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Fish spatial distribution in the littoral zone of Lake Pareloup (France) during summer

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With 5 figures and 1 table

Abstract: We studied the spatial distribution of 11 fish species in the littoral zone of Lake Pareloup (South-West of France) using a non-destructive Point Abundance Sampling by Scuba diving. The fish spatial assemblage was investigated with seven commonly used environmental variables (topographical, biological and substratum variables). Three fish groups colonising three different habitats were identified. The spatial distribution of each fish species was mainly influenced by two environmental factors: distance from the bank (highly correlated with depth) and vegetation cover. i) Young-of-the-year (YOY) cyprinids and northern pike were mainly associated with a small distance from the bank (less than 6 m). ii) Older cyprinids and perch (≥1+) were located between 6 and 12 m from the bank. iii) YOY perch and older northern pike (≥1+), occurred independently of the distance from the bank, but exhibited different responses to the percentage of vegetation cover: pike preferred areas with dense vegetation cover, while YOY perch abundance decreased rapidly with increasing vegetation cover. Thus, YOY fishes were common and abundant in shallow water, whereas large predators such as northern pike were found in vegetated areas. Therefore, vegetation cover, although generally considered as a crucial 0+ fish habitat, was here a secondary variable after distance from the bank. We hypothesised that the high density of predators (and especially northern pike) inside the vegetation as well as their high predation efficiency in this area could explain such a spatial distribution, shallow littoral areas being, in that case, safer from predation than vegetated ones for YOY fishes.

Key words: Point abundance sampling, shore distance, vegetation cover, correspondence analysis.

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Introduction

Compared to ecological knowledge derived from North American lakes, fish habitat use in littoral areas of European lakes is poorly documented. One of the main reasons is that most fish habitat studies have been performed using a large spatial scale (ROSSIER 1995, BROSSE et al. 1999 a) and more precise studies (i.e. microhabitat scale) have rarely been performed. The littoral zone constitutes the most heterogeneous part of lakes (FISCHER & ECKMANN 1997), where habitats and food resources are more diverse than in open water (PIERCE et al. 1994), leading to high fish densities (BROSSE et al. 1999 c). During summer, a 'littoralisation' phenomenon occurs in lakes, leading to an increased species richness in the littoral zone (WERNER et al. 1977, ROSSIER 1995, BROSSE et al. 1999 a, c) owing to the arrival of adults for spawning and then, to the presence of young-of-the-year (YOY) and juveniles (WERNER 1986, MITTELBACH 1988, CASSELMAN & LEWIS 1996). This phenomenon creates intense competition for feeding resources (MATENA 1995, SIMONIAN et al. 1995). Therefore, it appears important to study the spatial fish community distribution in littoral zones of lakes during this summer period.

In freshwater ecosystems, the two most frequently used sampling techniques to study fish spatial distribution and habitat use have been gillnets and electrofishing. However, these fishing techniques are known to be size- and species-selective and to induce fish escape behaviour (HAMLEY 1975, COPP 1989, BROSSE et al. 1999 b). To limit these biases, we used Point Abundance Sampling by Scuba diving (PASS). It was first employed in marine waters (BROCK 1954) and then in North American streams to investigate salmonid behaviour (ELLIS 1961, KEENLEYSIDE 1962) and microhabitat (BEECHER et al. 1993), but it has been little used in lakes. In Europe, the works of ROSSIER (1995) and BROSSE et al. (1999 b) are, as far as we are aware, the first habitat studies using scuba in a lake. PASS has recently proved to be a rapid and efficient method to assess fish microhabitat use (BROSSE et al. 1999 b).

The aim of this study was i) to identify the microhabitat of the fish community in a littoral zone of a European lake in summer, using the PASS method, ii) to identify the most important variables ruling fish spatial distribution and iii) to formulate hypotheses about the ecological processes that explain such a spatial assemblage.

Materials and methods

Study site

The study was undertaken during the summer of 1998 in Lake Pareloup (Fig. 1 A). This reservoir is located in the South-West of France, near the city of Rodez. It covers a to-

