Journal of Biological Research-Thessaloniki **19**: 139 – 149, 2013
J. Biol. Res.-Thessalon. is available online at http://www.jbr.gr
Indexed in: WoS (Web of Science, ISI Thomson), SCOPUS, CAS (Chemical Abstracts Service) and DOAJ (Directory of Open Access Journals)

Fish dietary patterns in the eutrophic Lake Volvi (East Mediterranean)

Dimitra C. BOBORI*, Ioanna SALVARINA and Evangelia MICHALOUDI

Laboratory of Ichthyology, Department of Zoology, School of Biology, Aristotle University of Thessaloniki, 54124 Thessaloniki, Greece

Received: 24 August 2012 Accepted after revision: 15 January 2013

The diet composition of ten fish species from the eutrophic East Mediterranean Lake Volvi was studied seasonally (summer 2005 – spring 2006) and in relation to body size. The index of relative importance (MI%) of each prey consumed varied within species. Diet diversity (Shannon-Wiener index, H') and diet breadth (Levins' standardized index, B') exhibited their highest values for almost all species in summer and in small size classes. Dietary overlap (Schoener's index, S) was higher between the different size classes of the same species. Cluster analysis, carried out on seasonal MI data, differentiated the following groups: (i) species feeding mainly on fish in all seasons (piscivorous), (ii) species feeding seasonally exclusively on zooplankton (zooplanktivorous), (iii) species with omnivorous feeding habits and preference in detritus and Chironomidae and (iv) omnivorous species that consumed mainly arthropods. Fish trophic niche widths were low, indicating a rather specialized feeding strategy for most species. The results will contribute to (a) understand species function in lake's food web, and (b) design commercial fisheries management strategies in the lake.

Key words: Diet overlap, gut content analysis, ontogenetic changes, seasonal variation, trophic guilds.

INTRODUCTION

Fish trophic ecology, food preferences, diet composition and diet overlap between coexisting species have been an issue of research for years (e.g. Hynes, 1950; Mendelson, 1975; Wootton, 1999). Knowledge of fish diet is important, among others, in defining the role of fish species in a system, their inter- and intra-specific relationships and their functioning within food webs (Pauly *et al*., 1998; Stergiou & Karpouzi, 2002), while it has been used for monitoring and management purposes (Zambrano *et al*., 2006). Furthermore, fish trophic ecology (trophic guilds, feeding habits) has been incorporated, among other metrics, in evaluating systems for the assessment of the ecological quality of the surface water ecosystems according to the European Water Framework Directive 2000/60/EC (European Commission, 2000).

* Corresponding author: tel.: +30 2310 998334, fax: +30 2310 998279, e-mail: bobori@bio.auth.gr

Fish feeding ecology and food preferences have been described for several marine and freshwater species (see Froese & Pauly, 2012). Especially for the Mediterranean region, such data is of major significance, due to the particulate importance of Mediterranean systems as biodiversity hotspots (Griffiths *et al*., 2004) and their recognized differences from other temperate systems (Alvarez Cobelas *et al*., 2005).

Fish communities in Greek lakes are characterized by the dominance of omnivorous cyprinids (Bobori & Economidis, 2006; Economou *et al*., 2007) and the rarity of piscivorous species. However, despite their wide dispersal, data concerning their diet composition are limited with most of them referring to a specific species from one lake (e.g. Iliadou, 1991; Politou *et al*., 1993; Kleanthidis & Sinis, 2001; Chrisafi *et al*., 2007; Gkenas *et al*., 2012).

The present study is the first effort to comprise information on the diet preferences of the most commercial fish species in Lake Volvi. The objectives were: (a) to provide qualitative and quantitative data on the seasonal and size related fish diet composition, and (b) to define trophic guilds and assess food utilization and competition within and among species.

MATERIALS AND METHODS

Study area

Lake Volvi, situated in N Greece (Fig. 1), at 37 m a.s.l. has a surface area of 68.6 km^2 and mean and maximum depth of 13.8 m and 19 m, respectively. It is a eutrophic lake that stratifies during summer (Moustaka-Gouni, 1988), it is listed under the 79/409/EEC Directive, the Ramsar Convention, it is included in NATURA 2000 sites and it is part of a National Wetland Park.

Fish sampling

Samples were collected seasonally (summer 2005 – spring 2006), during three to four consecutive days for each season, mainly from the western part of the lake (Fig. 1), since no spatial differences in the limnological features of the lake have been reported (Kaiserli *et al*., 2002; Gantidis *et al.*, 2007). When necessary, additional fish were collected from the eastern part. Gill nets (100 m long, 3 m height) of 8 different mesh sizes (from 12 to 60 mm knot to knot) were used. The nets were dropped in the evening and lifted the next morning, ensuring thus an approximate sampling duration of about 12 hrs. This approach was chosen due to the small number of fish caught when nets were left only for a few hours in order to avoid food digestion. Only *Alburnus* sp. Volvi specimens were collected after two hours netting, since a sufficient number of individuals was caught. All specimens were immediately preserved in 10% formalin solution. In the laboratory, individuals were identified to species level (nomenclature after Kottelat & Freyhof, 2007) and measured for total length (TL, cm) and total weight (W, g). For gut content analysis the recommendations suggested by Stergiou & Karpouzi (2002) were followed.

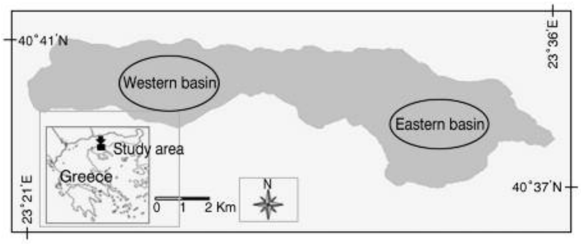

FIG. 1. Map of Lake Volvi with the fish sampling areas.

Diet analysis

For the diet analysis, the stomach contents (for the species *Anguilla anguilla*, *Esox lucius* and *Perca fluviatilis*) or the contents of the first 2/3 of the gastrointestinal track (for the rest of the cyprinid species) were used (Vašek *et al*., 2003) with the exception of *Alburnus* sp. Volvi for which the first 1/3 of its gastrointestinal track was used (according to Politou *et al*., 1993). Prey items were identified to the lowest possible taxonomic level, counted and weighted (wet weight, in g).

