

Trophic habits of the fish assemblage in an artificial freshwater ecosystem: the Joaquín Costa reservoir, Spain

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Received 15 March 2004; Accepted 19 November 2004

A b s t r a c t. The Joaquín Costa reservoir contains a mixed fish assemblage of native and exotic species. Feeding habits and feeding relationships of species in the fish assemblage were analysed over a one year cycle. Differences in diet composition were found both between species and within species among seasons. Food overlap and trophic similarity among species also showed seasonal variations. Cluster analysis differentiated four groups of predominant diet: (1) macroinvertebrates (trout and largemouth bass), (2) detritus (nase), (3) cladoceran crustaceans and (4) an omnivorous feeding regime, with large seasonal variations in food habits. Food of fish species included in groups 3 and 4 (roach, white bream, barbel, common and mirror carp) varied seasonally. Using graphical models of feeding strategies, similarity indexes, cluster and multivariate analyses based on the relative importance of food categories in the diet of the species, we illustrate that the fish assemblage showed food resource partitioning according to food habits and foraging habitats within the reservoir.

Key words: environmental fluctuations, exotic species, feeding strategies, native species, reservoir

Introduction

Until the last century, Spain was a country of rivers, most of them with a Mediterranean hydraulic regime characterised by the alternation of floods and drought periods. The evolution of native fish fauna yielded life strategies to cope with these fluctuating ecosystems. However, in recent years the epicontinental waterbodies of Spain have changed due to the construction of reservoirs. This change has resulted in a transformation of the original fish assemblage in many basins, with the disappearance of many native species and the appearance of exotic species, most introduced by fishermen, but sometimes also by the Public Administration (E l v i r a 1992, G r a n a d o - L o r e n c i o 1996). In many of these reservoirs we can find new fish assemblages but both the biotic relationships and the abiotic factors that structure them are virtually unknown. It is important to know how the trophic relationships essential for fish survival become established in these new assemblages. The purposes of the present study are: (1) to explore the seasonal variations in the trophic biology of the fish species in the Joaquín Costa reservoir; (2) to quantify the dietary overlap of these species in order to examine the evidence for partitioning and feeding niche shifts among species; (3) to examine how both native vs exotic and occasionally vs regularly species vary in food utilisation patterns, and (4) to relate how patterns of resource use, foraging strategies and trophic partitioning potentially influence the persistence of endemic species in poorly studied Mediterranean aquatic ecosystems.

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Study Area

The Joaquín Costa reservoir was built in 1932 in the Esera River basin at an altitude of 442 masl. The hydrographic basin has a surface of 1500 km². This reservoir has a volume of 92 Hm³, an area of 692 ha, a maximum depth of 60 m and a mean depth of 16 m. It belongs to group II of the classification of the Spanish reservoirs, characterized by carbonated waters (A r m e n g o l et al. 1991). According to its trophic characteristics it is classified as oligo-mesotrophic (R i e r a et al. 1992). It is of monomictic cycle, with summer stratification. Mean water temperature is of 15 °C with a maximum during summer (26 °C) and a minimum in winter (11 °C) (A r m e n g o l 1998). The fish assemblage of the reservoir is formed by a total of eight species and a sub-species, of which six are exotic (common carp, *Cyprinus carpio*; mirror carp, *C. carpio* var. *specularis*; roach, *Rutilus rutilus*; white bream, *Blicca bjoerkna*; pike-perch, *Stizostedion lucioperca* and largemouth bass, *Micropterus salmoides*). The remaining species (nase, *Chondrostoma toxostoma lemmingii*; barbel, *Barbus graellsii* and trout, *Salmo trutta fario*) belong to the native fish fauna of the biogeographical area of the Ebro River basin and the first two are endemic to the Iberian peninsula (G r a n a d o et al. 1998). The family Cyprinidae is numerically the most important, followed by Centrarchidae, Salmonidae and Percidae. Although the feeding habits of most of the fish species of the Joaquín Costa fish assemblage have been previously reported in their original, primary river ecosystems, nothing has been published on their diet and trophic relationships among them in this artificial mediterranean ecosystem.

Material and Methods

Fish were captured using trammel nets in the pelagic habitats and trap nets in the shallow habitats (M e l c o n 1964, G r a n a d o - L o r e n c i o 1996). Trap nets were used in habitats such as shallow coves, shoreline areas, banks and the tail end of the reservoir. The trap nets (or dutch trap nets) used in the study were 6 m long and had a single mesh of 15 mm. They are formed by a guide and four traps connected consecutively, each one of them of smaller entrance diameter to the previous one. They were set up in areas with development of vegetation, either macrophytes or other vegetative formations (i.e. roots or flooded old trees). Trammel nets (12 x 2 m) were set up in open water (depth over 2 m). These had a narrow inner mesh of 25 mm and an outer mesh of 100 mm. In areas deeper than 8 m, two nets were set up, one at the surface and one at the bottom. In areas shallower than 8 m, only one net was set up at mid depth. In all cases, nets were fishing during 24 hours, being examined twice during the period of exposition.

