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# Habitat heterogeneity and biodiversity in the shore zone of water bodies*

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**Abstract** – Habitat heterogeneity and high biological complexity are fundamental characteristics of the shore zone of water bodies. Water level fluctuations, shore slope and sediment structure are physical attributes of major importance in this zone, and macrophytes are its most important biotic element. Studies and experiments were done in the field in order to assess the relationships between habitat complexity and biodiversity in the lake shore zone. Biotic structure at sites with fluctuating water levels, as well as colonization of experimental near-shore pools by plants and animals were studied.

**Key words:** shore zone, water level fluctuations, macrophytes, invertebrates, habitat heterogeneity.

**Różnorodność siedliskowa i biotyczna strefy brzegowej zbiorników wodnych.** Różnorodność siedlisk i duża złożoność biologiczna są podstawowymi cechami strefy brzegowej zbiorników wodnych. Najważniejszymi właściwościami fizycznymi są wahania poziomu wody, nachylenie brzegu i struktura osadu, a wśród czynników biotycznych największe znaczenie mają makrofity. Celem przeprowadzonych badań i eksperymentów była ocena związku pomiędzy złożonością siedlisk i bioróżnorodnością w strefie brzegowej jeziora. Zbadano strukturę biotyczną stanowisk ze zmiennym poziomem wody jak również zasiedlanie przez rośliny i zwierzęta eksperymentalnych zbiorników przybrzeżnych.

## 1. Introduction

The physical and biological complexity of the shore-littoral zones of lakes, rivers and ponds has been stressed by a number of authors. A review of the literature shows that these ecotonal zones play a major role in supporting biological diversity and controlling nutrient dynamics in the whole water body (Dykyjova and Kvet 1978, Naiman and Decamps 1990, Holland et al. 1991, Hillbricht-Ilkowska and Pieczyńska 1993).

Shore zones are typical patchy environments, with the variety of macrophyte life forms and their mosaic distribution being especially important for the spatio-temporal organization of these habitats. Various natural or anthropogenic

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disturbances to the environment (e.g. fluctuation in water level) are significant in the regulation of species richness in the shore region (Keddy and Reznicek 1986, Sheldon 1986, Palomaki 1994).

Physical and biotic structures of the shore zone of lakes were studied in Mazurian lakes (northern Poland). Lake Mikołajskie (highly eutrophic, 460 ha) and Lake Roś (meso-eutrophic, 1888 ha) were the main objects of investigations.

## 2. Physical characteristics and communities

Water level fluctuations, shore terrace slope and shore sediment structure are physical attributes of major importance in the shore-littoral systems. The main variations in the boundary habitat depend on its periodic flooding and drying up. The same fluctuations in water level move the shore line on various distances depending on shore slope. For example, in Lake Mikołajskie, a difference in water level of 41 cm, moves the shore line by 12 m on average and a maximum of 103 m. In Lake Śniardwy, which has extensive shallow areas, the same amplitude of water level, give the much higher values of 53 m on average and a maximum of 296 m (Pieczyńska 1972).

At many shore sites, the accumulation of considerable amounts of plant detritus causes, at some water levels, the isolation of shallow near-shore pools. The size and distribution of these pools change during the season in relation to fluctuation in water level and the configuration of the bottom (fig. 1). The presence of these temporary water bodies of small, sometimes very small size ($< 1\ m^2$) gives a visible increase in shore habitat heterogeneity, especially by creating spatial and temporal discontinuity of ecotonal patches (Pieczyńska 1972, Pieczyńska and M. Zalewski unpubl.).

Shore and littoral plants are the most important biotic elements at the land-water interface. Plant cover in this zone depends strongly on the flooding and drying regime. On the basis of studies in the Great Lakes, Keddy and Reznicek (1986) and Keddy (1990) demonstrated that fluctuating water levels increase both the area of shore vegetation and its diversity. Periods of high water prevent terrestrial plants (especially woody ones) from occupying areas close to the water body. Low water periods allow plants of many species to regenerate from the very rich seed bank.

