DIETS OF *MICROPTERUS SALMOIDES* LAC. AND *ESOX LUCIUS* L. IN LAKE TRASIMENO (UMBRIA, ITALY) AND THEIR DIET OVERLAP.

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ABSTRACT

The aim of this study was to gather information about the feeding habits of *Micropterus salmoides* Lac., an exotic species recently introduced into Lake Trasimeno and *Esox lucius* L., in order to determine the degree of overlap between the two diets. The stomachs of 179 largemouth basses and 125 pikes were examined. The index of diet overlap (α) was determined by using a Prominence Value (*PV*) of each food item, using Schoener's formula. The value of the diet overlap index in the whole sample was 0.79. When the sample was divided in groups based on length, the index values were high and varied from a minimum of 0.623 to a maximum of 0.925. Based on theses results, a hypothesis of food competition between the two species in Lake Trasimeno could not be rejected.

Key-words : largemouth bass, pike, food, diet overlap, Lake Trasimeno.

ALIMENTATION DE *MICROPTERUS SALMOIDES* LAC. ET DE *ESOX LUCIUS* L. DANS LE LAC TRASIMENO (OMBRIE, ITALIE) ET CHEVAUCHEMENT DES RÉGIMES ALIMENTAIRES.

RÉSUMÉ

L'objet de cette étude a été d'obtenir des informations sur le régime alimentaire de l'achigan à grande bouche *Micropterus salmoides* Lac., une espèce récemment introduite dans le lac Trasimeno et celui du brochet *Esox lucius* L. pour déterminer le degré de chevauchement des régimes alimentaires. Les estomacs de 179 black bass à grande bouche et de 125 brochets ont été analysés. L'index de Schoener a été utilisée pour déterminer l'indice de chevauchement des régimes alimentaires en utilisant la valeur de la proéminence (*PV*) de chaque catégorie de proies. L'indice de chevauchement des régimes alimentaires pour tout l'échantillon est de 0,79. Quand l'échantillon est divisé en classes de taille, les valeurs de l'indice sont élevées et varient de 0,623 à 0,925. L'hypothèse de compétition alimentaire entre ces deux espèces ne peut pas être rejetée.

Mots-clés : achigan à grande bouche, brochet, alimentation, chevauchement des régimes alimentaires, lac Trasimeno.

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INTRODUCTION

Lake Trasimeno (43°9'11" Lat. N and 12°5' Long. E, F122 I.G.M.) is the largest laminar lake on the Italian peninsula (area = 126 km^2; average depth = 4.72 m; maximum depth = 6.3 m). From a trophic point of view, the lake is characterised by a high productivity (MEARELLI *et al.*, 1990) which has a positive influence on the fish population. In fact the lake has one of the largest groups of professional fishermen working on inland Italian lakes (NATALI, 1993). Currently, the fish fauna includes 19 species, dominated by cyprinids. In recent years marked changes have occurred due to the introduction of numerous exotic species, most of which have acclimated well but caused a decline in the number of native species (MEARELLI *et al.*, 1990). Pike (*Esox lucius*, L. 1758) have declined in Lake Trasimeno, as in many other Italian lakes, due to reduced spawning areas and an overall environmental degradation (LELEK, 1987; GANDOLFI *et al.*, 1991). Over fishing is also a factor in Lake Trasimeno (LORENZONI *et al.*, 1993; NATALI, 1993).

One of the most recently introduced species into Lake Trasimeno is the largemouth bass (*Micropterus salmoides* Lacépède, 1802): originally from the south-eastern United States, it has been reported in the lake since the end of the 1980's (NATALI, 1993). Earlier studies have clearly shown that the largemouth bass has acclimated well to the lake, having found environmental conditions that are particularly favourable to growth and reproduction (LORENZONI *et al.*, 1996) and the species is progressively colonising the entire lake. An exotic piscivorous species can change the pre-existing fish community through direct and indirect effects on its prey or by competition with other predators. In Lake Trasimeno there could be competition between *M. salmoides* and *E. lucius* that could cause a further depletion in the pike stock. The aim of this work was to study the feeding habits of the two species in Lake Trasimeno and determine the degree of diet overlap.