The sampling points were distributed throughout the reservoir to cover its whole area (Fig. 1). Sampling was carried during three seasons through a year, in February (winter), May (spring) and June (summer). From the fish caught with the different sampling gears we selected a representative number of each species within the single size range most frequent in the reservoir to avoid interference of ontogenic changes in the diet of the species (Table 1). Each fish was measured to the nearest mm (total and standard length) and weighed to the nearest gram. Specimens were dissected and either stomach contents (Centrarchidae and Salmonidae) or contents of the gastrointestinal tract (Cyprinidae) were removed (but in order to simplify, it will be referred also as stomach). Only fish with $\geq 75\%$ of their stomach or gastrointestinal tract full were selected. Fish with empty guts were replaced randomly by other individuals if they were sufficiently available. There were no significant differences

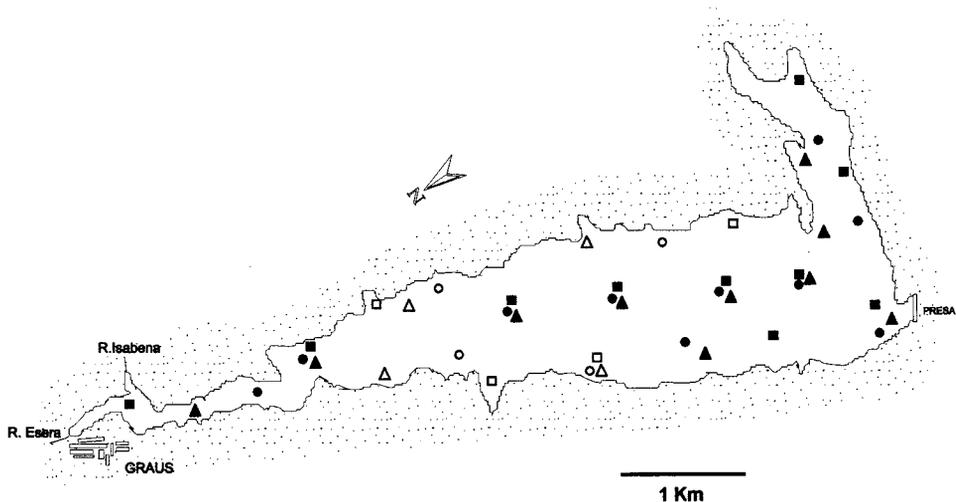


Fig. 1. Study area and sampling localities with trammel (black) and trap nets (white). Square: Winter; Triangle: Spring; Circle: Summer.

Table 1. Number of fish captured and fish analysed in each of the sampling periods and length of the fish selected for the trophic study.

Species	Fish captured (fish analysed)			Mean length (mm)	range (mm)
	Winter (February)	Spring (May)	Summer (June)		
Barbel	74 (30)	84 (30)	155 (30)	301	282–380
Nase	141 (30)	20 (20)	222 (30)	172	150–253
Mirror carp	23 (23)	7 (7)	125 (30)	306	286–325
Roach	14 (14)	48 (30)	29 (29)	183	153–282
Trout	-	2 (2)	5 (5)	400	367–512
Largemouth bass	-	9 (9)	-	142	110–186
White bream	-	-	44 (30)	131	100–165
Common carp	-	4 (4)	17 (17)	311	262–405

(Kruskall-Wallis and Mann Whitney' U test, $P > 0.05$) regarding the fish species captured nor between the different sampling gears nor between the different habitat (pelagic, benthic and littoral); neither regarding the food content between the individuals belong to the same species, so fishes were grouped according to species and season for diet analyses.

Diet items were identified under a dissecting microscope (up to 50 x magnification) or a high power microscope (100–400 x magnification) and later assigned to 15 food categories: cladocerans (Cla), copepods (Co), ephipids (Eph), crustacean eggs (CrEg), ostracods (Os), chironomid larvae (ChLa), chironomid pupae (ChPu), large invertebrates (aquatic and terrestrial) (Lma), fish eggs (FiEg), seeds (Se), vegetal debris (VeDe), macrophytes (Ma), benthic algae (BeAl) detritus (De) and substratum (sand and mud; Su). Gut contents were analysed according to volume. Three different measures for the description of the stomach contents were used to evaluate the importance of each food category: Frequency of Occurrence (% FO), Prey Abundance (% A) and Prey Specific Abundance (% P; H y s l o p 1980, A m u n d s e n 1995, A m u n d s e n et al. 1996).

