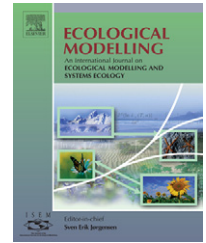


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Fish assemblages in the large lowland Narew River system (Poland): Application of the self-organizing map algorithm

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ARTICLE INFO

Article history:

Received 4 January 2005

Received in revised form

6 October 2005

Accepted 27 October 2005

Published on line 8 January 2007

Keywords:

Kohonen self-organizing map

The Narew River system

Habitat variables

Relative fish biomass

Fish assemblage structure

Diversity indices

ABSTRACT

The section of the lowland Narew River within Polish borders (432 km long) flowing between two big reservoirs, and its tributaries were selected for the study. At 321 sites a total of 49,675 fish and lamprey specimens, representing 36 taxa, were collected. The sites were classified using the Kohonen self-organizing map (SOM) on the basis of fish and lamprey relative biomass data. The trained SOM (lattice 6×4) showed three main clusters of samples assigned to the neurons: (1) A1–B4, (2) C1–D4, and (3) E1–F4, differing not only in fish fauna composition but also in some environmental variables not presented to the SOM. Generally, sites from small, regulated streams with few trees along banks were dominant in cluster AB, while sites from natural larger rivers with many trees along banks were assigned to cluster EF. Cluster CD contained sites of intermediate character. In AB we distinguished an assemblage with five species present in each neuron (gudgeon, loach, stickleback, ten-spined stickleback and pike), and in EF an assemblage with seven ones (stickleback, ide, perch, roach, pike, burbot and bleak), but 100% occurrence stability in each neuron was recorded only for roach in EF. A significantly lowest species richness and values of the Shannon index of biodiversity were recorded in AB, that is for the smallest streams. Additionally, many environmental, population and assemblage variables also showed more subtle gradients within each cluster. The clear differences between clusters and gradients within them, recorded even for variables indirectly analysed with SOM, prove that the obtained classification was very effective, which additionally testifies to the reliability of the distinguished fish assemblages. SOM provides more detailed information on the mutual relations between species through component planes than the detrended correspondence analysis through points in a multivariate space, thus being much useful for coenological studies. Moreover, such rich data as in this study diminish the legibility of scatterplots in the detrended correspondence analysis, while SOM provides much more clear visualization of results.

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1. Introduction

Researchers have long reflected on and disputed the problem of what controls distinguished by them fish assemblages, and

whether the latter are real and persistent despite being influenced by hardly predictable climate changes in the temperate zone (Mills, 1969; Connell, 1975; Grossman, 1982; Grossman et al., 1982; Schluter, 1986; Moyle and Herbold, 1987; Matthews,

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doi:10.1016/j.ecolmodel.2005.10.044

1998; Jackson et al., 2001; Oberdorff et al., 2001; Gevrey et al., 2005; Park et al., 2005a). Distinguishing assemblages is also difficult because pristine environments do not exist any more (Vannote et al., 1980; Penczak, 1994), invasions of non-native species may take place (Moyle, 1994; Penczak, 1999), fish assemblages may be strongly changed due to exploitation (Murawski, 1983), fish cannot be absolutely randomly sampled (Mahon and Smith, 1989), fish sampling gears are selective (Casselman et al., 1990; Głowacki and Penczak, 2005), different methods are applied to order fish data (James and McCulloch, 1990) and the ecological bases of defining assemblages are imprecise (Tyler et al., 1982; Jackson et al., 2001).

There is another problem that does not facilitate distinguishing of fish assemblages in river systems, namely the absence of decisive environmental preferences, which testifies to high adaptive capabilities of many species. In European rivers there are species exclusively adopted to running waters (rheophilic) as well as taxa that are classified as eurytopic, eurybiontic or facultative riverine (Wolter, 2001; Kruk and Penczak, 2003; Kruk, 2006); the latter are able to switch between stagnant and running waters during ontogeny because they are generalists (Jackson et al., 2001; Wolter, 2001; Irz et al., 2006). Presumably, the most generalist fish species in Europe are roach and perch (Schiemer and Wieser, 1992; Wolter and Vilcinskas, 1997; Kruk, 2006). They are getting dominant with high occurrence stability even in rivers where other eurytopic species can be threatened by extensive and harsh human stressors (Penczak and Koszalińska, 1993; Wolter and Vilcinskas, 1997; Kruk and Penczak, 2003).

We rather incline to the assemblage definition based on the dominance of species (Echelle et al., 1972; Johnson et al., 1977; Ryder and Kerr, 1978). For the classification of our ichthyofauna we cannot apply the proposal 'that species comprising

an assemblage are highly co-evolved, and interdependent, and that as one of the species reaches its distribution limits, the assemblage loses its integrity, giving way to another assemblage' (Mahon and Smith, 1989). If we chose this definition for distinguishing assemblages, their number would be high and their distribution would be unnaturally mosaic, despite the fact that the catchment is characterized by similar slope, discharge and temperature, although with various human stressors. Especial difficulty emerges when one wants to determine which human stressors are responsible for definitive or periodical elimination of rare and/or vulnerable species, because their effects overlap and interact (Northcote et al., 1985; Orth and White, 1993). In other large rivers of Central Poland, in a 40-year-long monitoring, differences were recorded even in the list of dominant species (Penczak, 1996; Kruk, 2006). However, changes in the presence or absence of rare species were much more often (Backiel and Penczak, 1989).

The fish fauna of the Narew River system was selected for the study because it covers over 1/6 of the territory of Poland. In some parts, this large lowland river system is moderately differentiated by environmental factors, but anthropogenic impacts and a high number of collected samples create some difficulties for ordination of fish populations with conventional statistical methods. The collected materials (1986-1991) have by now been used for inventory study only, made on the request of the Polish Anglers Association (Penczak et al., 1990a, 1990b, 1991a, 1991b, 1992). In the five above-cited papers only the species abundance along river courses was presented on diagrams, in a six-degree scale. Data on relative biomass was not published yet. Some attempts at comparisons and distinguishing of fish assemblages were undertaken but without applying statistical methods.

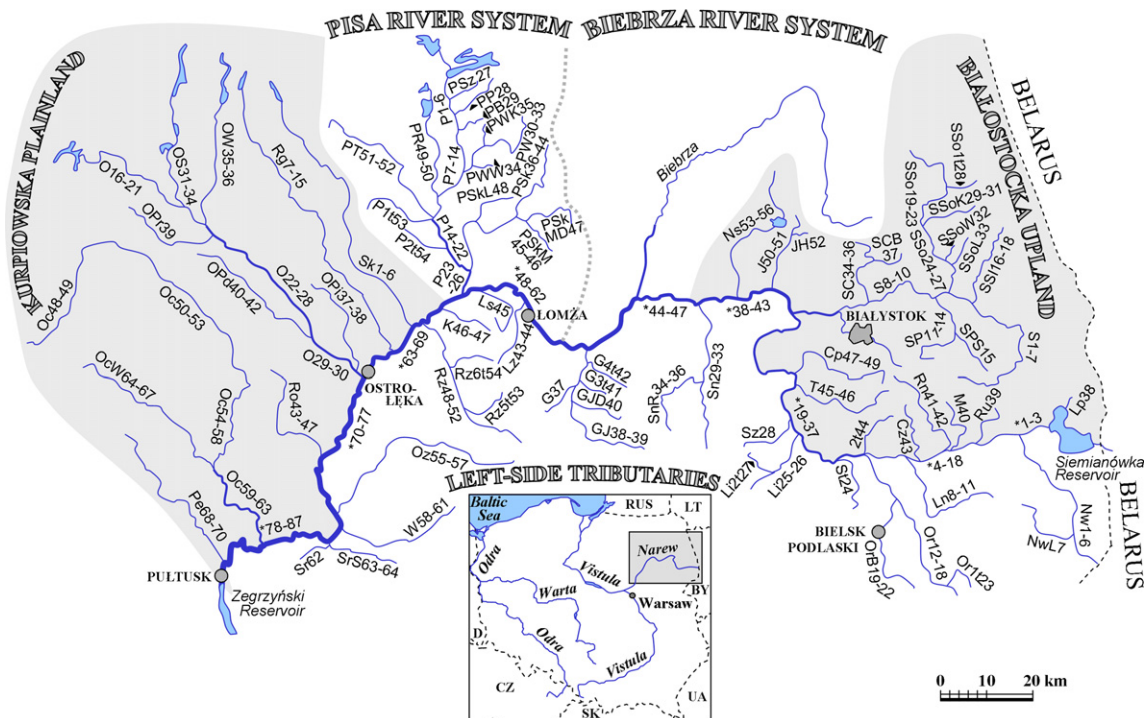


Fig. 1 – The Narew River system. Site codes for studied streams are the same as in Table 1.

Recently, in order to deal with the problem of complexity in ecological data, the Kohonen self-organizing map (SOM) (Kohonen, 1982, 2001) is proposed. It has been successfully used for diverse ecosystems (i.e., aquatic, forest, agricultural, etc.) (Lek and Guegan, 2000; Recknagel, 2003; Lek, 2005) for community classification (Chon et al., 1996, 2000; Park et al., 2001, 2003; Penczak et al., 2005; Kruk, 2006), water quality assessments (Walley et al., 2000; Aguilera et al., 2001), conservation strategies of endemic species (Park et al., 2003), even if other statistical methods failed (Cho, 1997; Park et al., 2005b). Hence the SOM was employed as the main method in this study.

The aim of the study is to: (1) assess the effectiveness of classification of numerous fish samples performed with use of the SOM and (2) determine how many fish assemblages can be distinguished in the lowland Narew River system, and whether they are characterized by repeatable species composition in different parts of the catchment.

2. Materials and methods

2.1. Study area and environments

The Narew River (total length 484 km) is 448 km long within Polish borders and its catchment comprises 53,787 km². The investigated 432 km long reach of the Narew River, limited by two big reservoirs, and its tributaries selected for the study, are presented in Fig. 1. The Biebrza River system was excluded from this study. This large Narew tributary was investigated previously by Witkowski (1984).

Electrofishing was conducted at 331 sites, but only 321 of them, those that were settled by fish, were selected for the study (Table 1). In the remaining ten fishless sites (*44, *46, S10, SSo21, SSo22, SSo1t28, Ns53, Ns54, Ns56, OcW66; Table 1) heavy water pollution and strong odour were recorded during sampling. The following environmental variables are available for each site (Penczak et al., 1990a, 1990b, 1991a, 1991b, 1992): distance from source (km), mean width (m), mean depth (m), bottom substratum, and the presence of submerged plants and trees along banks in four level scale (none: 0, little: 1, common: 2, abundant: 3). Also descriptive information is available on the types of hidings (fascine, fallen trees, branches, overhanging willow branches, roots), on the basis of which hidings diversity index was applied (expressed as a number of hidings). Information on areas adjacent to river banks (pasture, forest, arable land), and the character of sampled channel in three level scale (natural meandering: 2, not meandering but without signs of recent regulation: 1, or regulated: 0) was also gathered. The site numeration was maintained the same as in the original five papers, so that each site's characteristics is easy to find.

