



Fish communities and food web interactions in some shallow Mediterranean lakes

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Key words: fish, detritivory, zooplanktivory, Mediterranean lakes, Mugilidae

Abstract

Fish communities of five shallow Spanish Mediterranean lakes were studied and stomach content analysed to determine the foraging pattern of each species and the influence on the lake food web. Lakes ranged from 0.5 to 2300 ha with less than 3 m mean depth, while the trophic state varied from mesotrophy to hypertrophy. We fished during summer 2000 and 2001, and for one lake also during spring 2002. Almost no piscivores species were recorded and in general omnivorous species dominated independently of lake trophic state. Fish dietary differences were found among lakes and prey availabilities. Maximum fish biomass and diversity were found in the Albufera lake, where mugilids (*Mugil cephalus* and *Liza aurata*) and *Cyprinus carpio* dominated. The other lakes had young populations of *Atherina boyeri* and *Liza ramada*, endemic species (*Barbus guiraonis*, *Aphanius iberus*) or introduced species (*Lepomis gibbosus*, *Micropterus salmoides*, *Gambusia holbrooki*). Fish were mainly detritivorous and shifted to zooplanktivorous depending on abundance of large zooplankton. Fish demographic changes and facultative preys influenced food webs of the lakes by both direct predation and indirect nutrient recycling from the sediment. Omnivorous structure of fish communities in these Mediterranean warmer lakes resembles that described in some food webs of tropical lakes. Bottom-up mechanisms seem to be more relevant in warmer lakes and submerged plants were special key factors to maintain clear waters in the study lakes.

Introduction

Fish differences in dietary patterns observed among species inhabiting freshwaters are generally due to distinct feeding physiology, predator-prey behaviour and environmental constraints (e.g. O'Brien, 1987; Persson & Crowder, 1997). Fish do not only control quantitatively prey populations, but they can alter both diversity and demographic structure (and even morphology and behaviour) of prey (Vanni, 1986; Gliwicz, 1990; Hansen & Jeppesen, 1992; Moss, 1998; Jacobsen et al., 1997). Moreover, there is evidence that indirect effects can be determinant in trophic interactions, for instance fish can transport in the lakes nutrients vertically and horizontally, recycling nutrients though the food webs (Vanni, 1996; Hessen, 1997; Bertolo et al., 1999; Tátrai et al., 2003). Both direct

and indirect effects influence trophic structure of lakes and can be specially intense in eutrophic shallow lakes (Persson et al., 1996; Jeppesen et al., 1997; Moss et al., 1996). The presence of omnivorous and detritivorous fishes in shallow lakes are commonly associated with changes related to eutrophication (e.g. Horppila & Kairesalo, 1990; Karjalainen et al., 1999), such as the growth of rotiferan communities or the development of algal populations, both planktonic and epiphytic, displacing macrophytes as primary producers (Jeppesen et al., 1997; Scheffer, 1998).

Spanish freshwater ichthyofauna differs significantly from that of the rest of Europe (Granado-Lorencio, 1996). Some general hypotheses on food webs of shallow lakes accepted for temperate northern lakes, may need further research in warmer areas. Although fisheries has a long tradition in the Spanish

Mediterranean shallow lakes, there is a little knowledge of their ecology and impact on food webs, which can be generalized to other Mediterranean countries (Poizat & Crivelli, 1997; Gophen et al., 1998; Goren & Ortal, 1999). In this work, we present data about composition and feeding behaviour of fish communities of five shallow Mediterranean lakes (Valencia, Spain). We aim to relate the trophic state of the lakes with their fish composition and structure.

Materials and methods

Study sites

Five lakes were studied in the Spanish Mediterranean coast (Valencia region, East Spain). Lakes are located in wetland natural reserves. Lake size varied between 0.5 and 2300 ha with a mean depth less than 3 m (Table 1). They were oligohaline and brackish lakes, with trophic gradient from mesotrophy to hypertrophy. All lakes were sampled for fish during summers 2000 and 2001, except the lake Albufera that was fished during summer 2000 and spring 2002, when fish seasonally developed in the lake. The lake is connected to the Mediterranean sea by channels that are man-regulated for rice cultivation in the surrounded areas (Romo & Miracle, 1993). The lake of Cap de Terme was only sampled in summer 2001, since floating-plants (*Nymphaea*) prevented fishing with nets during summer 2000.

