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SOME TROPHIC RELATIONS IN THE BENTHOS OF SHALLOW PARTS OF MARION LAKE

ABSTRACT: Positive correlation in the distribution of the invertebrate predators and their prey was stated. The biomass of main predators slightly exceeded the biomass of their prey. Selectivity of the prey and daily food rations of predators (equalling 8–19% of predators' biomass) in situ were estimated by the method of "experimental cylinders". Predators feeding strongly depended on the presence of other predators of the same and other species, and decreased with their increasing density. The strong pressure of predators suggests either very short turnover time of their prey, or the immigration of the prey from other environments.

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1. INTRODUCTION

Marion Lake is a small (13.3 ha) and shallow (average depth 2.4 m) lake, at an altitude of 300 m a.s.l. in British Columbia, Canada. Being the subject of complex studies within the IBP, under the guidance of Dr. I. Efford, it has been well explored (Efford 1972, Efford and Hall in press).

This paper is an attempt to examine some trophic relations within the benthos. The following problems were analysed: (1) mutual distribution of animals, (2) influence of food on

the abundance of benthos and prey-predator relationships, (3) food selectivity and feeding intensity of the main predators.

Biocenotic relations, including trophic ones, are extremely sensitive to modifications of conditions, sometimes undetectable by the investigator, as has been demonstrated in a number of papers (K a j a k 1968, K a j a k and D u s o g e 1970). Thus, the only way to learn the real relationships in nature is to carry out experiments with natural communities of organisms, in as natural conditions as possible. For that reason the technique of experimental cylinders and enclosures in the lake was applied.

2. METHODS

The basic material consisted of a large series of experimental cylinders 20 cm² each, located in the lake for 2 days. The cylinders ensured completely normal environmental conditions and an entirely natural community of organisms, protecting it at the same time from large predators (including fish and salamanders), making impossible the migration of large benthic forms, and seriously limiting migration of the whole benthos. Each cylinder (a 16 cm deep piece of plastic tubing, 20 cm² in area, with 2 mm thick walls) was inserted into the bottom, its upper edge being at the mud surface. A cylindrical cap of netting (1 × 1 mm), 8 cm high, was placed over the cylinder, its top being 5 cm above the bottom (Fig. 1). From previous experience (Z. Kajak unpubl.) it appeared, that even a 0.5–1.0 cm protrusion of the cylinder above the mud surface could result in serious environmental modifications, influencing in turn the benthic community. To minimize the differences between the cylinders and neighbouring environment, a short exposure period (2 days) was used. At the end of the experiment the cylinders were lifted up a few cm, the cap was taken off, and the upper end of the plastic cylinder stoppered, which guaranteed that the mud remained in the cylinder. Later, after stoppering the lower end, the upper stopper was taken off, meiobenthic samples taken from the cylinder, and its contents placed in a container and preserved.

A series of samples from the experimental area were taken at the beginning of the experiment, using a transparent tube of the same diameter as the experimental cylinders. The surplus water from above the mud surface was let off through an aperture in the tube, so that sample could be compacted in the container.

The samples were not sieved, which guaranteed that even the smallest macrobenthic specimens were obtained. The material was sorted by flotation in a sugar solution (A n d e r s o n 1959, K a j a k, D u s o g e and P r e j s 1968). After stirring the sample the several times, with a glass-rod, until no organisms floated up, it was stirred for 5 minutes with a magnetic stirrer, which usually resulted in the floating up a few more organisms. The sample was then sorted on a tray, to pick up heavier organisms, mostly *Mollusca*.

From each sample, 2 subsamples of the meiobenthos were taken (using an 0.8 cm² transparent tube) from the surface 2 cm layer, and preserved with formalin. They were later sorted under the microscope (after being stained for 12 h in a solution of Rhodamine B); ultraviolet light was applied to make the organisms fluorescent.

Altogether in this part of the experiment the following variants were applied, and the following numbers of samples taken: (1) at the beginning of the experiment 20 IX 1970 – 60 samples to characterise the natural initial status of the benthos; (2) at the end of the experiment 22 IX 1970 – 60 control samples, to characterise the natural status of the benthos at that time; (2a) 60 samples in 4 variants, 15 samples in each of them. The following was added to particular variants at the beginning of the experiment: 1 *Crangonyx*, 2 *Crangonyx* + powdered milk, 1 *Crangonyx* + yeast.

