KOMITET EKOLOGICZNY-POLSKA AKADEMIA NAUK

EKOLOGIA POLSKA - SERIA A

Tom XII Warszawa 1964 Nr 2

Zdzisław KAJAK

EXPERIMENTAL INVESTIGATIONS OF BENTHOS ABUNDANCE ON THE BOTTOM OF LAKE ŚNIARDWY*

Examination of experimental cages containing mud and fauna from a given habitat, placed on the bottom of a lake, revealed after a few weeks that the number of species and the abundance of benthos had increased several times over, and also the rate of development of the organisms had been hastened in relation to the state found in the neighbourhood of the cages. These differences were not caused by the consumption of the benthos fauna by the large fish or by invertebrate predators, but were probably due to changes in the habitat in the cages caused, among others, by the activity of the benthos.

The comprehensive data now available on the abundance of benthos, its dynamics and the relations of the organisms make it possible to formulate some hypotheses as to the factors and mechanisms governing these matters. It would appear to be easier, quicker and more certain to check these hypotheses by means of field experiments than merely to collect material from different natural environments.

A relatively small number of field experiments have so far been made on benthos material. Eggleton (1931) made observations of the capacity for survival of different profundal species in glass jars (and therefore with considerable deformation of chemical conditions) submerged on to the bottom of a lake. Recently experiments have been increasingly frequently aimed at

* From the Institute of Ecology Polish Academy of Sciences, Warszawa.

one definite factor – consumption of the benthos by fish (Lachnovič 1953, Hayne and Ball 1956, Enaceanu 1957, Lellak 1957, Kajak 1958a, Assman 1958, 1960, Hruška 1961). Thus investigations were made by means of field experiments chiefly of two factors affecting the abundance of benthos – oxygen deficit and consumption by fish. There are undoubtedly far more factors affecting benthos and mechanisms determining its abundance (Kajak 1958b), and these may be discovered and understood by applying a sufficiently comprehensive range of experimental operations.

A kind of field experiment on a large scale (although not intentionally so) is formed by filling dam reservoirs and by the periodically flooded zones of these reservoirs. The fertilisation of ponds can also be included here (Ioffe 1954, 1957, Pankratova 1957). In all these cases the *Tendipedidae* larvae develop in large numbers and their development is accelerated (Morduchaj-Boltovskoj 1961, Kajak 1962). The reason for this is the abundance of food in the form of the bacteria developing on the decaying vegetation. These "experiments", although they yielded a large amount of interesting material, refer only to certain specific circumstances. An understanding of the causes determining the abundance of benthos in the whole range of natural situations remains to be investigated.

The application of experiments in the whole body of water (Lastočkin 1949, Hayne and Ball 1956, Olszewski 1961) is somewhat difficult and not always possible. The method of experiments in isolated sections of the natural habitat would seem far simpler and provides far greater opportunities of experimentation. Under conditions with maximum similarity to natural ones it is possible to trace and check the role played by defined ecological factors (by means of the variations in the intensity of these factors in the section of the habitat in relation to the neighbouring environment) in the abundance of organisms. I used the method of experimentation in sections of the natural habitat with considerable success in a shallow riverside lake (Kajak 1958a)[1]. It proved necessary to make suitable modifications to the experimental apparatus in the deeper parts of the profundal of lakes. Cubic cages were used measuring 30×30×30 cm, (Fig. 1a) consisting of an iron wire frame, Ø 5–6 mm, painted with enamel paint and then closely covered with plastic material to ensure isolation from the chemical action of iron and paint; the frame was then covered with fine nylon gauze, 0·4×0·4 mm mesh. This size of mesh prevents the adult forms from escaping from the cages, but permits of the free passage of the juvenile forms and free circulation of water from the surrounding environment. Using of similar experimental apparatus in the riverside lake (Kajak 1958a) revealed an analogical course of variations in the benthos inside the apparatus and in the neighbouring habitat. Experiments

[1] Grygierek (1958) used a similar type of equipment for her experimental investigations of plankton, and obtained results with a certain degree of similarity to those discussed in the present study.

of this type made in fish ponds, from the time the ponds were filled, and therefore a zero level of benthos, exhibited a greater abundance of *Tendipedidae* in the enclosures than in their neighbourhood, even in the cases in which the experimental cages covered at the top with polyethylene sheeting, thus making it impossible for eggs to be laid on their surface (Kajak – unpublished material). It is clear from the above that 1) the cages do not restrict the access of the juvenile forms, which is in agreement with data in literature on the planktonic spread of the first larval stage (Alekseev 1955, Morduchaj-Boltovskoj and Šilova 1955), 2) do not produce unfavourable changes in the confined habitat.

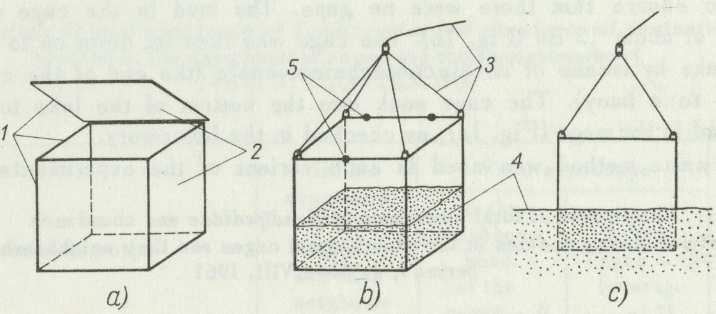

Fig. 1. Experimental cages

a – general view, *b* – cage after mud has been placed in it, ready to be submerged on to the bottom of the lake, *c* – cage on the bottom of the lake (cross-section). *1* – frame of wire painted and covered with plastic, *2* – miller gauze, *3* – electrotechnic cable or nylon string, *4* – mud, *5* – place in which the cover is fastened

Different types of experiment were carried out in the cages described above:

Variant 1. Artificially increased abundance of certain species of *Tendipedidae* in order to ascertain whether it is possible for a number of larvae, larger than that established naturally, to live in the given habitat (Kajak 1963).

Variant 2. Reduction of the abundance of certain species to ascertain whether this causes a compensatory increase in the number of larvae, and how this occurs.

Variant 3. Placing mud deprived of macrobenthos (by sieving) in a cage – for the same purposes as in the preceding variant.

Variant 4. Addition of readily decaying organic substance (cooked mashed potatoes, periphyton etc.) in order to ascertain whether the benthos in a given habitat has sufficient food.

