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Food partitioning among flatfish (Pisces: Pleuronectiforms) juveniles in a Mediterranean coastal shallow sandy area

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Diets of the four main flatfish species, *Arnoglossus laterna, Bothus podas* (Bothidae), *Buglossidium luteum* and *Solea solea* (Soleidae), inhabiting shallow sandy bottoms near the Gulf of Fos (north-west Mediterranean) were analysed to elucidate food partitioning between their juveniles (1^+ group) in nursery areas. The two Soleidae were principally active during the night, and the two Bothidae during the day. The four species all mainly fed on the three most abundant categories of prey in the area (polychaetes, molluscs and crustaceans) but showed different food preferences. *Arnoglossus laterna* and *B. luteum* mainly preyed on crustaceans and molluscs (gastropods and bivalves) whereas *Bothus podas* and *S. solea* preyed principally on polychaetes and bivalve molluscs. Food niche width was clearly higher in *A. laterna* and *Buglossidium luteum* (13.3 and 14.2 respectively) than in *Bothus podas* and *S. solea* (3.2 and 3.6 respectively). Overall food niche overlaps (T) obtained for each pair of fish ranged from 0.33 to 0.58. Overlap was higher between species of the same family but did not reach a significant level. Food niche overlap differed according to the period of the day but did not show any important seasonal variation. Differences in feeding rhythms, food preferences and body sizes, reduced the direct food competition between the juveniles of the four flatfish species, allowing their coexistence within the same nursery zone, despite close periods of settlement.

INTRODUCTION

Coastal shallow areas are used as nursery zones by numerous fish species and play an important role in their recruitment. The abundance and partitioning of food resources in these areas highly influence both survival and growth of juveniles, and determine the size of each species adult stock. Resource partitioning between species can be regarded as behaviour of near universal occurrence in fish assemblages (Bengtson, 1984). Nevertheless, its role in the maintenance of related species in the same biotope is highly controversial (Sale, 1977), as resource partitioning does not necessarily involve competition, if the food supply is abundant enough to cover all the specific needs of the various species present in the area (Thorman & Wiederholm, 1986). Among fish, trophic divisions seem to exercise a more important role than habitat divisions (Schoener, 1974). This hypothesis is controversial, but applies well to communities where the different species occupy the same spatial habitat, as in flatfish soft-bottom communities (Schoener, 1974; Ross, 1986). A considerable volume of work has been accumulated on food partitioning in fish assemblages in freshwater (e.g. Keast, 1978; Jachner, 1991), as well as in marine environments (e.g. MacPherson, 1981; Sala & Ballesteros, 1997; Labropoulou & Machias, 1998). Several studies focused on flatfish, but most of them were carried out in the Atlantic (Kravitz et al., 1976; Carter et al., 1991; Beyst et al., 1999) and, surprisingly, little work was made in the Mediterranean (Rogers & Jinadasa, 1989).

The shallow sandy bottoms in the Gulf of Fos (north-west Mediterranean) are used as nursery grounds by flatfish (Le Direac'h-Boursier, 1990), mainly the scaldfish *Arnoglossus laterna* (Walbaum, 1792), the wide-eyed flounder *Bothus podas* (Delaroche, 1809) (Pleuronectiforms, Bothidae), the solenette *Buglossidium luteum* (Risso, 1810), and the common sole *Solea solea* (Linnaeus, 1758) (Pleuronectiforms, Soleidae). Despite numerous studies on the feeding of the common sole in the Atlantic (e.g. Braber & De Groot, 1973; Lagardère, 1987), few data exist on this subject from the Mediterranean (Reys, 1960; Molinero & Flos, 1992). Little work has been done on the feeding of *A. laterna* (Tito de Morais, 1986; Avsar, 1993), *Bothus podas* (Nash et al., 1991; Schintu et al., 1994) and *Buglossidium luteum* (Tito de Morais, 1984, 1986). Nevertheless, close similarities in feeding rhythms and diets seem to exist between *A. laterna* and *Bothus podas*, and *Buglossidium luteum* and *S. solea* (De Groot, 1971). The occurrence, within the same zone, of juveniles of these four flatfish species could thus lead to an interspecific competition during this critical phase of their life cycle when they share the same spatial habitat (surface or subsurface of the sediment).

To test this hypothesis, the food resource partitioning between the juveniles of *A. laterna*, *Bothus podas*, *Buglossidium luteum* and *S. solea* was examined in a shallow sandy area in the Gulf of Fos (north-west Mediterranean), where they are commonly fished and constitute the major part of the flatfish community (93.5% of flatfish abundance). The diets of the four species juveniles and their variations

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according to the season and the period of the day were analysed and food niche overlaps were calculated for each pair of species.

MATERIALS AND METHODS

Sampling

The fish material used for the present study came from four 24-h cycles of sampling (two in August 1984 and two in February 1985) carried out near the Gulf of Fos (43°20′–43°26′N 04°50′–05°02′E), on the shallow sandy bottoms bordering the outer shore of the 'They de la Gracieuse'. Fish were collected at a depth of 7–10 m with a small (1.5×0.5 m) squid trawl (mesh size of 8-mm) that allowed small demersal fish catch. Samples consisting of 15 min trawls were conducted every two hours during each 24-h cycle. Digestive activity was immediately stopped by injection of formalin into the abdominal cavity of the fish, which were then preserved in 10% neutral formalin. Standard (SL, mm) and total length (TL, mm) and wet weight (W, g) of specimens were subsequently measured.