To assess the relative importance of food categories, we calculated an index of relative importance (IRI) for each food category, as described by *Windlell* (1971). Feeding strategy was studied according to *Costello* (1990) modified by *Amundsen et al.* (1996). To calculate food niche breadth in each species, the Shannon-Weaver index (H' , *Shannon & Weaver* 1949) was used. Low values indicated diets dominated by few prey items (specialist predators) and high values indicated generalist diets. In the present study, diets with values larger than 2 were considered high, whilst values smaller than 1 were considered low. The Baroni-Urbani-Buser similarity index (S) (in *Krebs* 1994) was used to describe the similarity of the dietary components between fish over a period of time. Trophic similarity was also evaluated by means of a cluster analysis based on squared Euclidean distance (*Sokal & Rohlf* 1981) carried out on IRI data. Diet overlap was calculated using the Morisita's index, C , as described by *Horn* (in *Krebs* 1994). Diet overlap increases as the Morisita's index increases from 0 to 1. Overlap is generally considered to be biologically significant when the value exceeds 0.6–0.8 (*Keast* 1978, *MacPherson* 1981, *Wallace* 1981, *Langton* 1982). A value bigger than 0.75 indicated significant overlap for our comparisons.

Seasonal variation in feeding habits within species, as well as differences in diet among species, were analysed by means of the Kruskal-Wallis and Mann Whitney' U test. Differences were considered significant at $P < 0.05$. Detrended Correspondence Analysis was used for the evaluation of the trophic niche segregation of the fish assemblage (with food categories as columns and species/seasons as rows). The new axes generated by the analysis maximise the correspondence between food categories and species, so that species/seasons with similar diets are positioned close to each other as are the food items eaten by similar sets of species/seasons. A measure of the importance of each ordination axis is given by the corresponding eigenvalue (*Magalhães* 1993).

Results

The fish catch composition in the reservoir showed seasonal fluctuations. There were seven fish species captured in spring and summer and only four species in winter. Common carp and trout were captured during spring and summer but not during winter. White bream were captured only during summer, whereas largemouth bass were caught only in spring. The pike-perch was not included in the study because only one individual was captured. Barbel, nase, mirror carp and roach were regularly captured and were abundant in the reservoir all year long. Figure 2 shows seasonal values for IRIs for each food category for these four regularly sampled species. Among all native species, the barbel is the one with the greatest trophic diversity (Table 2). This was the only species whose diet showed statistically significant seasonal changes (Kruskal-Wallis test; $\chi^2 = 10,315$; $P < 0.01$). During winter, barbel was mainly a bottom feeder, with chironomid larvae, benthic algae and detritus as principal food categories in its diet. From winter to summer, barbel increased the consumption of planktonic food items and decreased the consumption of benthic prey. In summer, barbel fed mainly on cladocerans. Accordingly, niche width decreased markedly from winter to summer. The nase (the other common native species) had a narrow dietary breadth, feeding almost exclusively on detritus in all seasons. Only during spring (Fig. 2) was the nase diet supplemented with other food categories concurrently sucked from the sediments (e.g. debris, seeds). During the other seasons the nase showed the lowest trophic diversity of less than as measured by Shannon-Weaver (Table 2).

Among the exotic fish, the mirror carp also showed seasonal changes in certain food items throughout the annual cycle (Mann-Whitney´ U test; $P < 0.05$), especially related to the consumption of cladocerans, although these changes were not sufficient to reflect statistically significant variations in their diet expressed as a whole (Kruskal-Wallis test; $P > 0.05$). Like the barbel, the mirror carp revealed a trend to increase consumption of cladocerans during spring and summer, although in the latter, detritus was an important food item also during the summer period (Fig. 2). The niche width in mirror carp decreased from winter to summer, though to a lesser extent than in barbel (Table 2). Roach, the other resident exotic in the reservoir had a narrow trophic niche (Table 2) and a highly specialised feeding strategy, preying primarily on cladocerans (Fig. 2).

The analysis of the feeding strategy of the species by means of the graphical method proposed by A m u n d s e n et al. (1996) indicated that barbel and mirror carp were the most generalist feeders (Fig. 3), in which both between and within phenotypic contribution to the

