Non-competitive coexistence between Mediterranean grey mullet: evidence from seasonal changes in food availability, niche breadth and trophic overlap

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Five grey mullet species in the Albufera des Grau lagoon (Balearic Islands, Western Mediterranean), reacted to the spring-summer reduction in the organic matter content of sediment by expanding their niche breadth, mainly due to higher algae consumption. However, trophic overlap did not change for most of the studied species pairs and when it did, overlap was higher in the warm than in the cold season. When all the assemblage was considered, niche overlap distribution was significantly skewed towards values higher than those predicted by null models, both in the warm and the cold season. These results are not consistent with the predictions from the niche theory, which suggests that grey mullet are under carrying capacity and hence competitive exclusion does not operate in the studied assemblage.

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INTRODUCTION

For a long time, competition was considered the major structuring force in natural communities (Giller, 1984). By the early 1980s, this paradigm was strongly challenged by the results of both theoretical and field studies and competition theory was no longer accepted uncritically (Gotelli & Graves, 1996; Tokeshi, 1999). Now, several other processes are recognized to be important in aquatic ecosystems and competition is thought to play a major role only in some situations, as wild populations are not always food limited (Townsend, 1991).

Three major theories summarize the relative importance of structuring forces in aquatic communities. The disturbance theory predicts that competitive exclusion takes place only in moderately harsh environments (Wiens, 1977; Menge & Sutherland, 1987), because where environmental stress is high, animal populations are rarely at carrying capacity and hence the competitive effects are important only during occasional ' resource crunches '. The top-down control theory (Hairston *et al.*, 1960; Carpenter *et al.*, 1985; Persson *et al.*, 1991; Foreman *et al.*, 1995) predicts that only the species of some trophic levels will reach carrying capacity and hence, competition will affect only them. Finally, the lottery theory (Sale & Dybdahl, 1975; Sale, 1978; Tokesi, 1999) states that in some situations recruitment is independent of previous adult performance and hence competitive exclusion does not operate.

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Grey mullet (Osteichthyes, Muglilidae) are detritivorous fishes, occurring in most warm-temperate estuaries around the world. They represent the bulk of fish assemblages in Mediterranean coastal lagoons (Kapetsky & Lasserre, 1984), where up to five species may coexist regardless of high interspecific trophic overlap (Drake *et al.*, 1984*a*; Ravagnan, 1992; Cardona, 1994). This situation has usually been considered a consequence of a high food availability (Drake *et al.*, 1984*a*), as grey mullet may be under carrying capacity due to massive summer fish kills (Cardona & Pretus, 1991; Brusle & Cambrony, 1992) and a high predation pressure by wintering birds (Volponi, 1994; Addis & Cau, 1997) and artisanal fishermen (Kapetsky & Lasserre, 1984). In such a situation, competition will not be a notable structuring phenomenon, as usually reported for other estuarine animal groups (Barnes, 1994).

On the other hand, there is wide evidence suggesting that estuarine detritivores, both vertebrates and invetebrates, may be food-limited in the warm season (Lasserre *et al.*, 1977; Drake *et al.*, 1984*b*; Walsh *et al.*, 1994; Foreman *et al.*, 1995; Rossi *et al.*, 1999, but see Cardona, 1999; Little, 2000), due to the seasonal dynamics of detritus production and degradation (Menéndez *et al.*, 1989, 1993; Cheng *et al.*, 1993; Gremare *et al.*, 1997; Rossi *et al.*, 1999). Indeed, competition between grey mullet and meiofauna may be intense in summer (Lasserre *et al.*, 1977) and hence, fishes may be food limited even where population density is low.

Theoretically, field experiments are the best way to test hypotheses in community ecology. However, constraints of money, time and resources severely limit replication and spatial dimension, hence reducing their utility. In such a situation, ' natural ' experiments and the use of null models still remain useful tools in community ecology (Gotelli & Graves, 1996). One system for assessing the importance of competition is testing predictions from the niche theory (Giller, 1984; Crowder, 1990). If Mediterranean grey mullet are seasonally food limited, niche theory predicts that trophic overlap and niche breadth will decrease in the warm season, when food is thought to be scarce. On the other hand, if resources are not limited, changes in trophic overlap and niche breadth will not be related to seasonal changes in food availability. The aim of this paper is to test these hypotheses.

MATERIALS AND METHODS

SITE DESCRIPTION

The study was carried out in 1989 in Albufera des Grau, a 72 ha brackish coastal lagoon located in Minorca (Balearic Islands) (39°57′N, 4°13′E). The mean depth is $1·2 \pm 0·52$ m and there is no tidal influence. The salinity level is highly variable, depending on rainfall, but throughout the study it ranged from 29 to 38‰. The lagoon fluctuates between summer transparent waters, which allow the development of a dense meadow of *Ruppia cirrhosa* (Petagna) Grande, and eutrophic winter waters, with dense phytoplankton blooms (Pretus, 1989). Five grey mullet species exist in the lagoon, *Chelon labrosus* (Risso), *Liza aurata* (Risso), *Liza ramada* (Risso), *Liza saliens* (Risso) and *Mugil cephalus* L. Other fish species present in the area are common eel *Anguilla anguilla* L., black goby *Gobius niger* L., sand smelt *Atherina boyeri* Risso, mosquitofish *Gambusia holbrooki* Girard and two banded sea bream *Diplodus vulgaris* (Geoffroy Saint-Hilaire).