Sampling and fishing methods

We determined the composition and relative abundance of the pelagic and benthic fish stock in the five lakes by multiple mesh-sized gill nets (6.5, 8, 10, 12, 17, 21, 25, 29, 32, 36, 42, 47, 60, 75 mm), the length of each size section and depth of gill nets being 3 and 1.5 m, respectively, and by simultaneously using fyke nets. The number of gill and fyke nets was dependent on lake size, and catch per unit effort (CPUE) of fish was calculated as mean catch per net and standardized to 18 hours (Jeppesen et al., 1997). The relations of weight (W) and length (L) for each fish species and the condition factor ($k_t = 100 W/L^3$) were calculated. Fish gut content was analyzed according to Blanco (2001). We selected randomly 20% of individuals (but never less than 20 individuals) and gut was removed from oesophagus to anus and fixed with ethanol 70% (v/v). Empty guts were

excluded from calculations. Guts were weighed before and after the removal of its content, and analysed under stereoscopic microscope ($\times 40$) in triplicate. A semiquantitative visual estimation of the abundance of dietary components (zooplankton, macroinvertebrates, macrophytes, algae, detritus and sediment) was made according to five categories: absent (0%), very rare (25%), rare (50%), abundant (75%) and very abundant (100%) following Collares-Pereira et al. (1996) and Karjalainen et al. (1999). Animal prey was quantified by identification to the lowest possible taxonomic level. For fractionated preys it was calculated the minimum number of individuals (MNI). We calculated the numeric percentage (NP, percentage of individuals of each prey type eaten by each fish) and frequency of occurrence (FO, percentage of fishes that preyed on each prey type; only when $n > 2$) according to Granado-Lorencio (1996) and Hyslop (1980). Neither gravimetric nor volumetric measures were made since the presence of sediment and detritus in gut contents make these impracticable, as well as fractionation and distinct digestibility of each dietary component could bias this measure (Cardona, 1991). Guts content were dehydrated until a constant weight, and later weighed and volume determined.

Results

In general, almost no piscivorous species were recorded and fish communities were dominated by omnivorous species independent of lake trophic state. Fish communities showed dietary differences among lakes and prey availability.

The Albufera lake had the maximum fish species richness (9 species) and biomass captured in summer 2000 ($> 40\%$ of total fish biomass captured, Table 2). Dominant species were flathead mullet (*Mugil cephalus* L.), golden mullet (*Liza aurata* Risso), and carp (*Cyprinus carpio* L.), and in less numbers sandsmelt (*Atherina boyeri* Risso), pumpkinseed sunfish (*Lepomis gibbosus* (L.)), and eels (*Anguilla anguilla* L.). Finally, the presence of potentially piscivorous species, such as pikeperch (*Sander lucioperca* L.) and sea bass (*Dicentrarchus labrax* (L.)) was insignificant (Table 2). In all the lakes mosquitofishes (*Gambusia holbrooki* Girard) were observed mainly in littoral zones, but were not captured. During spring 2002, fish biomass decreased to one third in the lake (Table 2). The predominant summer flathead mullet was not recorded, but carps, eels and golden mullets

Table 1. Morphometric and some trophic features of the study lakes. Limnological variables are mean summer values of 2000 and 2001 (modified from Alonso et al., 2002)

Lake	Mean depth (m)	Area (ha)	Conductivity ($\mu\text{S}\cdot\text{cm}^{-1}$)	Secchi depth (m)	Phytoplankton Chl- <i>a</i> ($\mu\text{g}\cdot\text{L}^{-1}$)	Submerged plants
Albufera	1	2300	2335	0.30	249	None
Cap de Terme	2.2	3.5	2665	0.45	93	scarce
Hondo	1	11	18380	Bottom	25	abundant
Baldoví	1.8	0.5	3020	Bottom	3	abundant
Cabanes	2.1	2.3	12693	Bottom	2	abundant

were captured, and pumpkinseed doubled its populations. Demographic structure revealed significant proportions of 0+ individuals for most species during both samplings (Fig. 1).