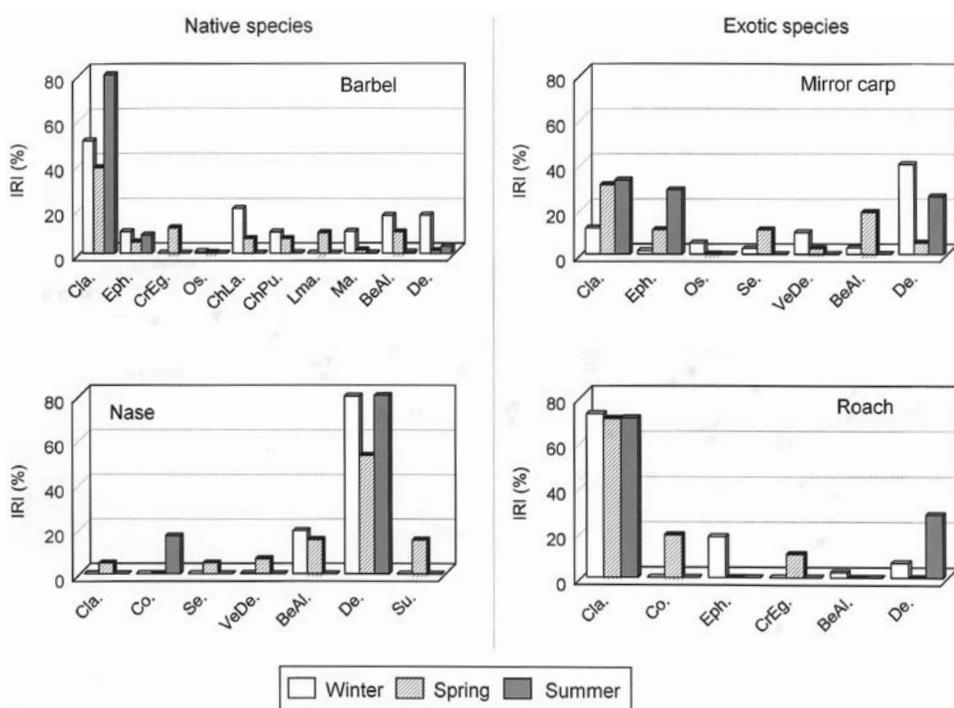


Fig. 2. Seasonal diet composition of regularly captured species in the Joaquín Costa reservoir.

Table 2. Seasonal values of the Shannon-Weaver index (H) calculated on the basis of IRI.

	Regularly captured species				Occasionally captured species			
	Native		Exotic		Native		Exotic	
	Barbel	Nase	Mirror carp	Roach	Trout	Largemouth bass	Common carp	White bream
Winter	3.267	0.789	3.156	1.212	-	-	-	-
Spring	2.999	1.991	2.642	1.191	1.196	0.710	1.191	-
Summer	1.180	0.844	2.050	0.974	0.976	-	0.974	2.364

trophic niche are important according to seasons. On the other hand, nase (detritivorous) and roach (planktophagous) were specialist feeders, with a high within phenotypic contribution to the trophic niche.

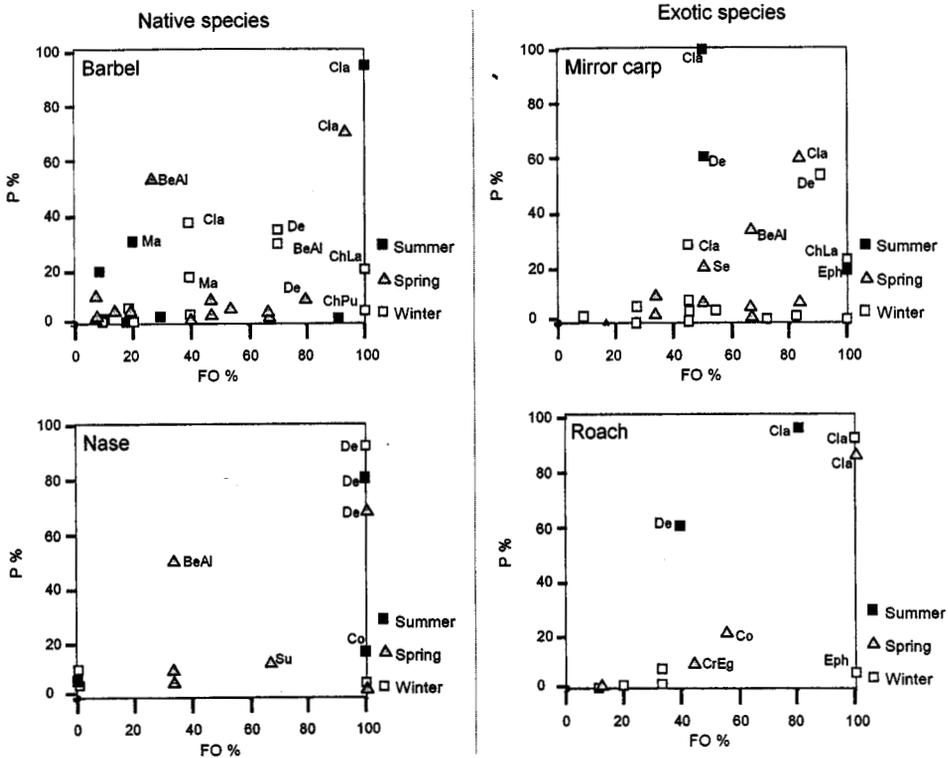


Fig. 3. Relationship between prey specific abundance (P%) and frequency of occurrence (FO%) of the main components of the diet of the regularly captured species in the Joaquín Costa reservoir.

