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DIFFERENCES IN CRUSTACEA PLANKTON BASED ON THE MORPHOLOGICAL CHARACTER OF THE LITTORAL OF THE LAKES*

Examination was made of the planktov *Crustacea* fauna in the littoral of 37 Mazurian lakes. The littoral habitat was classified according to morphological features into the following types of development sequence: the open, the accesible, the sheltered and the separate littorals. The three latter types were dealt with in these investigations. It was found that the proposed classification of the littoral coincides with the differences in the *Crustacea* zooplankton from the aspect of the character of the occurrence exhibited by the species composing it, and confirms the natural correctness of the division made in the habitat.

1. INTRODUCTION

This study forms part of the work carried out on results obtained from investigations of *Crustacea* plankton in the habitats of 37 lakes in the district of Węgorzewo (Mazurian lakes)¹ and constitutes a contribution to research on the formation of hydrobiological relations in the littoral of lakes. The faunistic material and research methods have been described in another study (M. Rybak, J. I. Rybak 1964).

Even a visual assessment of the littoral of lakes makes it possible to state that considerable differences exist in these habitats causing its great variability. A series of links side by side in this chain of variations can usually

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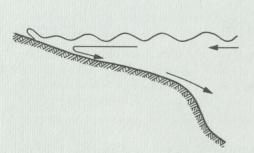
¹Descriptions from the limnological and fishery aspects of these lakes are contained in the exhaustive papers of Institute of Inland Water Fishery (Zawisza, Patalas 1960, Kondracki, Szostak 1960, Bernatowicz 1960, Patalas 1960a, 1960b, 1960c, 1960d).

be found in different lakes in a given region. Among the different principles of classification of littoral habitats the following may be mentioned: 1) differentiation in belts parallel to the edge of the lake and 2) the mosaic-like differences in vegetation (Welch 1935, Lityński 1952, Allee et al. 1958). The way in which the littoral is divided may be based for instance, on floristic character, formation of the bottom, kind of substratum, depth, morphology etc. In the present study we have concentrated on the features deciding the morphological character of the littoral.

Differences in the littoral result, among others, from the action of two opposite processes: 1) differentiating the habitat in the littoral itself and 2) processes levelling out differences and originating in the pelagial. Two opposed factors therefore occur: 1) factors isolating the littoral, leading to stagnation of the water, 2) accessibility to waves, which mix the habitat, carry in pelagial elements, carry away detritus etc. These circumstances, depending on the degree of intensity with which they operate, cause the formation of different easily recognised morphological types.

We have distinguished 4 types in our materials, and these have been partly discussed in the publication by Dobrowolski (1961).

1) Open littoral (latin: *apertus*). The margin is not occupied by vascular plants. Waves freely reach the shore. The bottom is most often stony or sandy. Typical beach. A zone affected by wave movement is situated near the shore, where organic and inorganic particles are deposited, the littoral of this type ends on the lake side in a normal sublittoral where the shells of molluscs settle. The littoral is not isolated in any way from the influences of the pelagial (Fig. 1).



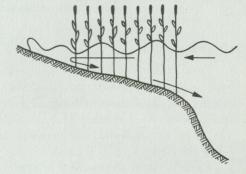
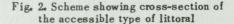


Fig. 1. Scheme showing cross-section of the open type of littoral



2) Accessible littoral (accessus). This type of littoral is usually occupied by reeds not growing densely, which weaken but do not restrain wave movement. There is a belt of unoccupied water between the reeds and the shore of the lake. Waves reach the shore, where a well-formed zone of wave movement is created. Typical sublittoral. This type of littoral is to a certain extent isolated from the influences of the pelagial (Fig. 2).

3) Sheltered littoral (protectus). This type of littoral is most often encountered in the lakes in the Mazurian Lakeland, and is characterised by densely growing reeds reaching right to the shore. Weaker waves do not in general reach the shore, there is no zone of wave movement. Organic particles accumulate in the reeds and are not carried out to the sublittoral. A littoral of this type is isolated to a considerable degree from the influences of the pelagial (Fig. 3). Examination was made in this type of littoral of the boundary between littoral plankton and pelagial plankton, an

unexpectedly sharp transition between them being found (Rybak 1960).

4) Separate littoral (separatus). This type of littoral is almost completely isolated from the pelagial. The water is stagnant. Waves cannot reach the shore through the reed barrier. The littoral between the isolating barrier and the edge of the lake is frequently occupied by soft vascular plants (Fig. 4).