A relationship between water level fluctuations and shore zone vegetation was also observed in the Mazurian lakes. A 1000 $m^2$ part of the flat shore of Lake Roś emergent in the summer of 1993 at low water was observed. A narrow, unvegetated sandy zone was found close to the shore line, while the upper area was overgrown by rather poor terrestrial vegetation (prevailingly grasses and some shrubs). The water level rose in autumn and the whole area studied was flooded. In the next summer (1994) some terrestrial (flood resistant) plants were still noticed on the flooded area (depth of 40 cm on average), while aquatic plants appeared in great quantity. Their distribution was very heterogenous and species diversity was visibly higher in the flooded areas. The biomass of submerged plants reached 5000 g FW $m^{-2}$. A moss (*Drepanocladus* sp.) appeared in masses and *Lemna trisulca* L., *L. minor* L., *Utricularia* sp. and floating mats of filamentous algae (predominantly *Cladophora* sp.) occurred abundantly. *Myriophyllum spicatum* L. and *Ceratophyllum demersum* L. were represented mainly by floating canopies, which were probably brought into the shore region from the deeper part of the lake by wave action. Emergent plants were represented mainly by *Phragmites australis*

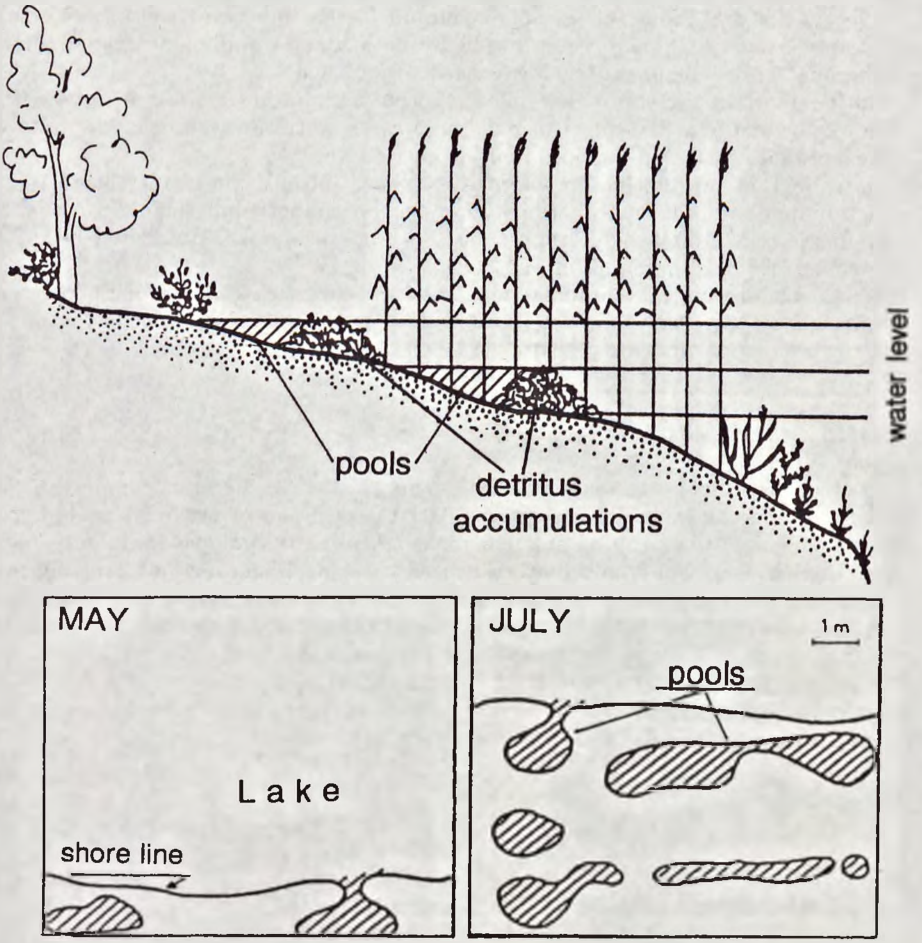


Fig. 1. Changes in shoreline position caused by water level fluctuations and location of near-shore pools on one site of Lake Mikołajskie.