For each species, feeding activity was evaluated by the vacuity index (VI%), estimated as the percentage of empty guts (Hureau, 1966). The fullness index (FI) was expressed for each specimen on an empirical scale, ranging from 0 (empty gut) to 5 (full gut).

The gut contents were assessed by calculating (a) the percentage of frequency of occurrence FO% = (number of guts containing a food item/total number of guts with food) × 100 and (b) the percentage gravimetric composition W% = (wet weight of each prey item/total gut content weight) × 100 (Hyslop, 1980). For small sized food categories, the weight of each prey item in each gut was estimated indirectly, using the individual weight of each species known from literature (for zooplankton: Michaloudi, 2005; for Chironomidae: Economidis, 1991; for nematodes and ostracods: Wolfram-Wais *et al*., 1999).

The index of relative importance (MI%) of each food item was estimated according to Castriota *et al*. (2005) as follows:

$$MI\% = [(FO\% \times W\%) / \Sigma\,(FO\% \times W\%)] \times 100$$

Diet diversity was measured by the Shannon-Wiener index (H') (Krebs, 1994) as:

$$H' = -\sum_{j=1}^{m} P_j \log_e (P_j),$$

where P_j is the proportion of the gravimetric contribution (W%) of food item *j* in the diet of species.

Diet breadth was estimated using Levins' standardized index (B') (Castriota *et al*., 2005):

$$B' = \frac{1}{n-1}\left(\frac{1}{\sum_j p_{ij}^2} - 1\right),$$

where B' is Levins' standardized index for species *i*, p_{ij} is the proportion of the index of relative importance (MI%) of food item *j* in the species *i* diet and *n* is the number of food items. The index ranges between 0 and 1 and is used to show the relative level of diet specialization of a species. Low index values characterise a species diet dominated by few prey items (specialist) while high values are indicative of a more generalist diet (e.g. Ellis *et al*., 1996).

The degree of niche overlap in the diet was estimated using Schoener's index (Schoener, 1970) as follows:

$$S = 1 - 0.5\left(\sum_{i=1}^{n}|p_{xi} - p_{yi}|\right),$$

where S is the Schoener's index, p_{xi} is the proportion of modified index of relative importance of food item i in the diet of species x, p_{yi} is the proportion of food item i in the diet of species y and n is the number of food categories (Castriota *et al*., 2005). The index ranges from 0 (no overlap) to 1 (total overlap); values greater than 0.60 are indicative of biologically meaningful diet overlap (Wallace, 1981; Clarke *et al*., 2005).

Statistical analysis

Analysis of variance (one-way ANOVA) and t-test were applied accordingly to test for seasonal differences in VI and FI values after running the Shapiro-Wilk test to check for normality (in all cases, $p > 0.05$). For within pair differences, the Fisher's LSD test was further performed. Testing for differences in diet composition per species per season, as well as per size class, Kruskal-Wallis test was applied on the MI% values of the most abundant species, after arcsine transformation. Size-related variations in fish diet were examined after dividing the most abundant species into three size classes: small (TL < 20 cm), medium (TL between 20.1 cm and 30 cm) and large (TL > 30.1 cm) except for *Alburnus* sp. Volvi, where no size classes were identified, due to the narrow length range of the specimens examined. For species where only two length classes were defined, the Mann-Whitney U test was applied accordingly. Functional feeding groups were identified by multivariate analysis (Cluster Analysis). Two matrices were constructed, based on the MI (%) composition for each species per season and per size class accordingly. Data were square root transformed, in order to reduce the weighting of abundant food categories, prior to calculation of similarity matrices based on Bray-Curtis similarity index (Bray & Curtis, 1957). Significant differences between groups resulted from Cluster analyses were tested by the Analysis of Similarities (ANOSIM). In addition, similarity percentage analysis (SIMPER) was used in order to identify the food items contributing to the similarity within and dissimilarity between groups (Clarke & Gorley, 2001). For all the above analyses the PRIMER (Clarke & Gorley, 2001), Statistica (StatSoft, Tulsa, OK, USA) and SPSS (SPSS Inc., Chicago, USA) software were used.

RESULTS

Diet analysis

A total of 964 specimens, belonging to 10 fish species and 4 families, were examined with TL ranging between 8.9 and 49.0 cm (Table 1). The number of the species caught varied among seasons, with the most numbered species being recorded in summer (Table 1). In general, for all species examined, mean VI values were higher during autumn (51.8%) and lower in summer (25.5%). However, no significant differences were found between any pair of seasonal VI and FI mean values (ANOVA, $p > 0.05$). Within species, seasonal differences of FI were observed for *Abramis brama*, *Alburnus* sp. Volvi, *Perca fluviatilis* and *Scardinius erythrophthalmus* (ANOVA, $F > 4.43$, $p < 0.005$), between summer-autumn and autumn-spring combinations (Fisher's LSD test, $p < 0.05$). Moreover, size related differences of FI values were apparent only in *Abramis brama*, between medium and large size classes ($F = 3.053$, $p < 0.05$).

Thirteen food items were identified in the guts examined. Within species, the index of relative importance (MI%) did not differ significantly among seasons (Kruskal-Wallis test, $p > 0.05$; Fig. 2) and size classes (Kruskal-Wallis test, $p > 0.05$; Fig. 3). *Abramis brama* consumed mostly Chironomidae (up to 83% in spring) and detritus (up to 80% in autumn), with the later being the most abundant food item (up to 75%) in the large sized specimens. *Vimba melanops* exhibited a high preference in arthropods (up to 90.9% in winter), which also dominated (76%) in the diet of the medium class individuals. *Alburnus* sp. Volvi was the only planktivorous species, with a narrow dietary breadth (Table 2), feeding almost exclusively on zooplankton in winter and spring (up to 99.9%), while in summer and autumn species diet was more diverse, including arthropods (up to 61.5% in autumn) and detritus (28.3% in summer). *Carassius gibelio* fed during summer and autumn mainly on detritus (up to 94.6%). Zooplankton was the most preferred item during winter and spring (68.9 and 87.6%, respectively), constituting up to 72% of the small size specimens' diet (Fig. 3). *Perca fluviatilis* was exclusively a piscivorous species, showing the lowest trophic diversity, while *Scardinius erythrophthalmus* exhibited a diverse and generalized diet (Table 2). The main food

