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**CAN PLANKTIVOROUS FISH KEEP  
IN CHECK PLANKTONIC CRUSTACEAN POPULATIONS?  
A TEST OF SIZE-EFFICIENCY HYPOTHESIS  
IN TYPICAL POLISH LAKES\***

**ABSTRACT:** Seasonal changes of food consumption rate of planktivorous fish (vendace, smelt and bleak) in two lakes with significantly different fish density, were compared with seasonal changes of (1) elimination of planktonic crustacean biomass, (2) mortality, (3) age structure in crustacean populations and (4) mean body weight of crustaceans. It was found that factors other than fish predation must be responsible for the seasonal and spatial changes of crustacean populations. This has been also confirmed by the results of an extensive analysis of zooplankton communities in 30 lakes with fish predation of varied intensity.

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## 1. INTRODUCTION

Few ecological hypotheses introduced in recent years have been so widely verified as the "size-efficiency hypothesis" of Brooks and Dodson (1965). This hypothesis evolved from the experiments of Hrbáček and his co-workers (Hrbáček 1958, 1962, Hrbáček et al. 1961), who after the removal of fish from small ponds in Czechoslovakia, attained the effect of quick domination of zooplankton by better adapted to competition large species of *Cladocera*, which previously were strongly controlled by fish and consequently present in small numbers. Brooks and Dodson (1965) observed the same phenomenon, but working the opposite way; the occurrence of plankton-feeding fish *Alosa aestivalis* (Mitchell) in Crystal Lake, Connecticut, caused the disappearance of large species of filter-feeding crustaceans, and the domination of zooplankton by smaller filter-feeding species which earlier were outnumbered by stronger competitively forms of larger sizes. According to the hypothesis of Brooks and Dodson (1965) the larger the species, the greater is its ability to compete, since its food collection is more efficient (higher filtering rate and a broader size range of available food particles), but at the same time it is more exposed to predation by planktivorous fish, which actively (eye sight) or passively (density of gillrakers) will choose larger forms from the environment. Consequently, the species composition of zooplankton will depend on stronger or weaker action of the plankton-feeding fish as a specialized predator.

One should think, that either Brooks and Dodson (1965) or Hrbáček (1962), considered predation by planktivorous fish as one of many possible biotic factors responsible for species composition of fresh-water zooplankton. However, their hypothesis is being regarded now as the basic interpretation of changes in composition of zooplankton communities both in space (either in different lakes – e.g., Northcote and Clarotto 1975, Sprules 1975, or within one lake – Gannon 1972) and in time, whether over the period of many years (e.g., Wels 1970, Kerfoot 1974, Stavn 1975), or during one vegetative season (e.g., Hall 1971, Limpadanai 1974). Many American and Scandinavian papers on the subject have set aside the old views presenting the development of fresh-water zooplankton communities as a result of joint interaction of many different biotic and abiotic factors for which various species show different tolerance limits.

The purpose of the present paper is to test to what degree predation by planktivorous fish can be responsible for species composition of pelagic zooplankton, its seasonal changes, mortality of individuals in crustacean populations and mean size of individuals, all in conditions typical for the Central European lakes of Northern Poland, where the main pelagic planktivorous fish is usually vendace (*Coregonus albula* (L.)) being in this region often accompanied by smelt (*Osmerus eperlanus* (L.)) and bleak (*Alburnus alburnus* (L.)). The test was carried out on materials from the vegetative period of May-September that is the period of the most intensive feeding and growth of fish.

The test was based on a quantitative analysis of seasonal changes in predation intensity of planktivorous fish and on a simultaneous analysis of seasonal changes in the elimination rate of zooplankton biomass, seasonal changes in the mortality and in numbers of crustacean populations as well as on the sequence of occurrence of the dominant species in two well known lakes.

In order to increase the possibility of interpretation of results obtained for the two lakes, the materials gathered over a short period of time from 30 lakes of Northern Poland have been also included in the analysis. Large number of lakes made it possible to use the regression analysis method to get a measure of the relationship between the structure of zooplankton communities and the intensity of predation by planktivorous fish.



## 2. THE LAKES, MATERIAL AND METHODS

Vendace occurs at present in 420 Polish lakes with a combined surface area of 127 km<sup>2</sup>, which is about 40% of the total surface area of lakes in Poland (Bernatowicz and Radziej 1974). Assuming that the size of catch indicates the real amount of biomass present, the density of this species varies greatly. According to Bernatowicz and Radziej (1974) the catches from majority of lakes are about 1 kg · ha<sup>-1</sup> · year<sup>-1</sup>. In only 29 lakes they exceed 20, and in one lake 40 kg · ha<sup>-1</sup> · year<sup>-1</sup>. Leopold (1972) stated that the average catches of vendace over the period 1950–1970 exceeded somewhat 3 kg · ha<sup>-1</sup> · year<sup>-1</sup>, while the mean biomass of the catchable part of the population was estimated to be 10 kg · ha<sup>-1</sup> (Dąbrowski and Leopold 1969).

Smelt and bleak, secondarily important consumers of pelagic zooplankton, have received less attention. It is well known, that both species occur in most of the water reservoirs inhabited by vendace. The catches of smelt and bleak also vary from lake to lake. According to data supplied by the State Fish Husbandry in Mikołajki the catches of smelt and bleak from many lakes can exceed the catches of vendace.

Extensive comparative research was done on materials obtained in June and July 1975 from 30 holomictic Pomeranian lakes strongly stratified during the summer. The lakes are of various trophic types (from  $\alpha$ -meso- to eutrophy) with the surface area ranging from 96 to 1,781 ha, the maximum depth from 20 to 80 m, and the average depth from 8 to 19 m (with one exception of a smaller and shallower lake; surface 17 ha, max. depth 10 m). They also have a wide range of the annual planktivorous fish catches; the catches of vendace range from 0 to 31 kg · ha<sup>-1</sup> · year<sup>-1</sup>. Detailed limnological characteristics of these lakes and their zooplankton are presented in the works of Sterzyńska (1976), Sterzyński (1976), and Gliwicz (in preparation).

More detailed research was carried on two holomictic and strongly stratified during the summer lakes of the Great Masurian Lakes; the eutrophic, Mikołajskie Lake (surface 460 ha, max. depth 27.8 m, average depth 11.0 m) and the  $\beta$ -mesotrophic Lake Tałtowisko (surface 327 ha, max. depth 39.5 m, average depth 14 m). The zooplankton communities of these lakes are well known (intensive research was done by the International Biological Programme – Productivity of Freshwaters), as well as their fish fauna (Kozikowska 1970, Prejs 1976). The analysis was done on materials which included detailed zooplankton data from 1966 (Mikołajskie Lake) and 1968 (Lake Tałtowisko).

Both lakes are being extensively used for fisheries. The catches from Mikołajskie Lake in the 1960-ties gave one the average 100 kg · ha<sup>-1</sup> · year<sup>-1</sup>, 60% of which was made up of pelagic species. Biomass of vendace and smelt exceeded 7 and 15 kg · ha<sup>-1</sup> · year<sup>-1</sup>, respectively, while the biomass of bleak reached 40 kg · ha<sup>-1</sup> · year<sup>-1</sup>. Besides that, significant part in the catches from this lake had bream and roach, species inhabiting chiefly the littoral and the bottom zones. In spite of an equally intensive fishing husbandry in both lakes, the results of catches from Lake Tałtowisko indicate a smaller fish stock than in Mikołajskie Lake. On the average, in the 1960-ties, the fish catches from Lake Tałtowisko were a little above 25 kg · ha<sup>-1</sup> · year<sup>-1</sup>, and the pelagic species made up only about 20% of the catches. The average biomass of vendace, smelt and bleak were respectively: 3, 1.5, and 1.1 kg · ha<sup>-1</sup> year<sup>-1</sup>. Largest share in the catches from this reservoir had roach and bream.

The following data were used for the analysis based on materials obtained from Mikołajskie Lake and Lake Tałtowisko:

1. Size of yearly catches of vendace, smelt, and bleak (kg · ha<sup>-1</sup> · year<sup>-1</sup>) in the years 1966 and 1967 from Mikołajskie Lake, and in the years 1968 and 1969 from Lake Tałtowisko.



2. Size of monthly catches of the same species ( $\text{kg} \cdot \text{ha}^{-1} \cdot 30 \text{ days}^{-1}$ ) from May to September (data pertaining both to yearly and monthly catches were obtained from the State Fishing Husbandry in Mikołajki).

3. Weight of zooplankton found in the stomachs of five specimens of vendace in the age group of  $2^+$ , which were caught in June in Mikołajskie Lake, and the data pertaining to the weight of zooplankton (Marciaik 1962) found in the stomachs of vendace of ages  $1^+$  and  $2^+$ , caught from May to September in Pluszne Lake,

4. Numbers ( $N$ ), mean body weight ( $W$ ) and biomass ( $B$ ) of various development stages, and daily biomass production ( $P_B$ ) of six dominant in both lakes species of *Crustacea* (*Daphnia cucullata* Sars, *Bosmina coregoni* Baird, *Diaphanosoma brachyurum* Liévin, *Chydorus sphaericus* (Müll.), *Eudiaptomus graciloides* (Lill.) and *Mesocyclops leuckarti* Claus) for 24 in the case of Mikołajskie Lake (15 April–26 September 1966) and 13 for Lake Tałtowisko (19 April–15 October 1968) points of time. The source materials provided by Dr. T. Węgleńska had been used for the publications of Hillbricht-Ilkowska and Węgleńska (1970), Hillbricht-Ilkowska et al. (1972), Gliwicz and Hillbricht-Ilkowska (1975), Węgleńska (in preparation).

The following parameters have been calculated on the basis of the above data:

1. Diurnal consumption of vendace, smelt and bleak  $C_B$  ( $\text{g f. w.} \cdot \text{m}^{-2} \cdot \text{day}^{-1}$ ) estimated as a monthly mean from May to September providing  $C_B = \bar{C}_{B_i} \cdot B_F$ , where  $\bar{C}_{B_i}$  is mean diurnal food consumption rate for each month (per cent of fish body weight  $\cdot \text{day}^{-1}$ ) and  $B_F$  is mean biomass (fresh weight) on fish in the pelagic zone each month.

Mean diurnal food consumption rate ( $\bar{C}_{B_i}$ ) has been calculated from a modified Bajkov (1935) equation:  $\bar{C}_{B_i} = K \cdot \bar{A}$ , where  $K$  is food overturn rate, or in other words, coefficient for daily renewal of the stomach content ( $\text{day}^{-1}$ ), and  $\bar{A}$  is mean fresh weight of zooplankters in fish stomachs per fish body weight unit ( $\text{mg f. w.} \cdot \text{g f. w.}^{-1}$ ) often expressed as per cent of fish body weight.

