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FEEDING HABITS OF THE MACEDONIAN SHAD, *ALOSA MACEDONICA* (VINCIGUERRA, 1921) IN LAKE VOLVI (GREECE): SEASONAL AND ONTOGENETIC CHANGES

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ABSTRACT

Feeding habits of the Macedonian shad (*Alosa macedonica*), an endemic species in Lake Volvi (Macedonia, Greece), were studied during the period October 1995–September 1996. At the beginning of summer and throughout autumn, feeding was more intense, decreasing during winter as well as in May and August. Feeding intensity was found to be directly dependent on water temperature. *A. macedonica* fed mainly on copepods (47.7% in terms of number), but according to Pearre's electivity index, cladocerans (18.5% in terms of number) were the most preferred prey. Although rotifers represented the third trophic group (17.1% in terms of number), they seem to be avoided. The diet composition changed with season and fish size. During summer–autumn, the diversity of food increased. Older fish (170–219 mm) were characterized by a consumption of larger prey, such as fish. Negative and positive selection was present for the smaller (100–200 µm) and the larger (200–300 µm) size class of *Bosmina longirostris*, respectively, only during the period of population explosion of this species.

INTRODUCTION

Several studies have been conducted on feeding in species of the genus *Alosa*, because their selective predation pressure on zooplankton communities of lakes eliminates the large-sized zooplankton and influences species composition (e.g., Wells, 1970; Hutchinson, 1971; Warshaw, 1972; Kohler and Ney, 1981).

In Lake Volvi, a study of the zooplankton community during 1984–1986 revealed the dominance of rotifers, the lack of large-sized cladocerans, and the limited zooplanktonic biomass during the warm season, all of which were attributed to selective feeding by *Alosa macedonica* (Zarfdjian, 1989), a freshwater, endemic species living only in this lake. The strong predatory pressure on zooplankton is related to the establishment of a large population of *A. macedonica* in Lake Volvi in recent years, as a result of its low commercial value and the overfishing of its main predators such as *Perca fluviatilis*, *Aspius aspius*, and *Silurus glanis* (Sinis, 1981; Zarfdjian et al., 1996). Although species

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composition of the lake zooplankton and the consequences of selective predation are known, few data exist on the feeding habits of *A. macedonica*. A preliminary, qualitative stomach content analysis of 20 individuals showed that the diet of young specimens consists mainly of zooplankton, whereas in the stomachs of 3–10-year-old specimens small fish were found (Economidis and Sinis, 1991).

As fish grow, they often show distinct ontogenetic shifts in diet, correlated with changed levels of energy efficiency, and subsequent effects on further growth (e.g., Ross, 1978; Stergiou and Fourtouni, 1991; Wootton, 1992; Jobling, 1995; Platell et al., 1998). In land-locked *Alosa* species, piscivory by adult individuals has frequently been observed (e.g., Berg and Grimaldi, 1966; Hoagman, 1974; Kohler and Ney, 1980; Brandt et al., 1987; Krueger et al., 1995; Mason and Brandt, 1996), and in some cases it has been proposed as a possible factor contributing to the decline of several native species in lakes (e.g., Smith, 1970; Eck and Wells, 1987).

The objectives of this article were: (1) to determine the food habits of *A. macedonica*; (2) to examine the monthly and size-related qualitative and quantitative variability in feeding; (3) to describe the changes in feeding intensity throughout the year; and (4) to assess prey selectivity, using Pearre's electivity index.

MATERIALS AND METHODS

Lake Volvi is situated in central Macedonia (Greece) (40°37'40"– 40°41'50"N and 23°21'10"– 23°36'40"E) at an altitude of 37 m. It is the second largest Hellenic lake, with a surface area of 68.6 km² and a mean depth of 13.5 m (maximum depth 23.5 m). It is a warm monomictic lake classified as mesotrophic to slightly eutrophic (Sinis, 1981; Moustaka, 1988; Zarfdjian, 1989). The fish community of Lake Volvi comprises 23 species (Economidis and Sinis, 1982).

Samples were taken monthly from October 1995 to September 1996, between 1000 and 1200 hours, using a series of vertical gill nets with nominal mesh sizes of 14, 18, 22, 26, and 30 mm (knot-to-knot). All fish were preserved in 10% formalin immediately after capture, in order to minimize post-capture digestion. Zooplankton samples were also collected by vertical haul, using nets with mesh sizes of 106 and 48 µm for the collection of crustaceans and rotifers, respectively. Zooplankton was fixed in 4% formalin final dilution. Water temperature, oxygen, pH, and transparency were also measured on site, using a Digital temperature–oxygen meter (OXI 196-WTW), a Digital pH meter (pH 90-WTW), and a Secchi disk, respectively.

For all fish, total length (TL), total wet weight (TW), gonad weight (GW), net somatic weight (NW; total wet weight minus gonad and gut weight), and sex were recorded and stomachs were removed. Diet composition was examined only for the contents of the blind sac of the stomach, as only there were the food items recognizable (Berg and Grimaldi, 1966; Aprahamian, 1989).

All organisms from the fish stomachs as well as the zooplankton samples were identified to species level or to the lowest possible taxonomic level and enumerated by counting three 1-ml subsamples, in a Sedwick-Rafter cell (Bowen, 1983).

Feeding intensity was estimated using the degree of stomach fullness (FD), according to the subjective scale of Lebedev (1946) from 0 (empty) to 5 (stomach fully distended with food), with the index of vacuity (V%) expressed as percentage of the stomachs not containing food to the total number of stomachs examined (Hureau, 1966). For a quantitative description of the diet, frequency of occurrence and the numerical method were chosen (Berg, 1979; Hyslop, 1980). Results were expressed as percentage of the stomachs containing food (F%), and as percentage of the total number of prey (N%) or mean number of ingested organisms per fish (N_{mean}).

The condition of fish was described using Le Cren's (1951) index of relative condition [$RC = NW/(a \times TL^b)$], where a and b were derived from the \log_{10} transformed total length–net somatic weight relationship for *A. macedonica*: Kleanthidis, unpublished data].

The mean RC values were tested for differences between months using one-way analysis of variance (ANOVA) and Fisher's least significance difference test (LSD) (Zar, 1984). All analyses were performed on log-transformed data. The median FD values were tested for differences between months using Kruskal–Wallis nonparametric analysis, followed by the Student–Newman–Keuls (SNK) multiple comparison test (Zar, 1984).