SAMPLING METHODS

Fish samples were collected monthly from January to December 1989. The sampling site was a shallow area (average depth $53·2 \pm 7·8$ cm) close to the drainage channel of the lagoon and covered by a *R. cirrhosa* meadow during the warm season. Fishes were caught with trammel nets of 25 mm stretched mesh size. After collection, they were stored on ice and frozen at $-20°$ C in <3 h. Once in the laboratory, fishes were defrosted, identified and stomachs removed. Monthly samples were pooled for diet and chemical analysis into seasons as follows: winter (January, February and March), spring (April and May), summer (June, July, August and September) and autumn (October, November and December).

DIET STUDY

The stomach contents of 394 individuals (110 *C. labrosus*, 101 *L. aurata*, 51 *L. ramada*, 94 *L. saliens* and 38 *M. cephalus*) were studied microscopically. The occurrence of detritus and sand in most of the stomachs made gravimetric or volumetric prey measurements impractical (Cardona, 1991). As a consequence, resource exploitation patterns were described using the frequency of occurrence of prey species (Hyslop, 1980).

The stomachs were defrosted, their contents removed, mixed with ethanol and stirred. Immediately after the sand had settled, five aliquotes of ethanol were collected with a micropipette and microalgae were identified and counted at $\times 400$ magnification, with the aid of a Newbauer chamber (Odum, 1970; Baker & Wolff, 1987). The rest of the sample was stained with Bengal rose (Whitfield, 1988) and invertebrates were counted with a dissection microscope at $\times 20$ magnification. Small invertebrates were collected with a pipette, mounted and identified under a light microscope. All prey were classified to the lowest possible taxonomical level. Occurrence of macroalgae, detritus and sand were also recorded.

To determine the minimum number of stomachs to examine each season, accumulated diversity of microalgae was measured using Margalef's (1986) equation. Three individuals were enough to characterize the feeding habits of *L. aurata*, *L. ramada* and *M. cephalus*, while six were needed for *L. saliens* and nine were required for *C. labrosus*. However, at least ten specimens were used for each season and species. Specimens from different size classes were pooled, because the feeding habits are very similar for all the specimens >5 cm (Drake *et al.*, 1984a).

DIET QUALITY

The amount of food present in an individual stomach was usually too small to allow chemical analysis and hence the stomach contents from the same species and season were mixed and divided into 20 subsamples of 800 mg. The number of specimens required was variable, but at least 15 specimens were used for each species and season. Only the contents of the cardiac stomach was used, because it did not contain mucus (Odum, 1968; Payne, 1976).

In order to measure moisture content, five subsamples were dried at $60°$ C for 48 h. They were then heated at $450°$ C for 8 h in order to calculate percentage organic matter (loss on ignition). Five subsamples were digested with diluted NaOH and mixed with concentrated H_2SO_4, H_2O_2 and HgO, in order to convert the nitrogen present in the amino acids to NH_4^+. Phenol, NaClO and sodium nitroprusiate were then added and light absorption of the solution was measured at 630 nm. $(NH_4)_2SO_4$ was used as a standard. NH_4^+ was used for calculating the concentration of nitrogen and a conversion factor of $\times 6·25$ was then used to determine the protein content in the original samples (Osborne & Voogt, 1978). A further five subsamples were dispersed in distilled water, treated with NaOH, mixed with a solution of $0·1\%$ anthrone in H_2SO_4 and boiled. Carbohydrate concentration was calculated after measuring light absorption at 630 nm. Glucose was used as a standard (Osborne & Voogt, 1978). The remaining five subsamples were used for lipid extraction with ether. They were boiled with diluted HCl and the lipids where extracted with a Soxhlet apparatus. The amount of lipids was calculated by weighing the sample before and after the extraction (Osborne & Voogt,

1978). Gross dietary energy was calculated from the chemical composition using values of 27·8, 39·5 and 17·6 kJ g^{-1} for protein, lipids and carbohydrates respectively (Henken *et al.*, 1986).

FOOD AVAILABILITY

Ten sediment samples were collected with a plastic core (5 cm internal diameter) in February, April, August and November. Samples were stored in ice and frozen at $-20°$ C in <3 h. Once in the laboratory, cores where defrosted and two sub-samples of 800 mg were taken from the upper cm of each core and analysed in the same way as stomach contents. Macrophyte cover was measured in February, April, August and November using 1 m^2 frame quadrats (Bullock, 1996). Ten samples were collected in each season.

TROPHIC OVERLAP AND NICHE BREADTH

Diet similarity among species caught in the same season was measured using the Morisitia-Horn index (Ricklefs & Lau, 1980), since it accepts resource use information expressed as occurrence frequencies and its bias is low (Ricklefs & Lau, 1980; Smith & Zaret, 1982). This index is defined as follows:

$$C_{hj} = 2 \ (\Sigma p_{hk} \cdot p_{jk}) \ (\Sigma p_{hk}^2 + p_{jk}^2)^{-1}$$

where C_{hj} is the similarity between the diets of species h and j, and p_{hk} and p_{jk} are measures of the use of the kth prey by the species h and j, respectively. The index C_{hj} varies from 0 when samples are completely different to 1 when they are identical with respect to food composition. Overlaps >0·6 are considered high and may be indicative of competition if resources are limiting (Zaret & Rand, 1971), whereas overlaps <0·5 are considered low and may represent a lack of competition (McArthur & Levins, 1967).