MATERIAL AND METHODS

Monthly samples were collected from the south-eastern part of the lake between the villages of San Savino and Sant'Arcangelo from April 1993 to May 1994. The sampling area is characterized by shallow water with very abundant aquatic vegetation, the preferred habitat of both species (GANDOLFI *et al.*, 1991). Samples were collected from a boat using an electric shocker (continual pulsed current, 4 kW).

All specimens were measured for total length (TL), with an accuracy of 1 mm. The age of the fish was determined using the microscopic scalimetric method (BAGENAL, 1978). The stomachs were removed immediately after capture and stored in formalin (10%) until the contents were analysed (BOWEN, 1996). The data are expressed as abundance (%N) = the number of individuals of each food item with respect to the total number of individuals and as occurrence (%S) = the number of stomachs containing each food item in relation to the total number of full stomachs. The Prominence Values (*PV*) of dietary component were estimated using the following formula (HICKLEY *et al.*, 1994):

$$PV = \%N * \sqrt{\%S}$$

The Diet Overlap Index (α) was evaluated using the prominence values of each food according to the following formula (SCHOENER, 1970):

$$\alpha = 1 - 0.5\left(\sum_{i=1}^{n} \left|PV_{xi} - PV_{yi}\right|\right)$$

where n is the number of food items, PV_{xi} is the prominence value of food item i in species x, PV_{yi} is the prominence values of food item i in species y. The index value varies from 0 (no diet overlap) to 1 (total diet overlap) and is used primarily when the prey abundance is unknown (WALLACE, 1981). Unidentified taxa (*e.g. Pisces indet.* and *Insecta indet.*) are reported in proportion to the identified categories from the same sampling period (MICHALETZ, 1997).

The seasonal comparison of the diets was carried out on the percentage occurrence data by dividing the samples into groups based on the sampling season. The analysis of the percentage abundance data was done by subdividing the samples by age. The degree of diet overlap was calculated by separating the specimens into classes based on length (SCOTT and ANGERMEIER, 1998): TL < 25 cm and TL > 25 cm for *M. salmoides* and TL < 40 cm and TL > 40 cm for *E. lucius*. The choice of length classes was based on the ontogenetic changes of the diet as reported in literature (MACEINA and MURPHY, 1988; RAAT, 1988; GODINHO and FERREIRA, 1994; HICKLEY *et al.*, 1994; NICOLA *et al.*, 1996; KANGUR and KANGUR, 1998).

RESULTS

The sample was made up of 179 *M. salmoides* specimens (mean TL ± SD = 24.95 ± 7.55) distributed in seven age classes: of the overall stomachs examined, 37 were empty (20.67%). For *E. lucius*, 125 specimens were examined (mean TL ± SD = 31.91 ± 10.16) distributed in seven age classes: of the overall stomachs examined, 41 were empty (32.80%).

The most common food of the largemouth bass was the grass shrimp *Palaemonetes antennarius* (Crustacea, Palaemonidae) (Table I). Fish were not frequent and insects were scarce. Eastern mosquitofish *Gambusia holbrooki* Gir., sand smelt *Atherina boyeri* Risso, pumpkinseed *Lepomis gibbosus* L., spined loach *Cobitis taenia* L., perch *Perca fluviatilis* L. were the fish species in the largemouth bass diet.

Table I
Abundance (%N), presence (%S) and Prominence Value (*PV*) of food items.

Tableau I
Abondance relative (% N), occurrence relative (% S) et valeur de la proéminence (*PV*) des catégories alimentaires.