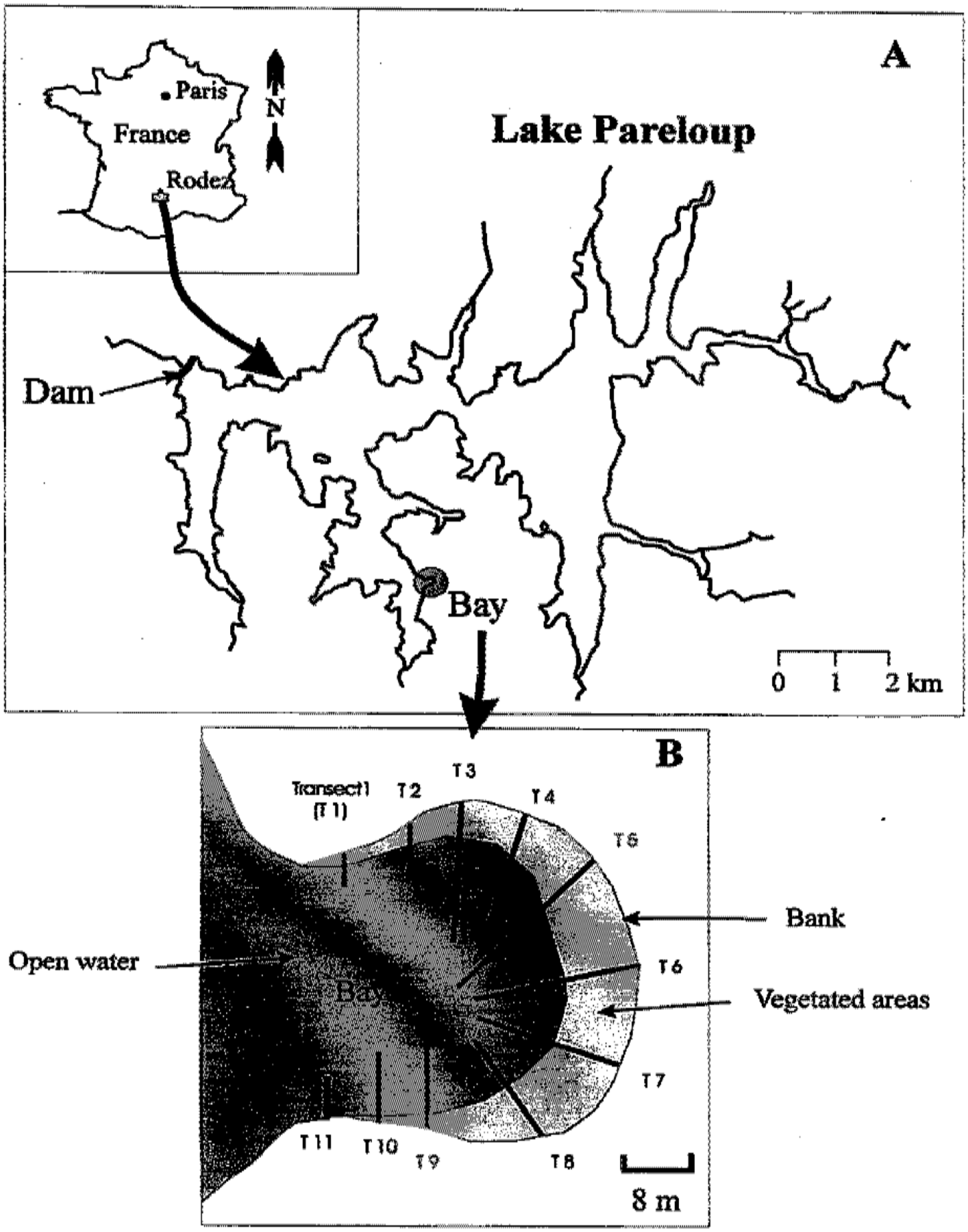

Fig. 1. Study site (**A**) and location of the transects (**B**).

tal area of 1,250 ha with a volume of about 168×10^6 m^3. Maximum depth is 37 m and average depth is 12.5 m. Lake Pareloup is a warm monomictic lake. It undergoes summer thermal stratification with low oxygen content below the thermocline (located about 10 m below the surface from early June to mid-September), which prevents the fish from colonising deep water during this period (Richeux et al. 1994 b, Brosse et al. 1999 c).

Fish were sampled weekly from the spawning period (mid May) to the juvenile period (late August), i.e. over 12 weeks, in a selected littoral zone of the lake. This sampling area was chosen for its topographical heterogeneity which provided a large range of habitat characteristics.

Sampling method

Sampling was performed using Point Abundance Sampling which was originally developed by Blondel et al. (1970) for studying nesting birds. It was intended to address clumped distribution, and it is based on the statistical theory that many small sample units provide more precise results than a few large samples; thus, it requires numerous small samples to be taken within the study area. Using that theory, Point Abundance Sampling by Scuba diving (PASS) (Brosse et al. 1999 b) was applied to study fish abundance in the shallow littoral areas of this lake.

Eleven transects were defined in the selected bay (Fig. 1B). Their length depended on the depth and varied between 4 and 32 m. Indeed, sampling was performed until depth reached 2 m and deeper areas were not considered in order to avoid fish underestimation caused by water turbidity and light intensity attenuation. Each transect was defined by a 2-m wide observation lane starting from the bank, with marks every 1 m. With this labelling, we obtained 230 sampling points. The diver was first located far from the bank in open water, he then swam towards the bank along one defined lane, covering the full surface of each sampling point. Water transparency was sufficient to identify and count the fish in each 2-m wide and 1-m long point. Fish counts were made while swimming along the transects and the results obtained were expressed as densities or through extrapolation as estimates of total number of individuals of each species occurring in each sample according to Sale (1980). When dense fish shoals were observed, counting was limited to a sub-sample, and then extrapolated over the entire volume of the sample. Out of the total of 2760 samples (230 sampling points × 12 weeks), this procedure was applied to 220 samples. This method, applied here to fish counts, has been proved efficient and is commonly used to study gregarious birds (Dervieux et al. 1980). As suggested by Northcote & Wilkie (1963) and Eklov (1997), a constant swimming speed of ca. 5 m/min was used in order to avoid disturbing the fish community. The shallowest areas (i.e. less than 50 cm deep) were investigated using the same scuba design, and provided fish abundance and occurrence results similar to those gathered by electrofishing methods (Wilcoxon non-parametric test, $Z = -0.50$, $p = 0.62$ for fish abundance and $Z = -0.20$, $p = 0.85$ for fish occurrence). For each fish species, individuals recorded were sorted into two categories: young-of-the-year (YOY, 0+) and older fish (≥1+; called 'adults') to avoid bias due to behavioural and habitat use differences between YOY and adult fishes. Fish age categories (0+ and ≥1+) were easily distinguished, as sampling was performed from the spawning to the juvenile period (from early May to late August), allowing us to follow the growth of each cohort. Owing to the temporal survey, fish species were correctly identified, with only one exception for YOY bleak (*Alburnus alburnus*) which can be confused with YOY roach (*Rutilus rutilus*) due to similar hatching periods, morphology and habitat during the earlier life stages, as shown by BROSSE et al. (in press) in the same environment. As a complement, fish species, length and age were checked weekly by punctual dipnet and electrofishing sampling.

At each sampling point, 8 environmental variables were measured in order to assess fish microhabitat: two topographical variables, distance from the bank and depth both expressed in metres, one biological variable, the flooded vegetation cover expressed as percent cover calculated for the area of each sampling point, and 5 substratum variables expressed as percentages of boulders, pebbles, gravel, sand, and silt using the CAILLEUX (1954) methodology.

Data processing

Among the 2,760 censuses, the 1,152 samples with no fish were removed from the data matrix in order to avoid an undue influence of the zero values which could induce biases in the analysis (TER BRAAK 1986, PENNINGTON 1996). As a consequence the final data matrix contained 1,608 samples. Prior to the statistical analysis and to respect normality of the distribution, the data were log (x + 1) transformed (FIELD et al. 1982).

A Canonical Correspondence Analysis (CCA) (TER BRAAK 1986) was used to describe the general trends of fish spatial occupancy with the aim of determining spatial distribution of the whole fish community and identifying the most influential environmental factors. Fish groups were identified by means of cluster analysis based on the fish densities data matrix using Ward's method (WARD 1963) which considers the average value of all objects in one cluster as the reference point for distances to other objects and the normalised Euclidiean distances (i.e. root mean squared distances). Fish microhabitats according to the two main environmental variables were studied in more detail. SPSS Release 8 (NORUSIS 1997) was used to set up scatterplots showing fish density according to each selected variable. To obtain maximum ecological reliability, data fitting was performed with a LOWESS (LOcally WEighted regression Scatterplot Smoothing) (CLEVELAND 1979) non-parametric regression model, which is known to reliably fit data tendencies and to respect natural non-linearity of data (TREXLER & TRAVIS 1993). In the smoothing procedure, 80 % of the samples were perfectly smoothed to provide a high level of accuracy.