Trophic niche breadth was calculated using Cardona's modification of Gladfelter-Johnson's index (Cardona, 1991), defined as follows:

$$B = (\Sigma p_k - \sigma) \ (100R)^{-1}$$

where p_k is the occurrence frequency of kth prey, σ is the standard deviation of the occurrence frequencies and R is the number of prey exploited by the guild (see below).

STATISTICAL ANALYSIS

ANOVA followed by Tukey's test (Sokal & Rohlf, 1981) were used to test differences in the mean contents of moisture, proteins, carbohydrates, lipids, organic matter and gross energy between samples of stomach contents collected in different seasons and between samples of sediment. The same statistical procedure was used to test seasonal differences in macrophyte cover. All the values expressed as percentages were previously transformed as arsin$\sqrt{x}$, where x was the percentage value.

Following Hall *et al.* (1990), the confidence interval (CI) of niche breadth and niche overlap was calculated using the boostrap procedure of Efron & Tibshironi (1986). Three thousand simulations were performed in each case.

Two of the randomization algorithms proposed by Lawlor (1980) were used to create null resource use patterns and estimate the frequency distribution of trophic overlap within the community in the absence of competition. Following Gotelli & Graves (1996), the RA2 and the RA3 procedures were selected. The RA2 algorithm replaced the occurrence frequency of each resource state with a random number between 0 and 100, but only for those resource states in which utilization in the observed matrix was >0. As occurrence frequencies are not additive, values were not rescaled in order to sum 1·0, as in the original procedure. The RA3 algorithm reassigned the observed occurrence frequencies to different resource categories, which allowed the retention of niche breadth for each species. One hundred null resource use patterns were created for each species and season and then null trophic overlaps were calculated. The χ^2 test at a

significance level of 0·02 was used to compare the observed frequency distribution of trophic overlaps with the frequency distribution provided by the two algorithms (Sokal & Rohlf, 1981).

RESULTS

The total length (L_T) of the studied specimens of *C. labrosus*, *L. aurata*, *L. ramada* and *L. saliens* usually ranged between 120 and 250 mm, but that of the specimens of *M. cephalus* ranged between 201 and 452 mm.

DIET STUDY AND FOOD QUALITY

All the specimens of *L. ramada*, *L. saliens* and *M. cephalus* caught in winter had empty stomachs or contained very little material, suggesting that they starved during the colder months. *Mugil cephalus* and *L. ramada* were too scarce in the summer samples for their diets to be studied. Consequently, only the spring and autumn samples provided information about the diet of the five species.

The commonest prey in the diet of *C. labrosus* throughout the study were detritus and the snail *Hydrobia acuta* (Fig. 1). The foraminiferan *Ammonia beccari* and the ostracod *Cypridopsis littoralis* were also abundant in winter, but scarce in summer and autumn. Blue-green algae (*Lyngbya* sp. and *Synechococcus* sp.), diatoms (*Cocconeis scutellum* and *Navicula digitoradiata*) and the filamentous green algae *Chaetomorpha crasa* were important only in spring and summer. The frequency of occurrence of planktonic prey was always low. Sand was abundant all year round in stomach contents, but its frequency of occurrence increased in summer. Niche breadth greatly increased in spring, remaining between 0·10 and 0·15 during the rest of the year (Fig. 2). Diet quality also increased in spring (Table I), when protein, carbohydrates, organic matter and energy were higher than in other seasons.

Liza aurata exploited principally detritus throughout the study (Fig. 1). Some animal prey (the amphipod *Corophium insidiosum* and adults of the snail *H. acuta*) were eaten more intensely in autumn, while the importance of blue-green algae (*Gomphosphaeria aponina*, *Lyngbya* sp. and *Synechococcus* sp.), and diatoms (*Cocconeis scutellum* and *N. digitoriadiata*) increased in spring and summer. Filamentous green algae (*C. crasa*) and planktonic prey were seldom consumed. Sand was abundant all year round in stomach contents, but its frequency of occurrence increased in summer. Niche breadth slightly increased in spring and summer (Fig. 2), being narrower in winter and autumn. Food quality was high in winter and spring, but decreased in summer and autumn (Table I) due to low protein, organic matter and energy content.

