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RIVER-LAKE SYSTEM AS MOSAIC PATTERN OF LANDSCAPE PATCHES AND THEIR TRANSITION ZONES (ECOTONES)

ABSTRACT : A river-lake system (i.e. a river flowing through the lakes) can be perceived as a system of lentic (lake) and lotic (river sections) landscape "patches" and the transitory zones between them. In this system transport and exchange of matter and biological information take place. Taking the Krutynia river (Masurian Lakeland, Poland) and its lakes as an example, transport of different biologically active compounds (like phosphorus) and non-active substances (like chlorides) was characterized. Phosphorus retention was estimated in successive "patches" of the system. The biotic structure and function of the river-lake-river transitory zones were described. They are the places where the particles selection and sedimentation of matter transported in the system take place as well as they are the sites where the selection and exchange of planktonic organisms of different size and reproduction strategy occur.

KEY WORDS: river-lake system, landscape, ecotone

1. INTRODUCTION

In the hilly lakeland landscape of north-eastern Poland (Kondracki 1972), river-lake systems, defined as distinct hydrographic units comprising running waters flowing out or passing across lakes, are a frequent and typical component. These systems can be considered at different spatial scales, depending on the river length, stage of development, and order (Strahler 1957), also on the number and morphometric features of the lakes the river crosses. These can be low order streams of different lenght draining small watersheds of several km^2 in area, and flowing through small and shallow lakes, as well as larger river systems (draining watersheds of the area of hundreds km^2) of orders 4–6, flowing through deep and large water bodies. The diversity of such systems in the lakeland landscape is particularly high, especially that they also include temporarily (flood period) the adjacent land systems such as marshes, wet meadows, swamps and similar riparian habitats.

In Poland, nearly half of the lakes (larger than 50 ha) have an area less than 300 ha and a mean depth between 1 and 5 m. At least two-thirds of them belong to the lakes with outlets or the through-flow lakes, that is, directly connected with the river system (Chojnowski 1986). In the landscape of Masurian Lakeland the river-lake systems of various size are widely distributed (Bajkiewicz-Grabowska 2002).

River-lake systems and the associated habitats, together with the relief (Smolska *et al.* 1995), land cover and land use (Dąbrowska-Prot and Łuczak, 1995), account for an extremely mosaic character of this landscape.

Landscape as a spatial fragment of the natural environment is perceived, defined, and described in a variety of ways (Dąbrowska-Prot and Hillbricht-Ilkowska 1991). For the needs of ecological research, the approach proposed by Forman and Godron (1986) is most useful. They perceive landscape as a spatial system of patches formed by ecosystems and sites interconnected by a system of boundaries (junction zones, contact zones, transition zones), generally named ecotones. All these components together form a spatial structure of the system that can be described and quantified with the different measures and indices (Mozgawa 1994). This spatial system of patches and ecotones creates the template for the movements, exchange, transformation, and retention of matter and nutrients as well as for biomass and organisms, i.e. biological information. These are ecological processes relative to landscape, determining geochemical activity and biotic diversity of the habitats.

The river-lake system may thus be perceived as a spatial system of two kinds of ecosystems or patches: a river and a lake connected with each other by surface water flow. Ecotonal zones of these patches would be formed by the water/land interface, as well as by the zones of mixing the lake water with the river water.

Connected with the Forman and Godron (1986) landscape theory, is the river continuum concept, firstly formulated by Vannotte *et al.* (1980). According to this concept (described among others in Hillbricht-Ilkowska 1984) "*... the river from its sources to the outlet is a system in which basic physical properties such as velocity and mass of flowing water, depth, character of the substrate and sediments vary continuously, forming a gradient. As a result of this physical gradient, species and populations form communities adapted to different ranges of the combination of physical factors, that is, they form a biotic continuum. The basic features of the functioning of a river are a continuous movement, temporal and spatial dislocation of matter in different stages of production, utilisation, and decomposition, and a permanent export and exchange of individuals in the population, which together with not assimilated matter (faeces, food remains) and the input of matter from outside form river drift (syrton). There is a directional variation in the stability and efficiency of the river system: from low stability (frequent dislocations) and low efficiency of utilisation of the matter produced or coming from outside, characteristic of the upper reaches, to a higher stability and efficiency in the lower reaches*". This description of the river continuum concept defines more precisely the basic process, which is transport and transformation of matter in multi-patch space. It is supplemented by the organic nutrient spiralling concept (Newbold *et al.* 1982) stating that as a result of the continuous, directional movement of water and drifting matter in the river channel, various stages of nutrient cycling are shifted with respect to each other, giving rise to a kind of spiral.