Data pertaining to the size of vendace catches during the research period in lakes Mikołajskie and Tałtowisko were taken as the base for calculations of the biomass of fish feeding in the pelagic zone ( $B_F$ ). Following the results of Dąbrowski and Leopold (1969) it has been calculated that these values equal 1/3 mean biomass of the catchable portion of vendace population. In turn, information pertaining to the sizes of catches in particular periods of the fishing season, and based on the age structure of the catchable vendace population (Marciaik 1970, Leopold 1972, Ciepielewski 1974), allowed us the reconstruction of the possible changes in biomass of the catchable part of population. Biomass of the remaining part of vendace population (fish of ages  $0^+$  and  $1^+$ )<sup>1</sup> has been calculated from the size of biomass gains predicted for the fishing population next year.

Assuming that Dąbrowski and Leopold's (1969) data of the ratio vendace catch sizes to mean biomass of the fishing population could be used for other pelagic species as well, the calculations of smelt and vendace biomass were done in the same manner.

2. Daily elimination of live crustacean mass calculated for each species as  $E_B = \frac{\Delta B + P_B}{\Delta t}$  ( $\text{g f. w.} \cdot \text{m}^{-2} \cdot \text{day}^{-1}$ ), where  $\Delta B = B_{t(x-1)} - B_{t_x}$  ( $\text{g f. w.} \cdot \text{m}^{-2}$ ) denotes decrease of

<sup>1</sup>For the purpose of the present work, fish of the age group  $1^+$ , which according to Marciaik (1970) and Ciepielewski (1974) make up less than 15% of the catchable biomass during the period May–September, have not been included in the fishing stock.



population biomass in time  $\Delta t$  (days), that is from the preceding date ( $t_{(x-1)}$ ) till the date of measurement ( $t_x$ ), and  $P_B$  is the cumulative population biomass production in time  $\Delta t$ .

3. Daily elimination of individuals from crustacean populations, that is mortality calculated for each species as  $E_N = \frac{\Delta N}{\Delta t} + P_e$  ( $\text{ind.} \cdot \text{m}^{-2} \cdot \text{day}^{-1}$ ), where  $\Delta N = N_{t_{(x-1)}} - N_{t_x}$  ( $\text{ind.} \cdot \text{m}^{-2}$ ) denotes decrease in total number of eggs, young and mature individuals in time  $\Delta t$ , and  $P_e = \frac{N_e}{D_e}$  ( $\text{eggs.} \cdot \text{m}^{-2} \cdot \text{day}^{-1}$ ) indicates daily population egg production, that is the mean number of eggs contained under  $1 \text{ m}^2$  of lake surface ( $N_e$ ) divided by the time of egg development in a given daily temperature, as calculated from the regression curve of Bottrell et al. (1976).

It should be indicated that both  $\Delta B$  and  $\Delta N$  can take negative values in cases when there is an increase of population biomass or population number in time  $\Delta t$ .

4. Maximum possible number of individuals of *Cladocera* or *Calanoida* taken by fish calculated with the assumption that fish do not select larger individuals, denoted as  $C_N = \frac{C_B}{\bar{W}}$ , where  $\bar{W} = \frac{B}{N_e + N_j + N_A}$  or  $\bar{W} = \frac{B}{N_e + N_n + N_k + N_A}$  indicates mean body weight of cladoceran individual of any age and species, or mean body weight of *Eudiaptomus graciloides* individual from any age group (eggs - e, juvenile cladocerans - j, nauplii - n, copepodites - k, adults - A).

### 3. RESULTS

#### 3.1. Fish predation on zooplankton in two Masurian lakes

##### 3.1.1. Estimation of planktivorous fish predation - consumption of zooplankton biomass and its seasonal changes

Predation intensity of planktivorous fish on zooplankton (total food consumption by vendace, smelt, and bleak under  $1 \text{ m}^2$  of lake surface) was calculated in such a way as to rather overestimate than underestimate its size. This is why many parameters for the estimation of the total fish predation were purposely chosen near their maximum.

The values of  $K$  (food overturn rate) necessary for the calculations of mean daily food consumption rate of fish in different months ( $\bar{C}_{B_i}$ ), are those of Brett and Higgs (1970), who found them for *Oncorhynchus nerka* (Walbaum), a planktivorous fish of the *Salmonidae* family. For May and September, when the epilimnion temperature of lakes Mikołajskie and Tałtowisko was below  $19^\circ\text{C}$ ,  $K = 2.5 \cdot \text{day}^{-1}$ , and for June, July and September  $K = 3 \cdot \text{day}^{-1}$ . The value of  $\bar{A}$  (mean zooplankton fresh weight in fish stomachs - Table I) was chosen near its maximum. For May and September  $\bar{A} = 1.1\%$  ( $11 \text{ mg f. w.} \cdot \text{g f. w. fish body}^{-1}$ ) and for June, July and August  $\bar{A} = 1.8\%$  ( $18 \text{ mg f. w.} \cdot \text{g f. w. fish body}^{-1}$ ). Values of  $\bar{A}$  for vendace were adopted also for smelt and bleak. Using values of  $K$  and  $\bar{A}$  it was calculated that  $\bar{C}_{B_i}$  (mean



Table I. Mean zooplankton biomass in stomachs of vendace as percentage of fish biomass (acc. to Marciak 1970 and own\* data)

Age group	Month		
	May	June-August	September
1+	no data	1.81	1.10
2+	1.00	1.41 1.70*	0.97

Table II. Biomass (g f. w.  $\cdot$  m<sup>-2</sup>) of vendace, smelt and bleak in the pelagic zone of Mikołajskie Lake (M) in 1966 and of Lake Tałtowisko (T) in 1968

Month	Vendace		Smelt		Bleak		Total	
	M	T	M	T	M	T	M	T
May	4.1	1.3	3.4	2.5	9.0	0.1	16.5	3.9
June	4.0	1.5	5.0	3.8	9.5	>0.1	18.5	5.3
July	4.2	1.6	5.9	4.5	12.3	0.2	22.4	6.3
August	5.6	1.9	6.4	4.8	13.4	0.2	25.5	6.9
September	5.6	1.9	5.5	4.1	14.0	0.2	25.2	6.2

Table III. Consumption of pelagic zooplankton biomass ( $C_B$ , g f.w.  $\cdot$  m<sup>-2</sup>  $\cdot$  day<sup>-1</sup>) by vendace, smelt and bleak in Mikołajskie Lake (M) in 1966 and in Lake Tałtowisko (T) in 1968

Month	Vendace		Smelt		Bleak		Total	
	M	T	M	T	M	T	M	T
May	0.102	0.032	0.105	0.062	0.110	0.002	0.317	0.096
June	0.217	0.081	0.271	0.206	0.253	>0.001	0.741	0.287
July	0.228	0.087	0.320	0.244	0.668	0.011	1.216	0.342
August	0.304	0.103	0.347	0.260	0.727	0.011	1.378	0.374
September	0.140	0.047	0.137	0.102	0.350	0.005	0.627	0.154



daily food consumption) for May and September equals 2.6%, and for June, July and August – 5.4%<sup>2</sup>.

Data pertaining to the biomass of vendace, smelt and bleak in different months ( $B_F$ ) in both lakes are given in Table II. S z y p u ł a (1970a) and D e m b i ń s k i (1971) stated, that vendace in the age group of 0<sup>+</sup> appears in the pelagic zone at the beginning of August; their statement was considered in our calculations.

Daily consumption of pelagic zooplankton by planktivorous fish in the period of May-September (Table III) was estimated on the basis of mean daily food consumption rate for different months ( $\bar{C}_{B_i}$ ) and the biomass of fish feeding in the pelagial ( $B_F$ ) during the same time. While calculating the consumption values for bleak, we considered the fact that sexually mature individuals of this species spend some time in May and June on spawning grounds of the littoral zone. This is why the bleak consumption values for May and June have been decreased to 50%.

Data in Table III show, that predation by vendace, smelt and bleak on pelagic zooplankton increases in both lakes from May till August, and then declines in September. Bleak seems to be the main consumer of zooplankton in Mikołajskie Lake, and smelt in Lake Tałtowisko.

Overestimation of values of fish predation on zooplankton ( $C_B$  – Table III) resulted from the fact, that the values of both the daily food consumption rate ( $\bar{C}_{B_i}$ ) and the biomass of vendace, smelt and bleak ( $B_F$ ) have been calculated near their maximum.

Daily food consumption rate ( $\bar{C}_{B_i}$ ) has been overestimated because of the assumption that its value for smelt and bleak is identical with the value for vendace. On the other hand, a lot indicates that the size of consumed zooplankton biomass per unit of fish body weight is much lower for bleak and smelt than for vendace. According to data supplied by several authors (data for smelt – C z e c z u g a (1959) and R e m b i s z e w s k i (1970), for bleak – G a s o w s k a (1962), for vendace – M a r c i a k (1962) and C i e p i e l e w s k i (1974)), the rate of increase of smelt and bleak biomass is considerably lower, than for vendace during the same period of time. As shown by P r e j s (1976), about 40% of food of mature bleak is obtained from air and littoral epiphytic fauna. D e m b i ń s k i (1971) who found an epilimnetic distribution of bleak, suggests that insects falling on to the water surface are the main factor which allures fish of this species to the pelagic zone during the summer time. In turn, C z e c z u g a (1959) and R e m b i s z e w s k i (1970) have stated that small fry is an important diet of the older age groups of smelt. Compared with these findings, vendace appears to be a purely planktivorous fish, and the few isolated cases of finding small fry and bottom fauna in its stomachs (M a r c i a k 1962, R a d z i e j 1965, S z y p u ł a 1970b) do not change the picture. This is why it can be accepted, that among the three mentioned species, only vendace consumes the assumed daily amount of zooplankton, and although in Mikołajskie Lake its biomass is smaller than the biomass of smelt and bleak, vendace uses as much food or more than these two species.

It should also be mentioned that the value of  $K$  used for the calculation of  $\bar{C}_{B_i}$  is for the temperature characteristic of epilimnion. At the same time it is known, that both smelt and

<sup>2</sup>It was tested if estimated value of mean daily food consumption could meet the energy demands of vendace. It was found that food consumption rate of 5.4% supplies a fish of 75 g with 6.0 g C · 30 days<sup>-1</sup>. Standard respiration consumes 2.1 g C · 30 days<sup>-1</sup> (15°C was accepted arbitrarily as mean daily temperature of water inhabited by vendace). Growth takes up 0.4 g C · 30 days<sup>-1</sup>. Hence, there remains more than twice as much (3.5 g C · 30 days<sup>-1</sup>) for other energy expenditures.



vendace stay mainly during the summer in meta- and hypolimnion (Dembiński 1971), where the temperature is about 10°C lower, and therefore the value of  $K$  (and consequently of  $\bar{C}_B$ ) would be accordingly smaller.

