EKOLOGIA POLSKA (Ekol. pol.)	25	1	59–74	1977

Tadeusz PRUS

Department of Ecological Bioenergetics, Institute of Ecology, Polish Academy of Sciences, Dziekanów Leśny near Warsaw

EXPERIMENTAL AND FIELD STUDIES ON ECOLOGICAL ENERGETICS OF *ASELLUS AQUATICUS* L. (*ISOPODA*)

III. POPULATION DYNAMICS ON THE BACKGROUND OF MACROBENTHOS OCCURRENCE IN THE LITTORAL ZONE OF POWSIŃSKIE LAKE*

ABSTRACT: The paper is an introduction to the field studies on bioenergetics of a natural population of *Asellus aquaticus* L. It gives a general outline of seasonal and annual changes in occurrence of macrobenthos with special attention paid to the species examined. The changes in numbers, biomass, and calorific equivalent of invertebrate benthic animals (except *Mollusca*) are given as a background of the population dynamics. Age, sex and size structures of *A. aquaticus* have been studied. The *A. aquaticus* population, abundant in late spring, was found to decline during summer with a certain tendency to restore in autumn. Annual changes point to the long-term population decline.

Contents

1. INTRODUCTION

Studies of energy flow through a population must rely upon a rather good knowledge of population dynamics in a natural habitat. According to the available literature the dynamics of *Asellus aquaticus* L. populations were up to now investigated by F i t z p a t r i c k (1968) and

*Praca wykonana w ramach problemu węzłowego nr 09.1.7 („Produktywność ekosystemów słodkowodnych").

Anderson (1969). Various types of water bodies were the objects of these studies. The study by Fitzpatrick (1968) resulted in energy budget of the population, whereas the study by Anderson (1969) resulted in an estimate of production by *A. aquaticus* populations occurring in two lakes.

Having ascertained: the assimilation efficiency of this species (Prus 1971), the energy budget for "productive" period of its life cycle (Prus 1972), and respiration in relation to temperature (Prus 1976), the field studies were initiated on a natural population inhabiting the littoral zone of a small lake.

The present paper aims at describing the dynamics of *A. aquaticus* population during three vegetation seasons (1972–1974), with a special attention paid to the population structure. In order to get some idea of the *A. aquaticus* importance in macrobenthos community of the lake, all invertebrate groups (except molluscs) were also investigated and the total macrobenthos occurrence was characterized as a background of the population studied.

2. STUDY AREA AND METHODS

The Powsińskie Lake was chosen as the study area. The lake is situated near Warsaw, along the village of Powsinek, west of Wilanów Palace. Premises on which such choice was made are the following: (1) proximity of the laboratory, (2) relatively small area of the water body, and (3) rather inconspicuous habitat differentiation.

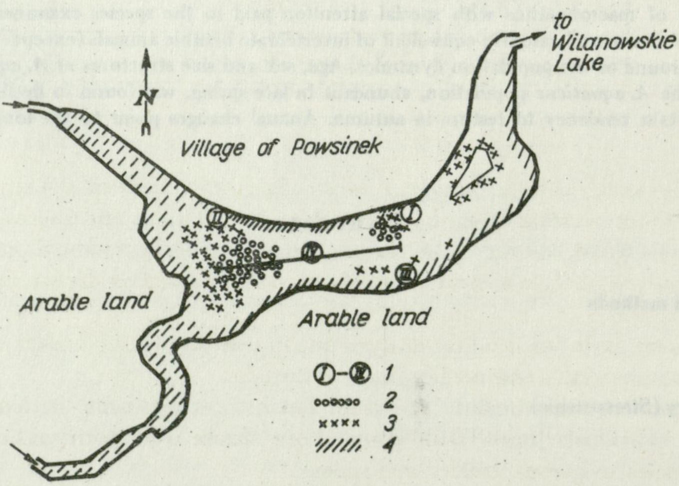

Fig. 1. Powsińskie Lake

1 – stations of sampling, *2* – *Nuphar luteum* L., *3* – *Myriophyllum* sp., *4* – emergent plants