The river continuum concept still has its adherents and opponents (e.g. Minshall *et al.* 1985); it has been argued that continuum is subject to various disturbances in each river or stream. These disturbances may be caused by local geomorphological structures, and most of all by anthropogenic processes (sewage discharge, raising of the water level, regulation of the channel and the riverside zone, and the like). As a result, the river system may be far away from the ideal continuum. Ward and Stanford , who developed the concept of so called "serial discontinuity" (Stanford *et al.* 1988; Ward and Stanford 1995) , argued that some "inserts" of this kind superimposed on the river continuum (e.g., water lifting) can in a way "rejuvenate" the system through pushing it back to the conditions characteristic of a stream (it concerns the character of a river flowing out from an impoundment reservoir).

The concept of river continuum is still blooming (Cummins *et al.* 1995). It clearly represents a useful approach to the study of fluvial systems. It joins them with the landscape, and also is a distinct and useful measure for description of individual river systems as both integrated continuous system (geochemically and biologically) and discontinuous system. It means that it is possible to measure the extent of disturbances in different river sections.

A question arises to what extent the lakes function as the "insert" systems disturbing river continuum and creating the discontinuity of processes occurring in the whole river system. Particularly, to what extent they modify matter transport in the river system in view of the fact that they are places of selective retention as well as transformation of organic matter, nutrients and pollutants; they also constitute a source of matter for lower fragments of the river system.

2. PROCESSES OF MATTER TRANSPORT AND TRANSFORMATION IN A RIVER-LAKE SYSTEM: CASE STUDY OF THE KRUTYNIA RIVER-LAKE SYSTEM ON MASURIAN LAKELAND

The Krutynia river (Fig. 1A) is about 100 km long. One-third of its drainage basin is located within the Masurian Landscape Park (Hillbricht-Ilkowska 1989). It drains an area of about 700 km^2 (about 60% arable land and 30% forests) and flows through 17 lakes that differ in morphometry (surface area of 24–841 ha, mean depth of 1.7–12.7 m) and rate of water exchange (annual exchange rate calculated as a ratio of the annual outflow to the lake volume ranged from 0.4 to 140.0). River sections connecting lakes differ in their length (from 0.5 to 25 km) and discharge (from 0.01 to 5 $m^3 s^{-1}$). The Krutynia is a typical river of the young post- glacial lakeland landscape, with diverse, meandering course, and discharge of no more than 4–5 $m^3 s^{-1}$ (at the outlet). The river starts as a small stream crossing arable land and flowing through a human settlement. This point source of pollution is located at the headwaters (Fig. 1A) and could be detected in the whole river downstream.

The measurements of the water discharge and chemical composition at inflows to and outflows from successive lakes in several hydrological periods (spring freshet, summer low water level) made possible the assessment of the retention of selective elements in successive lakes and river sections

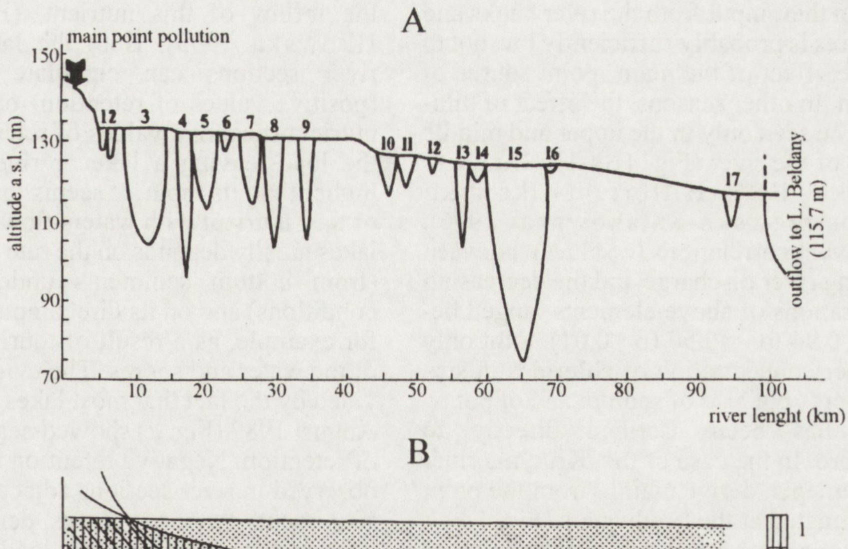

Fig. 1. Longitudinal profile of the river Krutynia (Masurian Lakeland, Poland) flowing through 17 lakes (A) and the schematic range of variation in the concentration (B) of selected biologically inactive compounds like chlorides, K and Na (1), and of some nutrients like nitrate-nitrogen (2) and total phosphorus (3) (after Hillbricht-Ilkowska and Bajkiewicz-Grabowska 1991, Hillbricht-Ilkowska and Kostrzewska-Szlakowska 1993, 1996 , modified).

of the system. This allows also to find a relationship between the discharge and the concentration of various compounds (Hillbricht-Ilkowska and Kostrzewska-Szlakowska 1993, 1996).