The biomass values for vendace, smelt and bleak in the pelagic zone of lakes Mikołajskie and Tałtowisko are very likely also overestimated. Dąbrowski and Leopold (1969) stated that in Polish lakes, on the average, only 37% of biomass of the catchable vendace stock is being fished, which shows a weak exploitation of this species. Both lakes mentioned above are the main fishing sites of a specialized husbandry, which suggests, that their fishing effectiveness is greater than the mean fishing effectiveness estimated for many lakes of varied intensity of exploitation. This in turn means that the real biomass and numbers of the catchable part of vendace population (and probably of the remaining pelagic species) are in the fishing season lower, than those calculated for the purpose of the present work.

Thus, the total daily consumption calculated for all three species has been in fact overestimated.

### 3.1.2. Predation by fish and elimination of crustacean biomass

As a result of considerable changes in biomass ( $B$ ) of the dominant crustacean species, the values of biomass elimination rate ( $E_B$ ) differ significantly from the values of production rate.

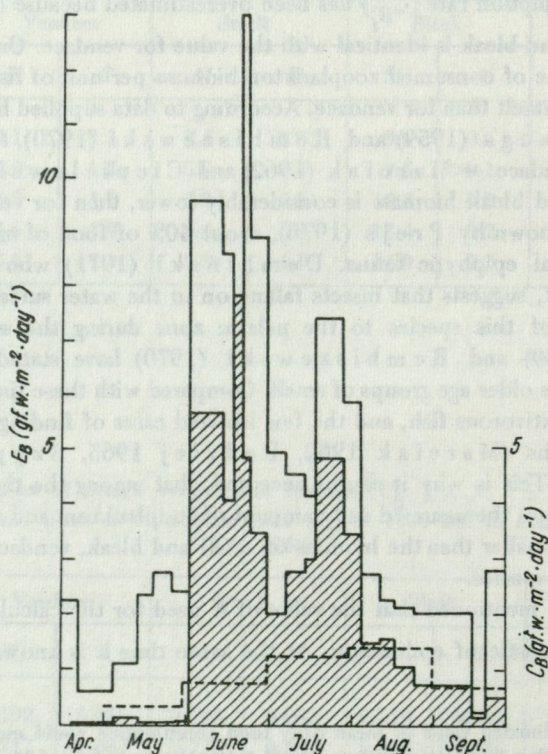


Fig. 1. Seasonal changes of cladoceran biomass (shaded) and copepod biomass (unshaded) eliminated daily under 1 m<sup>2</sup> of Mikołajskie Lake surface ( $E_B$ ) and changes in daily consumption of planktivorous fish under 1 m<sup>2</sup> surface of the lake ( $C_B$  - broken line) in 1966



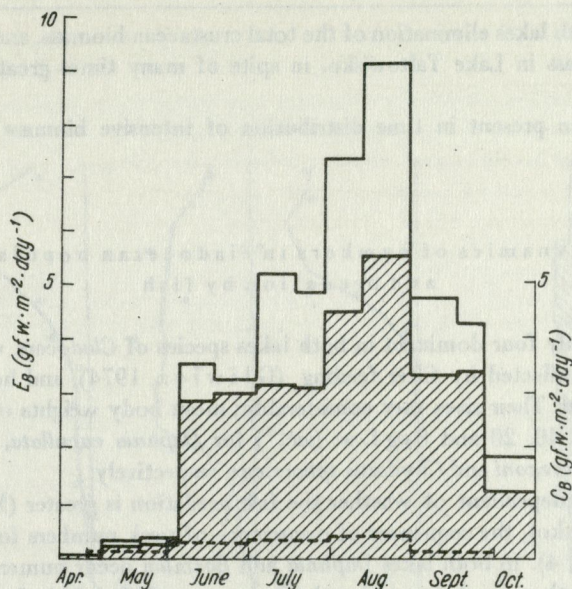


Fig. 2. Seasonal changes of cladoceran biomass (shaded) and copepod biomass (unshaded) eliminated daily under  $1 \text{ m}^2$  of Lake Tałtowisko surface ( $E_B$ ) and changes in daily consumption of planktivorous fish under  $1 \text{ m}^2$  surface of the lake ( $C_B$  - broken line) in 1968

For this reason, the values of biomass elimination rate, and not those of production rate, have been used in the analysis of the probable share of fish in the process of elimination of live *Crustacea* (Figs. 1, 2).

The sums of crustacean biomass eliminated during the season  $\Sigma E_B$  (the area under curve  $E_B$ ) are similar in both lakes. This results from the similar values of the yearly *Crustacea* net production received for these lakes for various years, including these analysed presently (see Hillbricht-Ilkowska, Gliwicz and Spodniewska 1966, Hillbricht-Ilkowska et al. 1972). Significantly larger is, however, the value of  $\Sigma E_B$  for *Cladocera* in Lake Tałtowisko, in spite of more than three times less intensive predation by fish ( $C_B$ ) in this lake.

Contribution by fish to the elimination of crustacean biomass during the entire season ( $\Sigma C_B \cdot \Sigma E_B^{-1} \cdot 100$ ) does not exceed 20% for Mikołajskie Lake and 8% for Lake Tałtowisko.

Distribution of elimination rate in the season does not correspond to the changes of fish predation. It is especially noticeable for Mikołajskie Lake (Fig. 1), where planktivorous fish must have a greater share in elimination of crustaceans. In August, the time of the most intensive predation ( $C_B$ ), the rate of biomass elimination ( $E_B$ ) is considerably lower than in June and July, when the values  $C_B$  are lower. Even if we assume, that the fish pressure is directed exclusively at *Cladocera*, only in May, and August-September could fish be considered as the main factor causing elimination of biomass. In June and July in Mikołajskie Lake, similarly as during the entire almost vegetative season in Lake Tałtowisko, the elimination of zooplankton biomass must be mainly caused by factors other than fish predation.

The following results of the above analysis show that it is not the predation by planktivorous fish which is decisive in the elimination of crustacean biomass:

1. low value of consumption by planktivorous fish in relation to the value of crustacean biomass elimination;



2. similar for both lakes elimination of the total crustacean biomass, and greater elimination of cladoceran biomass in Lake Tałtowisko, in spite of many times greater fish predation in Mikołajskie Lake;

3. no coincidence present in time distribution of intensive biomass elimination and of predation by fish.

### 3.1.3. Dynamics of numbers in cladoceran populations and predation by fish

Analysed were only four dominant in both lakes species of *Cladocera* which have the same demands for food collected by filter feeding (Gliwicz 1974), and hence may enter into competition for food. Their sizes vary considerably; mean body weights of mature individuals ( $\bar{W}_A$ ) are about 70, 40, 20 and  $8 \mu\text{g f. w.}$  (sic!<sup>3</sup>) for *Daphnia cucullata*, *Diaphanosoma brachyurum*, *Bosmina coregoni* and *Chydorus sphaericus*, respectively.

We found that independent of whether the fish predation is greater (Mikołajskie Lake) or lesser (Lake Tałtowisko), the sequences of occurrence of peak numbers for various species are identical (cf. Figs. 3, 4). In both lakes *Daphnia* and *Bosmina* occur numerously in late spring, and during summer they are being replaced to a greater (Mikołajskie Lake) or lesser degree (Lake Tałtowisko) by *Diaphanosoma* and *Chydorus*. This sequence in Lake Tałtowisko (Fig. 4) is somewhat delayed as compared with Mikołajskie Lake (Fig. 3).

If predation of planktivorous fish was responsible for this replacement of species, one should expect, that according to the observations of Hrbáček (1962) and the hypothesis of Brooks and Dodson (1965), large-sized species would give way to small-sized species. In fact, during the increase of fish predation ( $C_B$ ), the numbers of *Daphnia* ( $70 \mu\text{g f. w.}$ ), the largest of the four species, decrease, while the numbers of the smallest species – *Chydorus* ( $8 \mu\text{g f. w.}$ ) increase. At the same time, however, the numerical abundance of *Bosmina* ( $20 \mu\text{g f. w.}$ ) also decreases, and the abundance of *Diaphanosoma* ( $40 \mu\text{g f. w.}$ ), species twice as large as *Bosmina*, increases. It appears, then, that other factors must be responsible for the replacement of dominant species.

It is equally difficult to explain by fish predation the differences in numbers of *Leptodora kindtii* (Focke), the largest in both lakes species of *Cladocera* ( $\bar{W}_A = \text{about } 3,000 \mu\text{g f. w.}$ ), which according to Brooks and Dodson (1965) should be more intensively eliminated from Mikołajskie Lake than from Lake Tałtowisko.

In spite of several times greater predation by planktivorous fish in Mikołajskie Lake than in Lake Tałtowisko, the abundance of *Leptodora kindtii* in the former lake is twice as large, although the densities of *Crustacea*, which are the potential food of this predacious cladoceran, do not differ in both lakes. According to Karabin (1974) its peak numbers in July 1967 in the epi- and metalimnion were reaching  $940 \text{ ind.} \cdot \text{m}^{-3}$  in Mikołajskie Lake, and only  $530 \text{ ind.} \cdot \text{m}^{-3}$  in Lake Tałtowisko, while its mean biomass in July-September, the period of the highest fish predation, was respectively  $0.71$  and  $0.39 \text{ g f. w.} \cdot \text{m}^{-3}$ .

The following points show that it is not predation by fish which is responsible for the changes in numbers of large and small species of *Cladocera*:

<sup>3</sup>One more illustration for Hutchinson's (1959) hypothesis.