To identify changes in the diet composition related to month and fish size, multivariate techniques such as complementary hierarchical clustering and multidimensional scaling (MDS) (Stergiou and Fourtouni, 1991; Platell et al., 1998) were performed on the standardized prey numerical abundances per size class. Subsequently, cluster and MDS analyses were also performed on the standardized prey numerical abundances per each group of classes identified above for each sampling month. All data were transformed using the double square root transformation for down-weighting the importance of the abundant species (Clarke and Warwick, 1994). Both methods were based on the Bray and Curtis (1957) similarity index, and all the analyses were carried out using the PRIMER algorithms (Carr, 1997). The results of the cluster analysis are represented by dendrograms and those of MDS, by two-dimensional "maps". The adequacy of representation in only two dimensions is expressed by a "stress coefficient" (Field et al., 1982), and in general, stress values <0.2 imply good representation (Clarke and Warwick, 1994). Discontinuities in the diet between months and body sizes may be accepted as real when the results of the two methods agree (Field et al., 1982).

Prey preference was assessed using Pearre's electivity index (1982), based on a 2×2 contingency table incorporating Yates's correction for continuity for χ^2 :

$$C = \pm \left[\frac{\left(|a_d b_e - a_e b_d| - \frac{n}{2} \right)^2}{abde} \right]^{\frac{1}{2}}$$

where a and b represent the abundance of a given prey taxa and of all other prey taxa, respectively; subscripts d and e indicate the diet and the environment, and $a = a_d + a_e$,

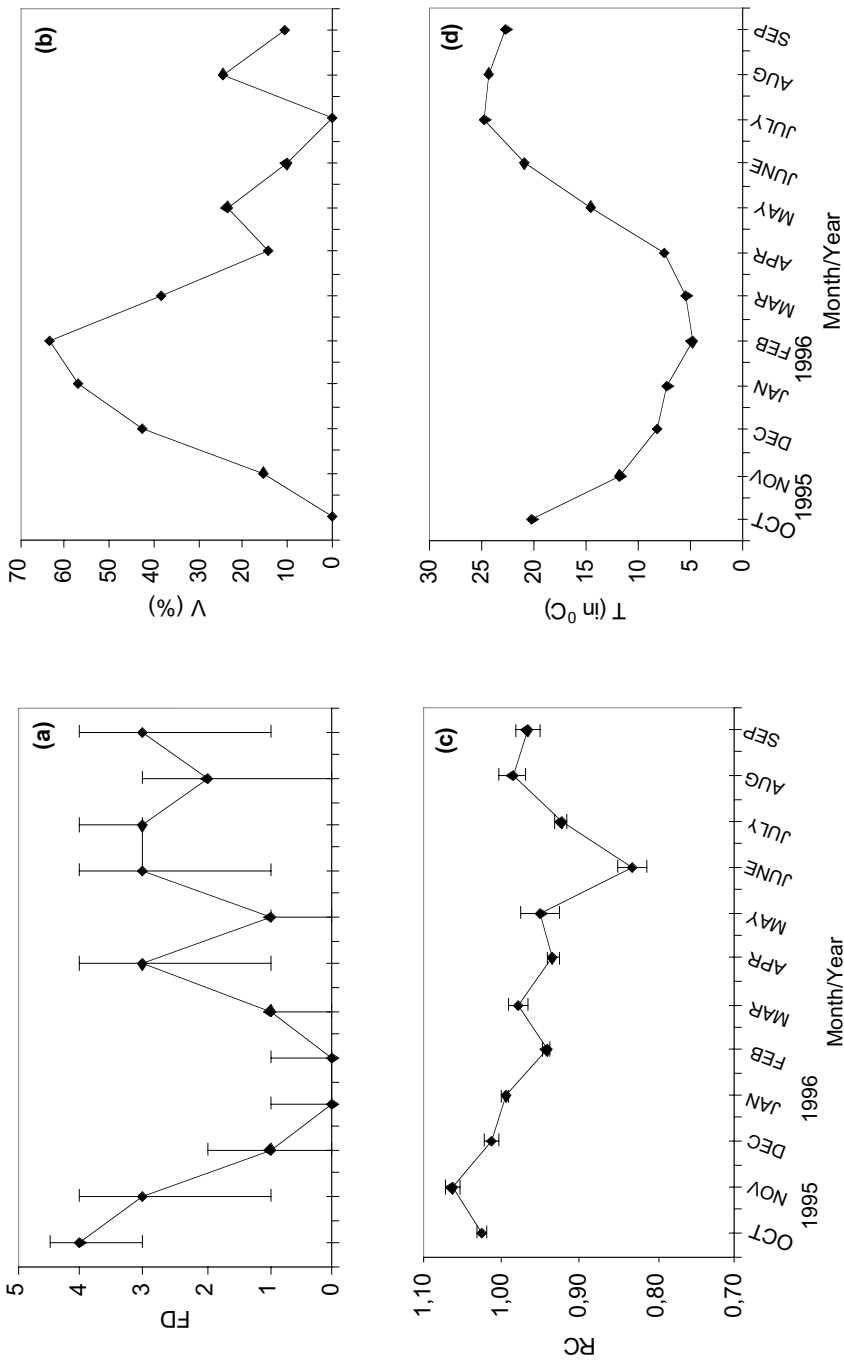


Fig. 1. Monthly variation in (a) median degree of stomach fullness (FD) (bars represent upper and lower quartile), (b) index of vacuity (V%), (c) condition factor (RC) of *Alosa macedonica* (95% confidence limits are given), and (d) mean monthly water temperature (°C) of Lake Volvi, October 1995–September 1996.

$b = b_e + b_d$, $d = a_d + b_d$, $e = a_e + b_e$, $n = a + b + d + e$. Pearre (1982) indicated that the sign of C must be given by inspection of $(a_d b_e - b_d a_e)$ and showed also that the index can be derived starting from χ^2 , as $C = \pm (\chi^2/n)^{1/2}$. The index can also be tested statistically using χ^2 test with one degree of freedom.

RESULTS

MONTHLY FEEDING INTENSITY

A total of 1161 stomachs were analyzed for diet. Of these, 799 (68.8%) contained food. The total length of the fish examined ranged from 102 to 214 mm.

