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Studying the spatiotemporal variation of the littoral fish community in a large prealpine lake, using self-organizing mapping

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Abstract: One of the most fundamental feature of freshwater systems is the spatiotemporal structure of their communities. In the present study, we used an artificial neural network model, i.e., self-organizing mapping, together with a likelihood ratio χ^2 statistic for proportions to investigate the influence of each factor of a complex sampling scheme (i.e., site, year, month, and time of day) on the littoral fish community of Lake Constance (south Germany). Based on self-organizing mapping, four clusters of samples were defined characterized by distinct fish communities. The samples gathered in clusters 1 and 2 were significantly related to the factors month and time of the day, while those in cluster 3 were related to the factors month and site and those in cluster 4 to each of the four factors. The results are discussed with regard to the temporal patterns of species succession in lakes and their similarities with the spatial patterns observable in streams, the importance of plasticity with regard to the fish nycthemeral preferences, the partitioning of habitat at a large spatial scale and its importance for the coexistence of species, and the effects of the reoligotrophication process in lakes.

Résumé : L'une des caractéristiques fondamentales des écosystèmes d'eau douce est la structure spatio-temporelle de leurs communautés. Dans cette étude, nous avons utilisé un réseau de neurones artificiels du type carte auto-organisatrice, associé à des tests sur les proportions, afin de mettre en évidence l'influence de facteurs d'un plan d'échantillonnage complexe (site, année, mois et période de la journée) sur la communauté de poissons de la zone littorale du lac de Constance (sud de l'Allemagne). Les résultats de la carte auto-organisatrice nous ont permis de définir quatre groupes d'échantillons, caractérisés par des peuplements distincts de poissons. Les échantillons des groupes 1 et 2 étaient significativement liés aux facteurs mois et période de la journée, ceux du groupe 3 aux facteurs mois et site d'échantillonnage et ceux du groupe 4 à chacun des quatre facteurs. Les résultats ont été discutés en considérant les patrons de succession temporels observables en lac et leurs similarités avec les patrons spatiaux observables en cours d'eau, l'importance de la plasticité dans l'occupation du nycthémère, le partage de l'habitat à large échelle et son rôle dans la coexistence des espèces et les effets du processus de re-oligotrophisation en lac.

Introduction

Ecosystems are structured in both space and time. Consequently, one of the most fundamental questions when studying an ecosystem and its component organisms is the strategy of its occupation with respect to space and time, and sampling plans built according to both spatial and temporal factors are often used by ecologists to address this issue.

The littoral areas of lakes are among the most diverse and complex habitats in aquatic ecosystems. Habitat and food resources here are normally more diverse than in other lake compartments (Pierce et al. 1994), resulting in a higher abundance and diversity of fish fauna (Keast 1985). Moreover, most freshwater fish, including those regarded as typically pelagic, often use the littoral zone for a short period of the year, either for spawning (Gafny et al. 1992) or during larval and juvenile development (Allen 1982; Werner et al. 1983). Nevertheless, studies examining the spatial and temporal variation in littoral zone fish communities are remarkably sparse (Hinch and Collins 1993; Pierce et al. 1994; Rundle and Jackson 1996).

Lake Constance (Germany) is the second largest prealpine lake in Europe. The fish community of Lake Constance comprises 33 species from 11 families (Eckmann and Rösch 1998) of which more than 95% are either obligate or facultative users of littoral resources. Previous works of Fischer

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and Eckmann (1997*a*, 1997*b*) have shown that abundances of littoral fish species in Lake Constance exhibit very high spatial and temporal variation at seasonal and diel scales. Based on these results, a routine sampling program was started in 1997 to assess the influence of temporal and spatial factors, i.e., year, month, site, and time of day, on the littoral fish community over longer time periods.

The complex nature of community data has been a catalyst for the rapid development and transfer of multivariate methods in ecology (Rundle and Jackson 1996). Ordination techniques, designed to summarize and simplify large data sets, can help to elucidate factors contributing to the structure of the community under consideration (Ludwig and Reynolds 1988). While multivariate approaches may offer an appropriate means for examining the spatial and temporal variation in an ecosystem (Resh and Rosenberg 1989), examples of these kinds of approaches are rare (Rundle and Jackson 1996).

Artificial neural networks provide a powerful, flexible learning technique for uncovering patterns in ecological data (e.g., Lek and Guégan 2000; Reyjol et al. 2001*a*; Olden and Jackson 2002). Among artificial neural networks, self-organizing mapping (SOM) (Kohonen 1982) is an unsupervised model that acts as a nonlinear clustering technique that has been previously used to characterize distribution patterns of ecological systems (Chon et al. 1996; Giraudel and Lek 2001; Park et al. 2003). It shares with conventional ordination methods the basic goal of displaying a multidimensional data set in a lower, usually two-dimensional, space. With SOM, the data set is projected in a nonlinear way onto a rectangular grid laid out on a hexagonal lattice, i.e., the Kohonen map.

The objective of this study was twofold. In terms of introducing new methodology, we have used SOM to cluster the data to test specific hypotheses concerning spatial and temporal variation. This study is similar in spirit to Rundle and Jackson (1996), who used an ordination technique (principal components analysis (PCA)) for the same purpose.

From an ecological point of view, we wanted to investigate the spatiotemporal variation of the littoral fish community of Lake Constance. Few studies have investigated this general aspect of lake functioning (Hinch and Collins 1993; Pierce et al. 1994; Rundle and Jackson 1996), despite the fact that littoral zones usually provide food, shelter against large predators, and favorable thermal conditions for a variety of species during most of the year (Hinch and Collins 1993; Pierce et al. 1994; Fischer and Eckmann 1997*b*).

Lake Constance has been characterized as having a high level of spatiotemporal variation (Fischer and Eckmann 1997*a*, 1997*b*), and as such, it represents a relevant study system to bring new general insights concerning the spatiotemporal variation in littoral fish communities in lakes. This study is the first to gather information on such a large number of spatiotemporal factors of variation for littoral fish communities.