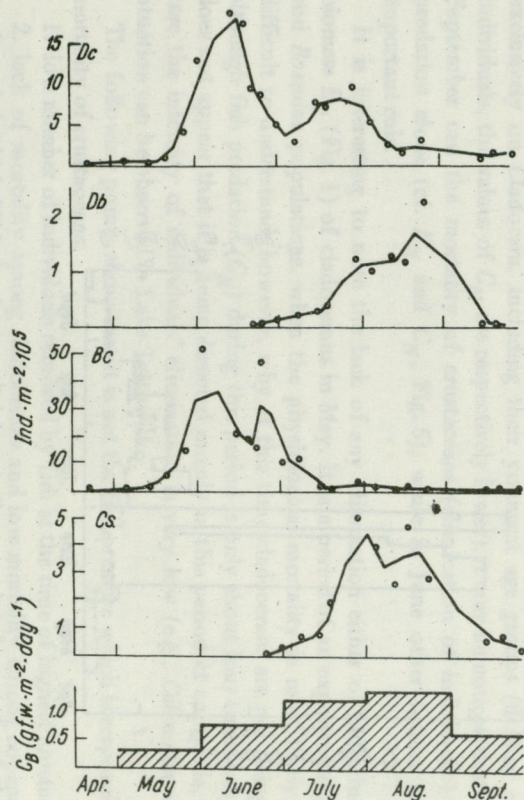


Fig. 3. Seasonal changes in population numbers of dominant cladoceran species (ind. · m<sup>-2</sup> · 10<sup>5</sup>) and changes in predation of planktivorous fish (C<sub>p</sub>, g f.w. · m<sup>-2</sup> · day<sup>-1</sup>), in Miłojaskie Lake in 1966

Dc – *Daphnia cucullata*, Db – *Diaphanosoma brachyurum*, Bc – *Bosmina coregoni*, Cs – *Chydorus sphaericus* (source materials of Węgleńska – in preparation)

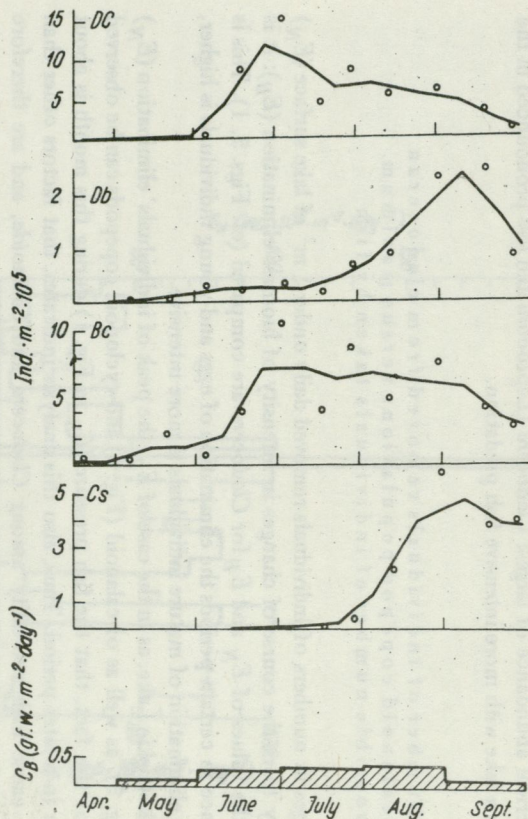


Fig. 4. Seasonal changes in population numbers of dominant cladoceran species (ind. · m<sup>-2</sup> · 10<sup>5</sup>) and changes in predation of planktivorous fish (C<sub>p</sub>, g f.w. · m<sup>-2</sup> · day<sup>-1</sup>) in Lake Tałtawisko in 1968

Dc, Db, Bc, Cs, as in Figure 3 (source materials of Węgleńska – in preparation)



1. identical sequence of peak numbers of *Cladocera* species in both lakes, in spite of differential predation;
2. reduction in numbers of smaller *Bosmina* and increase in numbers of twice as large *Diaphanosoma*, corresponding to the increase of fish predation;
3. greater numerical abundance of largest *Cladocera* (*Leptodora* and less pronounced in the case of *Daphnia*) in a lake with more intensive fish predation.

#### 3.1.4. Number of individuals removed from cladoceran and calanoid copepod populations versus maximum possible number of individuals taken by fish

Course of changes in numbers of individuals removed daily under  $1 \text{ m}^2$  of lake surface ( $E_N$ ) differs considerably from the course of changes in intensity of biomass elimination ( $E_B$ ): it is easy to see when the values of  $E_N$  and  $E_B$  for *Cladocera* are compared (cf. Figs. 5, 1). This is understandable, since in certain periods the elimination of eggs and young individuals is higher, while in others the elimination of mature individuals is more intensive.

However, in Mikołajskie Lake, as in the case of  $E_B$ , the peak of individuals' elimination ( $E_N$ ) of cladocerans (Fig. 5), as well as of calanoid (Fig. 6) and cyclopoid copepods can be observed in June, in spite of the fact, that the fish pressure ( $C_B$  in Fig. 1) during this month is about twice smaller than in a later period. Thus, also this analysis indicates, that factors other than predation by fish cause high mortality among *Cladocera* and *Calanoida*, and are therefore responsible for the high intensity of elimination of individuals from crustacean populations in June.

This is also noticeable, when comparing the changes of  $E_N$  with the changes of the maximum possible number of individuals taken by fish  $C_N$  (Figs. 5, 6). Even assuming that the fish feed

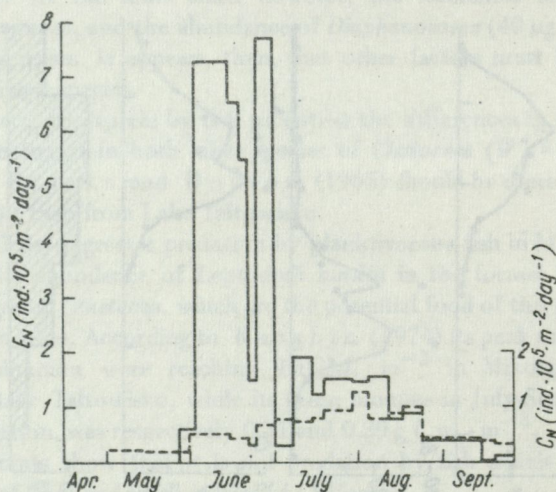


Fig. 5. Seasonal changes in numbers of cladocerans eliminated daily under  $1 \text{ m}^2$  of Mikołajskie Lake surface ( $E_N$  — solid line) in 1966 and changes in numbers of cladocerans eaten daily under  $1 \text{ m}^2$  surface of this lake by planktivorous fish (assuming that *Cladocera* are exclusive food of the fish —  $C_N$  — broken line)



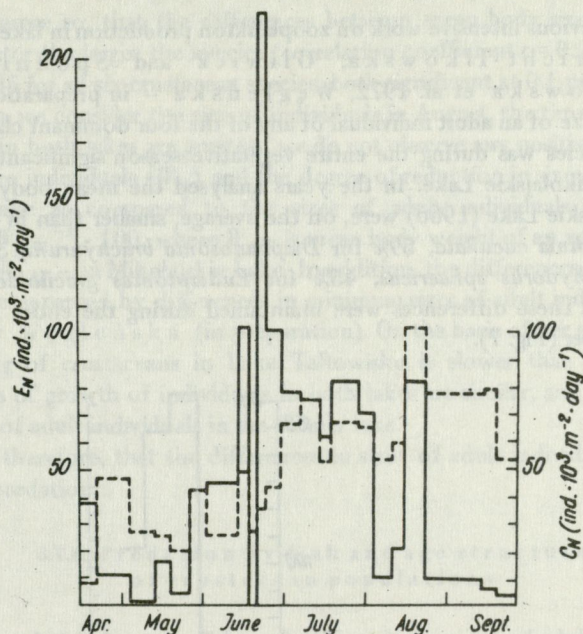


Fig. 6. Seasonal changes in numbers of calanoid copepods eliminated daily under  $1 \text{ m}^2$  surface of Mikołajskie Lake ( $E_N$  — solid line) in 1966, and changes in numbers of calanoid copepods eaten daily under  $1 \text{ m}^2$  surface of this lake by planktivorous fish (assuming that they are exclusive food of the fish —  $C_N$  — broken line)

exclusively on *Cladocera*, including their youngest age groups (if they choose only larger individuals, the values of  $C_N$  are respectively lower), it may be noticed that only in August and September can the mortality of crustaceans (elimination of individuals) be caused by fish predation alone (cf.  $E_N$  and  $C_N$ , Fig. 5), while in June other factors must play in it an important role.

It is interesting to note the lack of any elimination either of individuals  $E_N$  (Fig. 5) or biomass  $E_B$  (Fig. 1) of cladocerans in May. It is a period of an exponential growth of *Daphnia* and *Bosmina* populations, when the physiological mortality is most likely insignificant. It is difficult to understand, however, why at this time cladocerans are not being removed by fish, although fish predation ( $C_B$ ) during this period is only about four times less than in August. It does not appear that it is being directed mainly in this period at copepods, since also in their case the intensity of individuals' elimination is very low (e.g., *Calanoida* — Fig. 6). A similar situation can be observed in Lake Tałtowisko.

The following points show that it is not the fish pressure which is responsible mainly for the mortality of crustaceans:

1. low number of individuals removed by fish at the time of highest crustacean mortality;
2. lack of mortality among cladocerans and low mortality among copepods in May, when the number of individuals removed by fish is expected to be much greater (only about a half less than in June).



## 3.1.5. Predation by fish and body size of adult crustaceans

In the course of previous intensive work on zooplankton production in lakes Mikołajskie and Tańtowisko (Hillbricht-Ilkowska, Gliwicz and Spodniewska 1966, Hillbricht-Ilkowska et al. 1972, Węgleńska — in preparation) it was found, that the mean body size of an adult individual of any of the four dominant cladoceran species and two copepod species was during the entire vegetative season significantly larger in Lake Tańtowisko than in Mikołajskie Lake. In the years analysed the mean body sizes of mature individuals in Mikołajskie Lake (1966) were, on the average, smaller than in Lake Tańtowisko (1968): 66% for *Daphnia cucullata*, 59% for *Diaphanosoma brachyurum*, 36% for *Bosmina coregoni*, 43% for *Chydorus sphaericus*, 45% for *Eudiaptomus graciloides*, and 43% for *Mesocyclops leuckarti*. These differences were maintained during the entire vegetative season from May till September (Fig. 7).