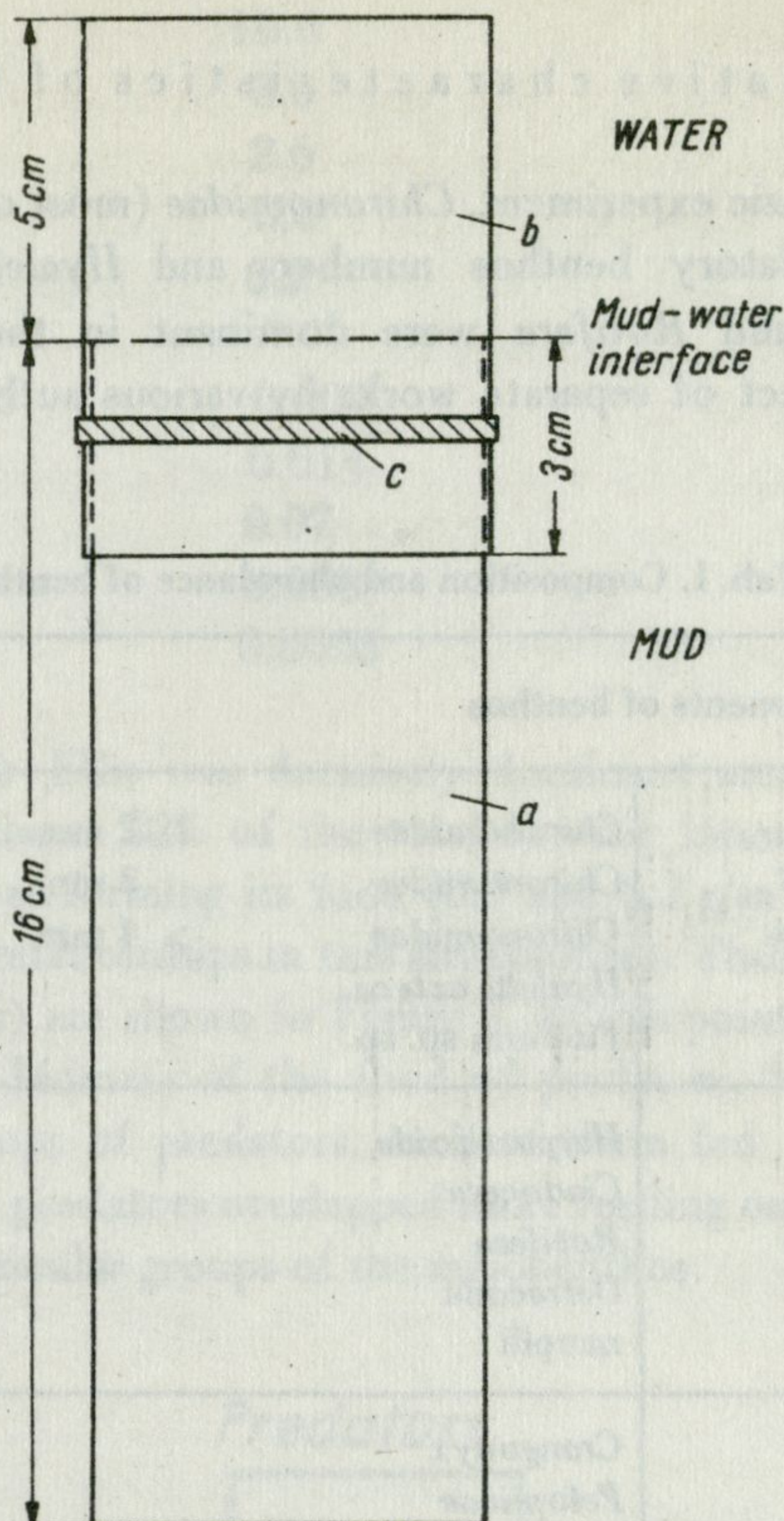


Fig. 1. Diagram of the experimental cylinder

a — solid cylinder (20 cm^2 , of internal area) allowing samples to be taken by pulling the set up about 5 cm, taking the netting off and closing the solid cylinder at both ends with rubber stoppers, *b* — cylinder made of netting, *c* — rubber band

Altogether in this part of the experiment 180 macrobenthic and 360 meiobenthic samples were taken. The cylinders were distributed 0.4 m each from other, over an area of about 15 m^2 in a uniform environment, about 40 cm deep.

At an other part of the lake (0.3 m depth) an experiment to improve the feeding conditions for the benthos, by the addition of powdered milk and yeast was carried out, in cages $60 \times 60 \text{ cm}$, with walls made of netting of $1 \times 1 \text{ mm}$ mesh size. 12 cages, 4 in each variant, 0.5 m distant each from the other, were used. The experiment lasted 10 days. The 100 samples of macrobenthos (20 at the beginning, and 20 in each variant and in the neighbourhood at the end of the experiment) were taken.

At the same place an experiment on the crowding of *Hyaella azteca* (Saussure) (15 cylinders, 5–15 individuals per cylinder, which gave a 3–6 fold increase of abundance) was carried out.

The bottom deposits at the locations where all the experiments were carried out, consisted of soft mud.

3. RESULTS

3.1. Quantitative characteristics of the benthos

At the location of the basic experiment, *Chironomidae* (most of them ≤ 5 mm) were clearly dominant in the non-predatory benthos numbers and *Hyaella azteca* in the biomass. *Harpacticoida*, *Cladocera* and *Rotifera* were dominant in the meiobenthos. The species composition has been subject of separate works by various authors (Efford 1970, 1971, 1972b).

Tab. I. Composition and abundance of benthos

Components of benthos		Ind. $\times 10^3/m^2$	g/m ²	
Non-predators	macrobenthos	<i>Chironomidae</i> 1-2 mm	16.6	0.2
		<i>Chironomidae</i> 3 mm	7.7	0.6
		<i>Chironomidae</i> ≥ 4 mm	21.0	4.0
		<i>Hyaella azteca</i>	5.1	15.4
		<i>Pisidium</i> sp. sp.	2.5	1.5
	meiobenthos	<i>Harpacticoida</i>	29.3	0.2
		<i>Cladocera</i>	16.5	1.2
		<i>Rotifera</i>	13.4	0.04
		<i>Ostracoda</i>	5.7	0.06
		nauplii	5.7	0.003
Predators	<i>Crangonyx</i>	0.44	4.4	
	<i>Pelopiinae</i>	0.48	1.7	
	<i>Heleidae</i>	0.24	0.6	
Benthos available as food for predatory invertebrates	macrobenthos		4.8	
	meiobenthos		1.5	
	total		6.3	
Benthos not available for predatory invertebrates (<i>Hyaella</i> , <i>Pisidium</i>)			16.9	
Non-predatory benthos (total)			23.2	
Predators (total)			6.7	
Biomass of benthos (total)			29.9	

Some groups of organisms not mentioned in Table I (*Hirudinea*, *Trichoptera*, *Gastropoda*, *Tabanidae*, *Nematoda*, *Oligochaeta*) occurred sporadically and will not be taken into account.