Materials and methods

Study area, sampling sites, and procedure

Lake Constance is the second largest, warm-monomictic lake north of the Alps mountain range. It is situated at the boundary of Austria, Germany, and Switzerland (47°N, 09°E) at an altitude of 395 m. Rivers entering the lake drain an area of 11 500 km^2 with two thirds of the water input originating from the River Rhine. The lake is morphologically divided in two basins (Kiefer 1972), the deep oligomesotrophic “Upper Lake” and the mesotrophic shallow “Lower Lake”, which are connected by the River Rhine (Fig. 1). The Upper Lake constitutes the major part of the lake, with a surface area of 475 km^2, a mean depth of 95 m (maximum 254 m), and a shoreline length of 186 km. Its littoral zone (sensu Wetzel 1983) extends to a water depth of about 5 m during high-water conditions in summer and covers about 10% of the entire lake area.

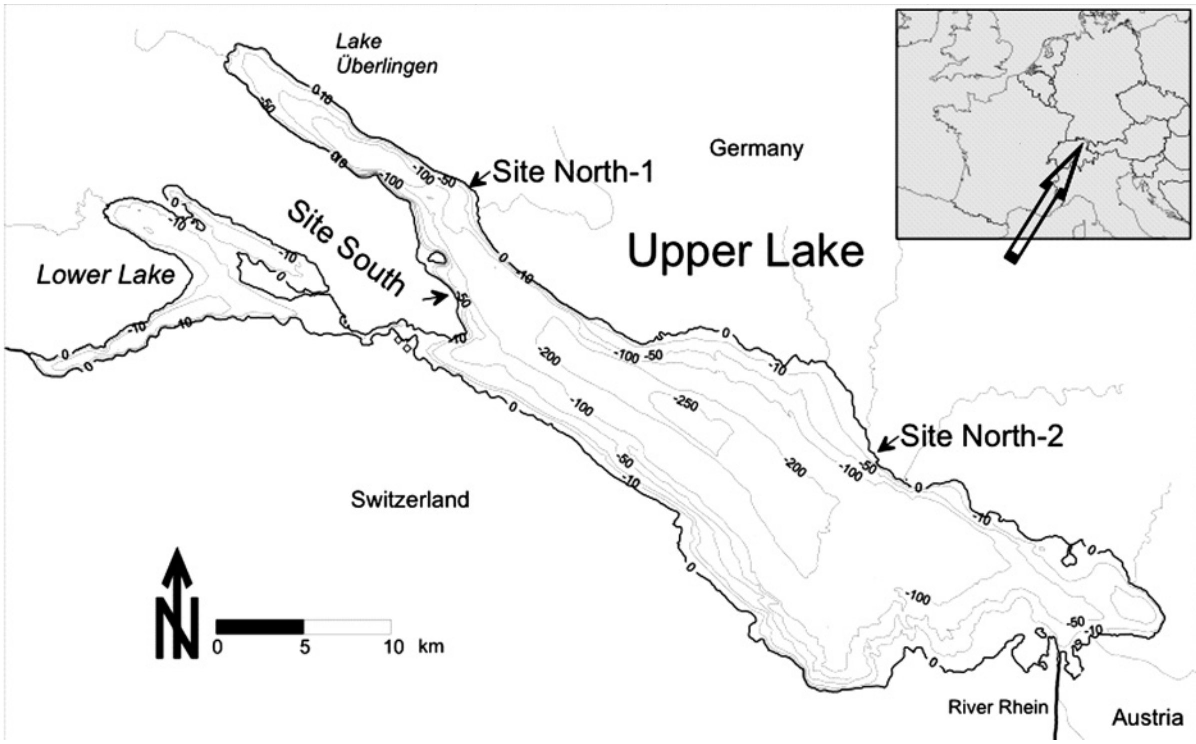
Sampling was carried out from 1997 to 2001 at three sites in the Upper Lake, each representing a different type of littoral zone. Site “South” is located on the southern shoreline of the lake (Fig. 1) and has a narrow (50 m) shelf-like littoral zone. Large stones and boulders providing distinct interstitial shelters characterize the uppermost shoreline, which is flooded only during high-water conditions from May to September. In contrast, interstitial shelter is sparse during the rest of the year, especially in winter when the substratum is mainly characterized by sand and pebbles interspersed with only slightly larger stones. Macrophyte coverage during summer is sparse, mainly dominated by *Potamogeton pectinatus*, *Potamogeton perfoliatus*, and *Chara* spp., and only present in a zone between 3 and 5 m deep. The site is exposed to winds from the northeast that, however, blow only a few days a year. During the remainder of the year, a landward ridge covering the major part of this shoreline protects the site.

Site “North-1” is located on the northwestern shoreline (Fig. 1) and has a lakeward extent of 200–300 m. The substratum of most of the area, including the uppermost shoreline, is characterized by gravel and pebbles providing a heterogeneous, but not as well-developed, interstitial coverage as the southern site. Soft sediments are present only in the deeper areas with sparse macrophyte coverage (mainly *P. pectinatus* and *Chara* spp.) during summer. The site is exposed to winds from the southeast, but owing to its geographical position within the fjord-like extension of the Upper Lake, “Lake Ueberlingen” (Fig. 1), the site is protected against strong wind and wave action year round.

The third site, “North-2”, is also located on the northern shoreline about 35 km east of North-1 (Fig. 1). This site has a littoral zone with a lakeward extension of 500–700 m. The substratum is composed of soft sediment with little rocky stone cover. Macrophytes are present in the deeper parts during summer even though the total coverage is sparse, with *P. pectinatus* presently the dominant species. This site has been subject to a dramatic decrease in macrophyte vegetation cover, a very dense population of *P. pectinatus* in the early 1990s being now reduced to only a few plants. Owing to its unprotected location, this site is the most exposed to winds coming from all directions.

Sampling was carried out at the three sites according to three temporal factors: year (from 1997 to 2001), month (from March to December), and time of day (day or twilight). The sampling plan applied in this study therefore consisted of four factors: site, year, month, and time of day. Sampling was standardized at all three sites, with beach

Fig. 1. Study area and sampling sites in Lake Constance situated at the boundary of Austria, Germany, and Switzerland.



seines (length 16 m, height 1 m, mesh size 4 mm (bar mesh)) being hauled from 1 m water depth (height of the seine) to the shoreline. On each sampling occasion, three replicate samples were collected so that for each month, a total of 18 samples (3 sites × 2 times (day and twilight) × 3 replicates) were taken. However, for various reasons (e.g., an extreme high water level in May 1999), this sampling schedule was not strictly adhered to over the entire 5 years. Nevertheless, because missing samples were few and occurred simultaneously at all sites, the number of samples remained comparable across sites. All fish caught within a seine haul were immediately killed with 2-phenoxyethanol solution, or alternatively clove oil, and stored on ice. In the laboratory, all fish were identified to species and counted.