Results

A total of 201,577 fishes, belonging to 11 species and 4 families, was sampled (Table 1). The mean density was ca. 36.5 fish per square metre for the total of 2,760 samples (62.7 fish per square metre for the 1,608 samples where at least one fish was present). Numerical abundance of the fish community was highly dominated by YOY roach and YOY rudd (*Scardinius erythrophthalmus*) which represented 41.8 % and 37.9 % of the total number of fish sampled, respectively.

Table 1. Stage (YOY: young-of-the-year; A: juveniles and adults ≥+), number of fish counted, frequency occurrence (% F, pecentage of samples were species i was present) and relative density occurrence (% N, numerical percentage of species i in fish community) of the fish community sampled. Species are listed in alphabetical order per family.

Family	Species	Common name	Stage	Number	% F	% N
Centrarchidae	*Lepomis gibbosus*	pumpinkseed	A	3	0.1	0.0
Cyprinidae	*Abramis brama*	bream	YOY	638	2.5	0.3
	Abramis brama	bream	A	36	1.1	0.0
	Alburnus alburnus	bleak	YOY	8,692	10.9	4.3
	Alburnus alburnus	bleak	A	728	3.6	0.4
	Cyprinus carpio	carp	A	24	1.3	0.0
	Gobio gobio	gudgeon	YOY	487	2.2	0.2
	Gobio gobio	gudgeon	A	455	1.5	0.2
	Rutilus rutilus	roach	YOY	84,315	18.0	41.8
	Rutilus rutilus	roach	A	1,800	9.5	0.9
	Scardinius erythrophthalmus	rudd	YOY	76,410	16.1	37.9
	Scardinius erythropthalmus	rudd	A	1,265	6.3	0.6
	Tinca tinca	tench	YOY	1,200	1.1	0.6
	Tinca tinca	tench	A	67	1.5	0.0
Esocidae	*Esox lucius*	northern pike	YOY	354	0.8	0.2
	Esox lucius	northern pike	A	63	1.1	0.0
Percidae	*Perca fluviatilis*	perch	YOY	23,147	12.5	11.5
	Perca fluviatilis	perch	A	1,839	10.2	0.9
	Stizostedion lucioperca	pike-perch	YOY	43	0.8	0.0
	Stizostedion lucioperca	pike-perch	A	11	0.2	0.0

Among microhabitat data, the Pearson correlation matrix (with Bonferroni post analysis) showed highly significant correlation between distance from the bank and depth ($r = 0.77$; $p < 0.001$). To avoid biases which could be induced by the co-linearity between variables, depth was removed from the data matrix. Consequently, the statistical analyses were performed on a set of seven variables, i.e. distance from the bank, percentage of silt, sand, gravel, pebbles, boulders, and flooded vegetation cover.

The CCA plane (Fig. 2) shows the associations among species and environmental variables. The first two axes of the CCA analysis accounted for 77 % of the variability (61 % and 16 %, respectively). The CCA bi-plot showed that the percentage of vegetation cover and distance from the bank (correlated with depth) were the most influential variables in the spatial distribution of the fish assemblage, they had the longest vector lengths; substratum variables were of lesser importance. The position of a species along the vector of a variable reflects its preference for that variable. Consequently, a more detailed study of the influence of the two most important variables on fish microhabitat was performed. To obtain reliable and representative results from an ecologi-

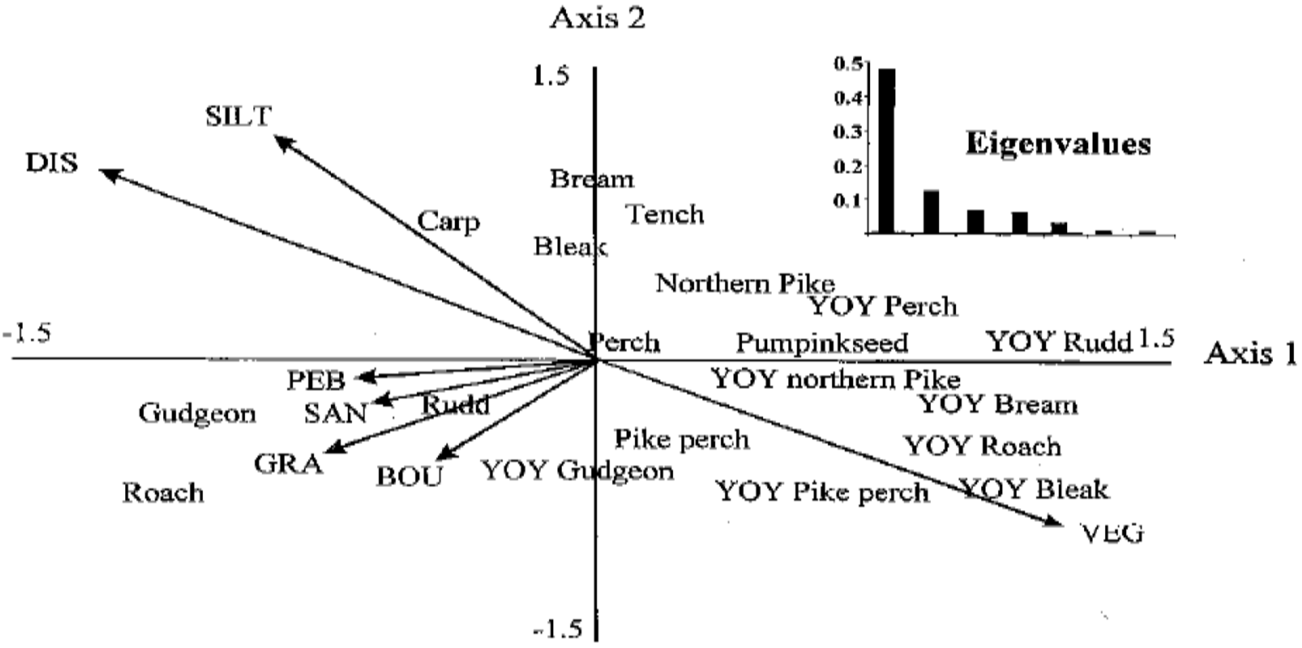

Fig. 2. F1×F2 plane of the Canonical Correspondence Analysis (CCA) between fish populations and environmental variables. DIS: distance from the bank, VEG: vegetation cover, SILT: silt, SAN: sand, PEB: pebbles, GRA: gravel, BOU: boulders, and YOY: Young-of-the-year.

cal point of view, only the most abundant and most frequent fish populations of the littoral zone of lake Pareloup, i.e. roach, rudd, perch (*Perca fluviatilis*), bleak, gudgeon (*Gobio gobio*), and northern pike (*Esox lucius*) (see Table 1) were studied in detail.