Types of littoral parallel to the trophic sequence of the lakes have been classified in the above descrip-

Isolating barrier

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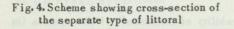
tions. Types 1 and 2 of the littoral are proper to more oligotrophic lakes, and types 3 and 4 proper to more eutrophic lakes, but these connections are of a statistical character only. It is impossible to establish complete adherence to these classes.

This form of classification defines the littoral according to the development sequence consisting in the gradually increasing isolation from the pelagial.

The boundaries between the types of littoral named here are not sharply defined, although each type can easily be distinguished in field investigations.

Apart from this group of littoral habitats there are also different retrogressive forms of the littoral such as, e.g. a sphagnum shore with artificial embankment, landslides etc.

The four types of littoral described above occur in the Węgorzewo group of lakes. Analysis has been



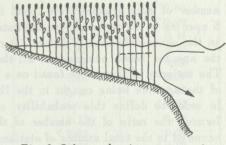


Fig. 3. Scheme showing cross-section of the sheltered type of littoral

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made in the present materials of the types most numerously represented: accessible, sheltered and separate littorals. The sheltered type occurs most frequently the accessible les frequently and most seldom - the separate type.

2. SPECIFIC FAUNA RELATIONS IN THE THREE MORPHOLOGICAL TYPES OF THE LITTORAL

A total of 34 species of *Cladocera* and *Copepoda* were found in all the littoral habitats examined. Eighteen species occurred in the accessible type of littoral, 28 species in the sheltered and 22 species in the separate type. Certain of these species occurred only in the littoral habitats of one type. The largest number of such species were found in the sheltered type habitats (7 species), 5 species in the separate type habitats and only 1 species (*Alona quadrangularis*) in the accessible type of littoral. It can be seen from our materials that none of the species found occurred on all the stations in the littoral of a given type. The majority of them were found on a few stations only. The probability of many of the species being caught in the littoral habitat of a given type was slight². In order to define this probability calculations were made of indices (Tab. I) forming the ratio of the number of these stations in which the given species occurred to the total number of stations of a given type.

Of the total number of 34 species occurring in the littoral stations examined 14 species have only very slight chances of occurring in each of three types of littoral (Tab. I) - value of the index in all the types of littoral did not exceed 0.09. Nine species occurred in one type of littoral only, 4 species in two types, while only 1 species *Alonella nana* occurred in all three types of littoral.

Of the list of 34 species 16 were not found in littorals of the accesible type. There was little chance of 8 other species being found. In littoral habitats of the sheltered lake type the figures are respectively: 6 species were not found at all, and 13 species had little chance of being found. In separate type habitats a total of 12 species were not found, and 9 had only slight chances of occurring (Tab. I).

The group of species possessing considerable chances of being found in all the types of habitats are given in Table II, from which it will be seen that the number of species with high probability of being found is smallest in the accessible type of littoral, is larger in the sheltered type, and largest in the separate type of littoral.

The majority of the littoral stations were settled by a small number of species. In the accessible type of littoral only 1-6 species were found on 92.9% of the stations; the same number on 77.5% of the sheltered type of littoral, while in the separate type there is no great difference in the number of stations represented by 1-6 species, or by 7-10 and more (Tab. III). It is clear from

²We distinguish between "index of probability of encounter" of the species (in a given physiographical region) and so-called "frequency", the latter being calculated from the same formula, but referring to one station uniform from the habitat aspect.