The plan of the lake, with aquatic vegetation and stations of sampling marked, is shown in Figure 1. The lake has an irregular shape, is elongated east-west, maximum length about 1 km, maximum width about 200 m, maximum depth about 4 m. Arable land constitutes the direct water basin of the lake and along the north shore there is the village of Powsinek. The lake is of a pond type, however, water fowl is present on it, which would point to natural character of this reservoir. The lake is highly eutrophic. The littoral zone is about 5 m wide, ending at a depth of about 2–3 m. The immergent plants (*Carex* spp. mainly) overgrow the small bays and the south shore, the north shore is almost void of higher plant vegetation. Submerged plants are Nuphar *spp.*, *Myriophyllum* spp. and *Potamogeton* spp.

Three stations were chosen for sampling in the littoral zone as marked in Figure 1. Samples in each station were arranged in a transect line along the littoral width. In 1973 an additional transect through the middle of the lake along its long axis was added (station IV).

The samples of benthos were taken every fortnight from a depth of 0.5 to 2.5 m with a modified bottom sampler of Morduchaj-Boltovskoj type (40 cm^2 of surface).

The sampling was done during vegetation seasons (about 6 months) of 3 consecutive years at 13, 12, and 11 time intervals in 1972, 1973, and 1974, respectively. A total of 1,310 samples were collected and the details of lake sampling are listed in Table I.

Table I. Outline of field studies on population of *A. aquaticus* in Powsińskie Lake

Year	Duration of studies		Number of samplings	Number of sites	Number of samples
	dates	days			
1972	16 May – 8 Nov	176	13	3	390
1973	27 March – 30 Oct.	217	12	4	480
1974	3 April – 2 Oct.	182	11	4	440
Total		575	36		1310

The samples were washed through a metal sieve with mesh of 0.4 mm, brought to the laboratory without fixation, placed into a refrigerator at 5°C, and successively sorted. The removed animals were classified to taxonomic groups or species, counted, measured and dried at a temperature of 60°C to a constant weight in order to ascertain dry weight of their biomass and calorific value.

Molluscs were excluded from the analysis due to a small catching surface of the sampler and uneven distribution of this taxonomic group in the lake.

Asellus aquaticus was similarly analyzed, but besides measuring its length, sex was also identified in individuals longer than 3 mm. Four classes were distinguished: juveniles, non--ovigerous females, ovigerous females, and males.

All animal material of taxonomic groups and classes of *A. aquaticus* was combusted in a bomb microcalorimeter of Phillipson (1964) or Klękowski and Bęczkowski (1973) type in order to assess its calorific values.

All the data (numbers, biomass and calorific equivalent) were related to 1 m^2 of the littoral surface.

The temperature of water was measured at the surface and at the bottom in each station, and oxygen samples were taken at these depths. Oxygen content in water was measured by a modified Winkler method (Just and Hermanowicz 1964).