Feeding habits of *L. ramada* during spring were based on the microalgae *Synechococcus* sp. and *N. digitoradiata* and the filamentous green algae *C. crasa* (Fig. 1). Copepod naupli were also abundant. The situation completely changed in autumn, when the diet was based on detritus and the planktonic dinoflagellate *Aerodinium pigmentosum*. Sand never occurred in more than 50% of the analysed stomachs. Niche breadth was higher in spring than in autumn (Fig. 2). Food quality was also higher in spring (Table I), due to an increase in protein, organic matter and energy content.
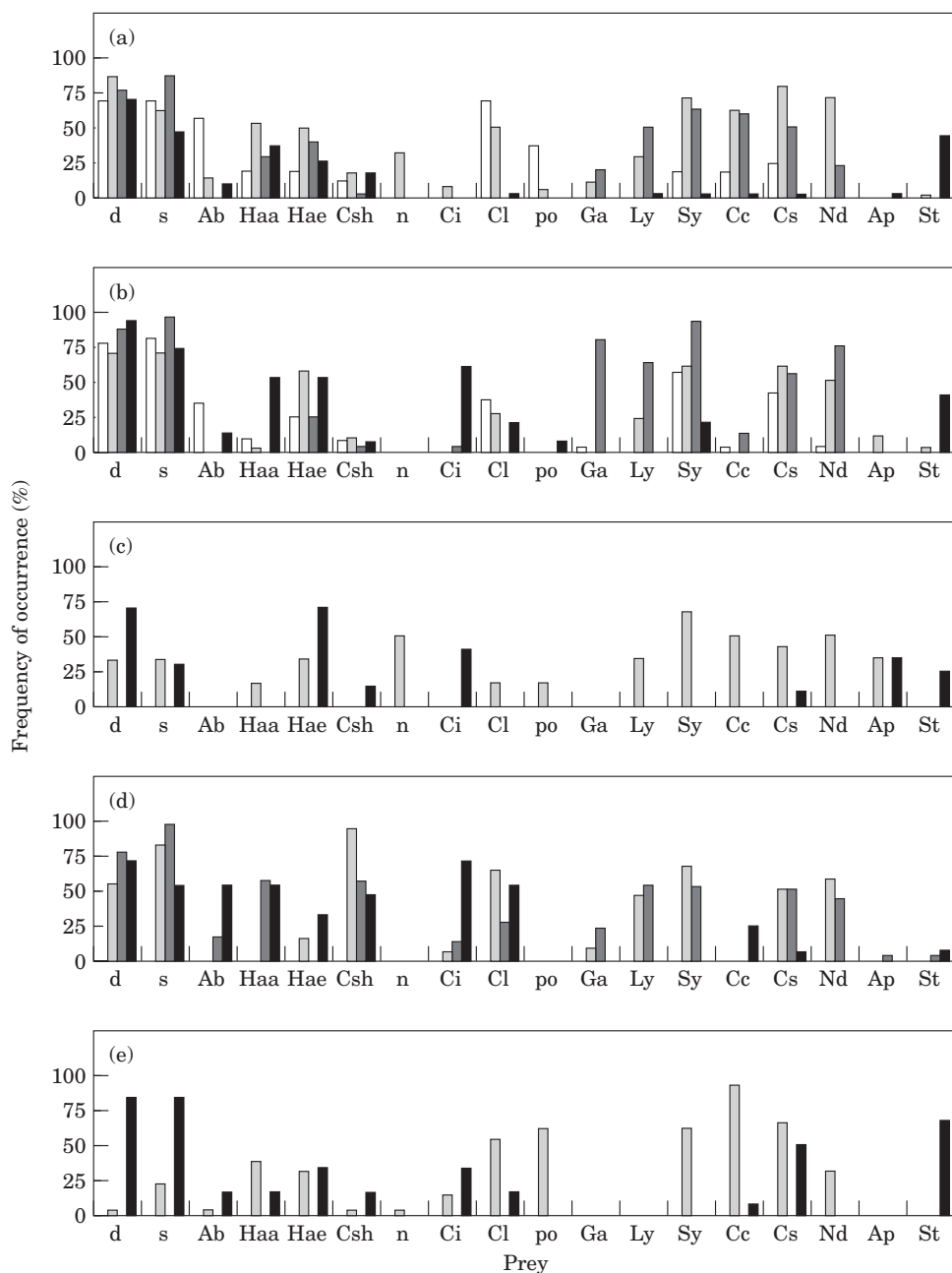
FIG. 1. Seasonal profile of the diet of the five grey mullet species, (a) *Chelon labrosus*, (b) *Liza aurata*, (c) *Liza ramada*, (d) *Liza saliens* and (e) *Mugil cephalus*, present in Albufera des Grau. Only those prey whose frequency of occurrence was at least >50% for one species are shown. d, Detritus; s, sand; Ab, *Ammonia beccari*; Haa, adults of *Hydrobia acuta*; Hae, eggs of *H. acuta*; Cs, larvae of *Chironomus salinarius*; n, copepod naupli; Ci, *Corophium insidiosum*; Cl, *Cyprideis littoralis*; p.o., podocopid ostracods; Ga, *Gomphosphaeria aponina*; Ly, *Lyngbya* sp.; Sy, *Synechococcus* sp.; Cc, *Chaetomorpha crasa*; Cs, *Cocconeis scutellum*; Nd, *Navicula digitoradiata*; Ap, *Aerodinium pigmentosum*; St, *Synedra tabulata*. □, Winter; ▨, spring; ▧, summer; ■, autumn.
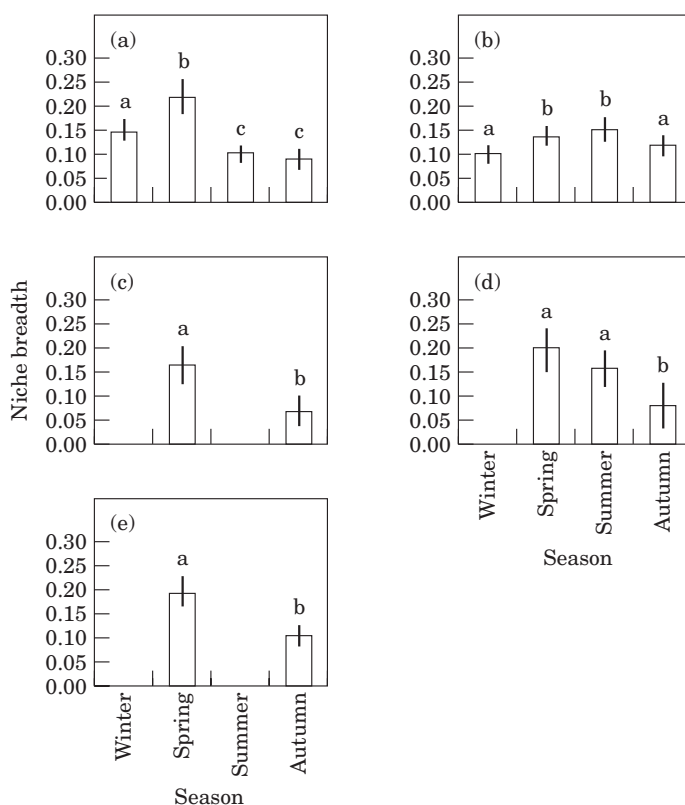
FIG. 2. Seasonal profile of the trophic niche breadth of (a) *Chelon labrosus*, (b) *Liza aurata*, (c) *Liza ramada*, (d) *Liza saliens* and (e) *Mugil cephalus*. Vertical bars show 95% bootstrap CL. Within a species, niche breadths with a different superscript are significantly different ($P<0.05$).

