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RELATIONSHIP BETWEEN THE ABUNDANCE OF LARVAE AND JUVENILE STAGE ASSEMBLAGES AND THE OCCURRENCE OF MACROPHYTES IN THE SHALLOW LITTORAL OF LAKE LICHEŃSKIE

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ABSTRACT. The aim of this paper was to identify the relationship between the degree of macrophyte cover on the lake bottom and the abundance and species richness of larva and juvenile stage assemblages. The analysis of the material verified the hypothesis that as the surface area of macrophyte cover increases so does the abundance, species richness, and diversity of fish aggregations. The investigations were conducted in the heated Lake Licheńskie in 2000-2003 during the period when underwater vegetation is at the height of development (June – September). The spatial differentiation of macrophyte occurrence had a significant impact on the occurrence and differentiation of the fry assemblages. It was confirmed that along with an increase in the macrophyte cover surface area there was also an increase in the species richness and diversity of juvenile fish assemblages. The locations that were most densely overgrown with vegetation had the highest fish biomass and individual weight. In littoral areas without macrophytes, abundant single-species concentrations of fish occurred. The bottom macrophyte cover did not have an impact on the numbers of fish.

Key words: JUVENILE STAGES, BOTTOM MACROPHYTE COVER, SPECIES RICHNESS, DIVERSITY, HEATED LAKES

INTRODUCTION

Aquatic vegetation is present in all types of inland waters. Its occurrence depends on light conditions, bottom topography, bottom sediment types, and water wavy motion (Duarte et al. 1986). The surface area of the littoral depends on the shape of the lake basin and the degree to which the shoreline is developed. Submerged vegetation usually occupies a significant amount of the surface area of shallow lakes, and its role in ecosystem processes decreases as the size of the lake increases (Carpenter and Lodge 1986).

The temporary and spatial differentiation in abundance and occurrence exhibited by littoral fish assemblages depend on the presence and species composition of macrophytes, among other factors (Hosn and Downing 1994, Growns et al. 2003).

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Due to its high water temperature and oxygen content, the nearshore zone offers advantageous conditions for the development of the spawn and youngest fry of many fish species (Petr 2000). Thickets of aquatic vegetation provide excellent refuge from predators (Savino and Stein 1989, Hindell et al. 2000). Additionally, few of the larger animals that feed on hatchlings and fry take the risk of feeding in shallow waters. Protection against predators and the opportunity of obtaining food are the two main factors that can explain the high densities of fish and food resources in littoral habitats rich in a diversified phytocoenosis structure (Carpenter and Lodge 1986, Rozas and Odum 1988).

Macrophytes enlarge the structure of the habitat impacting the diversity and abundance of animal assemblages. The abundance and diversity of fish assemblages are higher in habitats with macrophytes than in those without vegetation (Branzner and Magnuson 1994, Xie et al. 2000). The choice of habitat by the fish often depends on the presence of macrophytes, while the formation of different fish assemblages is related to the occurrence of diversified microhabitats (Chick and McIvor 1994).

There is a lack of information in Poland regarding the relationship between fish assemblages and the macrophyte content of lakes. The majority of publications that describe the fish-macrophyte bottom cover relationship in various water bodies in the world pertain to adult fish. This is also why the aim of the current work was to describe the relationship between the degree of macrophyte bottom coverage and the abundance, biomass, and species richness of larva and juvenile assemblages.

MATERIALS AND METHODS

STUDY AREA

Lake Licheńskie (52°18′N, 18°20′E), with a surface area of 147.6 ha and an average depth of 4.5 m, is a shallow, eutrophic, natural water body located in central Poland (Fig. 1). It is connected through a system of canals to lakes Ślesińskie and Pątnowskie. Since 1958 the lake has been part of the cooling system of the Pątnów and Konin Power Plant through the discharge channel located along the southwestern bank of the lake (Zdanowski 1994b). Of the five lakes that comprise the cooling system, Lake Licheńskie has the highest water temperature reaching as much as 32°C in nearshore areas in hot summers. The volume of post-cooling waters released into the lake range from 8.0 to 27.0 $m^3 s^{-1}$, and the residence time is approximately five days. The lake is mixed to the