The transport of biologically inactive substances such as chlorides is a continuous process, that is, the concentration of these compounds in water is progressively diluted down the river from the source of pollution and along the increase of discharge (Fig. 1 B) according to formula:

$$Cl\ (mg \times l^{-1}) = 12.25\ e^{-0.159Q} \quad (1)$$

where Q = flow ($m^3\ sec^{-1}$).

Successive lakes do not markedly disturb the rate of chloride transport (Hillbricht-Ilkowska and Bajkiewicz-Grabowska 1991, Hillbricht-Ilkowska and Kostrzewska-Szlakowska 1996). Other chemical components biologically inactive or low- assimilated, such as Ca, K, Na, and Mg, show a similar behaviour as chlorides. However, directional changes in their concentrations along with the increase of discharge are observed only in the periods of low water levels (like in June). It is the season when their input from the river banks and lake shores is probably sufficiently low not to mask the effect of the main point source of pollution. In other seasons the effect of dilution can be seen only in the upper and middle sections of the river (Fig. 1B) (Hillbricht-Ilkowska 1993, Hillbricht-Ilkowska and Kostrzewska-Szlakowska 1996). The relevant correlations (*r* values) between increasing river discharge and the decreasing concentrations of above elements ranged between –0.94 to – 0.50 ($p < 0.01$). Not only the higher concentration of chlorides in surface waters , but also of sodium and of potassium has been ascribed directly to agriculture. In the case of the Krutynia river these elements derive mainly from the point source situated at the headwaters (Fig. 1A).

The various forms of nutrients such as nitrate-nitrogen (Fig. 1B), the input of which is commonly ascribed to agriculture (Burt *et al.* 1993), show more irregular changes along river-lake course. Changes in the concentrations of this compounds downstream the point source of pollution are irregular, and variation in successive fragments of the river system is large (Fig. 1 B).The correlation with the river length or discharge is statistically significant ($r^2 = 62$, $p<0.01$) only in June i.e. the period of low water level course (Hillbricht-Ilkowska 1993, Hillbricht- Ilkowska and Kostrzewska-Szlakowska 1996).

Variation in phosphorus concentrations, the basic nutrient determining the productivity of the lakes under study, showed a different pattern. No directional changes were observed in its concentrations along successive sections of the river system (Fig. 1B). Variation in phosphorus concentration was large and not directional; no significant correlation was found with the river length or discharge (Hillbricht-Ilkowska and Bajkiewicz-Grabowska 1991, Hillbricht-Ilkowska 1993, Hillbricht-Ilkowska and Kostrzewska-Szlakowska 1996). The transport of this nutrient in the river-lake system was discontinuous. Successive lakes and river sections could function as systems cumulating as well as exporting this nutrient.

The retention of total phosphorus (in four hydrologically different months – Fig. 2) in successive lakes and river sections (Fig. 1A) was calculated as a difference between outflow and inflow (carried by the river and with precipitation), and expressed as part of the inflow of this nutrient. (Hillbricht-Ilkowska 1993). Both the lakes and the river sections can cumulate phosphorus (positive values of retention) or export this nutrient (negative values of retention), when the load leaving a lake or river section is higher than its input. It seems that the export of this nutrient with waters flowing out from lakes mostly depends on the rate of its release (from bottom sediments under anaerobic conditions) and on its direct input to the lake, for example, as a result of tourist utilisation of the water and shores. The evidence is provided by the fact that most lakes examined in August 1987 (Fig. 2) showed negative values of retention. Negative retention is frequently observed in river sections adjacent to human settlements or tourist camps, denoted as polluted in Fig. 2. Phosphorus load in their waters is often several times higher than in the water of the preceding lake (Fig. 2, data for June).