The median FD values (Fig. 1a) differed significantly between months (Kruskal-Wallis, $H_c = 429.3$, $p < 0.001$) and the application of the SNK multiple comparison test of mean rank sums indicated that the values were significantly lower in December 1995–March 1996 and in May and August 1996 than in the remaining months. On the other hand, during the same periods index of vacuity was high, whereas it was low in October 1995 and July 1996 (Fig. 1b). Stepwise regression analysis was attempted, using FD as the dependent variable and water temperature, pH, oxygen content, and water transparency as independent ones. Temperature was the only significant variable entering the model (Fig. 2):

$$FD = 1.535 \times \ln(\text{temperature}) - 1.848, r^2 = 0.48, p < 0.02, n = 12$$

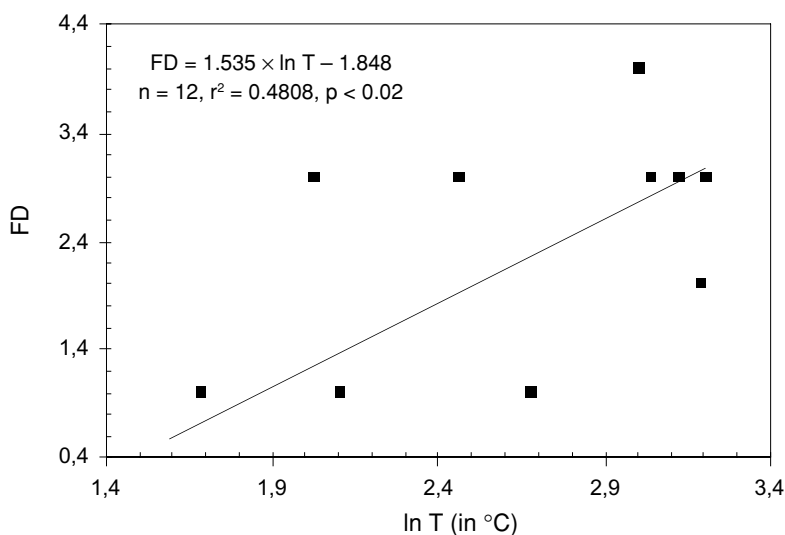


Fig. 2. Relationship between median degree of stomach fullness (FD) of *Alosa macedonica* and the natural logarithm of the water temperature (T in °C) of Lake Volvi.

CONDITION FACTOR

The mean RC (Fig. 1c) differed significantly between months (ANOVA, $F = 146.8$, $p < 0.05$), and the application of Fisher's LSD test showed a significant maximum in November, 1995 and significant minima in June and July 1996 (for all cases, $p < 0.05$).

TOTAL DIET COMPOSITION

Analysis of the stomach contents showed that copepods dominated the diet, comprising 47.7% in number and 98.1% in frequency of occurrence (Table 1). Copepodites and adult copepods (43.8% in number) comprised the major part of copepods, while nauplii represented only 3.8% in number. Cladocerans were the second prey group in the diet, both in number and in frequency of occurrence (Table 1), mainly consisting of *Bosmina longirostris* and *Diaphanosoma* cf. *mongolianum* (12.2% and 5.4% in number, respectively). Rotifers, mainly *Keratella quadrata* (8.9% in number), were less abundant (Table 1). Among the other invertebrate prey groups, insects (mainly *Chaoborus flavicans* larvae) had a low representation in number (0.01%), but a relatively high frequency of occurrence (17.2%). The fish *Knipowitschia caucasica* and *Rhodeus amarus* were also present (frequency of occurrence 1.3% and 0.3%, respectively) (Table 1). Finally, phytoplankton was relatively important in terms of number due to its small size and the high abundance in October and November, 1995 (Tables 1–3).

FEEDING VARIATION IN RELATION TO SIZE

Complementary clustering and ordination techniques revealed three main groups of fish size classes (Fig. 3, Table 4). The resulting stress for the two-dimensional plot was 0.07, implying an excellent representation. Group I (100–119 mm) was characterized by high consumption of crustaceans and rotifers (Table 4). Group II (120–169 mm) had the same consumption of crustaceans as Group I, but a much higher presence of rotifers (Table 4). Group III (170–219 mm) differed from the other two because of the lower presence of rotifers and increased frequency of occurrence of fish (Table 4). The number of prey groups and species differed significantly between groups (ANOVA, $F = 11.9$, $p < 0.001$) and the application of Fisher's LSD test indicated that it was significantly higher in Group I ($p < 0.05$) as compared to the other groups.

MONTHLY DIET VARIATION

Cluster and MDS analyses identified four groups of months (Fig. 4). The resulting stress for the two-dimensional plot was low, 0.1, implying a good representation in two dimensions. Group I was formed by May and was characterized by low consumption of food, composed mainly of the rotifers *Asplanchna priodonta*, *Brachionus angularis*, and *K. quadrata* (Table 3). Insects in May had a higher frequency of occurrence (81%) in comparison to the remaining months (Table 2). Group II was represented by the winter–spring period, December to April, with the stomachs being characterized by low quantity of food, with mainly copepods represented and high frequency of occurrence of insect larvae and fish (Tables 2,3). Group III comprised the months October and November (Fig. 4) and was characterized by high consumption of food, mainly crustaceans, as well as the increased presence of phytoplankton (Tables 2,3). Group IV comprised the

Table 1

Overall diet composition of *Alosa macedonica*, Lake Volvi, October 1995–September 1996
(F% = frequency of occurrence, N% = numerical percentage)

Taxon	F%	N%
ROTIFERA	83.45	17.07
<i>Keratella cochlearis</i>	26.44	0.26
<i>K. quadrata</i>	38.00	8.94
<i>Asplanchna priodonta</i>	9.80	3.38
<i>Brachionus angularis</i>	7.37	2.67
<i>B. calyciflorus</i>	2.88	0.02
<i>B. diversicornis</i>	32.15	1.38
<i>Trichocerca capucina</i>	24.93	0.31
<i>T. similis</i>	2.27	0.01
<i>Polyarthra</i> spp.	13.72	0.09
<i>Notholca squamula</i>	0.74	+
<i>Pompholyx sulcata</i>	2.64	0.01
CLADOCERA	97.13	18.53
<i>Bosmina longirostris</i>	95.15	12.24
<i>Daphnia cucullata</i>	0.17	+
<i>Diaphanosoma</i> cf. <i>mongolianum</i>	51.58	5.38
<i>Alona rectangula</i>	25.89	0.28
<i>Leptodora kindtii</i>	22.53	0.21
<i>Chydorus sphaericus</i>	0.13	+
<i>Leydigia leydigi</i>	2.08	+
<i>Ilyocryptus sordidus</i>	0.08	+
<i>Macrothrix laticornis</i>	0.32	+
Immature Cladocera	30.87	0.41
COPEPODA	98.06	47.67
Nauplii	87.04	3.83
Adults/Copepodites	98.06	43.82
Harpacticoida	4.38	0.02
HYDRACARINA	0.53	+
NEMATODA*	0.21	+
OSTRACODA*	4.24	0.03
INSECTA*	17.24	0.01
Larvae Chironomidae	6.72	+
Larvae <i>Chaoborus flavicans</i>	11.30	0.01
Nymphs Diptera	2.33	+
PISCES	1.84	+
<i>Rhodeus amarus</i>	0.30	+
<i>Knipowitschia caucasica</i>	1.34	+
Unidentified Pisces	0.46	+
PHYTOPLANKTON	40.57	16.70

*Benthic prey, + = < 0.01.