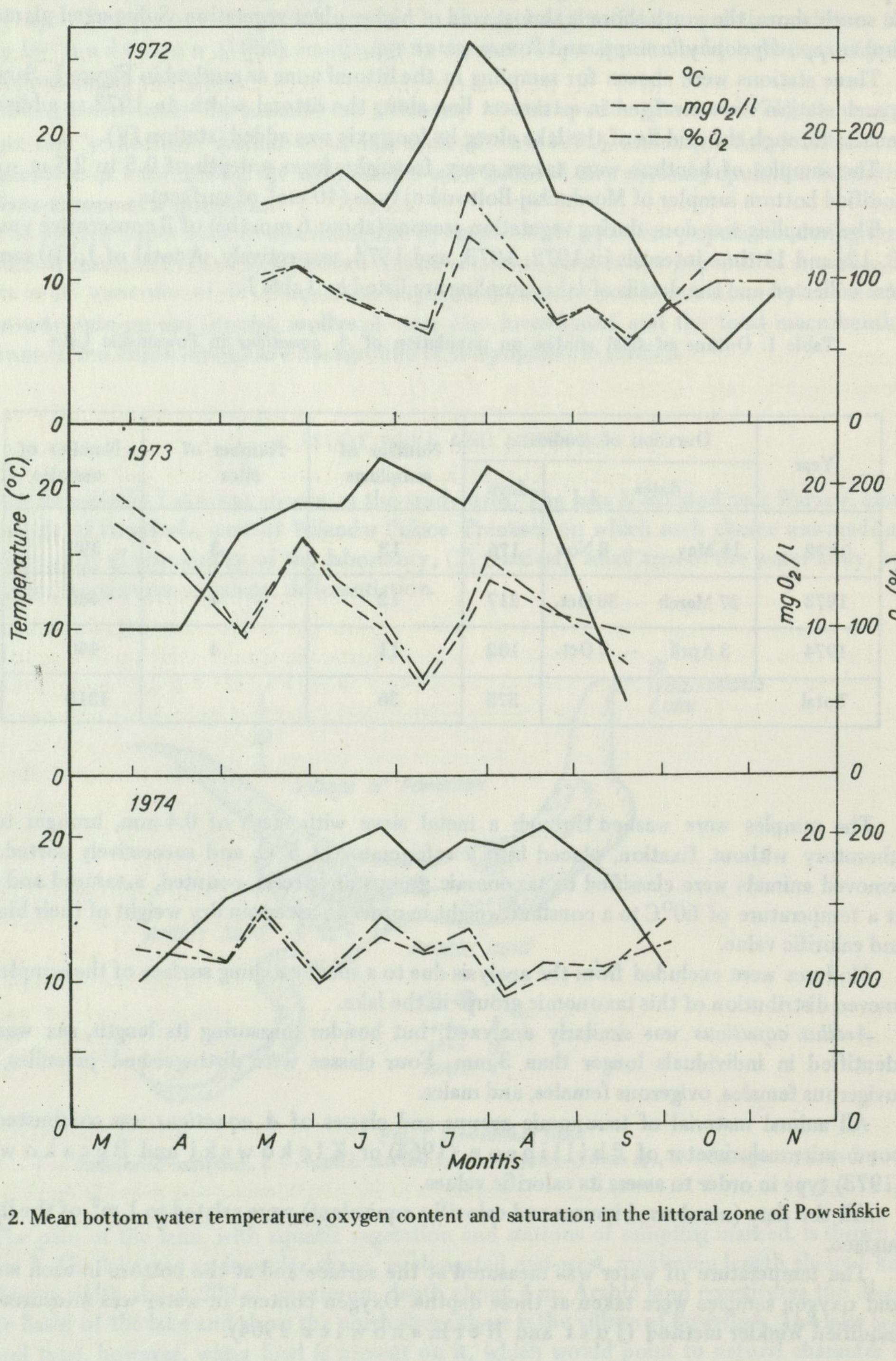

Fig. 2. Mean bottom water temperature, oxygen content and saturation in the littoral zone of Powsińskie Lake

3. RESULTS

T e m p e r a t u r e a n d o x y g e n c o n d i t i o n s. Thermic and oxygen conditions in the littoral zone expressed in ^{o}C, mg O_2/l and percentage of oxygen saturation, are presented in Figure 2.

These are means of 3 stations since the obtained values were almost identical on all stations sampled at a time. The water temperature ranged from 5 to 25°C within the study periods, showing thus a high variation, but during the majority of the season it ranged between 15–20°C.

Oxygen conditions near the bottom in the littoral zone can be considered as good (5–15 mg O_2/l, or 50–150% of saturation). A considerable oversaturation of water with oxygen in some periods coinciding with temperature peaks is probably connected with an intense growth of submerged plants and algae. In spite of a high oxygen content in water, the thin bottom surface layer can be deficient in oxygen.

B e n t h o s c h a r a c t e r i s t i c s. During the study period no considerable differences were found in changes of numbers, biomass and calorific equivalent of the benthic fauna among 3 stations. Thus for each sampling date the mean values were calculated and considered as representative for the whole littoral zone.