Variant 5. Transfer of certain species of *Tendipedidae* to a habitat in which they do not occur, or occur in very small numbers, to ascertain what is responsible for their absence – habitat conditions or biocenotic relations.

Only a few types of the experiments possible have, of course, been given above.

Control experiments were of course carried out to check how the enclosing of part of the habitat in a cage affects the abundance of benthos. Control experiments consisted in placing mud from a given habitat together with the macrofauna it contains into the cage. Partitions made of plywood were used while the mud was being placed in the cages to prevent the mud from overflowing; after the contents of 4 Ekman dredges had been placed in the cage, the partitions were removed, the cage covered by a lid (made of gauze of the same or rarer mesh – 1.5 × 1.5 mm) which was tightly secured with a nylon thread to ensure that there were no gaps. The mud in the cage reached to a height of about 12 cm (Fig. 1b). The cage was then let down on to the bottom of the lake by means of an electrotechnical cable (the end of the cable being fastened to a buoy). The cage sunk into the bottom of the lake to the level of the mud in the cage (Fig. 1c), as checked in the laboratory.

The same method was used in each variant of the experiments, the only

Comparison of total abundance of *Tendipedidae* and abundance of dominating species in the experimental cages and their neighbourhood Series *I*, 1.VII–3.VIII. 1961

Tab. I

Taxonomic groups	Initial abundance in the cages and their neigbourhood	Final abundance		*C/N*
		in the neighbourhood of the cages – *N*	in the cages – *C* (average of 3)	
Tendipedidae	289	471	1376	2.9
Tendipes plumosus L.	133	231	220	1.0
Tendipes anthracinus Zett.	0	9	189	21.0
Einfeldia carbonaria Mg.	89	0	11	<
Tanytarsus gregarius Kieff.	0	53	329	6.2
Limnochironomus tritomus Kieff.	0	18	74	4.1
Cryptochironomus viridulus F.	0	89	222	2.5
Cryptochironomus conjugens Kieff.	45	0	0	=
Procladius sp.	22	62	200	3.2
Orthocladiinae gen. *orielica* Tshern.	0	9	11	1.2
Pallasea quadrispinosa Sars.	0	0	63	<

Percentage in total abundance of *Tendipedidae* in the cages of the species which occurred in the neighbourhood of the cages during the course of the experiment was 95,8%.

difference being that before closing the cage the appropriate operation was carried out – increasing the density of certain species, addition of organic substance etc.

The cages were left on the bottom of the lake for several weeks. Samples of benthos were taken from the vicinity of the cages at the time when the latter were let down and at the time they were pulled up. At the end of the experiment the whole contents of the cage was sifted through a benthos sieve.

Experiments were made at different periods of the vegetation season (Tab. I–IV).

Comparison of total abundance of *Tendipedidae* and abundance of dominating species in the experimental cages and their neighbourhood
Series *II*, 11.IX–22.X.1960

Tab. II

Taxonomic groups	Initial abundance in the cages and their neigbour-hood	Final abundance		*C/N*
		in the neighbour-hood of the cages – *N*	in the cages – *C* (average of 3)	
Tendipedidae	710	599	1695	2.7
Tendipes plumosus L.	187	211	196	0.9
Einfeldia carbonaria Mg.	462	344	1396	4.0
Cryptochironomus defectus Kieff.	43	44	5	0.1
Procladius sp.	9	0	59	<
Ablabesmyia monilis L.	9	0	0	=
Pallasea quadrispinosa Sars.	0	0	5	<

Percentage in total abundance of *Tendipedidae* in the cages of the species which occurred in the neighbourhood of the cages during the course of the experiment was 96,2%.

I have limited myself here in principle to a discussion of the variations which were observed in the experimental control cages (and in those cages in which the abundance of the larvae of *Tendipes plumosus* was initially increased and which did not exhibit significant differences in the composition and abundance of fauna in comparison with the control cages) in relation to the surrounding environment. The experiments referred to were made in Lake Śniardwy, at a depth of 7–8 m, on a site about 2 km from the nearest edge. Lake Śniardwy is the largest lake in Poland, 102 km² in area, with a mean depth of 4.5 m (maximum depth – about 20 m – occurs only in a very

Comparison of total abundance of *Tendipedidae* and abundance of dominating species in the experimental cages and their neighbourhood
Series *III*, 11.IX–22.X.1960

Tab. III

Taxonomic groups	Initial abundance in the cages and their neigbour-hood	Final abundance		C/N
		in the neighbour-hood of the cages – N	in the cages – C (average of 3)	
Tendipedidae	187	452	1110	2.5
Tendipes plumosus L.	71	284	577	2.0
Tendipes anthracinus Zett.	0	44	76	1.7
Einfeldia carbonaria Mg.	98	115	266	2.3
Limnochironomus tritomus Kieff.	0	0	44	<
Cryptochironomus defectus F.	0	9	44	4.9
Procladius sp.	9	0	76	<
Tanytarsus gregarius Kieff.	9	0	0	=
Pallasea quadrispinosa Sars.	0	0	13	<

Percentage in total abundance of *Tendipedidae* in the cages of the species which occurred in the neighbourhood of the cages during the course of the experiment was 97,6%.

small fraction of the percentage of the lake's area). The whole area of the lake bottom lies within the epilimnion (Kosicki 1960, Olszewski and Paschalski 1961), and therefore the oxygen supply at the bottom during the season when there is no ice present is always maintained at nearly maximum level.

It must be stated in the first place that no reduction in the abundance of any species of *Tendipedidae* in the cages in relation to their surroundings was ever observed (with the exception of species which were very few in number, in which case it might be fortuitous). On the contrary, a significant, almost threefold, increase in abundance of *Tendipedidae* was usually observed (Tab. I–IV), and also an increase in the number of their species (Tab. V). The average increase in the number of species was over twofold, and in certain cases more than threefold, and in relation to the state in the lake at the end of the experiment (with which the final state in the experimental cage should properly be compared) in one case even sevenfold (Tab. V).