Table 2
Monthly diet composition of *Alosa macedonica* (frequency of occurrence, F%), Lake Volvi, October 1995–September 1996

Taxon	Oct.	Nov.	Dec.	Jan.	Feb.	Mar.	Apr.	May	Jun.	Jul.	Aug.	Sep.
Number of stomachs	98	136	123	205	174	42	121	34	29	99	53	47
Stomachs with food	98	115	71	88	64	26	104	26	26	99	40	42
ROTIFERA	84.7	72.7	72.7	87.2	88.9	88.0	100.0	84.6	34.6	87.9	100.0	100.0
<i>Keratella quadrata</i>	0.0	0.9	10.6	83.7	85.7	88.0	100.0	84.6	0.0	0.0	0.0	2.4
<i>Asplanchna priodonta</i>	0.0	0.0	0.0	0.0	0.0	8.0	25.0	84.6	0.0	0.0	0.0	0.0
<i>Brachionus angularis</i>	0.0	0.0	0.0	0.0	0.0	0.0	3.9	84.6	0.0	0.0	0.0	0.0
<i>B. diversicornis</i>	75.5	36.4	0.0	1.2	0.0	0.0	0.0	0.0	0.0	72.7	100.0	100.0
<i>Trichocerca capucina</i>	39.8	34.6	16.7	3.5	0.0	0.0	0.0	0.0	23.1	41.4	92.5	47.6
Other Rotifera	22.5	53.6	69.7	59.3	15.9	8.0	47.1	65.4	15.4	67.7	22.5	23.8
CLADOCERA	100.0	99.1	98.5	97.7	93.7	92.0	100.0	84.6	100.0	100.0	100.0	100.0
<i>Bosmina longirostris</i>	99.0	98.2	98.5	97.7	93.7	92.0	100.0	65.4	100.0	100.0	97.5	100.0
<i>Diaphanosoma cf. mong.</i>	100.0	78.2	48.5	0.0	0.0	0.0	0.0	0.0	92.3	100.0	100.0	100.0
<i>Alona rectangularis</i>	7.1	11.8	50.0	65.1	52.4	4.0	31.7	84.6	3.9	0.0	0.0	0.0
<i>Leptodora kindtii</i>	18.4	16.4	1.5	1.2	0.0	0.0	0.0	0.0	69.2	80.8	40.0	42.9
Other Cladocera	9.2	8.2	9.1	0.0	0.0	0.0	1.0	3.9	0.0	2.0	0.0	0.0
Immature Cladocera	3.1	7.3	7.6	8.1	3.2	0.0	1.9	46.2	84.6	54.6	82.5	71.4
COPEPODA	100.0	100.0	98.5	97.7	100.0	96.0	100.0	84.6	100.0	100.0	100.0	100.0
Nauplii	68.4	98.2	84.9	97.7	95.2	96.0	99.0	69.2	50.0	85.9	100.0	100.0
Adults/Copepodites	100.0	100.0	98.5	97.7	100.0	96.0	100.0	84.6	100.0	100.0	100.0	100.0
Harpacticoida	4.1	2.7	4.6	2.3	1.6	16.0	2.9	15.4	0.0	3.0	0.0	0.0
HYDRACARINA	0.0	0.0	0.0	0.0	1.6	0.0	1.0	3.9	0.0	0.0	0.0	0.0
NEMATODA	0.0	0.0	0.0	0.0	1.6	0.0	1.0	0.0	0.0	0.0	0.0	0.0
OSTRACODA	2.0	2.7	0.0	9.3	1.6	0.0	25.0	7.7	0.0	0.0	2.5	0.0
INSECTA (Larvae-Nymphs)	4.1	0.0	10.6	15.1	25.4	24.0	9.6	80.8	11.5	6.1	12.5	7.1
PISCES	2.0	2.7	7.6	1.1	4.8	0.0	0.0	0.0	3.9	0.0	0.0	0.0
PHYTOPLANKTON	100.0	99.1	16.7	18.6	9.5	24.0	18.3	65.4	84.6	7.1	15.0	28.6

Table 3
Monthly diet composition of *Alosa macedonica* (mean number of prey items per fish), Lake Volvi, October 1995–September 1996