To show approximate differences in water discharge, the product (WD) of channel width (W, in m) and mean channel depth (D, in m) was used. Slope (in m km⁻¹ of river length) in the investigated river system was rather low and amounted to: (1) 1.40 ± 0.63 m km⁻¹ (mean ± S.D.) in the rivers of the Białostocka Upland; (2) 2.00 ± 1.70 m km⁻¹ in northern Supraśl River tributaries flowing across postglacial moraines; (3) 0.23 ± 0.20 m km⁻¹ in the Pisa River and its tributaries; (4)

Table 1 – Studied rivers with site codes used in Figs. 1 and 3

Site code	River	Receiving river
*1–*87	Narew	Vistula
Pisa River system		
P1–P26	Pisa	Narew
PSz27	Szparka	Pisia
PP28	Pisza Woda	Pisia
PB29	Bogumiłka	Pisia
PW30–PW33	Wincenta	Pisia
PWW34	Wykówka	Wincenta
PWK35	Kulona	Wincenta
PSk36–PSk44	Skroda	Pisia
PSkM45–PSkM46	Mogilna	Skroda
PSkMD47	Dzierzbia	Mogilna
PSkL48	Łabna	Skroda
PR49–PR50	Rybница	Pisia
PT51–PT52	Turośl	Pisia
P1t53	Tributary No. 1	Pisia
P2t54	Tributary No. 2	Pisia
Białostocka Upland		
S1–S10	Supraśl	Narew
SP11–SP14	Płoska	Supraśl
SPS15	Świnobródka	Płoska
SS116–SS118	Słoja	Supraśl
SSo19–SSo27	Sokołda	Supraśl
SSo1t28	Tributary No. 1	Sokołda
SSoK29–SSoK31	Kamionka	Sokołda
SSoW32	Wielki Grud	Sokołda
SSoL33	Łanga	Sokołda
SC34–SC36	Czarna	Supraśl
SCB37	Bartoszycha	Czarna
Lp38	Łuplanka	Narew
Ru39	Ruda	Narew
M40	Małynka	Narew
Rn41–Rn42	Rudnia	Narew
Cz43	Czarna	Narew
2t44	Tributary No. 2	Narew
T45–T46	Turośnianka	Narew
Cp47–Cp49	Czaplinianka	Narew
J50–J51	Jaskranka	Narew
JH52	Hatka	Jaskranka
Ns53–Ns56	Nereśl	Narew
Left side tributaries		
Nw1–Nw6	Narewka	Narew
NwL7	Łutownia	Narewka
Ln8–Ln11	Łoknica	Narew
Or12–Or18	Orlanka	Narew
OrB19–OrB22	Biała	Orlanka
Or1t23	Tributary No. 1	Orlanka
St24	Strabla	Narew
Li25–26	Liza	Narew
Li2t27	Tributary No. 2	Liza
Sz28	Szeroka Struga	Narew
Sn29–Sn33	Ślina	Narew
SnR34–SnR36	Rokietnica	Ślina
G37	Gać	Narew
GJ38–GJ39	Jablonka	Gać
GJD40	Dąb	Jablonka
G3t41	Tributary No. 3	Gać
G4t42	Tributary No. 4	Gać
Lz43–Lz44	Łomżyczka	Narew
Ls45	Lepacka Struga	Narew
K46–K47	Krzywa Noga	Narew

Table 1 – (Continued)

Site code	River	Receiving river
Rz48–Rz52	Ruż	Narew
Rz5t53	Tributary No. 5	Ruż
Rz6t54	Tributary No. 6	Ruż
Oz55–Oz57	Orz	Narew
W58–W61	Wymakracz	Narew
Sr62	Struga	Narew
SrS63–SrS64	Strużka	Struga
Kurpiowska Plainland		
Sk1–Sk6	Szkwa	Narew
Rg7–Rg15	Rozoga	Narew
O16–O30	Omulew	Narew
OS31–OS34	Sawica	Omulew
OW35–OW36	Wałpusz	Omulew
OPi37–OPi38	Piasiecznica	Omulew
OPr39	Przędziecka Struga	Omulew
OPd40–OPd42	Płodownica	Omulew
Ro43–Ro47	Róż	Narew
Oc48–Oc63	Orzyc	Narew
OcW64–OcW67	Węgiełka	Orzyc
Pe68–Pe70	Pełta	Narew

$0.51 \pm 0.15 \text{ m km}^{-1}$ in the rivers of the Kurpiowska Plainland; (5) $1.44 \pm 0.72 \text{ m km}^{-1}$ in the left side tributaries of the Narew River; (6) 0.33 and 0.14 m km^{-1} in the reaches of the Narew River located between 64 and 380, and 380 and 432 km of the river course, respectively. Low slope values recorded there indicate that the WD values may provide some comparable data not only about river size but also about discharge.

A phenomenon common at that time consisted in emptying of cistern trucks with liquid manure from governmental cattle farms to ditches and small streams. Domestic sewers from small towns and villages also emptied to the rivers. Pure water, i.e., totally transparent and without flavour, was observed occasionally in small streams located in a forest or far away from domiciled areas.

In the river system we observed different forms of poaching with nets, explosives, harpoons and lamps at night, but these kinds of ‘harvesting’ were not directly investigated.

2.2. Fish assemblage data

Fish were caught from a boat or while wading, by two people, each operating an anode dipnet. Full-wave rectified, pulsed 230 V and 3–10 A dc current was taken from a 3 kW generator. Single electrofishing at each site was done in accordance with the Becklemishev’s rule (Penczak, 1967; Backiel and Penczak, 1989) stating that the length (area) of a sampled river section is considered to be satisfactory if further sampling does not add any new species to the species list. In practice that means that species relative abundance and biomass, i.e. per constant unit of effort (CPUE) were assessed in the Narew River system from both banks of a 100 m long reach when wading in shallow streams, and from a 500 m long reach when drifting in a boat along a bank. In this study the population abundance was expressed in relative biomass, which is equivalent to stock biomass or standing crop, and defined by Ricker (1968) as the amount of substances in (a) population(s) on the day

of sampling. It is well known that the potential energy of an ecosystem is not distributed proportionally between species (Odum, 1980). Expressing the importance of populations in an ecosystem in energy units is the best option but not always available. Biomass is much closer to energy and thus constitutes a more reliable variable than the number of specimens. The relative biomass data were log-transformed and then normalized in a scale of 0–1.

A total of 49,675 individuals of fish were caught and 36 species (Appendix A) were identified. Among them three rare species (nase, rudd, carp) occurring at less than three sites were removed from the dataset to prevent distortions of statistical analysis. Thus, the data matrix for ordering methods consisted of 33 species (columns) and 321 sites, i.e., samples (rows).

In the study we used the classification of species into reproductive guilds by Balon (1990) (Appendix A). It is a useful classification, although Orth (1980) noted that members of a guild can differ in reaction to human stressors, and that there are situations when some species from different guilds show similar trends in abundance. The most coherent guild in reaction to human stressors are lithophils (rheophilic species), which are most vulnerable and effectively indicate degradation of aquatic environment. Lack of this reproductive guild may result from pollution or engineering, and not only from the absence of suitable spawning conditions (Przybylski, 1993; Penczak and Kruk, 2000, 2005; Kruk, 2004).

2.3. Statistical analysis

The Kohonen self-organizing map (SOM), an unsupervised artificial neural network, was used in the study (Kohonen, 1982, 2001). The SOM consists of two (input and output) layers, each containing processing units (neurons). The input layer receives input values from the data matrix. The neurons in the output layer are usually arranged into a two-dimensional grid for better visualization of results. In this study, the output layer consists of 24 neurons arranged into a 6×4 hexagonal lattice according to our preliminary studies. We tried to employ smaller and larger lattices but the classifications of fish samples were not so clear as with that chosen for the study. During the learning process of the SOM, weights are modified to minimize the distance between weight and input vectors. The learning process is usually done in two phases: at first rough training for ordering with a large neighbourhood radius, and then fine-tuning with a small radius. Fitting of the model vectors is carried out by a sequential regression process, where $t = 1, 2, \dots$ is the step index: for each sample $x(t)$, first the winner index c (best match) is identified by the condition:

$$\forall i, \quad \|x(t) - m_c(t)\| \leq \|x(t) - m_i(t)\|.$$

After that, all model vectors or a subset of them that belong to neurons centred around neuron $c = c(x)$, are updated as

$$m_i(t+1) = m_i(t) + h_{c(x),i}(x(t) - m_i(t)),$$

where $h_{c(x),i}$ is the neighbourhood function, a decreasing function of the distance between the i th and c th neurons on the map grid. This regression is usually iterated over the available samples (Kohonen, 2001). The detailed algorithm of the SOM

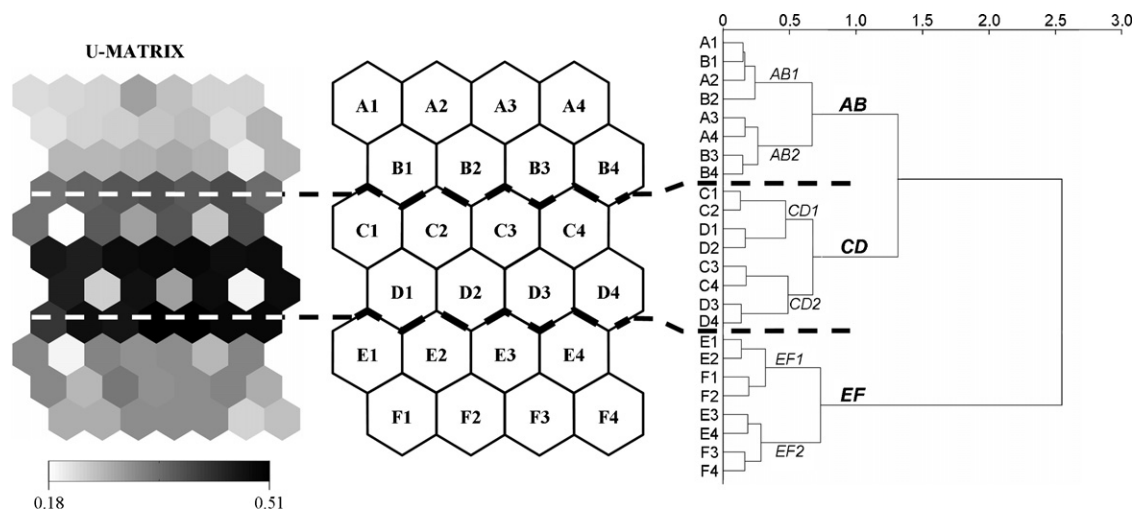


Fig. 2 – A self-organizing map formed by 24 hexagons representing neurons. Clusters of neurons AB, CD and EF were distinguished on the basis of the U-matrix (dark shading indicates big differences between neurons) and a hierarchical cluster analysis with Ward linkage method using Euclidean distance measure.

for ecological applications can be found in Chon et al. (1996), Giraudel et al. (2000) and Park et al. (2001, 2003, 2005b).

The map obtained after the learning process of the SOM represents all the fish samples assigned to neurons so that similar samples are located close to each other and far from those dissimilar. However, it is not easy to distinguish subsets because there are still no boundaries between possible clusters. Therefore, it is necessary to subdivide the output neurons into different groups according to their similarity. We used a hierarchical cluster analysis with the Ward linkage method using Euclidean distance measure to define the cluster boundaries in the neurons of the SOM map. Moreover, the neurons were clustered according to their similarities based on the unified distance matrix (U-matrix) (Ultsch, 1993). For each neuron information related to theoretical species composition is also available.

In order to assess the effectiveness of classification of fish samples performed with use of the SOM, medians of variables not presented to the SOM (direct environmental measurements) or not directly analysed by the SOM (fish assemblage variables and diversity indices) were calculated for each neuron.