Probability of finding species in each type of littoral

m	1	T
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Species	Accessible type 14 stations	Sheltered type 32 stations	Separate type 11 stations
1 – Daphnia longispina	< 0.07*	< 0.03	0.09
2 – Daphnia cucullata**	< 0.07	0.06	< 0.09
3 — Sida crystallina	0.28	0.21	0.45
4 - Diaphanosoma brachyu-	and the second	energy 1 1 to drag is to	a subspaces
гит	0.35	0.56	0.36
5 – Ceriodaphnia reticulata	0.07	0.12	< 0.09
6 – Ceriodaphnia megops	0.35	0.50	0.55
7 – Ceriodaphnia quadrangula	0.71	0.65	0.64
8 – Simocephalus vetulus	0.14	0.03	< 0.09
9 — Scapholeberis mucronata	0.14	0.12	0.18
10 — Bosmina longirostris**	0.50	0.43	0.45
11 – Bosmina coregoni**	< 0.07	0.06	0.09
12 — Eurycercus lamellatus	< 0.07	0.03	0.09
13 — Acroperus harpae	0.21	0.43	0.45
14 — Alona costata	< 0.07	0.03	< 0.09
15 – Alona guttata	0.07	0.15	0.09
16 – Alona rectangula	< 0.07	< 0.03	0.27
17 — Alona quadrangularis	0.07	< 0.03	< 0.09
18 — Alonella nana	0.07	0.09	0.09
19 – Alonella excisa	< 0.07	0.12	< 0.09
20 — Allonella exigua	< 0.07	< 0.03	0.09
21 — Camptocercus lilljeborgii	< 0.07	0.03	0.18
22 - Pleuroxus striatus	0.07	0.03	< 0.09
23 — Pleuro xus aduncus	0.07	0.15	0.09
24 – Pleuro xus uncinatus	< 0.07	0.06	< 0.09
25 — Peracantha truncata	0.07	0.12	0.27
26 - Chydorus sphaericus	0.14	0.31	0.55
27 — Graptoleberis testudinaria	< 0.07	0.03	0.09
28 – Polyphemus pediculus	0.21	0.15	< 0.09
29 — Cyclops vicinus	< 0.07	< 0.03	0.18
30 — Cyclops scutifer	< 0.07	0.06	< 0.09
31 - Mesocyclops (Th) crassus		0. 18	0.09
32 - Mesocyclops oithonoides	< 0.07	0.03	< 0.09
33 - Ectocyclops phaleratus	< 0.07	0.03	< 0.09
34 – Diaptomus graciloides	< 0.07	< 0.03	0.18

* Symbol " < " indicates occurrence in the habitat of a number of individuals smaller than the threshold value for the method used.

** Varieties within the species are not given. This is the result of fundamental uncertainty as to the ecological value attributed to these very labile units (unpublished material). This question cf. also Rybak, Rybak (1964).

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Distribution of species with greatest probability of being found in each type of littoral

Tab. II

Separate type	Sheltered type	Accessible type
	Separate type	Separate type Sheltered type

Distribution of littoral stations acc. to number of species Crustacea plankton

Tab. III

	Accessible	type	Sheltered	type	Separate type		
Number of species	Number of stations	%	Number of stations	%	Number of stations	%	
1-3	7	50.0	11	35.5	3	27.3	
4-6	6	42.9	13	.42.0	3	27.3	
7-9	- Lothe	-	6	19.4	3	27.3	
10 and more	1	7.1	1	3.1	2	18.1	

this that qualitatively the fauna of the accessible type of littoral is the poorest, and the fauna in the separate type the richest.

3. PERCENTAGE OF UBIQUITOUS AND PELAGIAL (I.E. IMMIGRANT) SPECIES IN THE CRUSTACEA PLANKTON FAUNA OF 3 MORPHOLOGICAL TYPES OF LITTORAL

The 34 species found were divided into 3 groups: littoral, pelagial and ubiquitous (Rybak, Rybak 1964). Species not typical of littoral habitats were included in the composition of the two last groups. These species occurred however in the great majority of the stations examined. It was only on 5 stations that not one species of this character were found (2 in the accessible type, 2 in the separate type and 1 in the sheltered type). These species occurred in numbers from 1 to 8 on all other stations examined (Tab. IV). The number of non-specific species most often encountered differed depending on the type of littoral. In the majority of the habitats of the accessible type (on 13 of the 14 stations examined) from 0 to 3 such species were encountered. In the sheltered type of habitats from 1 to 4 non-specific species were most often found (on 30 out of 32 stations examined). From 2 to 4 species of this type were found on the majority of the stations of the separate type (7 stations out of 11 examined - Tab. IV).

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Number of stations in the littoral acc. to the increase in number of non-specific species

Tab. IV

Number of non-specific	Number of littoral stations								
species	Accessible type	Sheltered type	Separate type						
0	2	1	2						
1	.4	8	1						
2	.4	11	2						
3	3	6	2						
4	1	5	.3						
5	0	0	1						
6	0	0	.0						
7	0	0	0						
8	0	1	0						

The number of non-specific species occurring on the stations varies depending on the type of littoral: it is smallest in the majority of habitats of the accessible type, and largest in habitats of the separate (Tab. IV).