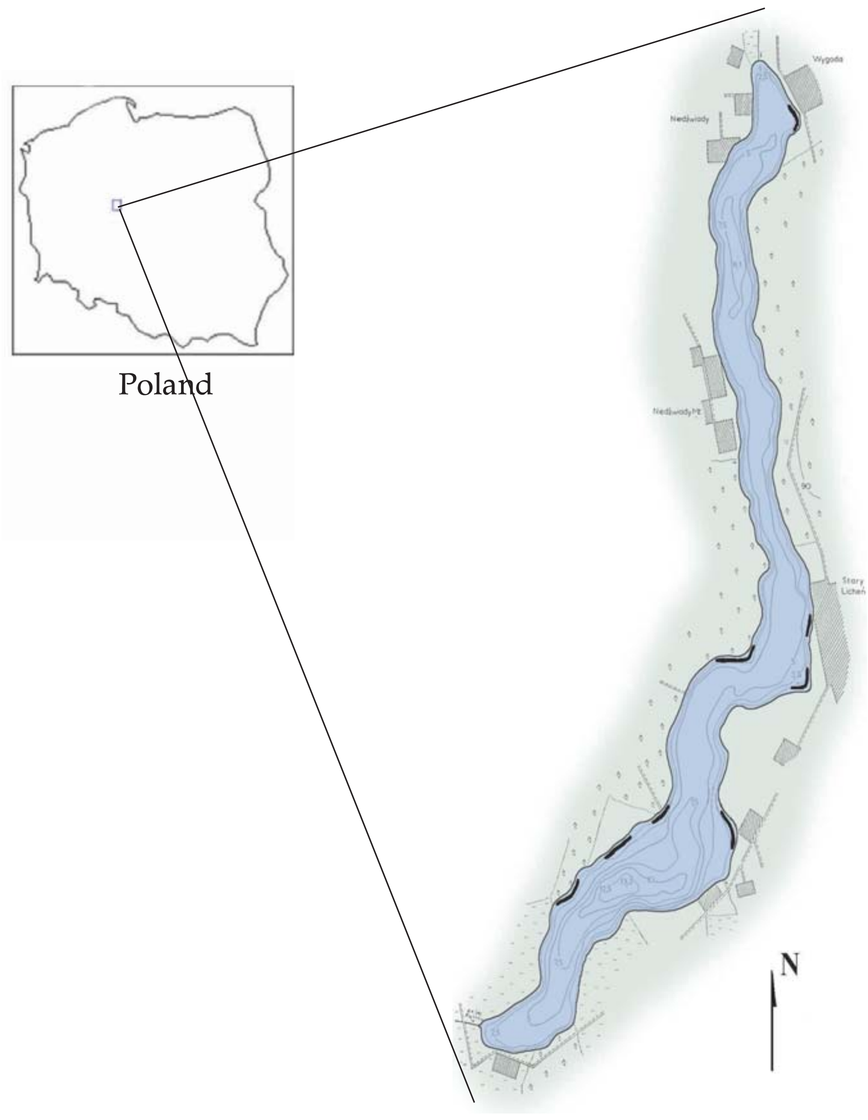

Fig. 1. Bathymetric map and location of Lake Licheńskie.

bottom beginning in early spring until late fall. The northern and southern shores, which are heated to a lesser degree, can freeze over in cold winters (Zdanowski 1994a).

The littoral of Lake Licheńskie is dominated by tape grass, *Vallisneria spiralis* L., an exotic macrophyte species in Polish waters that has occurred here since the early 1990s (Hutorowicz et al. 2003). It is a green, stolonate species that inhabits the shore zone; it occurs in Lake Licheńskie to a depth of 3 meters. Other species that occur sporadically in this lake include *Ceratophyllum demersum* L., *Najas marina* L., *Nuphar lutea* (L.) Sibth. & Sm., *Myriophyllum spicatum* L., *Potamogeton pectinatus* L., *P. lucens* L., *P. perfoliatus* L. and *P. natans* L. Patches of *Phragmites communis* Trin grew in a small, shallow area near the shore.