Taxon	Oct.	Nov.	Dec.	Jan.	Feb.	Mar.	Apr.	May	Jun.	Jul.	Aug.	Sep.
Number of stomachs	98	136	123	205	174	42	121	34	29	99	53	47
Stomachs with food	98	115	71	88	64	26	104	26	26	99	40	42
ROTIFERA	62.8	19.5	29.8	36.5	42.9	212.4	3451.3	1802	9.6	112.0	378.6	557.3
<i>Keratella quadrata</i>	0.0	0.1	4.3	28.9	37.6	211.3	34466	126.4	0.0	0.0	0.0	0.1
<i>Asplanchna priodonta</i>	0.0	0.0	0.0	0.0	0.0	0.8	14.9	920.9	0.0	0.0	0.0	0.0
<i>Brachionus angularis</i>	0.0	0.0	0.0	0.0	0.0	0.0	3.2	729.3	0.0	0.0	0.0	0.0
<i>B. diversicornis</i>	41.8	4.0	0.0	0.1	0.0	0.0	0.0	0.0	0.0	56.5	284.8	512.7
<i>Trichocerca capucina</i>	11.9	4.3	1.3	0.1	0.0	0.0	0.0	0.0	4.9	15.1	89.1	38.4
Other Rotifera	9.1	11.1	24.2	7.3	5.2	0.3	28.7	25.3	4.7	40.5	4.8	6.1
CLADOCERA	893.3	186.4	310.2	133.2	44.6	52.7	519.4	108.9	5892.8	2322.1	734.8	1973.9
<i>Bosmina longirostris</i>	582.5	158.5	299.6	128.0	37.7	52.6	500.8	46.6	5381.2	280.3	100.5	1425.3
<i>Diaphanosoma cf. mong.</i>	302.9	23.1	6.0	0.0	0.0	0.0	0.0	0.0	322.9	1957.4	572.5	497.2
<i>Alona rectangula</i>	1.4	1.3	3.3	4.6	6.9	0.1	17.5	53.5	0.4	0.0	0.0	0.0
<i>Leptodora kindtii</i>	3.1	1.5	0.1	0.1	0.0	0.0	0.0	0.0	90.4	45.4	5.1	8.1
Other Cladocera	3.1	0.9	0.5	0.0	0.0	0.0	0.1	0.9	0.0	0.8	0.0	0.0
Immature Cladocera	0.3	1.2	0.6	0.6	+	0.0	1.0	8.0	97.8	38.2	56.7	43.4
COPEPODA	3424.1	2167.0	1131.7	1220.1	1540.4	1333.7	6056.9	345.7	597.8	3166.0	2117.3	5106.2
Nauplii	47.1	215.0	65.0	297.5	55.1	97.5	435.5	9.7	16.9	76.5	178.1	145.4
Adults/Copepodites	3376.4	1951.8	1066.7	922.5	1485.2	1234.4	5620.4	334.2	580.9	3089.1	1939.2	4960.9
Harpacticoida	0.7	0.2	0.1	0.1	0.1	1.8	1.1	1.9	0.0	0.4	0.0	0.0
HYDRACARINA	0.0	0.0	0.0	0.0	+	0.0	+	+	0.0	0.0	0.0	0.0
NEMATODA	0.0	0.0	0.0	0.0	+	0.0	+	0.0	0.0	0.0	0.0	0.0
OSTRACODA	0.3	0.1	0.0	1.9	+	0.0	10.6	4.3	0.0	0.0	0.1	0.0
INSECTA (Larvae-Nymphs)	+	0.0	0.1	0.2	0.3	0.4	0.2	1.4	0.1	0.1	0.2	0.2
PISCES	+	0.1	0.1	+	0.1	0.0	0.0	0.0	+	0.0	0.0	0.0
TOTAL	4380.6	2373.0	1471.9	1392.0	1628.3	1599.2	41100	2262.4	6500.4	5600.2	3231.0	7637.6
PHYTOPLANKTON	449474	127871	7.7	1.5	1.3	2.6	28.8	13.1	91.9	2.3	2.9	8.7

+ = < 0.05.

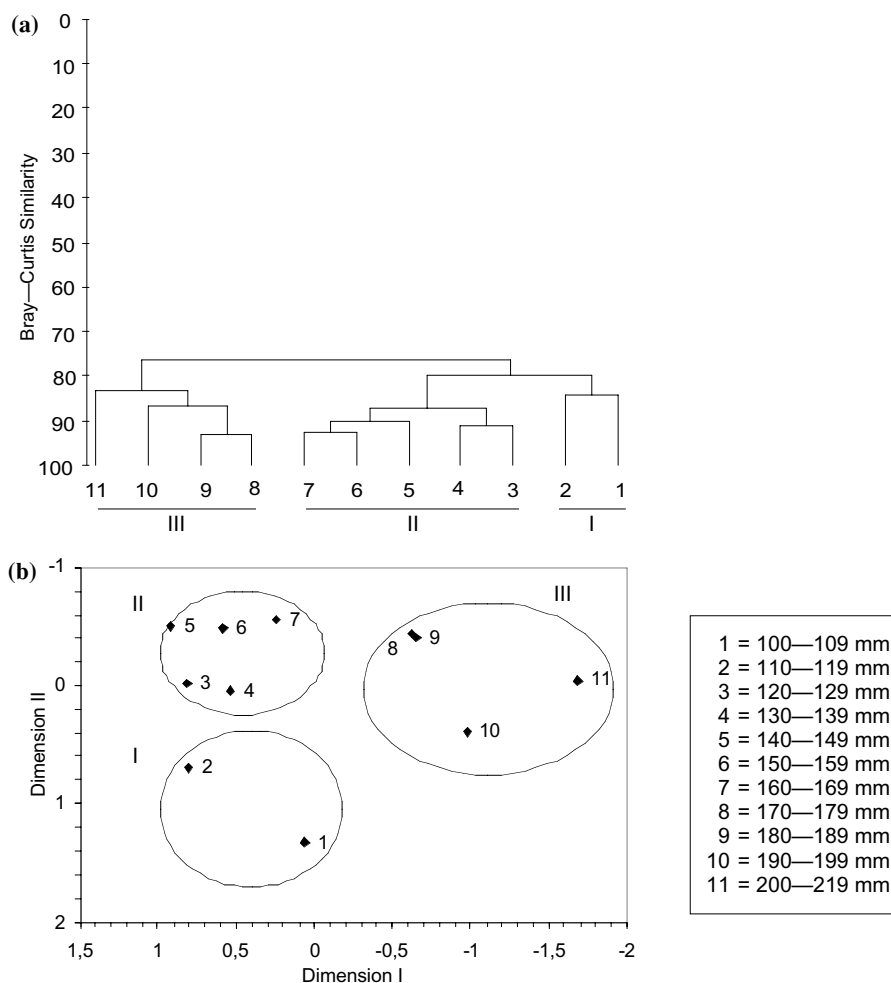


Fig. 3. Dendrogram (a) and multidimensional scaling configuration (b) based on the numerical abundance of the groups and prey species in the stomach content of *Alosa macedonica*, showing the classification by size into 3 main groups (I, II, III).

summer period, June–September (Fig. 4) and was characterized by a high consumption of food, mainly cladocerans (*B. longirostris*, *D. cf. mongolianum*, and *Leptodora kindtii*) and copepods (Tables 2,3).

PREY SELECTION

Pearre's electivity values for rotifers were negative (Fig. 5). Crustaceans were positively selected throughout the year, except in June when, for copepods, Pearre's

Table 4
Diet composition of *Alosa macedonica* in relation to body size groups indicated by multivariate analyses (for groupings, see Fig. 3)