The calorific values of animals occurring in Powsińskie Lake are presented in Table II. These are mean values of 5 combustions in a bomb microcalorimeter. Total material of a given group or species was homogenized prior to combustion. The Table includes general calorific values, ash-free calorific values, and per cent of ash in dry weight. The division into organisms feeding on detritus and predators is very tentative one with no particular studies made on feeding habits of collected animals. The average value for detritus feeders would be 4.80 kcal/g dry wt, ash-free value – 5.25 kcal/g dry wt of organic matter, the ash content being 9%. Corresponding values for predators would be 5.14 kcal/g dry wt, 5.44 kcal/g dry wt of organic matter, and ash – 5.48%. Grand mean for invertebrate bottom fauna of Powsińskie Lake (except *Mollusca*) is 5.0 kcal/g dry weight, 5.4 kcal/g ash free dry weight, and ash content is 6.8%. Attention should be drawn to a rather low calorific value of *A. aquaticus:* 3.58 kcal/g dry wt, 4.48 kcal/g dry wt of organic matter, and a very high ash content reaching 20%.

Total numbers, biomass (dry weight), and calorific equivalent of benthos in Powsińskie Lake are presented in Figure 3. The peaks of numbers, biomass and calorific equivalent occurred in June of the two first years of studies, amounting to about 18 thousand ind./m^2 which corresponds to about 7 g dry wt/m^2 and 35 kcal/m^2. After this period an intense decrease in occurrence of benthic fauna was observed reaching a fairly constant level of about 5–6 thousand ind./m^2 or 2–3 g dry wt/m^2 and about 10–15 kcal/m^2. In 1972 the peak of numbers coincided with that of biomass, in 1973 the biomass peak was delayed by about 2 weeks as compared with that of numbers.

Attention should be drawn to the fact of a very close coincidence of lines characterizing biomass and calorific equivalent, and also numbers in 1972 (Fig. 3). In 1973 and 1974, the coincidence is not so good. Especially the courses of lines of biomass and calorific equivalent are almost identical. If this would be true in other situations, one would expect that bioenergetics, dealing almost exclusively with calories, could also make use of earlier benthic data gathered as numbers or biomass only. As one can see from the graph, these units are recalculable and can be used one instead of other for benthos of Powsińskie Lake in 1972. The observed coincidence of the biomass and calorific equivalent lines is not a mere result of using one average calorific value of the whole benthos (5 kcal/g dry wt – Table II) when converting

Table II. Calorific values of benthic animals in Powsińskie Lake

No.	Taxonomic group or species		kcal/g dry wt	kcal/g ash-free dry wt	Ash (per cent)
1a	Detritus feeders	*Asellus aquaticus* ♂♂	3.3517	4.3019	22.09
1b		*A. aquaticus* ♀♀	3.7382	4.6204	19.09
1c		*A. aquaticus* juveniles	3.6455	4.5111	19.19
1		*Isopoda* (*A. aquaticus*)	3.5785	4.4778	20.10
2		*Nematoda*	5.3601	5.5059	2.65
3		*Oligochaeta*	5.2323	5.6740	7.78
4		*Ephemeroptera*	5.1463	5.5465	7.22
5a		*Tendipedidae* excl. *Pelopiinae* et *Tendipes* sp.	4.9032	5.3991	9.18
5b		*Tendipes* sp.	4.5037	4.9418	8.87
5		*Tendipedidae* excl. *Pelopiinae*	4.7035	5.1705	9.02
6		*Diptera* excl. *Tendipedidae*	4.7755	5.1434	7.15

I	Detritus feeders (mean)		4.7994	5.2530	8.99
1	Predators	*Turbelaria*	5.8397	6.0362	3.25
2		*Hirudinea*	5.5134	5.7437	4.01
3		*Hydracarina*	3.8727	4.1007	5.56
4		*Zygoptera*	4.8735	5.1190	4.80
5		*Neuroptera* (*Sialis* sp.)	5.5475	5.7491	3.51
6		*Trichoptera*	5.5276	5.7463	3.84
7		*Coleoptera*	5.8161	5.9718	2.60
8		*Ceratopogonidae*	5.0567	5.2898	4.41
9		*Culicidae* (*Chaoborus* sp.)	4.9792	5.2894	5.86
10		*Pelopiinae*	4.7019	5.1520	8.74
II	Predators (mean)		5.1413	5.4384	5.48
III	Benthic animals (grand mean)		5.0131	5.3689	6.79