TABLE 1. Vacuity Index (VI%), Fullness Index (FI) and descriptive statistics of the total length (TL, cm) of the fish species used for diet analysis per season. n: number of specimens, SU: summer, A: autumn, W: winter, SP: spring. Species names according to Kottelat & Freyhof (2007) (name abbreviations in parenthesis)

Family/Species	Season	n	VI %	FI mean ± SE	TL (cm) mean ± SE	Min-Max
Anguillidae						
Anguilla anguilla (Aa)	SU	1		1.0		32.0
Cyprinidae						
Abramis brama (Ab)	SU	38	47.37	1.2 ± 0.2	28.41 ± 0.72	20.4-38.3
	A	55	56.36	1.5 ± 0.2	30.54 ± 0.49	24.8-36.4
	W	83	73.49	0.7 ± 0.1	25.82 ± 0.36	17.5-33.0
	SP	41	56.10	1.1 ± 0.2	28.39 ± 0.97	19.7-44.0
Alburnus sp. Volvi (AspV)	SU	26	19.23	1.6 ± 0.3	12.34 ± 0.22	10.9-14.9
	A	34	35.29	1.5 ± 0.3	12.03 ± 0.16	10.5-14.1
	W	39	10.26	2.0 ± 0.2	11.52 ± 0.08	10.2-12.7
	SP	47	12.77	2.7 ± 0.2	11.22 ± 0.08	10.4-12.4
Alburnus volviticus (Av)	SU	1	0	3.0		16.2
	W	2	50.00	3.0	19.40 ± 0.40	19.0-19.8
	SP	6	16.67	1.8	15.65 ± 0.62	13.2-17.5
Carassius gibelio (Cg)	SU	34	32.35	2.1 ± 0.3	22.16 ± 0.65	14.8-28.7
	A	40	27.50	2.5 ± 0.3	25.88 ± 0.51	21.3-32.3
	W	41	14.63	1.9 ± 0.2	26.38 ± 0.51	12.9-31.0
	SP	29	10.34	2.2 ± 0.2	22.75 ± 0.50	18.2-27.3
Cyprinus carpio (Cc)	SU	7	28.57	1.9 ± 0.7	37.77 ± 2.86	26.2-49.0
	A	10	90.00	0.4 ± 0.3	27.87 ± 3.63	14.4-45.0
	W	6	50.00	1.0 ± 0.3	22.85 ± 1.35	21.5-24.2
	SP	3	100.00	0.0	29.93 ± 3.16	24.5-39.0
Scardinius erythrophthalmus (Se)	SU	8	12.50	1.9 ± 0.5	19.89 ± 0.32	18.7-21.2
	A	24	75.00	0.4 ± 0.2	21.16 ± 0.44	15.0-25.5
	W	25	56.00	0.5 ± 0.2	18.86 ± 0.29	17.3-22.9
Vimba melanops (Vm)	SU	36	44.44	1.4 ± 0.3	23.48 ± 0.45	17.5-31.7
	A	19	31.58	1.6 ± 0.3	23.34 ± 0.40	19.9-26.5
	W	64	32.81	1.8 ± 0.2	22.59 ± 0.26	16.3-29.6
	SP	22	18.18	1.3 ± 0.3	23.35 ± 0.60	16.0-27.2
Esocidae						
Esox lucius (El)	SU	2		1.5 ± 1.5	30.85 ± 2.65	28.2-33.5
	A	1		4.0		40.1
Percidae						
Perca fluviatilis (Pf)	SU	70	20.00	2.0 ± 0.2	15.83 ± 0.31	8.9-24.3
	A	36	47.22	1.7 ± 0.3	22.23 ± 0.57	12.9-36.0
	W	56	44.64	1.5 ± 0.2	18.66 ± 0.51	14.5-38.7
	SP	58	18.97	2.5 ± 0.2	23.86 ± 0.67	14.5-34.3

items consumed during summer were macrophytes (66.4%), followed by fish (17.1%) and arthropods (15.3%) while in autumn the diet of the species was supplemented with nematodes and detritus. The later was the most significant food item in the species diet during winter (72.3%, Fig. 2). Detritus was also abundant (50%) in the diet of the small sized class specimens, whereas, medium sized individuals of *Scardinius erythrophthalmus* preferred mainly macrophytes (80%). Generally, the studied species, with a few exceptions, exhibited a more diverse and generalized diet during summer and in small size classes