Diet studies

A total of 40 individuals of *Bothus podas* and 64 *Solea solea* were examined for their stomach contents (Table 1). As *Arnoglossus laterna* and *Buglossidium luteum* were numerous in the catches, the number of fish examined was reduced to ten individuals per trawl. This resulted in the analysis of 181 individuals of *A. laterna* and 231 individuals of *B. luteum* (Table 1). More than 85% of the individuals studied in the four species belonged to the 1^+ age class.

All prey in stomach contents were sorted under a binocular microscope, identified to broad taxonomic categories, and counted. Prey were identified down to the Class level in most cases, to the Order level for crustaceans and to the Family level for amphipods and polychaetes. Dry weight (including hard pieces) was determined to the nearest microgram for each prey category after drying 24 h at 60°C. Mean number (Nm) and mean weight (Wm) of prey per non empty stomach were then calculated for each fish species. The non-parametric Kruskal–Wallis ANOVA tested Nm and Wm differences between species. Post-hoc comparisons of means were performed using the Student–Newman–Keuls (SNK) test.

To study the dial rhythm of feeding activity, the fullness of the stomach (including oesophagus) was estimated using a fullness index (FI_S) ranging from 0 (empty) to 4 (full). Mean number and mean weight of prey per non-empty stomach were also calculated for the two main periods (day and night) of the 24-h cycle. As variance of data was not homogeneous, comparisons of means were performed using the non-parametric Mann–Whitney *U*-test.

Since important differences in size existed between the prey ingested; several conventional parameters proposed by Hureau (1970) were used to estimate the importance of the different prey categories in the diet of each species, as suggested by MacDonald & Green (1983). The occurrence (F) is the percentage of non-empty stomachs that contained a particular category of prey. Percentage number (N%) is the proportion of a given prey category related to the total number of prey consumed. The percentage by weight (W%) represents the ratio of the weight of a prey category to the total weight of all food types ingested. The prey alimentary coefficient Q (Q=N%×W%) gives an appreciation of the relative importance of each prey category in the fish diet in

Table 1. *Number and total length (TL, mm) of fish studied.*

Species	Total number of stomachs	Number of full stomachs	Median size of fish (TL, mm)	Size range of fish studied (TL, mm)	1^+ juveniles size ranges minimum–maximum (TL, mm)
Bothus podas	40	34	132	39–158	120–160
Arnoglossus laterna	181	148	80	29–122	50–90
Buglossidium luteum	231	175	84	20–99	50–90
Solea solea	64	36	207	135–370	140–240

Table 2. *Mean (±SD) number and weight of prey per stomach in the four flatfish species studied. Kruskal–Wallis analysis of variance (K–W ANOVA)=results of K–W ANOVAs with post-hoc comparisons of means (SNK test); similar letters indicate means which are not significantly different (*P>0.05*).*

Species	Mean number of prey/stomach (SD)	K–W ANOVA ($P<0.001$)	Mean weight of prey/stomach (SD)	K–W ANOVA ($P<0.0001$)
Bothus podas	32.24 (33.14)	A	113.39 (317.82)	A
Arnoglossus laterna	9.39 (8.52)	B	3.99 (2.55)	B
Buglossidium luteum	6.13 (4.27)	B C	1.27 (1.28)	B
Solea solea	4.43 (3.93)	C	21.15 (23.89)	B

combining number and weight of ingested prey and, so, was used in the present study, even if the efficiency of composite indices to describe diet were questioned by Tirasin & Jorgensen (1999). Following Hureau (1970), prey categories were considered as preferential when Q⩾200, as secondary prey when 20⩽Q<200, and as occasional or accidental prey when Q<20.

Similarity between global diets (expressed as weight percentages of prey) was analysed by cluster analysis. Single linkage (nearest neighbour) rule was used to elaborate the clustering tree based on the Euclidean distances found between the four species diets.

Food resource partitioning

Food niche width (*B*), which characterizes the food resource spectrum used by a fish species, was calculated following Piélou (1969) using the antilogarithm of the Shannon–Wiener index of diversity:

$$B = e^{H'},\ H' = -\sum pi \log_2 pi \qquad (1)$$

where *pi* is the proportion by weight represented by each specific prey category *i*. Prey weight rather than prey number in the diet was used, as the former better reflects food utilization in terms of energy. The interspecific resource overlap between each pair of fish species was calculated using the index (*T*) of Schoener (1970):

$$T = 1 - 0.5 \sum |Pxi\ Pyi| \qquad (2)$$

where *Pxi* and *Pyi* are the proportions of the total weight represented by each prey category *i* for all pairs of fish *x*, *y*. This index varies theoretically from zero, when the two species use totally different resources, to 1, when they use the same resources in the same proportions. An overlap equal or superior to 0.6 has been considered significant, following Keast (1978).