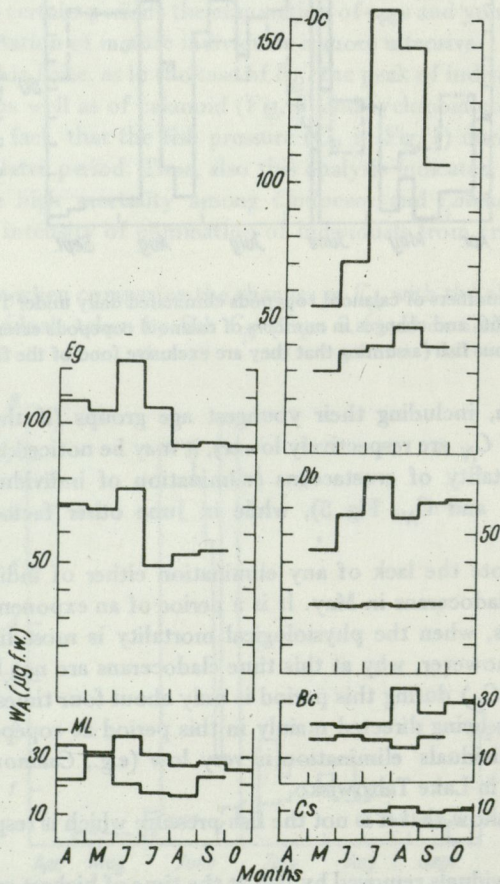


Fig. 7. Mean monthly weights of adult individual ( $W_A$ ) of dominant crustaceans in Mikołajskie Lake in 1966 (lower curves) and in Lake Tańtowisko in 1968 (upper curves)

*Eg* — *Eudiaptomus graciloides*, *ML* — *Mesocyclops leuckarti*, *Dc* — *Daphnia cucullata*, *Db* — *Diaphanosoma brachyurum*, *Bc* — *Bosmina coregoni*, *Cs* — *Chydorus sphaericus* (source materials of Węgleńska — in preparation)



According to Brooks and Dodson's (1965) hypothesis this could be explained by the effect of the several times greater fish pressure in Mikołajskie Lake as compared to Lake Tałtowisko. The more so, that the differences between mean body sizes of adult individuals ( $W_A$ ) are the greater the larger the species (correlation coefficient  $r = 0.90$  for four cladoceran species and  $r = 0.85$  for all six crustacean species, both significant at 0.1 probability level).

However, when we consider the size of individuals in August, the time when the differences in fish predation in both lakes are greatest, we do not observe any positive correlation between the sizes of mature individuals ( $W_A$ ) and the degree of reduction in sizes of mature individuals in Mikołajskie Lake as compared to the sizes of adult individuals in Lake Tałtowisko:  $(W_{AT} - W_{AM}) \cdot W_{AT}^{-1} \cdot 100$ , where  $W_{AT}$  is mean body weight of an adult individual in Lake Tałtowisko, and  $W_{AM}$  - in Mikołajskie Lake. In addition, the differences in mean sizes of adult individuals are accompanied by differences in minimum sizes of adult individuals, as was found for these lakes by Węgleńska (in preparation). On the basis of her results one can assume that the maturing of crustaceans in Lake Tałtowisko is slower than in Mikołajskie Lake, although the rates of growth of individuals in both lakes are similar, and this may be the cause of the larger sizes of adult individuals in the former lake.

It is doubtful, therefore, that the differences in sizes of adult individuals in both lakes are the result of fish predation.

### 3.1.6. Predation by fish and age structure of crustacean populations

Analysis of the relation between fish predation and mean size of adult individuals may give deceptive results, if we do not consider the abundance of juvenile stages and their survival until their maturity.

Lack of pertinent data makes it impossible to analyse the survivorship curves in both lakes during periods of weak and strong fish predation. On the basis of numbers in various developmental stages (eggs -  $N_e$ , juveniles -  $N_j$ , mature individuals -  $N_A$  for *Cladocera*, and eggs -  $N_e$ , nauplii -  $N_n$ , copepodites -  $N_k$  and adult individuals -  $N_A$  for *Copepoda*) and the data of duration of these stages ( $D_e = 2$ ,  $D_j = 6$ ,  $D_A = 30$  days for *Cladocera* and  $D_e = 4$ ,  $D_n = 10$ ,  $D_k = 14$ ,  $D_A = 50$  for *Copepoda*) which were adopted arbitrarily after authors cited by Hillbricht-Ilkowska and Patalas (1967) we obtained simplified survivorship curves for three periods. These periods for Mikołajskie Lake are: May 4-July 1, July 1-August 11, and August 11-September 26 of 1966. For Lake Tałtowisko they are: May 6-July 3, July 3-August 12 and August 12-October 15 of 1968. For each stage we found numbers in the age class every one day ( $N_1 = \bar{N} \cdot \frac{1}{D}$ , where  $\bar{N} = \frac{\sum N_t \cdot \Delta_t}{\sum \Delta_t}$ , and  $\bar{N}$  - mean numbers in a development stage during period analysed,  $\frac{1}{D}$  - the reverse of development time or stage duration,  $N_t$  - numbers in a given stage at the point of their estimation,  $\Delta_t$  - time elapsed between the previous and the next point of number estimation of this stage). Next,  $N_1$  for an egg ( $N_{1e}$ ) was assumed to be 100%, and  $N_1$  for other stages was taken as a per cent of  $N_{1e}$  (e.g.,  $N_{1j} \cdot N_{1e}^{-1} \cdot 100$ ), this was the basis for the simplified survivorship curves (see examples for one cladoceran species and one copepod species on Figure 8).

Assuming that the values of  $D$  for each stage are identical for both lakes analysed (in the previous section we assumed the contrary), comparison of the curves suggests, that in Mikołajskie Lake the elimination in younger stages is greater and in older stages smaller than in



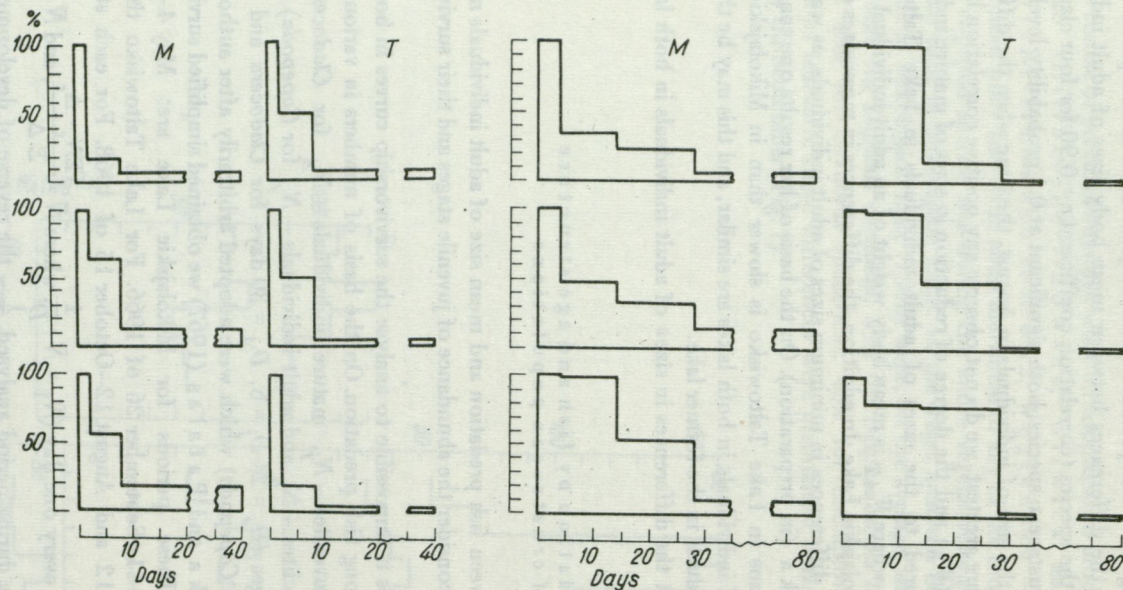


Fig. 8. Simplified survivorship curves for *Daphnia cucullata* (left) and *Eudiaptomus graciloides* (right) in Mikołajskie Lake (M) and in Lake Tańtowisko (T) for three different periods of fish predation to total crustacean biomass elimination ratio ( $C_B, E_B$ ): high (late spring – upper), very low (early summer – middle)

and very high (late summer – lower)

Three developmental stages have been distinguished for *Daphnia* (eggs, juveniles and adults) and four developmental stages for *Eudiaptomus* (eggs, nauplii, copepodites and adults)



Lake Tałtowisko. This can be seen from the much smaller degree of reduction of  $N_{1A}$  in relation to  $N_{1k}$  or  $N_{1j}$  in Mikołajskie Lake. In the next periods  $N_{1A}$  is for *Daphnia* 35, 20 and 32% of  $N_{1j}$  in Mikołajskie Lake, and 12, 10 and 21% of  $N_{1j}$  in Lake Tałtowisko, while for *Eudiaptomus* the values are 32, 44 and 20% of  $N_{1k}$  in Mikołajskie Lake and 18, 7 and 4% of  $N_{1k}$  for Lake Tałtowisko.

Any possible error involved here will rather act towards levelling this substantial difference, since if we assume, that fish predation is directed mainly at larger individuals and, therefore, the mean body size of an adult individual in Mikołajskie Lake would be as much lower (see section 3.1.5.), we will receive even higher values of  $N_{1A}$  in this lake as a result of increase of  $\frac{1}{D}$  (shortening of duration time for an adult individual).

Assuming then that as a result of a greater fish predation in Mikołajskie Lake, the mean life span of individuals is shortened (smaller sizes of adults), we can state, that this does not limit population reproduction, since although the life duration of an individual is shorter, however, much greater part of juvenile individuals enters the adult age and so the reproductive potential of a population is maintained at a high level.

It seems doubtful then, that fish predation could lead through a reduction of numbers of large adult individuals (as most susceptible to predation) to a significant reduction of population numbers of any of the species analysed, be it the result of an increased mortality, or the result of a decreased population reproduction.

### 3.2. Predation by fish and zooplankton in 30 Pomeranian lakes

As stated in section 3.1.1. there is a rather clear interdependence between the sizes of vendace catches, the mean density of vendace and mean biomass in a season, and also food consumption rate of vendace. Thus the size of vendace catches ( $\text{kg} \cdot \text{ha}^{-1} \cdot \text{year}^{-1}$ ) was assumed to be the relative measure of planktivorous fish predation on zooplankton ( $C$ ). It was necessary to exclude from calculations the contribution by smelt and bleak, assuming simultaneously that at a very wide variety of vendace density in 30 lakes analysed (catches vary between less than  $1 \text{ kg} \cdot \text{ha}^{-1} \cdot \text{year}^{-1}$  in four lakes and more than  $20 \text{ kg} \cdot \text{ha}^{-1} \cdot \text{year}^{-1}$  in five lakes) the fish predation on zooplankton is sufficiently differentiated to expect its significant correlations with a number of zooplankton characteristics.

The value of  $C$  was correlated with the following characteristics of zooplankton: (1) species diversity of crustacean community in the category of numbers, (2) production of unpredacious zooplankton (crustacean and rotifer) species; in both cases the value of the Shannon-Weaver index was used, (3–8) share (per cent) of each of the six different crustacean species in the total numbers of unpredacious crustaceans, and (9) total numbers of large cladocerans *Leptodora kindtii* and *Bythotrephes longimanus* Leydig ( $\text{ind.} \cdot \text{m}^{-3}$ ).

No significant correlation was found ( $p = 0.1$ ) between any of the above characteristics and the size of vendace catches ( $C$ ).