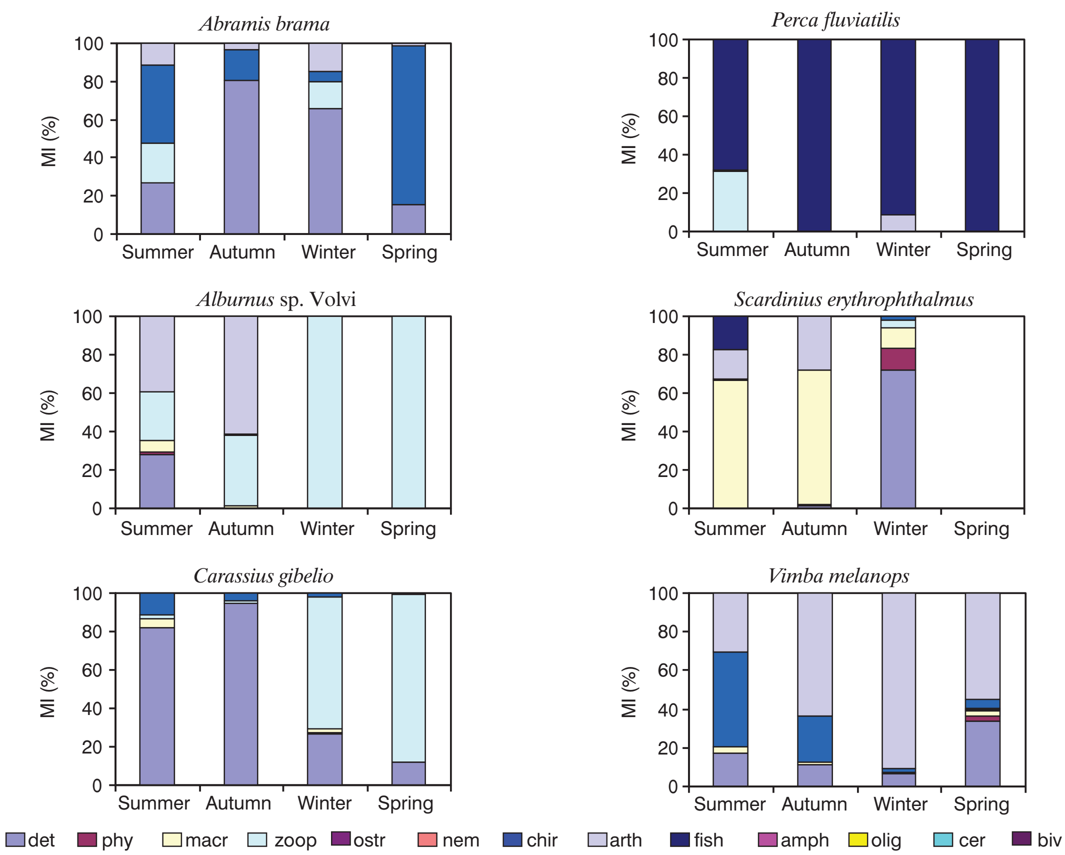

FIG. 2. Seasonal diet composition of the most abundant species based on the index of relative importance (MI%). Abbreviations: det: detritus, phy: phytoplankton, macr: macrophytes, zoop: zooplankton, ostr: ostracods, nem: nematods, chir: Chironomidae, arthr: arthropods, fish: fish, amph: amphipods, olig: oligochaets, cer: Ceratopogonidae, biv: bivalves.

TABLE 2. Shannon-Wiener diversity (H') and Levins' (B') indices of fish species diet per season and per size class

	Season								Size classes					
	Summer		Autumn		Winter		Spring		Small (<20 cm)		Medium (20.1-30 cm)		Large (>30.1 cm)	
Species	H'	B'	H'	B'	H'	B'	H'	B'	H'	B'	H'	B'	H'	B'
Abramis brama	1.33	0.47	0.89	0.08	1.16	0.22	0.69	0.10			1.13	0.24	0.91	0.05
Alburnus sp. Volvi	1.47	0.34	1.00	0.16	0.23	0.00	0.11	0.00						
Alburnus volviticus	0.92	0.59			0.25	0.06	0.67	0.50						
Carassius gibelio	0.84	0.07	0.52	0.02	0.54	0.14	0.04	0.05	0.96	0.12	1.16	0.18	0.89	0.21
Cyprinus carpio	0.69	0.03	0.00	0.00	0.00	0.01	0.00	0.00						
Perca fluviatilis	0.81	0.16	0.21	0.01	0.54	0.18	0.00	0.00	0.85	0.08	0.00	0.00	0.00	0.00
Scardinius erythrophthalmus	1.07	0.15	0.88	0.15	1.29	0.16				0.31		0.11		
Vimba melanops	1.18	0.35	1.07	0.18	0.84	0.03	0.91	0.20	1.92	0.27	1.59	0.06		

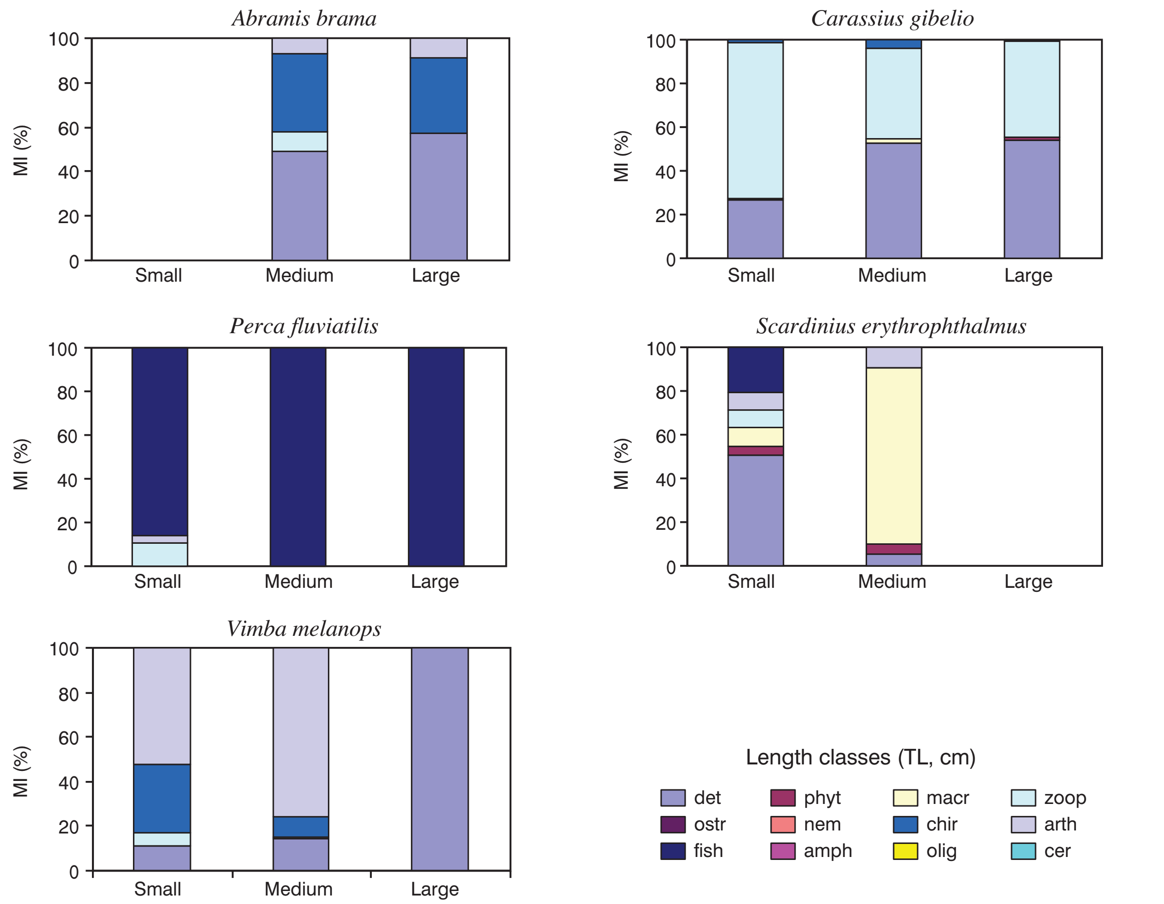

FIG. 3. Size-related diet composition of the most abundant species based on the index of relative importance (MI%). Abbreviations as in Figure 2.