RESULTS

Feeding strategies

No correlation was found between the median size (TL) of the fish studied and mean numbers (Nm) (r^2=0.003; *P*=0.946) nor weights (Wm) of prey per stomach (r^2=0.054; *P*=0.991). Thus, the values of Nm and Wm found for each species indicated interspecific differences in feeding strategy (Table 2) independently of the size range of the fish analysed. *Bothus podas*, with significantly higher mean number and weight of prey per stomach, ate more than the three other species and preferentially fed on

Table 3. *Overall diet of four flatfish species inhabiting shallow soft bottoms near the Gulf of Fos (north-west Mediterranean).*

	Arnoglossus laterna				*Bothus podas*				*Buglossidium luteum*				*Solea solea*			
	F	N%	W%	Q	F	N%	W%	Q	F	N%	W%	Q	F	N%	W%	Q
Actinians	—	—	—	—	—	—	—	—	0.6	0.1	0.2	+	5.6	1.2	0.9	1.1
Nemerteans	—	—		—	—	—	—	—	5.1	1.0	3.4	3.4	2.8	0.6	0.3	0.2
Polychaetes	33.1	5.6	15.6	87.4	76.5	19.0	19.2	364.8	56.6	16.9	38.9	657.4	72.2	28.7	77.5	2224.3
Bivalves	68.9	25.0	36.1	902.5	82.3	19.3	73.5	1418.6	49.1	14.3	11.9	170.2	69.4	44.5	10.1	449.5
Gastropods	—	—	—	—	35.3	2.0	0.1	0.2	27.4	15.4	10.1	155.5	5.6	1.2	0.4	0.5
Opistobranchs	—	—	—	—	—	—	—	—	0.6	0.1	0.1	+	—	—	—	—
Unident. molluscs	—	—	—	—	—	—	—	—	—	—	—	—	11.1	2.4	1.4	3.4
Ostracods	—	—	—	—	—	—	—	—	2.9	0.6	0.1	+	—	—	—	—
Copepods	2.7	0.3	0.4	0.1	32.4	3.1	+	0.1	46.9	14.1	0.8	11.3	—	—	—	—
Leptostraceans (*Nebalia* sp.)	—	—	—	—	—	—	—	—	1.1	0.2	0.3	+	2.8	0.6	+	+
Mysids	27.0	5.5	6.3	34.7	41.2	3.3	0.5	1.7	—	—	—	—	—	—	—	—
Cumaceans	20.3	5.3	1.2	6.4	41.2	4.9	0.1	0.5	6.3	1.6	1.1	1.8	5.6	1.2	0.3	0.4
Isopods	—	—	—	—	—	—	—	—	0.6	0.1	0.8	0.1	—	—	—	—
Amphipods	69.6	40.3	8.6	346.6	85.3	38.0	1.1	41.8	73.7	28.8	20.0	576.4	36.1	12.2	2.3	28.1
Shrimps	14.2	2.1	13.8	29.0	11.8	0.5	+	+	1.7	0.3	2.6	0.78	—	—	—	—
Pagurids	35.1	9.9	14.2	140.6	67.6	7.3	3.1	22.6	9.1	1.6	1.9	3.1	11.1	5.5	3.9	21.4
Brachyurids	2.0	0.3	1.5	0.5	26.5	1.2	1.2	1.4	0.6	0.1	0.7	0.1	2.8	0.6	0.3	0.2
Unident. crustaceans	—	—	—	—	—	—	—	—	0.6	0.1	0.3	+	—	—	—	—
Ophiuroids	—	—	—	—	5.9	0.2	0.2	+	6.3	1.7	1.2	2.0	—	—	—	—
Holothurians	—	—	—	—	2.9	0.1	0.2	+	—	—	—	—	—	—	—	—
Phoronidians	3.4	1.9	0.5	1.0	—	—	—	—	4.0	2.2	0.5	1.2	—	—	—	—
Unident. fish	4.1	0.5	1.4	0.7	32.4	1.1	0.8	0.9	—	—	—	—	—	—	—	—
Unident. eggs	4.7	3.3	0.4	1.3	—	—	—	—	1.1	0.7	0.1	0.1	—	—	—	—
Unident. prey	—	—	—	—	—	—	—	—	0.6	0.1	5.0	0.5	5.6	1.2	2.5	3.1

F, occurrence (% frequency) of prey; N%, percentage in number of prey; W%, percentage in weight of prey; Q, alimentary coefficient (Q=N%×W%). + indicates values <0.1.

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large preys. *Solea solea*, with a low Nm and a medium Wm, fed on few but also large preys. *Arnoglossus laterna* and *Buglossidium luteum* showed close feeding strategies with intermediate values of Nm and very low Wm indicating the consumption of numerous small preys.