Statistical treatment and data modeling

Community structure

First, a species abundance data set was arranged as a matrix of 184 rows (i.e., the samples) and 25 columns (i.e., the species). Each cell represented the mean number of individuals of a species caught during one sampling event based on the three replicates (e.g., 1997, July, site North-1, twilight). To have an overview of community structure according to species' mean abundance in the samples, we performed a hierarchical cluster analysis with the Ward linkage method.

SOM

Each of the 184 samples of the input data set can be considered as a vector of 25 dimensions in the n-dimensional space $\boldsymbol{R}^n$. The aim of the SOM is to project these samples on a two-dimensional space (i.e., the Kohonen map) preserving the neighborhood so that samples with close species abundances should be mapped together on the grid, and conversely, samples with very different species abundances should be mapped far from each others (full details on the method can be found in Ripley 1996; Lek and Guégan 2000; Kohonen 2001). The form of the Kohonen map is a hexagonal lattice because it does not favor horizontal or vertical directions as much as the rectangular array (Kohonen 2001). The SOM consists of two layers, i.e., one input layer and one output layer, connected with computational weights (i.e., connection intensities). The input layer is connected to each vector of the data set and the output layer corresponds to the Kohonen map. The input layer used for the present model consisted of 184 neurons, while the output layer consisted of 35 neurons organized on an array with seven cell-rows and five cell-columns. This configuration of the output layer was chosen because of the clarity of the representation obtained compared with other configurations.

The learning process of the SOM is as follows. Each neuron of the output layer comprised one virtual unit. The virtual units of the Kohonen map are initialized with random sample units drawn from the input data set. Then, the virtual units are updated in an iterative way: a sample unit is randomly chosen in the input data set. The Euclidian distance between this sample and every virtual unit is computed. The virtual unit that has the minimum distance with the input unit is selected as the best matching unit. For the best matching unit and its neighbors, the weight vectors are updated by the SOM learning rule. This results in training the network to classify the input vectors by the weight vectors that they are closest to.

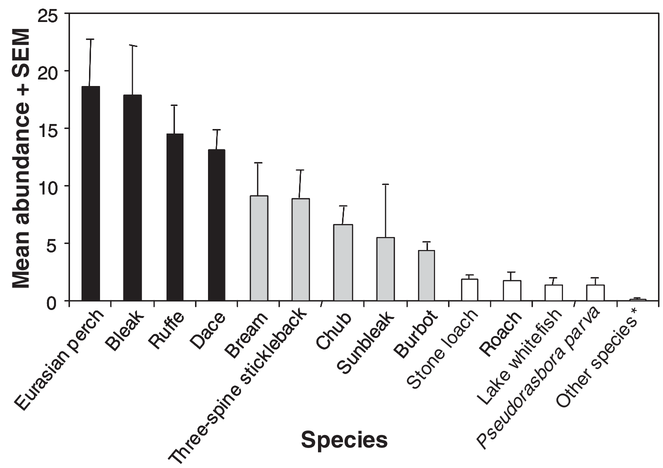
The virtual assemblages associated with the Kohonen map were visualized using a grey scale.

The SOM was performed using the toolbox developed by Alhoniemi et al. (2003) for Matlab.

Table 1. Common and scientific names of the species composing the littoral fish community of Lake Constance in the present study.

Common name	Scientific name
Eurasian perch	*Perca fluviatilis*
Bleak	*Alburnus alburnus*
Ruffe	*Gymnocephalus cernuus*
Dace	*Leuciscus leuciscus*
Bream	*Abramis brama*
Threespine stickleback	*Gasterosteus aculeatus*
Chub	*Leuciscus cephalus*
Sunbleak	*Leucaspius delineatus*
Burbot	*Lota lota*
Stone loach	*Barbatula barbatula*
Roach	*Rutilus rutilus*
Lake whitefish	*Coregonus lavaretus*
Stone moroko	*Pseudorasbora parva*
Common carp	*Cyprinus carpio*
Tench	*Tinca tinca*
Pikeperch	*Stizostedion lucioperca*
Rudd	*Scardinius erythrophthalmus*
European eel	*Anguilla anguilla*
Brown trout	*Salmo trutta*
Grayling	*Thymallus thymallus*
Prussian carp	*Carassius gibelio*
Northern pike	*Esox lucius*
Common barbel	*Barbus barbus*
Sculpin	*Cottus gobio*
Crucian carp	*Carassius carassius*

Fig. 2. Mean abundance and SEM for each species caught by seining the littoral zone of Lake Constance from 1997 to 2001. The different groups were separated according to a hierarchical cluster analysis with the Ward linkage method. Solid bars, species with a high level of abundance; shaded bars, species with an intermediate level of abundance; open bars, species with a low level of abundance. *Other species: common carp (*Cyprinus carpio*), tench (*Tinca tinca*), pikeperch (*Stizostedion lucioperca*), rudd (*Scardinius erythrophthalmus*), European eel (*Anguilla anguilla*), brown trout (*Salmo trutta*), grayling (*Thymallus thymallus*), Prussian carp (*Carassius gibelio*), northern pike (*Esox lucius*), common barbel (*Barbus barbus*), sculpin (*Cottus gobio*), and crucian carp (*Carassius carassius*).



Definition of SOM clusters

The weight vectors of each virtual unit were submitted to a hierarchical cluster analysis with the Ward linkage method to detect clusters on the trained SOM map. To associate each species to one cluster, we calculated the sum of the estimated abundances generated by the SOM for each species in the cells of each cluster and then assigned the species to the group with the highest value.