Algae found in guts content of all fish species of the Albufera lake during summer consisted mainly of colonial chroococcal cyanophytes and chlorophytes. In the gut sediment, rests of copepod eggs and ephippia were observed. During summer, *M. cephalus* had a benthic and pelagic feeding behaviour consuming mainly zooplankton (copepods amounted > 80% of preys), detritus and sediment. Although *L. aurata* is morphologically similar to this species, during summer it fed mainly on detritus and bottom sediment, animal components (gravid copepod females and eggs, and insects) amounting to only 22% of its diet. This changed markedly during spring, where insects, cladocerans (mostly *Daphnia magna*) and copepods were the main preys. Similarly, carps consumed detritus during summer but in spring selected cladocerans and copepods, increasing also the proportion of insects in the diet. It was observed that algae found in guts during spring were mainly filamentous chlorophytes and epipellic diatoms. The small *A. boyeri* (mean size 8 cm) was zooplanktivorous, predating mainly on copepods and insects. Detritus, algae and sediment was the predominant stomach content for *L. gibbosus* during summer, while cladocerans and dipterans represented 60% of the preys eaten in spring. Finally, *S. lucioperca* was the only piscivorous species in the Albufera, even though it was a young individual. Five small semi-digested fish (probably *Gambusia*) were found in its stomach together with some insects and zooplankton.

Lake Baldoví, young populations of Mediterranean barbel (*Barbus guiraonis* Steindachner) dominated the fish community, together but with much lower biomass of carp and flathead mullet (Table 2). All of them were detritivorous predating also on insects (Fig. 2).

During summer 2000, barbels ingested also an important quantity of copepod eggs and in the next summer large amounts of semi-digested *Ceratophyllum demersum*, especially in the bigger individuals, together with insects (Fig. 2). This plant sporadically developed in some parts of the lake during summer 2001.

Lake Hondo is a brackish lake (Table 1) with a fish community that changed interannually. There are important waterfowls in the reserve where the lake is located and lake water level varied markedly during the two study summers. The lake had in summer 2000 mainly eels and flathead mullets, while in summer 2001 a large population of 0+ sandsmelts, predominantly detritivorous (Figs. 1 and 2). Captured eels were clearly detritivorous, with animal preys focussed on insects, annelids and crayfish (Fig. 2).

Lake Cabanes is also brackish (Table 1) and located in a bird reserve area. In this lake was found one individual of the endemic and protected cyprinodont *Aphanius iberus* (Valenciennes in Cuvier & Valenciennes) (Table 2). The rest of the fish community consisted of young thin-lipped grey mullet (*Liza ramada* Risso), which was replaced in summer 2001 by the morphologically similar sandsmelt species. Some flathead mullets were also captured in the gill nets (Table 2). The diet of *L. ramada* consisted basically of detritus, with few individuals presenting important numbers of insects and copepods in the guts. The dominant *A. boyeri* in summer 2001 was detritivorous, but similarly to that observed in Hondo lake, here it also consumed non-dipteran insects.

Cap the Terme lake had a community consisting mostly of largemouth bass (*Micropterus salmoides* Lacèpede), an introduced species in Spain (Granado-Lorencio, 1996). Although it is a potential piscivorous species, the main dietary components for this species in the lake were detritus and insects.

Table 2. Length and weight of study fishes and related parameters ($W = a \cdot L^b$). n : number of fishes captured. k_i : condition factor. r^2 : Pearson's regression coefficient. N (mean catches per net) and weight (g) express CPUE (captures per unit of effort) calculated for <10 cm and > 10 cm total length (see 'Materials and methods' for further details)

