LONG-TERM CHANGES IN 0+ FISH ASSEMBLAGES IN LITTORAL ZONES OF HEATED LAKES. II. SPECIES STRUCTURE OF ICHTHYOFANA

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ABSTRACT. The aim of the study was to describe changes in the biodiversity of 0+ fish assemblages inhabiting lakes that differed in morphometry and the intensity and period of water heating. During the study larvae and fry of fish belonging to 24 species, three faunal assemblages, and three termal groups were caught. The most species were from the boreal lowland (10) and Ponto-Caspian freshwater (10) complexes, while the least were from the amphiboreal freshwater (3) complex. In all of the lakes studied, the most abundantly occurring fish were those belonging to the Ponto-Caspian complex. However, in consideration of thermal requirements, it was confirmed that the most numerously represented species are thermophilic (15), while the least represented belonged to eurythermic species that spawn in late spring (3). The marked congruity of the ichthyofauna composition of the studied lakes resulted from the limited spatial isolation of the individual lakes and the similarity of the environmental conditions that shaped the 0+ fish assemblages.

Key words: FAUNISTIC COMPLEX, 0+ FISH, FISH ASSEMBLAGES, LITTORAL ZONE, HEATED LAKES

INTRODUCTION

The ichthyofauna composition of freshwater lakes is shaped sporadically by single factors, while a range of factors are widely observed to have a simultaneous impact. The intensification of processes that shape the structure of the assemblages of organisms inhabiting a biocenosis are characteristic for a given ecosystem type and are dependent on local abiotic conditions (Weiner 2003). In the temperate zone, abiotic factors, i.e. climate change (Tonn 1990), lake size and depth (Amarasinghe and Welcomme 2002), habitat diversity (Benson and Magnuson 1992), temperature, water oxygen content and pH (Matuszek and Beggs 1988, Jeppesen et al. 2000), as well as biotic factors...
including the introduction of alien species and the expansion of endemic species (Wilkońska 1988, Tereshchenko and Strelnikov 1995, MacRae and Jackson 2001), predation and food competition (Robinson and Wilson 1994), and lake isolation (Olden et al. 2001) are often identified as the basic ones that determine species richness and the structure of fish assemblages.

All species exhibit a natural tendency to increase their area of occurrence within the limits of habitat conditions that meet their requirements. Nevertheless, habitats with similar conditions can support varied fauna assemblages due to differing possibilities for colonization and the occurrence of particular species (Magnuson et al. 1998, Olden et al. 2001).

The intense research of ichthyofauna conducted in the early twentieth century led to the formulation of the concept of faunal assemblages (faunistic complex) that include taxonomic groups linked by common geographical origin (Berg 1961, Nikolski 1980). In addition to common geographical origin, species belonging to one faunistic complex exhibit a certain degree of morphological and ecological adaptation to specific biotic factors and abiotic conditions (Nikolski 1970). This is why the analysis of the dynamics of the occurrence of fish belonging to a faunistic complex can assist in taking applied action and in protecting ichthyofauna.

The current study describes the assemblages of juvenile fish from three lakes that differ with respect to morphology and the intensity and period of water heating. The aim of the study was to create a zoogeographic description of the ichthyofauna and to determine the impact water heating and canal construction on the similarity of aggregations of 0+ fish inhabiting lakes that differ morphometrically.

MATERIALS AND METHODS

STUDY AREA

The study was conducted on three lakes known commonly as the Konin lakes, and differed in morphometry and thermal regime (Zdanowski 1994). The Konin lakes are connected by a system of artificial canals to fish ponds (272 ha), Lake Gópło (2154 ha), and the Warta River. Lakes Licheńskie and Gosławskie are heated year round, while Lake Ślesięńskie is only heated from May to September (Zdanowski 1994, Stawecki et al. 2007). Lake Gosławskie is a shallow pond-like basin, while lakes Licheńskie and
Ślesińskie are ribbon lakes. Fisheries are conducted in all of the lakes, and is based on roach, *Rutilus rutilus* (L.), bream, *Abramis brama* (L.), and white bream, *Abramis bjoerkna* (L.) as well as Asian cyprinid species that were introduced to the lake in the late 1960s and early 1970s: grass carp, *Ctenopharyngodon idella* (Val.), silver carp, *Hypophthalmichthys molitrix* (Val.) and bighead carp, *Aristichthys nobilis* (Richardson).