An attempt at ordination with the detrended correspondence analysis (DCA, version of DECORANA; Hill, 1979) was undertaken using the same dataset in order to compare the results between SOM and DCA. DCA is free of lax criteria for stability and a bug in the rescaling algorithm. The bug caused sensitivity of ordination results to sample order, mainly on the third axis and higher. These problems have been corrected in the multivariate analysis using PC-ORD statistical software (McCune and Mefford, 1992). Eigenvalues in DCA cannot be interpreted as proportions of the variance explained (Palmer, 2000) but the minimum value recommended for data interpretation is $\lambda_1 = 0.20$ (Matthews, 1998). For 1st and 2nd axes they appeared to be remarkably higher and accounted for 0.55 and 0.23, respectively. Our choice for scaling axes was the raw scores, which is arbitrary and dependent on the units of the original data.

3. Results

The trained SOM, according to the U-matrix distances, showed three main clusters of samples assigned to the output neurons: (1) A1-B4, (2) C1-D4, and (3) E1-F4 (Fig. 2). Such classification was confirmed with the conventional cluster analysis, which identified exactly the same clusters (Fig. 2). The two most distant clusters AB and EF are innerly homogenous (light shading on the U-matrix) unlike CD cluster (Fig. 2). This means that samples within CD are more diversified than others.

Cluster AB contains samples from small streams of the Narew River system, mainly from the left side tributaries of the Narew River (45 sites), the Białostocka Upland (41), the Kurpiowska Plainland (26) and the Pisa River system (19) (Fig. 3). Samples from the Narew River are absent in cluster AB, without exception. Clusters CD and EF contain sites from all the five distinguished parts of the Narew system, of course in different proportions. Cluster CD contains very diverse samples from the upper reach of the Narew River (24 sites located between the state border and the Biebrza River mouth, plus the most downstream site (No. *87), located in the backwater of the Zegrzyński Reservoir), 49 samples from the Kurpiowska Plainland, 27 samples from the left side tributaries of the Narew River, 14 from the Pisa River tributaries and 13 from the Białostocka Upland streams (Fig. 3). Cluster EF contains 69 sites from the Narew River, all 25 sites located along the course of the Pisa River inflowing from Lake Roś as a large, deep river, plus 12 sites from the lower courses of the Omulew, Orzyc, Supraśl and Narewka Rivers (Fig. 3).

Some available environmental variables exhibit a clear vertical gradient over SOM. Clusters AB, CD and EF differ significantly from each other in the product of width and depth (WD) (Fig. 4A), river naturalness (Fig. 4B) and the amount of trees along banks (Fig. 4C). Generally, in AB small, regulated streams with few trees along banks are dominant. Conversely, in EF there are mainly natural larger rivers with many trees along banks. Cluster CD contains sites of intermediate character-

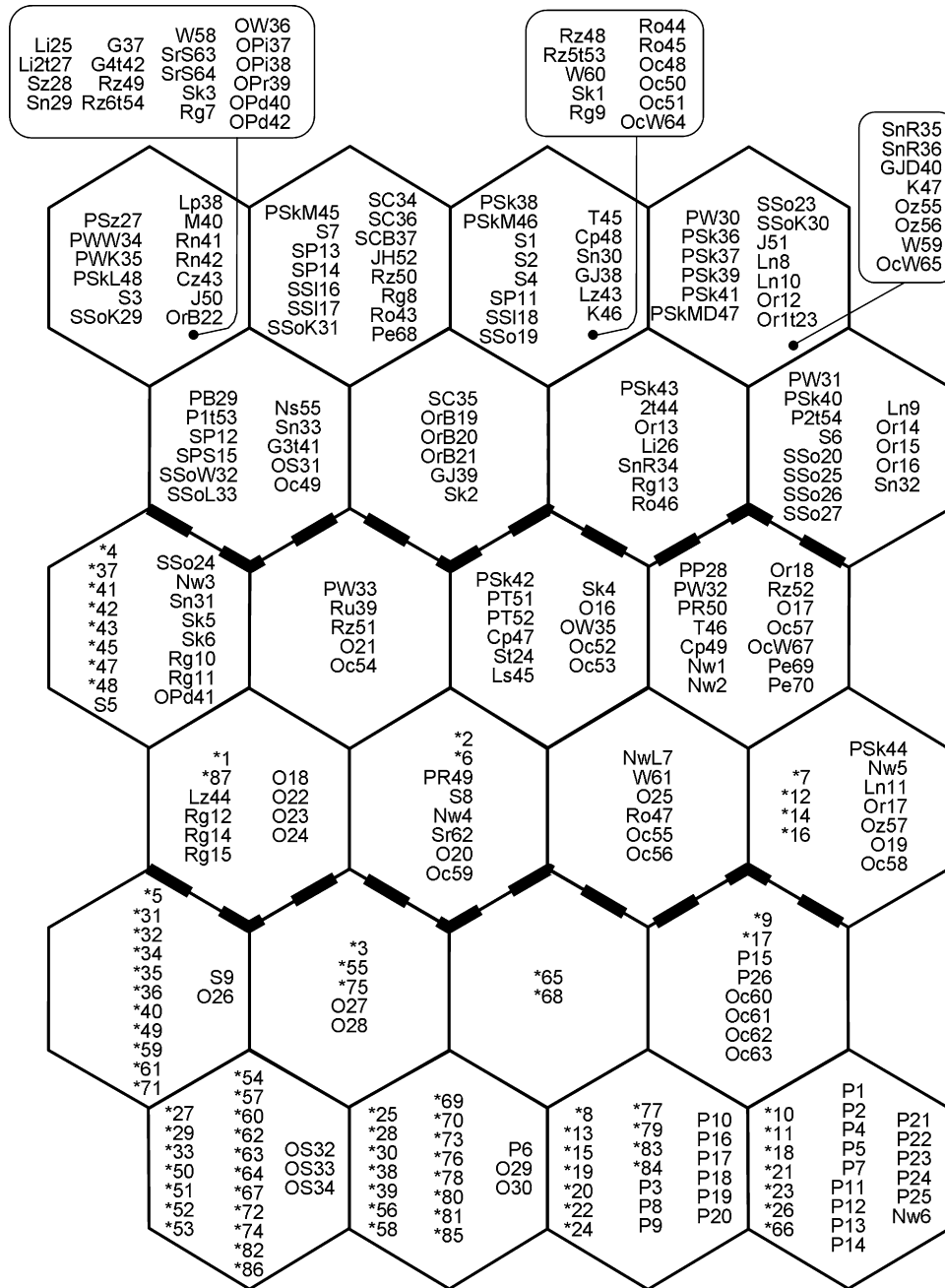


Fig. 3 – The 321 sites from the Narew River system assigned to SOM neurons. Sites from the Narew are marked with asterisks, and codes for sites from the tributaries are explained in Table 1. Symbols for the neurons are the same as in Fig. 2. Dashed lines show boundaries between clusters of neurons.

tics. Median values of the hidings diversity index do not differ between any of the clusters (AB, CD, EF), though differences between some single neurons are visible (Fig. 4D).

The most distant clusters, AB and EF, differ very much from each other in fish fauna composition (Fig. 5). Minnow, brown trout, gibel and sunbleak were present in AB and absent in EF while asp, spirlin, barbel, bream, ruffe, zander, silver bream and wels were present in EF and absent in AB (Table 3). In cluster AB the following species attained high occurrence stability in each neuron: gudgeon, loach, stickleback and ten-spined stickleback, while in EF—ide, perch, roach, pike, burbot and

bleak (Table 3). Stickleback in EF was also present in each neuron, but its occurrence stability never exceeded 50%. Pike was present in all hexagons of both clusters but in AB maximally in hundreds of grams (usually in tens of grams) and with lower occurrence stability, while in EF always in thousands of grams and with high occurrence stability (Tables 2 and 3).

Additional species creating the assemblage of cluster AB were Ukrainian lamprey and roach. The relative biomass of the latter was two orders of magnitude lower there than in EF, while biomass of the former species assumed similar values in both clusters. In cluster AB eight species, which were absent

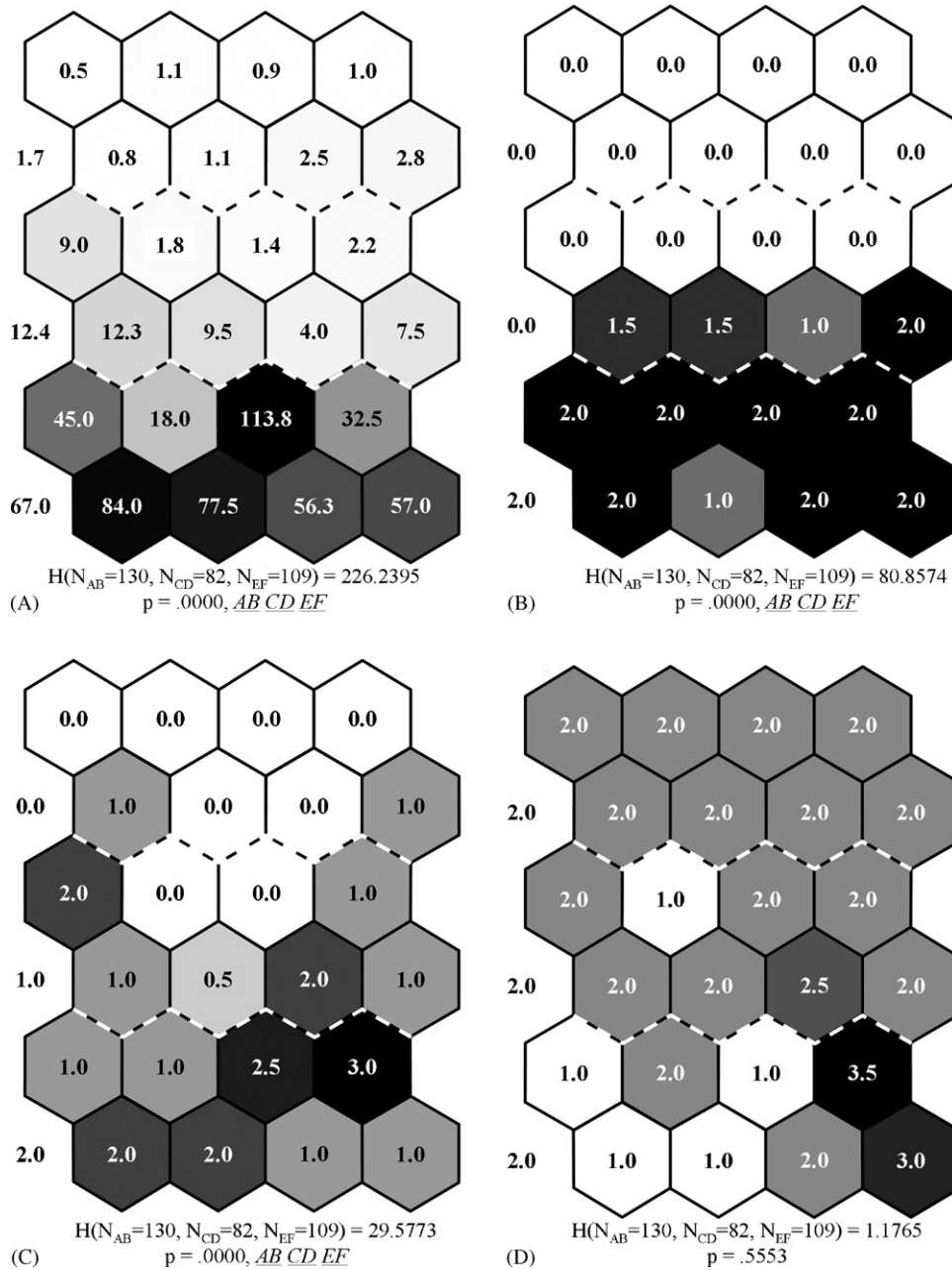


Fig. 4 – Environmental variables (not presented to the SOM) compared between clusters. (A) Product of depth and width (m²); (B) index of river naturalness (2: natural meandering, 1: not meandering but without signs of recent regulation, 0: regulated); (C) trees along banks (0: none, 1: little, 2: common, 3: abundant); (D) number of types of hiding places for fish. Explanations: Dark represents high values. Dashed lines show boundaries between clusters of neurons. Symbols for the clusters are the same as in Fig. 2. For each neuron a median is given. Medians for clusters are visible on the left side of SOM. Comparisons were made with use of the Kruskal–Wallis test. Between clusters of neurons underlined with the same line no significant difference was recorded.

in two neurons, were recorded: mud loach, minnow, brown trout, gibel, dace, perch, spined loach and sunbleak (Table 2). Among them minnow and brown trout reached their highest relative biomass in some samples from clean tributaries of the Białostocka Upland and the Pisa River.