Throughout the year, *L. saliens* fed mainly on detritus, *C. littoralis* and the larvae of the chironomid midge *Chironomus salinarius* (Fig. 1). The importance of other animal prey (*Ammonia beccari*, *H. acuta* and *C. insidiosum*) increased in summer and autumn, when that of *C. salinarius* decreased. However, the frequency of occurrence of microalgae increased in spring and summer. Sand was abundant all year round in stomach contents, but its frequency of occurrence increased in summer. The widest niche breadth was recorded in spring, decreasing in summer and autumn (Fig. 2). Food quality was significantly higher in November than during the warm season (Table I), due to a higher protein, carbohydrate, organic matter and energy content.

The spring diet of *M. cephalus* was based on the filamentous green alga *C. crasa*, together with some benthic microalgae and *C. littoralis* (Fig. 1). The situation changed in autumn, when they fed mainly on detritus and the benthic diatoms *Synedra tabulata* and *C. scutellum*. Sand was scarce in stomach contents of fish caught in spring, but was very common in those collected in autumn. Niche breadth was much higher in spring than in autumn (Fig. 2). Food quality was also higher in spring, due to a much higher content of protein, lipid and organic matter (Table I).

TABLE I. Proximate chemical composition and energy content (mean ± s.d.) of the stomach contents of grey mullet from Albufera des Grau. Values are on a wet matter basis. Average values of the same species in the same column and with a different superscript are significantly different (ANOVA; $P<0.05$). n is the number of samples analysed

	n	Moisture (%)	Protein (%)	Carbohydrate (%)	Lipid (%)	Organic matter (%)	Energy (kJ g^{-1})
Chelon labrosus							
February	5	83·4 ± 2·3	4·1 ± 2·1[a]	0·8 ± 0·1[a]	0·7 ± 0·1[a]	5·6 ± 0·9[a]	1·5 ± 0·2[a]
April	5	63·9 ± 3·9	14·1 ± 1·8[b]	2·0 ± 0·1[b]	0·3 ± 0·1[b]	16·4 ± 0·4[b]	4·4 ± 0·3[b]
August	5	78·0 ± 10·0	4·4 ± 1·5[a]	0·8 ± 0·2[c]	0·2 ± 0·1[b]	5·4 ± 0·9[a]	1·4 ± 0·2[a]
November	5	89·5 ± 4·2	3·4 ± 1·5[a]	0·5 ± 0·1[d]	0·2 ± 0·1[b]	3·4 ± 0·1[c]	1·1 ± 0·1[a]
Liza aurata							
February	5	72·6 ± 3·0	6·8 ± 1·3[a]	3·6 ± 0·4[a]	0·3 ± 0·1[a]	10·7 ± 3·5[a]	2·6 ± 0·4[a]
April	5	65·2 ± 3·3	6·2 ± 1·9[a]	2·1 ± 0·1[b]	0·3 ± 0·1[a]	8·6 ± 2·1[a]	2·2 ± 0·3[a,b]
August	5	53·5 ± 5·3	4·4 ± 1·5[b]	1·0 ± 0·2[c]	0·3 ± 0·1[a]	5·7 ± 2·2[b]	2·0 ± 0·2[b]
November	5	53·0 ± 1·0	4·0 ± 1·2[b]	1·0 ± 0·2[c]	0·3 ± 0·1[a]	4·9 ± 2·8[b]	1·4 ± 0·4[c]
Liza ramada							
April	5	78·0 ± 2·9	17·7 ± 0·6[a]	2·9 ± 0·3[a]	0·3 ± 0·2[a]	20·9 ± 1·5[a]	5·5 ± 0·2[a]
November	5	77·5 ± 4·2	7·0 ± 1·0[b]	2·9 ± 0·4[a]	1·2 ± 0·2[b]	11·0 ± 1·0[b]	2·9 ± 0·2[b]
Liza saliens							
April	5	49·5 ± 2·4[a]	9· ± 0·1[a]	0·6 ± 0·5[a]	0·2 ± 0·1[a]	9·7 ± 0·4[a]	2·6 ± 0·2[a]
August	5	61·9 ± 9·0[b]	6·4 ± 0·4[b]	0·7 ± 0·5[a]	0·7 ± 0·1[b]	7·9 ± 0·1[b]	2·2 ± 0·2[b]
November	5	76·7 ± 1·2[c]	9·3 ± 0·2[a]	1·8 ± 1·1[b]	0·6 ± 0·1[b]	11·7 ± 0·9[c]	3·1 ± 0·3[c]
Mugil cephalus							
April	5	67·0 ± 0·5	8·1 ± 0·1[a]	1·6 ± 0·6[a]	1·0 ± 0·4[a]	10·7 ± 1·7[a]	2·9 ± 0·2[a]
November	5	76·3 ± 0·5	2·7 ± 0·1[b]	1·1 ± 0·1[a]	0·3 ± 0·1[b]	4·2 ± 0·3[b]	1·1 ± 0·1[b]