	Largemouth bass			Pike		
	%N	%S	PV	%N	%S	PV
Palaemonetes	93.0	87.3	0.869	72.0	53.0	0.524
Total crustaceans	93.0	87.3	0.869	72.0	53.0	0.524
Eastern mosquitofish	1.5	4.9	0.003	6.8	14.4	0.026
Spined loach	0.2	1.4	0.001			
Largemouth bass				0.8	3.6	0.002
Pumpkinseed	0.3	2.1	0.001	1.1	4.8	0.002
Perch	0.1	0.7	0.001			
Sand smelt	0.6	2.1	0.001	7.3	13.2	0.027
Rudd				0.3	1.2	0.001
Tench				0.6	2.4	0.001
Pisces indet.	3.8	25.3	0.019	5.9	21.7	0.028
Total fish	6.3	36.6	0.038	22.9	59.0	0.176
Odonata	0.3	2.1	0.001	2.0	7.2	0.005
Ephemeroptera	0.2	0.7	0.001	0.3	1.2	0.001
Insecta indet.	0.3	1.4	0.001	2.8	6.0	0.007
Total insects	0.7	4.2	0.001	5.1	14.4	0.019

P. antennarius was also the most abundant food for pike but in contrast to *M. salmoides*, fish were also present in the diet as were a few insects, mostly Odonates. The eastern mosquitofish, sand smelt, pumpkinseed, tench *Tinca tinca* L., *M. salmoides* and rudd *Scardinius erythrophthalmus* L. were found in the pike's diet.

A marked seasonal variation in the percentage of empty stomachs was evident in both species between winter and the other seasons (Table II): differences were significant at *t*-test analysis (*M. salmoides*: t = 2.34, p = 0.021; *E. lucius*: t = 3.38, p = 0.001). The longer fish had more empty stomachs in both species (*M. salmoides*: mean TL ± SD specimens with full stomachs = 24.29 ± 7.29; with empty stomachs = 27.46 ± 8.11) (*E. lucius*: mean TL ± SD specimens with full stomachs = 27.33 ± 8.31; with empty stomachs = 30.11 ± 10.90). The average lengths of the specimens with empty stomachs was significantly different (*t*-test) for *M. salmoides* (t = 2.304; p = 0.02), but not for *E. lucius* (t = 1.584; p = 0.116).

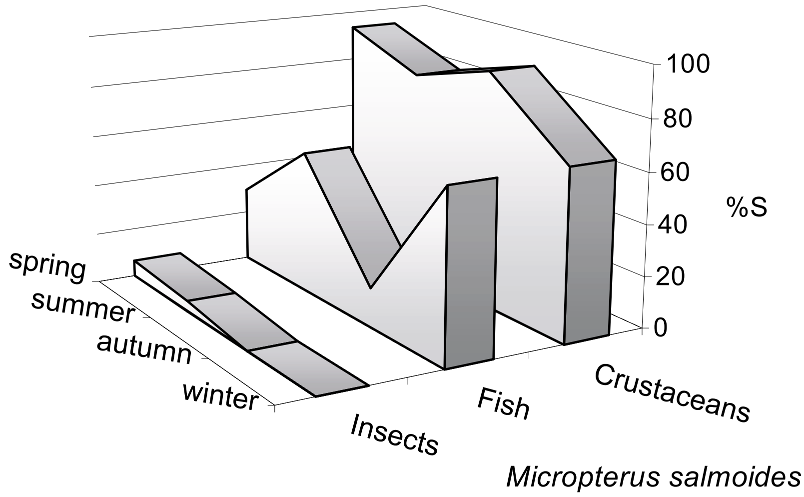
Table II
Seasonal trends of the percentages of empty stomachs.

Tableau II
Evolution saisonnière du pourcentage d'estomacs vides.

Largemouth bass				
	Winter	Spring	Summer	Autumn
N° of stomachs examined	14	71	61	33
N° of stomachs with food	8	53	55	26
% empty stomachs	42.86	25.35	9.84	21.21
TL range (cm)	13.00-32.80	13.10-43.60	6.50-41.70	13.30-39.50
Mean TL ± SD	20.99 ± 7.24	26.37 ± 7.16	23.51 ± 7.68	25.06 ± 7.83

Pike				
	Winter	Spring	Summer	Autumn
N° of stomachs examined	25	26	30	44
N° of stomachs with food	11	21	23	29
% empty stomachs	56.00	19.23	23.33	34.09
TL range (cm)	19.20-66.50	16.60-50.40	13.80-54.00	17.20-68.90
Mean TL ± SD	33.09 ± 11.75	33.55 ± 9.89	29.90 ± 8.06	32.25 ± 11.24

Figure 1 reports the seasonal trends of % occurrence (%S) for the principal food categories. Crustaceans presented the highest percentage in largemouth bass stomachs in all seasons. Insects accounted for a very small percentage of the diet and were only present in spring and summer. Fish were more numerous than the other food items in pike stomachs in the summer, while crustaceans were more prevalent in the other seasons. The insects were the most numerous in the summer but were scarce or absent in the other seasons.