**FISH SAMPLING AND DATA ANALYSES**

The fish were caught with a fry trawl (mesh size 1 mm) in the 1966-2000 period in the littoral zone in the same locations. Catches were made in the shore zone so the area of each haul was identical and the trawl extended in the water column from the surface to the bottom. The catches were sorted by species based on anatomical and morphological characters (Koblickaya 1966, Mooij 1989). The fish species occurring in the catches were divided into faunistic complexes (Nikolski 1980). Additionally, the fish species were placed in ecological groups according to threshold spawning and survival temperatures, and the dynamics were analyzed (Nikanorov 1974). Using data on fish spawning (Brylińska 2000), the various fish species were grouped according to the number of spawn batches deposited. The fish assemblage dynamics were evaluated based on the share of individual ecological groups that corresponded to the spawning groups.

**RESULTS**

**FAUNISTIC COMPLEXES**

Twenty-four species of larvae and fry were caught during the study (Table 1). The analysis did not include eel, *Anguilla anguilla* (L.), which spawns in the sea. The highest species richness were noted in Lake Licheński (23), while in lakes Gosławskie and Ślesińskie there were 20 and 16, respectively. Spirlin, *Alburnoides bipunctatus* (Bloch) and wels catfish, *Silurus glanis* (L.) occurred only in Lake Licheński, while nine-spine stickleback, *Pungitius pungitius* (L.) was only found in Lake Gosławskie. The fish occurring in these lakes belong to three faunistic complexes. The most numerous group of species is in the boreal lowland (10) and freshwater Pontic-Caspian (10), while the fewest number of species was in the freshwater amphiboreal complex (3). The most frequently occurring fish in all the lakes were from the Pontic-Caspian complex (Fig. 1).
Species belonging to the amphiboreal complex (pikeperch, *Sander lucioperca* (L.), bitterling, *Rhodeus amarus* (Bloch)) were only a significant part of the fish assemblage in Lake Šlesińskie in the period preceding water heating (1966-1970) and in the 1990s (Fig. 1c). The lowest share of fish from the boreal complex was noted in Lake Gosławskie (from 2 to 80%, mean 22%), and the largest share in Lake Licheńskie.