In littoral habitats in which the greatest number of non-specific species occurred, a total of 10 such species was found, 4 of which were pelagial. Three species also occurred frequently in all the types of littoral. These are ubiquitous species – Bosmina longirostris, Ceriodaphnia quadrangula and Diaphanosoma brachyurum. The remaining 7 species were found to occur mainly in the sheltered and separate types of habitats, and rarely appear in habitats of the accessible type. These are either pelagial species: Daphnia cucullata, Diaptomus graciloides, Cyclops scutifer and C. vicinus, or ubiquitous species: Chydorus sphaericus, Bosmina coregoni, Mesocyclops (Th.) crassus. The lack of occurrence of pelagial species despite the free penetration there of water from the middle of the lake, in the littoral which is most accessible to wave movement is remarkable. It is possible that it is a question here of the sensitiveness of these forms to the effects of being beaten against hard underwater obstacles in the constantly moving water of the littoral.

4. DOMINATION OF SPECIES IN EACH TYPE OF LITTORAL

The species represented by the greatest number of individuals in a given littoral habitat was taken as a dominating species, percentages never being lower than 25% of the total number of individuals of all the species. In the case of an equal number of individuals of two or more species they were considered as jointly dominating.

The littoral stations examined were fairly considerably differentiated from the aspect of the domination of different species (Tab. V and VI). This differentiation was especially distinct in habitats of the separate type, in almost

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Littoral of the accessible type Dominating species	Biała Kuta L ₁ 13.IX.54	Głęboka Kuta 14.IX.54	Lemięt 31. VIII. 54	Swięcajty 10.IX.54	Brzozówka 3.IX.54	Duźy Siniec 17.IX.54	Krzywa Kuta L ₁ 13.IX.54	Piecek L ₁ 19. VII. 54	Żywy L1 15.IX.54	Krzywa Kuta L ₂ 13.IX.54	Stregiel L ₂ 9. VII. 54	Rydzówka La 4. VIII.54	Gołdopiwo L2 2.1X.54	Głęboka Kuta 10.IX.55
Ceriodaphnia quadrangula Ceriodaphnia megops	x	x		x x	x				x					
Bosmina longirostris Acroperus harpae Diaphanosoma brachyrum	Ree	n eX		x	8	x	x	x	x	x				
Polyphemus pediculus Ceriodaphnia reticulata Simocephalus vetulus Scapholeberis mucronata	silo a	0_80 \$2.00	0.03	00 A	oin a allas	18. 2. 19. 31	Line al.:	18-18 a 105	11. 10 14. 14	, and	x	x	x	x

Cases of domination of Crustacea plankton

Littoral of the sheltered type Dominating species	Żywy L 1 15.IX.54	Węgielsztyńskie 13. VII.55	Przyleśne L ₂ 25. VIII. 55	Wilkus L ₂ 14.VIII.54	Bimbinek L I 3.IX.54	Soltmany L ₁ 15.IX.54	Krzywa Kuta L ₃ 13.1X.54	Mały Siniec 17.IX.54	Oświn L ₂ 14.IX.54	Ciche 23.VIII.54	Surwille 6. VIII.54	Piecek L ₁ 19, VII.54	Czarna Kuta L ₁ 14.IX.54
Ceriodaphnia quadrangula Acroperus harpae Ceriodaphnia megops Bosmina longirostris Diaphanosoma brachyurum	x	x	x	x	x	x	x	x x	x x	x	x	x	x
Polyphemus pediculus Pleuroxus aduncus Chydonus sphaericus Alona guttata	certer i la sub la suble Cassioni		s pris type a filte action								in the	lerne IV),	
Mesocyclops (Th) crassus Daphnia cucullata Ceriodaphnia reticulata Bosmina coregoni	a alan Matan Malad		akji Loos	o dest Danti	iena iveito	olina na dia nana	12 - 04 20-94	is to trea	sea parte bath	an da a da a da		ident detteb	

Cases of domination of Crustacea plankton in

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Differences in (
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Crustacea	
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littoral habitats of the accessible and separate types

Ceriodaphnia quadrangula Ceriodaphnia megops Bosmina lor girostris Acroperus harpae Pleuroxus aduncus Alona rectangula Alona quadrangularis Bosmina coregoni Bosmina coregoni Mesocyclops (Th) crassus Cyclops vicinus	Littoral of the separate Dominating species
×	Jagoczany 20. VIII. 55
×	Arklickie 1.IX.54
×	Pniewskie L ₁ 10.VII.54
ж	Łękuk 16.IX.54
н	Purwin 24. VIII. 55
×	Rominty L ₂ 16. VII. 55
м	Bartelnik 9. VII. 55
×	Arklickie 26.VIII.55
н	Jagoczany 124.VIII.54
н	Rominty L1 16.VII.55
×	Pniewskie L ₂ 10.VII.54