TABLE 3. Diet overlap (Schoener's index, *S*) for the pairs of species per season and size class. Only significant similarities for *S* > 0.60 are indicated. S: Small (TL < 20 cm), M: Medium (20.1 cm < TL < 30 cm) and L: Large (TL > 30.1 cm) size classes. Species name abbreviations as in Table 1

	Season				Size class	
	Summer	Autumn	Winter	Spring		
Ab-Cg		0.843			AspV(S)-*Cg*(S)	0.731
Ab-Se			0.716		*Cg*(S)-*Cg*(M)	0.692
Ab-Vm	0.698				*Cg*(S)-*Cg*(L)	0.715
AspV-*Av*	0.615				*Pf*(S)-*Ab*(M)	0.860
AspV-*Cg*			0.692	0.876	*Pf*(S)-*Pf*(M)	0.860
AspV-*Cc*		0.615			*Pf*(S)-*Pf*(L)	0.860
AspV-*Vm*		0.628			*Se*(S)-*Ab*(M)	0.635
Aa-El	1.000				*Se*(S)-*Cg*(M)	0.605
Aa-Pf	0.679				*Vm*(S)-*Vm*(M)	0.727
Av-Cc	0.675			0.643	*Ab*(M)-*Cg*(M)	0.623
Av-Pf			0.916		*Ab*(M)-*Ab*(L)	0.750
El-Pf	0.679	0.997			*Cg*(M)-*Cg*(L)	0.949
					Pf(M)-*Pf*(L)	1.000

(Table 2). *Scardinius erythrophthalmus* was the only species where diet diversity (H') and dietary breadth (B') were higher during winter. A more generalized diet was also observed for *Carassius gibelio* during winter and for the large sized individuals, as B' values were progressively increased with body size (Table 2). The dietary overlap (S) varied with season and body size (Table 3). In general, it was higher between the different size classes of the same species (e.g. *Perca fluviatilis*, *Carassius gibelio*), than between the size classes of different species.

Functional feeding guilds

Cluster analysis, differentiated two main groups (ANOSIM, R = 0.439, $p = 0.0001$; Fig. 4a and Table 4): (i) species feeding mainly on fish in all seasons (Group I), and (ii) the species (Group II) feeding seasonally on one or more prey categories. The latter group was further divided into three sub-groups (ANOSIM, R= 0.646, $p = 0.0001$), that included: (a) species feeding during winter and spring exclusively (*Alburnus* sp. Volvi) or almost exclusively (*Carassius gibelio*) on zooplankton (sub-group IIa), (b) species with omnivorous feeding habits and preference on detritus and Chironomidae all year through (*Abramis brama*) or seasonally (*Carassius gibelio*), forming sub-group IIb, and (c) species that consumed mainly arthropods (sub-group IIc; *Vimba melanops*, *Cyprinus carpio*). The cumulative contribution (SIMPER analysis) of the main food categories to the average Bray-Curtis similarity within each group is shown in Table 4. Moreover, cluster analysis based on the size related variation in diet composition revealed three main groups (ANOSIM, R = 0.945, $p = 0.0003$; Fig. 4b, Table 4). In group I, fish was the prey almost exclusively consumed by all size classes of *Perca fluviatilis*. Group II was consisted of the medium sized individuals of *Scardinius erythrophthalmus*. The formed group III was further divided into two sub-groups (ANOSIM, R = 0.906, $p = 0.0001$). In sub-group IIIa (consisted of medium and large specimens of *Abramis brama* and small and medium individuals of *Vimba melanops*), Chironomidae (cumulative contribution 33.1%; Table 4), detritus (31.2%) and arthropods (28.4%) were almost equally contributed to the total prey eaten, while in sub-group IIIb (formed mainly by all size classes of *Carassius gibelio*), zooplankton (37.8%) was the second more frequent eaten prey after detritus (48.5%; Table 4).

DISCUSSION

We studied the seasonal variation and size-related variation of the diet composition of the most commercially exploited and more frequent caught species in the eutrophic Lake Volvi in order to examine diet overlap among species and define the trophic guilds of the fish assemblage. All species examined consumed a variety of food items, that is generally in agreement with the literature (e.g. Michel & Oberdorff, 1995; Froese & Pauly, 2012), with a few exceptions (*Abramis brama*; Biró *et al*., 1991). Some preys like fish, arthropods, Chironomidae, zooplankton and detritus, contributed greater in the diet of the species examined, reflecting either the species preference for certain food categories or their presence, being the result of a slower digestion rate (zooplankton crustaceans; Wootton, 1999), compared to others that are digested faster and are not easily recognised.

In fish diet research, seasonal variations in diet composition have been related, among others, to water temperature (Jardas *et al*., 2004) and have been previously reported also for *Alosa macedonica* from

TABLE 4. Percentage contribution (%) of each food category to the average Bray-Curtis similarity (%) within each group discriminated by multivariate analysis. Numbers below groups indicate the overall similarity within each group

	Groups based on season				Groups based on size classes			
	I	IIa	IIb	IIc	I	II	IIIa	IIIb
Average similarity (%)	84.8	76.8	60.4	58.3	83.5		70.1	70.0
Fish	98.8				99.5			
Zooplankton		90.7						37.8
Arthropods			10.8	80.0			28.4	
Detritus			52.2	5.7			31.2	48.5
Chironomidae			28.7				33.1	5.1
Macrophytes				8.3				