(Cav.) Trin. ex Steudel, *Heleocharis palustris* (L.) R. et Sch. and *Schoenoplectus lacustris* (L.) Palla. Macrophytes serve as essential sites for rich assemblages of invertebrates, and Lake Roś resembled previously-studied Mazurian lakes (Pieczyńska 1972), in having an especially rich fauna in sheltered areas with differentiated vegetation and a high degree of accumulation of plant detritus.

There is generally a clear relationship between habitat heterogeneity and biodiversity. Shore areas of high habitat complexity provide sites for many plant species as well as animals — permanent inhabitants of this zone and temporary visitors from adjacent aquatic and terrestrial patches. Various typical limnetic organisms (invertebrates and fish) found the necessary conditions for spawning, rearing and feeding in this zone.

Pieczyńska and Zalewski (unpubl.) pointed to the important cascade effects in the water body which may be initiated by both abiotic and biotic factors in the shore zone. Three major patterns can be distinguished:

1. Biotic factors in the shore zone may generate a chain of abiotic reactions within the ecosystem (e.g. the effect of macrophytes on nutrient cycling in the lake via the uptake, release or accumulation of nutrients).
2. Biotic factors originating in shore areas may initiate biotic responses in the system (e.g. the influence of macrophytes on limnetic phytoplankton via the production of allelopathic substances, competition for nutrients, and the provision refuges for plankton feeders).
3. Abiotic factors in the boundary zone may initiate a cascade of biotic reactions reflected by the ecosystem (e.g. the effect of periodic flooding and drying out on the reproduction and growth of fish).

## 3. Field experiments

Field experiments to assess relationships between habitat complexity and biodiversity in the lake shore zone involved the creation of artificial pools by the digging of holes in a area of uniform reeds (*P. australis*) above the shore line of Lake Roś (fig. 2). The pools (with surfaces covering about 0.4 $m^2$ and depth of 60 cm) filled naturally over several hours with infiltrating lake water. They were observed and restored (if necessary) between 1990 and 1994 and the results of the experiments conducted in 1993 and 1994 are presented here.

Changes in the level of the lake gave changes in the amount of water in the pools which were thus typical astatic water bodies, similar in this respect to natural near-shore pools noted previously (fig. 1).

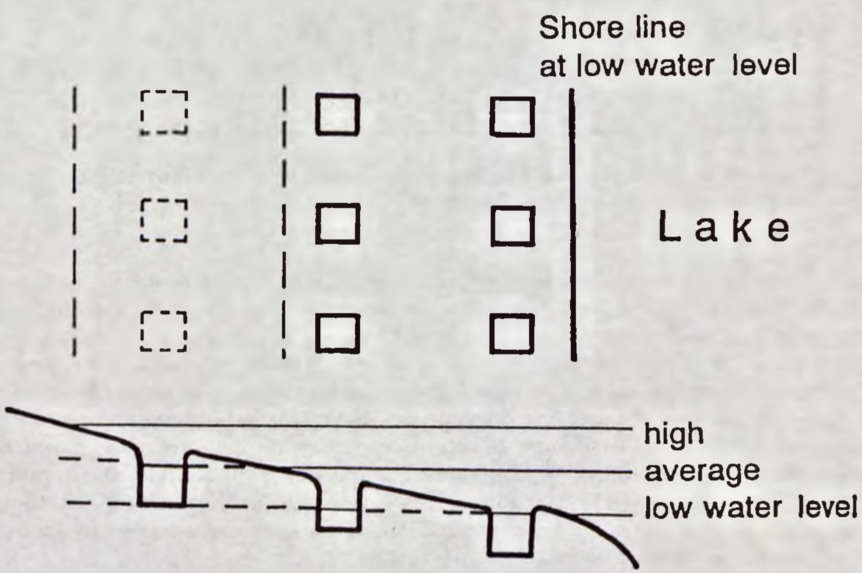


Fig. 2. Location of experimental pools in the shore zone of Lake Roś.