in the littoral habitats of the sheltered type

Tab. VI

	Siewki
×	3.IX.54
×	Pozezdrze 16.IX.54
н н	Babka 5.VIII.54
х х	Kirsajty L ₁ 10.VII.54
ни н	Silec L ₁ 17.IX.54
H	Białe 2.IX.54
н н	Rydzówka L2 4.VIII.54
H	Bimbinek L ₂ 3.IX.54
н	Kirsajty L 2 10.VII.54
нн	Wilkus L ₁ 14.VIII.54
H	Przerwanki 24. VIII.55
11. 124 183	Przyleśne L ₁ 14.VIII.54
×	Przyleśne L ₁ 25.VIII.55
×	Gołdopiwo L ₂ 2.IX.54
×	Przyleśne L ₁ 14. VIII.54
×	Stręgiel L 1 9.VII.54
×	Upinek L ₁ 31.VIII.54
н	Rydzówka L 2 4.VIII.54
	Żabinki 5.VIII.54

[9]

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each of which a different species dominated. In all in the 11 littoral stations examined of the stagnant type, the domination of 10 different species was established (Tab. V).

In 32 littoral stations of the sheltered type as many as 13 species occurred as dominants. The reat majority of the stations (28) had joint dominants, the species most often encountered being *Ceriodaphnia quadrangula*, then *Bosmina longirostris.*] Of the remaining species - 2 dominated in 4 habitats, 1 species in 3 habitats, and the remainder completely sporadically (1-2 stations) (Tab.VI).

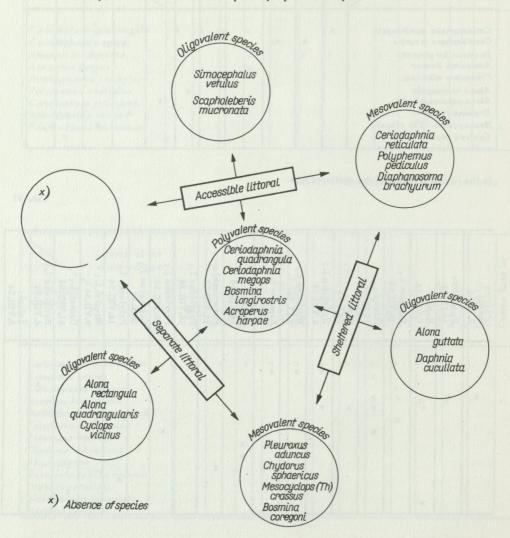


Fig. 5. Scheme showing differences in the dominating species in different types of littoral

A total of 9 species dominated in 14 littoral stations of the accessible type - most often *Bosmina longirostris* and *Ceriodaphnia quadrangula*. The remaining species were dominants only in 1 or 2 habitats (Tab. V).

The specific coincidence of occurrence in the domiration of different species with defined types of the littoral is illustrated by a scheme (Fig. 5).

As can be seen from this plan there are only a few polyvalent species, that is, species which can dominate in all three types of littoral. The remainder either dominate only in one of them (oligovalent), or in two (mesovalent): accessible and sheltered, or sheltered and separate types. It is interesting to find that there are no species (apart from polyvalents) dominating simultaneously in habitats of the accessible and separate types (Tab. V, Fig. 5). These are habitats with extreme specialisation: one in the direction of accessibility to water from the lake, the other in the direction of stagnation.

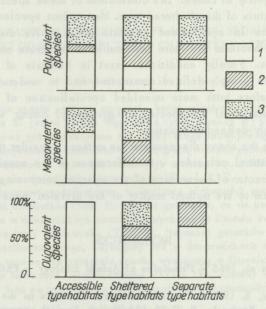


Fig. 6. Percentage of habitats with different degree of sharpness of domination of species in different types of littoral

1 - sharply defined domination, 2 - moderate domination, 3 - unformed domination

If we compare the degree of domination then we find that the particular species did not occupy the littoral habitats to a uniform degree.

The stations examined were divided into three groups: 1) with sharply-defined domination of species — these are stations where the given species dominated very distinctly, 2) stations with moderate domination, where the species occupied the habitat less distinctly; and finally, 3) stations with unformed domination, where there was no dominating species or it occupied the habitat

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to an insignificant degree. These relations, connected with data from preceding discussions, are shown jointly in Fig. 6.