Consequently, multiple regression analysis was used in which all the above characteristics were treated as variables dependent on the following six independent variables: (1) size of vendace pressure expressed by the size of yearly catches ( $\text{kg} \cdot \text{ha}^{-1} \cdot \text{year}^{-1}$ ), (2) degree of hypolimnion deoxygenation (per cent from 100% saturation), (3) bottom area in the reach of



epilimnion in relation to the total bottom surface area of the lake (per cent), (4) amount of particulate organic carbon in seston particles smaller than  $50 \mu\text{m}$  in diameter ( $\text{mg} \cdot \text{l}^{-1}$ ), (5) ratio of lake shore line to total surface area of the lake ( $\text{m} \cdot \text{ha}^{-1}$ ) and (6) mean diameter of the largest ellipse inscribed in a lake surface with relation of diameters  $\leq 2/1$ .

Thus, considered was the fact that not only predation by planktivorous fish, but also other factors act on the structural characteristics of zooplankton community. These factors are connected with the lake trophic type (degree of hypolimnion deoxidation and bottom area in the reach of epilimnion), the amount of food accessible for zooplankters (particulate organic carbon in particles smaller than  $50 \mu\text{m}$ ), or with the probable influence of the littoral zone on pelagic zooplankton (ratio of lake shore line to total lake surface and the mean diameter of the largest ellipse inscribed in a lake surface treated as an indicator of the distance from the sampling station to the shore). Values of these factors and their discussion can be found in another paper (Gliwicz — in preparation).

Multiple regression analysis was used on June data from 30 lakes and July data from 15 lakes. Among 12 correlations with significant statistically coefficients of correlation (obtained after the sixth step in the regression) most important were independent variables pertaining to the trophy of the lake (oxygen depletion and per cent of bottom in the reach of epilimnion), and the influence of the littoral zone on pelagic zooplankton (size of ellipse inscribed in lake's surface). The remaining independent variables did not elevate significantly the values of multiple correlation coefficients.

Fish pressure ( $C$ ) turned out to be a significant independent variable in only four out of twelve regression analyses (Fig. 9). It appeared to be one of the factors responsible for the

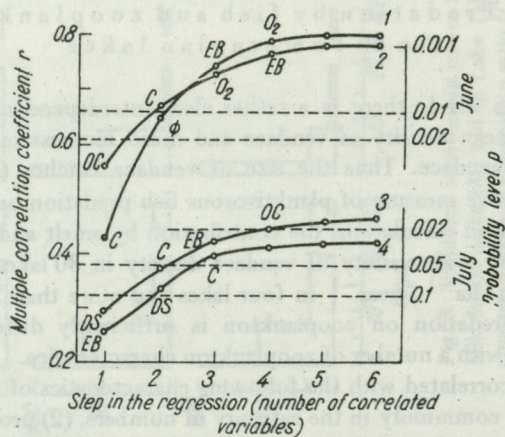


Fig. 9. Dependence of share of *Daphnia cucullata* (1) and of *Eudiaptomus graciloides* (2) in total numbers of unpredacious planktonic crustaceans (in June 1975) on six independent variables (upper), and dependence of species diversity of planktonic crustaceans expressed by the Shannon and Weaver index (3) and (4) of total numbers of *Leptodora* and *Bythotrephes* (in June 1975) on the same six independent variables (lower):  $C$  — intensity of planktivorous vendace predation on zooplankton expressed by size of yearly catches ( $\text{kg} \cdot \text{ha}^{-1} \cdot \text{year}^{-1}$ ),  $O_2$  — degree of hypolimnion deoxidation (per cent from 100% saturation),  $OC$  — amount of organic carbon in particles  $< 50 \mu\text{m}$  ( $\text{mg C} \cdot \text{l}^{-1}$ ),  $EB$  — share of bottom area in the reach of epilimnion in total bottom area of the lake (per cent),  $DS$  — ratio of lake shore line to lake total area ( $\text{m} \cdot \text{ha}^{-1}$ ),  $\phi$  — mean diameter of largest ellipse with diameter ratio  $\leq 2/1$  inscribed in lake surface. Multiple regression analysis for 14 lakes (July) and 30 lakes (June 1975)



contribution of larger species, such as *Daphnia cucullata* and *Eudiaptomus graciloides* in the total crustacean numbers in June, but not in July when fish predation most likely increases. There was no significant correlation either between fish pressure and the contribution of a large species *Daphnia longispina* O. F. Müller to the total numbers of unpredacious crustaceans during both months.

It can be accepted then, that in lakes of Northern Poland fish predation is not the main factor responsible for the species composition of pelagic crustaceans, although it is not unlikely, that together with other biotic and abiotic environmental factors, it may act in the shaping of the structure of zooplankton communities.

#### 4. DISCUSSION

The results of the present paper show, that in typical Polish lakes, where vendace accompanied often by smelt and bleak is the main planktivorous fish feeding in the pelagic zone, predation by planktivores cannot be considered as the main factor influencing the species composition and seasonal succession of zooplankton. This conclusion will not change even then, if the consumption of zooplankton biomass by planktivorous fish happens to be greater from the value obtained in this work, since there still remains open the question of the seasonal changes and differences between lakes.

The concept of the decisive role of planktivorous fish on the shaping of zooplankton communities arose from observations made on small and shallow reservoirs having much greater stocks of fish than large lakes of Northern Poland. In backwaters and ponds of Czechoslovakia and Poland, where the effect of fish pressure on the elimination of large and the development of smaller zooplankton forms was observed by Hrbáček (1958, 1962), Gurzęda (1960), Grygierek (1962, 1967), Hillbricht-Ilkowska (1962), Straškraba (1965), and others, the fish biomass was reaching  $900 \text{ kg} \cdot \text{ha}^{-1}$ , and fish numbers  $60,000 \text{ ind.} \cdot \text{ha}^{-1}$  (in backwaters — Hrbáček and Novotná-Dvořáková 1965) or  $20,000 \text{ ind.} \cdot \text{ha}^{-1}$  (in ponds — Grygierek, Hillbricht-Ilkowska and Spodniewska 1966). On the other hand, it appears, that the biomass and numbers of vendace in the pelagic zone of Polish lakes do not exceed<sup>4</sup>  $270 \text{ kg} \cdot \text{ha}^{-1}$  and  $10,000 \text{ ind.} \cdot \text{ha}^{-1}$  (in Mikołajskie Lake  $56 \text{ kg} \cdot \text{ha}^{-1}$  and  $2,000 \text{ ind.} \cdot \text{ha}^{-1}$ ). At the same time the fish there penetrate a water column at least ten times greater and therefore their pressure on zooplankton is respectively many times smaller.

<sup>4</sup>These numbers have been obtained for Lake Buszno, where according to Bernatowicz and Radziej (1974) the catches are about  $41 \text{ kg} \cdot \text{ha}^{-1} \cdot \text{year}^{-1}$ , which is a record for Polish lakes.

Vendace biomass in the pelagic zone has been calculated according to the scheme shown in section 2. Numerical abundance was calculated on the basis of the age structure data of the catchable portion of population (Marciak 1970, Leopold 1972, Ciepielewski 1974) and on the basis of data on biomass increase of different age groups (Marciak 1962, Ciepielewski 1974).

Dąbrowski and Leopold (1969) stated that in Polish lakes the catches of vendace are about 1/3 of the average biomass of the catchable stock of this species; the calculations of vendace biomass in the pelagic zone are based on this statement. According to these authors, this intensity of vendace exploitation, a short living species, is not adequate and, on the average, vendace populations are improperly exploited. This would mean that the higher than in other lakes vendace catches in Lake Buszno, are not as much the result of a greater biomass as the result of a much more intensive exploitation. Thus, it can be accepted that the real biomass and numbers of vendace in the pelagic zone of this reservoir are much lower than estimated.



However, the concept of Hrbáček (1958) was soon confirmed on lake samples and announced by Brooks and Dodson (1965) as the universal "size-efficiency hypothesis", verified later many times in numerous publications. It is characteristic, however, that most of the examples of the evident planktivorous fish predation effect on the replacement of large crustacean forms by smaller forms and rotifers, are from oligotrophic lakes, mostly of the alpine type (e.g., Gliwicz 1963, 1967, Galbraith 1967, Anderson 1972, Sprules 1975) or located at high latitudes (Nilsson 1972, Nilsson and Pejler 1973) where the lakes are sometimes small and shallow (e.g., Stenson 1972) and in addition stocked with several closely related species of the *Salmonidae* family.

If the effect of fish predation in more eutrophic lakes seemed at times questionable (e.g., Gannon 1972), it was usually clear in oligotrophic lakes, although the fish stock there must have been several times smaller than in ponds and backwaters. This can be explained by several causes. First of all, in lakes of little advanced eutrophication, there is an abundance of large crustaceans, which do not occur in eutrophic lakes, even those with a very small stock of planktivorous fish. These forms maybe large and desirable enough to make it worth-while for the fish to search after, and thus must increase the degree of their selection as opposed to smaller forms. Transparent waters of oligotrophic lakes, and distinct red or blue colouration of crustaceans inhabiting cooler alpine and subarctic waters, help fish in choosing larger and consequently better visible individuals. Not less important is much lower temperature of these lakes and smaller food concentration, which do not allow fast increase of biomass and intensive reproduction of crustaceans. The ratio of elimination rate of individuals from crustacean populations to their reproductive rate may, therefore, approach or exceed 1, even when fish pressure is not very high. It is even more so probable, that in these conditions, the better visible and slower moving egg-producing females (Gliwicz 1967) are most readily preyed upon by planktivorous fish. Finally, not less important is the fact, that in an environment with small food concentration, specialization of fish in food searching may increase (as shown, e.g., by Zaret and Rand 1971) by changing from collecting into selecting technics.

In the environment of meso- and eutrophic lakes in Poland all these factors are of little importance. Less or more passive collection of food on gillrakers cannot act selectively enough to spare the 300–600  $\mu\text{m}$  *Bosmina* or *Chydorus* and choose the 800–1,400  $\mu\text{m}$  *Daphnia* or *Diaphanosoma*. At the abundance of other, although smaller species, searching for distinctly larger food morsels such as *Leptodora* or *Bythotrephes* becomes unprofitable, although it happens to vendace, as found by Marciaik (1962) and Szypuła (1965).

Perhaps of some importance in these lakes is hunting for one-species clouds of crustaceans. This, however, happens rather in the littoral zone; guts of fish caught in this region often contained one-species mass of crustaceans (e.g., *Bosmina*, *Sida* or *Ceriodaphnia* — Prejs 1973, 1976).

However, regardless of the degree of food selectivity by vendace, smelt and bleak, the planktivorous fish in the pelagic zone of the lakes analysed have most likely little effect on the structure of zooplankton community, which is shown by the value of planktonic crustacean biomass elimination many times greater than the value of the overestimated planktonic food consumption by all three species of fish.