The water in pools was rich in nutrients. For example, in July 1993 concentrations of phosphorus in the 6 (one-year-old) pools varied between 59 and 203 µg $dm^{-3}$ P-$PO_4$, as compared with only 12 µg $dm^{-3}$ in the adjacent lake littoral. Data for nitrogen show similar regularities. The differences noted between the pools were related to their locations and specific colonization by plants and animals.

From the high concentrations of nutrients observed in pools throughout the period of their existence it may be suggested that there is a permanent supply of material transported from the catchment area. It may thus be expected that experimental near-shore water bodies can serve as traps for nutrients carried from uplands to aquatic system.

The creation of new near-shore microhabitats had a marked effect on plant cover. After one year, pools had been colonized by a rich vegetation. The pools varied in volume of water depending on position, and there were also differences in nutrient concentrations and light conditions, with the latter reflecting various degrees of shading by shore trees and emergent macrophytes. These differences led to differences in colonization by plants.

New plant species appeared where *P. australis* was eliminated (fig. 3). Some (mainly semi-aquatic) plants grew from buried seeds or seeds transported by the wind or animals. Others (like *P. australis* itself) grew from remaining rhizomes or (in the cases *M. spicatum* and *C. demersum)* from initially small fragments collected at times of high water, when the pools were temporarily connected with the lake. Filamentous algae (*Cladophora* sp. with associated algae) and *L. trisulca* appeared in masses in some pools.

The artificial pools were colonized by very rich assemblages of animals of various origin. The three main types of colonization involve:

1. The reproduction of individuals originating in the lake, collected from it during high water and later trapped by the fall in water level. Typical of this type of colonization are Rotatoria, Cladocera and Copepoda.
2. The migration of actively-moving animals, like certain snails, and also insects (e.g. Hemiptera, Coleoptera and Collembola), which can fly or otherwise move between the various water bodies. The passive transport of organisms by wind or larger animals may also occur.
3. Colonization by insects (e.g. Diptera, Trichoptera, and Ephemeroptera), which have aerial adults laying eggs on the water surface.

In his review paper on the ecology of temporary waters Williams (1987) demonstrates the very complex mechanisms responsible for the colonization of these types of habitats and for survival in the face of frequent changes in habitat conditions (mainly due to flooding or droughts). Animals colonizing both natural and artificial water bodies includes both species of very broad tolerances occurring in many aquatic and semi-aquatic habitats, and those of very restricted range.

The experimental pools in the shore zone of Lake Roś had invertebrate assemblages of very high density and taxonomic diversity. For example, in July 1993, in 1 litre of water 600 individuals of Cladocera (> 80% *Ceriodaphnia* sp.), 560 Copepoda (> 80% nauplii), and 155 Ephemeroptera larvae were recorded. These densities were significantly higher than they were in the adjacent lake littoral. Furthermore several other important groups occasionally occurring in pools in a mass were practically absent from typical lake littoral. They were primarily mosquitoes (*Culex* sp. up to 50 ind. $dm^{-3}$), Collembola and some representatives of Coleoptera. The pools and lake margins were also permanently colonized by dense populations of the snail *Lymnaea (Galba) turricula* (Held).