All the species found in the experimental cages also occurred in the lake (although they were frequently not found in the immediate neighbourhood of the cages during the course of the experiment). This is evidence that there

Comparison of total abundance of *Tendipedidae* and abundance of dominating species in the experimental cages and their neighbourhood
Series *IV*, 27.VI–29.VII.1960

Tab. IV

Taxonomic groups	Initial abundance in the cages and their neighbourhood	Final abundance		C/N
		in the neighbourhood of the cages – N	in the cages – C (average of 3)	
Tendipedidae	444	320	1043	3.3
Tendipes plumosus L.	300	249	644	2.6
Einfeldia carbonaria Mg.	78	0	22	<
Microtendipes chloris Mg.	0	0	155	<
Limnochironomus tritomus Kieff.	11	0	78	<
Tanytarsus gregarius Kieff.	0	9	22	2.4
Procladius sp.	55	53	56	1.0
Cryptochironomus conjugens Kieff.	0	9	22	2,4
Valvata piscinalis (Müll.)	0	0	255	<

Percentage in total abundance of *Tendipedidae* in the cages of the species which occurred in the neighbourhood of the cages during the course of the experiment was 81%.

are no species specially privileged by the cage. Increase in abundance in the cages, in relation to their neighbourhood, was as a rule decided by the species which occurred and dominated at that time in the lake. The participation of other species was relatively small – usually only a few %. It is also probably that the majority of these "other" species were not perceived in the lake on account of the small numbers in which they occurred; owing to the general tendency to an increase in abundance of each species in the experimental cages, the same size of area sampled permitted of grasping a larger number of species.

Certain species proved capable of attaining in the cages an abundance several times (Tab. I–IV), and in one case even 21 times, greater (*Tendipes anthracinus* – Tab. I) than in their surroundings at the bottom of the lake. The greater abundance in the cages in relation to their surroundings was particularly distinct in those species which increased in abundance in the lake during the course of the experiment. This was usually the case when the increase in abundance in the lake was caused by the appearance of young larvae (see below).

Species, the abundance of which decreased or was maintained on the same level in the lake during the experiment, did not generally occur in large numbers

Comparison of number of species of *Tendipedidae* in the experimental cages and neighbouring environment
(Upper row for the given series – range of fluctuations in the number of species, lower row – arithmetical mean)

Tab. V

Series and duration of the experiment	Number of species: neighbourhood of the cages (beginning – end of the experiment)	Number of species: cages (end of experiment)	Number of cages
I 1.VII–3.VIII 1961	4–7	11–14	3
	5.5	12.3	
II 11.IX–22.X 1960	6–3	7–9	4
	4.5	7.5	
III 11.IX–22.X 1960	4–4	–	1
	4.0	8.0	
IV 27.VI–29.VII 1960	4–2	8–14	3
	3.0	10.7	
Average of all series	4.25	9.7	11

in the cages, or only in slightly larger numbers in relation to the lake (*Einfeldia carbonaria*, *Cryptochironomus conjugens* – Tab. I, *Ablabesmyia monilis* – Tab. II, *Procladius* – Tab. IV etc.). Nevertheless the abundance of certain species in the cages increased even when the numbers in the lake either remained unaltered or decreased (*Tendipes plumosus*, *Microtendipes chloris*, *Limnochironomus tritomus* – Tab. IV, *Einfeldia carbonaria*, *Procladius*, sp. *Limnochironomus tritomus* – Tab. III, *Einfeldia carbonaria* – Tab. II). This occurred in the cases in which, despite the decrease or maintainence of the same numbers in the lake, appearance of the young forms took place (see later, Tab. VI and VII). These facts are evidence of the greater capacity for survival of the juvenile stages of certain species of *Tendipedidae* in the cages than in the lake. Sometimes a considerable amount of young larvae were found in the cages despite the fact that in the lake the reduction in their numbers was so great that they were never encountered at all throughout the entire duration of the experiment (Tab. VI, VIII). Cases in which there were large numbers of young larvae in the cages, with simultaneous complete absence in the lake at the moment the experiment was ended, were frequent (Tab. VI, No. 1, 6, 7). It may be imagined that it is not a case here of the greater capacity for survival, but that the cage "entices" the larvae of *Tendipedidae*, Comparison of age structure of *Tendipedidae* in the experimental cages and their neighbourhood

Tab. VI

Duration of the experiment	Series	Number of cages	Species	Classes of length of larvae in mm	Number of individuals*: neighbourhood of cages – beginning	Number of individuals*: neighbourhood of cages – end of experiment	Number of individuals*: cages (end of experiment)	No.
1. VII–3. VIII 1961	I	3	*Procladius* sp.	5–8	2	0	11	1
				9–11	2	6	7	
			Cryptochironomus viridulus	0–5	0	8	11	2
				6–8	0	0	10	
			Tanytarsus gregarius	3–6	0	4	25	3
				7–8	6	0	2	
11.IX–22.X 1960	II	4	*Tendipes plumosus*	5–10	0	0	4	4
				> 10	11	18	15	
			Einfeldia carbonaria	4–6	41	6	55	5
				7–9	0	19	78	
	III	1	*Tendipes plumosus*	5–15	2	0	12	6
				> 15	5	26	40	
			Einfeldia carbonaria	0–6	8	0	8	7
				7–10	1	11	16	
27.VI–29.VII 1960	IV	3	*Tendipes plumosus*	0–12	0	0	35	8
				> 20	22	23	23	

*The number of individuals per area of experimental cage (900 cm^2) is given.

Detailed comparison of age structure in experimental cages and their neighbourhood, using several examples (number of individuals per area of experimental cage = 900 cm²)

Tab. VII

Procladius sp. Series *I*			*Tendipes plumosus* Series *II*			*Einfeldia carbonaria* Series *III*			*Tendipes plumosus* Series *IV*		
length mm	number of larvae: in neighbourhood of cages	number of larvae: in cages	length mm	number of larvae: in neighbourhood of cages	number of larvae: in cages	length mm	number of larvae: in neighbourhood of cages	number of larvae: in cages	length mm	number of larvae: in neighbourhood of cages	number of larvae: in cages
5	0	0.3	5–10	0	5.2	4	0	2.7	0–5	0	1.0
6	0	2.0	10–15	0	6.8	5	0	2.7	5–10	0	29.0
7	0	4.7	15–20	1.6	21.2	6	0	2.7	10–20	0.5	5.0
8	0	3.7	20–25	18.4	17.2	7	1.6	7.7	20–25	13.0	18.0
9	2.3	4.0	>25	5.6	1.2	8	2.4	6.7	>25	9.0	5.0
10	0.7	2.7				9	2.4	2.7			
11	2.3	0.7				10	5.0	0.0			

is attractive to them, that the forms of a size which make it possible to pass through the net into the cage accumulate in them. The fact that forms of relatively small dimensions (and which can therefore pass through the mesh of the net even in the older larval stages) e.g. *Cryptochironomus conjugens*, *Tanytarsus gregarius*, do not exhibit significant differences in their abundance in the cages and lake than other species (Tab. I–IV) hower, argue against this explanation.