The biomass of the benthos has been calculated, taking the following coefficients (fresh weight in mg) for the average size (in mm) of particular groups:

	(mm)	(mg)
<i>Chironomidae</i>	1-2	0.01
<i>Chironomidae</i>	3	0.08

	(mm)	(mg)
<i>Chironomidae</i>	4	0.19
<i>Crangonyx</i>	7.5	10.0
<i>Pelopiinae</i>	10.0	3.6
<i>Heleidae</i>	12.0	2.6
<i>Hyaella</i>	4.5	3.0
<i>Pisidium</i>	2-3	0.2
(without shell)		
<i>Harpacticoida</i>	0.7	0.007
<i>Cyclopidae</i>	0.9	0.014
<i>Cladocera</i>	1.2	0.07
<i>Rotatoria</i>	0.5	0.003
<i>nauplii</i>	0.1	0.0005

Crangonyx richmondensis Ellis was decisively dominant among benthic predators. The predatory benthos formed about 22% of the total benthic biomass, but about equalled the biomass of the benthic species forming its food (6.7 and 6.3 g/m² accordingly), which shows the very tense prey-predator relationships in this environment. These data, including the trophic links (to be discussed further) are shown in Figure 2. At this point we would like to stress that the main component in the biomass of the food of predators, the *Chironomidae*, was partitioned among particular groups of predators; each of them fed mostly on a particular size group of *Chironomidae*. The predators overlapped more feeding on the meiobenthos; there was no clear selectivity of the particular groups of the meiobenthos.

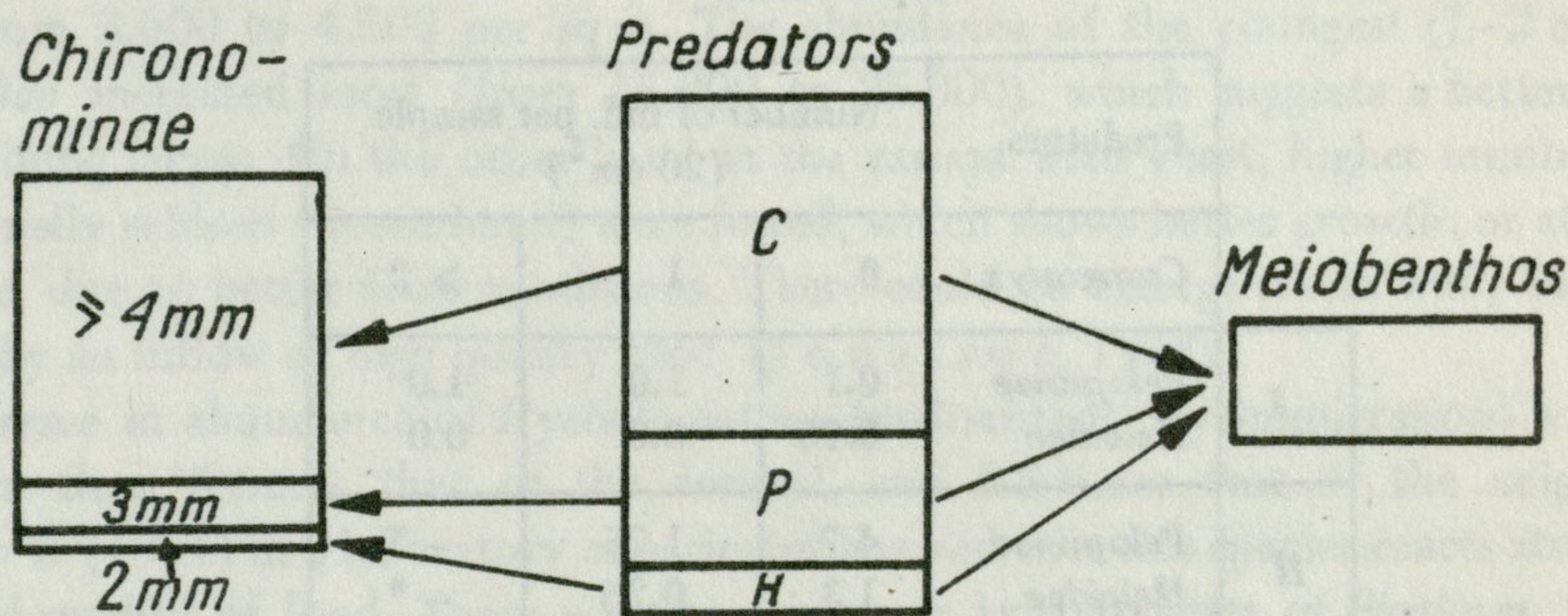


Fig. 2. Prey-predator links

Area of rectangles proportional to the biomass of benthic components; 1 cm² = 1 g/m²; C - *Crangonyx*, P - *Pelopiinae*, H - *Heleidae*

3.2. Distribution of benthic organisms

A clear positive correlation between the distribution of most of the groups of macro- and meiobenthos on one hand, and *Crangonyx richmondensis* on the other (and thus between these groups as well) has been found (Fig. 3). Obviously the non-predatory organisms gather in some places due to environmental (possibly food) reasons. *Crangonyx* in turn could gather there due to plenty of prey.