Species absent in only one neuron in cluster EF were Ukrainian lamprey, loach, dace, chub and spined loach, and this concerns neurons E1, E2 and E3 (Table 2), containing

mainly samples from more polluted reaches of the Narew River. Gudgeon, silver bream and eel were absent in some E neurons, and gudgeon additionally in F2. It should be underlined that only roach reached occurrence stability equal 100% in cluster EF, whereas pike was absent at one site of neuron E1 (92% of occurrence stability) (Table 3). The occurrence of perch and burbot was <100% in two and three neurons, respectively. Other dominants creating the frame of the distinguished two

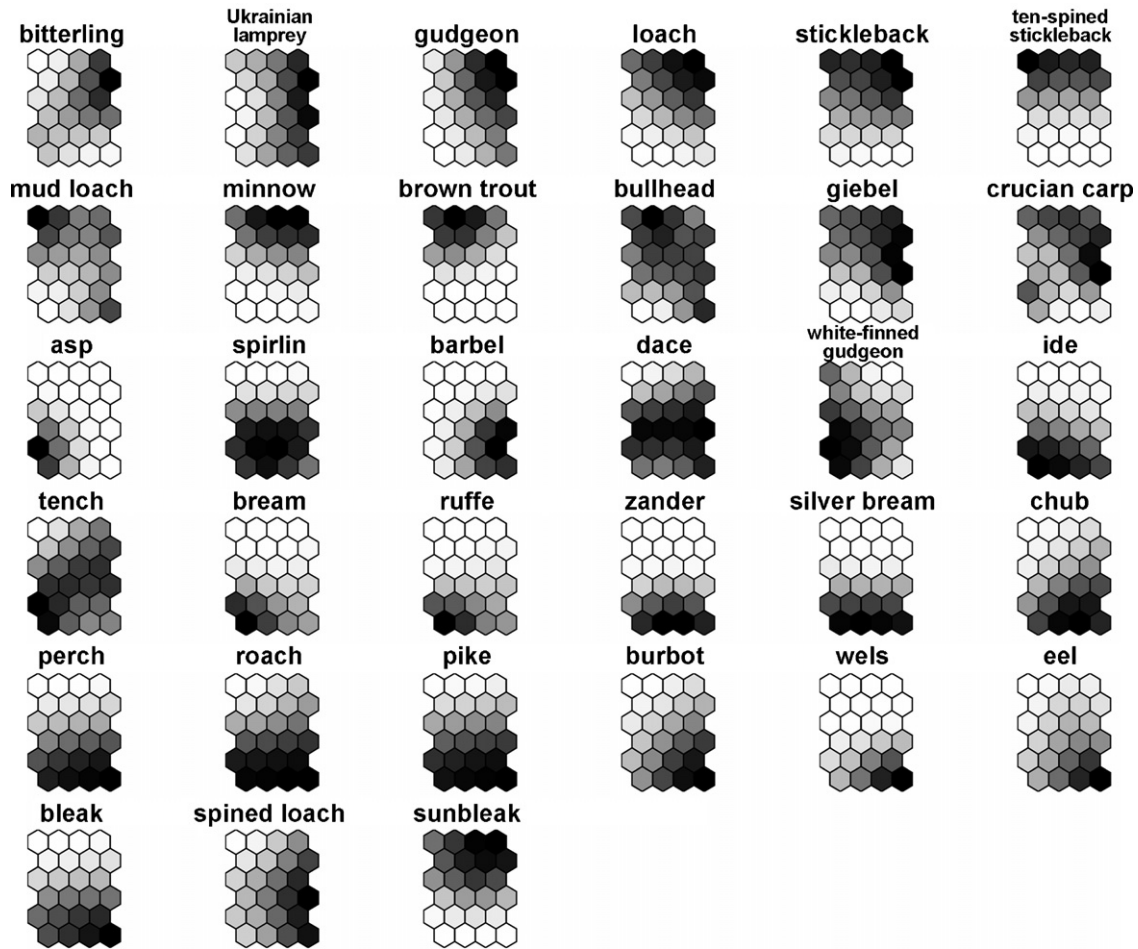


Fig. 5 – Importance of 33 fish species on SOM listed according to the most activated regions of SOM. Dark (normalised for a given species) represents high values. Symbols for the neurons are the same as in Fig. 2.

Table 2 – Species participating in creation of repeatable fish assemblages in the Narew River system in the distinguished by SOM two most distinct clusters AB and EF

Cluster AB (eight neurons)			Cluster EF (eight neurons)		
Species	Neurons without species	Biomass (g)	Species	Neurons without species	Biomass (g)
Gudgeon		xxx ₃	Stickleback		x
Loach		xx-xxx	Ide		xxxx-xxxxx ₁
Stickleback		xx ₂	Perch		xxxx ₃
Ten-spined stickleback		x-xx	Roach		xxxx-xxxxx
Pike		xx-xxx ₂	Pike		xxxx
Ukrainian lamprey	B2	xx ₂ ¹	Burbot		xxx-xxxx ₂
Roach	A2	xx-xxx ₂	Bleak		xxx ₂
Mud loach	A3, B3	xx ₁	Ukrainian lamprey	E1	x-xx
Minnow	A1, B1	x-xx ¹	Loach	E3	x ¹
Brown trout	B3, B4	xx ₁ ¹	Dace	E3	xx-xxx ₂
Gibel	B1, B3	x	Chub	E1	xxxx ₃
Dace	A2, B1	x ¹	Spined loach	E2	x-xx ¹
Perch	A2, B2	x-xx	Gudgeon	E2, F2	x-xx ¹
Spined loach	A2, B2	x-xx	Silver bream	E2, E3	xxx ₁ ¹
Sunbleak	A2, B3	x	Eel	E1, E3	xxx ₁
			Bream	E2, E3, E4	xx-xxx

Order of biomass magnitude is presented only: x, grams; xx, tens of grams; xxx, hundreds of grams; xxxx, kilograms; xxxxx, tens of kilograms; subscript, number of exceptions with lower biomass; superscript, number of exceptions with biomass higher than presented. Species listed according to the number of neurons they are absent in.

Table 3 – Occurrence stability (%) of the 33 studied fish and lamprey species within SOM output neurons

Neuron	Number of samples	Species															
		Bitterling	Ukrainian lamprey	Gudgeon	Loach	Stickleback	Ten-spined stickleback	Mud loach	Minnow	Brown trout	Bullhead	Giebel	Crucian carp	Asp	Spirilin	Barbel	Dace
A1	32		16	9	63	88	100	41		3		3	6				3
A2	15		47	47	100	80	80	33	53	60	53	7	7				
A3	25		28	96	100	76	80		12	20	4	4	16				4
A4	21	24	43	100	100	95	76	24	24	5		10					5
B1	11	9	9	18	45	64	64	9		27							
B2	6			100	50	50	67	33	17	17	17	17					17
B3	7		43	100	100	71	29		14								14
B4	13	62	69	100	100	100	69	46	15		31	8	8				38
C1	17		6	18	12	12	12	6				6					12
C2	5		20	20	100	60		20			40						40
C3	11	18	18	91	73	82	18	9	9		9						27
C4	14	21	50	93	86	71	43	7			14	14	14			7	43
D1	10		20	10	40	70	20	20			30					40	70
D2	8	13	13	63	25	63	13				13						38
D3	6	17	33	17	67	67					17					33	17
D4	11	9	82	73	91	45	9	27	9		9	18	18			9	27
E1	13	15		31	8	15					8		15	23			15
E2	5		20		40	40											40
E3	2		100	100		50											50
E4	8		13	63	13	50					13					25	25
F1	21	5	14	14	14	14								5			10
F2	18		17		6	11										11	11
F3	20		40	25	15	5		10								5	5
F4	22		32	77	27	9	5	36			23						32

Neuron	Number of samples	Species															
		White-finned gudgeon	Ide	Tench	Bream	Ruffe	Zander	Silver bream	Chub	Perch	Roach	Pike	Burbot	Wels	Eel	Bleak	Spined loach
A1	32	16								3	3	9	3		3	3	6
A2	15											27					
A3	25			4						4	12	4	4			4	20
A4	21			10					5	5	48	10	14		5	33	10
B1	11			9						36	9	27				9	27
B2	6		17						17		33	67					17
B3	7			14						14	57	57	14	14		14	
B4	13			15					23	38	85	69	46		8	62	31
C1	17	12		12			6			24	59	53	12		12	12	6
C2	5			20	20				20	40	20	80	40			80	
C3	11			18	18					45	64	73	45	36	9	27	
C4	14	7		21	7		7		14	36	86	64	71		36	79	27
D1	10	40		70	10					70	100	70	20		50	10	
D2	8	13		13	13				13	88	100	100	38		88	50	
D3	6	17		17	17				50	100	100	83	83		67	50	
D4	11	9		9	18	9	9	18	18	82	100	100	100		18	100	
E1	13	8		100	15	15		38		69	100	92	31		31	15	
E2	5	20		100					20	100	100	100	60	20	100		
E3	2			100					50	100	100	100	100		100	50	
E4	8			25			13	13	50	100	100	100	88	25	63	50	
F1	21	14		95	14	33	62	5	14	100	100	100	19	10	5	48	10
F2	18	11		94		17	33	17	39	94	100	100	100	6	11	61	6
F3	20			95	5	5		5	35	100	100	100	100	15	20	55	45
F4	22			55	5	9	14	5	9	100	100	100	100	14	32	82	59