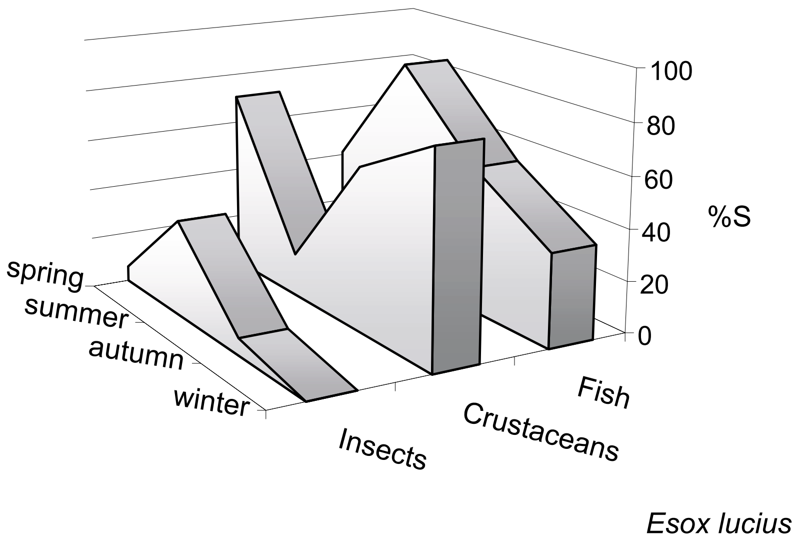


Figure 1
Seasonal trends of the presence (%S) of food items.

Figure 1
Evolution saisonnière de l'occurrence (% S) des catégories alimentaires.

The % abundance (%N) of the principal food items was reported (Figure 2) by age classes. The presence of fish in *M. salmoides* diet decreases with age; diet of older specimens was almost exclusively made up of crustaceans with a few insects in all age classes. The abundance of crustaceans in *E. lucius* was particularly high in the younger age classes; the highest value (around 80%) was observed in the 2+ and 3+ age classes; crustaceans were absent in 4+ age group. The highest values of fish in the diet occurred in the 0+ (50%) and 4+ (87.5%) age classes. Insects were never particularly abundant and the maximum value, 12.5%, was observed in the 4+ age class. Differences in the diets among largemouth bass specimens divided according to size (TL < 25 cm and TL > 25 cm) were not significant (*t*-test) for any food item (crustaceans: $t = 1.50$, $p = 0.067$; fish: $t = 1.10$, $p = 0.21$; insects: $t = 0.24$, $p = 0.40$): the shift from a piscivorous diet to an invertebrate-based one occurs when the TL of fish is less than 25 cm and was therefore not detected by t-test analysis. For pike the differences between the specimens divided according to size (TL < 40 cm and TL > 40 cm) were not significant for insects ($t = 0.69$, $p = 0.22$) or crustaceans ($t = 1.11$, $p = 0.13$) but were significant for fish ($t = 1.79$, $p = 0.038$) with the larger fish having more fish in their diets.