The above processes characterising the functioning of the river-lake system on the example of Krutynia river (Masurian Lakeland) are summarised in Hillbricht-Ilkowska (1999) as follows:

– the river flowing through the lakes represents a diversified landscape system

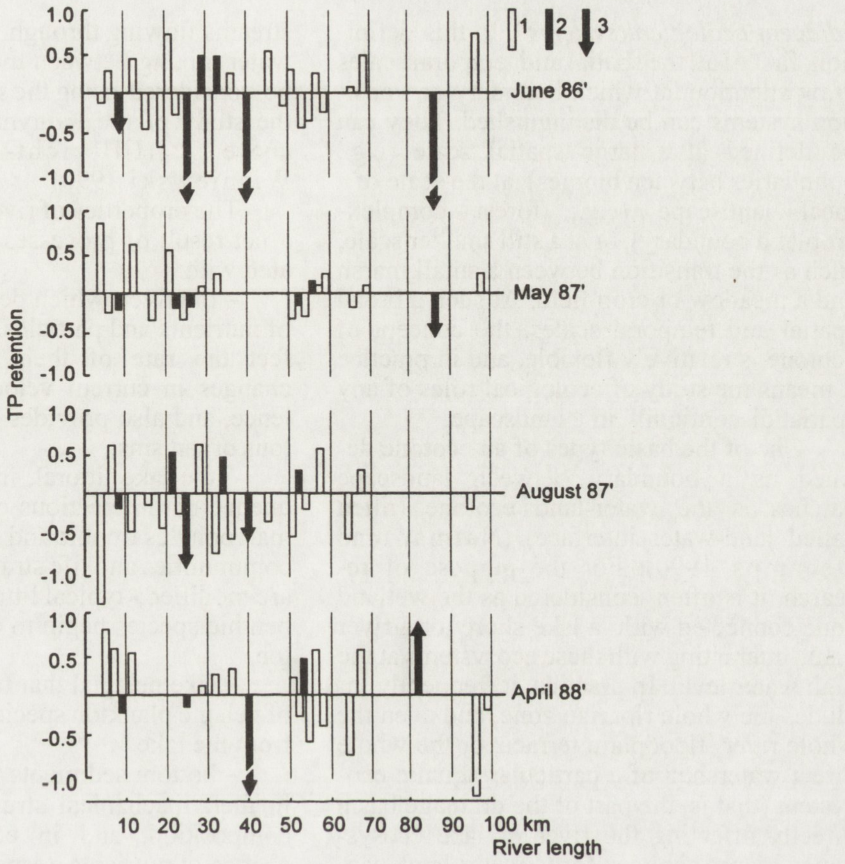

Fig. 2. Indices of the net retention of total phosphorus (TP) for successive lakes (1) and unpolluted (2) and polluted (3) fragments of the river Krutynia (see Fig. 1) in four different months (after Hillbricht-Ilkowska, 1993, modified). Net retention expressed as the ratio of the difference between load in inflow *minus* load in outflow to load in inflow.

composed of lotic patches (river sections) and lentic patches (lake fragments).

– in the case of the transport of biologically inactive compounds loaded to a river from point sources of pollution, this system can be compared to a river contonuum.

– the presence of lakes in a river system basically eliminates the continuity of nutrient transport, especially of phosphorus; lakes and river sections connecting them function in this system as "inserts" cumulating or exporting this nutrient.

– a tendency was observed to an alternate occurrence of nutrient cumulating systems (that is, with a positive retention) and exporting systems (with a negative retention) along the river course; both lakes and river sections can retain or export (Fig. 2) but most often the latter are exporters of phosphorus.

3. FUNCTIONING OF THE MIXING ZONES OF RIVER AND LAKE WATERS AS ECOTONES

In the history of ecological concepts, the concept of ecotone goes back to 1905, when Clements (1905) used it to define the zone of transition from one plant community to another, where competition and displacement of various components occur. In the world literature, especially in the field of landscape ecology this concept is being extended, and it can be used for various systems formed at the junction of different landscape fragments (ecosystems, habitats). According to Naiman and Decamps (1990) the ecotone is "*...a zone of transition between adjacent ecological systems, having a set of characteristics uniquely defined by space and time scales and by the strength of the interaction between* *adjacent ecological systems*". In this definition, first of all the spatial and temporal scales draw attention, at which boundary or transition systems can be distinguished. They can be defined at a large spatial scale (e.g., boundaries between biomes), at the scale of a local landscape (e.g., forest complex-cropland boundary), or at a still smaller scale, such as the transition between a small marsh and a meadow or crop field. At such a broad spatial and temporal scales, the concept of ecotone is relatively flexible, and in practice it means the study of ecological roles of any spatial discontinuity in a landscape.

