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Fish assemblage patterns in the littoral zone of a European reservoir

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SUMMARY

1. Although reservoirs are common aquatic habitats in Europe, there is little quantitative information on the spatial organisation of fish assemblages inhabiting their littoral zones. Consequently, we characterised fish assemblage structure in the littoral zone of a reservoir (Lake Pareloup) in SW France during late spring, summer and early autumn (the growing season).
2. We measured the relative abundance of fish, weekly from mid-May to mid-October, using point abundance sampling by electrofishing. We identified temporal patterns in assemblage structure using hierarchical cluster analysis, and then characterised the spatial distribution of 17 defined ecospecies using a Kohonen self-organising map (SOM, an unsupervised Artificial Neural Network).
3. Our analyses revealed three distinct faunal structures within the littoral zone. From mid-May to mid-July, adults and young-of-the-year (0+) occupied separate habitats, with most 0+ fish in vegetated habitats and adults in open water. From mid-July to late August, some 0+ co-occurred with adults, but most 0+ fishes remained in vegetated areas. Finally, from late August to mid-October, most fish (both 0+ and adults) left the vegetation for unvegetated littoral habitats, the exception being fish species known to be dependent on macrophytes.
4. Contrary to patterns for adult fishes, the 0+ fish assemblage was dynamic. These dynamics were driven by ontogenetic species-specific habitat changes. Consequently, there was little evidence of stable assemblages or strong assemblage–habitat relationships that would be expected of an 'interactive' assemblage. It is likely that the patterns observed are a result of species-specific response to habitat availability in the lake.

Keywords: artificial neural network, Kohonen neural network, perch, pike, roach, rudd, self-organising map, temporal variation

Introduction

Studies on the spatial distribution of fish in lakes and reservoirs suggest that littoral habitats are particularly important for many species (Keast, 1985; Brosse, Lek & Dauba, 1999; Pierce *et al.*, 2001). The substantial productivity and habitat diversity of reservoir littoral zones may be responsible for the high biomass and diversity of fishes in these habitats (Fischer & Eckmann, 1997; Lewin, Okun & Mehner, 2004). This has led some investigators to postulate that the littoral zone is crucial fish reservoirs (Laffaille *et al.*, 2001; Winfield, 2004; Reyjol *et al.*, 2005). Nevertheless, because littoral fish assemblages typically are dominated by 0+ fish, their dynamics are likely to vary substantially during the growing season due to species-specific ontogenic changes in diet and habitat preferences (Copp, 1990; Brosse & Lek, 2000). Perhaps

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as a consequence of this variability, studies of the temporal dynamics of fish assemblages are uncommon in European reservoirs, although they are well studied in North American reservoirs (Pierce *et al.*, 2001; Eggleton *et al.*, 2005).

Spatially explicit data on fish assemblages are of increasing importance to aquatic ecologists (Grossman, Hill & Petty, 1995; Eros & Grossman, 2005). Nonetheless, these data typically require complicated statistical approaches because of the non-linear relationships inherent in large ecological data sets (James & McCulloch, 1990; Lek *et al.*, 2005). Artificial Neural Networks (ANN) are a useful technique for identifying complex habitat–species relationships in such ecological data sets (Lek *et al.*, 2005). An ANN may be used in one of two primary forms: with supervised or unsupervised learning. Under supervised learning, the network is trained to recognise specific categories through the use of reference samples (Lek *et al.*, 2005). Artificial Neural Networks with supervised learning have been used to predict species abundances (Baran *et al.*, 1996; Lek *et al.*, 1996), determine the main factors affecting species richness and distribution (Guegan, Lek & Oberdorff, 1998; Brosse & Lek, 2001, 2002), and modelling the use of spatial resources by fishes (Brosse *et al.*, 1999). In contrast, unsupervised ANNs do not have predefined groups, and the network searches for organisation within the data set itself. An unsupervised ANN provides a more objective picture of the ecological structure in a data set, because it is not influenced by preconceived notions regarding the samples or environment. With this approach, it is customary to use the Kohonen self-organising map (SOM) (Kohonen, 2001) to depict graphically relationships among samples (Blayo & Demartines, 1991; Chon *et al.*, 1996; Giraudel *et al.*, 1999; Reyjol *et al.*, 2005).

Our first aim was to measure the distribution and abundance dynamics of fish during the growing season in the littoral zone of Lake Pareloup, a previously studied hydroelectric reservoir in southwest France (Brosse *et al.*, 1999; Brosse & Lek, 2001, 2002). Based on habitat characteristics, we were then able to distinguish distinct environmental periods during the growing season. Finally, we used the SOM to characterise the spatial distribution of 17 defined ecospecies during these environmental periods. These analyses enabled us to describe the dynamics of the fish assemblage in the littoral zone of the lake.