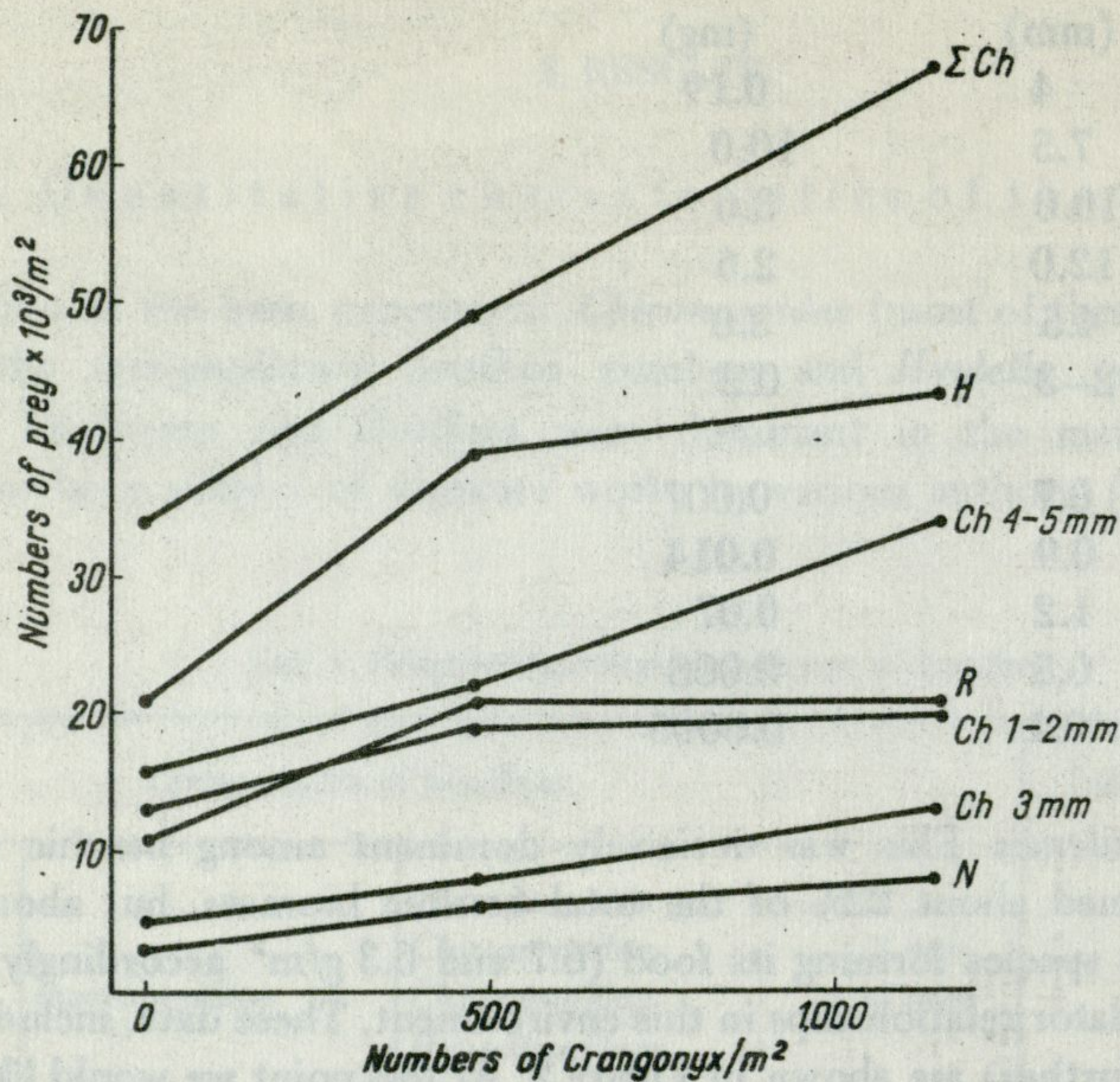


Fig. 3. Correlation of the predator (*Crangonyx*) and prey numbers at the beginning (t_0) of the experiment

Ch – Chironomidae, H – Harpacticoida, R – Rotifera, N – nauplii

Tab. II. Distribution of benthic predators (all differences statistically significant, with χ^2 criterium)
I – main experimental site, II – additional experimental site (crowding of *Hyalella*, addition of food);
depth 30 cm

Predators		Number of ind. per sample (20 cm ²)		
		0	1	≥ 2
I	<i>Crangonyx</i>	0	1	≥ 2
	<i>Pelopiinae</i>	0.1	1.0	1.0
	<i>Heleidae</i>	0.75	0.0	0.0
II	<i>Pelopiinae</i>	4.7	1.75	– *
	<i>Heleidae</i>	1.3	0.25	– *

*Never more than 1 *Crangonyx* per sample.

Tab. III. Correlation between all predators and non-predatory *Chironomidae*
Number of individuals per sample. Correlation coefficient – 0.6, statistically significant at 5% level

	Predators			
	0	1	2	≥ 3
Non-predatory <i>Chironomidae</i>	45	50	76	110

With regard to the other predators the *Pelopiinae* correlated positively with *Crangonyx* and non-predatory groups, but *Heleidae* correlated negatively (Tab. II). The numbers of *Pelopiinae* increased during the experiment in variants with the addition of *Crangonyx*, which suggests that they somehow profit by the presence of this species, e.g. its activity increases the availability of food for *Pelopiinae*. The tendency of these 2 groups to be together is not however the rule. In the other environment where *Chironomidae* were 3 times more abundant, *Pelopiinae* showed the same behaviour as the *Heleidae* and avoided *Crangonyx* (Tab. II).