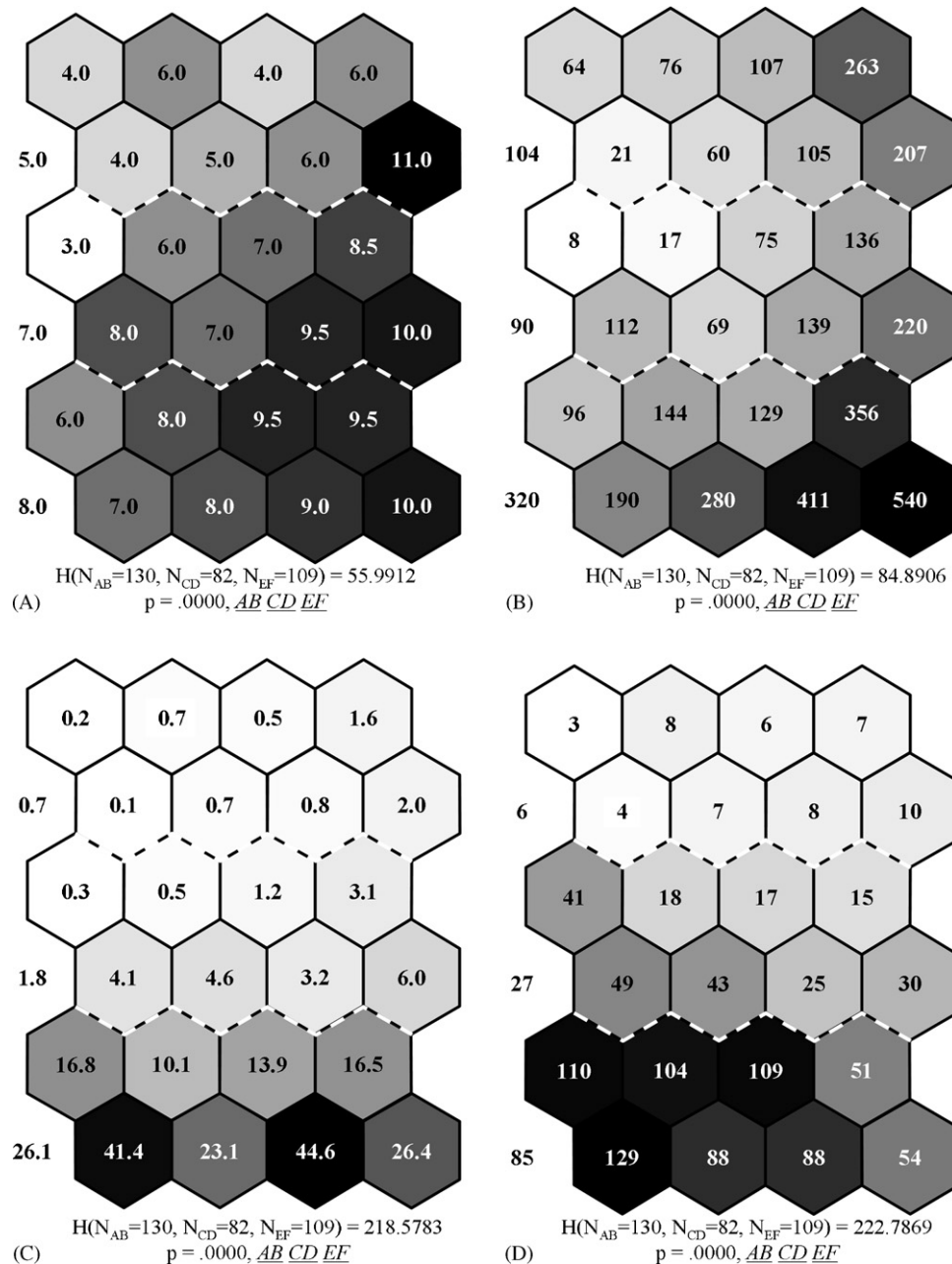


Fig. 6 – Assemblage variables compared between clusters: (A) number of species in a sample; (B) number of fish collected (CPUE); (C) fish relative biomass (kg); (D) mean body weight of a specimen (g). Explanations as in Fig. 4.

assemblages were characterized by occurrence stability values much lower than 100% (Table 3). Cluster CD, because of its intermediate character, does not have any exclusive species (Fig. 5, Table 3).

The clusters also differ significantly in the number of species and the total relative biomass, exhibiting a clear vertical gradient (Fig. 6A and C). Along with increase in river size (Fig. 4A), an increase in both variables was observed. The fish number collected at sites was significantly highest in cluster EF, but the difference between clusters AB and CD was insignificant (Fig. 6B) despite the fact that the CD sites were located on streams on average seven times larger than those of AB (Fig. 4A). Fish mean body weight, complying with expectation,

increased with river size (Fig. 4A) and differences between the three clusters were significant (Fig. 6D).

The main channel sites retained little or no rheophils, whose biggest contribution to fish assemblages was recorded in cluster AB, in streams located on the Białostocka Upland, in the Pisa River system, and partly in the Kurpiowska Plainland in the Omulew, Orzyc and Pełta Rivers (Fig. 7A). Conversely, the significantly biggest contribution of facultative riverine fish to assemblages was in cluster EF, and decreased successively from the bottom to the top of the SOM (Fig. 7B).

The significantly lowest median of the Shannon index of biodiversity was recorded in cluster AB, that is for the small-

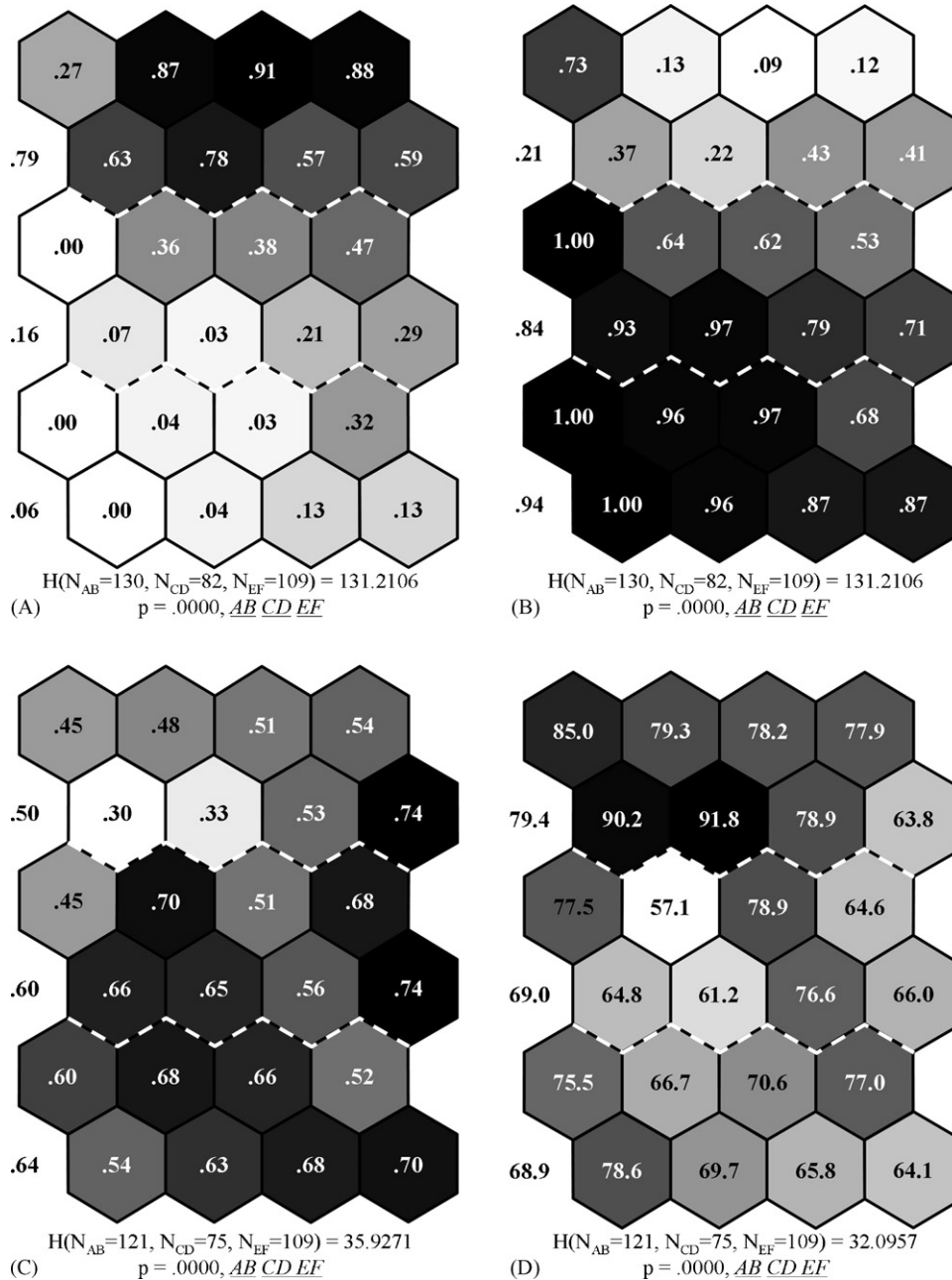


Fig. 7 – Assemblage variables compared between clusters: (A) the contribution of biomass of rheophilic species to the total biomass; (B) the contribution of biomass of facultative riverine species to the total biomass; (C) Shannon index of biodiversity (samples with less than three species were excluded); (D) community dominance index (CDI) (%) (samples with less than three species were excluded). Explanations as in Fig. 4.

est streams (Fig. 7C). The lowest species richness in cluster AB (Fig. 6A) was accompanied by a high median (79.4%) of the community dominance index (CDI, i.e. the contribution of the two most dominant species to the total number of specimens) (Fig. 7D). The CDI values in CD and EF were similar and significantly lower from AB (Fig. 7D).

Some of the environmental and assemblage variables also showed a quite distinct horizontal gradient within each cluster (Fig. 6A–D). In AB an increase in stream size (from the left to the right of SOM) (Fig. 4A) was accompanied by an increase in species richness, number of specimens and total

biomass, mean body weight of a specimen and the Shannon index (Figs. 6A–D and 7C) and by a decrease in the CDI index (Fig. 7D). In CD and EF in larger streams and rivers (left side of SOM) (Fig. 4A) on the one hand bigger specimen were caught (Fig. 6D), but on the other hand fewer species, including rheophils, and fewer specimens were recorded (Figs. 6A and B and 7A). Moreover, in EF samples assigned to the left side of SOM were coming from ecomorphologically simplified sites, i.e., with fewer hiding places (Fig. 4D) and, to some extent, fewer trees on banks (Fig. 4C). The existence of these horizontal gradients was confirmed by the cluster anal-

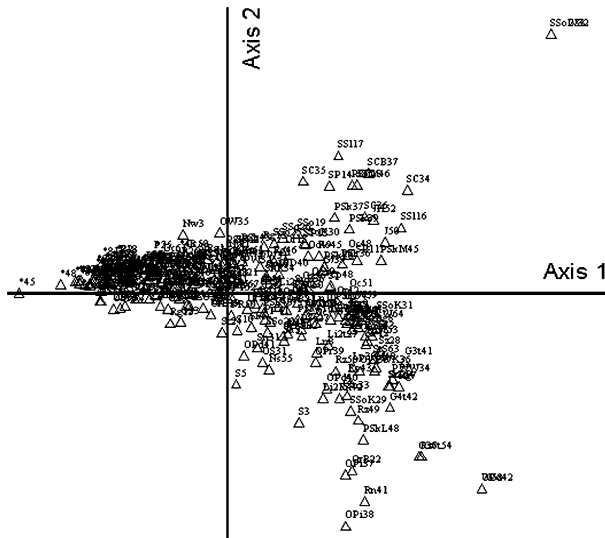


Fig. 8 – Sites from the Narew River system ordered by DCA on the basis of relative biomass of fish species. Codes for sites are explained in Table 1.

ysis, which divided each cluster into the left (AB1, CD1, EF1) and right (AB2, CD2, EF2) halves (Fig. 2).

The DCA (DECORANA) after logarithmic transformation of relative biomass data, and general relativization provided a scatterplot with over 250 sites (including all sites from the Narew) forming an elliptic ‘black cloud’, in which sites and their codes are illegible (Fig. 8). Outside of the ‘black cloud’ there are only some sites from the rivers of the Białostocka Upland and the Kurpiowska Plainland.

The DCA scatterplot for species is not clear, either (Fig. 9). Species are freely dispersed without a clearly determined pattern in the multivariate space of the scatterplot. Moreover, the scatterplot presents data for all 321 sites analysed together, hence we cannot read what is a given species importance in different parts of the Narew River system. The importance of each species was however clearly visible in the clusters distinguished by SOM (Fig. 5).