Methods

Study site and sampling

Lake Pareloup is located in southwest France (44.20°N, 2.76°E) and has a total surface area of 1250 ha, a volume of *c.* 168×10^6 m^3, and a maximum and mean depth of 37 m and 12.5 m, respectively. Because water levels fluctuate substantially in late autumn, winter and early spring (i.e. from 2 to 10 m), we conducted our study between late spring and early autumn. Water levels decrease in late autumn and winter because of hydroelectric generation, and increase in early spring to store water for recreational purposes during warm months (see below) and power generation the next winter. Water level stabilises in mid-spring and, for recreational purposes (variation in depth never exceeded 0.10 m), lake levels were kept relatively constant up to mid-autumn.

We sampled fish populations weekly between mid-May and mid-October 1998 (20 weeks) in the littoral zone of the reservoir. For most species, this sampling period enabled us to follow the 0+ age class through the summer. When we began sampling, only 0+ pike and roach were present (Fig. 1). At this time, 0+ pike were early stage juveniles and measured from 40 to 50 mm total length; 0+ roach were of 7–10 mm total length and were still in the free embryonic phase [i.e. step F in the classification of Cerny (1977)]. In each weekly sample, we collected point electrofishing samples over 500 m of shoreline that comprised heterogeneous micro-habitats varying from soft mud

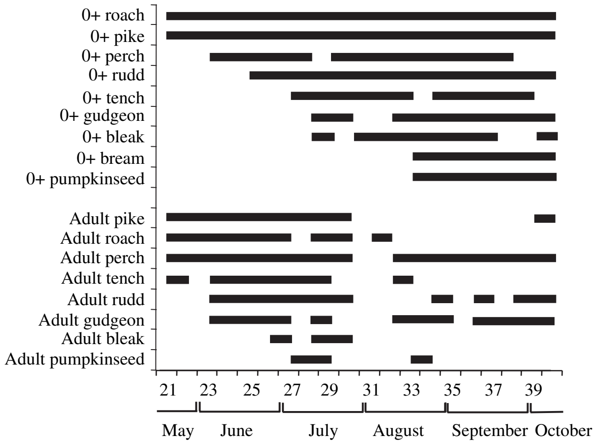

Fig. 1 Chronology of 0+ and adult fish sampled in the littoral zone of lake Pareloup from mid-May (week 21) to mid-October (week 40).

bottoms with emergent vegetation to rocky shores. Each site (i.e. sampling point) was sampled only once. We sampled only between 0 and 1 m depth to maximise sampling efficiency. Samples were collected between 09.00 and 18.00 h to characterise diurnal habitat use. Fishes were sampled with a backpack electrofisher (DEKA 4000, DEKA, Germany) using the point abundance method of Nelva, Persat & Chessel (1979). We sampled fish by swiftly immersing the anode in water and then collecting stunned fish with a fine-mesh dip net. Each week, we haphazardly sampled 100–150 points that were separated by 5–10 m to minimise sampling disturbance.

For each point, we measured depth (cm) (measured in the centre of each point using a metre stick) and the percentage of vegetation cover (visual estimate of percent bottom coverage, in a 1 m^2 bottom area corresponding to each sample), to provide an overall description of the environment. We focused on the relationship between fish abundance and depth and vegetation cover because previous studies have shown these variables to be important for littoral fishes in lentic systems (Rossier, 1995; Fischer & Eckmann, 1997; Laffaille *et al.*, 2001; Lewin *et al.*, 2004), and allows for greater comparability with previous work (e.g. Holland & Huston, 1984; Rheinberger, Hofer & Wieser, 1987; Matena, 1995; Rossier, 1995; Eklöv, 1997; Fischer & Eckmann, 1997; Laffaille *et al.*, 2001; Lewin *et al.*, 2004). Fishes from each point sample were preserved in 4% formaldehyde. The samples were returned to the laboratory and the fish counted and identified to species. We classified individuals of each species into 'ecospecies' representing either young-of-the-year (0+) or older fish (hereafter called adults). We used these ecospecies classifications because there is much evidence that resource use varies with size/age in freshwater fish (Hjelm, Persson & Christensen, 2000; Persson *et al.*, 2000, 2004).