One of the basic types of an ecotone defined as a boundary between landscape patches is the water-land ecotone (often called land-water interface) (Naiman and Decamps 1990). For the purpose of research, it is often considered as the wetland zone connected with a lake shore or a river bank interacting with these ecosystems at the high water level. In practice, it frequently includes the whole riparian zone, and even the whole river floodplain terrace, or the whole direct watershed of a particular aquatic ecosystem (that is, the part of the drainage basin directly affecting the river or lake ecosystem). Many habitats form water-land ecotones. The habitats associated with the river – riparian habitats (riverine marshes, alluvial forests, wet meadows, etc.) are typical examples of an ecotone of this type. The lacustrine ecotones involve lake shoreline sites like beaches, lake littoral sites and macrophyte vegetation as well as the surface – ground water interface (hyporeic zone) (Naiman and Decamps 1990). The papers in this volume address mainly to the above lacustrine ecotones.

A special kind of ecotones associated with aquatic ecosystems is the river-lake interface, or the zone where the mixing of water of these two different aquatic ecosystems take place and in effect the delta type site is formed.

The spatial scale of this "delta" zone can vary from many square km to one or several ha, depending on the river and lake size. In contrast to land ecotones the mixing zones of river and lake waters have not been adequately studied on their spatial and temporal scales. In a typical lakeland landscape prevailing in north-eastern Europe, including Masurian Lakeland in Poland, these zones are particularly frequent; most lakes occurring there form a integrated system with rivers or streams flowing through them. The zones of water mixing between these ecosystems will be considered using the selected results from the study of the Krutynia river, mentioned above (Hillbricht-Ilkowska and Wiśniewski 1996).

The properties of river-lake ecotones are a net result of processes and factors associated with:

– the river, which determines the inflow of nutrients and particles suspension, and affect the rate of their sedimentation, the changes in current velocity and in turbulence, and also provides habitat for rheophilous organisms;

– the lake littoral, in which as a consequence of interactions of river waters with macrophytes trophic and spatial structures of communities and life strategies of organisms are modified; typical littoral, periphyton and benthic species begin to occurr in the plankton

– lake pelagial that functions as a source of pelagic plankton species in inflow/outflow from the lake

– bottom sediments which are different in their mechanical structure and chemical composition, and in consequence in exchange of nutrients, (especially phosphorus), between sediments and the water over the bottom.

The zone of a river inflow to a lake functions as a barrier system and filter of incoming organic matter, nutrients, and mineral suspension. The river carries to the lake particles of different composition and properties. Kufel (1993) studied the selective sedimentation of this material in several river-lake ecotones of the Krutynia river. Heavier mineral particles form a sandy deposit, poor in phosphorus and nitrogen, at a distance of a dozen or so metres from the outlet. Lighter, smaller particles of the suspension are richer in phosphorus and nitrogen. As a consequence, the contents of phosphorus and nitrogen in deposits increase with distance from the river inflow towards the open lake (Kufel 1993).

In the zone of the river inflow to a lake, lake waters may be totally exchanged into river waters, or only partially mixed (vertically and horizontally). These processes occur in a smaller or larger section of the littoral, depending on the velocity of the river current, differences in the trophic conditions of the lake and the river flowing into it, and on the bottom coverage with macrophytes.

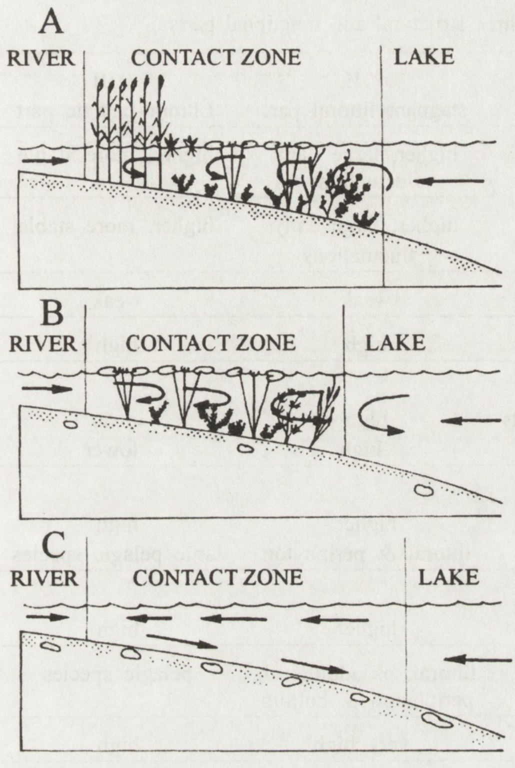

Fig. 3. Scheme of the range of the contact zone (and water mixing) of river and lake waters (arrows) in the lake littoral covered with dense emergent and submerged vegetation (A), or with vegetation with floating leaves and submerged vegetation (B) and in the "open" littoral without vegetation(C).