The fish species appearing occasionally in the catches belonged to two feeding groups: 1) species feeding mainly on cladocerans but with detritus as an important complementary food category (common carp and white bream), and 2) species feeding mainly (trout) or exclusively (largemouth bass) on aquatic and terrestrial macroinvertebrates (Fig. 4). Among these species the trout was the only native one. It was captured only during spring and summer. Largemouth bass showed a narrower dietary breadth than trout. This exotic species was captured only during spring. Individuals captured fed exclusively on aquatic and terrestrial macroinvertebrates. During spring, the common carp fed mainly on cladocerans, whereas in summer the decrease of cladoceran consumption was compensated by an increase of detritus consumption. White bream were captured only during summer in the reservoir. This exotic species feeds both on cladocerans and detritus as main food categories. The analysis of the feeding strategy by means of the Amundsen et al. method indicated that white bream was the species with most generalist feeding habits (Fig. 5), whereas trout and largemouth bass were specialist feeders with a narrow diet breadth (Table 2).

The similarity index (Table 3) and cluster analysis carried out on IRI data (Fig. 6) differentiated three trophic groups in the reservoir: a) species eating macroinvertebrates: trout

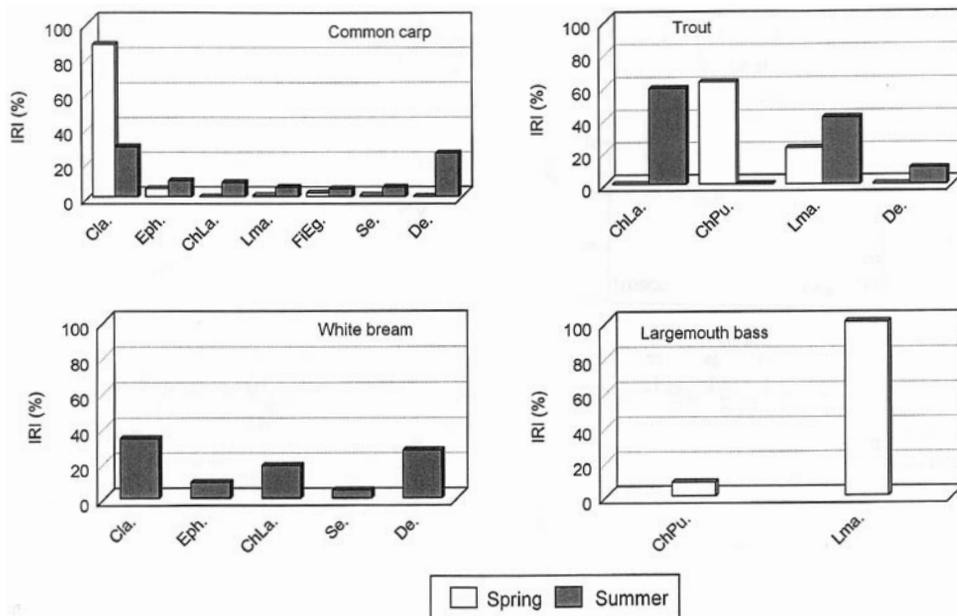


Fig. 4. Seasonal diet composition of occasionally captured species in the Joaquín Costa reservoir.

and largemouth bass; b) species with a feeding strategy specialised on one food category. The fish species included in this stenophagous group varied seasonally: in winter and spring it included nase (detritivorous) and roach, which preyed on cladocerans almost exclusively. In summer, the nase was the only species that remained in this group, whereas roach was grouped together with barbel, mirror carp and white bream; c) species with omnivorous feeding habits and a broad trophic niche in which both planktonic and benthic food categories were consumed. In winter, barbel and mirror carp were clustered into this group. In spring, the common carp also appeared in this group, and in summer it was associated with roach and white bream. Results from detrended analysis located these three trophic groups in a three-dimensional space defined by the three first components axis from the analysis (Fig. 7). DC I was a general bottom-foraging-habitat-related, DC II was mainly defined by the consumption of cladocerans and ephipids, and DC III by the consumption of macroinvertebrates (Table 4). These three components were able to absorb the 73.7% of the data variance.

All analyses showed an important trophic overlap for several species of the fish assemblage during summer. Values obtained for the Morisita index were in agreement with these results (Table 5). Except for nase (highly specialised on detritus consumption) and trout and largemouth bass (feeding almost exclusively on macroinvertebrates) all the species showed high values for the Morisita index (> 75%, even up to 95%). Among them, roach, mirror carp, common carp and white bream had the highest trophic overlap values due to their convergence in the exploitation of both planktonic (with cladocerans as the main food category) and bottom (detritus mainly) food resources. Barbel had a lower overlap value because its consumption on detritus decreased in summer. However, during spring the barbel, with a more omnivorous feeding regime, showed high trophic overlap with roach and the two carp species. Common carp and roach also had high values for the Morisita index due to their convergence in cladoceran consumption. The season when the lowest trophic overlap was registered was winter.