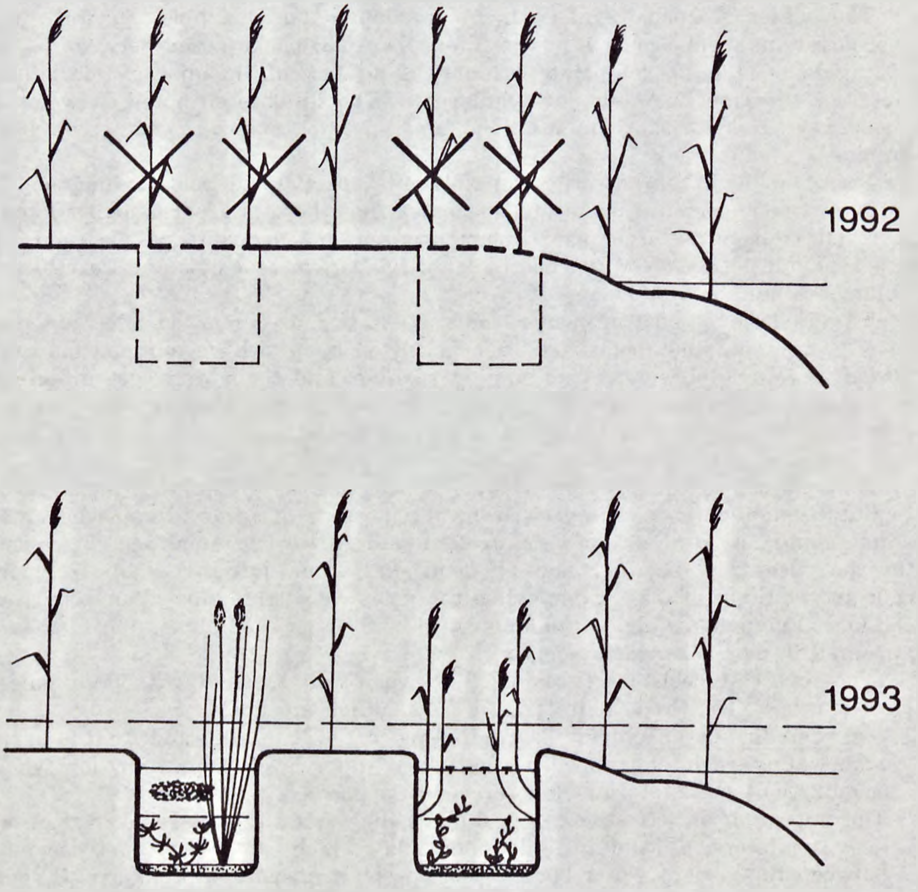


Fig. 3. Response of macrophytes to creation of artificial pools (Lake Roś, July 1992 and 1993).

The mass appearances of invertebrates in pools are usually ephemeral, with the fates of such organisms including emigration, losses to predation and mortality due to rapid changes in the environment. It is probable that most of organisms colonizing pools die before they reach the age for reproduction or emergence. Thus the mass hatching of insect eggs in pools is of limited importance from the point of view of the existence of their populations. But the laying of eggs on the surface of near-shore pools allows a part of the life cycle to be realized. This is very important to the community (for example by providing additional food resources to predators). The eggs of the insects are, of course, also laid on the lake surface, but conditions in the open littoral, especially wave action, do not allow the larvae of many species to exist.

## 4. Conclusion

The shore zone plays a significant role in controlling the transfer of material from a catchment area to a water body and in the maintenance of biodiversity in both the shore region and the water body as a whole. The degree to which these functions are fulfilled is strongly related to the heterogeneity of the system. Differentiated shore areas serve as essential sites for rich assemblages of plants and animals and they are also most effective in the removal of excess nutrient and pollutant inputs.

Various programmes for the protection of water bodies from excessive eutrophication and pollution involve reconstructions of degraded shore zones, as well as creations of new littoral-wetland areas (see reviews in Olson 1992, Hillbricht-Ilkowska and Pieczyńska 1993). The management practices involved are usually large-scale and very expensive. In contrast, the data from the field experiments presented in this paper albeit preliminary, do suggest that very simple operations (the creation of small near-shore pools) may increase shore habitat heterogeneity and biodiversity and may thus have a beneficial effect on the protective functions of the shore zone.

It is obvious that the shore zones of water bodies are and will be subject to unfavourable changes resulting from various management practices in both the water body and watershed. Increasing its habitat heterogeneity would thus seem to be of primary importance if beneficial effect of the shore zone on water body functioning are to be retained.

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