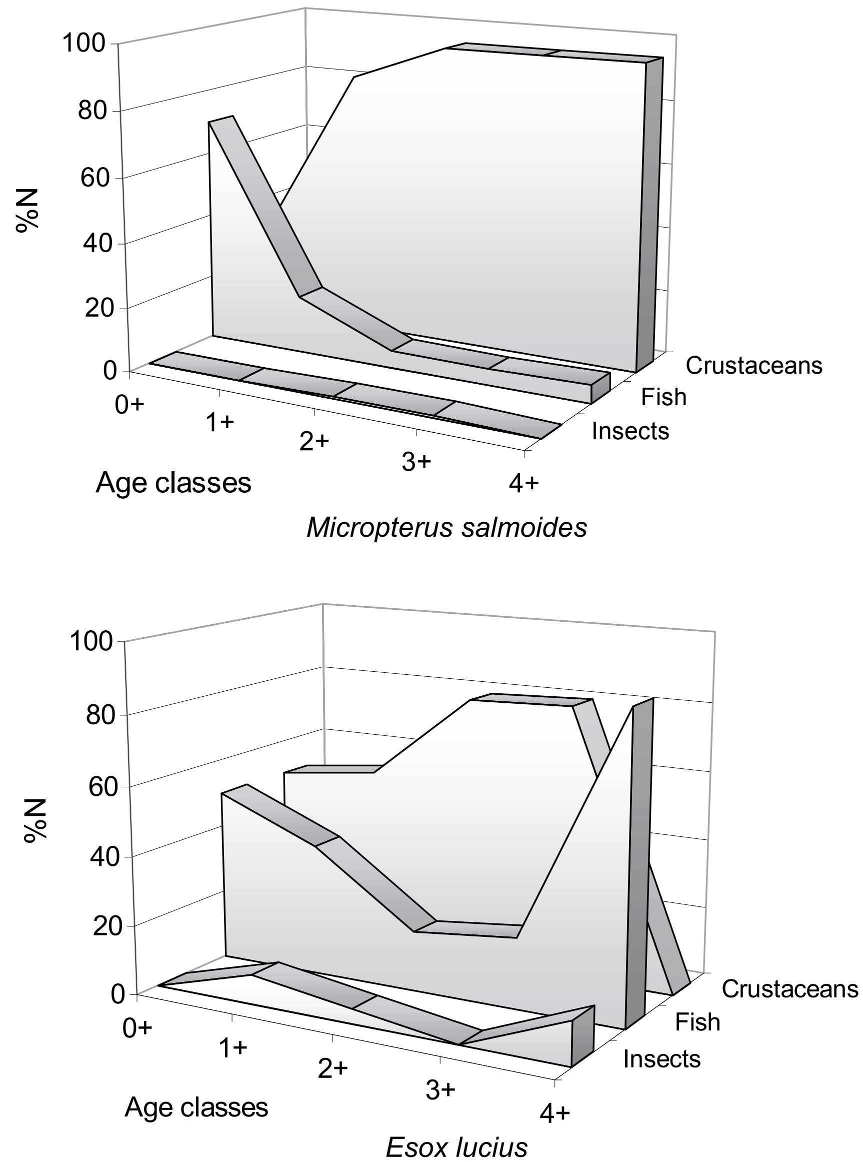


Figure 2
Abundance (%N) of food items divided into age classes.

Figure 2
Abondances relatives (% N) des catégories alimentaires par classes d'âge.

The diet overlap index for the whole sample was 0.79, but when the sample was divided into size classes, the index showed a marked variability with a minimum value of 0.623 (between the entire largemouth bass sample and the TL > 40 cm pike) and a maximum of 0.925 (entire largemouth bass sample and TL < 40 cm pike) (Table III).

Table III
Dietary overlap index for the whole sample and for the sample divided into size classes.

Tableau III
Indice du chevauchement des régimes alimentaires de l'échantillon complet et de l'échantillon divisé en classes de taille.

		Pike		
		ALL (n°84) (mean TL ± SD = 30.99 ± 9.31)	TL < 40 cm (n°59) (mean TL ± SD = 27.23 ± 5.94)	TL > 40 cm (n°25) (mean TL ± SD = 45.35 ± 4.62)
Largemouth bass	ALL (n°142) (mean TL ± SD = 24.24 ± 7.30)	0.790	0.925	0.623
	TL < 25 cm (n°74) (mean TL ± SD = 18.34 ± 3.93)	0.824	0.895	0.654
	T L > 25 cm (n°68) (mean TL ± SD = 30.58 ± 3.99)	0.857	0.855	0.694