FOOD AVAILABILITY

The percentage of organic matter and protein, and the energy content of the sediment were high throughout the cold season and significantly lower in April and August (Table II).

The macrophyte community included four major species: one filamentous green alga (*C. crasa*), two red algae (*Gracillaria verrucosa* and *Polysiphonia* sp.) and one vascular plant (*R. cirrhosa*). Only *C. crasa* is known to be regularly consumed by grey mullet (see above). This species covered a large part of the study area in February and April, but it almost disappeared in August. A slight recovery was observed in November (Fig. 3).

TROPHIC OVERLAP

The diets of the five species studied were very similar, as shown by the high trophic overlaps that were >0·6 in 22 of the species pair comparisons (Fig. 4). Lower overlaps were recorded only in April for the pairs *L. aurata*–*M. cephalus* and *L. saliens*–*M. cephalus*. In both cases, the diet of one member was based on the filamentous green alga *C. crasa* and that of the other on detritus. Trophic overlap did not change throughout the year for most of the studied species-pairs, but for *C. labrosus*–*M. cephalus*, *L. aurata*–*M. cephalus*, *L. saliens*–*M. cephalus* and *L. ramada*–*L. saliens* it clearly increased in autumn. This was due to an increase in the importance of detritus in the diet of *L. ramada* and *M. cephalus*.

Comparison of the observed trophic overlap distribution with those resulting from null resource use patterns created with algorithms RA2 and RA3 yield similar results (Fig. 5). In both cases, the distribution frequency of observed trophic overlap was skewed toward higher than expected values (χ^2; d.f.=1; $P<0.02$).

DISCUSSION

The grey mullet assemblage from Albufera d'es Grau lagoon was affected in late June and early July by a dystrophic crisis that killed unknown fish numbers and modified water quality and which probably explained why the green algae *C. crasa* was so scarce in mid-summer (Pretus, 1989; Cardona & Pretus, 1991). However, the seasonal change of sediment quality was not affected by this phenomenon and the percentage of organic matter, the percentage of protein and the energy content of the sediment changed as predicted, i.e. were high in winter, decreased in the warm season and peaked again in autumn. This result also demonstrates that microphytobenthos development during the warm season cannot compensate for a decrease of sediment quality due to detritus degradation.

Diet analysis showed that the five species studied foraged intensely on detritus during the cold season, when it was abundant, although some species starved due to very low water temperatures (Cardona, 1999). The five species reacted to the detritus shortage observed in the warm season by an expansion of their niche breadths, mainly increasing algal consumption. *Chelon labrosus*, *L. ramada* and *M. cephalus* increased the use of both microphytobenthos and filamentous green algae, which increased the food quality of these three species. On the other hand, *L. saliens* and *L. aurata* did not use macroalgae and the quality of their stomach content followed the changes undergone by sediment quality. *Liza saliens*

TABLE II. Proximate chemical composition and energy content (mean ± s.D.) of the top 1 cm of sediment from Albufera des Grau. Values are on a dry matter basis, except moisture. Average values in the same column and with a different superscript are significantly different (ANOVA; $P<0.05$). n number of samples analysed