Influence of time and space on the fish community

The last step was to assess the relationships between the fish community associated with each cluster and the factors of the sampling plan (year, month, site, and time of day), which were not used in the SOM learning process. To do so, we calculated for each cluster the relative contribution of each modality (e.g., July) of a certain factor (e.g., month) to the total number of modalities of the factor. Then, we tested for the H_0 that no significant differences were present among these relative values using a test for proportions based on the likelihood ratio χ^2 statistics (Sachs 1997). The SOM was computed using MATLAB® software (The MathWorks, Inc., Natick, Massachusetts). All subsequent proportion tests were done in Microsoft Excel® based on the calculation procedures of Sachs (1997).

Community structure

A total of 57 557 fish belonging to 25 species were caught during the 5-year sampling program (Table 1). According to a cluster analysis, four of these species were found with high average ± SEM abundances over the entire sampling period (from 18.7 ± 4.1 to 13.2 ± 1.8 individuals per replicate), five species were found at an intermediate level of abundance (from 9.1 ± 2.8 to 4.4 ± 0.6 individuals per replicate), and 16 species were found in low abundances (<2.0 ± 0.3 individuals per replicate) (Fig. 2).

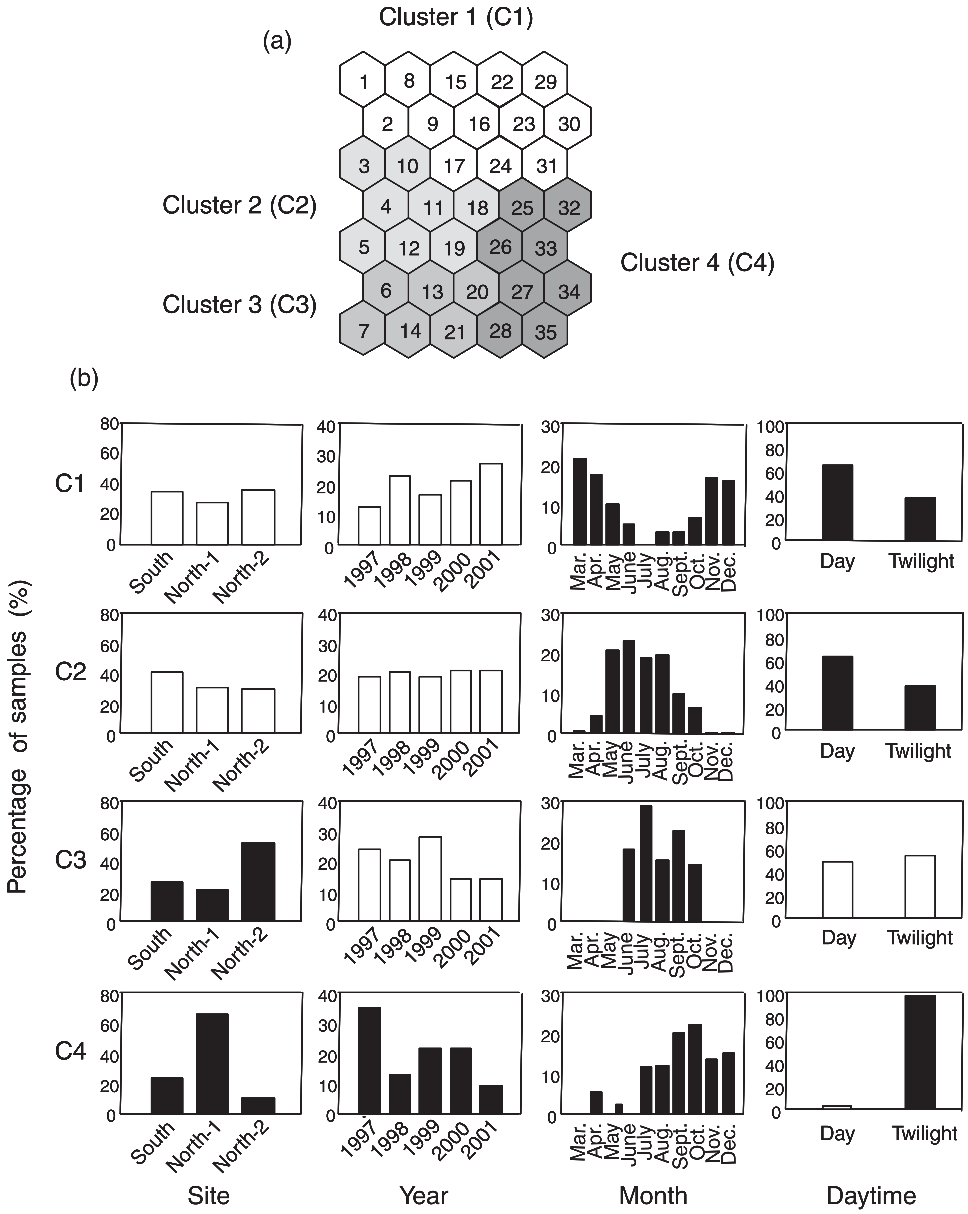
SOM

According to the cluster analysis used to detect the cluster boundaries on the trained SOM map, four clusters were defined, which encompassed 74, 49, 29, and 32 samples, respectively.

The tests for proportions revealed significant patterns for the four factors of the sampling design. Considering cluster 1, the samples were significantly related to the factors month ($G = 49.4$, df = 9, $p < 0.05$) and time of day ($G = 7.7$, df = 1, $p < 0.05$). This cluster grouped together samples from March and April with samples from November and December, i.e., winter and early spring samples. Considering time of day, cluster 1 included significantly more day than twilight samples (Fig. 3*b*). The corresponding fish community was made up of sculpin (*Cottus gobio*), brown trout (*Salmo trutta*), and grayling (*Thymallus thymallus*) in decreasing order of the sum of their estimated abundance in the cluster (Fig. 4).

The samples within cluster 2 were significantly related to month ($G = 78.1$, df = 9, $p < 0.05$) and time of day ($G = 6.0$, df = 1, $p < 0.05$). As for cluster 1, this cluster included significantly more day than twilight samples but corresponded to samples taken from May through August, i.e., late spring and summer samples (Fig. 3*b*). Fish species typically associated with this cluster were crucian carp (*Carassius carassius*),

Fig. 3. (*a*) Two-dimensional SOM. Each cell represents one neuron, which groups together several samples. The clusters (C1–C4) of the SOM defined by the hierarchical analysis are illustrated with different shades of gray. (*b*) Relative contribution of each modality of a certain factor to the total number of modalities of the factor. Solid bars, significant relationships ($p < 0.05$).