The sampling sites were designed so that the littoral assemblages were as diversified as possible and the large sampling areas (500-800 m^2) were as homogeneous as possible. Due to the hydrotechnical structure on the southeastern shore of the lake, this area was omitted from the study. The term "shallow littoral" refers to the area that is delineated by the shoreline on one side and the 1 m isobath on the other. The surface area of the shallow littoral was determined with satellite GPS to be approximately 13.5 ha.

MACROPHYTE STUDY METHOD

The study encompassed vegetation that was submerged (Elodeids and Isoetids) and that with floating leaves (Nimfeids), which are referred to collectively in this paper as "macrophytes". The Casper and Krausch (1980) and Matuszkiewicz (2001) keys were used to identify the macrophytes. At sites where fish were caught, the surface area of the bottom overgrown with vegetation was measured. Next, in the areas where catches were conducted, the percentage of bottom covered by macrophytes was estimated visually (Braun-Blanquet 1964) with the following five-degree scale: 0 (no vegetation); I (1-25%); II (25-50%); III (50-75%); IV (> 75%). In order to describe the impact of vegetation on the fry assemblages, the samples obtained were categorized depending on the abundance of macrophytes occurring within the area of the fishing grounds.

FISH CATCHES

The material was collected during catches with a fry net measuring 5 × 0.6-0.8 m (mesh bar length 1 mm) from April to September in 2001-2003. Catches were conducted either once or twice monthly in the nearshore zone following procedures that ensured that the area of each haul was identical and the net extended from the water surface to the bottom. The net was weighted with a groundrope that adheres to the bottom during catches. In order to reduce the impact of the diel variation in fish activity, catches made on sunny days were conducted at the same time (09.30 – 14.30). The fish caught in each haul were placed in separate containers and preserved in a 4% formaldehyde solution. Species were identified under a stereo microscope based on anatomical and morphological characters (Koblickaya 1966, Mooij 1989, Pinder 2001).

ANALYSIS OF FISH ASSEMBLAGE PARAMETERS

The structure and diversity of the fish assemblages was described by analyzing the following: abundance; permanence of occurrence; biomass; average fish body weight, species richness described as the number of species occurring in the sample (S); species diversity described by the Simpson species diversity coefficient (Magurran 1988). The abundance of fish at the fishing grounds was determined using the method proposed by Zippin (1958) and taking into account the littoral catch effectivity model of Pierce et al. (1990). The biomass of the fish caught was calculated for surface area units disregarding the effectiveness of the gear used. The permanence of occurrence was described as the ratio of the number of hauls in which a given species was found to the total number of hauls. The analysis of the relationship between the degree of bottom covered by macrophytes and the abundance, biomass, and species richness of the larva assemblages and juvenile stages was performed with samples from months in which the macrophytes achieved the greatest degree of vegetative development (June - September).

STATISTICAL ANALYSES

The distribution of the variables and homogeneity of variance were verified with the Shapiro-Wilk and Levene tests. Neither the transformation (log(x+1)) nor standardization of data produced normal distributions. Thus, the hypothesis of a significant difference between the parameters that describe fish assemblages in the various classes of macrophyte bottom cover was verified with the non-parametric analysis of variance (Kruskal-Wallis test). After obtaining a statistically significant value using the Dunn test, the groups that differed were determined. In order to identify sets and to more easily illustrate the obtained results, the curve was fitted to the average values using the least squares method weighted with distances. The statistical analyses were done with STATISTICA 6.0 and GraphPad Prism 4 software.

RESULTS

Approximately 41000 larvae and juveniles belonging to 20 species were caught (Table 1).