### TABLE 1


<table>
<thead>
<tr>
<th>Ecological reproductive group</th>
<th>Species name</th>
<th>Faunistic complex</th>
<th>Thermal group</th>
<th>Spawning</th>
</tr>
</thead>
<tbody>
<tr>
<td>Non-guarding, eggs distributed on open substrate</td>
<td><em>Leuciscus cephalus</em> (L.)</td>
<td>C</td>
<td>L</td>
<td>P</td>
</tr>
<tr>
<td></td>
<td><em>Alburnoides bipunctatus</em> (Bloch)</td>
<td>C</td>
<td>T</td>
<td>E</td>
</tr>
<tr>
<td>Lithophilous</td>
<td><em>Rutilus rutilus</em> (L.)</td>
<td>B</td>
<td>W</td>
<td>E</td>
</tr>
<tr>
<td>Phyto-lithophilous</td>
<td><em>Alburnus alburnus</em> (L.)</td>
<td>C</td>
<td>T</td>
<td>P</td>
</tr>
<tr>
<td></td>
<td><em>Abramis bjoerkna</em> (L.)</td>
<td>C</td>
<td>T</td>
<td>P</td>
</tr>
<tr>
<td></td>
<td><em>Abramis brama</em> (L.)</td>
<td>C</td>
<td>L</td>
<td>E</td>
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<td></td>
<td><em>Perca fluviatilis</em> L.</td>
<td>B</td>
<td>W</td>
<td>E</td>
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<td></td>
<td><em>Gymnocephalus cernuus</em> (L.)</td>
<td>B</td>
<td>W</td>
<td>P</td>
</tr>
<tr>
<td>Phytophilous</td>
<td><em>Leuciscus idus</em> (L.)</td>
<td>B</td>
<td>W</td>
<td>E</td>
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<td></td>
<td><em>Scardinius erythrophthalmus</em> (L.)</td>
<td>C</td>
<td>T</td>
<td>P</td>
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<td></td>
<td><em>Tinca tinca</em> (L.)</td>
<td>B</td>
<td>T</td>
<td>P</td>
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<tr>
<td></td>
<td><em>Carassius gibelio</em> (Bloch)</td>
<td>B</td>
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<td></td>
<td><em>Carassius carassius</em> (L.)</td>
<td>B</td>
<td>T</td>
<td>P</td>
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<tr>
<td></td>
<td><em>Cyprinus carpio</em> L.</td>
<td>A</td>
<td>T</td>
<td>P</td>
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<tr>
<td></td>
<td><em>Esox lucius</em> L.</td>
<td>B</td>
<td>W</td>
<td>E</td>
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<tr>
<td></td>
<td><em>Cobitis taenia</em> L.</td>
<td>B</td>
<td>T</td>
<td>P</td>
</tr>
<tr>
<td>Psammophilous</td>
<td><em>Gobio gobio</em> (L.)</td>
<td>B</td>
<td>T</td>
<td>P</td>
</tr>
<tr>
<td>Non-guarding, eggs hidden</td>
<td><em>Rhodeus amarus</em> (Bloch)</td>
<td>A</td>
<td>T</td>
<td>E</td>
</tr>
<tr>
<td>Ostracophilous</td>
<td><em>Leucaspius delineatus</em> (Heck.)</td>
<td>C</td>
<td>T</td>
<td>P</td>
</tr>
<tr>
<td>Guarding and supervising hatch</td>
<td><em>Silius glanis</em> L.</td>
<td>C</td>
<td>T</td>
<td>E</td>
</tr>
<tr>
<td>Phytophilous</td>
<td><em>Gasterosteus aculeatus</em> L.</td>
<td>C</td>
<td>T</td>
<td>P</td>
</tr>
<tr>
<td>Guarding and nesting</td>
<td><em>Pungitius pungitius</em> (L.)</td>
<td>C</td>
<td>T</td>
<td>P</td>
</tr>
<tr>
<td>Ariadnophilous</td>
<td><em>Sander lucioperca</em> (L.)</td>
<td>A</td>
<td>L</td>
<td>E</td>
</tr>
</tbody>
</table>

Fig. 1. Dynamics in the shares of 0+ fish belonging to the amphiboreal freshwater (1), the boreal lowland (2), and the Ponto-Caspian freshwater (3) complexes in lakes Gosławskie (a), Licheński (b), and Ślesiński (c).
(mean 43%). The abundance of the small share of this complex in Lake Gosławskie was noted to fluctuate widely, which was linked to the occurrence of strong generations of roach (boreal complex) and bleak, *Alburnus alburnus* (L.) and stickleback, *Gasterosteus aculeatus* L., (Ponto-Caspian complex). A corresponding degree of fluctuation was confirmed in the boreal complex in Lake Licheńskie. The share of this complex varied over a cycle of approximately ten years, and the highest share of it was noted in catches made in the mid 1970s and 1980s and in the second half of the 1990s when it constituted from 60 to 70% of the fish assemblage. The increased share of species from the boreal complex in Lake Ślesińskie, was preceded by short-term increases in the significance of species belonging to the amphiboreal complex (Fig. 1). This situation occurred in the late 1960s and early 1970s and in the second half of the 1990s.