Lake	Year	Species	L – W relationship					CPUE			
			n	a	b	r^2	k_i	< 10 cm		> 10 cm	
								N	Weight	N	Weight
Albufera	Summer 2000	<i>M. cephalus</i>	182	0.017	2.90	0.96	2.04	13	211	58	7712
		<i>C. carpio</i>	112	0.053	2.65	0.98	4.09	16	123	20	5427
		<i>L. gibbosus</i>	17	0.042	2.68	0.86	2.29	2	22	.25	4
		<i>S. lucioperca</i>	1	–	–	–	1.27			.5	14
		<i>L. aurata</i>	65	0.011	3.05	0.99	1.7			15	1923
		<i>A. boyeri</i>	11	0.06	2.23	0.84	1.74	4	16	0.12	3
		<i>A. anguilla</i>	1	–	–	–	0.13			0.12	4
		<i>D. labrax</i>	1	–	–	–	1.32			0.12	76
		Total						35	372	94.11	15163
	Spring 2002	<i>A. anguilla</i>	3	–	–	–	0.21			0.33	18
		<i>C. carpio</i>	10	0.016	3.04	0.99	2.43			4	3503
		<i>L. gibbosus</i>	38	0.04	2.58	0.89	2.27	3	19	1	13
		<i>L. aurata</i>	32	0.01	3.01	0.99	2.36	3	19	11	1724
		Total						6	38	16.33	5258
Baldoví	Summer 2000	<i>C. carpio</i>	2	–	–	–	1.91			2	128
		<i>L. aurata</i>	2	–	–	–	1.4			2	514
		<i>B. guiraois</i>	74	0.016	2.98	0.98	4.02	56	363	38	5392
		Total						56	363	42	6034
	Summer 2001	<i>B. guiraois</i>	57	0.017	2.95	0.98	6.08	30	142	13	3284
Hondo	Summer 2000	<i>M. cephalus</i>	1	–	–	–	1.06			1	1429
		<i>A. anguilla</i>	7	0.007	2.63	0.93	0.19			3	937
		Total								4	2366
	Summer 2001	<i>A. boyeri</i>	219	0.008	3.12	0.56	1.02	394	930		
		<i>G. holbrooki</i>	1	–	–	–	1.56	1	2		
		<i>A. anguilla</i>	2	–	–	–	0.22			3	2239
		Total						395	932	3	2239
Cabanes	Summer 2000	<i>A. iberus</i>	1	–	–	–	4.66	1	3		
		<i>L. ramada</i>	54	0.009	3.04	0.83	1.1	91	321	1	16
		Total						92	324	1	16
	Summer 2001	<i>M. cephalus</i>	2	–	–	–	0.55			3	969
		<i>A. boyeri</i>	96	0.030	2.36	0.12	0.99	142	676	1	13
		Total						142	676	4	982
	Summer 2001	<i>M. salmoides</i>	4	–	–	–	5.15	3	20	1	447

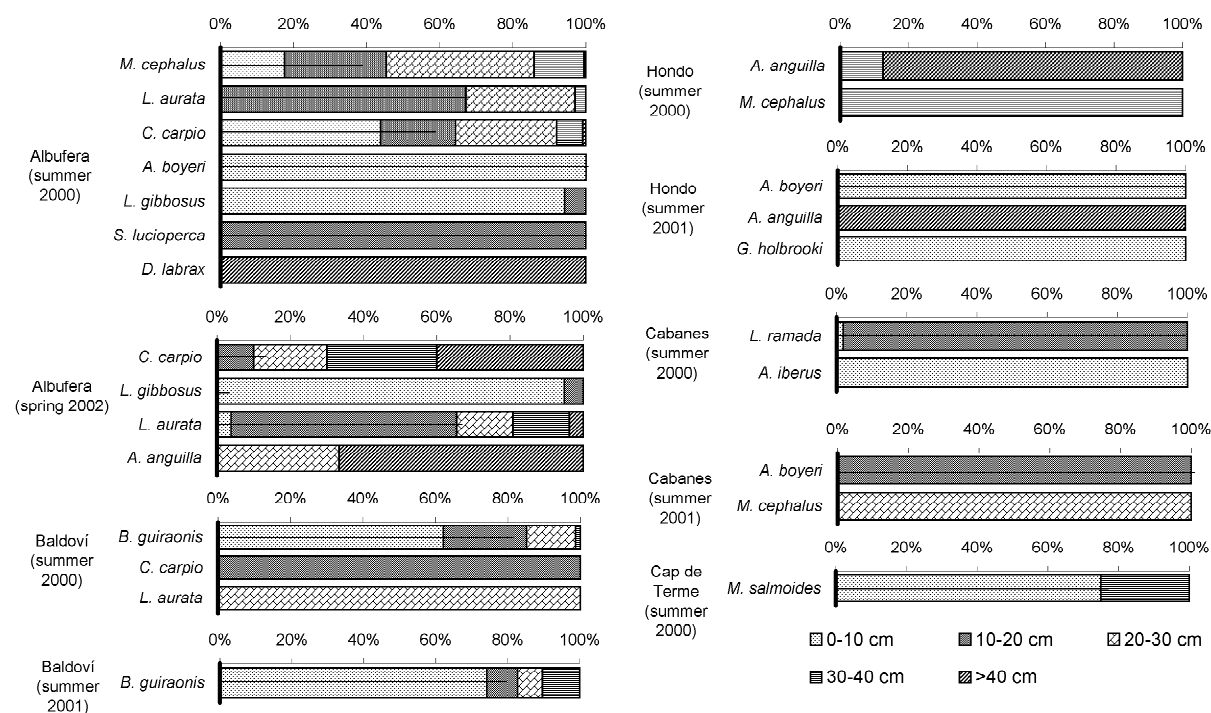


Figure 1. Frequency of each fish species length class (TL). Horizontal lines express the frequency of 0+ individuals.