TABLE 1

Species composition of larvae and juvenile fish in Lake Licheńskie in 2001-2003 categorized by permanence of occurrence and relative abundance

Species	Percentage in catches		Permanence of occurrence
	Abundance	Biomass	
Alburnus alburnus (L.)	67	34	58
Rutilus rutilus (L.)	23	39	49
Scardinius erythrophthalmus (L.)	4	15	36
Tinca tinca (L.)	2	5	36
Abramis bjoerkna (L.)	2	3	28
Pseudorasbora parva (Schlegel)	1	<1	6
Abramis brama (L.)	<1	<1	10
Carassius gibelio (Bloch)	<1	1	4
Perca fluviatilis L.	<1	1	8
Leuciscus cephalus (L.)	<1	<1	9
Rhodeus sericeus (Bloch)	<1	<1	3
Cyprinus carpio L.	<1	<1	1
Gasterosteus aculeatus L.	<1	<1	2
Sander lucioperca (L.)	<1	<1	<1
Gobio gobio (L.)	<1	<1	<1
Cobitis taenia L.	<1	<1	<1
Silurus glanis L.	<1	<1	<1
Esox lucius L.	<1	<1	<1
Gymnocephalus cernuus (L.)	<1	<1	<1
Oreochromis niloticus (L.)	<1	<1	<1

The highest abundance of fish in the 0+ age group that reached a maximum of approximately 260 indiv. m^{-2} was recorded in May. The highest species richness was noted in June (Table 2).

TABLE 2

Species richness, total number, and biomass of larvae and juvenile fish caught in Lake Licheńskie 2001-2003 (N – number of hauls)

Month	N	Species richness	Number (indiv.)	Biomass (g)
April	27	5	241	4.0
May	40	12	19069	957.4
June	34	14	12179	1740.5
July	31	11	6989	1637.3
August	24	11	1652	1833.0
September	27	11	1271	1052.7

Two species – bleak, *Alburnus alburnus* (L.), and roach, *Rutilus rutilus* (L.), dominated in the littoral of Lake Licheńskie, and cyprinids comprised the most abundant and the most frequently caught fish group. Of them, five species comprised approximately 98% of all the fish caught.

The impact of the occurrence of submerged vegetation is visible in the increases in diversity ($P < 0.0001$, $N = 97$) and species richness of juvenile assemblages ($P < 0.0001$, $N = 97$). As the surface area of macrophyte cover increased, a significant increase occurred in the diversity and species richness of juvenile assemblages (Fig. 2).

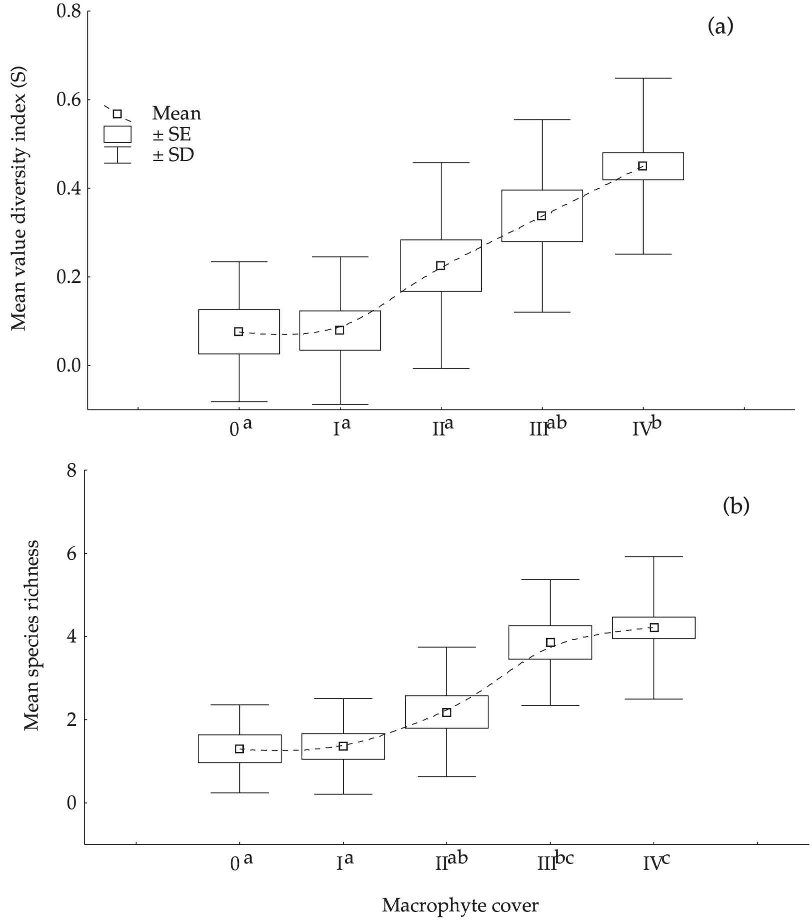

Fig. 2. Comparison of diversity (a) and species richness (b) of juvenile fish assemblages and macrophyte cover (0 – no vegetation, I – 1- 25%, II – 25-50%, III – 50-75%, IV –above 75%. The broken line curve was fitted with the least squares smoothing procedure. Data denoted with the same letter index do not vary significantly statistically (P > 0.05).