An analysis of the material shows that in habitats more specialised, i.e. in habitats of the accessible type — with a high degree of contact with the mass of the lake water and in habitats of the separate type — the most isolated type of habitat — that there are clearly more favourable conditions of sharply — defined domination for the species occupying the habitat, this taking place to a greater degree in habitats of the accessible type than in habitats of the separate type. Habitats of the sheltered type, on the other hand, exhibit a geater tendency to more faintly defined, moderate domination, particularly for species occupying other types of habitat also.

In assessing the degree of domination of species according to their valency it must be stated that the oligovalent, more specialised species dominate sharply in the majority of cases. The domination of these species is not formed only in a few habitats of the sheltered type. Mesovalent species exhibit sharply defined domination in specialised habitats also, while conditions in the sheltered type of habitats are more favourable to moderate and not distinctly formed domination. Finally conditions exist in habitats of all three types favourable both to sharply-defined domination and to moderate and unformed domination. Therefore both more onesided specialisation of the habitat and narrower specialisation of the species (oligovalency) concur with the frequent formation of sharply-defined domination.

In summing up the above discussions the authors consider that the proposed division of the littoral coincides with differences in the zooplankton from the aspect of the character of occurrence of the species composing it. This proves the correspondence to the natural reality of the division made of the habitats.

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ZRÓŻNICOWANIE PRZYBRZEZNEGO PLANKTONU SKORUPIAKOWEGO W ZALEŻNOŚCI OD MORFOLOGICZNEGO CHARAKTERU LITORALU JEZIOR

Streszczenie

Niniejsza praca oparta jest na materiale badań planktonu skorupiakowego prowadzonych w litoralu 37 jezior okolic Węgorzewa (por. również Rybak, Rybak 1964). Środowiską litoralowe poklasyfikowano na 4 typy ciągu rozwojowego: litoral lotyczny, wielkojeziorny, małojeziorny i sadzawkowy³ oraz grupę róźnych postaci litoralu uwstecznionego (brzegi sucharowe, sztuczne obudowy, urwiska itp.). Badaniami objęto - 3 typy: wielkojeziorny, małojeziorny i sadzawkowy (Fig. 1, 2, 3).

Stwierdzono, że prawdopodobieństwo znalezienia większości gatunków skorupiaków planktonowych jest niewielkie (Tab. I). Liczba gatunków, co do których istnieje duża szansa znalezienia w środowiskach poszczególnych typów litoralu zwiększa się w miarę wzrostu stopnia izolacji środowiska (Tab. II). Najmniej gatunków znaleziono w środowiskach typu wielkojeziornego, najwięcej zaś w środowiskach typu sadzawkowego (Tab. III). Gatunki typowe dla pelagialu rzadko występują w litoralu, który jest najbardziej dostępny dla falowania (wielkojeziorny – Tab. IV). Autorzy sądzą, że chodzi tu o wrażliwość tych form na rozbijanie o twarde podwodne przeszkody w ruchliwej wodzie litoralu.

Badane środowiska litoralowe były dość znacznie zróżnicowane pod względem dominacji poszczególnych gatunków (Tab. V, VI). Zaledwie kilka gatunków dominowało we wszystkich trzech typach litoralu (poliwalentne), pozostałe dominują tylko w jednym z nich (oligowalentne) albo w dwóch (mezowalentne). Jest rzeczą interesują-

³ Przytoczonymi nazwami posługują się ekipy badawcze tego terenu. Wprowadzone zostały do literatury przez Dobrowolskiego (1961). W tekście angielskim używa sie odpowiedników: lotyczny – open (otwarty), wielkojeziorny – accessible (dostępny), małojeziorny – sheltered (osłonięty), sadzawkowy – separate (izolowany). Terminy te lepiej odpowiadają strukturalnemu charakterowi wyróżnionych środowisk niż tradycyjnie dotąd używane nazwy.

cą, że nie ma takich gatunków (prócz poliwalentnych) które by dominowały jednocześnie w środowiskach o skrajnej specjalizacji (wielkojezionych i sadzawkowych) (Fig. 5). W środowiskach bardziej jednostronnie wyspecjalizowanych istnieją wyraźnie korzystniejsze warunki ostrej, wyraźnej dominacji dla gatunku opanowującego środowisko, natomiast środowiska typu małojeziornego stwarzają warunki dla miernej tylko dominacji, zwłaszcza jeżeli chodzi o gatunki opanowujące także i inne typy środowisk (Fig. [6]). Gatunki oligowalentne dominują najczęściej w sposób ostry.

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