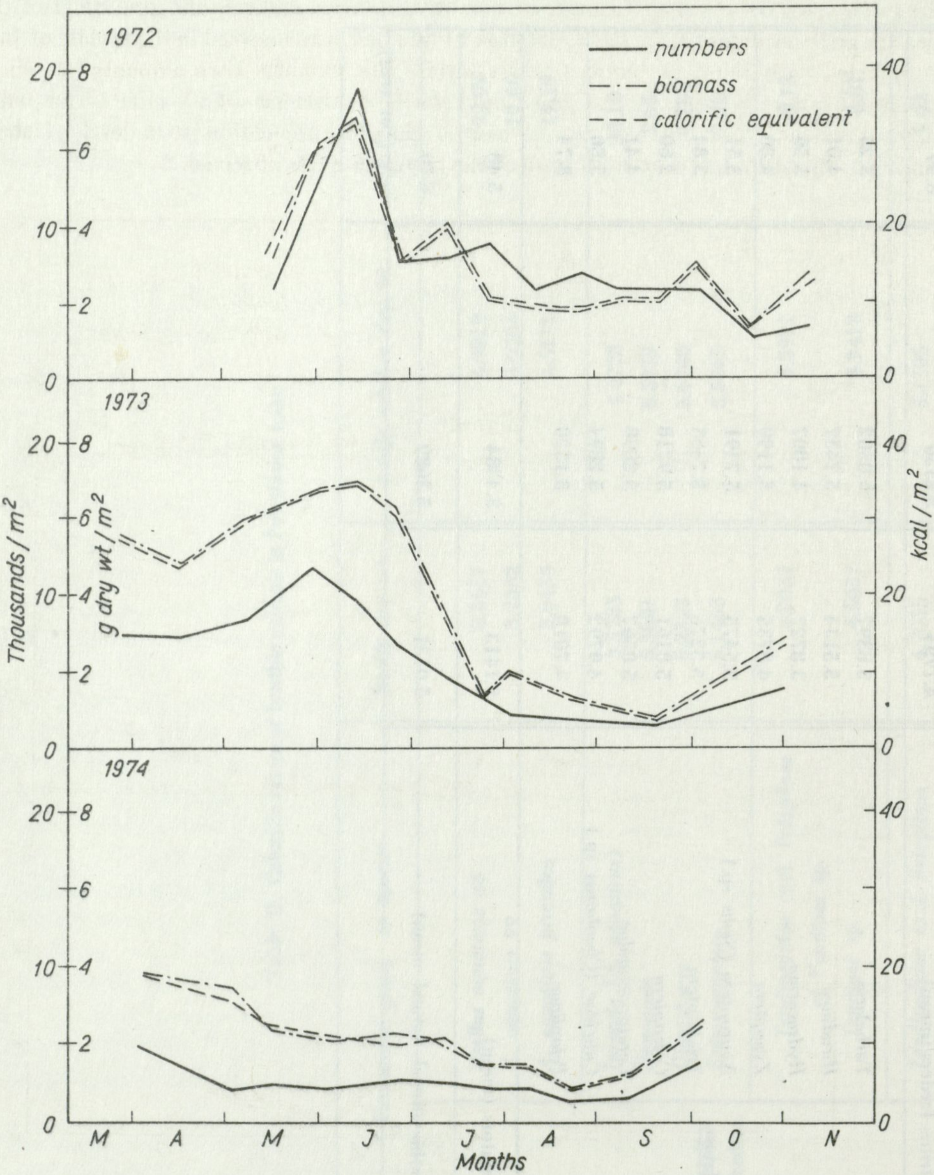

Fig. 3. Numbers, biomass, and calorific equivalent of benthic animals in the littoral zone of Powsińskie Lake

biomass into calories, but particular calorific values of each taxonomic group or species listed in this Table.

Asellus aquaticus. Changes in numbers, biomass, and calorific equivalent of this species are given in Figure 4. In 1972, the peak of numbers was observed in the middle of June and coincided with those of biomass and calories. The numbers then amounted to about 2.7 thousand ind./m^2, biomass – 1.7 g/m^2 and calorific equivalent – 4.5 kcal/m^2. The period of high abundance was followed by a sharp decline of population to a level of about 100 ind./m^2. In autumn, certain restitution of the population was observed.