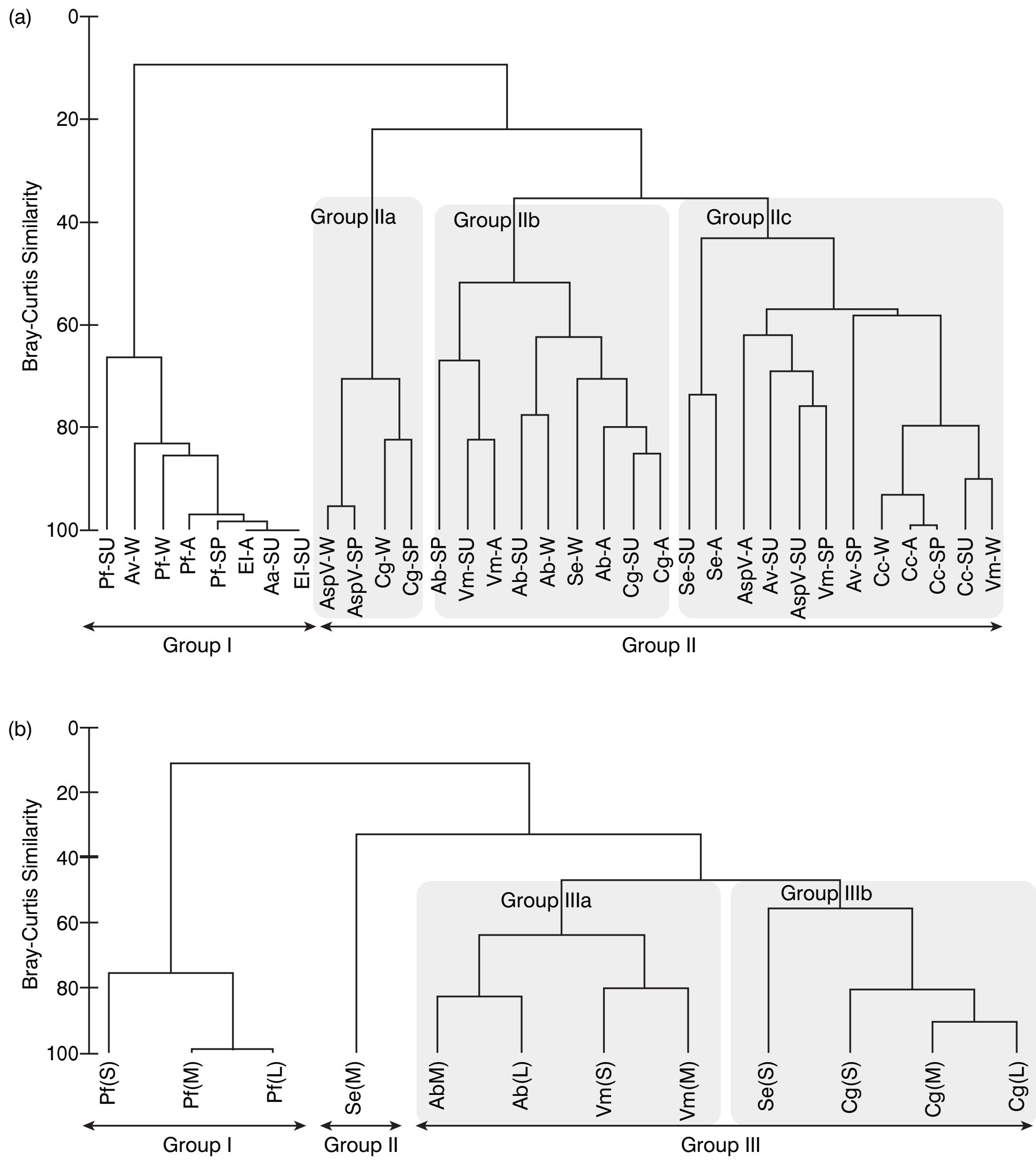

FIG. 4. Cluster analysis (group average linkage) based on the Bray-Curtis similarities of the index of relative importance (MI%, square root transformed) of each food category identified in the diet of each species (a) per season, and (b) per size class. Abbreviations as in Table 1.

the Lake Volvi (Kleanthidis & Sinis, 2001) and *Alburnus alburnus* from the nearby Lake Koronia (Politou *et al*., 1993). However, it is well known that several other factors such as the food availability (Encina *et al*., 2004; Bănaru & Harmelin-Vivien, 2009) may account for seasonal variations in fish diet. The diet composition of the species examined here exhibited a moderate variation depending on seasons that could not generally be considered as indicative of any discontinuity in their food preferences. The species *Alburnus* sp. Volvi and *Carassius gibelio*, which consumed zooplankton in spring and almost exclusively during winter, seemed to follow the general seasonal pattern of zooplankton abundance described for Lake Volvi (Zarfdjian *et al*., 1990). The zooplanktivorous feeding behavior of the above species was not evident during summer and autumn, when both species behaved as bottom feeders. The consumption by *Abramis brama* of Chironomidae larvae during spring and summer, when the densities of this prey are higher (Economidis, 1991), may also be indicative that fish exploit food resources depending on the availability and abundance of the food prey. During winter the omnivorous species (Group IIb) exhibited a preference on detritus (mainly *Abramis brama* and *Scardinius erythrophthalmus*). Detritus is a food resource that is accessible for benthic fish all year through and is considered to be consumed in variable quantities especially by cyprinids (Tolonen *et al*., 2000). It can be selected or be consumed accidentally (Michelsen *et al*., 1994) due to the habitat the fish is feeding. According to more recent studies, detritus could potentially act as a valuable food resource for several fish species, having higher nutritional value than algae (Wilson *et al*., 2003). However, as the protein content of detritus varies, fish species that feed on it have to supplement their diet with other food categories (invertebrates) in order to meet their nutritional requirements (Bowen *et al*., 1995). This feeding strategy seems to be followed by the species *Abramis brama*, *Carassius gibelio* and *Vimba melanops*, which complemented their detritivorous diet with other animal preys. Finally, the high contribution of zooplankton to *Perca fluviatilis* diet during summer should be attributed to the smaller bodied specimens caught this period compared to the other seasons.

It is well known that fish select their prey not only in relation to the above mentioned factors but also in relation to their body size (e.g. Pen & Potter, 2006). Such ontogenetic shifts in fish diet are documented for only a few freshwater Greek species (e.g. Gkenas *et al*., 2012), and are mostly referred to the use of larger and most diverse preys as the species grow. Although this is a general phenomenon, it was not so clearly observed for the species studied, except for *Perca fluviatilis*. The larger size classes exhibited the lower breadth values and a dominance of fish in species diet, indicating a piscivorous status at the top of lake's food web. Fish had also a significant contribution to the smaller (<20 cm) *Perca fluviatilis* specimens that could probably be indicative of a possible onset of piscivory. Fish dominantly consumption by specimens of *Perca fluviatilis* <8 cm, is reported (Akin *et al.,* 2011) and is attributed to ontogenetic development and food availability.