The cluster analysis indicated that fish could be assembled into three groups at the 75 % probability level on the basis of dissimilarities between species abundance and samples (Fig. 3):

Cluster A was composed of adult fish (≥1+) except adult pike (i.e., cyprinids and perch). Most gudgeon, rudd, and bleak were distributed about 10 m from the bank. Roach and perch were equally distributed over the entire range of variation of this variable (Fig. 4 A). Fish habitat features according to the flooded vegetation cover (Fig. 5 A) showed that roach, rudd and perch were observed everywhere in the bay with a certain preference for open water. Most gudgeon were located in the transition zone between dense vegetation and open water, about 50 % of vegetation cover. Bleak preferred two zones: the open water without vegetation and highly vegetated areas (100 % of vegetation cover).

Cluster B was composed of all YOY fish, except perch (i.e., cyprinids and pike). Most of these remained less than 8 m from the bank, which represents between 70 and 80 cm depth. Beyond this distance, YOY fish abundance decreased rapidly. YOY gudgeon had the narrowest distribution range of distance (0–10 m from the bank) followed by YOY bleak and YOY rudd (0–16 m) and

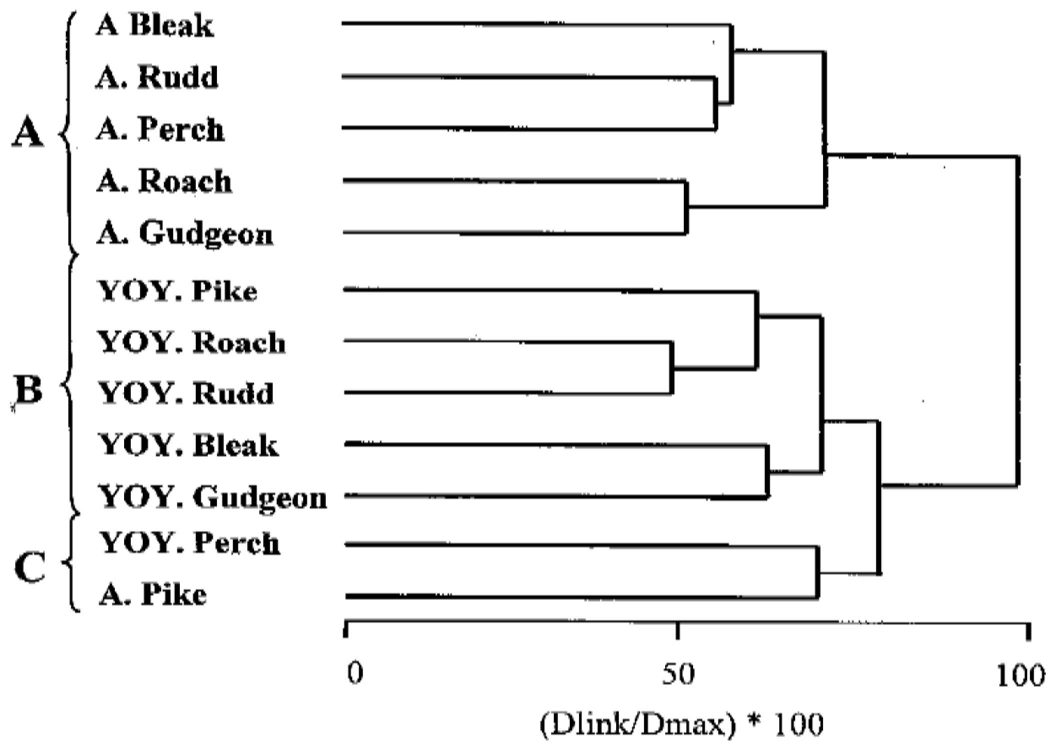

Fig. 3. Cluster analysis (Ward's method, Euclidean distances) of fish abundance. The linkage distance (Dlink) is presented as a percentage of the maximum linkage distance (Dmax). YOY: Young-of-the-year; A: older fishes.

finally by the ubiquitous YOY roach (Fig. 4 B). YOY roach and rudd were hardly affected by vegetation cover, whereas YOY pike abundances increased with vegetation cover up to ca. 70 % cover (Fig. 5 B). In contrast the abundance of YOY bleak and gudgeon decreased rapidly in areas with more than 40 % vegetation cover.

Cluster C was composed of YOY perch, and adult pike (≥1+). Distance from the bank did not influence the spatial distribution of these two populations (Fig. 4 C) whereas they responded differently to the percentage of vegetation cover: pike showed a preference for areas with some vegetation cover (more than 30 %), while YOY perch abundance greatly decreased with increasing vegetation cover above 30 % (Fig. 5 C).