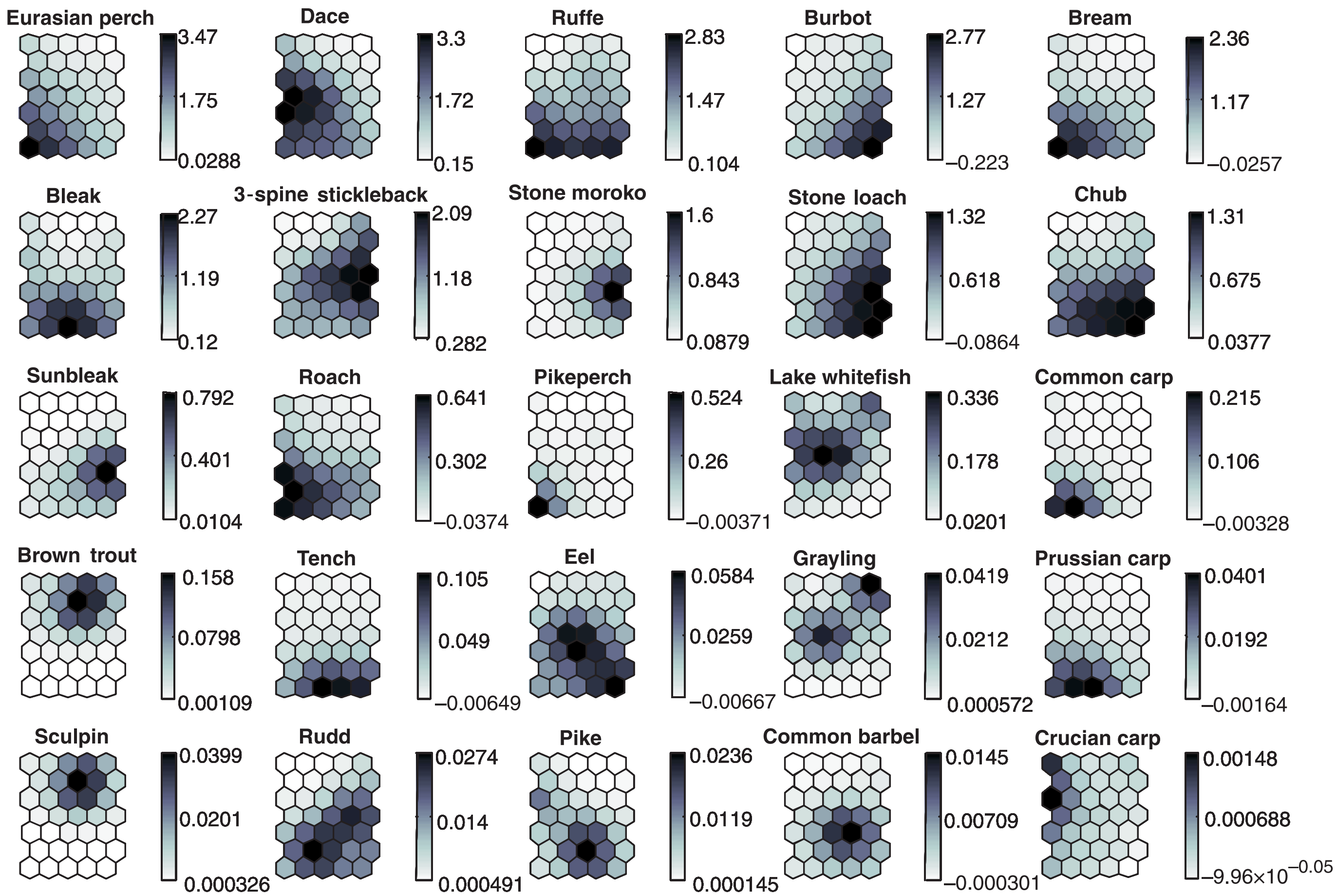


lake whitefish (*Coregonus lavaretus*), dace (*Leuciscus leuciscus*), and northern pike (*Esox lucius*) (Fig. 4).

The samples grouped in cluster 3 were significantly related to month ($G = 102.9$, df = 9, $p < 0.05$) and to sampling site ($G = 16.9$, df = 2, $p < 0.05$). They mainly represented the summer months, i.e., June through September, as well as samples taken at site North-2 (Fig. 3*b*). The corresponding fish community was composed of common carp (*Cyprinus carpio*), pikeperch (*Stizostedion lucioperca*), Prussian carp (*Carassius gibelio*), bream (*Abramis brama*), roach (*Rutilus rutilus*), Eurasian perch (*Perca fluviatilis*), and bleak (*Alburnus alburnus*) (Fig. 4).

Finally, the samples composing cluster 4 were significantly linked to every factor of the sampling design: month ($G = 61.4$, df = 9, $p < 0.05$), time of day ($G = 88.4$, df = 1, $p < 0.05$), site ($G = 49.6$, df = 2, $p < 0.05$), and year ($G = 19.7$, df = 4, $p < 0.05$). In this cluster, samples from July through December were overrepresented (especially September and October, i.e., partly autumn), as well as samples taken from site North-1 and twilight samples. The samples grouped within this cluster also showed a significant negative trend over the sampling period as a whole, with the highest proportion value in 1997 and the lowest in 2001 (Fig. 3*b*). The associated fish community comprised sunbleak (*Leucaspius delineatus*), burbot (*Lota lota*), stone moroko (*Pseudorasbora parva*), stone loach (*Barbatula barbatula*), tench (*Tinca tinca*), common barbel (*Barbus barbus*), chub (*Leuciscus cephalus*), European eel (*Anguilla anguilla*), rudd

Fig. 4. Estimated abundance of each species in each cell of the SOM. Species are presented in decreasing order of maximal estimated abundance (from top left to bottom right).



(*Scardinius erythrophthalmus*), threespine stickleback (*Gasterosteus aculeatus*), and ruffe (*Gymnocephalus cernuus*) (Fig. 4).