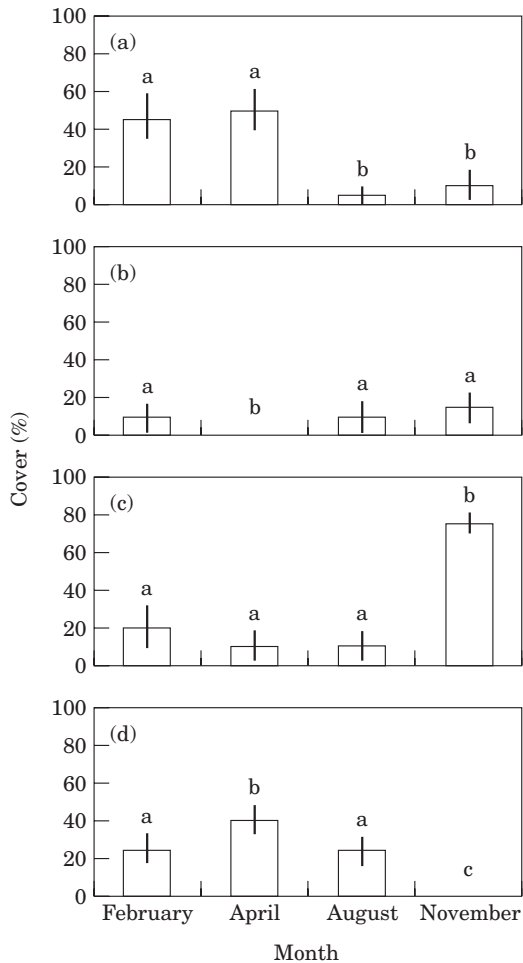|	n	Moisture (%)	Protein (%)	Carbohydrate (%)	Lipid (%)	Organic matter (%)	Energy (kJ g^{-1})
February	10	53·5 ± 3·4[a]	16·7 ± 2·3[a]	3·4 ± 0·5[a]	0·6 ± 0·1[a]	20·7 ± 3·5[b]	5·5 ± 0·2[a]
April	10	42·6 ± 3·4[b]	11·1 ± 1·8[b]	1·4 ± 0·2[b]	0·7 ± 0·1[a]	13·2 ± 2·0[a]	3·6 ± 0·2[b]
August	10	56·3 ± 5·2[a,c]	13·9 ± 1·7[b]	0·8 ± 0·5[b]	0·5 ± 0·2[a]	15·2 ± 2·1[a]	4·2 ± 0·4[b]
November	10	63·4 ± 3·3[c]	19·1 ± 3·8[a]	5·4 ± 0·9[a]	0·7 ± 0·2[a]	25·2 ± 5·3[b]	6·5 ± 0·7[a]

FIG. 3. Seasonal profiles of macrophyte cover (a) *Chaetomorpha crasa*, (b) *Gracillara verrucosa*, (c) *Polysiphonia* sp. and (d) *Ruppia cirrhosa* in Albufera d'es Grau. Vertical bars show s.D. Within a species, the cover values with a different superscript are significantly different (ANOVA and Tukey's test; $n=10$; $P<0.05$).

overcame this problem increasing foraging time and daily rations, which allowed them to maintain high growth throughout the warm season, regardless of the poor quality of their food (Cardona, 1999).

According to niche theory, the niche breadth of the five species should have decreased in the warm season (Giller, 1984; Wootton, 1992), when sediment quality decreased probably because less detritus was available. However, all species showed the opposite pattern, which suggests that grey mullet were not food limited. Niche theory also predicts that trophic overlap should decrease when food supply decreases, if limited (Giller, 1984; Wootton, 1992). Again, the predictions failed and trophic overlap remained constant throughout the year for most of the species pairs. The only significant increases were observed in autumn, when the green filamentous alga *C. crasa* became scarce and *L. ramada* and *M. cephalus* shifted to detritus. Furthermore, when the whole assemblage is
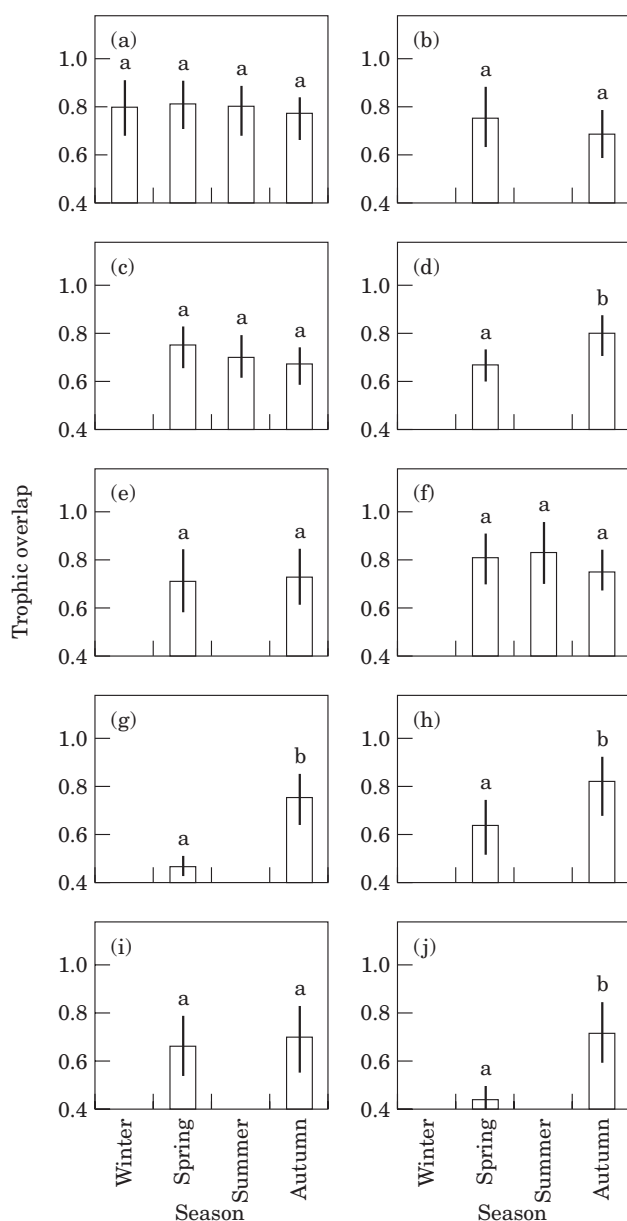
FIG. 4. Seasonal profile of the trophic niche overlap between the five studied species. Vertical bars show 95% bootstrap CL. The niche breadths within species comparisons with a different superscript are significantly different ($P<0.05$). (a) *C. labrosus–L.aurata*, (b) *C. labrosus–L. ramada*, (c) *C. labrosus–L. saliens*, (d) *C. labrosus–M. cephalus*, (e) *L. aurata–L. ramada*, (f) *L. aurata–L. saliens*, (g) *L. aurata–M. cephalus*, (h) *L. ramada–L. saliens*, (i) *L. ramada–M. cephalus* and (j) *L. saliens–M. cephalus.*