Discussion

Community assemblage studies require reliable sampling designs, which permit the whole fish assemblage to be sampled. Underwater visual sampling (PASS) is known as an appropriate method for the census of fish populations. PASS provided reliable information, as it does not affect the environment and the welfare of the fish (see Brosse et al. 1999 b). Using this method, of the 15

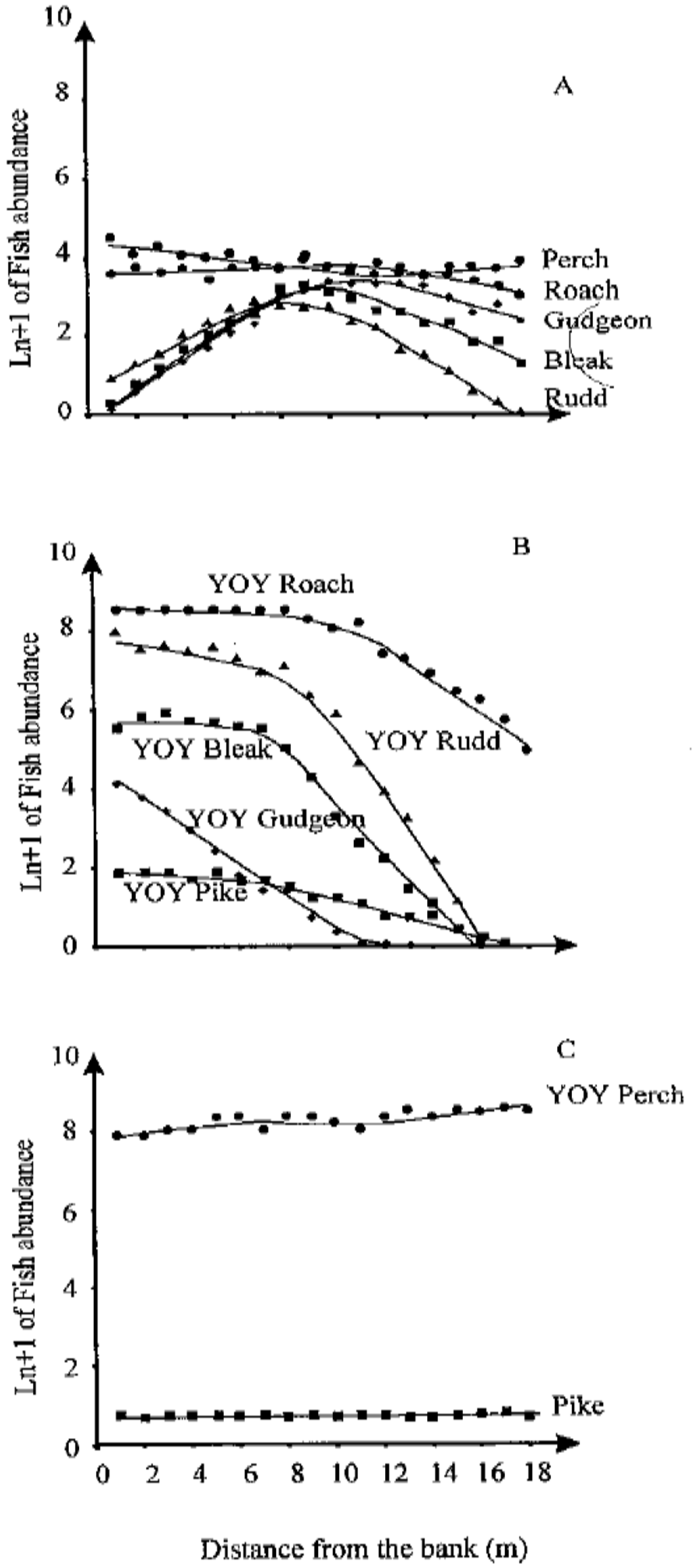

Fig. 4. Location of each fish group (log transformed fish density) versus distance from the bank. **A:** cluster A (older cyprinids and perch); **B:** cluster B (YOY cyprinids and pike); **C:** cluster C (YOY perch and older pike). Smoothing was performed using LOWESS non-parametric smoother (solid lines) with tension (*f*) = 0.8 (see text for detail). YOY: Young-of-the-year.