Groups	I		II		III	
Length classes (in mm)	100–119		120–169		170–219	
Number of stomachs	74		883		204	
Stomachs with food	56		589		154	
<i>Taxon</i>	F%	N _{mean}	F %	N _{mean}	F %	N _{mean}
ROTIFERA	100.0	2195.0	87.4	6181.8	71.1	90.6
<i>Keratella quadrata</i>	23.6	1973.8	43.6	6035.7	11.8	7.1
<i>Asplanchna priodonta</i>	0.0	0.0	8.1	43.2	2.0	3.6
<i>Brachionus angularis</i>	0.0	0.0	4.0	27.3	2.0	23.2
<i>B. diversicornis</i>	70.9	154.7	28.4	48.4	43.4	43.2
<i>Trichocerca capucina</i>	67.3	38.2	21.3	9.5	23.0	6.0
Other Rotifera	65.5	28.3	47.6	17.6	23.0	7.5
CLADOCERA	100.0	998.5	97.9	784.3	98.7	1237.6
<i>Bosmina longirostris</i>	100.0	657.6	96.9	463.9	97.4	588.8
<i>Diaphanosoma cf. mong.</i>	76.4	321.8	46.2	293.0	73.7	602.2
<i>Alona rectangula</i>	18.2	0.8	28.7	7.2	15.1	2.4
<i>Leptodora kindtii</i>	34.5	9.8	19.2	7.9	26.3	18.1
Other Cladocera	3.6	0.3	2.3	0.3	8.6	2.4
Immature Cladocera	32.7	8.2	22.7	12.0	19.1	23.7
COPEPODA	100.0	2178.2	98.8	2644.4	99.3	3307.4
Nauplii	100.0	179.7	90.8	194.5	78.9	56.0
Adults/Copepodites	100.0	1998.0	98.8	2449.5	99.3	3250.8
Harpacticoida	3.6	0.5	3.1	0.4	4.6	0.5
HYDRACARINA	0.0	0.0	0.3	+	0.7	+
NEMATODA	0.0	0.0	0.3	+	0.0	0.0
OSTRACODA	0.0	0.0	6.2	2.3	4.6	0.8
INSECTA (Larvae-Nymphs)	3.6	+	13.3	0.2	9.9	0.2
PISCES	0.0	0.0	1.4	+	4.6	0.1
TOTAL	100.0	5371.8	100.0	9612.9	100.0	4636.5
PHYTOPLANKTON	38.2	20234.9	36.2	52434.4	65.1	175667.8

F% = frequency of occurrence; N_{mean} = mean number of prey items per fish; + = < 0.05.

index showed random selection (Fig. 5). Electivity values for *B. longirostris* and *D. cf. mongolianum* were positive for almost all months during which these species were present in the lake (Fig. 5). For the size classes of *B. longirostris*, Pearre's index in June showed significant negative and positive selection for the size classes of 100–200 μm and 200–300 μm of *B. longirostris*, respectively (Fig. 5). Pearre's index presented

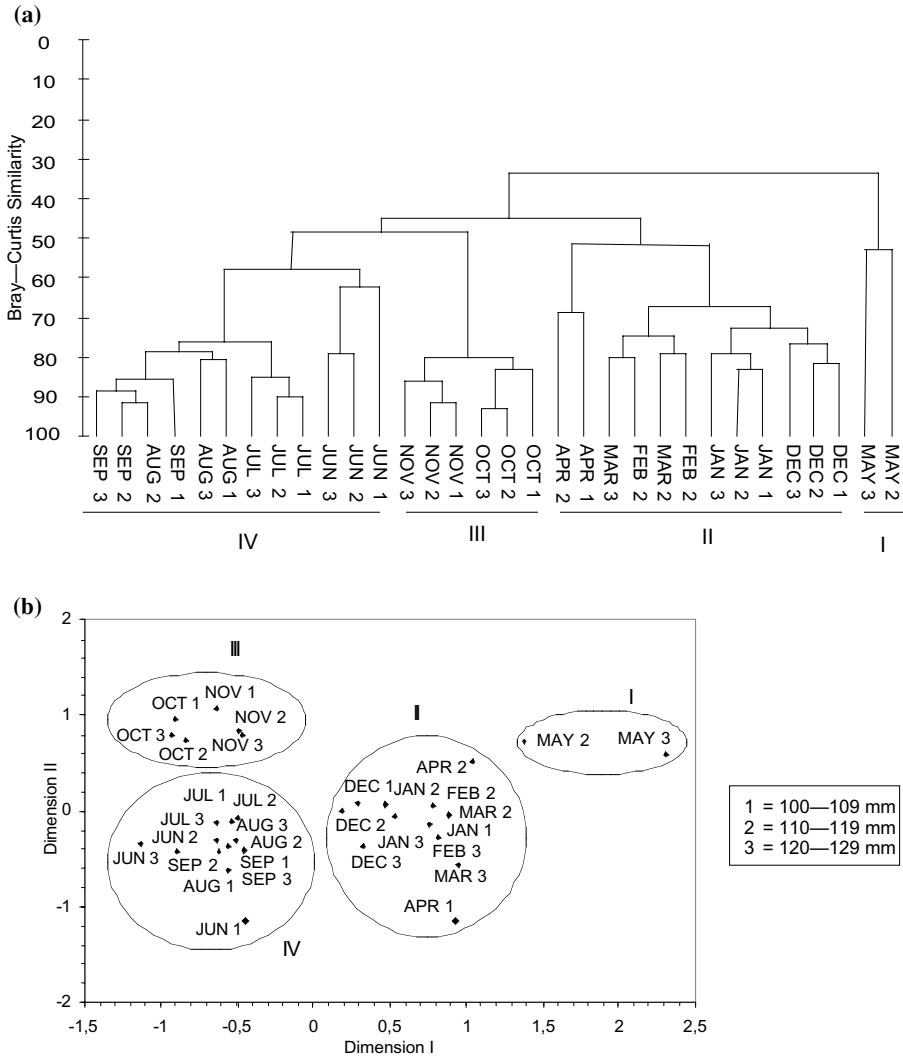


Fig. 4. Dendrogram (a) and multidimensional scaling configuration (b) based on the numerical abundance of the groups and prey species in the stomach content of *Alosa macedonica*, showing the classification by month into 4 main groups (I, II, III, IV).

significant positive values for nauplii only in November 1995 and January and March 1996 (Fig. 5). Electivity values for copepodites were highly positive in winter–spring (Fig. 5). Finally, electivity for adult copepods was positive, except in September, when Pearre’s index did not show a statistically significant positive selection (Fig. 5).

