>				1.3 $\pm$ 1.3	2.0 $\pm$ 2.0
<i>Peyssonnelia rubra</i>				46.0 $\pm$ 9.0	
<i>Rhodymeria ardissonae</i>				2.0 $\pm$ 2.0	
<i>Aglaozonia parvula</i> stadium					15.3 $\pm$ 8.0
<i>Amphiroa cryptarthrodia</i>					8.0 $\pm$ 3.7
<i>Codium bursa</i>					6.0 $\pm$ 4.6
<i>Cystoseira</i> cf. <i>spinosa</i>					35.2 $\pm$ 8.2
<i>Eupogodon spinellus</i>					1.3 $\pm$ 1.3
<i>Gelidium latifolium</i>					2.7 $\pm$ 2.7
<i>Jania</i> cf. <i>longiarthro</i>					2.7 $\pm$ 2.0
<i>Sphaerococcus coronopifolius</i>					2.0 $\pm$ 2.0
<i>Wrangelia penicillata</i>					2.0 $\pm$ 2.0

Table 5. *Diplodus* spp. Spearman correlation coefficients among algal abundance in fish stomach contents and in the 5 habitats. SZ: surge zone; SW: shallow walls; PP: photophilic plain; HP: hemisciaphilic plain; ScW: sciaphilic walls. NS: non significant; \* $p < 0.05$ , \*\* $p < 0.01$ , \*\*\* $p < 0.001$

	SZ	SW	PP	HP	ScW
<i>D. sargus</i>	0.55*	0.03 <sup>NS</sup>	-0.20 <sup>NS</sup>	-0.27 <sup>NS</sup>	-0.40 <sup>NS</sup>
<i>D. vulgaris</i>	-0.21 <sup>NS</sup>	0.62**	0.76***	0.81***	0.55*
<i>D. puntazzo</i>	-0.62*	0.23 <sup>NS</sup>	0.46 <sup>NS</sup>	0.69**	0.80***

significantly and positively correlated with algae for all habitats, except SZ, and highest correlation coefficients were found for PP and HP. The algae found in *D. puntazzo* were positively and significantly correlated with algae found in HP and ScW, and significantly and negatively correlated with algae from SZ.

## DISCUSSION

Consideration of both distributions and food habits indicates clear differences in resource use among the 3 *Diplodus* species, although they may overlap in some cases. Although the results of the stomach content analysis showed a significant feeding overlap between *D. sargus* and *D. vulgaris*, we suggest that they may not be sharing resources with each other, because the trophic activities of the 2 species are segregated by differences in habitat use. As observational studies and correlation analysis indicate, *D. sargus* mainly exploited the surge zone, whereas *D. vulgaris* fed more frequently in the hemisciaphilic plain. The spatial distributions of these 2 species also suggests a negative relationship between their activity range. Moreover, *D. vulgaris* was not present in the surge zone, and thus may not present a substantial drain on the food resources it shares with *D. sargus*. However, there may be an interaction between small individuals of both species in the shallow zone, since they exhibited a significant habitat overlap. Nevertheless, the availability of the same kind and different kinds of prey in very close habitats may allow the coexistence of both species, in spite of much higher overall abundance of *D. sargus*. The 'niche complementarity' hypothesis implies that co-occurring species that show a high degree of overlap in one niche dimension (e.g. diet) separate out along another dimension (habitat) (Ebeling & Hixon 1991). Furthermore, as each species partitioned resources among size classes, both species may coexist in very high numbers within a relatively small habitat.

On sciaphilic walls there was another case of niche complementarity. Density of *Diplodus vulgaris* was higher than *D. puntazzo* density in deep waters, while

feeding use of sciaphilic walls was almost the same for both species. Results from observational studies suggest that there was a high and significant habitat overlap between the 2 species, especially between medium-sized *D. puntazzo* and large-sized *D. vulgaris*. However, the stomach content analysis showed that these 2 species exploit different food resources. Therefore, the 2 species displayed a high degree of overlap in the spatial dimension but separated out along the diet dimension.

Of special interest concerning the segregation in food resource use was the substantial consumption of sponges by *Diplodus puntazzo*. This species exploited a resource that is apparently not used by any other species of littoral fish in the western Mediterranean, although sponges are an important prey item for some coral-reef fishes (Dunlap & Pawlik 1996). Exploitation of sponges may segregate *D. puntazzo* ecologically from the other *Diplodus* species and thereby may help to minimize whatever level of competition for food resources may occur between them.

Ross (1986) suggested that among marine fish assemblages trophic segregation plays a more important role than habitat separation, but this hypothesis is highly controversial, since several other authors found that habitat separation may be as important as trophic segregation in structuring fish assemblages (among others, Gladfelter & Johnson 1983, Bouchon-Navaro 1986, Harmelin-Vivien et al. 1989). Furthermore, Schoener (1974) pointed out that habitat separation is far more effective than food separation in preventing species overlap, although it is more frequent in terrestrial than in aquatic systems. In this study, habitat partitioning appeared as important as food partitioning in structuring fish assemblages.

We recognize that our study is limited in several significant ways. We considered only 3 species—although 2 of them are by far the most abundant species in the habitat studied—at one local site. We did not investigate seasonal trends in resource partitioning, because of the insufficient number of fish caught in some seasons. We examined only habitat-trophic use relationships, and did not evaluate competitive relationships between these species. Observational and diet studies are not appropriate for properly establishing the existence of competition (Connell 1983, Hastings 1987), and therefore experimental studies are needed to ascertain whether the patterns observed are a result of competition between species. We suggest that effort should be focused on the relationship between *D. sargus* and *D. vulgaris*, since *D. puntazzo* already exhibits morphological differences: it has a longer intestine than either of the other 2 species, and thus it appears to be adapted to feeding on 'low-digestible' organisms, like algae and sponges (Sala 1996).

In this study, visual census of habitat use patterns was combined with gut content analysis and the spatial distribution of algae among habitat types. The combined data provided a very convincing argument that the 3 species partition space and food resources. Although observational study may be carried out easily and relatively quickly, and provides a clear assessment of the use of habitats by fishes, the use of both methods (gut content analysis and visual census) jointly provides more reliable data. The use of a single method might have led to mistaken conclusions concerning resource partitioning. Conversely, it appears that algal stomach contents provide good estimates of habitat use for omnivorous fish in the Mediterranean rocky infralittoral.

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