Comparison of age structure, mean length of larvae and percentage of pupae in the experimental cage and its neighbourhood, at the time the experiment was ended

Tab. VIII

Length of larvae mm	Number of individuals	
	in the neighbourhood of the cage	in the cage
15–25	8	6
> 25	13	12
Average length of larvae measuring ⩾ 20 mm	26.5	27.5
% of pupae	11.5	44.4

The number of individuals per area of experimental cage (=900 cm^2) is given.

In addition to the fact itself of finding greater abundance of several species in the cages than in their surroundings, a second matter is important – whether, despite the greater abundance, conditions for the development of the larvae do not deteriorate, in other words – whether under the given conditions it is possible for a larger number of larvae to develop. Comparison of the age structure (Tab. VI) in the cages and their surroundings shows that in the former the number of young larvae is usually greater, which, as mentioned above, is evidence of the greater capacity for survival in the cages; apart from this, however, the abundance of larvae of greater dimensions is generally also higher, which is proof that not only is the rate of development not decreased, but sometimes even increased. The few cases of a lower abundance of larvae of the greatest dimensions (Tab. VII) do not contradict this; it must be presumed that there as well acceleration of development has taken place, ending in the emergence of the oldest forms (hence their absence), and in the meantime the larvae of smaller dimensions, of which there is usually a greater number in the cages, have succeeded in growing to a size almost the same as that of the larvae in the neighbourhood of the cages. Detailed data on age structure (Tab. VII) provide convincing evidence of this.

In those cases in which appearance of the young larvae did not take place, the age structure in the cages and lake was similar (Tab. VIII), and the average dimensions of the larvae in the cages greater than in the neighbourhood of the latter. Further, there was a far greater participation of pupae in the cage; part of them had probably already changed into imagines, which explains the slightly smaller number of larvae in the cage than in its neighbourhood. These facts provide evidence that the development of the larvae in the cages is more rapid than that in the situation found in the lake.

With regard to *Oligochaeta*, the differences in their abundance between cages and lake were less regular than was the case with *Tendipedidae*. On an average the abundance of *Oligochaeta* was similar in the cages and in their neighbourhood at the bottom of the lake (Tab. IX).

Comparison of abundance of *Oligochaeta* in experimental cages and their neighbouring environment

Tab. IX

Series and duration of experiment	Range of fluctuations in abundance		Number of cages
	neighbourhood of cages (beginning – end of experiment)	cages (end of experiment)	
I 1.VII–3.VIII.1961	35.5–97.7	33.3–55.5	3
II 11.IX–22.X.1960	79.2–188.7	77.7–177.6	4
III 11.IX–22.X.1960	53.0–275.3	652.7	1
IV 27.VI–29.VII.1960	26.0–333.0	155.4–1110.0	3
Average of all series	136.1	165.0*	

*Excluding one case – exceptionally high abundance (1100 individuals per 1 m²).

The two groups discussed – *Tendipedidae* and *Oligochaeta*, formed almost 100% of the benthos in the lake habitat examined. Of the other organisms occurring is small numbers, *Pallasea quadrispinosa* Sars, *Valvata piscinalis* (Müll) and *Chaoborus crystallinus* Degeer deserve discussion. *Pallasea quadrispinosa* exhibited the same regularity as *Tendipedidae* – it occurred far more numerously in the cages than at the bottom of the lake in the area surrounding the cages. It occurred sporadically in the lake, and during the experiments it was not even found in the neighbourhood of the cages (hence its numbers were less than 1 individual per 1 m²), whereas in the experimental cages its numbers varied from approximately 5 to 10 individuals per 1 m² (Tab. I–IV) (maximum abundance found was 90 individuals per 1 m²). These were mainly young individuals, which is evidence, as in the case of *Tendipedidae*, of their greater capacity for survival in the cages than in their neighbourhood.

Valvata piscinalis generally occurred in very small numbers both in the cages and in their neighbourhood; it was only in one series (Tab. IV) that a considerable amount of this species occurred in the cages. It is worthy of note that the exceptionally high abundance – about 1800 individuals per 1 m^2 – occurred in the cage containing mud deprived of macrofauna (Kajak 1963); it is possible that this is evidence of the unfavourable influence exerted by *Oligochaeta* and *Tendipedidae* on this species – as these forms had been removed *Valvata piscinalis* could occur abundantly. Even in the cage containing a very thin layer of mud (several mm only) the numbers of *Valvata* were lower (about 800 individuals/ 1 m^2), despite the fact that field observations have shown the tendency of benthos snails to settle on hard substrata.

Chaoborus crystallinus occurred in very small numbers both in the cages and in the lake – up to approximately 60–70 individuals per 1 m^2.

DISCUSSION

It was found in the experiments discussed above that after the cages had been left for several weeks on the bottom of the lake, the number of species and the abundance of benthos in the cages increased several times over in relation to the state found in the neighbourhood of the cages. The rate of development of the organisms was also greater in the cages.

The interpretation of the greater abundance and more rapid development of the majority of benthos organisms in the cages in relation to the neighbouring bottom of the lake requires further investigation. There are many factors, generally not investigated, which might affect the abundance of benthos (Kajak 1958b). Nevertheless, the results obtained, make it possible to exclude a certain number of factors and put forward certain hypotheses.

As regards invertebrate predators which might fundamentally affect the abundance of benthos(Belavskaja and Konstantinov 1956, Luferov 1958) these cannot be held responsible for the differences between the numbers present in the cages and in the neighbourhood of the cages, since like the other species of *Tendipedidae* they exhibit a tendency to more numerous occurrence in the cages. The abundance of the chief predator feeding on the larvae of *Tendipedidae* – *Procladius* sp., increased in the majority of cases in the cages by at least as many times as the total abundance of *Tendipedidae* (Tab. I–IV). Of the other invertebrate predators, *Hydracarina* were sporadically encountered, and these predators also occurred slightly more abundantly in the cages than in the lake.