All predators (*Crangonyx*, *Pelopiinae*, *Heleidae*, *Hirudinea*) at the beginning of the experiment were positively correlated with the number of non-predatory *Chironomidae* (Tab. III); they obviously gather in places with a higher abundance of prey. A similar correlation has been shown for the distribution of the main predator – *Crangonyx richmondensis* and particular groups of non-predatory benthos (Fig. 3).

3.3. Influence of food

This was analysed by the addition of powdered milk or baker's yeast (as direct food or a substrate for bacteria) with two techniques: (1) cages (0.6 × 0.6 m of) netting, 1 × 1 mm mesh size and (2) experimental cylinders. The enclosures were to restrain the access of vertebrates and larger invertebrates to the trophically enriched places.

The experiment in cages lasted from 20 IX to 3 X 1970, the food was added at the starting point. The suspension of food was delicately placed at the very bottom of the cages, which prevented its serious dispersal. The food enrichment resulted in a distinct increase of benthos abundance: *Chironomidae* from 28,000 to 38,000, *Hyaella azteca* from 3,000 to 7,500, *Pisidium* from 3,600 to 4,500 per sq m. The abundance of the youngest (1–2 mm) class of *Chironomidae* increased most (from 15,000 to 25,000), which suggests a better survival of hatching, young larvae. On the other hand in the variant with yeast, higher numbers of 5 mm larvae (normally seldom encountered) were found, which shows better growth, or attainment of a larger size, due to better food conditions. There could be emergence as well, which is often stimulated by an inflow of high quality food (Jonasson 1972).

The increase in abundance of *Hyaella azteca* (undoubtedly by immigration) was especially high – more than 5 times that of the control, and 2.5 times that of the neighbourhood. Hargrave (1971) in a laboratory experiment showed that this species reacts strongly to the amount and quality of food. There was some increase in abundance of *Pisidium*, but none of the meiobenthos and other less numerous groups.

Less food per an unit of area was added to the experimental cylinders than to the cages discussed above. The main goal for the cylinders was to compare the prey-predator relations under conditions of increased predator abundance and improved food conditions for the prey, as related to normal food conditions. Small *Crangonyx* individuals could migrate through the meshes. In the variant with the addition of food and crowding of *Crangonyx*, its numbers were notably (30%) higher than in the control (crowding of *Crangonyx*, but no food addition). It could be a result of better food conditions leading to higher numbers of prey, as found in the cages mentioned above. The final numbers of prey, were not significantly higher, probably due to their elimination by *Crangonyx*. The abundance of groups not eliminated (*Hyaella*, *Pisidium*) was markedly (55 and 25%) higher, especially in the variant with added milk.

3.4. Reaction of the population to artificial crowding

Crowding of *Crangonyx* or *Hyalella* resulted as a rule in their emigration. This was however smaller in those variants with the addition of food; under these conditions 28% of *Crangonyx* emigrated (addition of milk or yeast obviously resulted in the immigration of the fauna consisting the food for *Crangonyx*, thus improving its food conditions), whereas when food was not added, 65% of the *Crangonyx* emigrated. In the control cylinders, without food or the addition of *Crangonyx* 10% immigration of *Crangonyx* took place.

In the variants with 5 and 15 *Hyalella* added (that is with 3 and 6 times increased abundance) strong emigration was found. The numbers after 10 days were only 10% (in the variant with 5 *Hyalella* added) higher than in the control. Only *Pisidium* reacted clearly on the increased numbers of *Hyalella* – its abundance was 60% lower than in the control.

3.5. Feeding of predators – food selectivity and food rations

It has been proved that the conditions, the density of the food and the consumer inclusive, are decisive for feeding and mutual relationships (Kajak 1968, Kajak and Dusoge 1970, Hargrave 1971). As shown above even in the given, natural environment predators do choose particular places and in particular, higher food densities. That is why in this work a method was applied that provided natural environmental conditions, natural density and relationships of organisms. The only difference to natural conditions was some limitation of the mobility of the benthos. It was assumed that due to these natural conditions there was no any reason for directional migration between the cylinders and their neighbourhood. At the same time, forcing large predators to stay in the same place (experimental cylinder) resulted in the decrease of the prey numbers (by their elimination) which made it possible to estimate the food selectivity and food rations of predators. The 2 days period of exposure proved to be proper, because the decrease in prey numbers was great enough for an estimation of the selectivity and amount of the food taken by predators, and short enough not to change seriously the feeding conditions during the experiment. As far as the distribution of prey and predators was positively correlated at the beginning of the experiment the amount of food (prey) eaten was analysed within the groups of samples with the given (1–2–3) number of *Crangonyx* (the main predator) deducting the final number of prey per one predator, from the initial value. To calculate the daily food ration of one *Crangonyx*, the amount of food eaten by *Pelopiinae* and *Heleidae* present in the sample (cylinder) was deducted from the above mentioned value.

The food rations for *Pelopiinae* and *Heleidae* were calculated by comparing (in the final series of the experiment) the abundance of prey¹ in groups of samples with various (0–1–2) numbers of the given predator, within the group with the same (0–1–2–3) number of *Crangonyx*.

The same method was applied to estimate the selection of food by particular predators (Fig. 2) and the amount of food eaten; the examples of *Chironomidae* eaten in particular

¹There was the rise in the water level during the experiment, and this probably caused some immigration of *Chironomidae* to the environment analysed. This was found by comparing the initial and final samples without predators, thus having no reason other than immigration for the change in the numbers of prey. It was assumed that the same intensity of immigration took place in all variants of the experiment excluding those with the food added.