Fish assemblage dynamics and habitat relationships

We first used linear regression to characterise temporal trends in fish abundance using weekly fish density estimates. We then tested for temporal trends in assemblage structure by performing a hierarchical cluster analysis on a presence/absence matrix for the 17 ecospecies X 20 weekly point samples. Presence/absence data were preferable in this analysis because there were strong temporal trends in fish abundance (see Results). Due to the binary nature of the data, Euclidean distance and average linkage were used as clustering algorithms. We used discriminant function analysis (DFA) to confirm that clusters identified in the cluster analysis differed significantly and these results were validated using Monte-Carlo tests (1000 permutations) (Manly, 1994). Statistical calculations were performed using R (Ihaka & Gentleman, 1996).

We quantified assemblage structure in the periods identified by the cluster analysis by producing a Kohonen SOM (Kohonen, 2001) for fish density data from point samples within each period. In the SOM model, input samples can be considered as a vector of 17 dimensions (i.e. ecospecies) in n-dimensional space $\boldsymbol{R}^n$. The SOM reduces the dimensionality of these data to a two-dimensional map (i.e. the Kohonen map) while preserving the spatial relationships of the original samples. Hence, points with similar assemblage structures (i.e. species composition) map together on the two dimensional grid (i.e. in the same or a neighbouring cell); conversely, samples with very different assemblage structures (i.e. different species composition) should map far apart, depending of the degree of difference. Full details on the method can be found in Ripley (1996); Kohonen (2001) and Lek *et al.* (2005). The form of the Kohonen map is a hexagonal lattice (Kohonen, 2001) and the SOM consists of two layers (i.e. one input layer and one output layer), connected to each vector of the data set. The output layer corresponds to the Kohonen map. In this study, three independent SOM models were calculated (i.e. one for each of the three periods identified by the cluster analysis, see Results). The input layer used for each of the three data sets (one for each period) corresponded to the number of samples, i.e. 799 (i.e. abundance data for the 17 ecospecies in the 799 sampling sites), 523 and 1155 samples, respectively, whereas the output layers of the three independent SOM models had the same size, consisting of 150 neurons organised on an array of 15 cell-rows and 10 cell-columns. This configuration yielded the clearest representation of the data (Lek *et al.*, 2005), and permitted comparisons among the three Kohonen maps (one for each period).

The learning process of the SOM is as follows. Each neuron of the output layer comprised one virtual unit (i.e. virtual sampling site). The virtual units of the Kohonen map are initialised by random sampling from the input data set (i.e. real sampling sites, hereafter called sample units). The virtual units are then updated in an iterative way: a sample unit is randomly chosen in the input data set (initial unit) and the Euclidian distance between that sample and every virtual unit is computed. The virtual unit that has the lowest Euclidian distance from the initial virtual unit is then selected as the best matching unit (the winner) and placed adjacent to the initial unit. A weighting vector is produced for this pair of units using the SOM learning rule and the process continues iteratively, with the weighting vector updated during each iteration, until all sampling units are located on the SOM. The map produced by this analysis graphically depicts similarities and differences in fish assemblage structure of sample units (i.e. sampling sites patterns), but also represents the probability of the presence of each species in each cell of the map. Then, to identify groups of ecospecies on the map, the weight vector of each virtual unit (i.e. cell) was used in a hierarchical cluster analysis (Ward linkage method). Results of the cluster analysis were validated as described previously using DFA and Monte-Carlo tests (1000 permutations) in R with ADE4 package (Thioulouse *et al.*, 1997). The SOM was performed using the toolbox developed by Alhoniemi *et al.* (2003) for Matlab. Finally, to elucidate relationships between habitat characteristics of sample units in different clusters we used ANOVA and Tukey *post-hoc* tests on depth and vegetation coverage data.

Results

Fish assemblage dynamics and habitat relationships

We captured 17 ecospecies belonging to nine species: nine juvenile ecospecies and eight adult ecospecies (Table 1). Adult bream (*Abramis brama*) were not recorded in the littoral zone during sampling. Approximately 98% of individuals captured were 0+ (i.e. >34 000 individuals) with the remaining 2% adults (i.e. 674 individuals). Only three ecospecies represented >1% of the total catch: 0+ roach, *Rutilus rutilus*, (22 739 fish, 67%); 0+ rudd, *Scardinius erythrophthalmus* (8967 fish, 26%), and 0+ perch, *Perca fluviatilis*, (645 fish, 2%) (Table 1), and represented approximately 95% of the total catch. Total fish density in the littoral of Lake Pareloup decreased significantly over time ($P < 0.01$; $r^2 = 0.854$, Fig. 2). Fish assemblage structure also varied during our study (Table 1). For example, the species richness of the 0+ assemblage tended to increase through time, whereas adult species richness was highest early in the year and decreased after July (Fig. 1).