**THERMAL AND REPRODUCTIVE GROUPS**

The fish species confirmed during the current study belong to three thermal groups (Table 1). The most abundantly represented species are thermophilic (15), while the fewest representatives of ichthyofauna in the lakes analyzed belong to eurythermal species that spawn in late spring (3). Species belonging to the thermophilic group dominated in terms of numbers in all the lakes. The dynamics of the share of the particular termal groups varied in the studied lakes. In Lake Gosławskie, the increase in the share of thermophilic species corresponded with the initiation of water heating. In subsequent years, slight fluctuations in the abundance of thermophilic species occurred until the mid 1980s and alternately with the increased share of eurythermal species that spawn in early spring (Fig. 2a). Following this period, there was a short period of domination by eurythermal fish that spawn in late spring (1983-1985), and then, at the cost of thermophilic species, the significance increased of eurythermal species that spawn in early spring. Changes in the share of species that spawn once or in batches were similar (Fig. 3a). Initially, the batch spawners dominated, but in the 1990s they were displaced by fish that spawn once. Fluctuations in the abundance of fish belonging to the various thermal groups was substantially higher in Lake Licheńskie than in Lake Gosławskie. The domination of thermophilic species and batch spawners was periodically interrupted by the domination of eurythermal fish that spawn in early spring (Figs. 2b and 3b). The heating of the waters in Lake Ślesińskie
Fig. 2. Dynamics of the shares of 0+ fish belonging to the eurythermic with early spring spawning (1), eurythermic with late spring spawning (2), and thermophilic (3) groups in lakes Gosławskie (a), Licheński (b), and Ślesiński (c).
Fig. 3. Dynamics of the shares of 0+ fish belonging to single spawning (1) and multiple spawning (2) groups in lakes Gosławskie (a), Licheński (b), and Ślesiński (c).
coincides with the increased share of thermophilic batch-spawning species (bleak, white bream), and from the mid 1970s also with eurythermic species that spawn in late spring (Figs. 2c and 3c). The complete change in the structure of these groups occurred in the mid 1990s, when the share of species that spawn once in early spring increased to 70-90%.

DISCUSSION

Dispersion processes result in the ichthyofauna of freshwater ecosystems being comprised of representatives of various faunistic complexes (Banarescu 1992). The structure of fish assemblages in lakes is shaped by spatial and temporal interactions among a range of internal and external factors. Global processes tend to have a greater impact on the structure of fish assemblages than do regional ones (Van Zyll de Jong et al. 2005). One of the effects of global climate change is the displacement of the representatives of one complex by those from another faunistic group. Changes such as these are often very complicated, can be cyclic, and are dependent on the nature of the processes shaping the ichthyofauna (Nikolski 1970, Tereshchenko et al. 2004). In Lake Licheńskie, periodic fluctuations were confirmed in the share of fish from the boreal complex. The species of this complex dominated in three periods in this lake in ten-year cycles. Due to the limited range of this phenomenon, local factors should be considered to establish its cause. Lake Licheńskie has a stable, short period of water retention and is also the most intensely heated of the Konin lakes (Zdanowski 1994, Stawecki et al. 2007), which is why it can be postulated that in this instance the fluctuations in fish abundance are rather linked to the occurrence of strong generations (Mooij et al. 1996) and interspecific interactions (Wilkońska 1994b) than to the immediate impact of abiotic factors.

Using the lake as a reservoir for power plant post-cooling waters has effected radical modifications in environmental conditions. The range and rate of the changes depend foremost on the volume of post-cooling waters released into the lake (Zdanowski 1994). Modifications of hydrological, thermal, and trophic conditions impacts the structure of the fish assemblages. The increased water flow resulting from the construction of canals increased the possibility for species expansion (Saunders et al. 1991). While the increased water temperature might limit the occurrence of species,
the lack of them in the basin does not necessarily indicate that temperature is the limiting factor (Lampert and Sommer 2001).