Tab. IV. Numbers of *Chironomidae* larvae eaten daily by predators in situations with various numbers of *Crangonyx* (calculated per 1 *Crangonyx* as the main predator)*

Size of prey (mm)	Samples with naturally differentiated <i>Crangonyx</i> numbers		Samples with addition of <i>Crangonyx</i> **	
	1 C./sample	2 C./sample	+ 1 C. (1.2 C./sample)	+ 2 C. (1.6 C./sample)
1-2	1.5	1.0	2.8	0.1
3	2.3	2.1	2.4	1.1
4	5.2	7.9	4.7	4.8
> 4	8.9	11.0	9.8	6.0

*Real food rations of *Crangonyx* are given in Table IX.

**In the samples (cylinders) with the addition of *Crangonyx* its final numbers (given in brackets) were smaller than the initial ones, due to emigration of some specimens.

variants of the experiments are given in Table IV. The amount of food eaten out in the samples with naturally differentiated *Crangonyx* numbers, especially the amount of the preferred 4 mm larvae was higher at naturally higher *Crangonyx* numbers (2 individuals in a sample); it is logically connected with the above discussed fact, that the numbers of prey were higher in the samples with higher numbers of *Crangonyx* (Fig. 3). In the variant with 1 *Crangonyx* added, the amount of *Chironomidae* eaten out was similar to that in the samples with natural *Crangonyx* numbers, because due to its emigration, final *Crangonyx* numbers were almost equal to natural ones. However in the variant with 2 *Crangonyx* added, where the numbers of the predator were much higher during the whole time of the experiment than in the control, the amount of prey eaten out by 1 predator was much smaller. This was especially so for the small (1-2 mm) *Chironomidae*, possibly due to competition with other predators (*Pelopiinae*, *Heleidae*). On the other hand, the intense elimination of "large" (≥ 4) *Chironomidae* probably resulted from their immigration; as far as they had not located safely yet in the new environment, they were more readily available to predators. One can suppose that if there was no immigration during the experiment, the numbers of prey eliminated could be lower.

Consumption of the meiobenthos by *Crangonyx* was also inversely correlated with the number of *Crangonyx* in the sample (Tab. V).

Tab. V. Amounts of meiobenthos eaten daily by predators in situations with various numbers of *Crangonyx* (calculated per 1 *Crangonyx* as the main predator)*

	Average number of <i>Crangonyx</i> in cylinder			
	1.0	1.6	2.0	2.4
Consumption mg/ind. per 24 h	0.7	0.3	0.3	0.2

*Feeding of the other predators present has not been deducted, so the real food rations of 1 *Crangonyx* would be slightly lower; real food rations are given in Table IX.

Tab. VI. Numbers of *Chironomidae* (1–2 mm) larvae eaten daily by 1 *Heleidae* in various situations

	Control samples with a natural density of <i>Crangonyx</i> (average 0.8 in a sample)	Samples with addition of <i>Crangonyx</i>	
		1 <i>Crangonyx</i> in a sample	2 <i>Crangonyx</i> in a sample
No. of <i>Heleidae</i> /sample	1.2	2.2	1.2
No. of prey eaten by 1 <i>Heleidae</i> /day	5.0	1.7	1.7

Tab. VII. Amount of meiobenthos eaten daily by 1 *Heleidae* at various densities of *Crangonyx*

	Average number of <i>Crangonyx</i> in cylinder		
	0	1	2.5
Amount of food eaten by 1 <i>Heleidae</i> (mg/24 h)	0.4	0.06	0.0

Tab. VIII. Numbers of *Chironomidae* larvae (3 mm) eaten daily by 1 *Pelopiinae* in various situations

	Samples with natural density of <i>Crangonyx</i> (average 0.8 in a sample)	Samples with addition of <i>Crangonyx</i>	
		1 C. in a sample	2 C. in a sample
No. of <i>Pelopiinae</i> /sample	0.9	1.2	1.3
No. of prey eaten by 1 <i>Pelopiinae</i> /day	1.2	0.4	0.3

There was a much greater dependence of the feeding of *Heleidae* (the distribution of which was, as mentioned above – Tab. II, negatively correlated with that of other predators) on the presence of *Crangonyx*. The numbers of *Chironomidae* consumed by *Heleidae* were much lower whilst the presence of *Crangonyx*, and especially whilst it was artificially crowded (Tab. VI); it was even clearer for the meiobenthos – 7 times smaller consumption by *Heleidae* in the presence of 1 *Crangonyx* in the cylinder, and no consumption in cylinders with 2 and more *Crangonyx* (Tab. VII). It was not caused by the amount of food because this was positively correlated with *Crangonyx* numbers, thus the only possible interpretation is the influence of *Crangonyx*, limiting the feeding of other predators. The same pattern, although not so strongly pronounced, was true for *Pelopiinae* (Tab. VIII). Of course the decreasing (with increasing *Crangonyx* density) amount of food eaten out was hypothetically attributed to *Heleidae* or

Pelopiinae (Tabs. VII and VIII) it could well be that both *Crangonyx* and *Heleidae* (or *Pelopiinae*), ate less whilst influencing each other, and thus the amount of food consumed by *Heleidae* and *Pelopiinae* (in the presence of *Crangonyx*) were higher than shown in Tables VI–X. *Pelopiinae* ate less both in the presence of *Crangonyx* and at a higher density of their own population (Tab. IX).