DISCUSSION

Largemouth bass are opportunistic predators that have a varied diet depending on their environment (HE *et al.*, 1994; HICKLEY *et al.*, 1994; GODINHO *et al.*, 1997). In other European sites where the species has been introduced the dominant food items in its diet were not only fish, but mainly crayfish and insects (ALESSIO, 1983; RODRÍGUEZ-JIMÉNEZ, 1989; GODINHO and FERREIRA, 1994; NICOLA *et al.*, 1996; GODINHO *et al.*, 1997; GODINHO and FERREIRA, 1998). In Lake Trasimeno the main food of *M. salmoides* was the grass shrimp *P. antennarius*; diet of older specimens was almost exclusively made up of crustaceans; fish are the dominant food item in the youngest specimens, insects are scarce in the diet of all age classes. In Spain NICOLA *et al.* (1996) have found that while insects were important prey for smaller largemouth bass, they were present in all size classes; crayfish and fish were also present in all size classes, but rose in importance in older largemouth bass. In a Portuguese stream GODINHO and FERREIRA (1998) have found that besides a few Odonata nymphs, *M. salmoides* over 20 cm in TL preyed exclusively upon fish and Decapoda, but they strongly favoured Deacapoda when the food items are expressed as abundance (%N).

That the pike is a piscivorous predator has been demonstrated in numerous studies which showed a predominance of fish in the diet beginning at an early age (AVIAN *et al.*, 1998; FILLEUL and LE LOUARN, 1998; KANGUR and KANGUR, 1998). However in Lake Trasimeno the pike's diet is varied and not exclusively fish-based, but fish were more important in its diet than for largemouth bass. *P. antennarius* was also the most abundant food in *E. lucius* diet but fish were the second most important food category in terms of occurrence. The variety of fish in the pike's diet, which included largemouth bass, was greater than for *M. salmoides*. No cases of cannibalism by pike, a frequent phenomenon in other environments, were recorded (AVIAN *et al.*, 1998; MARGENAU *et al.*, 1998).

Marked seasonal variations in the feeding activities of *E. lucius* and *M. salmoides* were observed and both species had the most empty stomachs in the winter. The seasonal trend in the feeding activities is related to water temperature and the typical reduction in foraging activity during the reproductive period in both species (HEIDINGER, 1976; ALESSIO, 1983; RAAT, 1988; ROSENBLUM *et al.*, 1994). In Lake Trasimeno *E. lucius* usually reproduce in February (NATALI, 1993) and have the greatest feeding activity in the spring. *M. salmoides* is spawning in spring, reason why the number of empty stomachs remains high also in this season. Its greatest feeding activity in Lake Trasimeno occurs in the summer and the least activity is in the winter as occurs in other Italian (ALESSIO, 1983) and European lakes (NICOLA *et al.*, 1996).

E. lucius and *M. salmoides* are both considered non-selective predators (RAAT, 1988; ADAMS, 1991; HE *et al.*, 1994; HICKLEY *et al.*, 1994; NICOLA *et al.*, 1996; GODINHO *et al.*, 1997; MARGENAU *et al.*, 1998); and their diets are strongly influenced by food availability. Fish and shrimps seemed to be the food alternatives of pike and largemouth bass based on their abundance and vulnerability which vary seasonally. *M. salmoides* are less efficient foragers than *E. lucius* in areas that are thick with hydrophytes that provide refuge for the fish prey (OLSON *et al.*, 1998) and its foraging success has been shown to decrease with the increasing abundance of submerged vegetation (GODINHO *et al.*, 1997). In manipulative experiments in a Texas reservoir BETTOLLI *et al.* (1992) have found that before aquatic vegetation removal the diet of largemouth bass was made mainly of insects, amphipods and *P. antennarius*, whereas after the removal of the vegetation piscivory increased significantly. Lake Trasimeno is subject to marked changes in water level with the highest levels during winter and the maximum presence of fish in largemouth bass stomachs may be related to less aquatic vegetation and higher water levels. This was confirmed by the winter high percentage of sand smelts found in largemouth bass stomachs, because these fish are generally associated with vegetation-free water in Lake Trasimeno (NATALI, 1993). In Lake Trasimeno, *P. antennarius* is a food source that guarantees optimal growth (LORENZONI *et al.*, 1996) in contrast to what occurs in most environments in which *M. salmoides* have a fish-poor diet.