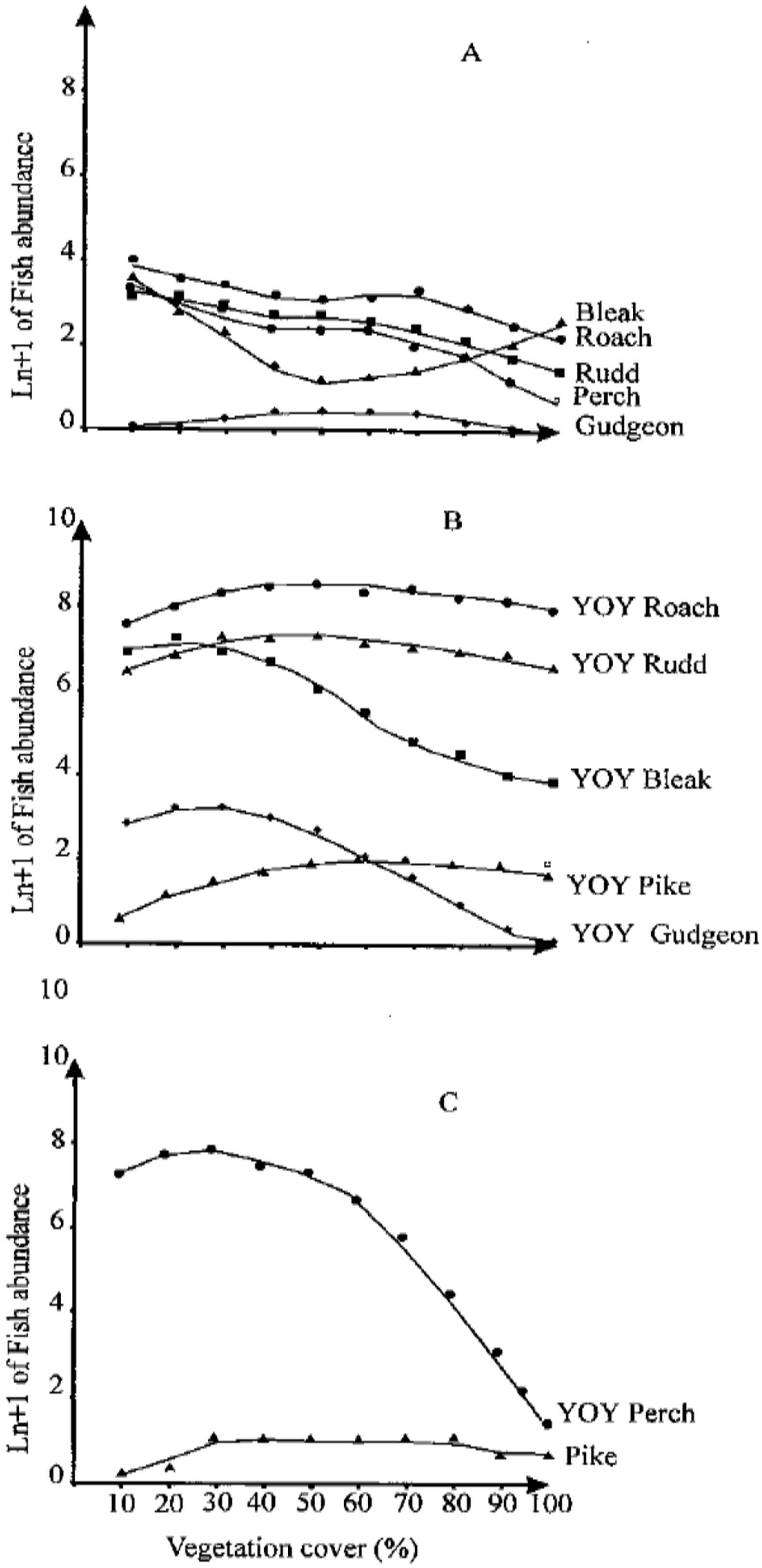

Fig. 5. Location of each fish group versus vegetation cover. Same captions as in Fig. 4.

fish species described in the lake (BROSSE 1999), 11 were recorded in the littoral zone during the summer stratification. These species could be considered as three distinct groups that exhibited different spatial occupancy according to environmental factors. Moreover, an important spatial separation was found between YOY and older individuals.

The maximal abundance of fish belonging to the first group, without species distinction (i.e. ≥1+ old perch and cyprinids) was observed between 6 and 12 m from the bank and with little vegetation cover. However, some differences in fish distribution were revealed according to the species. Adult cyprinids (≥1+) were more dispersed than YOY, and this distribution pattern can be ascribed to an opportunistic habitat use behaviour, which parallels previous studies considering feeding habits (MICHEL & OBERDORFF 1995). The age ≥1+ fish were mainly located in the open water, therefore reducing predation risk by adult pike in the vegetation, as previously demonstrated by experimental studies using pike and a cyprinid prey (EKLOV & HAMRIN 1989). However, the relevance of experimental studies using cages or experimental ponds is questionable (ENGLUND 1997) and should be verified in natural environments (TOWNSEND et al. 2000). Our study therefore adds weight to previous results that considered the influence of predation on prey habitat use in artificial environments. Adult perch were distributed evenly along the transects whereas their usual fish prey, i.e. YOY fish (MICHEL & OBERDORFF 1995), were mainly located in the shallow areas. This could signify that YOY fish marginally contribute to adult perch diet and therefore to their spatial distribution. Indeed, in Lake Pareloup, RICHEUX et al. (1994 a) demonstrated that adult perch and adult cyprinids mainly prey on benthic invertebrates and zooplankton, which therefore justifies a similar habitat use. Finally, the particular bimodal habitat-use by age ≥1+ bleak may be considered as two distinct behavioural traits: the use of dense vegetation during the spawning period, whereas resting and feeding areas were mainly located in open water.

The second group, composed of YOY cyprinids and YOY pike, mainly colonised areas close to the bank. In our study, vegetation did not appear as a primary key factor, although it is usually assumed to be very important for YOY fish (WERNER et al. 1977, RAHEL 1984, GRENOUILLET et al. 2000) which use this habitat as a refuge from predators and as feeding grounds (WERNER et al. 1983, ROZAS & ODUM 1988). However, some experimental studies showed that under high predation pressure, prey feeding behaviour decreases and refuge occupation increases (PERSSON & EKLOV 1995). In our study, vegetation located in far from the bank and deep areas did not constitute an efficient refuge against predators as both 0+ and adult pike prey efficiently inside vegetation (CASSELMAN & LEWIS 1996, EKLOV 1997). Therefore, under this predation pressure, only shallow areas (with or without vegetation) were safe from aquatic predators due to the avoidance of shallow waters by large fish (HOL-

LAND & HUSTON 1984, CASSELMAN & LEWIS 1996). However, we can hypothesise that the discrepancy between this study and several previous ones considering the lack of preference for vegetation in shallow waters could be ascribed to the scarcity of aerial predators such as grey heron (*Ardea cinerdea*) in the littoral zone of that lake. As a consequence, these results gathered in a natural and undisturbed environment confirm and add weight to experimental and theoretical demonstrations (WERNER et al. 1983, ROZAS & ODUM 1988, DIEHL & EKLOV 1995) which stress the importance of both structural characteristics and predation on habitat use by YOY fish.

Particular distribution features were found for the third group constituted by YOY perch and adult pike, both occurred over the whole transects. Adult pike hid inside vegetation cover ≥30 %, adopting a "sit and wait" position on the bottom, in relation with their predation behaviour, in agreement with TURNER & MACKAY (1985) and EKLOV (1997). In contrast, most YOY perch were found outside aquatic vegetation. Such a behaviour could be the result of a trade-off between maximisation of feeding rate and predation avoidance. On one hand, YOY perch avoidance of shallow and vegetated areas, which sustain high macroinvertebrate biomass, could be related to the presence of YOY roach which outcompete them (PERSSON 1983, DIEHL 1988, BERGMAN 1990). On the other hand, YOY perch are little consumed by adult perch in the presence of YOY cyprinids (BROSSE, unpubl. data) because of their dorsal spines which afford a relative protection against predation (PERSSON 1986) and this allowed them to colonise open waters.

Even if fish abundance and microhabitat use are strongly affected by underlying biotic interactions such as competition, predation and resource limitation, the fish spatial assemblage and the associated species interactions are usually evidently connected to the environmental features (GROSSMAN et al. 1982, WERNER & GILLIAM 1984, FISCHER & ECKMANN 1997, GROSSMAN et al. 1998). Our results gathered in the littoral area of the lake contrast with those obtained in stream systems (COPP 1992, 1993, 1997), in contrast to streams, substratum variables played a secondary role in fish assemblage distribution. In lakes, distance from the bank, depth and particularly vegetation cover are usually considered as key environmental factors in the littoral fish community organisation (at least for YOY) (HALL & WERNER 1977, CONROW et al. 1990, CHICK & MCIVOR 1994, EKLOV 1997). However, in our study, distance from the bank, and hence depth (it was not possible to separate the distance from the bank and depth, as they were highly correlated as in numerous lakes) were crucial for fish. In the light of our results, we can formulate the hypothesis that shallow littoral water provided efficient shelter against predators feeding inside macrophytes which could explain the primary importance of the distance from the bank and then the secondary role of vegetation cover. In this way, this study adds weight to the theoretical "top-down" view of fish structure (sensu NORTHCOTE 1988) which stipulates that predators can structure the space occupation by their prey.