The Konin lakes differ in morphology and the intensity and period of water heating, but their ichthyofauna is comprised of species from the same faunistic complex. The species richness of the fish assemblages were very similar in all the lakes studied. This is why it can be assumed that the conditions shaping the fish assemblages were similar. The occurrence of cold water species in the Konin lakes was limited by water heating. Currently, these fish occur most numerously and most frequently in Lake Ślesińskie, which is the coolest lake in the system and also that which has been heated for the shortest period. Additionally, the thermal and hydrological conditions of the studied lakes, are more advantageous to multispawners species. This type of spawning lessens the possibility of the young generation dying out completely under the influence of disadvantageous abiotic conditions and ensures better feeding conditions for the larvae that are beginning to feed on plankton (McEvoy and McEvoy 1992). Juvenile stages of nearly all fish species feed on zooplankton for either shorter or longer periods (Miller et al. 1988), which is why their development, survival, and growth are positively correlated with the plentiful occurrence of the appropriate prey (Pepin et al. 2003). The development of zooplankton in the Konin lakes is limited by high mortality that occurs in the cooling systems (Tunowski 1988, 1994), the continual weakening of populations, water heating and short retention time, and pressure from planktivorous fish (Ejsmont-Karabin and Węgleńska 1988). This means that when the larvae switch to exogenous feeding, they often starve (Wilkońska and Strelnikova 2000), which ultimately leads to significant losses among 0+ fish (Wilkońska 1994a). In the first years of heating in the lakes studied, the domination of batch-spawning species probably resulted from the dynamic changes in the ecosystem (Hillbricht-Ilkowska and Zdanowski 1988, Zdanowski 1994). Meanwhile, in the 1990s the increasing share in catches of roach, a species that spawns once, may suggest that this fish has achieved a certain degree of adaptation to the prevailing conditions (Wilkońska 1994b, Ciepielewski 1994).

Independently of biotic and abiotic factors that shape the species richness and ichthyofauna structure, spatial isolation does have a fundamental impact on the structure of fish assemblages. The consequences of the spatial isolation of lakes might be of decisive importance in understanding the primary factors that shape populations
and fish assemblage dynamics and also impact the regulation and protection of fish stocks (Olden et al. 2001). In the case of the Konin lakes, the substantial similarity in ichthyofauna composition is the result of the small level of isolation of the individual lakes. The small distances among the studied lakes and the construction of canals that either directly or indirectly connect them means that the assemblages in the individual lakes do not exhibit a great degree of distinctiveness.

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STRESZCZENIE

DŁUGOTERMINOWE ZMIANY W ZESPOŁACH RYB 0+ W LITORALU JEZIOR PODGRZEWANYCH. II. STRUKTURA GATUNKOWA

Przedmiotem badań była charakterystyka zoogeograficzna zespołów ryb 0+ zasiedlających jeziora różniące się morfometrią oraz intensywnością i długością okresu podgrzewania wód. W czasie badań złowiono larwy i narybek należący do 24 gatunków, 3 zespołów faunistycznych oraz 3 grup termicznych (tab. 1). Najliczniejsza grupa gatunków pochodzi z zespołu borealnego równinnego (10) i pontokaspijskiego słodkowodnego (10), a najmniejsza z amfiborealnego słodkowodnego (3). We wszystkich jeziorach najliczniej występują ryby należące do kompleksu pontokaspijskiego. Natomiast uwzględniając wymagania termiczne stwierdzono, że najliczniej reprezentowane są gatunki termofilne (15), a najmniej przedstawieni w ichtiofaunie analizowanych jezior należy do gatunków eurytermicznych o tarle późnowiosennym (3). Znaczna zbieżność składu ichtiofauny badanych jezior była efektem niewielkiej izolacji przestrzennej poszczególnych zbiorników oraz podobieństwa warunków środowiskowych kształtujących zespoły ryb 0+.