The cluster analysis identified three distinct faunal groups (Monte-Carlo test, $P < 0.001$) correlated with

Table 1 Mean fish abundance per electrofishing point sample

	Pooled	Period 1	Period 2	Period 3
0+ Roach (*Rutilus rutilus* L.)	9.18	22.23	0.57	0.43
0+ Rudd (*Scardinius erythrophthalmus* L.)	3.62	4.91	5.27	1.51
0+ Perch (*Perca fluviatilis* L.)	0.26	0.51	0.09	0.10
0+ Bream (*Abramis brama* L.)	0.12			0.29
0+ Tench (*Tinca tinca* L.)	0.08	0.02	0.34	0.01
0+ Pike (*Esox lucius* L.)	0.07	0.13	0.03	0.04
0+ Bleak (*Alburnus alburnus* L.)	0.07		0.04	0.14
0+ Gudgeon (*Gobio gobio* L.)	0.04		0.07	0.05
0+ Pumpkinseed (*Lepomis gibbosus* L.)	0.03			0.08
Adult roach (*R. rutilus* L.)	0.10	0.24	0.01	
Adult perch (*P. fluviatilis* L.)	0.07	0.14	<0.01	0.04
Adult gudgeon (*G. gobio* L.)	0.04	0.08		0.02
Adult rudd (*S. erythrophthalmus* L.)	0.02	0.05	<0.01	0.01
Adult bleak (*A. alburnus* L.)	0.02	0.03	0.02	
Adult tench (*T. tinca* L.)	0.01	0.03		<0.01
Adult pike (*E. lucius* L.)	0.01	0.03	<0.01	<0.01
Adult pumpkinseed (*L. gibbosus* L.)	<0.01	<0.01		<0.01

Pooled: data from the entire sampling period (mid-May to mid-October).
The three periods were identified by the hierarchical cluster analysis (see Fig. 3). Period 1: mid-May to mid-July; period 2: mid-July to late August; period 3: late August to mid-October.

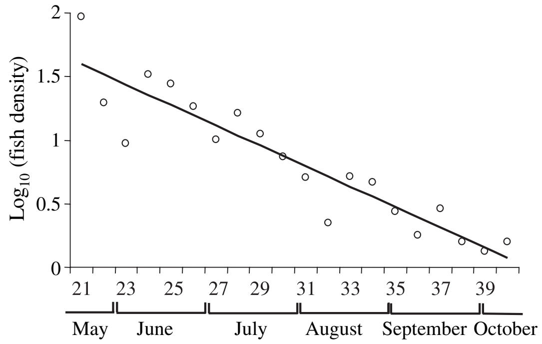

Fig. 2 Changes in total fish density (log transformed mean number of fish per sample) in the littoral zone of lake Pareloup over the study period. Equation of the exponential model: Fish density $= 47.352e^{-0.1842x}$. Numbers on the x-axis are weeks of the year.

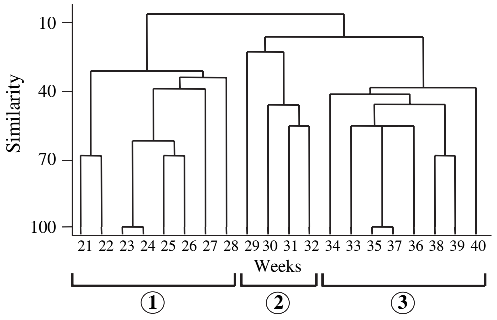

Fig. 3 Hierarchical cluster analysis (Euclidean distance and average linkage) of the 20 weekly samples based on fish occurrences. The three time periods indicated on the figure were validated by discriminant function analysis and Monte-Carlo tests (see text).

sampling date (Fig. 3). Although depth and vegetation varied significantly during the study (ANOVA $0.05 > P > 0.01$ for depth and ANOVA $0.05 > P > 0.01$ for vegetation), these differences are unlikely to be ecologically significant (<0.06 m for depth and <8% for vegetation cover, Table 2) and probably because of large sample sizes. From mid-May to mid-July (period 1), the fish assemblage was diverse and comprised both 0+ and adult fish (Figs 1 & 3). During this period, 0+ fish richness increased (Fig. 1), but numerical abundance within the fish assemblage was dominated by 0+ roach (78% of the fish) and to a lesser extent 0+ rudd and 0+ perch. Although adults were less common, they represented >2% (476) of the 22 687 fish captured during this period (Table 1). The SOM identified the three faunal assemblages shown on the cluster dendrogram and validated by Monte-Carlo test ($P < 0.01$) (Fig. 4a). Adult and 0+ fish (except 0+ and adult pike, *Esox lucius*) generally showed independent spatial distributions with most 0+ occupying vegetation habitats (clusters B and C), whereas adults (cluster A) occupied mainly open water habitats. This was confirmed by a significant difference in depth and vegetation characteristics between samples grouped in clusters B and C (both 0+ clusters) and in cluster A (Tukey test, $P < 0.001$). Zero plus roach and perch (cluster C) inhabited deeper areas (>0.4 m), than either 0+ tench (*Tinca tinca*), or 0+ rudd and adult pike (<0.3 m; cluster B) (Tukey test, $P < 0.001$) (Fig. 4a).