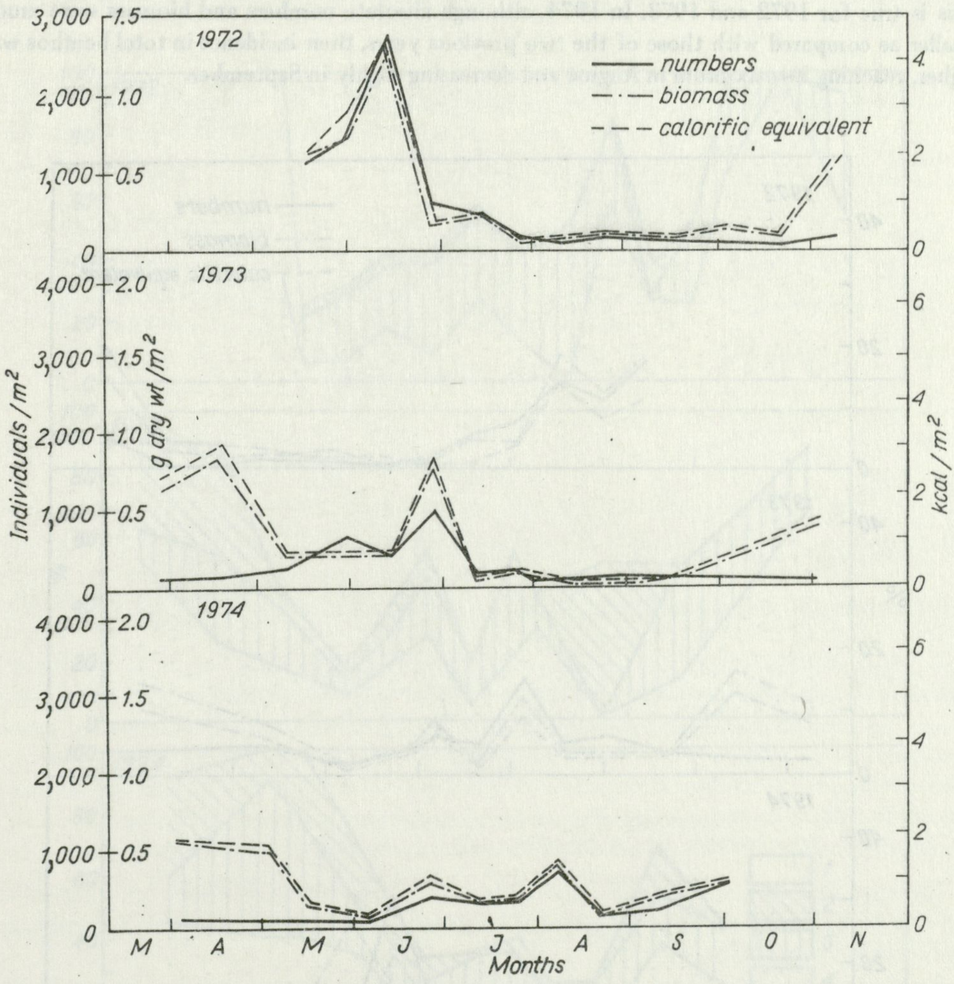

Fig. 4. Numbers, biomass, and calorific equivalent of *A. aquaticus* in the littoral zone of Powsińskie Lake

In 1973, the spring peak of numbers was smaller, and shifted to the end of June. In March and April a high biomass and calorofic contents were recorded in spite of small numbers of individuals. This was due to the presence of large, old specimens which have hibernated. In these months the biomass was about 0.7 g/m^2 and calorific content about 3 kcal/m^2. In July, August and September the population showed the lowest level of occurrence with a certain tendency to increase in the end of sampling period. The biomass in those months was about 0.3 g/m^2 and calorific content 1 kcal/m^2. In 1974, the summer peak of occurrence of *A. aquaticus* is poorly expressed and extended towards the middle of August.