In locations without submerged vegetation, either one fish species or no fish at all occurred most frequently (Fig. 3). Most often very abundant densities of roach and bleak occurred periodically in these areas. When macrophytes covered over 75% of the bottom (class IV) most often four to five species of juvenile fish were noted. There was a statistically significant relationship between the biomass of juvenile stages in the littoral ($P < 0.0001$, $N = 97$) and the average weight of fish ($P = 0.0003$, $N = 97$) and the abundance of macrophytes. The biomass and weight of fish caught in zones with abundant submerged vegetation was higher (Fig. 4). The robust development of macrophytes stimulated the occurrence of a larger number of species and more diversity in the juvenile stage assemblages. However, the average abundance of juvenile fish was not related to the amount of macrophyte cover on the littoral bottom

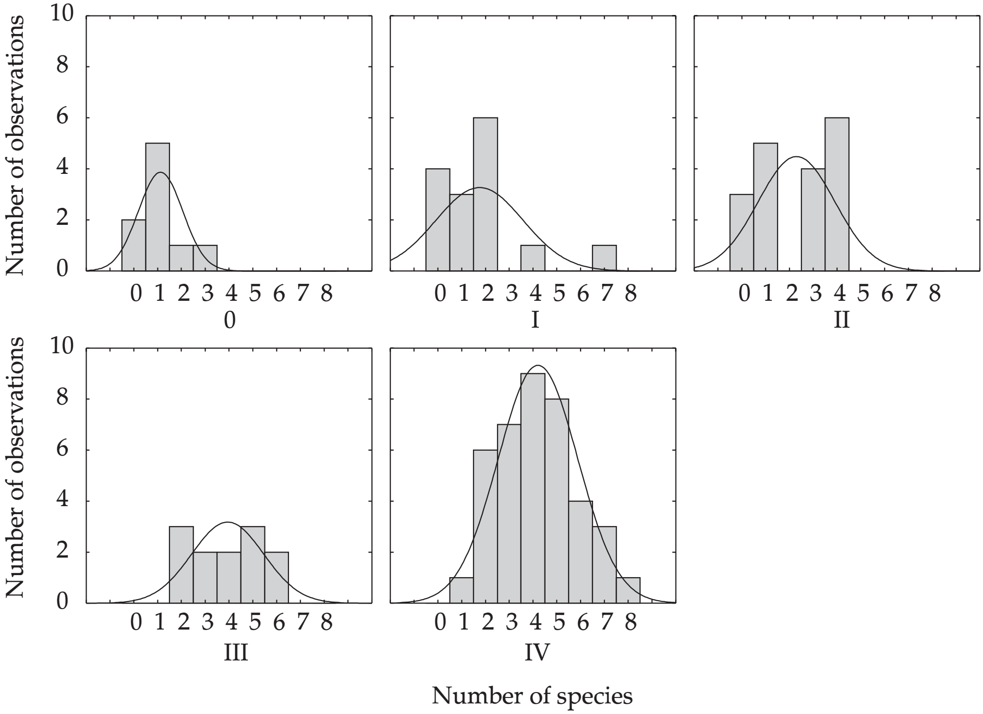

Fig. 3. Categorized histogram of the number of fish species in comparison with macrophyte cover. The line denotes the normal distribution. Descriptions as in Fig. 2.