Discussion

From a total of 33 fish species in Lake Constance (Eckmann and Rösch 1998), 25 species were found in the littoral zone during this 5-year study (i.e., more than 75%). This high percentage confirms the important role played by littoral areas for fish populations and assemblages (Crowder and Cooper 1982; Werner et al. 1983; Lobb and Orth 1991). Compared with the previous work by Fischer and Eckmann (1997*b*) on Lake Constance, more species were found in the present study (25 versus 19). This difference is probably attributable to a different sampling strategy, since more sites were sampled by Fischer and Eckmann (1997*b*) but over a shorter time period and mainly during daytime.

According to the tests for proportions, every factor of the sampling design appeared to significantly influence one or several of the fish assemblages isolated by the SOM. The clearest patterns observed were those related to the annual cycle (factor month), which has to be related to the annual littoral thermal regime of the lake and to the species' thermal preferences. The winter to early spring assemblage revealed by the SOM corresponded with sculpin, brown trout, and grayling, which are usually classified as cold stenotherms and characteristic of cold-water areas with high oxygen content (e.g., Pickering 1981; Matthews 1998; Reyjol et al. 2001*b*). The late spring to summer community comprised species like lake whitefish and dace, which are also cold-water species, although they tolerate warmer water temperatures (Mann 1996). Finally, the summer and autumn communities clearly gathered typical warmwater species, e.g., bream, roach, Eurasian perch, bleak, common carp, Prussian carp, tench, and ruffe (Pickering 1981; Mann 1996). Studies describing such a monthly pattern of succession for European freshwater species in lakes are only sparse (but see Fischer and Eckmann 1997*a*, 1997*b*). Most of our knowledge on the distribution patterns of fish according to their thermal preferences comes from the spatial pattern of succession observable from upstream to downstream of rivers as temperature increases (for details, see Matthews 1998). It is most striking that SOM revealed temporal patterns of succession in the littoral fish community in Lake Constance that are very close to the spatial pattern of succession in the fish community in streams. This might become especially important for future studies on littoral fish communities of large lakes. Compared with stream ecology, our knowledge on littoral fish communities in large lakes and especially on the factors determining the temporal and spatial distribution of fish in certain habitats is still restricted. Our SOM analysis provided some evidence that the mechanisms determining the distribution of fish in streams and lakes might be similar even though expressed in different scales (spatial scale in streams versus a temporal scale in lakes). This, however, would allow the transfer of ecological concepts developed in stream ecology to large lake ecosystems and therefore provides the opportunity to enhance our restricted knowledge on large lake ecosystems in general. The fact that our modified SOM analysis revealed these patterns in Lake Constance is all the more precious because Lake Constance is the second largest prealpine lake in Europe and therefore can be well assumed as a most relevant model system for many other temperate large lake ecosystems on the Northern Hemisphere.

The second result of the SOM was the clear gradient from a strictly daytime community notably constituted by sculpin, brown trout, grayling, dace, and lake whitefish to a twilight community gathering sunbleak, burbot, stone moroko, stone loach, chub, threespine stickleback, and ruffe. The results obtained for the daytime community associated with cluster 1 have to be considered carefully because of the very low catches recorded for the species over the entire sampling period ($<2.0 \pm 0.3$ individuals per replicate). On the contrary, the other results fit with previous studies on fish nycthemeral habits, especially for burbot and stone loach, previously described as typically crepuscular species hiding within substratum interstices during daytime (Burdeyron and Buisson 1982; Fischer 2000). The twilight preference of the other species is much less documented in the literature and has to be considered with interest. The fact that SOM revealed a gradient instead of a simple dichotomy (daytime versus crepuscular species) in the present study is most interesting. This would suggest that a strict nycthemeral preference is more the exception than the rule and only expressed in few species related to species-specific physiological and probably genetic adaptation (e.g., burbot and stone loach). The results suggest that most other species are probably more plastic with regard to this biological trait allowing more a flexible and species-specific pattern of habitat partitioning with regard to daytime. This is especially true with regard to dace, which was found in the present study as a typical daytime species, while Clough and Ladle (1997) previously found it as a nocturnal species in the River Frome. Diel activity patterns especially in juvenile fish are generally assumed as a biological trait between the need for somatic growth to increase individual fitness and the need for refuge against predation by larger piscivorous daytime predators such as pike (Bain et al. 1988; Ruiz et al. 1993; Gibson and Robb 1996). Assuming optimal foraging, to optimize a behavior within these two conflicting demands, a highly plastic behavior with respect to diel activity patterns is much more likely to exist (in an evolutionary way) than a strict bimodal daytime–nocturnal decision with little chance for modulation. More than 90% of the fish in the present study were juveniles. Such a plastic behavior is especially important during the first year of life, during which fish have to grow as fast as possible to limit predation pressure and after which resource allocation progressively switches to maintenance and reproduction (Wooton 1998).

Considering sampling site, the SOM clearly isolated two distinct assemblages. The first one associated site North-2 with common carp, pikeperch, Prussian carp, bream, roach, Eurasian perch, and bleak, while the second one gathered sunbleak, burbot, stone moroko, stone loach, chub, threespine stickleback, and ruffe within site North-1. Compared with site South, which has a comparatively narrow shelf-littoral area, both North sites are characterized by a low slope and therefore an extended littoral area. Site North-1, however, differs from site North-2 by its very heterogeneous substratum composed of large stones and cobbles. This substratum type provides large interstices where crepuscular benthic species such as burbot and stone loach can shelter. On the contrary, site North-2 is characterized by fine sediments with dense stand of submerged macrophytes, which are know to be suitable habitats for species like bream, roach, and Eurasian perch (Hinch and Collins 1993; Fischer and Eckmann 1997*a*, 1997*b*). Habitat partitioning in lakes has especially been studied at the scale of the study site, where some species have been found to colonize shorelines, while others colonize substratum or more or less deep areas (Pierce et al. 1994; Fischer and Eckmann 1997*a*, 1997*b*). The present study gives an example of how habitat can be partitioned within different sampling sites and therefore at the scale of the whole lake, which probably has an influence on the coexistence of different species populations within a lake. Even if only three sampling sites were considered in the present study, a similar habitat partitioning can be found in Fischer and Eckmann (1997*a*, 1997*b*) where more sites were considered. This testifies to the necessity of maintaining habitat diversity in littoral zones of lakes to promote fish diversity.