Tab. IX. Amount of meiobenthos eaten daily by 1 *Pelopiinae* depending on density of *Crangonyx* and of *Pelopiinae*

	Number of <i>Crangonyx</i> per cylinder			
	0		1	
Number of <i>Pelopiinae</i> per cylinder	1	2	1	2
Consumption (mg/ind. per 24 h)	0.45	0.30	0.026	0.0021

Tab. X. Consumption (in fresh weight) by benthic predators

		<i>Crangonyx</i>	<i>Pelopiinae</i>	<i>Heleidae</i>
Consumed by 1 predator (mg/24 h)	Macrobenthos	1.33	0.1	0.05
	Meiobenthos	0.55	0.2	0.2
	(A) Total	1.88	0.3	0.25
(B) Biomass of 1 specimen of predator (mg)		10.0	3.6	2.6
Daily food ration (A/B, %)		19	8	10

The daily food rations of the main predators equalled 8–19% of their biomass (Tab. X). The predators together ate daily about 0.6 g/m² *Chironomidae* (only about 3% of the biomass in the water body of the 2 mm class, 11–14% from the older 3–4 mm class) at a *Chironomidae* biomass of 4.8 g/m². This gives a turnover time (assuming that the standing crop is stable and total production is eliminated by invertebrate predators) of 4.8:0.6 = 8 days. Daily elimination of meiobenthos is 0.7 g/m² and average biomass 2.6 g/m² which gives a turnover time of 2.6:0.7 = 3.6 days. These are short turnover times. The one for *Chironomidae* is similar to that observed in temperate fish ponds (Wójcik - Miętała 1968, Zięba 1973). The estimated daily food rations (8–19%) do not seem too high. Often much higher values are noted for planktonic (Monakov and Sorokin 1972) and benthic (Kajak and Dusoge 1970) predators. Even assuming food rations several times lower, that is several per cent (and one hardly can assume lower than that) turnover time would become 30–40 days for *Chironomidae* and about 15 for meiobenthos which is still short, when compared to the usually assumed yearly generation times, and accordingly (Waters 1969) a 2–4 month turnover time. However one cannot exclude that this environment is not self-sufficient in the food for predators and profits by immigration from neighbouring environments. Immigration was found

during this study. It is highly probable that it stimulated consumption by predators, due to a higher availability of immigrants, not yet safely located in the new environment. Considering other possible reasons of the high intensity of the feeding of predators in the experiment (cylinders), it is possible that protection against fish and salamanders, allowed quiet, uninterrupted feeding to invertebrate predators. But we must stress once more that the food rations were not unreasonably high.

The long (yearly) life cycles assumed for most of the Marion Lake benthic species are surprising. In the shallow environment, with a high production of benthic algae, which is the most valuable food for the *Chironomidae* (Kajak and Warda 1968), the dominant prey group, the generation times should be shorter. This leads to the hypothesis about the influence of the mutual relationships on the prolongation of the life cycle. This has been proved for Esrom Lake (Jonasson 1972) – a shorter generation time occurred when the abundance of organisms was lower. Kajak (1968) found limitation of growth and survival of *Chironomidae* by competition. High abundance and activity of necto-benthic organisms in Marion Lake (*Hyaella*, *Crangonyx*) can cause limitation of the feeding time of non-predatory species, and consequently of their rate of growth and development.

The high pressure of invertebrate predators can keep the benthos abundance below the trophic capacity of the environment, by elimination of the excess, including young forms. The elimination of young can occur as well when the mud is stirred by benthic organisms (Kajak 1968).

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4. SUMMARY

The work was carried out in the shallow (0.4 m) part of the Marion Lake (13.3 ha, 2.4 m average depth), British Columbia, Canada. The aim of the work was the analysis of feeding and trophic relations of benthic invertebrate predators. As the main technique experimental cylinders were applied (16 cm long plastic tubings covered with miller gauze) inserted in the mud and taken out after the 2 days exposure time, the bottom sample in them. The sampling area of both the experimental cylinders and the bottom sampler was 20 cm². The exposure time was short enough to provide the unchanged environmental and biocenotic situation in the cylinders, and long enough to find the changes in macro- and meiobenthos numbers which had resulted from predators activity.

The selectivity and the amount of food consumed by invertebrate predators was estimated by comparing the amount of prey at the beginning and at the end of exposure in experimental cylinders with various numbers of un predatory and predatory benthos; both the natural differentiation of numbers and the experimental crowding of predators were used in this purpose.

The effects of trophic enrichment (by the addition of yeast and powdered milk) were also analysed.

All the macrobenthic material was sorted out by flotation, meiobenthic one was sorted out in the ultraviolet light, after staining by Rhodamine B.

Total benthic biomass was 29.9 g/m², the dominants being *Hyaella azteca* (Saussure) (15.4 g/m²) and *Chironomidae* (4.8 g/m²). Invertebrate predators were very abundant (6.7 g/m²), the dominant being *Crangonyx richmondensis* Ellis (4.4 g/m²), *Pelopiinae* (1.7 g/m²) and *Heleidae* (0.6 g/m²). The biomass of predators slightly exceeded that of their prey (Tab. I).

The distribution of non-predatory benthos was very differentiated, and the distribution of invertebrate predators was positively correlated with the distribution of their potential food (Fig. 3, Tab. III), excluding *Heleidae* which avoided *Crangonyx* (Tab. II).

Addition of food resulted in an increase of the abundance and growth rate of several benthic groups. It also resulted in less emigration of artificially crowded *Crangonyx*, probably due to a higher abundance of its potential food.