Discussion

Fish feeding behaviour changed significantly among lakes and within the same lake. According to Lammen & Hoogenboezem (1991) fish diet in shallow lakes will relate to prey density, distribution and its availability. We observed that similar size-individuals of sandsmelt consumed zooplankton and insects in the Albufera lake, but detritus in the lakes Hondo and Cabanes. This ecological adaptation to food resources was also observed within the same lake, e.g. in the lake Albufera mostly species predated on zooplankton (large cladocerans) when they became dominant and visible during the spring clear water phases, but were mainly benthivorous during the summer turbid state. In this lake, mugilids played a key role in removing sediment (and possible indirectly nutrients) and large zooplankton, influencing likely the dominance in the lake of rotifers (Oltra et al., 2001) and stabilizing its turbid state. Fishing of these species in the lake by local fishermen is fixed between October and May, with maximum catches (about 150 kg.ha⁻¹) before clear water phases (January–March). Although nutrients in the lake are still high (e.g. mean TP > 0.3 mg L⁻¹, Villena & Romo, 2003), reduction of mullets could accelerate restoration of the Albufera

lake. They have a complex life cycle cohabiting in both marine and coastal lagoons (Cardona, 2000). In the Albufera lake, mugilids steeply increased with eutrophication of the lake in 1970s and specially after submerged macrophytes dissappeared (S. Romo, pers. comm.). Probably both dense cover of macrophytes and the presence of piscivorous species (specially *Dicentrarchus labrax*, Docavo, 1979) prevented their massive entry from the sea and development in the lake. Therefore, reestablishment of submerged macrophytes together with reduction of their populations could be complementary measures to restore the lake.

Mulletts were found almost in all the study lakes under different salinities and trophic states. They can be detritivorous (Porter et al., 1996), as well as benthivorous (Cardona & Castelló, 1989) and planktivorous (Cardona et al., 1996; Torras et al., 2000). Our dietary analysis supports that they feed on zooplankton, benthic insects, microalgae and detritus, this latter being an important resource. Cardona (2001) described for a coastal lagoon (Albufera des Grau, Balearic Islands) that spring diet of flathead mullet was based on algae but shifting to detritus, diatoms and sand in autumn, observing that mugilids reacted to detritus shortage by an expansion of its niche, consuming algae. In the Albufera, algae consumption may relate