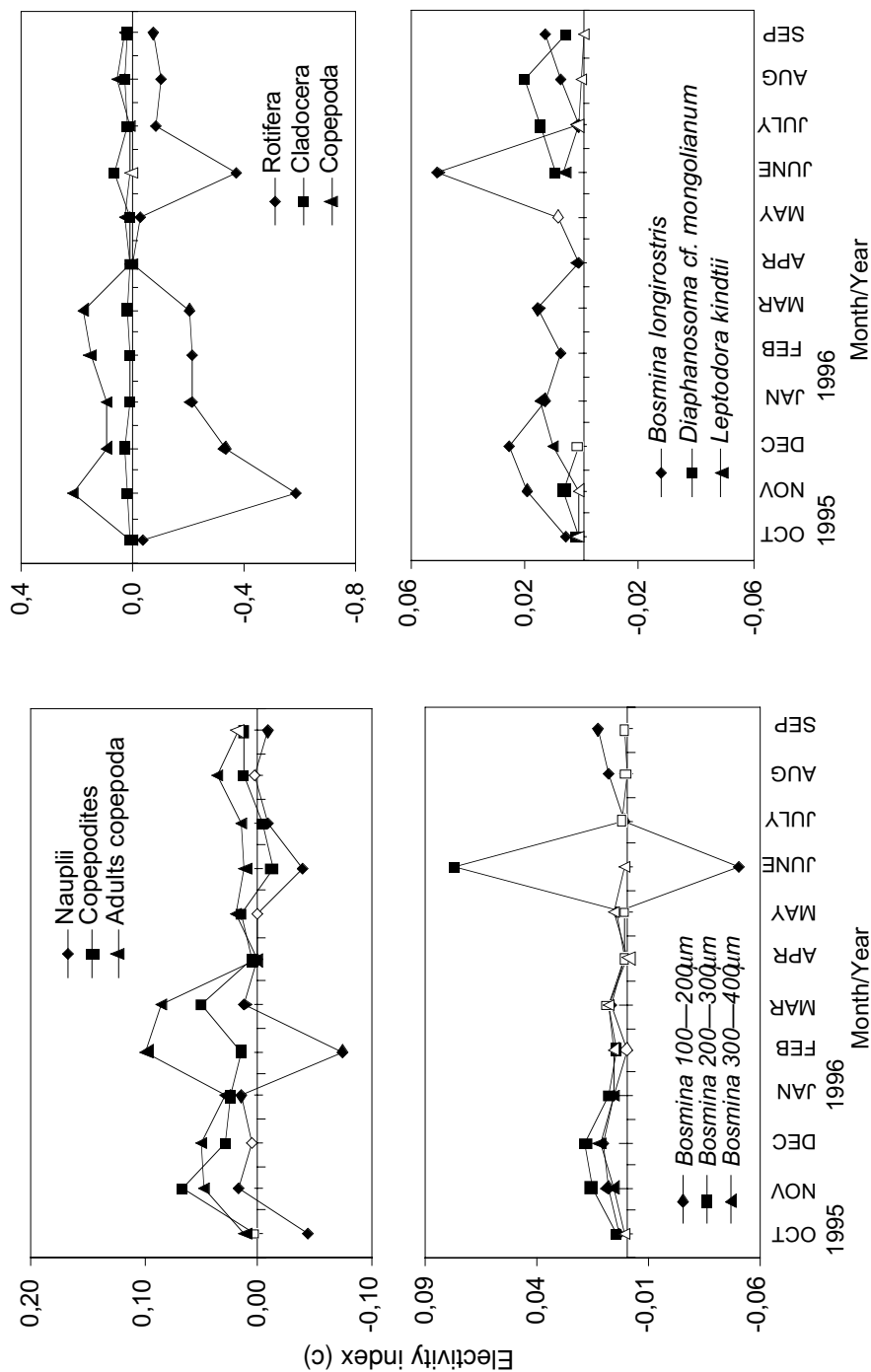


Fig. 5. Monthly variation of Pearson's electivity index (black markers indicated $p < 0.05$) for the main groups or species of the zooplankton and for the size groups of *Bosmina longirostris* of Lake Volvi, October 1995–September 1996.

DISCUSSION

Although the feeding habits of other *Alosa* anadromous species and land-locked populations have been studied (e.g., Berg and Grimaldi, 1966; Hutchinson, 1971; Burbidge, 1974; Guest and Drenner, 1991; Mills et al., 1992), those of *A. macedonica*, one of the four indigenous exclusively freshwater *Alosa* species in the world, have never been examined before. The present analysis of feeding habits shows that *A. macedonica* is a selective zooplanktivore, influencing the size and species composition of the zooplankton community in Lake Volvi, and also indicates that large-sized individuals of *A. macedonica* can be occasional piscivores. Given the large *A. macedonica* population in Lake Volvi established in recent years as a result of fisheries management (Zarfdjian et al., 1996), one may assume that trophic competition and piscivory by *A. macedonica* might constitute one of the major causes for the reduced growth rates and fisheries production of the other fish species in this lake.

Janssen (1976) describes three planktivory modes for *Alosa pseudoharengus* feeding on zooplankton: particulate feeding, filter feeding, and gulping. The shift among these feeding modes depends on the fish size and the size and abundance of available prey (Janssen, 1976; Crowder and Binkowski, 1983). The same authors also point out that filter feeding is observed mainly when high densities and small prey sizes are found in the environment, whereas particulate feeding prevails when low densities and large prey sizes predominate.

Seasonal *A. macedonica* diet shifts reflected the changes in availability of organisms. Our results show that copepods represented the major part of the food, and although they were consumed throughout the year, their representation was less in summer (Tables 2,3), when cladoceran abundance increased in the lake (Zarfdjian, 1989). A similar switch to cladocerans in summer was also observed for *A. fallax lacustris* (Berg and Grimaldi, 1966) and for *Coregonus* sp. (De Bernardi and Giussani, 1975; Mookerji et al., 1998). Within the group of copepods, the strongest selection was observed for adult copepods and the weakest for nauplii (Fig. 5), and this is probably based on size (Burbidge, 1974). Although cladocerans, due to their slow but continuous and trembling motion, are more vulnerable prey to fish predation than copepods (e.g., O'Brien, 1979; Mookerji et al., 1998), they made only a minor contribution to the diet (Table 1). This could be attributed to their low abundance in the lake, caused by the heavy size-selective predation pressure on the zooplankton in recent years (Zarfdjian, 1989). Nevertheless, the preference of *A. macedonica* for cladocerans was clear in June (Fig. 5, Tables 2,3), when *B. longirostris* is abundant in the lake (Kleanthidis, unpublished data). Moreover, when *D. cf. mongolianum* density increased during summer in the lake, the selection for *B. longirostris*, the smallest (>400 μm) and relatively low-energy-value cladoceran (Skurdal et al., 1985; Kankaala et al., 1990), decreased (Fig. 5). Regarding rotifers, these are considered a poor diet because of their small individual size and low energy content (Sarvala et al., 1988). The use of Pearre's electivity index showed (Fig. 5) that they were selected against by *A. macedonica*. However, they had a relative high contribution to the diet (17.1%), most probably related to the low abundance of large-sized prey (crustaceans) in the lake and the high food requirements of *A. macedonica*.