The influence of consumption by large fish is also doubtful; as is known, the food most intensively sought by them is *Tendipes plumosus* and therefore, assuming intensive consumption of benthos by fish, this species in particular should be more numerous in the cages than in their neighbourhood, whereas the abundance of the large larvae of *Tendipes plumosus* is not usually greater in the cages than in the lake (Tab. X). In addition, as discussed above, the greater abundance in the cages is caused chiefly, in the case of various species, by the young larvae, and not the grown ones, of larger dimensions, which are more sought after by large fish. All this shows that consumption by large fish is not the factor responsible for differences in abundance in the cages and their neighbourhood. On the other hand it is not possible to exclude the activities of fry in the habitat examined, as the occurrence of young (3–4 cm) *Acerina cernua* was confirmed there.

Comparison of abundance of large larvae of *Tendipes plumosus* in the lake and in cages at the moment of ending the experiment (abundance per area of 1 cage = 900 cm²)

Tab. X

Length of larvae mm	Duration of experiment	Number of larvae	
		neighbourhood of cages	cages
> 20	27.VI–29.VII.1960	23	23
> 15	11.IX–22.X.1960	17	15
> 15	1.VII–3.VIII.1960	21	18

The greater abundance of *Tendipedidae* in the cages is perhaps the effect of the greater calm in the cages, in the sense of the reduction in the intensity of water movement of this fairly stormy lake, and also the fact that the benthos is not disturbed by fish. Owing to the greater calm in the cages, the larvae can spend more time on feeding, and get more food from the habitat. It is rather an indisputable fact that the condition of the animal, its fecundity, capacity for survival, and as a result its population numbers, are dependent on the amount and quality of food which the animal is capable of acquiring and using (Nikolskij 1950, Borodič 1956, Konstantinov 1958, Beverton 1962, Nikolskij 1962). In turn this naturally depends on many other habitat and biocenotic factors (Ivlev 1955).

It is also possible that on account of a certain reduction in the circulation of water between the cage and its surrounding, a concentration occurs of nutritive substances discharged from the mud to the water at the bottom, (review of literature on substance interchange between mud and water – Rossolimo 1958), which creates better food conditions for the benthos. In this connection it is worth to note, that the benthos organisms themselves play an important part in the interchange of substance between mud and water (Rossolimo 1939, Sinica 1941, Ganapatti 1949, Edwards 1958). Possibly, owing to the greater calm in the cages, transformation of the habitat by the organisms was more intensive. The fact that the abundance of *Tendipedidae* usually increased while that of *Oligochaeta* remained, on the average, unchanged, indicates that the conditions on the surface of the mud or in the water immediately above the bootom were decisive here; as we know, *Oligochaeta* obtain their food from a certain depth below the surface of the mud (Poddubnaja and Sorokin 1961, Poddubnaja 1962), while *Tendipedidae* obtain their food on and above the surface of the mud (Konstantinov 1958).

It is also probable that a different structure, different type of relations and interrelations are formed within the cages, making it possible for a larger number of benthos to live there. Facts are known in literature of considerable increase in the density of the animals per unit of area being obtained by a change in the organisation of the population, and in the character of the interrelations of the organisms in the population (research on mice – Petrusewicz 1957, 1960). As I have shown previously (Kajak 1963) the interaction of the benthos organisms, even when density is not great, are very strong, which makes it possible to assume that in the case of benthos also, the role of population (and of the whole community) organisation is very great. The fact is worth emphasising that despite the situation discussed of the spontaneous increase in the abundance of many species, attempts at artificial increasing of numbers by introducing larger numbers of larvae from the same habitat did not give great results (Kajak 1963). The position is similar in the case of attempts at increasing density per unit of area of other biological objects (Kajak, Stańczykowska – attempts at increasing the numbers of *Viviparus fasciatus* Müll. – unpublished materials; Ryszkowski – in press). These facts are evidence of the extremely important part played by the organisation of populations and biocenoses. We know very little about this organisation as yet and as a result we do not know what stimulus should be used and at what moment to change the organisation of the biocenosis in the direction of increased abundance and productivity.

There are a certain number of facts which form evidence that in certain situations the organisms can so strongly influence the habitat that they completely change the character of circulation of matter. For instance, instead of settling on the bottom, the greater part of organic matter is quickly mineralised and returns to circulation, causing greater abundance, more rapid tempo of production, changes in the ratios of the species, and even in the species composition. An example of such influence may be the activities of nutria or ducks in fish ponds, counteracting the aging of the pond and leading to an increase in the production of all the production links in the pond (Wolny 1956, Ehrlich 1961). The influence of a large fish population on the circulation of matter in a pond is similar (Cahn 1929, Hrbaček and others 1961, Grygierek 1962, Wolny 1962, Hillbricht-Ilkowska 1963); the large fish population does not only cause exhaustion of the food supply of the habitat, but on the contrary – transforms the latter in such a way, that intensiveness of the circulation of matter and production of different food links in the pond increases.

It will be interesting to ascertain whether the increase in abundance of benthos discussed here consists in the better use made of the existing supply of food only, or whether in addition in the transformation of the habitat causing greater production of food, and in effect an increase in abundance and in the rate of development of the benthos.

On the basis of material so far examined it may be stated without doubt that the increase in the production of benthos in the cages was not determined by the amount of organic matter, which remained the same as in the lake, nor the amount of oxygen, nor consumption by large fish, nor nonvertebrate predators. All the factors mentioned are, as we know, most frequently considered as determining the abundance of benthos. In the situations analysed it was probably some small differences in the conditions between the bottom of the lake and the interior of the experimental cages at the beginning of the experiment, which were decisive.

*

The far greater abundance of benthos obtained in the cages described above under natural conditions gives grounds for hoping for: 1) more rapid discovery of the causes and mechanisms determining the abundance of benthos, 2) the possibilities of interference in the abundance of benthos in bodies of water – the increasing of their abundance and production.

Increase in the numbers of benthos would have not only direct food effects (greater amount of food for fish) but would also affect in other ways the circulation of matter in a body of water; as is well known the participation of benthos organisms in the interchange of substances between water and mud is considerable (Rossolimo 1939, Sinica 1941, Ganapatti 1949, Edwards 1958); and owing to mechanisms transferring substances from the bottom to the water (Ohle 1958, Rossolimo 1958) the effects of the activities of benthos could be quickly spread over the whole basin.

CONCLUSIONS

1. The experimental apparatus described (Fig. 1) ensure good conditions for the development of the benthos fauna.

2. The number of species inside the experimental cages were found to have increased several times over in relation to the neighbouring habitat (Tab. V).