Table 2 Mean depth (±SE, m) and vegetation cover (±SE, percentage) for the three periods identified by the hierarchical cluster analysis (see text and Fig. 3). The sample size (Nb samples) is also given for each period

	Nb samples	Depth	Vegetation
Period 1	799	0.54 ± 0.011	38.1 ± 1.49
Period 2	523	0.56 ± 0.015	32.4 ± 1.77
Period 3	1155	0.59 ± 0.009	39.5 ± 1.25

From mid-July to late August (period 2), 0+ species richness remained similar to that of in Spring, whereas adult richness decreased (Fig. 1). The relative abundance of 0+ roach also decreased and this ecospecies represented only 8.8% of fish numbers during period 2, whereas 0+ rudd were numerically dominant (82%). Among 0+ individuals, tench also increased in abundance (5%). Moreover, adults were scarce and represented only 0.5% of fish numbers. The three clusters indicated on the Kohonen map (Fig. 4b) showed a clear separation between most 0+ fish and adults (except for 0+ pike and 0+ tench). There were habitat differences among 0+ ecospecies with fishes in clusters A and C differing by depth (0+ perch, 0+ roach and 0+ gudgeon (*Gobio gobio*) in deeper areas; 0+ rudd and 0+ bleak (*Alburnus alburnus*) in shallower areas with dense vegetation) (Tukey tests, $P < 0.001$). The third cluster (cluster B) contained adults, 0+ pike and 0+ tench, which occupied shallow water habitats with little vegetation (Fig. 4b).

From late August to mid-October (period 3) species richness of the 0+ fish reached a maximum, with 0+ rudd and 0+ roach again dominating the assemblage numerically (Table 1). These two ecospecies represented 55% and 16%, respectively, of fish total numbers. Moreover, three additional 0+ ecospecies were