considered, niche overlap distribution is always significantly skewed towards values higher that those predicted by null models, a pattern suggesting that grey mullet did not modify their feeding habits to reduce trophic overlap (Gotelli & Graves, 1996; Tokeshi, 1999). These results strongly support the hypothesis that
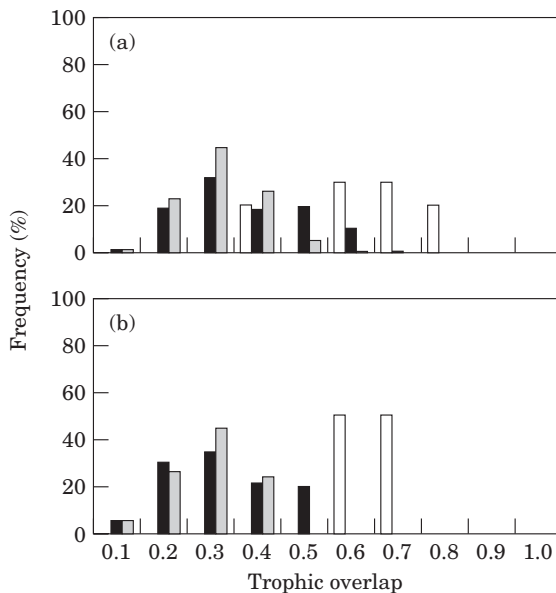
FIG. 5. Observed (□) and predicted, (■) RA2 and (▨) RA3, niche overlap among grey mullet in (a) spring and (b) autumn. In both cases, there are significant differences between observed and expected distributions (χ^2; d.f.=1; $P<0.05$).

grey mullet from Albufera d'es Grau were not food limited and hence competition was not important in defining the assemblage structure. Available information does not provide the answer to why grey mullet are under carrying capacity (summer kills, predation or poor recruitment), but perhaps this is not really important, as coexistence with high trophic overlap has also been reported for other grey mullet assemblages from estuarine systems where food supply is supposed to be limited.

Cadiz fish-ponds (south-western Spain) are artificial coastal lagoons where grey mullet fry freely enter at high tide, but larger fish cannot return to the sea due to the screens at the channel (Arias & Drake, 1990). Ponds are not fertilized and artificial feeds are not supplied, so grey mullet growth depends on the natural production of ponds. In this situation, growth rates are negatively correlated with grey mullet density (Drake *et al.*, 1984*b*), which suggests food limitation. However, five grey mullet species coexist, regardless of high interspecific trophic overlap (Drake *et al.*, 1984*a*). The explanation for such a paradox is the absence of any link between growth performance and recruitment, as adults are prevented from migrating off-shore for spawning (Arias & Drake, 1990). Indeed, the grey mullet populations inhabiting Cadiz fish-ponds depend on the offspring produced by other populations, probably from Cadiz Bay and the Guadalquivir estuary. In this situation, competition has a minor role in defining assemblage structure, although a competitive juvenile bottle-neck may exist, because after recruitment, grey mullet assemblages change as predicted by Gisbert *et al.* (1996) (Arias & Drake, 1990).

Coexistence with high trophic overlap is possible both with an unlimited food supply (Albufera d'es Grau lagoon) and under food-limitation (Cadiz fish-ponds). As the top-down control theory (Hairston *et al.*, 1960; Carpenter *et al.*,

1985; Persson *et al.*, 1991; Foreman *et al.*, 1995) and the disturbance theory (Wiens, 1977; Menge & Sutherland, 1987) are based on the assumption of no food-limitation, they cannot explain the present results and alternative hypotheses are needed.

A similar situation of coexistence with high trophic overlap had previously been reported from some African grey mullet assemblages, but trophic overlap was thought to be reduced because each species used a different range of particle size (Blaber, 1976, 1977; Payne, 1976). This explanation is not useful for Mediterranean grey mullet assemblages, as many species also overlap in particle size (Mariani *et al.*, 1987; Cardona, 1990) and hence trophic overlap remains high even when particle size is considered. The exploitation of different microhabitats has also been suggested (Ravagan, 1992), but there is no evidence to support this explanation.

All the above attempt to identify new niche dimensions that allow grey mullet to reduce trophic overlap, in agreement with the classical view of competition in natural communities (Giller, 1984). An alternative explanation relies on the reproductive biology of grey mullet, as they spawn off-shore and fry are dispersed over a wide geographic area (Brusle, 1981). Hence, recruitment at a particular lagoon or estuary is probably decoupled from growth performance of that species in the area, as in Cadiz fish-ponds, and hence competitive exclusion does not operate even when food supply is limited (Sale, 1978; Wootton, 1992). However, further research is needed to test this hypothesis.

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