3. The abundance of *Tendipedidae* in the cages was as a rule several times greater than in the lake (Tab. I–IV), this difference being caused chiefly by the species which predominated in the lake in the neighbourhood of the cages.

4. The increase in the numbers of *Tendipedidae* larvae in the cages was caused by the greater survival of the juvenile stages of several species (different in different periods) in the cages than in their neighbourhood.

5. Certain data indicate that the development of the larvae is more rapid in the cages than in their neighbourhood.

6. Like *Tendipedidae, Pallasea quadrispinosa,* and in some cases also *Valvata piscinalis,* occurred in far greater numbers in the cages than in the neighbouring habitat.

7. *Oligochaeta* occurred on an average in approximately the same numbers in the cages as in their vicinity; in certain cases they occurred more abundantly in the cages, or more abundantly in their neighbourhood; no regularity was found here (Tab. IX).

8. The difference in abundance of many benthic forms in the experimental cages and in their neighbourhood is not the result of the activities of large fish, but it is not possible to exclude the consumption of benthos by the fry or the disturbance of the benthos by fish.

9. The facts presented show that a far larger number of animals than that determined naturally, is capable of living in the study habitat at the bottom of the lake. The most probable cause of the greater abundance of benthos would seem to be either the possibility of getting greater quantity of food in the habitat owing to the greater calm in the cages, or the change in habitat conditions in the cages, actually caused to a considerable extent by the life activity of the benthos, resulting in the greater production of the kinds of food favoured by the benthos.

REFERENCES

1. Alekseev, N. K. 1955 – O rasselenii ličinok chironomid po vodoemu – Vopr. Ichtiol. 5: 145–149.
2. Assmann, A. V. 1958 – Nekotyre dannye o vyedanii bentosa rybami – Dokl. Akad. Nauk SSSR 122: 932–935.
3. Assmann, A. V. 1960 – Izmenenie dostupnosti ličinok *Chironomidae* pri vyedanii rybami – Izv. Akad. Nauk SSSR, s. biol. 5: 670–685.
4. Belavskaja, L. I., Konstantinov, A. S. 1956 – Pitanie ličinok *Procladius choreus* Meig. i uščerb nanosimyj imi kormovoj baze ryb – Vopr. Ichtiol. 7: 193–203.
5. Beverton, R. J. H. 1962 – Long term dynamics of certain north sea fish populations – The exploatation of natural animal populations – British Ecol. Soc. Symp. II. Oxford: 242–258.
6. Borodič, N. D. 1956 – O pitanii ličinok *Chironomus* f. l. *plumosus* i o zimovkie ich w gruntach spuščonnych rybovodnych prudov – Trudy vsesojuzn. gidrobiol. Obšč. 7: 123–147.
7. Cahn, A. R. 1929 – The effect of carp on a small lake; the carp as a dominant – Ecology 10: 271–274.
8. Edwards, R. W. 1958 – The effect of larvae of *Chironomus riparius* Meig. on the redox potentials of settled activated sludge – Ann. appl. Biol. 46: 457–464.
9. Eggleton, F. 1931 – A limnological study on the profundal bottom fauna of certain fresh-water lakes – Ecol. Monogr. 1: 231–331.
10. Ehrlich, S. 1961 – Experiments in reversion of the filling up processes in fish ponds – Hydrobiologia, 18: 136–154.

11. Enaceanu, V. 1957 – Contributioni la determinarea productivitatii apelor piscicole – Bul. Inst. Cercet. piscic. 16: 83–84.
12. Ganapatii, S. V. 1949 – The role of the blood-worm, *Chironomus plumosus* in accounting for the presence of phosphates and excessive free ammonia in the filtrates from the slow sand filters of the Madras Water Works – J. Zool. Soc. India 1: 41–43.
13. Grygierek, E. 1958 – Eksperymentalne badania nad dynamiką liczebności skorupiaków w naturalnych warunkach – Ekol. Pol. A, 6: 167–182.
14. Grygierek, E. 1962 – Wpływ zagęszczenia narybku karpi na faunę skorupiaków planktonowych – Rocz. Nauk. roln. 81, B: 189–208.
15. Hayne, D. W., Ball, R. C. 1956 – Benthic productivity as influenced by fish predation – Limnol.Oceanogr. 1: 162–175.
16. Hillbricht-Ilkowska,A. 1963 – Effect of carp fry as predators on some rotifer (*Rotatoria*) species – Bull. Acad. pol. Sci. cl. 2, 11: 88–89.
17. Hrbaček, J., Dvorakova, M., Korinek, V., and Prochazkova, 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. Vercing Limnol. 14: 192–195.
18. Hruška, V. 1961 – An attempt at a direct investigation of the influence of the carp stock on the bottom fauna of two ponds – Verh. int. Vereinig. Limnol. 14: 732–736.
19. Ioffe, C. I. 1954 – Povyšenie kormovoj bazy prudov organičeskimi udobrenijami – Trudy probl. Sovešč. 2: 112–121.
20. Ioffe, C. I. 1957 – Vlijanie udobrenija na povyšenie kormovoj bazy prudov – Probl. gidrobiol. vnutr. vod. – Trudy probl. sovešč. 7: 68–72.
21. Ivlev, V. S. 1955 – Eksperimentalnaja ekologija pitanija ryb – Moskva, 252 pp.
22. Kajak, Z. 1958a – Próba interpretacji dynamiki liczebności *Tendipedidae* bentosowych w wybranym środowisku łachy wiślanej Konfederatka – Ekol. Pol. A, 6: 205–291.
23. Kajak, Z. 1958b – W sprawie badań warunków życiowych bentosu – Ekol. Pol. B, 4: 189–201.
24. Kajak, Z. 1962 – Przegląd piśmiennictwa dotyczącego bentosu zbiorników zaporowych, w związku z budową zbiornika Dębe na Bugu i Narwi – Ekol. Pol. B, 8: 3–27.
25. Kajak, Z. 1963 – The effect of experimentally induced variations in the abundance of *Tendipes plumosus* L. larvae on intraspecific and interspecific relations – Ekol. Pol. A, 11: 355–367.
26. Konstantinov, A. S. 1958 – Biologija chironomid i ich razvedenie – Saratov, 362 pp.
27. Kosicki, S. 1960 – Pionowe rozmieszczenie wrotków pelagicznych w okresie stagnacji letniej w jeziorach Mikołajskim i Śniardwy – Pol. Arch. Hydrobiol. 8: 9–57.
28. Lachnovič, V. T. 1953 – Estestvennaja kormovaja baza nerestovo-vyrostnych i nagulnych prudov rybchoza "Volma" – Učen. Zap. belorus. gos. Univ. s. biol. 17: 256–273.
29. Lastočkin, D. L. 1949 – Biocenozy sapropelej v ich vzaimootnošenii s sapropelevoj sredoj – Trudy Lab. sapropelev. otloženij 3: 7–28.
30. Lellak, J. 1957 – Der Einfluss der Fresstätigkeit des Fischbestandes auf die Bodenfauna der Fischteiche – Z. Fischerei,8: 621–633.
31. Luferov, V. P. 1958 – Issledovanija po biologii chiščnych ličinok *Tendipedidae* (*Diptera*) Rybinskogo vodochranilišča – Avtoref dissert. – Jaroslavl: 1–19.
32. Morduchaj-Boltovskoj, F. D. 1961 – Process formirovanija donnoj fauny v Gorkovskom i Kujbyševskom vodochraniliščach – Trudy Inst. Biol. Vodochr. 4/7: 49–177.
33. Morduchaj-Boltovskoj, F. D. i Šilova, A. I. 1955 – O vremenno planktonnom obraze žizni ličinok *Glyptotendipes* (*Diptera, Chironomidae*) – Dokl. Akad. Nauk. SSSR, 105: 163–165.