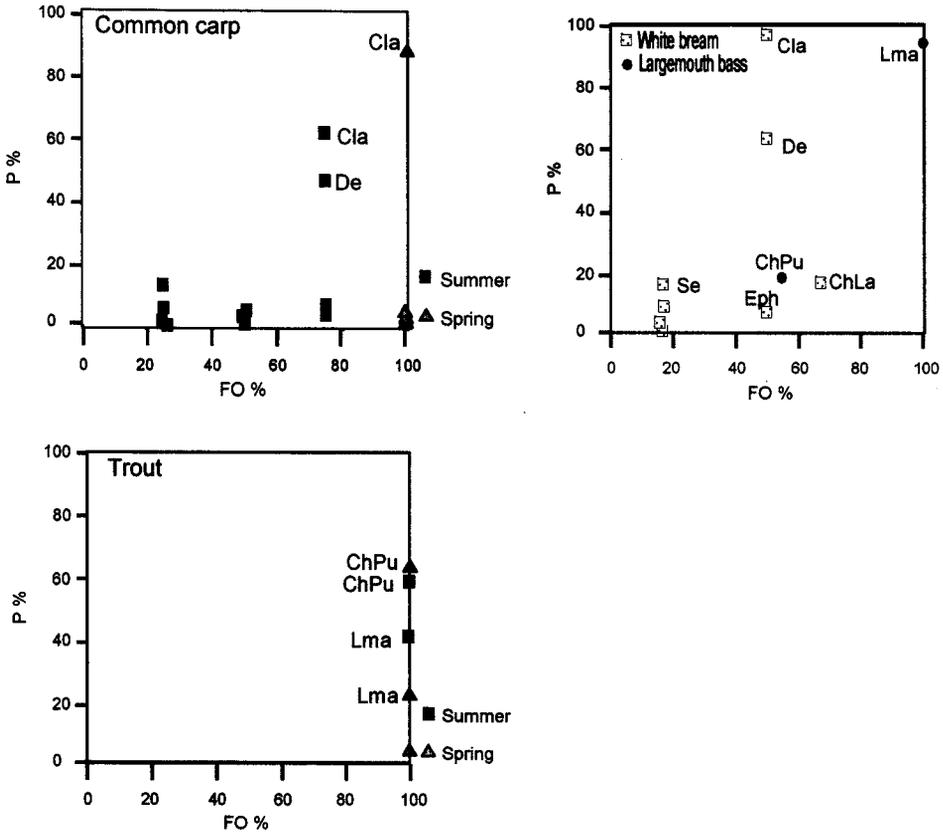


Fig. 5. Relationship between prey specific abundance (P%) and frequency of occurrence (FO%) of the main components of the diet of the occasionally captured species in the Joaquín Costa reservoir.

Discussion

The results obtained reveal a trophic partitioning of resources among the species in the reservoir. Regularly captured species were segregated into three feeding strategies: 1) specialists on detritus foraging (nase, a native species), 2) specialists on plankton foraging (roach, an exotic species) and 3) generalist feeders (barbel and mirror carp, native and exotic species respectively). The species occasionally captured include the predators on macroinvertebrates (trout and largemouth bass, native and exotic species respectively), and two species with omnivorous feeding habits (white bream and common carp, exotic species).

The results of the present study suggest that the food resource use by the Joaquín Costa fish assemblage is highly dynamic and diverse. Every method of analysis of dietary data illustrates variation in the diet and foraging strategies over time for some species of the fish assemblage. On the other hand, other fish species showed little variation and were characterised by a single food category.

From the point of view of the trophic strategies, some species were specialists, others showed generalist feeding strategies, and others showed seasonal shifts from generalist to specialist and viceversa. This trophic dynamism is related with the spatial distribution and

Table 3. Seasonal values of the index of diet similarity of Urbani-Baroni-Buser (S).

		Winter				
	Barbel	Nase	Mirror carp			
Nase	0.631					
Mirror carp	0.742	0.704				
Roach	0.667	0.603	0.640			
		Spring				
	Barbel	Nase	Mirror carp	Common carp	Roach	Trout
Nase	0.400					
Mirror carp	0.800	0.429				
Common carp	0.467	0.440	0.698			
Roach	0.267	0.489	0.353	0.438		
Trout	0.267	0.000	0.483	0.483	0.389	
Largemouth bass	0.067	0.000	0.199	0.389	0.000	0.589
		Summer				
	Barbel	Nase	Mirror carp	Common carp	Roach	White bream
Nase	0.392					
Mirror carp	0.585	0.609				
Common carp	0.706	0.769	0.559			
Roach	0.392	0.267	0.809	0.400		
White bream	0.686	0.603	0.640	0.642	0.603	
Trout	0.264	0.000	0.444	0.308	0.000	0.301

Table 4. Eigenvalues matrix for the three first axis resulted from the Detrended correspondence analysis.