The diet of the four flatfish species studied was mainly composed of the same three categories of prey, namely polychaetes, molluscs and crustaceans, but in different proportions (Table 3). Global diet composition differed mainly according to fish body size, resulting in two pairs of species showing close food preferences (Figure 1). The two larger species, *S. solea* and *Bothus podas* could be qualified as 'polychaete–mollusc' feeders, these two prey categories representing more than 88% by weight of their food (Table 3). The diet of *S. solea* was clearly dominated by polychaetes, mostly Owenidae and Maldanidae (Table 4). Molluscs, the second preferential prey of this fish (Table 3), consisted of small bivalves and numerous siphons torn out from larger ones. *Solea solea* also ate crustaceans as secondary prey, mainly amphipods (*Pontocrates* sp. and *Leucothoe* sp.) and pagurids. It occasionally fed on actinians, nemerteans and gastropods. *Bothus podas* mainly fed on bivalves, both small individuals and feet of larger ones. This species also consumed a large amount of polychaetes, eating small and medium sized individuals as well as tentacles of larger ones, and preying on a wide range of families (Table 4). Crustaceans were frequent and abundant, but represented a low percentage by weight in the diet of *B. podas* (Table 3). They mainly consisted of amphipods (*Pariambus typicus*, *Ampelisca brevicornis* and other gammarids) and pagurids. In addition, *B. podas* occasionally fed on juvenile echinoderms (ophiuroids, holothurians) and small fish. The two smaller fish species, *Buglossidium luteum* and *Arnoglossus laterna* could be considered as 'crustacean–mollusc' feeders, as these two prey categories represented more than 68% by number and 50% by weight of their food (Table 3). The diet of *B. luteum* was dominated by crustaceans, principally amphipods (mostly Oedicerotidae) and copepods. This species also consumed a large proportion of molluscs, selecting bivalve syphons and juvenile gastropods. The third preferential prey category was polychaetes, mostly Lumbrineridae. *Buglossidium luteum* could also feed occasionally on actinians, nemerteans, ophiuroids and phoronidians. *Arnoglossus laterna* principally concentrated its predation effort on crustaceans, mainly amphipods (*Pariambus typicus* and *Ampelisca brevicornis*), pagurids, mysids and shrimps. The second preferential prey category of *Arnoglossus laterna* was molluscs, principally feet of bivalves. This species also consumed polychaetes (mostly Spionidae) as secondary prey, and occasionally phoronidians and small fish.

Diel variation in diet composition

The flatfish species studied showed different feeding rhythms (Figure 2). The feeding activity took place principally during night hours in the two Soleidae (*B. luteum* and *S. solea*), with significantly higher mean stomach fullness index (FI_S) at night, whereas the two

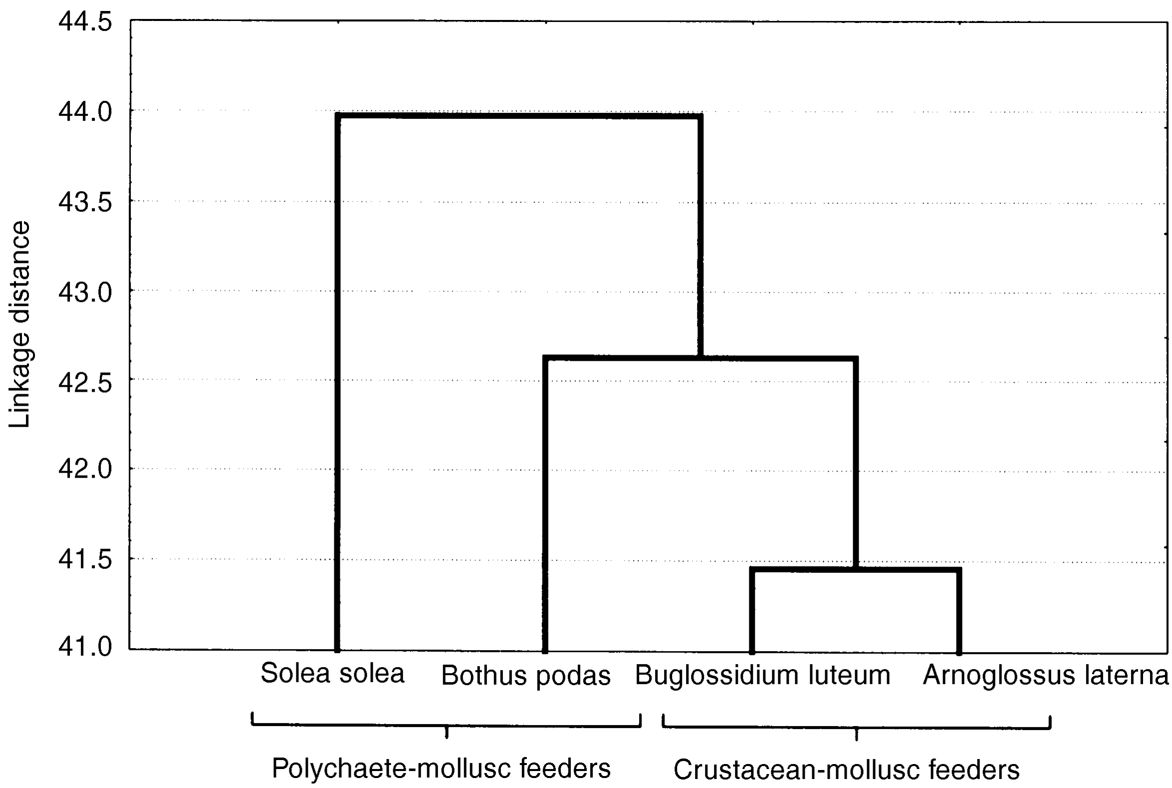

Figure 1. Global diet similarity between four flatfish species inhabiting the shallow sandy bottoms near the Gulf of Fos (north-west Mediterranean): clustering tree (single linkage rule) based on Euclidean distances between diets expressed as weight percentages of prey.