34. Nikolskij, F. V. 1950 – O dinamike čislennosti stada ryb i o tak nazyvaemoj probleme produktivnosti vodojomov – Zool. Ž. 29: 489–500.
35. Nikolskij, G. V. 1962 – On some adaptations to the regulation of population density in fish species with different types of stock structure. The exploatation of natural animal populations – British Ecol. Soc. Symposia II, Oxford: 265–282.
36. Ohle, W. 1958 – Die Stoffwechseldynamik der Seen in Abhängikeit von den Gasausscheidung ihereres Schlammes – Vom Wasser 15: 127–149.
37. Olszewski, P. 1961 – Versuch einer Ableitung des hypolimnischen Wassers aus einem See. Ergebnisse des erster Versuchsjahres – Verh. int. Vereinig. Limnol. 14: 855–861.
38. Olszewski, P. i Paschalski, J. 1961 – Wstępna charakterystyka limnologiczna niektórych jezior Pojezierza Mazurskiego – Zesz. nauk. WSR Olsztyn, 4: 1–109.
39. Pankratova, V. J. 1957 – Vlijanie udobrenija na razvitie donnoj fauny prudov rybcogo-semajnogo pitomnika – Trudy probl. Sovešč. 7: 46–51.
40. Petrusewicz, K. 1957 – Investigation of experimentally induced population growth – Ekol. Pol. A, 5: 281–309.
41. Petrusewicz, K. 1960 – An increase in mice population induced by disturbance of the ecological structure of the population – Bull. Acad. pol. Sci. cl. 2, 8: 301–304.
42. Poddubnaja, T. L. 1962 – Issledovanija po biologii massovych vidov tubificid (*Limnodrillus newaensis* Mich. i *Limnodrillus hoffmeisteri* Clap.) Rybinskogo vodochranilišča – Avtoref. dissert. Moskva, 1–22.
43. Poddubnaja, T. L. i Sorokin, J. I. 1961 – Glubina sloja optimalnogo pitanija tubificid v sviazi s ich peremeščenijami v grunte – Bjull. Biol. Vodochr. 10: 14–17.
44. Rossolimo, L.L. 1939 – Rol ličinok *Chironomus plumosus* v obmene veščestvom meždu ilovymi otloženijami i vodoj ozera – Trudy limn. Stanc. Kosino, 22: 35–52.
45. Rossolimo, L. L. 1958 – Sovremennoe sostojanie voprosa ob obmene rastvorennymi veščestvami meždu vodoj i gruntom ozer i prudov – Trudy mosk. techn. Inst. ryb. prom. 4 Choz. 9: 3–62.
46. Ryszkowski, L. in press – Zależności wewnątrzpopulacyjne wśród nutrii *Myocaster coypus* (Molina) – Ekol. Pol. A.
47. Sinica, T. I. 1941 – Izmenenie soderžanija nekotorych organiceskich veščestv v sapropele pod vlijaniem processov piščevarenija u ličinok *Chironomidae* – Trudy Labor. Genezisa sapropelja 2: 159–167.
48. Wolny, P. 1956 – Wpływ stada kaczek na biocenozę stawów karpiowych – Biul. Zakł. Biol. Stawów PAN 3: 47–67.
49. Wolny, P. 1962 – Przydatność oczyszczonych ścieków miejskich do hodowli ryb – Roczn. Nauk roln.81, B: 231–249.

EKSPERYMENTALNE BADANIA NAD LICZEBNOŚCIĄ BENTOSU W STREFIE DENNEJ JEZIORA ŚNIARDWY

Streszczenie

Przeprowadzono badania eksperymentalne nad bentosem w śródjezierzu Śniardw, około 2 km od najbliższego brzegu. Eksperymenty polegały na umieszczeniu w specjalnych klatkach na dnie jeziora mułu wraz z fauną, pobranego w danym miejscu jeziora. Klatki o wymiarach 30 × 30 × 30 cm miały szkielet z grubego drutu pomalowanego farbą i obciągniętego folią polietylenową dla izolacji zawartości klatki od wpływów chemicznych żelaza i farby; szkielet był obciągnięty gazą perlonową o wymiarach oczek 0,5 × × 0,5 mm, a więc takich, jakie najczęściej używa się w sitach bentosowych. Klatki opuszczano na dno jeziora, gdzie zanurzano je mniej więcej do poziomu mułu wewnątrz

klatki (fig. 1). Spuszczano je na kablu elektrotechnicznym, którego koniec przywiązywano do boi. Na początku i końcu eksperymentu pobierano próby bentosu w sąsiedztwie klatek.

Klatki były przeznaczone do przeprowadzania w nich różnych eksperymentów z bentosem, np. obserwacji efektów zwiększania lub zmniejszania liczebności fauny w stosunku do stanu w ich sąsiedztwie (Kajak 1963), efektów zwiększania ilości substancji oganicznej, zwiększania ilości drapieżców itd.