4. Discussion

SOM, just on the basis of fish relative biomass, effectively grouped samples differing also in other variables not directly analysed by SOM, both environmental (Fig. 4A–C) and assemblage ones (Figs. 6B and D and 7A–D). The three clusters exhibit the most distinct differences (vertical gradient), while within each cluster a further horizontal, more subtle gradient is observed. In small streams (cluster AB) the limiting factor was stream size and probably resulting from its problems with food base and instability of environment, e.g. periodical lack of water flow in summers or frost penetration in winters (Horowitz, 1978). This is why increase in stream size in AB (from the left to the right of SOM) (Fig. 4A) led to improvement in assemblage variables (Figs. 6A–D and 7A–D). In CD and EF for larger streams and rivers (left side of SOM) (Fig. 4A) many assemblage variables worsened (Figs. 6A and B and 7A). However, for these larger streams and rivers the channel size is not a limiting factor. In general, larger water bodies that we studied were more human-impacted. On the right side of SOM in CD and EF there are samples from the upper Narew, Narew near backwater, mouth sections of some left-side tributaries

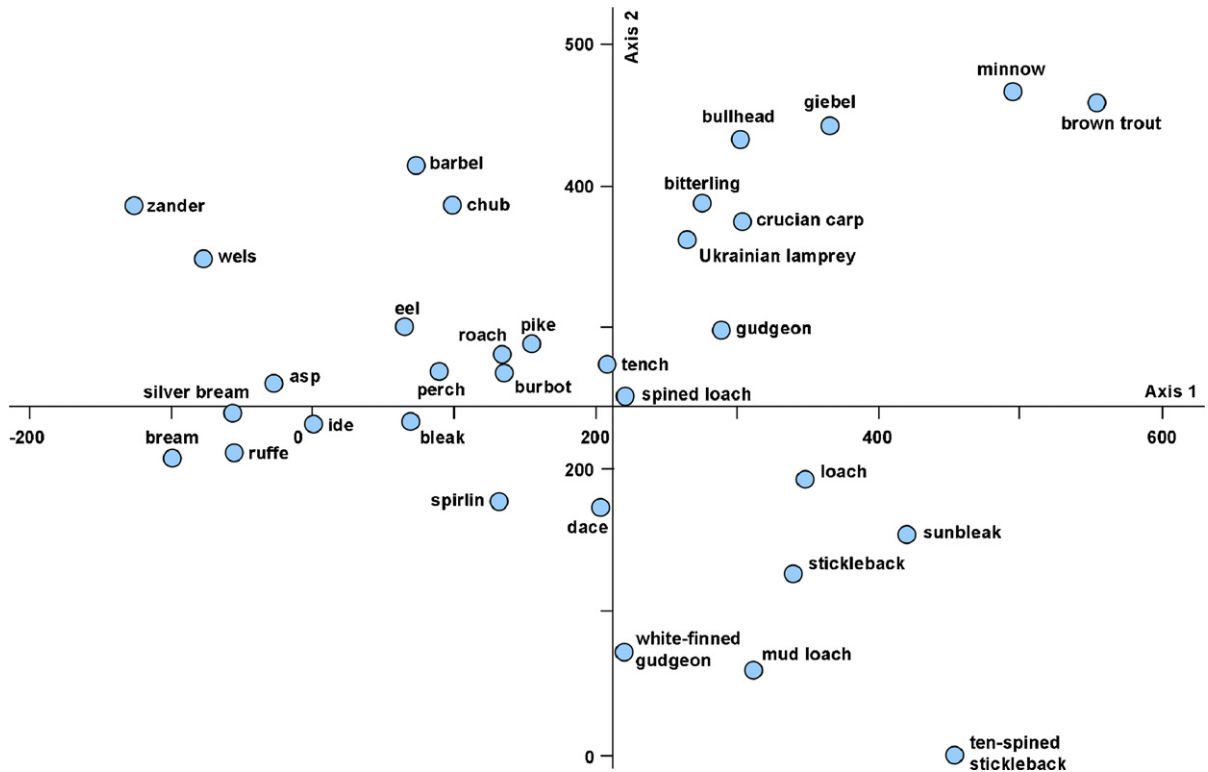


Fig. 9 – Species sampled in the Narew River system on the multivariate space of DCA.

and other small streams, the Pisa system and the Orzyc River (Fig. 3). All of them were little modified as far as both channel structure (Fig. 4C and D) and water chemistry (Penczak et al., 1990a, 1990b, 1991a, 1991b, 1992) are concerned.

In this study few environmental variables have displayed significant relationship with fish assemblages, perhaps because their cumulative effect in many rivers' reaches masks their separate roles (Northcote et al., 1985). Rose (2000), while analysing this problem in detail, stated that quantitative relationships between environmental quality and fish populations are elusive, controversial and difficult to determine. Mahon and Smith (1989) stated that fish species on the Scotian Shelf are distributed independently on environmental gradients if assemblages consist of highly co-evolved, interdependent species.

In cluster AB we distinguished an assemblage with five species present in each hexagon (gudgeon, loach, stickleback, ten-spined stickleback and pike), and in EF with seven ones (stickleback, ide, perch, roach, pike, burbot and bleak), but occurrence stability in each hexagon equal 100% was recorded only for roach in cluster EF (Table 3). The two fish assemblages are characterized by 'repeatable occurrence' (Tyler et al., 1982). Their credibility is confirmed by the described effective classification obtained with SOM.

For the two fish assemblages distinguished in clusters AB and EF there are two common species: pike and stickleback, though their contribution to the total relative biomass in clusters AB and EF is not the same. The median relative biomass of pike in hexagons of cluster AB is in the range 5.5–338.8 g, while in EF 3086.5–7045.8 g. Stickleback in hexagons AB and EF has median relative biomass in the ranges 3.5–93.0 and 0.1–3.0 g, respectively. Their importance in energy flow through fish populations, in the two clusters, is thus considerably different (Odum, 1980; Wootton, 1990). This is comprehensible because cluster AB contains samples from small streams (Fig. 4A), settled mainly by small short living species (Table 2), while cluster EF has gathered sites from the main channel and lower courses of the biggest tributaries, where large, long living species are representative and dominant (Lamouroux et al., 2002).

Presumably, before the impact of human stressors, the Narew River had the same dominant and subdominant species along its whole course, and only rare ones were varying in number and distribution according to subtle differences in the dimension and character of the channel (Matthews and Robison, 1998; Marsh-Matthews and Matthews, 2000; Silva Abes and Agostinho, 2001). Such an expectation is supported by the fact that the Narew sites *8–26 (upper course) and *76–86 (close to the backwater) have a similar ichthyofauna composition (neurons F2–F4, Fig. 3). Downstream of the Orłanka River outlet the number of lithophilic species and their abundance in the main channel has begun slightly decreasing (first slight human impact). Downstream of the Szeroka Struga River, receiving pollutants from a sugar-factory sewer, qualitative losses in lithophils were very conspicuous. Similarly, from the outlet of the Supraśl River, collecting sewage of the large city of Białystok via the Biała River, lithophils were absent in the Narew, and many representatives of other spawning guilds were endangered or already extirpated. Most fish samples from this river fragment were

assigned to the neuron D1 located far from the neurons F2–F4 (Fig. 3). Some improvement in species richness and fish abundance is visible downstream of the Biebrza River outlet, but lithophils appeared again in the channel from the Orzyc River outlet, and were also present in the Narew reach close to the backwater of the Zegrzyński Reservoir. As water quality was improving, the samples were assigned to neurons located closer to F2–F4 (mainly in E1 and F1) or even in F2–F4 (Fig. 3), which is another reflection of the horizontal gradients, well visible also in the distribution of lithophils over SOM (Fig. 5).

Do distinguished by us fish assemblages are repeatable in other lowland Polish rivers investigated at a similar time? Grossman (1982) stated that deterministic assemblages should be characterized by persistence. However, an assemblage is defined by two properties: persistence (i.e., presence or absence of a given species) and stability (i.e., relative constancy of species abundance over time). Hence, in this definition 'stability' has quantitative values, but 'persistence' is qualitative (Meffle and Berra, 1988). Despite the fact that fish populations apply migration tactics during environmental perturbation (Stott and Buckley, 1979), only serious long-lasting perturbation of the environment, such as sewage input or extended engineering, can have a permanent effect on respective assemblages (Przybylski, 1994). Thus, it is easy to distinguish fish assemblages on the basis of persistence, but on the basis of stability it is rather difficult. In other lowland river systems in Poland the assemblage from cluster EF (stickleback, ide, perch, roach, pike, burbot and bleak) was recorded in the lower course of the Gwda River (Penczak et al., 1998), in the Noteć River below the Drawa tributary (Penczak et al., 1999), in the Warta River downstream of the city of Poznań (Kruk et al., 2000), in the lower course of the Nida River (Penczak, 1972) and at 7 out of 38 sites of the Biebrza River system (Witkowski, 1984). If we could accept the lack of one or two species (mainly burbot and/or ide) in the assemblage, then much more Polish rivers would be listed here, including the Pilica River system (Penczak et al., 2005).

The assemblage with gudgeon, loach, stickleback, ten-spined stickleback and pike, distinguished in cluster AB, was quite frequently repeatable in small streams of the Narew River system, including small tributaries of the Biebrza River (Witkowski, 1984). However, in other Polish lowland rivers such an assemblage was found in two rivers from the Bzura River system (Czarnawka and Skierniewka) (Penczak et al., 2000) and in the Wkra River system (Penczak et al., 2001; Marszał et al., 2005). In the Pilica and Warta River systems the assemblage without ten-spined stickleback was recorded at many sites (Penczak, 1969; Kostrzewa et al., 2001).

In general, DCA provides good results for sedentary species (rich literature on this subject for plants) but not for migratory ones, as fish for example. In case of plants, if in a multivariate space of DCA the distance of over 4S.D. between two sites or two groups of sites is recorded, the latter do not contain common species (Gauch, 1982). For fish, cases of site pairs sharing several species in common are recorded when the sites are located at a distance of even 6S.D. (Penczak et al., 2003). This is an important proof that such rich data as in this study restrain the interpretation of scatterplots in DCA and other gradient analyses (Brosse et al., 2001; Giraudel

and Lek, 2001). Additionally, in scatterplots the position of a species in a multivariate space is presented with a single point, whose position is determined on the basis of all fish samples. SOM provides the information on species distribution in form of a gradient over plane, that is for each neuron (and sites assigned to it). This much more detailed way of visualizing results, allows to analyse mutual relations between species and changes in species importance in different parts of SOM, thus being much more useful for coenological studies. In the latter book, edited by Lek et al. (2005), this and a few other drawbacks, while applying DCA, were

pointed out in the case of fish, macroinvertebrates and other organisms.

Acknowledgements

The authors thank very much Professor Tae-Soo Chon and two anonymous referees for helpful comments on the manuscript. We thank Łukasz Głowacki for English improvements. Field research was financially supported by the Polish Anglers Association and the University of Łódź.