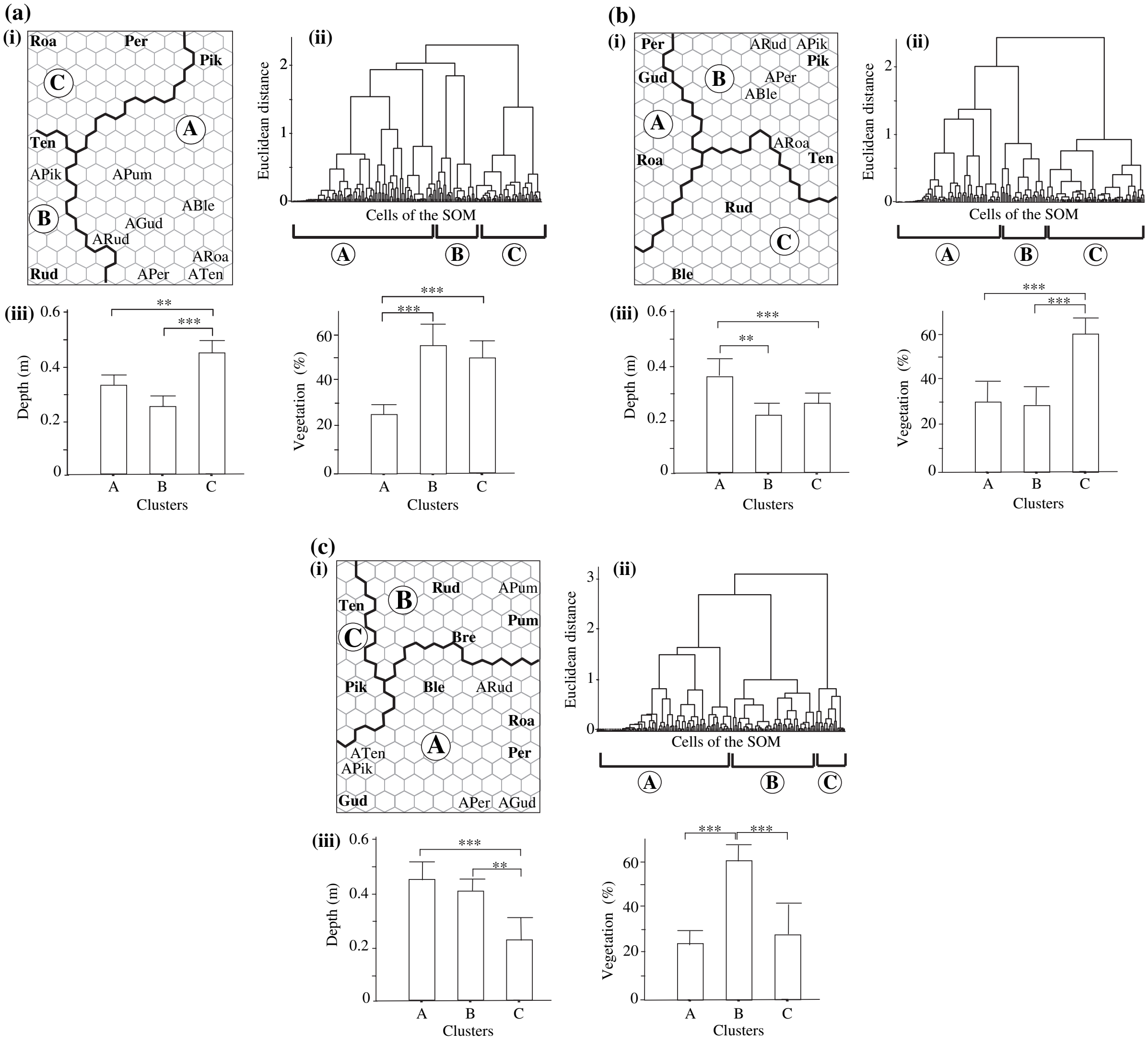

Fig. 4 Fish assemblage structure patterns identified using the self-organising map (SOM) method during the three periods (see Fig. 3). (a) Period 1: mid-May to mid-July; (b) period 2: mid-July to late August; (c) period 3: late August to mid-October. (i) The Kohonen SOM map with ecospecies represented on the 15 × 10 cells output map. Then the 150 cells were classified into three clusters (A, B and C) based on a hierarchical cluster analysis. The three clusters were delineated with bold lines. (ii) Hierarchical classification of the 150 SOM cells (Ward method). (iii) Environmental characteristics of each of the three clusters. Depth and vegetation cover of the samples gathered in the three clusters were compared using ANOVA and *post hoc* Tukey tests. Only significant differences were indicated, $^{**}P < 0.01$; $^{***}P < 0.001$. Species abbreviations as follows: 0+ fish are bolded. Adults are in normal font and acronyms preceded by A. Bleak (*Alburnus alburnus*): Ble; bream (*Abramis brama*): Bre; pike (*Esox lucius*): Pik; gudgeon (*Gobio gobio*): Gud; pumpkinseed (*Lepomis gibbosus*): Pum; perch (*Perca fluviatilis*): per; roach (*Rutilus rutilus*): roa; rudd (*Scardinius erythrophthalmus*): rud; tench (*Tinca tinca*): ten.

present in relatively high abundance: 0+ bream (11%), 0+ bleak (5%) and 0+ perch (4%) (Table 1). Although adults represented 2% of the total fish numbers, 75% of adults were perch. Adults of the remaining species only occurred occasionally in the littoral zone during period 3. The spatial habitat patterns identified by the SOM in period 3 (Fig. 4c), differed from the two previous periods. Adult and 0+ ecospecies co-occurred, and most ecospecies (both 0+ and adults) left vegetated habitats for open water. This was supported by the highly significant differences (Tukey test, $P < 0.001$) between the amount of vegetation occupied by species in cluster B versus clusters A and C (Fig. 4c). Finally, we first captured 0+ pumpkinseed (*Lepomis gibbosus*), a North American exotic species (about 100 individuals captured) during this period.