Generally, the present results revealed a higher interspecific and intraspecific dietary diversity and a more generalized diet of the small body specimens, indicating their ability to shift their diet to available food sources. This is also evident by the observed diet overlap, which was generally low for most of the species/seasons pair combinations. In precise, higher and more pronounced diet overlap was recorded for the piscivorous species, while for the rest of the species combinations, seasonal variations were observed, indicating that different species in each season segregate the same food resources, depending possibly on their availability. The partitioning of feeding niche among species permits them to coexist in the same system (Mendelson, 1975). Even when species consume the same food categories, they may feed in different microhabitats (e.g.Wolfram-Wais *et al*., 1999). As concerns *Perca fluviatilis*, it exhibited high dietary overlap not only with the other piscivorous species, but also with *Alburnus volviticus* in winter. The shift of the latter species to piscivory diet during winter may be the result of the congregation of species assemblage in the profundal zone of the lake, where a wider range of fish communities is supported (e.g. Winfield, 2004) and hence a wider range of preys is provided.

In conclusion, the results obtained in the present study revealed a trophic partitioning of the food resources among the fish species. Fish trophic niche widths were low, since most of our species consumed a few food categories available in the lake, exhibiting thus a rather specialized feeding strategy depending on the season. However, most of the species studied showed a feeding plasticity by adapting their diet to prey categories that are more available in the system in each season. Generally, the fish assemblage studied was dominated by omnivorous cyprinid species that often dominate in eutrophic Mediterranean lakes (Blanco *et al*., 2003). However, since their role in the lake's food web structure and dynamics is poorly known, the results provided here will contribute to (a) understand species function in biomass flow and (b) extract trophic guild metrics for the ecological evaluation of the lake in accordance to the European Water Framework Directive 2000/60/EC. Given that fish ecology and fish community dynamics are crucial issues of ecosystem-based approaches for fisheries management (Pikitch *et al*., 2004), our results will also contribute in designing commercial fisheries management strategies in the lake.

ACKNOWLEDGEMENTS

The authors would like to thank Dr. Lourdes Encina for her assistance in diet analysis. Current address of IS is Limnological Institute, University of Konstanz, Mainaustrasse 252, 78464 Konstanz, Germany.

REFERENCES

Akin Ş, Sahin Ç, Verep B, Turan D, Gözler AM, Bozkurt A, Çelik K, Çetin E, Araci A, Sargın I, 2011. Feeding habits of introduced European perch (*Perca fluviatilis*) in an impounded large river system in Turkey. *African Journal of Agricultural Research*, 6: 4293-4307.

Alvarez Cobelas M, Rojo C, Angeler DG, 2005. Mediterranean limnology: current status, gaps and the future. *Journal of Limnology*, 64: 13-29.

Bănaru D, Harmelin-Vivien M, 2009. Feeding behavior of Black Sea bottom fishes: did it change over time? *Acta Oecologica*, 35: 769-777.

Biró S, Sadek SE, Paulovits G, 1991. The food of bream (*Abramis brama* L.) in two basins of Lake Balaton of different trophic status. *Hydrobiologia*, 209: 51-58.

Blanco S, Romo S, Villena M-J, Martínez S, 2003. Fish communities and food web interactions in some shallow Mediterranean lakes. *Hydrobiologia*, 506-509: 473-480.

Bobori DC, Economidis PS, 2006. Freshwater fishes of Greece: their biodiversity, fisheries and habitats. *Aquatic Ecosystem Health & Management*, 9: 407-418.

Bowen SH, Lutz EV, Ahlgren MO, 1995. Dietary protein and energy as determinants of food quality: trophic strategies compared. *Ecology*, 76: 899-907.

Bray JR, Curtis JT, 1957. An ordination of the upland forest communities of southern Wisconsin. *Ecological Monographs*, 27: 325-349.

Castriota L, Scarabello MP, Finoia MG, Sinopoli M, Andaloro F, 2005. Food and feeding habits of pearly razorfish, *Xyrichtys novacula* (Linnaeus, 1758), in the southern Tyrrhenian Sea: variation by sex and size. *Environmental Biology of Fishes*, 72: 123-133.

Chrisafi E, Kaspiris P, Katselis G, 2007. Feeding habits of sand smelt (*Atherina boyeri*, Risso 1810) in Trichonis Lake (Western Greece). *Journal of Applied Ichthyology*, 23: 209-214.

Clarke KR, Gorley RN, 2001. *PRIMER v5: User Manual/Tutorial*. PRIMER-E, Plymouth.

Clarke LR, Vidergar DT, Bennett DH, 2005. Stable isotopes and gut content show diet overlap among native and introduced piscivores in a large oligotrophic lake. *Ecology of Freshwater Fish*, 14: 267-277.

Economidis GB, 1991. Bionomic study of the benthic macrofauna of Lake Volvi. Ph. D. Thesis, Aristotle University of Thessaloniki.

Economou AN, Giakoumi S, Vardakas L, Barbieri R, Stoumboudi M, Zogaris S, 2007. The freshwater ichthyofauna of Greece- an update based on a hydrographic basin survey. *Mediterranean Marine Science*, 8: 91-166.

Ellis JR, Pawson MG, Shackley SE, 1996. The comparative feeding ecology of six species of shark and four species of ray (Elasmobranchii) in the north-east Atlantic. *Journal of the Marine Biological Association of the United Kingdom*, 76: 89-106.

Encina L, Rodríguez-Ruiz A, Granado-Lorencio C, 2004. Trophic habits of the fish assemblage in an artificial freshwater ecosystem: the Joaquín Costa reservoir, Spain. *Folia Zoologica*, 53: 437-449.

European Commission, 2000. Directive 2000/60/EC of the European Parliament and the council 23rd October establishing a framework for community action in the field of water policy. *Official journal of the European Communities*.

Froese R, Pauly D, 2012. *FishBase. World Wide Web electronic publication*. www.fishbase.org, version (08/2012).

Gantidis N, Pervolarakis M, Fytianos K, 2007. Assessment of the quality characteristics of two lakes (Koronia and Volvi) of N. Greece. *Environmental Monitoring and Assessment*, 125: 175-181.