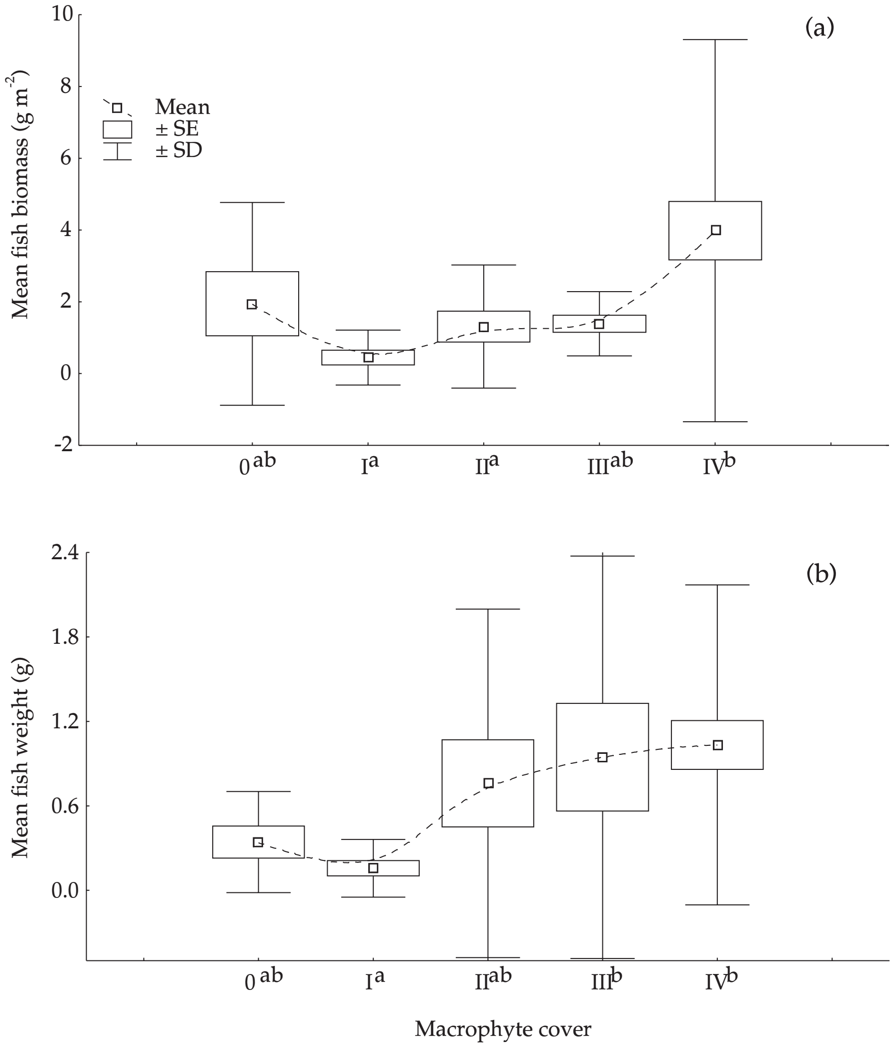

Fig. 4. Comparison of the biomass (a) and weight of caught fish (b) and macrophyte cover. Description as in Fig. 2. Data denoted with the same letter index do not vary significantly statistically ($P > 0.05$).

($P = 0.0649$, $N = 97$). Regardless of the surface area covered by macrophytes, the fish densities were similar in all zones (Fig. 5a). Conversely, in August and September (Fig. 5b), when the submerged vegetation covered 80-100% of the littoral bottom, there was a statistically significant decrease in fish abundance ($P = 0.0318$, $N = 97$).