Discussion

Littoral assemblage composition

The fish assemblages of most lowland European lakes and reservoirs are dominated numerically by roach and perch (Matena, 1995; Rossier, 1995; Irz *et al*., 2002; Lewin *et al*., 2004) with pike as the top fish predator (Eklöv, 1997; Irz *et al*., 2002). In addition, the rudd is widespread in lowland lentic systems in Europe (Bruslé & Guignard, 2001; Irz *et al*., 2002), where it may comprise a substantial portion of the littoral fish assemblage (Matena, 1995; Jeppesen *et al*., 2006). The remaining fish species in reservoirs are generally uncommon and differ according to geography or the physical characteristics of the system (Kubecka, 1993; Irz *et al*., 2002; Jeppesen *et al*., 2006). Consequently, many European lowland lentic systems have fish assemblages similar to Lake Pareloup (see Irz *et al*., 2002 for French reservoirs; Duncan & Kubecka, 1995 for Czech and English reservoirs; Jeppesen *et al*., 2006 for Danish lakes; Reyjol *et al*., 2005 for Lake Constance in Germany; Rossier, 1995 for Lake Geneva on the Swiss–French border), and hence, our results may have some generality.

Despite the fact that lowland lakes and reservoirs are common in Europe, there are few studies that focus on their littoral fish assemblages. Duncan & Kubecka (1995) and Matena (1995) also found that most 0+ fishes occupy shallow, highly vegetated littoral habitats in natural lakes, whereas adults are most common in open waters. In addition, Fischer & Eckmann (1997) showed that Lake Constance fishes display both seasonal and ontogenetic shifts in spatial distributions. Consequently, patterns in assemblage structure and habitat use in natural systems are similar from those of Lake Pareloup.

Dynamics of fish abundance and assemblage structure

The exponential decrease in fish abundance observed during our study was primarily attributable to the decline in 0+ fish, which represented about 98% of the fish collected. Although it was not possible to quantify the relative importance of the major processes influencing 0+ fish abundance (i.e. emigration, mortality, immigration and recruitment) during our study, it is well known that almost all 0+ fishes experience high mortality rates (Kubecka & Svatora, 1993; Wang & Eckmann, 1994; Bystrom, Persson & Wahlstrom, 1998; Quist, Pember & Guy, 2004) and generally remain within the littoral zone (Rossier, 1995; Fischer & Eckmann, 1997). Perch represent an exception to this generalisation, because after hatching larval perch become pelagic although they return to the littoral after several weeks of pelagic life (this occurred on week 23) (Wang & Eckmann, 1994; Urho, 1996; Hjelm *et al*., 2000). Similar to the other species, perch abundance generally declines during the first weeks of life and the fish that enter the littoral zone represent only a small fraction of the initial year class (Wang & Eckmann, 1994). This may explain why 0+ perch represented only 2% of the littoral fish community. Alternatively, adults emigration from the littoral zone probably was significant after spring.

Temporal variation in the fish assemblage

We chose to use presence–absence data to identify patterns in fish assemblage structure to prevent trivial clustering due to the decline in fish abundance over time. We then used the SOM to describe finer scale habitat-related patterns in assemblage structure. An ANN was preferable to traditional multivariate methods (e.g. MDS, PCA and CCA) for a variety of reasons, including a lack of bias incurred via over-emphasis of rare species in the analysis (Gevrey *et al*., 2004; Park *et al*., 2006). Although we originally analysed our data using traditional multivariate methods (e.g. MDS, PCA and CCA), these results were not presented because they were much less interpretable than those of the ANN; a result similar to that of Olden & Jackson (2002). In addition, comparisons between SOM and traditional multivariate statistics can be found in other papers (Brosse, Giraudel & Lek, 2001; Giraudel & Lek, 2001; Lee *et al*., 2006). As an alternative to SOM, we also attempted to analyse our data using simple map overlays of general habitat structure and fish abundance, but due to the patchiness of the physical environment, this technique did not yield clear results in comparison with those obtained via the ANN. In contrast, the SOM method provided easily interpretable patterns within the littoral zone fish assemblages. Similar to our findings regarding the utility of the SOM, other investigators have found this technique useful in pattern recognition within large and complex ecological data sets dealing with various kinds of plants and animals: algae (Gevrey *et al*., 2004; Park *et al*., 2006), birds (Lee *et al.*, 2006), fish (Reyjol *et al.*, 2005), insects (Worner & Gevrey, 2006), trees (Giraudel & Lek, 2001).

The identification of temporal patterns in Lake Pareloup littoral fish assemblages was complicated by the absence of stable assemblages throughout the study period. However, two general patterns were apparent. First, adult fish co-occurred in open waters (i.e. low vegetation cover) throughout the study (except for adult pike in period 1 and adult pumpkinseed in period 3). This result suggests that adults share similar habitat requirements in this system. The co-occurrence of adult fishes has been observed in other systems and may be linked to the greater swimming ability of adults in open water habitats (Duncan & Kubecka, 1995; Fischer & Eckmann, 1997). In contrast, the two exceptions to this generalisation (pike and pumpkinseed) are known to be strongly dependent on vegetated habitats (Bruslé & Guignard, 2001). Hence, spatial differences in habitat use by most adults was limited to variation in depth, which changed little throughout the study. Consequently, the adult fish assemblage can be considered as stable during our study.