It seems then, that the influence of planktivorous fish on *Crustacea* in meso- and eutrophic lakes should not be treated as the effect of a specialized predator, but rather as the effect of an unspecialized predator, which according to the concept of Gause (1935) (after Slobodkin 1963) modifies the results of interspecific competition by giving greater chances to species of increased presently ecological reproductivity, even then, if these are weaker competitors. Thus



some other environmental factor which selectively modifies the reproduction of various species would be responsible for the kind of species dominating in a lake. According to an earlier paper (Gliwicz 1977), planktivorous fish as an unspecialized predator, would only help in the elimination of species of reduced reproductivity, even of those competitively stronger; in case of filter feeding cladocerans — those large-sized species.

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## 5. SUMMARY

Seasonal changes of daily elimination of planktonic crustacean biomass  $E_B$  in two lakes were compared with seasonal changes of the total daily consumption of the crustacean biomass by three species of planktivorous fish: vendace, bleak and smelt (Figs. 1, 2). The analysis was done for two Masurian lakes (Mikołajskie and Tańtowisko) of varied, but typical for lakes in Poland, density of planktivorous fish (Table II) and of varied — as a consequence — predation of fish on zooplankton.

It was found that fish predation is not the main factor responsible for the elimination of crustacean biomass. This is evident from: (1) low for both lakes value of biomass consumption by fish ( $C_B$ ) in relation to the value of total elimination of biomass ( $E_B$ ), (2) close for both lakes values of  $E_B$  for crustaceans, and greater value  $E_B$  for cladocerans in Lake Tańtowisko in spite of greater fish predation in Mikołajskie Lake, (3) divergence in distribution of values  $E_B$  and  $C_B$  during the season analysed.

Analysis of seasonal dynamics of numbers in cladoceran populations (Figs. 3, 4) showed that fish predation is not the chief factor effecting the changes in numbers ( $N$ ) of cladoceran species with larger and smaller mean body weights ( $\bar{W}$ ). This is evident from: (1) identical sequence of peak numbers of cladoceran species in both lakes which differ in intensity of fish predation, (2) reduction in numbers of *Bosmina* with small  $\bar{W}$  and increase in numbers of *Diaphanosoma* with twice as large value of  $\bar{W}$ , in time of the gradual increase in fish pressure, and (3) greater numbers of largest *Cladocera* (*Leptodora*, and to a smaller degree *Daphnia*) in a lake with more intensive fish predation.

Comparison of changes in elimination of individuals from populations of *Cladocera* and *Calanoida* ( $E_N$ ) with changes in numbers of *Cladocera* and *Calanoida* eaten by fish ( $C_N$ , Figs. 5, 6) also showed, that fish predation is not the main factor causing mortality among crustaceans. It is evident from: (1) small number of *Crustacea* possibly taken by fish ( $C_N$ ) at the time of highest crustacean mortality ( $E_N$ ) and (2) lack of mortality ( $E_N = 0$ ) in *Cladocera* and low mortality of *Calanoida* in May, when the value of  $C_N$  is already relatively high.

It was also found, that fish pressure cannot be considered as the factor causing essential differences in the average sizes of adult individuals in both lakes, the greater, the larger is the crustacean species (Fig. 7). Analysis of simplified survivorship curves for various crustacean species in both lakes, during periods of greater and less intensive fish predation (Fig. 8) showed, that it is doubtful if reduction of numbers of larger mature individuals by fish can lead to any essential reduction of population numbers of any analysed crustacean species, be it the result of increased mortality or the result of diminished reproductivity of populations.

It turned out also, that fish predation is of little importance in effecting the species composition and species diversity of crustacean communities in 30 Pomeranian lakes with varied density of vendace (lack of simple correlations). The results of multiple regression analysis, in which various parameters pertaining to zooplankton community structure were treated as dependent variables, dependent on many independent variables, such as density of vendace or food resources of lakes, showed that only in few cases did fish predation elevate the value of multiple regression coefficients (Fig. 9).

It seems then reasonable to state that the effect of planktivorous fish on planktonic *Crustacea* in meso- and eutrophic lakes should not be regarded as the influence of a specialized predator according to the "size-efficiency hypothesis" of Brooks and Dodson (1965), but rather as the effect of an unspecialized predator, which according to the concept of Gause (1935) (after Slobodkin 1963)



modifies the results of interspecific competition by giving greater chances to species of higher at present ecological reproductivity, even then if these are competitively weaker forms.

## 6. POLISH SUMMARY (STRESZCZENIE)

W dwóch jeziorach mazurskich (Mikołajskie i Tałtowisko) o różnym, lecz typowym dla jezior w Polsce, zagęszczeniu ryb planktonożernych (sielawa, ukleja i stynka) w pelagialu (tab. II) i – w konsekwencji – odmiennej presji tych ryb na zooplankton, porównano sezonowe zmiany dobowej eliminacji biomasy skorupiaków planktonowych  $E_B$  z sezonowymi zmianami łącznej dobowej konsumpcji tej biomasy przez wszystkie trzy gatunki ryb (fig. 1, 2).

Stwierdzono, że presja ryb nie jest głównym czynnikiem decydującym o eliminacji biomasy skorupiaków, o czym świadczy: 1) niska w obu jeziorach wartość konsumpcji tej biomasy przez ryby ( $C_B$ ) w stosunku do wartości całkowitej eliminacji tej biomasy ( $E_B$ ), 2) zbliżona wartość  $E_B$  skorupiaków i większa wartość  $E_B$  wioślarek w Tałtowisku pomimo kilkakrotnie mniejszej niż w Mikołajskim presji ryb, 3) brak zgodności w rozkładzie wartości  $E_B$  i  $C_B$  w czasie sezonu.

Analizując sezonową dynamikę liczebności populacji wioślarek (fig. 3, 4) stwierdzono, że presja ryb nie jest również głównym czynnikiem decydującym o zmianach liczebności ( $N$ ) gatunków wioślarek o większych i mniejszych średnich ciężarach ciała ( $\bar{W}$ ), o czym świadczy: 1) identyczna sekwencja szczytów liczebności gatunków wioślarek w obu jeziorach, mimo odmiennej presji ryb, 2) redukcja liczebności *Bosmina* o małej  $\bar{W}$  i wzrost liczebności *Diaphanosoma* o 2-krotnie większej  $\bar{W}$ , wraz ze wzrostem presji ryb oraz 3) większe liczebności największych wioślarek (*Leptodora*, w mniejszym stopniu również *Daphnia*) w jeziorze o większej presji ryb.

Porównując zmiany eliminacji osobników z populacji wioślarek i widłonogów *Calanoida* ( $E_N$ ) ze zmianami liczby zjadanych przez ryby wioślarek i widłonogów *Calanoida* ( $C_N$ , fig. 5, 6) stwierdzono, że presja ryb nie jest również głównym czynnikiem powodującym śmiertelność skorupiaków, o czym świadczy: 1) mała liczba skorupiaków eliminowanych przez ryby ( $C_N$ ) w okresie ich największej śmiertelności ( $E_N$ ) oraz 2) brak śmiertelności ( $E_N = 0$ ) wioślarek i niska śmiertelność widłonogów w maju, gdy wartość  $C_N$  jest znaczna.

Stwierdzono też, że trudno uznać presję ryb za czynnik powodujący istotne różnice w średniej wielkości dojrzałych osobników w obu jeziorach, tym większe, im większy gatunek skorupiaków (fig. 7). Wyniki analizy uproszczonych krzywych przeżywalności różnych gatunków skorupiaków w obu jeziorach, w okresach większego i mniejszego znaczenia presji ryb (fig. 8), poddały też w wątpliwość, by ryby mogły poprzez redukcję liczebności większych dojrzałych osobników prowadzić do istotnej redukcji liczebności populacji któregośkolwiek z analizowanych gatunków skorupiaków, czy to na skutek zwiększenia śmiertelności, czy też na skutek zmniejszenia rozrodczości populacji.

Presja ryb okazała się również mało istotnym czynnikiem przy analizie jej wpływu na skład gatunkowy i zróżnicowanie gatunkowe zespołów zooplanktonu skorupiakowego w 30 jeziorach Pomorza o różnym zagęszczeniu sielawy (brak korelacji jednostkowych). W wynikach analizy regresji wielokrotnej różnych wskaźników struktury zooplanktonu, z których każdy potraktowano jako zmienną zależną od szeregu zmiennych niezależnych (w tym wskaźnik zagęszczenia sielawy oraz wskaźniki zasobności pokarmowej wód jeziornych i inne), presja ryb tylko w nielicznych przypadkach miała istotne znaczenie dla podniesienia wartości współczynnika korelacji wielokrotnej (fig. 9).

Wydaje się zatem, iż wpływ ryb planktonożernych na skorupiaki planktonowe w warunkach jezior mezo- i eutroficznych rozpatrywany być winien nie jako działanie drapieżcy wyspecjalizowanego, zgodnie z „size-efficiency hypothesis” Brooksa i Dodsona (1965), lecz raczej jako działanie drapieżcy niespecjalizowanego, który zgodnie z koncepcją Gausego (1935) (według Slobodkina 1963) modyfikuje wynik konkurencji międzygatunkowej dając większe szanse gatunkom o wyższej aktualnie rozrodczości ekologicznej, nawet wtedy gdy są to gatunki konkurencyjnie słabsze.

## 7. REFERENCES

1. Anderson R. S. 1972 – Zooplankton composition and change in an alpine lake – Verh. int. Verein. Limnol. 18: 264–268.
2. Bajkov A. D. 1935 – How to estimate the daily food consumption of fish under natural conditions – Trans. Am. Fish. Soc. 65: 288–289.