On Fig. 3, three typical situations found in the river Krutynia system are presented. In the open, macrophytes-free littoral the mixing of the river and lake waters can be gradual, and lotic conditions can be replaced continually by lentic conditions (Fig. 3C). In case of littoral covered with macrophytes the violent changes can occur within a small space when river waters with a higher velocity meet a dense belt of hard emergent vegetation such as a reedbed. (Fig. 3A) or the area covered by submerged vegetation (Fig. 3 B).

In case of littoral covered with macrophytes the transition zone can be divided into three parts (Ejsmont-Karabin *et al.* 1993, Ejsmont-Karabin and Węgleńska 1996).

In the current zone of the first part (Table 1), the river has a clear inhibiting effect on the development of submerged vegetation and vegetation with floating leaves, resulting from a heavy hydraulic stress (Królikowska 1990, 1996). The elimination of this vegetation, or simplification of its species composition reduce ecological niches for many species of zooplankton associated with the vegetation and its epiphytes. For many species of zooplankton (especially, for large species of cladocerans), thickets of macrophytes are shelters from predators (fry and adult fish), particularly during the day. Reduction in the density of macrophytes increases the vulnerability of large zooplankton to predation (Lauridsen *et al.* 1996)

Speed current and increased turbulence in this part of the transition zone can modify the structure and abundance of the plankton in many ways. Firstly, it has a selective effect on the spatial structure of plankton populations because of a differential response of individual species to hydraulic stress. Secondly, it can "dilute" zooplankton populations occurring in the transition zone by eliminating individuals with a low reproductive rate, unable to compensate for the losses due to increased mortality or removal beyond this zone. Thirdly, by modifying local environmental conditions, it has an indirect effect on the abundance and species composition of the plankton. The elimination of individuals by their destruction or removal from this part of the habitat cause a permanent decline in population numbers. This, in turn, accounts for an increased reproduction of surviving individuals like higher rate of cell divisions of the phytoplankton (Puchalski, unpublished) and increased zooplankton fecundity (Ejsmont-Karabin and Węgleńska 1996) .

The "current" part of the transition zone (Fig. 3 C) was characterised by lower water temperatures, lower oxygen and lower chlorophyll concentrations, as compared with those recorded in the stagnant littoral zone (Simm, unpublished). The phytoplankton community was dominated by diatoms and green algae typical of rivers (Puchalski, unpublished). The zooplankton community mainly consisted of opportunistic species with r-strategy, such as rotifers and crustaceans feeding on detritus and bacteria. They are the eurytopic forms, with a broad food spectrum, well adapted to low and variable food concentrations, lower oxygen concentrations and lower temperatures. They are also resistant to high concentrations of mineral suspension in the water due to a structure of the feeding apparatus precluding clogging of the alimentary tract (Ejsmont-Karabin

Table 1. Division of the river-lake transitory zone into three structural and functional parts

Parameters	I current part	II stagnant littoral part	III Littoral-pelagic part
Temperature	lower	higher, large daily fluctuations	higher, more stable
O_2 concentration	lower	higher, large daily fluctuations	higher, more stable
Turbulence	strong	weak	weak
Chlorophyll content	low	high	high
Macrophytes:			
density	very low or no plants	high	lower
species diversity	low	high	lower
Phytoplankton:			
density	low	higher	high
species composition	potamoplankton	littoral & periphyton	large pelagic species
Zooplankton:			
density	low	higher	high
species composition	potamoplankton	littoral, pseudolittoral, periphyton & bottom	pelagic species
species diversity	small	very high	high
fecundity of dominant species	small	high	high
trophic type of zooplankton	microfiltrators, sedimentators (detritus, bacteria)	filtrators, sedimentators, graspers, scrapers (algae, detritus, bacteria)	macro- and microfiltrators, sedimentators (algae, detritus, bacteria) predatory species

et al. 1993, Ejsmont-Karabin and Węgleńska 1996).

The second part of the transition zone, "out of current", comprises the belt of the lake littoral supporting emergent and submerged plant (Fig. 3A,B). This area is characterised by the higher than in the river and current parts abundance of the plankton, and by a high species diversity (Table 1). The plankton of this part of the ecotone consists of the typical littoral species (like rotifer *Euchlanis dilatata*), highly specialised, with K-strategy, associated with specific macrophyte types, and also of the peryphyton , rheophilous, pelagic, and benthic species (Ejsmont-Karabin and Węgleńska 1996). Basu *et al.* (2000) has found also several times higher abundance of zooplankton in the macrophytes patches of fluvial lakes as well as their higher diversity.

The third part of this zone, being a transition between the littoral and pelagial, is characterised by a relatively high, although lower than in the second part, species diversity, but at manifold higher plankton abundance. Plankton community in this part of the transition zone consists of a mixture of littoral and pelagic forms, with increasing prevalence of the latter towards the zone of open water.