The variability in the seasonal trends of the various food items in pike stomachs is also related to the seasonal availability of the different food sources. In contrast to *M. salmoides*, the predator behaviour of *E. lucius* takes advantage of aquatic vegetation (GRIMM, 1991); in Lake Trasimeno the high percentage of *P. antennarius* in the pike diet during the winter can be attributed to the reduced availability of forage fish. In a study on the trophic ecology of *E. lucius* and *M. salmoides* in six lakes located in Minnesota (U.S.A.) SOUPIR *et al.* (2000) have found that pike was more selective in summer, when the highest proportion of its diet was composed of fish; the uppermost proportions of other food items, mainly insects, were ingested when prey fish densities were lowest. This pattern was similar in both allopatric and sympatric assemblages and was likely due to a fish diet preference in pike.

The overall value of the diet overlap index between *E. lucius* and *M. salmoides* was very high (α = 0.79) and the probability of a strong negative interaction between the two species could not be excluded. MACEINA and MURPHY (1988) consider 0.80 to be an index value which indicates a high level of diet similarity; values $>$ 0.60 should be considered biologically significant and indicative of interspecific competition if the resources are limited (ZARET and RAND, 1971). When the sample was divided in size, the index values showed that the overlap of largemouth bass diet was greater with respect to the whole sample for younger pike, while it decreased with respect to older pike. This can be explained by the fact that in Lake Trasimeno, *M. salmoides* are primarily fish-eaters in the young stages, while the older specimens feed mostly on *P. antennarius*. In contrast, the piscivorous tendency in *E. lucius* progressively increases with age, while the crustaceans are a very important component in the diets of younger specimens. The make-up of the sample and the number of empty stomachs prevented the use of the 5+-age class in *E. lucius* in the comparison but if the sample included more fish in the older age class, the phenomenon would probably be even more evident (RAAT, 1988; AVIAN *et al.*, 1998).

CONCLUSION

Competition does not necessarily occur among sympatric species that use the same food resources. This can be avoided by partitioning the different food resources (HODGSON *et al.*, 1997). In particular, significant differences in habitat selection seem to be an efficient mechanism that can guarantee the coexistence among species that use the same food source (WERNER *et al.*, 1981; SCOTT and ANGERMEIER, 1998). The interaction between *E. lucius* and *M. salmoides* does not seem to be in this category since the two species have the same habitat preference. This is confirmed by the recent expansion of largemouth bass into the same lake zones where pike were formerly more abundant.

Food competition between *E. lucius* and *M. salmoides* has not been demonstrated to date and has even been excluded by ALESSIO (1983) for other Italian environments. To evaluate the potential intensity of competition between two sympatric species diet overlap must be examined under conditions of allopatry and sympatry. A change in trophic niche between these conditions is an indication of competition (HEARN, 1987). In six lakes of Minnesota the diets of pike and largemouth bass in sympatric assemblages are indicating the potential for competition, especially during periods of low prey availability (SOUPIR *et al.*, 2000); in this study, however, the food consumed by pike did not differ between sympatric and allopatric assemblages, contrarily of what happens for largemouth bass. It would indicate that *M. salmoides* are at a significant disadvantage when coexisting with *E. lucius.* Unfortunately there is a lack of information about the feeding of the pike in the Lake Trasimeno before the introduction of largemouth bass. Based on the results of our study, however, the hypothesis of food competition between *E. lucius* and *M. salmoides* cannot be completely rejected because the data showed a high probability of competition between the two species when the resources were limited. This potential interaction could be reduced by different spatial and temporal allocation of the resources (HEARN, 1987; ARMSTRONG *et al.*, 1998). The analysis of the seasonal trends of feeding activity showed some substantial differences between the two species. In addition, the method used to analyse the stomach contents which gives more weight to the numerical presence rather than the biomass of the food categories found in the fish stomachs could have caused an overestimation of the level of food overlap between the two species. Further study of the degree of interaction between the two species is needed.

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