Appendix A

List of fish species recorded in the Narew river system; reproductive guilds according to Balon (1990):

Non-guarding and open substratum egg scattering (A.1)

Pelagophil (A.1.1.)	<i>Anguilla anguilla</i> (L.)	Eel
Lithopelagophil (A.1.2)	<i>Lota lota</i> (L.)	Burbot
Lithophil (A.1.3)	<i>Phoxinus phoxinus</i> (L.)	Minnow
	<i>Alburnoides bipunctatus</i> (Bloch)	Spirlin
	<i>Aspius aspius</i> (L.)	Asp
	<i>Chondrostoma nasus</i> (L.)	Nase
	<i>Barbus barbus</i> (L.)	Barbel
	<i>Leuciscus cephalus</i> (L.)	Chub
Phytolithophils (A.1.4)	<i>Leuciscus leuciscus</i> (L.)	Dace
	<i>Leuciscus idus</i> (L.)	Ide
	<i>Rutilus rutilus</i> (L.)	Roach
	<i>Alburnus alburnus</i> (L.)	Bleak
	<i>Abramis brama</i> (L.)	Bream
	<i>Blicca bjoerkna</i> (L.)	Silver bream
	<i>Perca fluviatilis</i> L.	Perch
	<i>Gymnocephalus cernuus</i> (L.)	Ruffe
Phytophils (A.1.5)	<i>Esox lucius</i> L.	Pike
	<i>Scardinius erythrophthalmus</i> (L.)	Rudd
	<i>Tinca tinca</i> (L.)	Tench
	<i>Cyprinus carpio</i> L.	Carp
	<i>Carassius carassius</i> (L.)	Crucian carp
	<i>Carassius auratus gibelio</i> (Bloch)	Gibel
	<i>Misgurnus fossilis</i> (L.)	Mud loach
	<i>Cobitis taenia</i> (L.)	Spined loach
Psammophils (A.1.6)	<i>Barbatula barbatula</i> (L.)	Loach
	<i>Gobio gobio</i> (L.)	Gudgeon
	<i>Gobio albipinnatus</i> Lukasz	White-finned gudgeon
Non-guarding and brood hiding (A.2)		
Lithophil (A.2.3)	<i>Salmo trutta</i> L.	Brown trout
	<i>Eudontomyzon mariae</i> (Berg)	Ukrainian lamprey
Ostracophil (A.2.4)	<i>Rhodeus sericeus</i> (Pallas)	Bitterling
Guarding and clutch tending (B.1)		
Phytophils (B.1.4)	<i>Leucaspis delineatus</i> (Heckel)	Sunbleak
	<i>Silurus glanis</i> L.	Wels
Guarding and nesting (B.2)		
Ariadnophils (B.2.4)	<i>Gasterosteus aculeatus</i> L.	Stickleback
	<i>Pungitius pungitius</i> (L.)	Ten-spined stickleback
Phytophil (B.2.5)	<i>Stizostedion lucioperca</i> (L.)	Zander
Speleophil (B.2.7)	<i>Cottus gobio</i> L.	Bullhead

REFERENCES

- Aguilera, P.A., Garrido Frenich, A., Torres, J.A., Castro, H., Martinez Vidal, J.L., Canton, M., 2001. Application of the Kohonen neural network in coastal water management: methodological development for the assessment and prediction of water quality. *Water Res.* 35, 4053–4062.
- Backiel, T., Penczak, T., 1989. The fish and fisheries in the Vistula River and its tributary, the Pilica River. In: Dodge, D.P. (Ed.), *Proceedings of the International Large River Symposium*, Honey Harbour, Ontario, Canada. *Can. Spec. Publ. Fish. Aquat. Sci.*, pp. 488–503.
- Balon, E.K., 1990. Epigenesis of an epigeneticist: the development of some alternative concepts on the early ontogeny and evolution of fishes. *Guelph Ichthyol. Rev.* 1, 1–48.
- Brosse, S., Giraudel, J.L., Lek, S., 2001. Utilization of non-supervised neural networks and principal component analysis to study fish assemblages. *Ecol. Modell.* 146, 159–166.
- Casselman, J.M., Penczak, T., Carl, L., Mann, R.H.K., Holcik, J., Woitowich, W.A., 1990. An evaluation of fish sampling methodologies for large river systems. *Pol. Arch. Hydrobiol.* 37, 521–551.
- Cho, S.B., 1997. Self-organizing map with dynamical node-splitting: application to handwritten digit recognition. *Neural Comput.* 9, 1345–1355.
- Chon, T.S., Park, Y.S., Moon, K.H., Cha, E.Y., 1996. Patternizing communities by using an artificial neural network. *Ecol. Modell.* 90, 69–78.
- Chon, T.S., Park, Y.S., Park, J.H., 2000. Determining temporal pattern of community dynamics by using unsupervised learning algorithms. *Ecol. Modell.* 132, 151–166.
- Connell, J.H., 1975. Some mechanisms producing structure in natural communities: a model and some evidence from field experiments. In: Cody, M.L., Diamond, J.M. (Eds.), *Ecology and Evolution of Communities*. Belknap, Cambridge, MA, pp. 460–490.
- Echelle, A.A., Echelle, A.F., Hill, L.G., 1972. Interspecific interactions and limiting factors of abundance and distribution. I. The Red River pupfish, *Cyprinodon rubrofluvialtilis*. *Am. Midl. Nat.* 88, 109–130.
- Gauch, H.G., 1982. *Multivariate Analysis in Community Ecology*. Cambridge University Press, Cambridge.
- Gevrey, M., Park, Y.S., Oberdorff, T., Lek, S., 2005. Predicting fish assemblages in France and evaluating the influence of their environmental variables. In: Lek, S., Scardi, M., Verdonschot, P.F.M., Descy, J.P., Park, Y.S. (Eds.), *Modelling Community Structure in Freshwater Ecosystems*. Springer-Verlag, Berlin, pp. 54–63.
- Giraudel, J.L., Lek, S., 2001. A comparison of self-organizing map algorithm and some conventional statistical methods for ecological community ordination. *Ecol. Modell.* 146, 329–339.
- Giraudel, J.L., Aurelle, D., Berrebi, P., Lek, S., 2000. Application of the self-organizing mapping and fuzzy clustering microsatellite data: how to detect genetic structure in brown trout (*Salmo trutta*) populations. In: Lek, S., Guegan, J.F. (Eds.), *Artificial Neural Networks: Application to Ecology and Evolution*, Environmental Science. Springer, Berlin, pp. 187–202.
- Głowacki, Ł., Penczak, T., 2005. Species richness estimators applied to fish in a small tropical river sampled by conventional methods and rotenone. *Aquat. Living Resour.* 18, 159–168.
- Grossman, G.D., 1982. Dynamics and organization of a rocky intertidal fish assemblage: the persistence and resilience of taxocene structure. *Am. Nat.* 119, 611–637.
- Grossman, G.D., Moyle, P.B., Whitaker, J.O., 1982. Stochasticity in structural and functional characteristics of an Indiana stream fish assemblage: a test of community theory. *Am. Nat.* 120, 423–454.
- Hill, M.O., 1979. DECORANA—a FORTRAN program for detrended correspondence analysis and reciprocal averaging. In: *Ecology and Systematics*. Cornell University, Ithaca, NY.
- Horowitz, A.J., 1978. Temporal variability patterns and the distributional patterns of stream fishes. *Ecol. Monogr.* 48, 307–321.
- Irz, P., Odion, M., Argillier, C., Pont, D., 2006. Comparison between the fish communities of lakes, reservoirs and rivers: can natural systems help define the ecological potential of reservoirs? *Aquat. Sci.* 68, 109–116.
- Jackson, D.A., Peres-Neto, P.R., Olden, J.D., 2001. What controls who is where in freshwater fish communities—the roles of biotic, abiotic and spatial factors. *Can. J. Fish. Aquat. Sci.* 58, 157–170.
- James, F.C., McCulloch, C.E., 1990. Multivariate analysis in ecology and systematics: Panacea or Pandora's Box? *Annu. Rev. Ecol. Syst.* 21, 129–166.
- Johnson, M.G., Leach, J.H., Minns, C.K., Olver, C.H., 1977. Limnological characteristics of Ontario lakes in relation to associations of walleye (*Stizostedion vitreum vitreum*), northern pike (*Esox lucius*), lake trout (*Salvelinus namaycush*), and small-mouth bass (*Micropterus dolomieu*). *J. Fish. Res. Board Can.* 34, 1592–1601.
- Kohonen, T., 1982. Self-organized formation of topologically correct feature maps. *Biol. Cybern.* 43, 59–69.
- Kohonen, T., 2001. *Self-organizing Maps*, Third Extended Edition. Springer, Berlin.
- Kostrzewa, J., Penczak, T., Koszaliński, H., Marszał, L., Kruk, A., Tłoczek, K., 2001. Fish fauna of the Liswarta River drainage basin. *Sci. Annu. Polish Anglers Assoc.* 14, 19–38 (in Polish, with English summary).
- Kruk, A., 2004. Decline in migratory fish in the Warta River, Poland. *Ecohydrol. Hydrobiol.* 2, 147–155.
- Kruk, A., 2006. Self-organizing maps in revealing variation in non obligatory riverine fish in long-term data. *Hydrobiologia* 553, 43–57.
- Kruk, A., Penczak, T., 2003. Impoundment impact on populations of facultative riverine fish. *Ann. Limnol.: Int. J. Lim.* 39, 197–210.
- Kruk, A., Penczak, T., Galicka, W., Koszaliński, H., Tłoczek, K., Kostrzewa, J., Marszał, L., 2000. Fish fauna of the Warta River. *Sci. Annu. Polish Anglers Assoc.* 13, 35–67 (in Polish, with English summary).
- Lamouroux, N., Poff, N.L., Angermeier, P.L., 2002. Intercontinental convergence of stream fish community traits along geomorphic and hydraulic gradients. *Ecology* 83, 1792–1807.
- Lek, S., 2005. Fish community assemblages. In: Lek, S., Scardi, M., Verdonschot, P.F.M., Descy, J.P., Park, Y.S. (Eds.), *Modelling Community Structure in Freshwater Ecosystems*. Springer-Verlag, Berlin, pp. 41–42.
- Lek, S., Guegan, J.F. (Eds.), 2000. *Artificial Neuronal Networks: Application to Ecology and Evolution*. Springer, Berlin.
- Lek, S., Scardi, M., Verdonschot, P.F.M., Descy, J.P., Park, Y.S. (Eds.), 2005. *Modelling Community Structure in Freshwater Ecosystems*. Springer-Verlag, Berlin.
- Mahon, R., Smith, R.W., 1989. Demersal fish assemblages on the Scotian Shelf. Northwest Atlantic: spatial distribution and persistence. *Can. J. Fish. Aquat. Sci.* 46 (Suppl. 1), 134–152.
- Marsh-Matthews, E., Matthews, W.J., 2000. Geographic, terrestrial and aquatic factors: which most influence the structure of stream fish assemblages in the midwestern United States? *Ecol. Freshwater Fish* 9, 9–21.
- Marszał, L., Kruk, A., Koszaliński, H., Tybulczuk, S., Zięba, G., Grabowska, J., Penczak, T., 2005. Fish fauna of the Wkra River system. Part II. Tributaries. *Sci. Annu. Polish Anglers Assoc.* 18, 5–28 (in Polish, with English summary).