Table 4. *Importance of various polychaetes and amphipods families in the diets of four flatfish species inhabiting shallow soft bottoms near the Gulf of Fos.*

	Arnoglossus laterna	*Bothus podas*	*Buglossidium luteum*	*Solea solea*
I. POLYCHAETES				
Dorvilleidae		*		
Ampharetidae	*			
Nereidae			*	
Chaetopteridae			*	
Cirratulidae			*	
Hesionidae			*	
Sphaerodoridae			*	
Orbiniidae	*		*	
Magelonidae		*	*	
Paraonidae		*	**	
Glyceridae		***	*	
Onuphidae	**	***		
Lumbrineridae		***	***	*
Nephthyidae	*	***	**	*
Spionidae	***	***	**	*
Phyllodocidae	**	***	*	**
Owenidae	*	****		***
Capitellidae		*	*	**
Pectinariidae		*		*
Syllidae			*	*
Maldanidae			*	***
Sabellidae	**			**
Terebellidae	*			*
Pilargidae				*
Indet. polychaetes	*			
II. AMPHIPODS				
Gammaridea	***	****	****	****
Eusiridae				*
Melitidae				*
Lysianassidae				*
Phoxocephalidae				*
Pontoporeidae		*	**	*
Leucothoïdae	*	***	*	***
Oedicerotidae	**	***	***	***
Ampeliscidae	***	***	*	*
Dexaminidae	**	**	*	
Megaluropidae	**	***	*	
Aoridae	*	**		
Corophiidae	*			
Indet. Gammaridea	****	****	***	**
Caprellidea	***	****	*	

Nm, mean number of individuals per stomach containing food calculated for each family of the two prey categories: I, polychaetes; II, amphipods. ****, Nm ⩾ 1; ***, 0.1 ⩽ Nm < 1; **, 0.05 ⩽ Nm < 0.1; *, Nm < 0.05.

Bothidae (*A. laterna* and *Bothus podas*) were preferentially active during the day hours with significantly higher diurnal FI_S (Table 5).

Diets were more diversified during the period of maximum feeding activity in *A. laterna*, *B. podas* and *S. solea*, with a higher consumption of occasional prey (Table 6). *Buglossidium luteum* ingested a similar number of prey categories by day and night. The composition of the diet differed between day and night in the four flatfish species, but the preferential prey categories generally remained the same. Polychaetes and molluscs (bivalves) were always the preferential prey categories, with crustaceans as secondary prey, in the diet of *S. solea*. The common sole clearly preferred polychaetes at night, whereas it consumed a large number of bivalve syphons during the day. The crustaceans eaten were mostly pagurids at night and amphipods by day. This change in diet composition resulted in a higher mean weight of prey per stomach at night ($P<0.01$; Table 7) when the largest prey categories (polychaetes and pagurids) were preferentially ingested.

Whatever the period, crustaceans, molluscs and polychaetes were the three preferential prey categories of *B. luteum*. However, this fish fed more on crustaceans (amphipods) and molluscs at night, and polychaetes by day. The type of molluscs ingested differed between night (bivalve syphons) and day (juvenile gastropods). This resulted in a higher mean weight of prey per stomach during the day ($P<0.051$; Table 7). The preferential preys of *A. laterna* were crustaceans (amphipods, pagurids, mysids and shrimps) and molluscs (bivalves) whatever the period, whereas polychaetes were mainly caught during the day. By day, this fish showed a significant increase in mean number ($P<0.051$; Table 7) and decrease in mean weight ($P<0.05$) of prey per stomach due to the consumption of small prey such as copepods, phoronidians and eggs. *Bothus podas* fed mainly on molluscs (bivalve feet), crustaceans (amphipods and pagurids) and polychaetes during the day. At night, it preyed mainly upon molluscs (bivalve feet) and polychaetes, its consumption of crustaceans being highly reduced, which resulted in a lower, but non significant, mean weight of prey per stomach during this period.

Seasonal variations of feeding

Seasonal variations (summer vs winter) in diet composition have been studied only for *Buglossidium luteum* and *A. laterna*, as the low numbers of *Bothus podas* and *S. solea* caught in winter prevented any seasonal comparison of the feeding of these last two species. The feeding activity of *Buglossidium luteum* did not differ significantly with season ($FI_{Swinter}=1.97\pm1.34$ vs $FI_{Ssummer}=1.74\pm1.48$; $P=0.238$). However, this species presented a more diversified diet in summer (19 prey types in summer vs 11 in winter) due to an increase in the catch of occasional prey. In summer, the preferential preys of *B. luteum* were polychaetes, amphipods and gastropods, with bivalves as secondary prey (Figure 2A). In winter, the preferential preys were amphipods, polychaetes and bivalves, with all the other prey types occasional. The seasonal variation of feeding was more obvious in *A. laterna* with a significantly higher feeding activity in summer ($FI_{Swinter}=2.25\pm1.60$ vs $FI_{Ssummer}=3.26\pm1.08$; $P<0.001$), despite a total number of prey categories similar in summer and in winter (11 vs 10). In summer, *A. laterna* preferentially consumed amphipods and pagurids, plus some polychaetes, bivalves and mysids as secondary prey (Figure 2B). In winter, the diet of