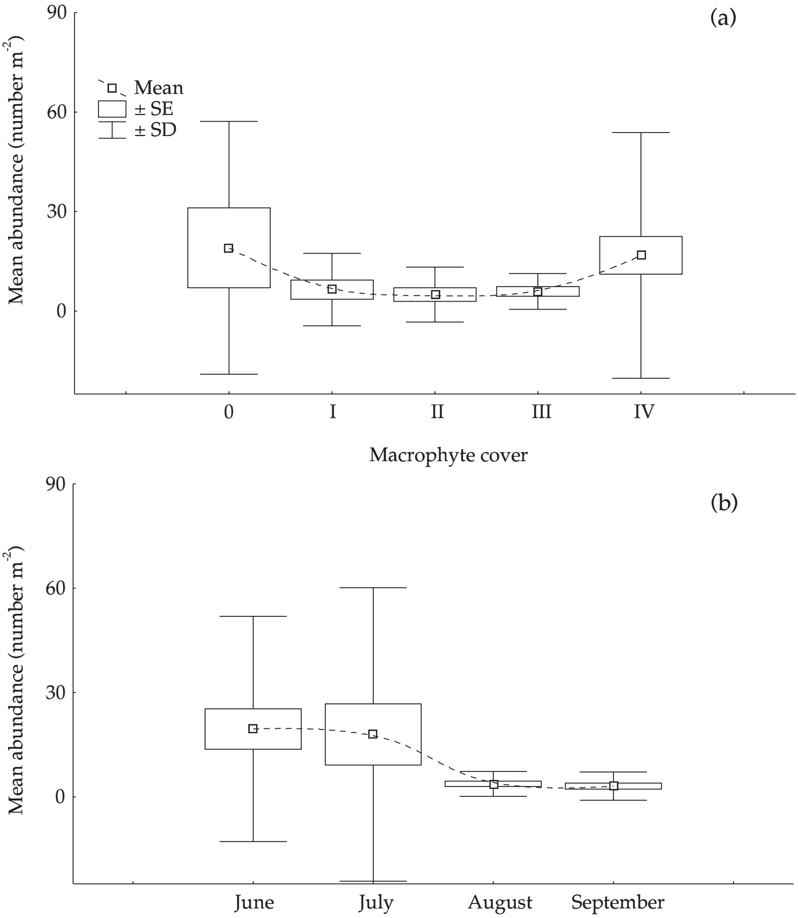

Fig. 5. Comparison of the abundance of juvenile stage assemblages dependent on the macrophyte bottom cover (a) and subsequent study months (b). Description as in Fig. 2.

DISCUSSION

In water bodies without submerged vegetation fry limit their activity to shallow waters (De Vries 1990). In littoral areas with robust macrophyte cover, fish spend approximately eight times more time among the vegetation than they do in open water zones (Chapman and Mackay 1984, Hosn and Downing 1994). Randall et al. (1996), who studied the impact of macrophyte bottom cover on littoral fish assemblages, reported that the production, species richness, and number of fish caught increased along with increased cover. The lowest abundance and number of species were recorded by these authors at sites without submerged vegetation, while the greatest number of species was noted at sites where the macrophytes covered from 30 to 70% of the bottom. The highest abundance was noted, however, when macrophyte cover was at its densest (> 70%). These authors also maintained that the heaviest fish were caught in habitats without vegetation, while the biomass of the fish in all habitats was similar and did not depend on the amount of macrophyte cover on the littoral bottom. Increases in the bottom macrophyte cover in Lake Licheńskie had an impact on the species richness, assemblage diversity, and average body fish weight. It was confirmed that the larvae and juvenile stages of many species prefer habitats that have abundant macrophyte cover. Tape grass was in the growth phase at the height of the juvenile fish assemblage differentiation phase (Hutorowicz et al. 2003). Even in places where growth was thick, tape grass leaves rarely reached the surface, and there was an open water zone above them. This created advantageous conditions for many taxa, which was reflected in the species richness of the fish assemblages. From July the macrophytes reached the surface of the water, and there were few areas free of vegetation. Simultaneously, there was a significant decline in species richness. The macrophyte cover did not have an impact on the abundance of juvenile fish in the littoral, but it was here that factors were identified that shaped the biomass of larvae and juveniles. The highest biomass of juvenile fish was noted in areas either without macrophytes or in those with the most dense submerged vegetation cover, *i.e.*, areas where the most abundant temporary densities of bleak juveniles (0 class) or very abundant juvenile assemblages (IV class) occurred. The effect of this was a statistically significant ($P < 0.0001$) differentiation between fish biomass depending on the degree of bottom macrophyte cover.