The spatial habitat differentiation described above, and also structural and functional diversity of the plankton observed in the mixing zone of the river and lake waters is stable in the period of vegetation development, and recurrent in time both in the daily cycle and in successive years (Ejsmont-Karabin *et al.* 1993, Ejsmont-Karabin and Węgleńska 1996).

The zone of the mixing of lake and river waters, that is, the zone of the river outflow from the lake, when lake waters give rise to a stream or river, constitutes an ecotone with a different structure and function. This is a frequent situation for the Krutynia river (Ejsmont-Karabin and Węgleńska 1996).

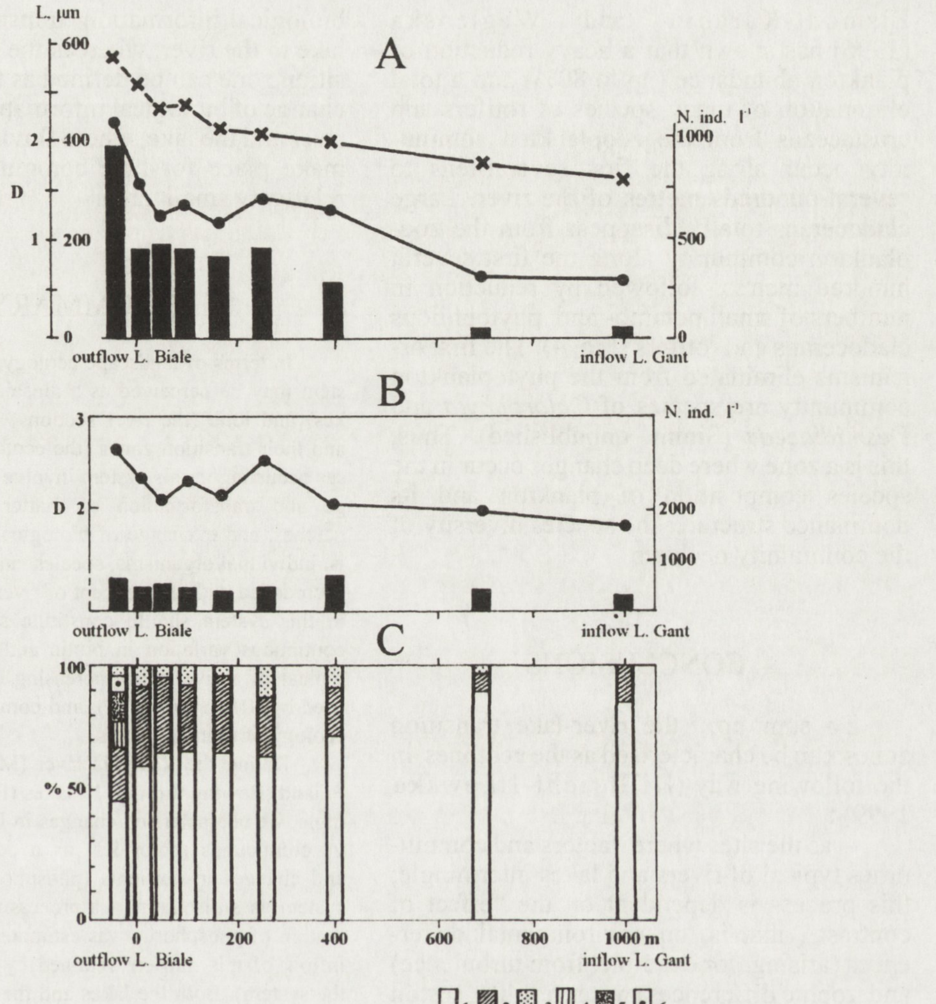

Fig. 4. Changes in the index of species diversity (D, closed circles), mean body lenght per sample (L, crosses), total number of individuals (N, columns) of Crustacea (A) and Rotatoria (B), and contribution of more important taxons to the total numbers of Crustacea (C) along the river Krutynia fragment (about 1 km long) between the outflow from Lake Białe and the inflow to Lake Gant. 1 – *Cyclopoida*, 2 – *Calanoida*, 3 – *Cladocera* (small size species), 4 – *Daphnia cucullata*, 5 – *Bosmina coregoni*, 6 – *Diaphanosoma brachyurum* (after Ejsmont-Karabin and Węglęńska, 1996).

The zone of the river outflow from the lake is strongly and directly influenced by the open lake water. As a result, the abundance and structure of plankton communities are often similar between the pelagial and the zone of outflow.