Artificial crowding of organisms (*Hyaella*, *Crangonyx*), led as a rule to their emigration, so as to achieve the previous level of abundance.

Crangonyx richmondensis distinctly selected larger class of *Chironomidae* (≥ 4 mm), *Pelopiinae* selected medium one (3 mm), *Heleidae* the smallest one (2 mm), only slightly overlapping with each other in this respect. All these predators fed on meiobenthos as well, without distinct selectivity of particular groups (Fig. 2).

The food rations of predators were in the range of 8–19% of their body weight per 24 h (Tab. X). Due to the high biomass of predators, the total amount of prey eaten was very high, and the calculated turnover time for *Chironomidae* was about 8 days and for meiobenthos – about 4 days. Even assuming several times lower food rations (taking into account the possibility of the food rations in this work being untypically high, due to the immigration of *Chironomidae* connected with the rise of the water level) we would still get a comparatively short turnover time, some 30–40 days for *Chironomidae* and 15 for meiobenthos.

The predators ate less at higher densities of their own and other predatory species (Tabs. IV–IX).

5. POLISH SUMMARY (STRESZCZENIE)

Badania przeprowadzono w płytkiej (0,4 m) części jeziora Marion (13,3 ha, średnia głębokość 2,4 m), położonego w Kolumbii Brytyjskiej w Kanadzie. Celem pracy była analiza odżywiania i stosunków troficznych drapieżnych bezkręgowców bentosowych. Jako główną technikę badań zastosowano cylinderki eksperymentalne (16-centymetrowe rury plastikowe nakryte od góry gazą młyńską) wciskane w muł, a następnie wyjmowane wraz z próbą mułu po dwudniowej ekspozycji. Powierzchnie przekroju cylinderków oraz chwytacza rurowego wynosiły 20 cm². Czas ekspozycji cylinderków był na tyle krótki, że gwarantował zasadniczo nie zmienione warunki środowiskowe i biocenotyczne wewnątrz cylinderków, a z drugiej strony dostatecznie długi, aby móc stwierdzić zmiany w makro- i meiobentosie zasze pod wpływem drapieżców.

Wybiórczość pokarmową i ilość pokarmu pobieranego przez drapieżce określono przez porównanie liczby ofiar w cylinderkach eksperymentalnych z różnymi liczebnościami drapieżców na początku i na końcu ekspozycji. Wykorzystano tu naturalne zróżnicowanie liczebności drapieżców, jak również sztuczne ich zagęszczenie.

Analizowano również efekty wzbogacenia troficznego środowiska (dodatek drożdży i mleka w proszku).

Makrobentos sortowano makroskopowo metodą flotacji, a meiobentos – pod mikroskopem w świetle ultrafioletowym po zabarwieniu rodaminą B.

Całkowita biomasa bentosu wynosiła 29,9 g/m³, dominantami były *Hyaella azteca* (Saussure) (15,4 g/m³) i *Chironomidae* (4,8 g/m³). Bardzo liczne były drapieżne bezkręgowce (6,7 g/m²), wśród których dominowały *Crangonyx richmondensis* Ellis (4,4 g/m²), *Pelopiinae* (1,7 g/m²) i *Heleidae* (0,6 g/m²). Biomasa drapieżców nieco przewyższała biomasę ich ofiar (tab. I).

Zróżnicowanie liczebności bentosu niedrapieżnego w próbach było bardzo duże. Rozmieszczenie drapieżnych bezkręgowców było skorelowane pozytywnie z rozmieszczeniem ich potencjalnego pokarmu (fig. 3, tab. III), co nie dotyczy jedynie *Heleidae*, które unikały *Crangonyx* (tab. II).

Dodanie pokarmu spowodowało wzrost liczebności i tempa wzrostu kilku grup bentosu, jak również zmniejszyło emigrację sztucznie zagęszczonego *Crangonyx*, prawdopodobnie dzięki większej obfitości jego potencjalnego pokarmu.

Sztuczne zagęszczenie organizmów (*Hyaella*, *Crangonyx*) z reguły prowadziło do ich emigracji, a w następstwie do osiągnięcia wyjściowego poziomu zagęszczenia.

Crangonyx richmondensis zdecydowanie preferował największą klasę wielkości *Chironomidae* (≥ 4 mm), *Pelopiinae* preferowały średnią (3 mm), *Heleidae* – najmniejszą (2 mm). Tak więc ich nisze pokarmowe w zakresie makrobentosu zachodziły na siebie jedynie nieznacznie. Wszystkie te drapieżce odżywiały się także meiobentosem, bez wyraźnej wybiórczości pokarmowej poszczególnych grup (fig. 2).

Dobowe racje pokarmowe drapieżców wahały się w granicach 8–19% wagi ich ciała (tab. X). Ze względu na wysoką biomasę drapieżców całkowita ilość zjadanych ofiar była duża i wyliczony czas obrotu (turnover) biomasy *Chironomidae* wynosił około 8 dni, zaś meiobentosu – około 4. Gdyby nawet racje pokarmowe były kilkakrotnie niższe (biorąc pod uwagę możliwość zwiększonej intensywności odżywiania w badanej sytuacji wskutek imigracji *Chironomidae* z podwyższeniem się stanu wody w trakcie eksperymentu), nadal

uzyskamy stosunkowo krótki czas obrotu biomasy – około 30–40 dni dla *Chironomidae* i 15 dla meiobentosu.

Drapieżce żerowały mniej intensywnie przy wysokich liczebnościach własnego lub innych gatunków drapieżnych (tab. IV–IX).

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