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References

BEECHER, H. A., JOHNSON, T. H. & CARLETON, J. P. (1993): Predicting microdistributions of steelhead (*Oncorhynchus mykiss*) parr from depth and velocity preference criteria: test of an assumption of the instream flow incremental methodology. – Can. J. Fish. Aquat. Sci. **50:** 1380–1387.

BERGMAN, E. (1990): Effects of roach (*Rutilus rutilus*) on two percids, *Perca fluviatilis* and *Gymnocephalus cernua*: importance of species interaction for diet shifts. – Oikos **57:** 241–249.

BLONDEL, J., FERRY, C. & FROCHOT, B. (1970): La méthode des indices ponctuels d' abondance (IPA) ou des relevés d'avifaune par "stations d'écoute". – Alauda **38:** 55–71.

BROCK, V. (1954): A preliminary report on a method of estimating reef fish populations. – J. Wildlife Managem. **18:** 297–308.

BROSSE, S. (1999): Habitat, dynamique spatiale et structure des communautés pisciaires en milieu lacustre. Etude de la retenue de Pareloup (Aveyron, France). – Ph.D. University of Toulouse 3, France.

BROSSE, S., DAUBA, F., OBERDORFF, T. & LEK, S. (1999 a): Influence of some topographical variables on the spatial distribution of lake fish during summer stratification. – Arch. Hydrobiol. **145:** 359–371.

BROSSE, S., GABAS, S., CEVER, K. & LEK, S. (1999 b): Comparison of two Point Abundance Sampling methods to assess young roach (*Rutilus rutilus* L.) microhabitat in the littoral zone of lake Pareloup (France). – Annls Limnol. **35:** 199–204.

BROSSE, S., LEK, S. & DAUBA, F. (1999 c): Predicting fish distribution in a mesotrophic lake by hydroacoustic survey and artificial neural networks. – Limnol. Oceanogr. **44:** 1293–1303.

BROSSE, S., LAFFAILLE, P., GABAS, S. & LEK, S. (in press): Is scuba sampling a relevant method to study fish microhabitat in lakes? Examples and comparisons for three common European species. – Ecol. Freshwat. Fish.

CAILLEUX, A. (1954): Limites dimentionnelles des noms des fractions granulométriques. – Bull. Soc. Géol. Fr. **4:** 643–646.

CASSELMAN, J. M. & LEWIS, C. A. (1996): Habitat requirements of northern pike (*Esox lucius*). – Can. J. Fish. Aquat. Sci. **53:** 161–174.

CHICK, J. H. & MCIVOR, C. C. (1994): Patterns in the abundance and composition of fishes among beds of different macrophytes: viewing a littoral zone as a landscape. – Can. J. Fish. Aquat. Sci. **51:** 2873–2882.

CLEVELAND, W. S. (1979): Robust locally weighted regression and smoothing scatterplots. – J. Amer. Statist. Assoc. **74:** 829–836.

CONROW, R., ZALE, A. V. & GREGORY, R. W. (1990): Distributions and abundances of early life stages in a Florida lake dominated by aquatic macrophytes. – Trans. Amer. Fish. Soc. **119:** 521–528.

COPP, G. H. (1989): Electrofishing for fish larvae and juveniles: equipment modifications for increased efficiency with short fishes. – Aquacult. Fish. Managem. **20:** 453–462.

– (1992): Comparative microhabitat use of cyprinid larvae in a lotic floodplain channel. – Env. Biol. Fish **33:** 181–193.

– (1993): Microhabitat use of fish larvae and 0+ juveniles in a small abandoned channel of the upper River Rhône, France. – Folia Zool. **42:** 153–164.

– (1997): Microhabitat use of fish larvae and 0+ juveniles in a highly regulated section of the river Great Ouse. – Regul. River **13:** 267–276.

DERVIEUX, A., LEBRETON, J. D. & TAMISIER, A. (1980): Technique et fiabilité des dénombrements aériens de canards et de foulques hivernant en Camargue. – Rev. Ecol. (Terre & Vie) **34:** 69–99.

DIEHL, S. (1988): Foraging efficiency of three freshwater fish: effects of structural complexity and light. – Oikos **53:** 207–214.

DIEHL, S. & EKLOV, P. (1995): Effects of piscivore-mediated habitat use on resources, diet, and growth or perch. – Ecology **76:** 1712–1726.

EKLOV, P. (1997): Effects of habitat complexity and prey abundance on the spatial and temporal distributions of perch (*Perca fluviatilis*) and pike (*Esox lucius*). – Can. J. Fish. Aquat. Sci. **54:** 1520–1531.

EKLOV, P. & HAMRIN, S. F. (1989): Predator efficiency and prey selection: interactions between pike (*Esox lucius*), perch (*Perca fluviatilis*) and rudd (*Scardinius erythrophthalmus*). – Oikos **56:** 149–156.

ELLIS, D. V. (1961): Diving and photographic techniques for observing and recording salmon activities. – J. Fish. Res. Bd. Can. **18:** 1159–1166.

ENGLUND, G. (1997): Importance of spatial scale and prey movements in predator caging experiments. – Ecology **78:** 2316–2325.

FIELD, S. G., CLARKE, K. R. & WARWICK, R. M. (1982): A practical strategy for analyzing multispecies distribution patterns. – Mar. Ecol. Prog. Ser. **8:** 37–52.

FISCHER, P. & ECKMANN, R. (1997): Spatial distribution of littoral fish species in a large European lake, Lake Constance, Germany. – Arch. Hydrobiol. **140:** 91–116.

GRENOUILLET, G., PONT, D. & OLIVIER, J. M. (2000): Habitat occupancy pattern of juvenile fishes in a large lowland river: interactions with macrophytes. – Arch. Hydrobiol. **149:** 307–326.

GROSSMAN, G. D., MOYLE, P. B. & WHITAKER, J. O. Jr. (1982): Stochasticity in structural and functional characteristics of an Indiana stream fish assemblage: a test of community theory. – Amer. Midl. Nat. **120:** 423–454.