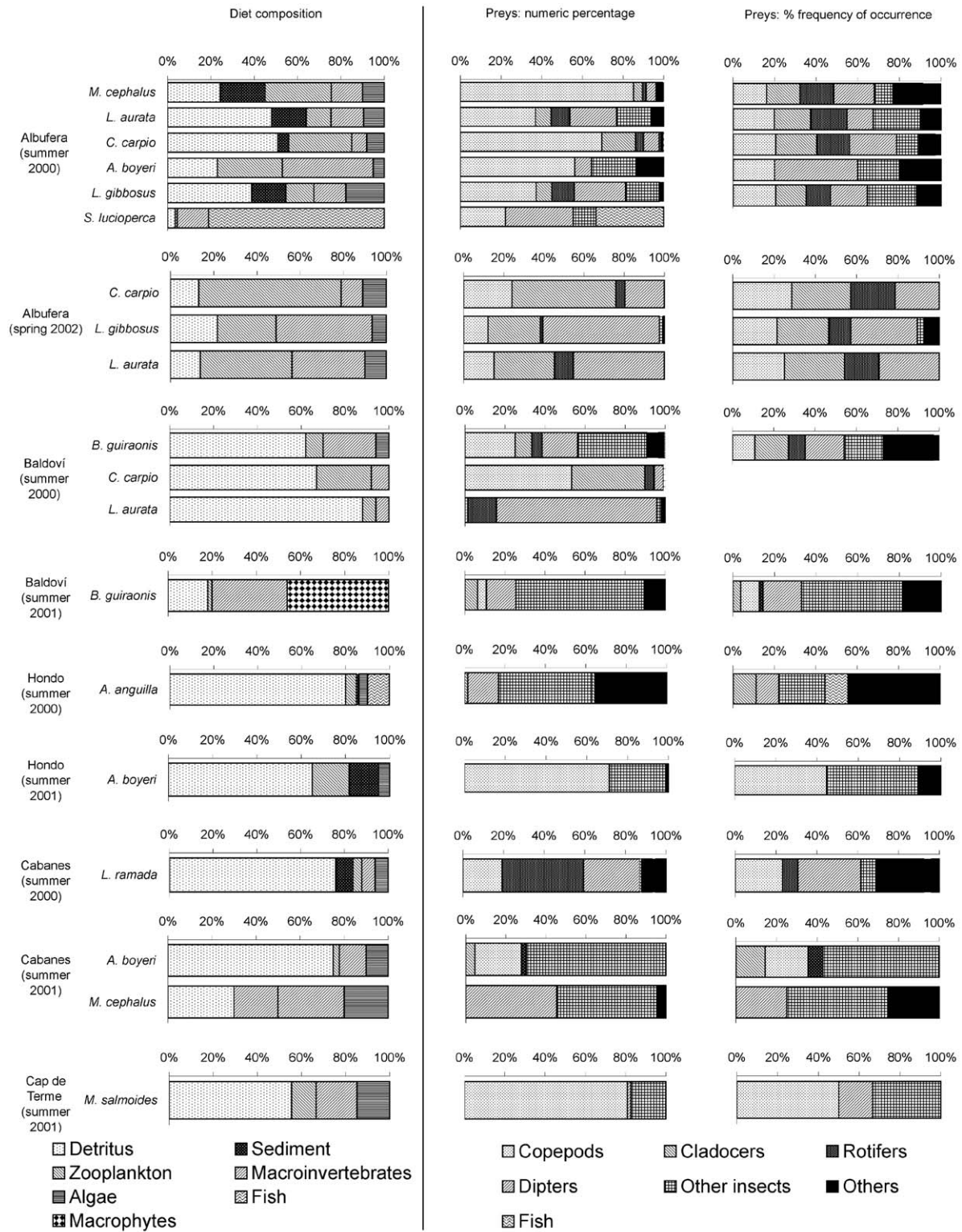


Figure 2. Fish diet composition, numeric percentage and frequency of occurrence (%) of prey for each fish species (see 'Materials and methods' for further details).

to fish feeding mainly on the surface mat-sediment, while in the lakes covered by macrophytes detritus and algae probably comes from periphyton. The effect on the food web may then vary, increasing nutrient recycling from the sediment in turbid lakes and maintaining macrophytes by removing periphyton.

In the study of Mediterranean shallow lakes, abundance of detritivorous and sedimentivorous species contrasts with zooplanktivorous and piscivorous species in Northern Europe (Jeppesen et al., 1990; Jacobsen et al., 1997; Tátrai et al., 2003) and North America (Carpenter & Kitchell, 1993) lakes. The recent introduction of piscivorous species like pikeperch can have unknown consequences. For instance, the widespread mosquitofish in shallow Spanish lakes has been detrimental for endemic species, such as *Aphanius iberus* or *Valencia hispanica* (García-Berthou & Moreno-Amich, 2000; Caiola et al., 2001). The dominance of generalistic and opportunistic fish species and the absence of piscivorous predators in the study lakes agree with that described in some food webs of tropical lakes (Lazzaro, 1997). Lack of fish control by piscivorous, the abundance of waterfowls in southern shallow lakes, together with lake water variations due to climate in the Mediterranean area lead to a high degree of fish community variability, such as was observed in the replacement of species from year to year, e.g. in Hondo and Cabanes lakes (Table 2). Annual floods allow interconnection between lakes from the same area that could also explain interannual changes in fish structure and the dominance of 0+ size fish. The cascading effect of fish predation became then rather unpredictable. The view that warmer lakes are predominantly controlled by bottom-up mechanisms (Lazzaro, 1997), was in part supported by our results since with similar functional fish species, clear water phases were maintained in those lakes with submerged plants and low nutrient levels (Cabanes, Baldoví and Hondo). This should imply a stronger environmental policy for water quality and vegetation conservation in these countries, but paradoxically contrast with their social tradition. Overall, more comparative studies from tropical, sub-tropical and warmer areas, such as the Mediterranean are needed.

Acknowledgements

We want to thank to Juan Miguel Benavent, Boro, José Luis Echevarría, José Manuel Poquet and the

guards from Parque Natural del Hondo for their useful help during the study. We are also grateful to the Consellería de Medio Ambiente de la Comunidad Valenciana and the Oficina Técnica Devesa-Albufera for the facilities given. This work was funded during by a European Community project (Environment Project ECOFRAME EVK1-CT-1999-00039).

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