Finally, the last trend revealed by the analyses was a significant decreasing proportion of samples in which sunbleak, burbot, stone moroko, stone loach, chub, threespine stickleback, and ruffe were present from 1997 to 2001. While chub and ruffe dominated the cyprinid and percid community during the 90s of the last century (Fischer and Eckmann 1997*b*), recent studies on Lake Constance showed that these species underwent a strong decrease in abundance over the last years. This decline probably reflects the significant change in the trophic status of Lake Constance from a mesotrophic to eutrophic lake in the late 1980s (i.e., $>80\ \mu g\ P{\cdot}L^{-1}$) to an oligotrophic lake at present (i.e., $<12\ \mu g\ P{\cdot}L^{-1}$). In contrast with the process of eutrophication, for which effects like an increase in total catches in cyprinids together with the decrease in percids, salmonids, and coregonids are well documented, the effects of the reoligotrophication process on lake fish communities are almost entirely lacking. Assuming a simple reversal of the process and effects of eutrophication can hardly be assumed, especially when new species have been introduced into the system. In Lake Constance, ruffe was found for the first time in 1987, and since then, its population increased dramatically until 1995 (Rösch and Schmid 1996). Our SOM results now revealed that for Lake Constance, among percids, only ruffe but not perch was associated with a decreasing trend. This indicates that ruffe might be much more affected by the long-term changes in the tropic status compared with Eurasian perch. If a higher or earlier sensitivity to the reoligotrophication process of ruffe compared with Eurasian perch would be confirmed, this species could be considered as a relevant biological sentinel to follow the reoligotrophication process in lakes. The theoretical following step for the littoral fish community of Lake Constance in the next years should be the increase of species which were dominant during the first half of the last century when Lake Constance was on a trophic state similar to nowadays. Exactly this is observed today with a strong increase in bleak and with lake whitefish becoming again more important in the commercial fishery. Especially the latter development, i.e., the refreshment of lake whitefish, is most interesting, not only in terms of importance to the local fishermen but also in terms of intraspecific interactions with ruffe. Rösch and Schmid (1996) showed that in Lake Constance during the spawning season of lake whitefish, ruffe almost entirely switches to lake whitefish eggs as a main prey. If long-term changes in the trophic status of the lake selectively negatively affect ruffe abundance, the decrease in the nutrition load of the lake not only positively affects lake whitefish recruitment itself by an increase in egg survival in the deep profundal areas. It also may indirectly affect stock size by a decrease in one of its main predators on the most critical ontogenetic stage of development.

In addition to using SOM on these data, we did try a number of more traditional approaches. We initially ran a PCA on instrumental variables (PCAiv), a method that was developed for focusing on the different effects of factors in sampling designs (Sabatier et al. 1989; Lebreton et al. 1991). The results from this method were difficult to interpret, probably owing to the large number of factors used here. A classical PCA was also used on the data to cluster the samples to investigate the effects of the different factors, but the results from this analysis were also difficult to interpret.

Multivariate analysis of variance (MANOVA) seemed to be a natural contender here and with this approach, we found that the results were similar to those from SOM with regard to the effects of month and daytime but there were major differences between the two methods concerning the factors site and year. That is, significant associations with site South were found for some species with MANOVA, and SOM only detected the interannual decreasing trend observed for burbot, ruffe, and chub from 1997 to 2001, while other relationships were found with MANOVA.

In MANOVA, each fish species was related to each of the factors and the grouping of species with similar ecological responses was made after the fact. On the other hand, with the SOM approach, species were clustered first and then the significance of trends for the sampling design factors was tested using χ^2 statistics. Despite these differences in approach and while MANOVA detected more significant relationships than SOM did, a number of the trends revealed by the SOM approach were confirmed by MANOVA, testifying to their robustness. While using more than one kind of statistical model for the same data can identify the more robust findings, we believe that the SOM method used here allows for a very interesting view of the whole community organization and functioning with respect to space and time (superimposition of Figs. 3 and 4), which as far as we know has never been documented for such a complex sampling design as used here.

In conclusion, the SOM methodology used in this study clearly separated distinct communities according to site, year, month, and time of day. The explicit, simultaneous consideration of spatial and temporal variation allowed a valuable interpretation of temporal and spatial patterns, as previously suggested by Resh and Rosenberg (1989). Consequently, SOM appears to be a very promising approach to analyzing large data sets built according to complex sampling designs. With regard to lake functioning in general, this study clearly illustrated how habitat utilization is partitioned by fish both spatially (i.e., among sites) and temporally (i.e., between daytime and twilight), which highlighted the complexity of fish community organization and functioning in the littoral zones of lakes.

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References

Alhoniemi, E., Himberg, J., Parhankangas, J., and Vesanto, J. 2003. SOM toolbox 2.0 [online]. Laboratory of Computer and Information Science, Neural Networks Research Centre, Helsinki, Finland. Available from http://www.cis.hut.fi/projects/somtoolbox/ [accessed 14 April 2003].

Allen, L.G. 1982. Seasonal abundance, composition, and productivity of the littoral fish assemblage in upper Network Bay, California. Fish. Bull. **80**: 769–790.

Bain, M.B., Finn, J.T., and Booke, H.E. 1988. Streamflow regulation and fish community structure. Ecology, **69**: 382–392.

Burdeyron, H., and Buisson, B. 1982. On a circadian endogenous locomotor rhythm of loaches (*Noemacheilus barbatulus* L., Pisces, Cobitidae). Zool. Jahrb. Physiol. **86**: 82–89.

Chon, T.S., Park, Y.S., Moon, K.H., and Cha, E.Y. 1996. Patternizing communities by using an artificial neural network. Ecol. Model. **90**: 69–78.

Clough, S., and Ladle, M. 1997. Diel migration and site fidelity in a stream dwelling cyprinid, *Leuciscus leuciscus*. J. Fish Biol. **50**: 1117–1119.

Crowder, L.B., and Cooper, W.E. 1982. Habitat structural complexity and the interactions between bluegills and their prey. Ecology, **63**:1802–1813.