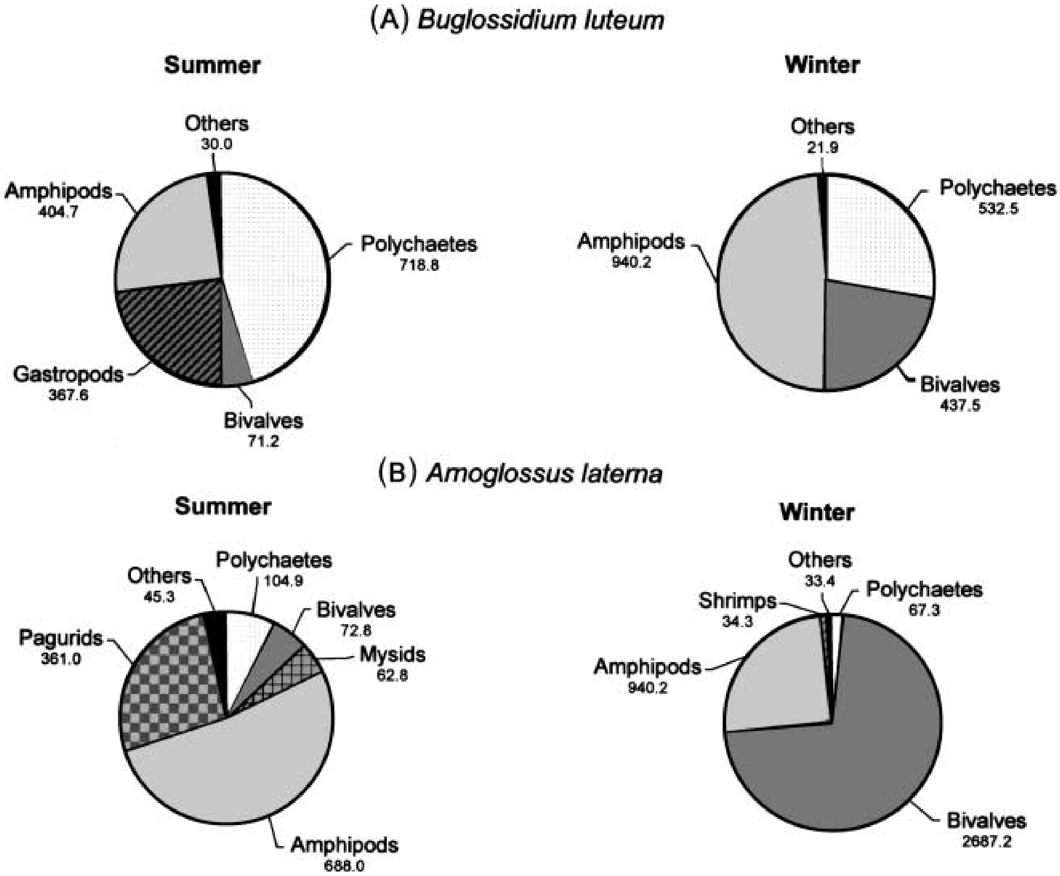

Figure 2. Seasonal variations (summer vs winter) in diet composition for *Buglossidium luteum* (A) and *Arnoglossus laterna* (B) on shallow sandy bottoms near the Gulf of Fos (north-west Mediterranean). Numbers given correspond to each prey alimentary coefficient (Q=N%×W%).

A. laterna was largely dominated by bivalves, the importance of secondary prey (amphipods, polychaetes and shrimps) being reduced. Both flatfish species showed a higher consumption of polychaetes in summer, and bivalves in winter. However, they showed opposite pattern in amphipod consumption, as these preys were eaten preferentially in winter by *B. luteum*, and in summer by *A. laterna*.

Resources partitioning

Although the four flatfish investigated preferentially consumed the same categories of prey, the width of their food niches (*B*) differed. It was wider in the two smaller species, *A. laterna* (*B*=14.2) and *B. luteum* (*B*=13.3), and narrower in *Bothus podas* (*B*=3.6) and *S. solea* (*B*=3.2), the two larger species. In *A. laterna*, *B. podas* and *Buglossidium luteum*, the niche width was wider during the main feeding activity period (Table 8), i.e. during the day for the two Bothidae and at night for *B. luteum*. However, *S. solea* showed a narrower food niche at night due to a high consumption of polychaetes during this period in spite of a higher number of prey categories ingested. A large increase in food niche width was observed in summer for both *A. laterna* (*B*=16.1 in summer vs 7.1 in winter) and *B. luteum* (*B*=14.7 in summer vs 7.3 in winter). The overall feeding niche overlaps (*T*) obtained for each pair of fish ranged from 0.33 to 0.58 (Table 9). Overall niche overlap was higher between the two Bothidae, and the two Soleidae, the values found being close to the significant level (0.60) defined by Keast (1978). For the other fish pairs, overall overlap was well below this significant level. Nevertheless, the food niche overlap between each pair of species was higher during the day than at night (Table 10). The diurnal niche overlap was high and significant between *S. solea* and the three other species ($0.62 \leqslant T \leqslant 0.78$), and between *Bothus podas* and *Buglossidium luteum* (*T*=0.69). No seasonal variation in feeding niche overlap was found between *A. laterna* and *B. luteum* (*T*=0.56 in summer and 0.54 in winter) despite a larger food niche width in summer.