This zone forms a natural barrier to most pelagic species of the plankton on their way down the river (Fig. 4). Individual organisms and species are eliminated, depending on their susceptibility to hydraulic stress, their shape and size, and vulnerability to mechanical damage. First of all, this concerns adult individuals of large cladoceran species. Some of them (e.g., of the genera *Daphnia, Diaphanosoma, Leptodora*) can also actively withstand floating with water current if its velocity does not exceed several m/sec. As a result, clear changes occur in the age structure and size structure of the plankton community carried from the lake by the river. The dominance of younger developmental stages increases, and the mean body length of individuals in the community declines (Fig. 4).

The elimination of plankton is continued in the river below its outlet. The study by

Ejsmont-Karabin and Węgleńska (1996) has shown that a heavy reduction of plankton abundance (up to 80%) and a total elimination of many species of rotifers and crustaceans from the zooplankton community occur along the first several-tens to several-hundreds metres of the river. Large cladocerans totally disappear from the zooplankton community along the first several hundred metres, followed by reduction in numbers of small potamo- and phytophilous cladocerans and rotifers (Fig. 4). The first organisms eliminated from the phytoplankton community are species of *Chlorophyta* and *Desmidiaceae* (Simm, unpublished). Thus, this is a zone where deep changes occur in the species composition of plankton and its dominance structure; the species diversity of the community declines.

4. CONCLUSIONS

To sum up, the river-lake transition zones can be characterised as the ecotones in the following way (Hillbricht-Ilkowska 1999) :

– as the sites where factors and communities typical of rivers and lakes intermingle; this process is dependent on the "effect of contrast", that is, on environmental differences (arising, for example, from turbulence) and trophic differences (water fertility, seston abundance) between lake and river waters. When the contrast is large, secondary division is observed into three zones with differential plankton responses at the individual, population, and community levels;

– among factors determining the development of these zones as ecotones, are macrophytes of the lake littoral, especially emergent vegetation (when its density and range are high), which functions as a dense barrier hindering the effects of the river on the lake;

– river-lake transition zones are sites of sedimentation and selection of organic matter and nutrients, thus, these are boundary zones (ecotones) that influence the rate of matter transport and exchange between ecosystems;

– the transition zone formed by the inflow of lake waters into rivers functions first of all as the site of a strong selection of living material deriving from the lake. An ecotone of this type, that is, a transition lake-river zone can be defined as the place of a filter of biological information transmitted from the lake to the river, whereas the river-lake transition zone can be defined as the place of exchange of biological information between the river and the lake, where fluvial communities make place for lake communities within a relatively small area.

5. SUMMARY

In terms of landscape ecology, the river-lake system may be perceived as a mosaic of lentic (the lakes) and lotic (the river sections) landscape patches and their transition zones (the ecotones). The processes occurring in this system involve transport, exchange and transformation of matter among different patches, and exchange of biological information, that is, individual organisms, species, and communities. In accordance with the concept of river continuum, lakes in this system should constitute systems disturbing continuous variation in biotic and abiotic structures typical of a river with increasing order in the sense used by Strahler (1957), and commonly used in the ecology of running waters.

Taking the Krutynia river (Masurian Lakeland, Poland) flowing through 17 lakes (Fig. 1A) as an example, we characterised changes in biologically inactive compounds (chlorides) as a continuous process, and changes in nutrients (phosphorus) in successive system as a discontinuous process (Fig. 1B). The retention of phosphorus was estimated (as a part of the inflow of this nutrient retained by or exported from the system). Both the lakes and the river sections can function with equal probability as systems retaining phosphorus (positive retention) or exporting it (negative retention). However, lakes in summer, as well as polluted river sections more often export this nutrient than retain it (Fig. 2).

We also characterised the function and structure of transition (contact) zones between river and lake waters, that is, ecotones that can be distinguished at the river inflow to and outflow from the successive lakes of the Krutynia river. Differences were found in the species composition and degree of the development of littoral macrophytes occurring in these zones. Depending on the degree of development and the vegetation cover of the contact zone (Fig. 3), velocity of the current, and trophic conditions of the river and lake waters, the contact zones function as barriers and filters of incoming organic matter, nutrients, and mineral suspension. This is also the zone of exchange of plankton species occurring in the river for those occurring in the lake, that differ in their life strategy, foraging, and reproduction (Table 1). Also changes in the composition and abundance of the plankton in zones of lake water outflow were analysed (Fig. 4). It has been found that the river-lake transition zones,

constituting the places of sedimentation and selection of organic matter and nutrients, influence the rate of transport and matter exchange between river and lake ecosystems, and that they are places of the exchange of biological information in the form of changes in the species composition of the plankton.

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