Wstępne próby wykazały, że względna izolacja bentosu w klatkach przez okres kilku tygodni powoduje istotne różnice w stanie bentosu w stosunku do sąsiedztwa klatek. We wszystkich czterech seriach eksperymentów, przeprowadzonych w różnych okresach roku (z wyjątkiem zimy), liczebność *Tendipedidae* (oraz niektórych innych form – *Pallasea quadrispinosa* Sars , *Valvata piscinalis* (Müll.) wzrastała kilkakrotnie w stosunku do stanu w sąsiedztwie klatek (tab. I–IV). (Liczebność *Oligochaeta* w klatkach była przeciętnie zbliżona do liczebności w ich sąsiedztwie – tab. IX). Wzrastała również z reguły liczba gatunków *Tendipedidae* (tab. V). Wzrost liczebności wykazywały wszystkie, różne w różnych seriach eksperymentów, gatunki *Tendipedidae*. Świadczy to o tym, że przyczyną były jakieś czynniki ogólne wpływające dodatnio na wszystkie *Tendipedidae*, a nie tylko na poszczególne gatunki.

Wzrost liczebności *Tendipedidae* w klatkach powodowały głównie te gatunki, które występowały w sąsiedztwie klatek w trakcie trwania eksperymentu; udział innych gatunków nie przekraczał na ogół kilku procent (tab. I–IV). Wszystkie gatunki stwierdzone w klatkach są formami bentosowymi.

Wzrost liczebności w klatkach w stosunku do jeziora powodowały głównie formy młode. Niejednokrotnie nawet w sąsiedztwie klatek w ogóle nie stwierdzono obecności młodych larw danego gatunku, podczas gdy w klatkach występowały one licznie (tab. VI). Oczywiście przy końcu eksperymentu w klatkach stwierdzono większą liczebność nie tylko młodych, ale i starszych stadiów (tab. VI), gdyż część młodych larw dorosła. W tych wypadkach, gdy przebiega ostra granica między młodą i starszą generacją, stwierdzono zwiększenie tempa wzrostu i rozwoju larw w klatkach w stosunku do ich sąsiedztwa. (tab. VIII). Zdarzające się wypadki mniejszej liczebności najstarszych larw w klatkach w porównaniu z ich sąsiedztwem (tab. VII) nie przeczą temu; mniejsza liczba najstarszych larw w klatkach jest prawdopodobnie spowodowana przez wylot najbardziej wyrośniętych osobników (właśnie dzięki szybszemu tempu rozwoju w klatkach) i zajęcia ich miejsca przez larwy młodsze, które jeszcze nie osiągnęły maksymalnych rozmiarów.

Czynników wpływających na bentos jest bardzo wiele (Kajak 1958a). W obecnym etapie badań trudno stwierdzić, który z nich spowodował większą liczebność fauny w klatkach. Niemniej można wysunąć pewne hipotezy i wykluczyć działanie niektórych czynników. W piśmiennictwie najczęściej wymieniane są jako decydujące o stanie bentosu takie czynniki, jak tlen, ilość substancji organicznej, temperatura. Rzeczywiście decydują one w znacznej liczbie wypadków, wszędzie tam, gdzie odgrywają rolę limitującą. W omawianych tu eksperymentach te czynniki z pewnością nie decydowały; żaden z nich nie mógł mieć wartości korzystniejszych dla bentosu w klatkach niż w ich sąsiedztwie. Różnic liczebności w klatkach i ich sąsiedztwie nie mogły także wywoływać drapieżce bezkręgowe (*Pelopiinae*), gdyż liczebność ich w klatkach była większa niż w jeziorze, podobnie jak liczebność innych gatunków, niedrapieżnych.

W wypadkach istnienia wyraźnej granicy między pokoleniem młodym i starszym, co zdarzało się tylko u *Tendipes plumosus* L., stwierdzono, że liczebność dużych larw jest zbliżona w klatkach i jeziorze (tab. X), co przemawia za tym, że ryby te nie powodują znaczniejszej redukcji liczebności bentosu w badanym środowisku i nie są odpowiedzialne za różnice liczebności w klatkach i ich sąsiedztwie. Nie badano natomiast wpływu małych ryb, występujących w tym środowisku.

Zarówno duże, jak i małe ryby mogą „niepokoić" faunę bentosową, co zmniejsza jej możliwości żerowania, powodując pogorszenie kondycji, a w efekcie zmniejszenie liczebności fauny bentosowej.

Prawdopodobnie pewne procesy biologiczne przebiegały inaczej w klatkach niż w ich sąsiedztwie, mogło też, w wyniku osłabienia wymiany wody wnętrza klatek z otoczeniem, dochodzić do większej koncentracji substancji chemicznych w wodzie przydennej, co z kolei mogło stymulować rozwój mikroflory i mikrofauny. Omówiony wyżej wzrost liczebności *Tendipedidae* przy niezmienionej liczebności *Oligochaeta* świadczy o tym, że zmiany zachodziły głównie na powierzchni mułu lub nad jego powierzchnią; jak wiadomo, tam właśnie głównie żerują *Tendipedidae* (Konstantinov 1958), *Oligochaeta* zaś żerują w głębi mułu (Poddubnaja i Sorokin 1961, Poddubnaja 1962).

W literaturze opisano kilka wypadków zmiany środowiska przez organizmy wodne i to zmiany tego typu, że możliwe się staje liczniejsze występowanie tych zwierząt (Cahn 1929, Hrbaček i in. 1961, Hillbricht-Ilkowska 1963).

Jak wiadomo (Rossolimo 1939, Sinica 1941, Ganapatti 1949, Edwards 1958), *Tendipedidae* również bardzo intensywnie przekształcają środowisko przydenne. Być może, że w warunkach omawianych klatek eksperymentalnych na dnie jeziora zachodzi przekształcanie środowiska przez zespół organizmów bentosowych, co umożliwia liczniejsze występowanie tych organizmów.

Najbardziej prawdopodobnymi przyczynami większej liczebności bentosu w klatkach w porównaniu z ich sąsiedztwem są więc: 1) możność lepszego wykorzystania warunków troficznych w klatkach niż w ich sąsiedztwie, dzięki większemu spokojowi w klatkach, albo 2) zmiana warunków w klatkach, wywołana w znacznej mierze działalnością życiową bentosu, a powodująca większą produkcję pożądanych przez bentos rodzajów pokarmu.

AUTHOR'S ADDRESS:
Dr. Zdzisław Kajak,
Institute of Ecology, Warszawa, ul. Nowy Świat 72,
Poland.