Single-species macrophyte meadows do not provide advantageous conditions for large densities of invertebrates; this contributes to a reduction in the diversity of fish assemblages (Keast 1984, Killgore et al. 1989). Macrophytes that are equally distributed on a lake are usually divided into patches of varying size surrounded by open waters with bottoms free of vegetation. The patchiness of macrophyte occurrence increases the structure of the littoral habitat; one consequence of which is an increase in the abundance and diversity of fish assemblages. Conversely, the spatial diversity of the littoral can limit the number of preferred habitats thus limiting the occurrence of species (Matthews et al. 1994, Weaver et al. 1997). The impact of the spread of warm-water tape grass in Lake Licheńskie was the heavy cover on the littoral bottom and in the post-cooling water discharge canal. At the height of its growth, tape grass covered approximately 92% of the shallow littoral (Hutorowicz et al. 2003). This had an impact on the occurrence of rheophile species. In comparison with the period prior to the occurrence of tape grass, significant declines in the abundance and occurrence locations of chub, *Leuciscus cephalus* (L.), were noted (Wilkońska 1994). The distribution of chub in the lake is limited only to the area near the post-cooling water discharge channel. However, small clumps of macrophytes have already created advantageous conditions for tench, *Tinca tinca* (L.), which occur regularly in such places. Increases in the size of macrophyte patches were accompanied by increases in the abundance and biomass of tench. This is evidence of the equivocal impact of the occurrence of tape grass on fish assemblage occurrence. Species that prefer the littoral gained a significant amount of substrate on which to spawn; however, a portion of the fish species that had occurred up to this point in this basin curbed their abundance. One consequence of the lake being overgrown was the disappearance of habitats preferred by many species and the disappearance from the lake, for example, of chub. Additionally, the dense overgrowth of the lake causes increased sedimentation and decreased water flow, and decaying vegetation pollutes the nearshore zone.

CONCLUSIONS

Spatial differences in the distribution of macrophytes had a significant impact on the juvenile stage assemblages. As the surface area covered by macrophytes increased, and increases in the species richness and assemblage diversity of juvenile fish were noted. Fish with the highest biomass and individual weight were noted in locations that were most robustly overgrown with submerged vegetation. Abundant single-species densities of fish were confirmed in littoral zones without macrophytes. The degree of bottom macrophyte cover did not have an impact on the abundance of fish.

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STRESZCZENIE

RELACJE POMIĘDZY LICZEBNOŚCIĄ, BIOMASĄ I BOGACTWEM GATUNKOWYM ZESPOŁÓW NARYBKU A WYSTĘPOWANIEM MAKROFITÓW W PŁYTKIM LITORALU

Celem niniejszej pracy było określenie relacji pomiędzy stopniem pokrycia dna makrofitami a liczebnością, biomasą oraz bogactwem gatunkowym zespołów larw i narybku. Analizując uzyskany materiał weryfikowano hipotezę zakładającą, że wraz ze wzrostem powierzchni zajmowanej przez makrofity rośnie obfitość, bogactwo gatunkowe i różnorodność zespołów ryb. Badania prowadzono w podgrzanym Jeziorze Licheńskim (rys. 1) w latach 2001-2003. W tym okresie złowiono ok. 41000 larw i narybku należących do 20 gatunków (tab. 1). Najwyższe bogactwo gatunkowe stwierdzono w czerwcu (tab. 2). W okresie największego rozwoju wegetacyjnego roślinności zanurzonej (czerwiec-wrzesień) przestrzenne zróżnicowanie rozmieszczenia makrofitów w istotny sposób determinowało występowanie i zróżnicowanie zespołów narybku. Wraz ze wzrostem powierzchni zajmowanej przez makrofity stwierdzono wzrost bogactwa gatunkowego i różnorodności zespołów juwenalnych ryb (rys. 2). W miejscach pozbawionych roślinności zanurzonej najczęściej występował 1 gatunek lub nie stwierdzono występowania ryb (rys. 3). Miejsca najsilniej porośnięte roślinnością zanurzoną charakteryzowały się najwyższą biomasą i osobniczą masą ciała ryb (rys. 4). W strefach litoralu pozbawionych makrofitów stwierdzono występowanie obfitych, jednogatunkowych skupisk ryb. Pokrycie dna makrofitami nie miało wpływu na liczebność ryb (rys. 5).