The low presence of benthic prey in the diet (Table 1) probably indicates that *A. macedonica* feeds mainly in the water column. *Alosa* species have difficulty capturing prey near or at the bottom due to their superior mouth position (Brooks, 1968; Aprahamian, 1989), so that predation on insect larvae is carried out during larval movement to the surface, while Ostracoda are consumed when found free in the water column. The low contribution of phytoplankton to the diet almost throughout the year (Tables 2,3), and its lower nutritional value compared with animal food (Hickling, 1966; Persson, 1983), probably indicate that phytoplankton was consumed opportunistically. Phytoplankton was present in the stomachs only during October–November (Tables 2,3), when its biomass peaks in the lake (Moustaka, 1988). During these months, the high phytoplankton biomass probably decreased visibility in the lake, and *A. macedonica* fed mainly through filter feeding, thus consuming phytoplankton passively.

The low percentage of large-sized *B. longirostris* in the lake zooplankton made assessment of selective predation towards large-sized individuals unclear, except in June, when *B. longirostris* exhibited its highest density in the lake (Fig. 5).

Fish undergo changes in diet during the course of development (Ross, 1978; Jobling, 1995). Usually, as fish increase in size, the size of prey also increases, while the number of prey per stomach decreases (Grossman, 1980; Stergiou and Fourtouni, 1991; Milton et al., 1994), and there is a general tendency for fish to become more specialized (Gibson and Ezzi, 1987). This seems to be true for *A. macedonica* as well. Thus, the younger individuals (<119 mm) were characterized by a wider trophic spectrum and consumption of smaller organisms, whereas the diet of older fish shifted towards larger organisms, such as fish (Fig. 3, Table 4).

Piscivory by *Alosa* species on larval fish has been observed in the laboratory (Hoagman, 1974; Krueger et al., 1995) and the field (Berg and Grimaldi, 1966; Kohler and Ney, 1980; Brandt et al., 1987; Krueger et al., 1995; Mason and Brandt, 1996). Economidis and Sinis (1991) found, in the stomach of large *A. macedonica*, fish such as *Rutilus rutilus*, *Alburnus alburnus*, and *Knipowitschia caucasica*, and also observed that the shift to piscivory is reflected by the erosion of the gill rakers along the inner parts of the gill arches, an adaptation that limits the ability of older fish to utilize small prey. In the present study, only *K. caucasica* and *R. amarus* were identified. Piscivory was observed at the end of autumn and in winter, as well as in June 1996 (Tables 2,3). Monthly frequency of occurrence of fish in the diet of *A. macedonica* was not correlated with abundance of either total zooplankton ($r = 0.187$, $p > 0.05$, $n = 12$) or crustaceans ($r = 0.209$, $p > 0.05$, $n = 12$) in the lake. On the other hand, *K. caucasica* and *R. amarus* prefer shallow waters near the shore (Economidis, 1974) while *A. macedonica* in winter forms schools near the bottom and migrates toward the shore before the beginning of the spawning season (Sinis, 1981). Therefore, the presence of fish in their stomach content appears to be related to the migration of *A. macedonica* near the bottom in winter, and toward the shore in June. Because *K. caucasica*, the most preferred fish in the diet (Table 1), is a sluggishly moving fish, its selection may also be associated with a shorter pursuit/handling time. The smallest *A. macedonica* to consume fish was 153.4 mm TL, whereas the largest fish found in an *A. macedonica* stomach was a *R. amarus* of 44.8 mm TL. The total length of a consumed fish, however, was not correlated with the total length of

A. macedonica ($r = 0.117$, $p > 0.05$, $n = 9$). The number of fish found in *A. macedonica* stomachs usually ranged from 1 to 3, and only in one specimen were 9 individuals of *K. caucasica* found.

Seasonal variations in physical condition indicate gonadal maturation and/or changes in feeding intensity and are related to temporal variations in environmental factors, such as food supply and water temperature (Flath and Diana, 1985; Encina and Granado-Lorencio, 1997). Thus, the limited consumption of food in winter (Fig. 1a,b), resulted in the low RC values at the end of winter and in spring (Fig. 1c). The high feeding intensity from the beginning of summer (Fig. 1a,b) was reflected in the increased RC (Fig. 1c) and was probably related to the storage of energy for reproduction. In August, when reproduction takes place (Sinis, 1981; Kleanthidis, unpublished data), feeding intensity was low (Fig. 1a,b), whereas in September, RC decreased (Fig. 1c). As reported by Encina and Granado-Lorencio (1997), conditions deteriorated after reproduction, which may reflect some energy transfer from somatic tissues to gonads.

FD was very low in May (Fig. 1a) and RC displayed a minimum (ANOVA, $p < 0.05$) one month later, in June (Fig. 1c). These facts could be related to the limited die-off of fish, mainly *A. macedonica*, observed in Lake Volvi during the first week of June 1996 (Kleanthidis, pers. observ.). The low feeding intensity in May is unexpected, since under normal conditions, the rise of water temperature in spring (Fig. 1d) should lead to high food consumption (Wootton, 1992). The most probable explanation is the low crustacean abundance in the lake zooplankton in May (Kleanthidis, unpublished data). During this month, the percentage of stomachs containing food was relatively high, while FD was low (Fig. 1a,b). Most fish had consumed small-sized prey. The dominance of rotifers in the stomach content of *A. macedonica* (Tables 2,3), as well as the positive electivity values for some of them in May, reinforce this observation. The differentiation of the diet composition in May is also apparent in the dendrogram (Fig. 4a) and in the two-dimensional plot (Fig. 4b), where May composed a single group due to the high presence of rotifers and the high frequency of occurrence of insect larvae and nymphs, both of which have a low presence during the other months of the year (Tables 2,3). Rotifer consumption in May (Table 3) was obligate due to low abundance of crustaceans in the lake.

Die-off is a common phenomenon in landlocked populations of *Alosa* (e.g., Wells, 1970; Warshaw, 1972; Kohler and Ney, 1981; O'Gorman and Schneider, 1986). The cause of *A. macedonica* die-off in Lake Volvi is believed to be a decrease in crustacean abundance in the lake, leaving the *A. macedonica* population in poor condition, with some individuals dying. Condition is directly correlated with the quantity of available food in the environment (Berg and Grimaldi, 1966; Burbidge, 1974) and is inversely related to changes in population density (Brown, 1972; O'Gorman and Schneider, 1986). Furthermore, annual die-offs correspond with seasonal energy lows, indicating that mortalities may be induced by insufficient feeding the previous autumn (Flath and Diana, 1985). The die-off in Lake Volvi may lead to a decrease in the previously overabundant *A. macedonica* population, thus increasing the food supply for the remaining individuals and improving the condition of the pre-spawning fish, leading to better reproductive success.

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