- Matthews, W.J., 1998. Patterns in Freshwater Fish Ecology. Chapman & Hall, Int. Thomson Publ., New York.
- Matthews, W.J., Robison, H.W., 1998. Influence of drainage connectivity, drainage area and regional species richness on fishes of the interior highlands in Arkansas. *Am. Midl. Nat.* 139, 1–19.
- McCune, B., Mefford, M.J., 1992. *PcOrd: multivariate analysis of ecological data*, Version 2.0. Oregon, Glenden Beach, MjM Software Design.
- Meffle, G.K., Berra, T.M., 1988. Temporal characteristics of fish assemblage structure in an Ohio stream. *Copeia* 1988, 684–690.
- Mills, E.L., 1969. The community concept in marine zoology, with comments on continua and instability in some communities: a review. *J. Fish. Res. Board Can.* 26, 1415–1428.
- Moyle, P.B., 1994. Biodiversity, biomonitoring and structure of stream fish communities. In: Loeb, S.L., Spacie, A. (Eds.), *Biological Monitoring of Aquatic Systems*. Lewis Publisher, Boca Raton, pp. 171–186.
- Moyle, P.B., Herbold, B., 1987. Life-history patterns and community structure in stream fishes of western North America: comparisons with eastern North America and Europe. In: Matthews, W.J., Heins, D.C. (Eds.), *Community and Evolutionary Ecology of North American Stream Fishes*. University of Oklahoma Press, Oklahoma, pp. 25–32.
- Murawski, S.A., 1983. Mixed-species yield-per-recruitment analyses accounting for technological interactions. *Can. J. Fish. Aquat. Sci.* 41, 897–916.
- Northcote, T.G., Arcifa, M.S., Froehlich, O., 1985. Effects of impoundment and drawdown on the fish community of a South American river. *Verh. Int. Ver. Limnol.* 22, 2704–2711.
- Oberdorff, T., Pont, D., Hugueny, B., Chessel, D., 2001. A probabilistic model characterizing fish assemblages of French rivers: a framework for environmental assessment. *Freshw. Biol.* 46, 399–415.
- Odum, E.P., 1980. *Ecology*. Holt-Saunders, London.
- Orth, D.J., 1980. Changes in the fish community of Lake Carl Blackwell Oklahoma (1967–1977) and a test of the reproductive guild concept. *Proc. Okla. Acad. Sci.* 60, 10–17.
- Orth, D.J., White, R.J., 1993. Stream habitat management. In: Kohler, C.C., Hubert, W.A. (Eds.), *Inland Fisheries Management in North America*. American Fisheries Society, Blacksburg, pp. 205–230.
- Palmer, M., 2000. Ordination methods for ecologists. <http://www.okstate.edu/artsci/botany/ordinate>.
- Park, Y.S., Kwak, I.S., Chon, T.S., Kim, J.K., Jørgensen, S.E., 2001. Implementation of artificial neural networks in patterning and prediction of exergy in response to temporal dynamics of benthic macroinvertebrate communities in streams. *Ecol. Modell.* 146, 143–157.
- Park, Y.S., Céréghino, R., Compin, A., Lek, S., 2003. Applications of artificial neural networks for patterning and predicting aquatic insect species richness in running waters. *Ecol. Modell.* 160, 265–280.
- Park, Y.S., Oberdorff, T., Lek, S., 2005a. Patterning riverine fish assemblages using an unsupervised neural network. In: Lek, S., Scardi, M., Verdonschot, P.F.M., Descy, J.P., Park, Y.S. (Eds.), *Modelling Community Structure in Freshwater Ecosystems*. Springer-Verlag, Berlin, pp. 43–53.
- Park, Y.S., Verdonschot, P.F.M., Lek, S., 2005b. Review of modelling techniques. In: Lek, S., Scardi, M., Verdonschot, P.F.M., Descy, J.P., Park, Y.S. (Eds.), *Modelling Community Structure in Freshwater Ecosystems*. Springer-Verlag, Berlin, pp. 21–40.
- Penczak, T., 1967. The biological and technical principles of the fishing by use of direct-current field. *Prz. Zool.* 11, 114–131 (in Polish, with English summary).
- Penczak, T., 1969. The ichthyofauna of the rivers of the Łódź Upland and adjacent areas. Part I. The hydrography and fishes of the Warta basin. *Acta Hydrobiol.* 11, 69–118 (in Polish, with English summary).
- Penczak, T., 1972. Structure of fish groupings in the rivers and streams of the River Nida drainage basin. *Ekol. Pol.* 20, 327–344.
- Penczak, T., 1994. Problems of river ichthyology. In: Singh, H.R. (Ed.), *Advances in Fish Biology*, vol. 1. Hindustan Publishing Corporation, Delhi, pp. 292–299.
- Penczak, T., 1996. Natural regeneration of endangered fish populations in the Pilica drainage basin after reducing human impacts. In: Kirchhofer, A., Hefti, D. (Eds.), *Conservation of Endangered Freshwater Fish in Europe*. Advances in Life Sciences. Birkhäuser Verlag, Basel, p. 341.
- Penczak, T., 1999. Impact of introduced brown trout on native fish communities in the Pilica River catchment (Poland). *Environ. Biol. Fish.* 54, 237–252.
- Penczak, T., Koszalińska, M., 1993. Populations of dominant fish species in the Narew River under human impacts. *Pol. Arch. Hydrobiol.* 40 (1), 59–75.
- Penczak, T., Kruk, A., 2000. Threatened obligatory riverine fishes in human-modified Polish rivers. *Ecol. Freshwater Fish* 9, 109–117.
- Penczak, T., Kruk, A., 2005. Patternizing of impoundment impact (1985–2002) on fish assemblages in a lowland river using the Kohonen algorithm. *J. Appl. Ichthyol.* 21, 169–177.
- Penczak, T., Koszaliński, H., Buczyńska, M., Jakuciewicz, H., 1990a. The ichthyofauna of the Narew River drainage basin. Part I. The Narew River. *Sci. Annu. Polish Anglers Assoc.* 3, 81–94 (in Polish, with English summary).
- Penczak, T., Mann, R.H.K., Koszaliński, H., Pietrowska, M., 1990b. Ichthyofauna of the Narew River drainage basin. Part II. The Pisa River and its tributaries. *Sci. Annu. Polish Anglers Assoc.* 3, 95–114 (in Polish, with English summary).
- Penczak, T., Zaczyński, A., Koszaliński, H., Galicka, W., Ułańska, M., Koszalińska, M., 1991a. Ichthyofauna of the Narew River drainage basin. Part III. The Supraśl River and other rivers of the Białostocka Upland. *Sci. Annu. Polish Anglers Assoc.* 4, 65–81 (in Polish, with English summary).
- Penczak, T., Zaczyński, A., Koszaliński, H., Koszalińska, M., Ułańska, M., 1991b. Ichthyofauna of the Narew River drainage basin. Part IV. Left side tributaries of the Narew River. *Sci. Annu. Polish Anglers Assoc.* 4, 83–99 (in Polish, with English summary).
- Penczak, T., Koszaliński, H., Zaczyński, A., Koszalińska, M., Ułańska, M., 1992. Ichthyofauna of the Narew River drainage basin. Part V. Rivers of the Kurpiowska Plainland. *Sci. Annu. Polish Anglers Assoc.* 5, 155–172 (in Polish, with English summary).
- Penczak, T., Kruk, A., Koszaliński, H., Marszał, L., Kostrzewa, J., 1998. Monitoring of fish fauna in the Gwda drainage basin. *Sci. Annu. Polish Anglers Assoc.* 11, 5–28 (in Polish, with English summary).
- Penczak, T., Kostrzewa, J., Marszał, L., Koszaliński, H., Kruk, A., 1999. Fish fauna of the Noteć River. *Sci. Annu. Polish Anglers Assoc.* 12, 81–94 (in Polish, with English summary).
- Penczak, T., Kruk, A., Koszaliński, H., Zięba, G., 2000. Fish fauna of the Bzura River. *Sci. Annu. Polish Anglers Assoc.* 13, 23–33 (in Polish, with English summary).
- Penczak, T., Kostrzewa, J., Kruk, A., Marszał, L., Zięba, G., Koszaliński, H., 2001. Ichthyofauna of the Wkra River drainage basin. Part I. Wkra. *Sci. Annu. Polish Anglers Assoc.* 14, 5–19 (in Polish, with English summary).
- Penczak, T., Glowacki, Ł., Kostrzewa, J., Kruk, A., Koszaliński, H., Galicka, W., Marszał, L., Zięba, G., 2003. Influence of climate-related temporal changes on fish assemblages in oxbow lakes and in their parent Pilica River (continuation). *Ecology Hydrobiol.* 3, 71–85.
- Penczak, T., Kruk, A., Park, Y.S., Lek, S., 2005. Patterning spatial variations in fish assemblage structures and diversity in the Pilica River system. In: Lek, S., Scardi, M., Verdonschot, P.F.M.,

- Descy, J.P., Park, Y.S. (Eds.), *Modelling Community Structure in Freshwater Ecosystems*. Springer-Verlag, Berlin, pp. 100–113.
- Przybylski, M., 1993. Longitudinal pattern in fish assemblages in the upper Warta River, Poland. *Arch. Hydrobiol.* 126, 499–512.
- Przybylski, M., 1994. Are the fish communities persistent and stable in European rivers? *Pol. Arch. Hydrobiol.* 41, 365–375.
- Recknagel, E., 2003. *Ecological Informatics: Understanding Ecology by Biologically Inspired Computation*. Springer-Verlag, Heidelberg.
- Ricker, W.E., 1968. Methods for assessment of fish production in fresh waters. In: *IBP Handbook No. 3*. Balckwell Science Publishers, Oxford.
- Rose, K.A., 2000. Why are quantitative relationships between environmental quality and fish populations so elusive? *Ecol. Appl.* 10, 367–385.
- Ryder, R.A., Kerr, S.R., 1978. The adult walleye in the percid community—a niche definition on feeding behavior and food specificity. In: Kendall, R.L. (Ed.), *Selected Coolwater Fishes of North America*, 11. *Am. Fish. Soc. Spec. Publ.*, pp. 39–51.
- Schiemer, F., Wieser, W., 1992. Epilogue: food and feeding ecomorphology, energy assimilation and conversion in cyprinids. *Environ. Biol. Fish.* 33, 223–227.
- Schluter, D., 1986. Tests for similarity and convergence of finch communities. *Ecology* 67, 1073–1085.
- Silva Abes, S., Agostinho, A.A., 2001. Spatial patterns in fish distributions and structure of the ichthyocenosis in the Agua Nanci stream, upper Paraná River basin, Brazil. *Hydrobiologia* 445, 217–227.
- Stott, B., Buckley, B.R., 1979. Avoidance experiments with homing shoals of minnows. *Phoxinus phoxinus* in a laboratory stream channel. *J. Fish. Biol.* 14, 135–146.
- Tyler, A.V., Gabriel, W.L., Overholtz, W.J., 1982. Adaptive management based on structure of fish assemblages on northern continental shelves. *Can. Spec. Publ. Fish.* 59, 149–156.
- Ultsch, A., 1993. Self-organizing neural networks for visualization and classification. In: Opitz, O., Lausen, B., Klar, R. (Eds.), *Information and Classification*. Springer, Berlin, pp. 307–313.
- Vannote, R.L., Minshall, G.W., Cummins, K.W., Sedell, J.R., Cushing, C.E., 1980. The river continuum concept. *Can. J. Fish. Aquat. Sci.* 37, 130–137.
- Walley, W.J., Martin, R.W., O'Connor, M.A., 2000. Self-organizing maps for the classification of river quality from biological and environmental data. In: Denzer, R., Swayne, D.A., Purvis, M., Schimak, G. (Eds.), *Environmental Software Systems: Environmental Information and Decision Support*. Kluwer Academic, Dordrecht, pp. 27–41.
- Witkowski, A., 1984. Structure of communities and biomass of ichthyofauna in the Biebrza River, its old river beds and effluents. *Pol. Ecol. Stud.* 10, 447–474.
- Wolter, C., 2001. Conservation of fish species diversity in navigable waterways. *Landscape Urban Plan.* 53, 135–144.
- Wolter, C., Vilcinskis, A., 1997. Perch (*Perca fluviatilis*) as an indicator species for structural degradation in regulated rivers and canals in the lowlands of Germany. *Ecol. Freshwater Fish* 6, 174–181.
- Wootton, R.J., 1990. *Ecology of Teleost Fishes*. Chapman & Hall, London.