Eckmann, R., and Rösch, R. 1998. Lake Constance fisheries and fish ecology. Arch. Hydrobiol. Spec. Issues Adv. Limnol. **53**: 285–301.

Fischer, P. 2000. An experimental test of metabolic and behavioural responses of benthic fish species to different types of substrate. Can. J. Fish. Aquat. Sci. **57**: 2336–2344.

Fischer, P., and Eckman, R. 1997*a*. Seasonal changes in fish abundance, biomass and species richness in the littoral zone of a large European lake, Lake Constance, Germany. Arch. Hydrobiol. **139**: 433–448.

Fischer, P., and Eckman, R. 1997*b*. Spatial distribution of littoral fish species in a large European lake, Lake Constance, Germany. Arch. Hydrobiol. **140**: 91–116.

Gafny, S., Gasith, A., and Goren, M. 1992. Effect of water level fluctuation on shore spawning of *Mirogrex terraesanctae*

(Steinitz) (Cyprinidae) in Lake Kinnereth, Israel. J. Fish Biol. **41**: 863–871.

Gibson, R.N., and Robb, L. 1996. Piscine predation on juvenile fishes on a Scottish sandy beach. J. Fish Biol. **49**: 120–138.

Giraudel, J.-L., and Lek, S. 2001. A comparison of self-organizing map algorithm and some conventional statistical methods for ecological community ordination. Ecol. Model. **146**: 329–339.

Hinch, S.G., and Collins, N.C. 1993. Relationships of littoral fish abundance to water chemistry and macrophyte variables in central Ontario lakes. Can. J. Fish. Aquat. Sci. **50**: 1870–1878.

Keast, A. 1985. The piscivore feeding guilds of fishes in small freshwater ecosystems. Environ. Biol. Fishes, **12**: 119–129.

Kiefer, F. 1972. Naturkunde des Bodensees. J. Thorbecke, Sigmaringen.

Kohonen, T. 1982. Analysis of a simple self-organizing process. Biol. Cybern. **44**: 135–140.

Kohonen, T. 2001. Self-organizing maps. 3rd extended ed. Springer Series in Information Sciences. Vol. 30. Springer, New York.

Lebreton, J., Sabatier, R., Banco, G., and Bacou, A. 1991. Principal component and correspondence analyses with respect to instrumental variables: an overview of their role in studies of structure–activity and species–environment relationships. *In* Applied multivariate analysis in SAR and environmental studies. *Edited by* Devilliers and Karcher. Kluver Academic Publishers, Dordrecht, Boston, London. pp. 85–114.

Lek, S., and Guégan, J.-F. (*Editors*). 2000. Artificial neuronal networks: application to ecology and evolution. Springer-Verlag, Berlin/Heidelberg.

Lobb, M.D., and Orth, D.J. 1991. Habitat use by an assemblage of fish in a large warmwater stream. Trans. Am. Fish. Soc. **120**: 65–78.

Ludwig, J.A., and Reynolds, J.F. 1988. Statistical ecology. A primer on methods and computing. John Wiley & Sons, Chichester, UK.

Mann, R.K.H. 1996. Environmental requirements of European non-salmonid fish in rivers. Hydrobiologia, **323**: 223–235.

Matthews, W.J. 1998. Patterns in freshwater fish ecology. Chapman and Hall, New York.

Olden, J.D., and Jackson, D.A. 2002. A comparison of statistical approaches for modeling fish species distributions. Freshw. Biol. **47**: 1976–1995.

Park, Y.S., Cereghino, R., Compin, A., and Lek, S. 2003. Applications of neural networks for patterning and predicting aquatic insect species richness in running waters. Ecol. Model. **160**: 265–280.

Pickering, A.D. 1981. Stress and fish. Academic Press, Inc., New York.

Pierce, C.L., Rasmussen, J.B., and 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.

Resh, V.H., and Rosenberg, D.M. 1989. Spatial–temporal variability and the study of aquatic insects. Can. Entomol. **121**: 941–963.

Reyjol, Y., Lim, P., Belaud, A., and Lek, S. 2001*a*. Modelling of microhabitat used by fish in natural and regulated flows in the river Garonne (France). Ecol. Model. **146**: 131–142.

Reyjol, Y., Lim, P., Dauba, F., Baran, P., and Belaud, A. 2001*b*. Role of temperature and flow regulation on the Salmoniform–Cypriniform transition. Arch. Hydrobiol. **152**: 567–582.

Ripley, B.D. 1996. Pattern recognition and neural nets. Cambridge University Press, Cambridge, UK.

Rösch, R., and Schmid, W. 1996. Ruffe (*Gymnocephalus cernuus* L.), newly introduced into Lake Constance: preliminary data on population biology and possible effects on whitefish (*Coregonus lavaretus* L.). Ann. Zool. Fenn. **33**: 467–471.

Ruiz, G.M., Hines, A.H., and Posey, M.H. 1993. Shallow water as a refuge habitat for fish and crustaceans in non-vegetated estuaries: an example from Chesapeake Bay. Mar. Ecol. Prog. Ser. **99**: 1–16.

Rundle, H.D., and Jackson, D.A. 1996. Spatial and temporal variation in littoral-zone fish communities: a new statistical approach. Can. J. Fish. Aquat. Sci. **53**: 2167–2176.

Sabatier, R., Lebreton, J., and Chessel, D. 1989. Principal component analysis with instrumental variables as a tool for modelling composition data. *In* Multiway data analysis. *Edited by* R. Coppi and S. Bolasco. Elsevier Science Publishers B.V., North-Holland, Amsterdam, Netherlands. pp. 341–352.

Sachs, L. 1997. Angewandte Statistik. 8th ed. Springer, Berlin.

Werner, E.E., Gilliam, J.F., Hall, D.J., and Mittelbach, G.G. 1983. An experimental test on the effects of predation risk on habitat use in fish. Ecology, **64**: 1540–1548.

Wetzel, R.G. 1983. Limnology. Sounders College Publication, Philadelphia, Pa.

Wooton, R.J. 1998. Ecology of teleost fishes. 2nd ed. Fish and Fisheries Series 1. Chapman and Hall, London, UK.