	Detrended Component		
	I	II	III
Cladocerans	-0.058	0.763	-0.445
Copepods	0.261	-0.503	-0.421
Ehipipids	-0.059	0.703	-0.218
Crustaceans eggs	0.372	-0.012	-0.030
Ostracods	0.662	-0.142	0.205
Chironomid larvae	0.778	-0.197	-0.086
Chironomid pupae	-0.431	-0.219	0.668
Large invertebrates	-0.600	-0.266	0.533
Fish eggs	-0.258	0.356	0.534
Seeds	0.335	0.658	0.291
Debris	0.596	0.434	0.328
Macrophytes	0.557	-0.078	0.253
Benthic algae	0.495	0.256	0.336
Detritus	0.620	-0.447	-0.155
Substratum	0.501	-0.164	0.269

seasonal variations of the resources in the reservoir. The Joaquín Costa is a highly unstable reservoir because it was built for electrical production. This particular use creates important environmental changes and water level oscillations. The presence and stability of certain

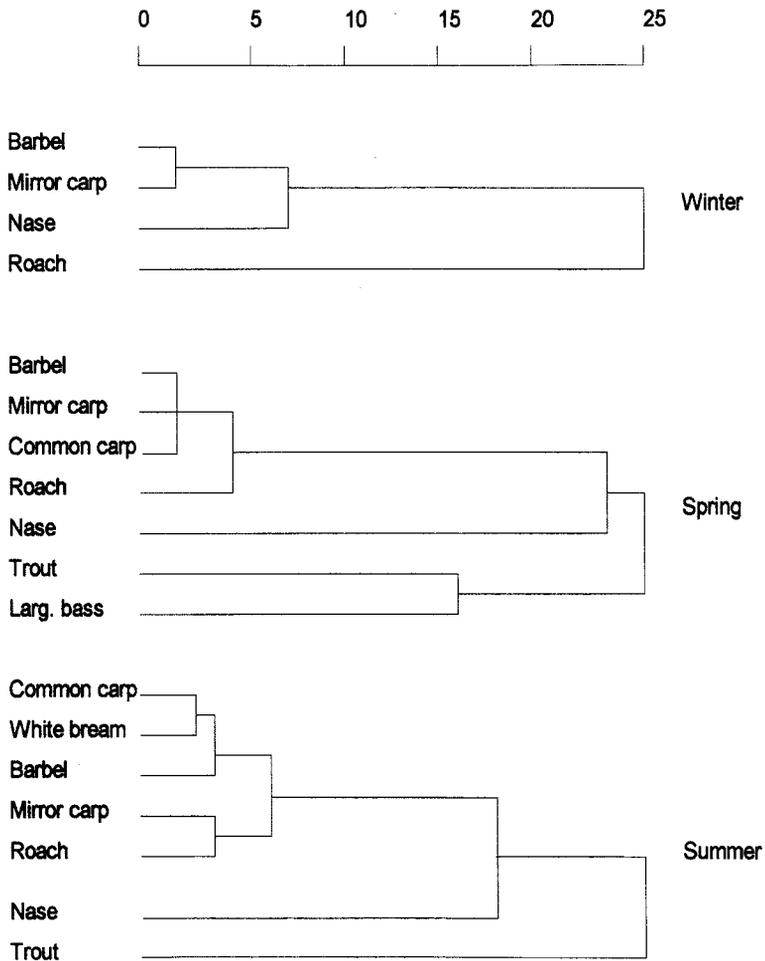


Fig. 6. Dendrograms based on results of the cluster analysis using average linkage between group from the IRI data of the fish species.

populations will be the result of interactions between the effect of environmental changes and species adaptive capacities.

The species regularly captured in the reservoir with specialist feeding habits base their diet on food items that are abundant in all seasons, such as detritus and plankton. Detritus is well recognized as an important food resource in severe fluctuating environments, in which it frequently represents the only available one (Persson 1983, Granada-Lorenzo 1991, 1992, Hofer 1991, Magalhães 1992). Native species (nase and barbel), that evolved in Mediterranean streams, use efficiently this element as an important food resource (Encina & Granada-Lorenzo 1994). In Mediterranean streams the barbel feeds also on macroinvertebrates, periphyton algae, macrophytes and other elements, shifting from one to another seasonally, according to the resources available in the environment (Encina 1991, Magalhães 1992). This great plasticity in the amplitude of the trophic niche of this species contributes to its survival in the reservoir. In the new