3. Bernatowicz S., Radziej J. 1974 – Rozsiedlenie sielawy (*Coregonus albula* L.) w jeziorach Polski – Acta Hydrobiol. 16: 209–219.
4. Bottrell H. H., Duncan A., Gliwicz Z. M., Grygierek E., Herzig A., Hillbricht-Ilkowska A., Kurasawa H., Larsson P., Węgleńska T. 1976 – A review of some problems in zooplankton production studies – Norw. J. Zool. 24: 419–456.
5. Brett J. R., Higgs D. A. 1970 – Effect of temperature on the rate of gastric digestion in fingerling sockeye salmon, *Oncorhynchus nerka* – J. Fish. Res. Bd Can. 27: 1767–1779.
6. Brooks J. L., Dodson S. 1965 – Predation, body size and composition of the plankton – Science, N. Y. 150: 28–35.
7. Ciepielewski W. 1974 – Wzrost, śmiertelność i stosunek produkcji do biomasy populacji sielawy w jeziorze Maróz – Roczn. Nauk roln. 96–H–2: 7–23.
8. Czeczuga B. 1959 – Stynka (*Osmerus eperlanus* L.) w Jeziorze Rajgrodzkim i jej biologia – Pol. Arch. Hydrobiol. 5: 131–146.
9. Dąbrowski B., Leopold M. 1969 – Próba oceny przeciętnego stanu zagęszczenia populacji sielawy (*Coregonus albula* L.) w jeziorach polskich – Roczn. Nauk roln. 91–H–1: 75–82.
10. Dembiński W. 1971 – Vertical distribution of vendace *Coregonus albula* L. and other pelagic fish species in some Polish lakes – J. Fish. Biol. 3: 341–357.
11. Galbraith M. G. 1967 – Size-selective predation on *Daphnia* by rainbow trout and yellow perch – Trans. Am. Fish. Soc. 96: 1–10.
12. Gannon J. E. 1972 – Effects of eutrophication and fish predation on recent changes in zooplankton *Crustacea* species composition in Lake Michigan – Trans. Am. microsc. Soc. 91: 82–84.
13. Gąsowska M. 1962 – Krągłoustę i ryby – PWN, Warszawa-Kraków, 240 pp.
14. Gliwicz Z. M. 1963 – Wpływ zarybienia na biocenozę jezior tatrzańskich – Chronimy Przyr. ojcz. 19, 6: 27–35.
15. Gliwicz Z. M. 1967 – Zooplankton and temperature-oxygen conditions of two alpine lakes of Tatra Mts. – Pol. Arch. Hydrobiol. 14: 53–72.
16. Gliwicz Z. M. 1974 – Status troficzny gatunków zooplanktonu słodkowodnego – Wiad. ekol. 20: 197–206.
17. Gliwicz Z. M. 1977 – Food size selection and seasonal succession of filter feeding zooplankton in an eutrophic lake – Ekol. pol. 25: 179–225.
18. Gliwicz Z. M. (in preparation) – Factors affecting planktonic crustacean populations in 30 Polish lakes.
19. Gliwicz Z. M., Hillbricht-Ilkowska A. 1975 – Ecosystem of Mikołajskie Lake. Elimination of phytoplankton biomass and its further fate in the lake throughout the year – Pol. Arch. Hydrobiol. 22: 39–52.
20. Grygierek E. 1962 – The influence of increasing carp fry population on crustacean plankton – Roczn. Nauk roln. B, 81: 189–210.
21. Grygierek E. 1967 – Formation of fish pond biocenosis exemplified by planktonic crustaceans – Ekol. pol. A, 15: 155–181.
22. Grygierek E., Hillbricht-Ilkowska A., Spodniewska I. 1966 – The effect of fish on plankton community in ponds – Verh. int. Verein. Limnol. 16: 1359–1366.
23. Gurzęda A. 1960 – Wpływ presji narybku karpia na dynamikę liczebności *Tendipedidae* i *Cladocera* – Ekol. pol. B, 6: 257–268.
24. Hall D. J. 1971 – Predator-prey relationships between yellow perch and *Daphnia* in a large temperate lake – Trans. Am. microsc. Soc. 90: 106–107.
25. Hillbricht-Ilkowska A. 1962 – Euplanktonic rotifers (*Rotatoria*) in ponds varying stocked with carp fry – Bull. Acad. pol. Sci. Cl. II. Sér. Sci. biol. 10: 537–540.
26. Hillbricht-Ilkowska A., Gliwicz Z. M., Spodniewska I. 1966 – Zooplankton production and some trophic dependences in the pelagic zone of two Masurian lakes – Verh. int. Verein. Limnol. 16: 432–440.
27. Hillbricht-Ilkowska A., Patalas K. 1967 – Metody oceny produkcji i biomasy oraz niektóre problemy metodyki ilościowej zooplanktonu – Ekol. pol. B, 13: 139–172.
28. Hillbricht-Ilkowska A., Spodniewska I., Węgleńska T., Karabin A. 1972 – The seasonal variation of some ecological efficiencies and production rates in the plankton community of several Polish lakes of different trophic (In: Productivity problems of freshwaters, Eds. Z. Kajak, A. Hillbricht-Ilkowska) – PWN–Polish Scientific Publishers, Warszawa-Kraków, 111–127.



29. Hillbricht-Ilkowska A., Węgleńska T. 1970 – The effect of sampling frequency and the method of assessment of the production values obtained for several zooplankton species – *Ekol. pol.* A, 18: 539–557.
30. Hrbáček J. 1958 – Typologie und Produktivität der teichartigen Gewässer – *Verh. int. Verein. Limnol.* 13: 394–399.
31. Hrbáček J. 1962 – Species composition and the amount of zooplankton in relation to the fish stock – *Rozpr. čsl. Akad. Věd. Řada mat. přír. Věd.* 72: 1–116.
32. Hrbáček J., Dvořáková M., Kořinek V., Procházková L. 1961 – Demonstration of the effect of the fish stock on the species composition of zooplankton and the intensity of metabolism of the whole plankton association – *Verh. int. Verein. Limnol.* 14: 192–195.
33. Hrbáček J., Novotná-Dvořáková M. 1965 – Plankton of four backwaters related to their size and fish stock – *Rozpr. čsl. Akad. Věd. Řada mat. přír. Věd.* 75: 1–65.
34. Hutchinson G. E. 1959 – Homage to Santa Rosalia or why are there so many kinds of animals? – *Am. Nat.* 93: 145–149.
35. Karabin A. 1974 – Studies on the predatory role of the cladoceran, *Leptodora kindtii* (Focke), in secondary production of two lakes with different trophy – *Ekol. pol.* 22: 295–310.
36. Kerfoot W. C. 1974 – Net accumulation rates and the history of cladoceran communities – *Ecology*, 55: 51–61.
37. Kozikowska Z. 1970 – Analiza populacji ryb w jeziorach okolic Mikołajek na Mazurach – *Acta Univ. Wratislav.* III, 119: 1–119.
38. Leopold M. 1972 – Metodyka prognozy i oceny połowów ryb o krótkim cyklu życiowym w jeziorach polskich (na przykładzie sielawy – *Coregonus albula* (Linnaeus)) – *Roczn. Nauk roln.* 94–H–4: 9–98.
39. Limpadanai D. 1974 – Production of zooplankton communities, determined by <sup>14</sup>C in situ method – Ph. D. Thesis, Department of Limnology, University of Helsinki, Helsinki, 68 pp.
40. Marciak Z. 1962 – Sezonowe zmiany w odżywianiu się i wzroście sielawy (*Coregonus albula* L.) z jeziora Pluszne – *Roczn. Nauk roln.* 81–B–2: 335–357.
41. Marciak Z. 1970 – Podstawa przyrodnicza gospodarki sielawowej – *Inst. Ryb. śródl., Olsztyn*, 39: 8–14.
42. Nilsson N. A. 1972 – Effects of introductions of salmonids into barren lakes – *J. Fish. Res. Bd Can.* 29: 693–697.
43. Nilsson N. A., Pejler B. 1973 – On the relation between fish fauna and zooplankton composition in North Swedish Lakes – *Rep. Inst. Freshwat. Res. Drottningholm*, 53: 51–77.
44. Northcote T. G., Clarotto R. 1975 – Limnetic macrozooplankton and fish predation in some coastal British Columbia lakes – *Verh. int. Verein. Limnol.* 19: 2378–2393.
45. Prejs A. 1973 – Experimentally increased fish stock in the pond-type Lake Warniak. IV. Feeding of introduced and autochthonous non-predatory fish – *Ekol. pol.* 21: 465–505.
46. Prejs A. 1976 – Fishes and their feeding habits (In: Selected problems of lake littoral ecology, Ed. E. Pieczyńska) – *Wydawnictwa Uniwersytetu Warszawskiego, Warszawa*, 152–172.
47. Radziej J. 1965 – Studium limnologiczne pod kątem zróżnicowania sielawy (*Coregonus albula* L.) jeziora Narie i jeziora Kańskiego – Ph. D. Thesis, Higher School of Agriculture, Olsztyn, 83 pp.
48. Rembiszewski J. M. 1970 – Population variation in smelt – *Osmerus eperlanus* (Linnaeus, 1758) (*Pisces*) in Poland – *Annl. zool., Warsz.* 28: 65–95.
49. Slobodkin L. B. 1963 – Growth and regulation of animal population – Holt, Rinehart and Winston, New York-Chicago-San Francisco-London, 184 pp.
50. Sprules W. G. 1975 – Factors affecting the structure of limnetic crustacean communities in central Ontario lakes – *Verh. int. Verein. Limnol.* 19: 635–643.
51. Stavn R. H. 1975 – The effects of predator pressure on species composition and vertical distribution of *Daphnia* in Piedmont lakes of North Carolina, USA – *Verh. int. Verein. Limnol.* 19: 2891–2897.
52. Stenson J. A. E. 1972 – Fish predation effect on the species composition of the zooplankton community in eight small forest lakes – *Rep. Inst. Freshwat. Res. Drottningholm*, 52: 132–148.
53. Sterzyńska M. 1976 – Zróżnicowanie gatunkowe zooplanktonu w 30 jeziorach pomorskich o różnej trofii – M. Sc. Thesis, University of Warsaw, Warszawa, 51 pp.
54. Sterzyński W. 1976 – Płodność i zmienność morfologiczna wrotków planktonowych w jeziorach o różnej zasobności pokarmowej – M. Sc. Thesis, University of Warsaw, Warszawa, 73 pp.
55. Straškraba M. 1965 – The effect of fish on the number of invertebrates in ponds and streams – *Mitt. int. Verein. Limnol.* 13: 106–127.



56. Szypuła J. 1965 – Odżywianie się sielawy (*Coregonus albula* L.) w Jeziorze Legińskim – Zesz. nauk. wyższ. Szk. roln. Olsztyn, 20: 213–224.
57. Szypuła J. 1970a – Wzrost i rozmieszczenie narybku sielawy w jeziorze Legińskim i Wydryńskim – Roczn. Nauk roln. 92–H–2: 45–60.
58. Szypuła J. 1970b – Odżywianie się narybku sielawy w jeziorze Legińskim i Wydryńskim – Roczn. Nauk roln. 92–H–3: 61–83.
59. Węgleńska T. (in preparation) – Variability of production rate in freshwater planktonic crustaceans.
60. Wells L. 1970 – Effects of alewife predation on zooplankton populations in Lake Michigan – Limnol. Oceanogr. 15: 556–565.
61. Zaret T. M., Rand A. S. 1971 – Composition in tropical stream fishes: support for the competitive exclusion principle – Ecology, 52: 336–342.

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