Gkenas Ch, Malavasi S, Leonardos I, 2012. Diet and feeding habits of *Economidichthys pygmaeus* (Perciformes: Gobiidae) in Lake Pamvotis, NW Greece. *Journal of Applied Ichthyology*, 28: 75-81.

Griffiths HI, Krytufek B, Reed JM, 2004. *Balkan Biodiversity: pattern and process in the european hotspot.* Kluwer Academic Publishers, Dordrecht, The Netherlands.

Hureau JC, 1966. Biologie comparée de quelques poissons antartique (Nototheniidae). *Bulletin de l'institut Oceanographique (Monaco)*, 68: 1-244.

Hynes HBN, 1950. The food of fresh-water sticklebacks (*Gasterosteus aculea*tus and *Pygosteus pungitius*), with a review of methods used in studies of the food of fishes. *Journal of Animal Ecology*, 19: 36-58.

Hyslop EJ, 1980. Stomach content analysis- a review of methods and their application. *Journal of Fish Biology*, 17: 411-429.

Iliadou K, 1991. Feeding of *Scardinius acarnanicus* Stephanidis, 1939 (Pisces: Cyprinidae) from lakes Lysimachia and Trichonis, Greece. *Journal of Fish Biology*, 38: 669-680.

Jardas I, Šantić M, Pallaoro A, 2004. Diet composition and feeding intensity of horse mackerel, *Trachurus trachurus* (Osteichthyes: Carangidae) in the eastern Adriatic. *Marine Biology*, 144: 1051-1056.

Kaiserli A, Voutsa D, Samara C, 2002. Phosphorus fractionation in lake sediments – Lakes Volvi and Koronia, N. Greece. *Chemosphere*, 46: 1147-1155.

Kleanthidis PK, Sinis AI, 2001. Feeding habits of the Macedonian shad, *Alosa macedonica* (Vinciguerra, 1921) in Lake Volvi (Greece): seasonal and ontogenetic changes. *Israel Journal of Zoology*, 47: 213-232.

Kottelat M, Freyhof J, 2007. *Handbook of European freshwater fish.* Kottelat, Cornol and Freyhof, Berlin.

Krebs CJ, 1994. *Ecological methodology*. Addison Wesley, Longman Inc., London.

Mendelson J, 1975. Feeding relationships among species of *Notropis* (Pisces: Cyprinidae) in a Wisconsin stream. *Ecological Monographs*, 45: 199-230.

Michaloudi E, 2005. Dry weights of the zooplankton of Lake Mikri Prespa (Macedonia, Greece). *Belgian Journal* *of Zoology*, 135: 223-227.

Michel P, Oberdorff T, 1995. Feeding habits of fourteen European freshwater fish species. *Cybium*, 19: 5-46.

Michelsen K, Pedersen J, Christoffersen K, Jensen F, 1994. Ecological consequences of food partitioning for the fish population structure in a eutrophic lake. *Hydrobiologia*, 291: 35-45.

Moustaka-Gouni M, 1988. The structure and dynamics of the phytoplankton assemblages in Lake Volvi, Greece. I. Phytoplankton composition and abundance during the period March 1984 – March 1985. *Archiv für Hydrobiologie*, 112: 251-264.

Pauly D, Trites AW, Capuli E, Christensen V, 1998. Diet composition and trophic levels of marine mammals. *ICES Journal of Marine Science*, 55: 467-481.

Pen LJ, Potter IC, 2006. Seasonal and size related changes in the diet of perch, *Perca fluviatilis* L., in the shallows of an Australian river, and their implications for the conservation of indigenous teleosts. *Aquatic Conservation: Marine and Freshwater Ecosystems*, 2: 243-253.

Pikitch EK, Santora C, Babcock EA, Bakun A, Bonfil R, Conover DO, Dayton P, Doukakis P, Fluharty D, Heneman B, *et al.*, 2004. Ecosystem-based fishery management. *Science*, 305: 346-347.

Politou CY, Economidis PS, Sinis AI, 1993. Feeding biology of bleak, *Alburnus alburnus*, in Lake Koronia, northern Greece. *Journal of Fish Biology*, 43: 33-43.

Schoener TW, 1970. Non-synchronous spatial overlap of lizards in patchy habitats. *Ecology*, 51: 408-418.

Stergiou KI, Karpouzi VS, 2002. Feeding habits and trophic levels of Mediterranean fish. *Reviews in Fish Biology and Fisheries*, 11: 217-254.

Tolonen KT, Karjalainen J, Staff S, Leppä M, 2000. Individual and population-level food consumption by cyprinids and percids in a mesotrophic lake. *Ecology of Freshwater Fish*, 9: 153-162.

Vašek M, Kubečka J, Sed'a J, 2003. Cyprinid predation on zooplankton along the longitudinal profile of a canyon-shaped reservoir. *Archiv für Hydrobiologie*, 156: 535-550.

Wallace RK, 1981. An assessment of diet-overlap indexes. *Transactions of the American Fisheries Society*, 110: 72-76.

Wilson SK, Bellwood DR, Choat JH, Furnas MJ, 2003. Detritus in the epilithic algal matrix and its use by coral reef fishes. *Oceanography and Marine Biology*, 41: 279-309.

Winfield IJ, 2004. Fish in the littoral zone: ecology, threats and management. *Limnologica*, 34: 124-131.

Wolfram-Wais A, Wolfram G, Auer B, Mikschi E, Hain A, 1999. Feeding habits of two introduced fish species (*Lepomis gibbosus*, *Pseudorasbora parva*) in Neusiedler See (Austria), with special reference to chironomid larvae (Diptera: Chironomidae). *Hydrobiologia*, 408/409: 123-129.

Wootton RJ, 1999. *Ecology of Teleost Fishes*. Kluwer Academic Publishers, Dordrecht, The Netherlands.

Zambrano L, Perrow MR, Sayer CD, Tomlinson ML, Davidson TA, 2006. Relationships between fish feeding guild and trophic structure in English lowland shallow lakes subject to anthropogenic influence: implications for lake restoration. *Aquatic Ecology*, 40: 391-405.

Zarfdjian M, Vranovský M, Economidis PS, 1990. Les invertébrés planctoniques du lac Volvi (Macédoine, Grèce). *International Revue der Gesamten Hydrobiologie*, 75: 403-412.