Table 5. *Day and night mean (±SD) values of stomach fullness index (FI_S) in four flatfish species inhabiting shallow soft bottoms near the Gulf of Fos (north-west Mediterranean).*

Species	N fish D–N	FI_S by day	FI_S by night	*P*
Bothus podas	27–13	2.82 (1.11)	1.53 (1.80)	*
Arnoglossus laterna	115–66	3.08 (1.06)	1.86 (1.83)	***
Buglossidium luteum	21–110	1.50 (1.46)	2.17 (1.30)	***
Solea solea	33–31	0.88 (1.26)	1.81 (1.55)	*

N fish, number of fish analysed in each species by day (D) and night (N); P, probability associated with the Mann–Whitney *U*-test of comparison of means; *, $P<0.05$; **, $P<0.01$; ***, $P<0.001$.

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Table 6. *Diel variations of prey alimentary coefficients (Q=N%×W%) in the diet of four flatfish species inhabiting shallow soft bottoms near the Gulf of Fos (north-west Mediterranean).*

	Arnoglossus laterna		*Bothus podas*		*Buglossidium luteum*		*Solea solea*	
	day	night	day	night	day	night	day	night
Actinians	—	—	—	—	—	0.1	—	1.9
Nemerteans	—	—	—	—	2.3	4.3	—	0.1
Polychaetes	137.3	5.5	374.4	752.2	1018.8	359.7	2085.2	1774.5
Bivalves	682.8	3118.8	399.8	1444.3	44.5	364.0	1235.7	340.9
Gastropods	—	—	2.0	—	183.6	136.8	—	0.9
Opistobranchs	—	—	—	—	—	+	—	—
Unident. molluscs	—	—	—	—	—	—	31.5	0.9
Ostracods	—	—	—	—	—	0.3	—	—
Copepods	0.2	—	0.3	—	14.7	8.4	—	—
Leptostraceans	—	—	—	—	+	0.1	—	+
Mysids	50.6	6.8	7.2	0.1	—	—	—	—
Cumaceans	6.7	9.8	2.5	+	—	5.9	2.0	0.1
Isopods	—	—	—	—	0.3	—	—	—
Amphipods	393.9	309.9	281.6	1.2	422.1	755.6	106.3	18.0
Shrimps	14.8	62.3	0.1	—	—	2.7	—	—
Pagurids	159.3	143.0	43.4	15.9	6.0	1.6	—	35.9
Brachyurids	0.1	5.6	8.8	0.1	0.3	—	—	0.3
Unident. crustaceans	—	—	—	—	0.1	—	—	—
Ophiuroids	—	—	—	0.2	+	6.2	—	—
Holothurians	—	—	0.2	—	—	—	—	—
Phoronidians	1.5	—	—	—	+	3.8	—	—
Unident. fishes	0.9	0.1	5.5	0.1	—	—	—	—
Unident. eggs	1.9	—	—	—	0.3	—	—	—
Unident. preys	—	—	—	—	1.9	—	—	5.2
Total N of prey category	**12**	**9**	**12**	**9**	**15**	**15**	**5**	**12**

+, indicates Q smaller than 0.1.

Table 7. *Day and night values of mean (±SD) number and weight of prey per stomach in four flatfish species inhabiting shallow soft bottoms near the Gulf of Fos (north-west Mediterranean).*

Species	Mean number of prey/stomach (SD) Day–Night	*U*-test	Mean weight of prey/stomach (SD) Day–Night	*U*-test
Bothus podas	32.54 ±25.22–31.25 ±53.89	ns	127.55 ±360.32–67.39 ±96.74	ns
Arnoglossus laterna	10.32 ±9.08–6.50 ±5.69	*	3.68 ±2.39–4.93 ±2.83	*
Buglossidium luteum	5.98 ±4.55–6.32 ±3.92	ns	1.72 ±1.72–0.87 ±0.37	*
Solea solea	3.60 ±3.33–5.00 ±4.27	ns	4.43 ±3.93–32.23 ±33.14	**

U-test=result of the Mann–Whitney *U*-test of comparison of means between day and night. *, $P<0.05$; **, $P<0.01$; ns, not significant.

Table 8. *Food niche width (B) of the juveniles (1^+) of four Mediterranean flatfish species during the day and at night.*

B	*Arnoglossus laterna*	*Bothus podas*	*Buglossidium luteum*	*Solea solea*
Day	14.7	9.2	7.9	4.0
Night	8.1	2.2	18.1	2.7

Table 9. *Global feeding niche overlaps (T) found between the juveniles (1^+) of four Mediterranean flatfish species.*

	Bothus podas	*Buglossidium luteum*	*Solea solea*
Arnoglossus laterna	0.58	0.44	0.33
Bothus podas		0.36	0.34
Buglossidium luteum			0.58

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Table 10. *Variation of the feeding niche overlap (T) during the day and at night among the juveniles (1^+) of four Mediterranean flatfish species.*

	Arnoglossus laterna	*Bothus podas*	*Buglossidium luteum*	*Solea solea*	
Arnoglossus laterna		0.51	0.41	0.17	**NIGHT**
Bothus podas	0.58		0.36	0.23	
Buglossidium luteum	0.42	0.69		0.29	
Solea solea	0.62	0.78	0.67		
		DAY			