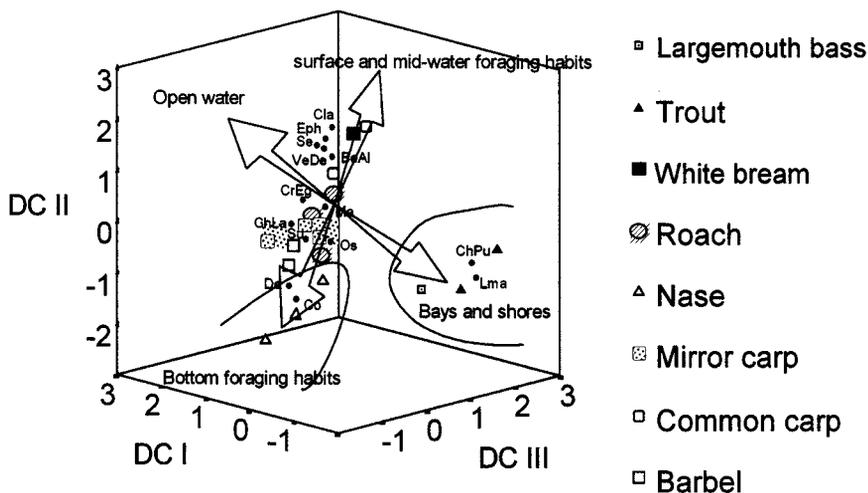


Fig. 7. Plot of the first three axes obtained from the detrended correspondence analysis. Food categories are represented as black circles. (legend see text).

ecosystems, barbel feed on a great diversity of food items and show the greatest amplitude in their trophic niche. Cladocerans are also an important element in their diet, especially during summer.

Cladocerans are an important food resource in the reservoir all year long but mainly during spring and summer. The roach, one of the exotic species regularly captured in

Table 5. Seasonal trophic overlap between species pairs in the Joaquín Costa reservoir.

	Winter						
	Barbel	Mirror carp	Nase				
Mirror carp	0.316	1.000					
Nase	0.287	0.738	1.000				
Roach	0.908	0.079	0.093				
	Spring						
	Barbel	Mirror carp	Nase	Roach	Common carp	Trout	
Mirror carp	0.899	1.000					
Nase	0.159	0.309	1.000				
Roach	0.779	0.623	0.077	1.000			
Common carp	0.709	0.595	0.084	0.938	1.000		
Trout	0.209	0.211	0.000	0.007	0.003	1.000	
Largemouth bass	0.156	0.139	0.000	0.000	0.008	0.307	
	Summer						
	Barbel	Mirror carp	Common carp	Nase	White bream	Roach	
Mirror carp	0.646	1.000					
Common carp	0.606	0.882	1.000				
Nase	0.048	0.445	0.483	1.000			
White bream	0.655	0.885	0.950	0.502	1.000		
Roach	0.936	0.726	0.736	0.358	0.786	1.000	
Trout	0.002	0.077	0.097	0.000	0.013	0.000	

the reservoir, is a specialist feeder on cladocerans, with a narrow niche breadth. In their original ecosystems, planktonic crustaceans are a common item in roach diet (García-Berthou 1999). In Joaquín Costa reservoir, this species has a high trophic overlap with carp, white bream and barbel, which all converge on the use of cladocerans, especially in spring and summer. The intensive consumption of cladocerans during both periods was related to their high availability (Palau, per. com.), when they are known to be abundant and hatch in large densities. With a superabundance of available food and consequently a low search time, the fish could afford to specialise on this single food category (Masón & MacDonald 1982). Their consumption decreased towards winter as the density of cladocerans diminished, except for the roach. During winter, these species tend towards a trophic segregation in their feeding niches, their dietary overlap being relatively low. This suggests that food resources were well partitioned among them.

The exotic mirror carp has similar feeding habits to the barbel: generalist and omnivorous. As with barbel, this feeding plasticity allows carp to live in the reservoir. Both species showed high trophic overlap during spring and summer, when the production of the reservoir is higher, but during winter, when the resource availability is lower, barbel and mirror carp partitioned their resources: barbel fed mainly on cladocerans and mirror carp on detritus and chironomid larvae.

Regarding the occasionally captured species, the diets of trout and largemouth bass could explain the scarce presence of both species in the reservoir, where the water fluctuation greatly affects the macroinvertebrates communities, their main food items (Fisher & Lavoy 1972, Petts 1984, Merz & Vanicek 1996). Variations of water flow cause dramatic level fluctuations that affect the benthic littoral and cause reductions of foraging habitats. In the cases of common carp and white bream it is difficult to withdraw any conclusion because of the low number of specimens captured during the study.

Feeding strategies and seasonal diet variability described in this work can be used to define some aspects of the life history of fishes, which permit their survival in reservoir ecosystems.

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