GROSSMAN, G. D., RATAJCZAK, R. E. Jr., CRAWFORD, M. & FREEMAN, M. C. (1998): Assemblage organization in stream fishes: effects of environmental variation and interspecific interactions. – Ecol. Monogr. **68:** 395–420.

HALL, D. J. & WERNER, E. E. (1977): Seasonal distribution and abundance of fishes in the littoral zone of a Michigan lake. – Trans. Amer. Fish. Soc. **106:** 545–555.

HAMLEY, J. M. (1975): Review of gillnet selectivity. – J. Fish. Res. Bd. Can. **32:** 1943–1969.

HOLLAND, L. E. & HUSTON, M. L. (1984): Relationship of young-of-the-year northern pike to aquatic vegetation types in brackwaters of the upper Mississippi river. – N. Amer. J. Fish. Managem. **4:** 514–522.

KEENLEYSIDE, M. H. A. (1962): Skin-diving observations of Atlantic salmon and brook trout in the Miramichi River, New Brunswick. – J. Fish. Res. Bd. Can. **19:** 625–634.

MATENA, J. (1995): The role of ecotones as feeding grounds for fish fry in a Bohemian water supply reservoir. – Hydrobiologia **303:** 31–38.

MICHEL, P. & OBERDORFF, T. (1995): Feeding habits of fourteen European freshwater fish species. – Cybim **19:** 5–46.

MITTELBACH, G. (1988): Competition among refuging sunfishes and effects of fish density on littoral zone invertebrates. – Ecology **69:** 614–623.

NORTHCOTE, T. G. (1988): Fish in the structure and function of freshwater ecosystems: a 'top-down' view. – Can. J. Fish. Aquat. Sci. **45:** 361–379.

NORTHCOTE, T. G. & WILKIE, D. (1963): Underwater census of stream fish populations. – Trans. Amer. Fish. Soc. **92:** 146–151.

NORUSIS, M. J. (1997): SPSS for Windows, Advanced Statistics 7.5. – SPSS Inc., Chicago, IL, USA.

PENNINGTON, M. (1996): Estimating the mean and variance from highly skewed marine data. – Fish. Bull. **94:** 498–505.

PERSSON, L. (1983): Effects of intra- and interspecific competition on dynamics and size structure of a perch (*Perca fluviatilis*) and a roach (*Rutilus rutilus*) population. – Oikos **41:** 126–132.

– (1986): Effects of reduced interspecific competition on resource utilization in perch (*Perca fluviatilis*). – Ecology **67:** 355–364.

PERSSON, L. & EKLOV, P. (1995): Prey refuges affecting interactions between piscivorous perch and juvenile perch and roach. – Ecology **76:** 70–81.

PIERCE, C. L., RASMUSSEN, J. B. & LEGGETT, W. C. (1994): Littoral fish communities in Southern Quebec lakes: relationships with limnological and prey resource variables. – Can. J. Fish. Aquat. Sci. **51:** 1128–1138.

RAHEL, F. J. (1984): Factors influencing fish assemblages along a bog lake successional gradient. – Ecology **65:** 1276–1289.

RICHEUX, C., ARIAS-GONZALES, J. E. & TOURENQ, J. N. (1994a): Régime et comportement alimentaire du gardon (*Rutilus rutilus* L.) et de la perche (*Perca fluviatilis* L.) de la retenue de Pareloup. II. Les adultes. – Hydroécol. appl. **6:** 243–256.

RICHEUX, C., NOGUES, J.-F., TOURENQ, J.-N. & ARAGON, B. (1994b): Inventaire piscicole de la retenue hydroélectrique de Pareloup (Aveyron, France) lors de la vidange de juin 1993. Essai d'un nouveau système d'acquisition et de traitement des signaux d'un écosondeur. – Hydroécol. appl. **6:** 197–226.

ROSSIER, O. (1995): Spatial and temporal separation of littoral zone fishes of Lake Geneva (Switzerland-France). – Hydrobiologia **300/301:** 321–327.

ROZAS, L. P. & ODUM, W. E. (1988): Occupation of submerged aquatic vegetation by fishes: testing the roles of food and refuge. – Oecologia **77:** 101–106.

SALE, P. F. (1980): Assemblages of fish on patch reefs – predictable or unpredictable? – Environ. Biol. Fish. **5:** 243–249.

SIMONIAN, A., TATRAI, I., BIRO, P., PAULOVITS, G., TOTH, L. G. & LAKATOS, G. (1995): Biomass of planktonic crustaceans and the food of young cyprinids in the littoral zone of Lake Balaton. – Hydrobiologia **303:** 39–48.

TER BRAAK, C. J. K. (1986): Canonical Correspondence analysis: a new eigenvector technique for multivariate direct gradient analysis. – Ecology **67:** 1167–1179.

TOWNSEND, C. R., HARPER, J. L. & BEGON, M. (2000): Essentials of ecology. – Blackwell Science, Malden, USA, 552 p.

TREXLER, J. C. & TRAVIS, J. (1993): Nontraditional regression analyses. – Ecology **74:** 1629–1637.

TURNER, L. J. & MACKAY, W. C. (1985): Use of visual census for estimating population size in northern pike (*Esox lucius*). – Can. J. Fish. Aquat. Sci. **42:** 1835–1840.

WARD, J. H. (1963): Hierarchical grouping to optimize an objective function. – J. Amer. Stat. Assoc. **58:** 236–244.

WERNER, E. E. (1986): Species interactions in fresh water fish communities. – In: DIAMOND, J. & CASE, T. J. (eds.): Community ecology. – Harper and Row, New York, USA, pp. 344–358.

WERNER, E. E. & GILLIAM, J. F. (1984): The ontogenetic niche and species interactions in size-structured populations. – Annu. Rev. Ecol. Syst. **15:** 393–425.

WERNER, E. E., GILLIAM, J. F., HALL, D. J. & MITTELBACH, G. G. (1983): An experimental test of the effects of predation risk on habitat use in fish. – Ecology **64:** 1540–1548.

WERNER, E. E., HALL, D. J., LAUGHLIN, D. R., WAGNER, D. J., WILSMANN, L. A. & FUNK, F. C. (1977): Habitat partitioning in a freshwater fish community. – J. Fish. Res. Bd. Can. **34:** 360–370.

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