DISCUSSION

The low global overlaps found between the food niches of *Arnoglossus laterna*, *Bothus podas*, *Buglossidium luteum* and *Solea solea* indicated that the four flatfish species have succeeded in partitioning the food supply between their juveniles on the shallow sandy bottoms bordering the Gulf of Fos. The prey a fish can capture is dependent upon its foraging methods and the morphology of its alimentary tract (De Groot, 1971). Differences in gut morphology and foraging behaviour exist between Soleidae and Bothidae, with consequences on their respective diets. *Solea solea* and *B. luteum* are morphologically adapted to prey on vulnerable and slow moving prey and, so, are supposed to mainly feed on polychaetes and molluscs (De Groot, 1971). On the contrary, *A. laterna* and *Bothus podas* should be able to capture larger and more resistant prey that move quickly such as fish and crustaceans. However, in the present study, the four flatfish species showed close food preferences, all mainly eating polychaetes, molluscs and crustaceans. The diets observed in the present work are representative of the 1^+ juveniles feeding and, as stated by Nikolskii (1969), the food of young fish is usually more similar than that of adults. When immature, *S. solea* has been recorded as generally feeding on worms, molluscs (juveniles and bivalve syphons), and crustaceans (De Groot, 1971; Braber & De Groot, 1973; Lagardère, 1987). This totally fits with our observations. Avsar (1993) confirms the abundance of crustaceans in the diet of *A. laterna* and the frequent ingestion of molluscs and small fish by 1^+ juveniles. The 1^+ juveniles of both *B. podas* (Nash et al., 1991) and *Buglossidium luteum* (Tito de Morais, 1986), are supposed to predominantly feed on crustaceans. Near the Gulf of Fos, their diets were unusually diversified, and they abundantly fed on molluscs and polychaetes, prey they are rarely mentioned to eat in other areas. Such diet switches are common among flatfish (De Groot, 1971) and could result from a present or past competition in food supply use (Gerking, 1994). They also reflect the high trophic adaptability of *B. luteum* and *Bothus podas* juveniles, which can adapt their diet in consuming an abundant type of prey (here molluscs and polychaetes), when confronted to a reduction of their preferential preys (crustaceans) (Tito de Morais, 1984; Schintu et al., 1994).

Polychaetes, molluscs and crustaceans are the three main groups of benthic invertebrates in the Gulf of Fos, where they represent respectively 34, 31 and 32% in abundance of the sandy bottoms benthic fauna (Massé, 1971). Such dietary overlap, only concerning the most abundant prey categories, has already been recorded in flatfish (Beyst et al., 1999) and suggests an opportunistic utilization of these available food resources by the flatfish species involved. In general, interspecific competition among juveniles is avoided by differences in recruitment periods (Nikolskii, 1969). In the north-west Mediterranean, the juveniles of the four flatfish species studied recruit simultaneously on the same shallow sandy bottoms from spring to early summer (Shehata, 1984) with a higher overlap in recruitment time between species of the same family. Once settled, these species present a common annual pattern of migration, their juveniles moving down to deeper waters in winter in order to avoid cold water temperatures (Woodhead, 1964; Tito de Morais, 1986; Nash et al., 1991). This period also corresponds to a reduction of their feeding activity in *S. solea* and *B. luteum* (De Groot, 1969; Tito de Morais, 1984). Thus, the food competition between the four species studied should be maximal in summer. However, the summer values of food niche overlap indicated that, in the Gulf of Fos, food competition remained low between these four species even during this period of maximal density and feeding activity.

The absence of competition resulted mainly in part from differences in feeding rhythms, as *A. laterna* and *B. podas* fed mainly during the day, and *Buglossidium luteum* and *S. solea* at night. Our results agree with the available literature on the feeding activity of these species (De Groot, 1971; Tito de Morais, 1984; Nash et al., 1991). The existence in fish assemblage of different feeding rhythms is thought to facilitate interspecific partitioning of available food (Carter et al., 1991). The competition in prey consumption was also reduced by the selection of different prey at the family level (Table 4). In addition, within each prey family, the species ingested could differ from one fish to another. Food competition was higher between species of the same family, which displayed the same period of maximal feeding activity. However, the two Soleidae clearly showed different food preferences during their common period of maximal feeding (night): *S. solea* then selected polychaetes whereas *B. luteum* mostly ate crustaceans. The two species both ate a lot of polychaetes during the day, resulting in a higher and significant niche overlap during this period. However, the polychaete families ingested differed in size and ethology (Fauchald & Jumars, 1979). *Solea solea* generally preferred large tubicolous polychaetes (Owenidae, Sabellidae and Maldanidae), whereas *B. luteum* consumed small individuals belonging to motile families (Lumbrineridae and Nephthyidae). This could be related to the fact that the 1^+ juveniles of *S. solea* are twice the size of *B. luteum* (Table 1). Difference in size could also decrease food competition between the two Bothidae, the 1^+ juveniles of *A. laterna* being smaller than those of *Bothus podas* (Table 1). *Arnoglossus laterna* mostly preyed on small crustaceans, whereas *B. podas* consumed larger prey like bivalves.

The juveniles of *A. laterna*, *B. podas*, *Buglossidium luteum* and *S. solea* have succeeded in partitioning their food resources on the shallow sandy bottoms bordering the Gulf of Fos. In winter, interspecific food competition is low and reduced by simultaneous decrease in fish abundance and feeding intensity. In summer, several factors reduce the direct food competition that could occur as a consequence of the sharp increase in both fish density and feeding intensity. Differences in feeding rhythms, food preferences and, within the same age class (1^+ juveniles), in body sizes allow the juveniles of these four flatfish to share the same nursery areas, despite similar spatial distributions and close periods of recruitment.

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