Among 0+ fishes, roach and perch formed a second group of stably co-occurring species; an association that has also been identified in other littoral systems (Bystrom *et al.*, 1998; Brosse & Lek, 2001, 2002). However, the remaining 0+ ecospecies did not co-occur in a consistent manner and, hence, assemblage-level properties were composites of species-specific habitat associations rather than emergent properties of the assemblage itself. The lack of stable associations among most ecospecies was probably due to ontogenetic differences in habitat and feeding preferences. These processes have been extensively studied for individual species (Rheinberger *et al.*, 1987; Kucharczyk *et al.*, 1998; Brosse & Lek, 2000), but their relationship to fish assemblage structure in lentic systems is poorly known. Although our data are correlational and do not allow inference of causal mechanisms, existing experimental studies suggest that the factors structuring the 0+ fish assemblage are complex and probably include both physical and biotic (competition and/or predation) processes (Bystrom *et al.*, 1998; Persson *et al.*, 2004).

Our results suggest that the apparent association between 0+ fish and vegetation (i.e. cover) (Conrow, Zale & Gregory, 1990; Matena, 1995; Laffaille *et al.*, 2001) may need re-examination. Although most 0+ ecospecies occupied vegetated habitat in the first sampling period (mid-May to mid-July), they did not for the two later periods. Consequently, this habitat association occurred when 0+ fish were smallest and had limited swimming capability (Cerny, 1977; Blaxter, 1986; Copp, 1990). This relationship was supported by data for 0+ rudd and 0+ bleak, which reproduce later in the year and larvae of these species occupied vegetated habitats from mid-July to late August.

Temporal variation in fish–habitat relationships

Lake Pareloup has been the subject of previous studies on littoral fishes, including 0+ fishes, which makes it useful for long-term comparisons. In fact, several of our results differ from those of previous studies, especially those for 0+ roach and perch, which demonstrate a strong association between 0+ fish and vegetation cover (Brosse & Lek, 2000, 2002). Given results from the present paper, which encompass a longer time period during the year; previous results should be viewed with caution. The strong association of fish with aquatic vegetation is true only for the first time period (mid-May to mid-July; Fig. 4a), when most species are still in larval and early juvenile developmental steps. In addition, differences between our results and previous studies certainly were influenced by the steep decline in fish abundance during summer and autumn, which was not recorded in previous studies due to more limited sampling. Similarly, the habitat models proposed by Brosse & Lek (2000, 2002) were strongly influenced by the high abundance of 0+ fish in a data set collected over a shorter time span than the current study. A similar problem exists in the habitat relationships observed for both 0+ tench and the association between pike and 0+ roach or 0+ rudd found by Brosse *et al.* (2001). These examples emphasise the importance of sampling 0+ fish over a time period adequate to encompass both habitat changes and changes in fish assemblage structure. Another surprising result was that 0+ and adult pike were rarely associated with dense vegetation, and instead frequented vegetated ‘habitat edges’. This result is consistent with the hunting behaviour of pike, which hide in the vegetation and ambush prey in the open water (S. Brosse, unpublished). This hunting strategy is probably more efficient than hunting in highly vegetated habitats, where prey have many potential refuges (Holland & Huston, 1984; Eklöv, 1997). Nonetheless, our sampling could not detect 'edge habitats' such as those occupied by pike.

Moreover, the above-mentioned discrepancies between this study and previous works may be partly due to different statistical approaches, but also because previous studies used abundance-based approaches, that weight periods of high abundance (early period) more heavily than periods of lower abundance (later two periods). Given that our findings cover a broader time span they are probably more reliable than those of the more limited previous studies. These examples illustrate that studies of habitat use and assemblage dynamics of 0+ fishes need to consider both shifting patterns of habitat use and changes in abundance of assemblage members over the course of the study.

In conclusion, depth and vegetation cover remained relatively stable in Lake Pareloup during our study period and therefore the dynamic patterns of fish abundance in the littoral zone probably were a function of ontogenetic changes in habitat preferences of the ecospecies (Copp, 1990; Brosse & Lek, 2000). Moreover, although we cannot infer the processes influencing variation in these assemblages, a variety of descriptive studies suggest that non-interactive factors (species-specific differences in habitat preferences; Grossman & de Sostoa, 1994a,b) affect the patterns observed in this system.

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