In order to evaluate the rôle of *A. aquaticus* in the total macrobenthos community of the Powsińskie Lake, the percentage incidence of numbers, biomass, and calorific equivalent was calculated (Fig. 5). In early spring and during the period of mass occurrence in June, *A. aquaticus* formed about 10–20% ot the total benthos biomass and energy content. During summer months the percentage incidence was relatively small, increasing again in the autumn. This is true for 1972 and 1973. In 1974, although absolute numbers and biomass were much smaller as compared with those of the two previous years, their incidence in total benthos was higher, reaching its maximum in August and decreasing slighly in September.

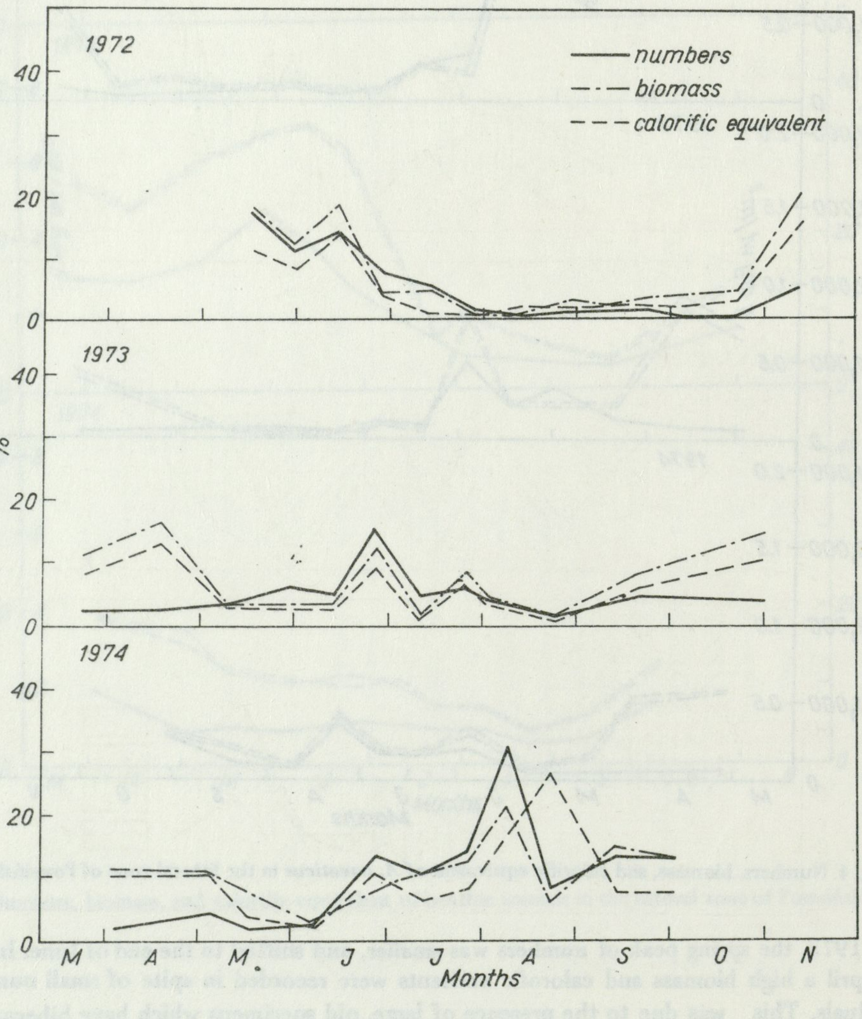

Fig. 5. Percentage incidence of *A. aquaticus* in benthic animals of the littoral zone of Powsińskie Lake

Population structure. The population was divided into 4 groups of individuals: juveniles, ovigerous females, non-ovigerous females, and males for there are reasons to expect that these groups will differ in terms of bioenergetics. Percentage incidences of these groups in total population numbers during 3 consecutive vegetation seasons are presented in Figure 6. Attention is drawn to a relatively high proportion of juveniles found during most of the vegetation season. The sex ratio is close to 1, with males prevailing numerically in autumn. From the percentage incidence of ovigerous females it is inferred that the population, besides a period of an intense reproduction in early spring, during the whole vegetation season has always a small proportion of reproducing females.

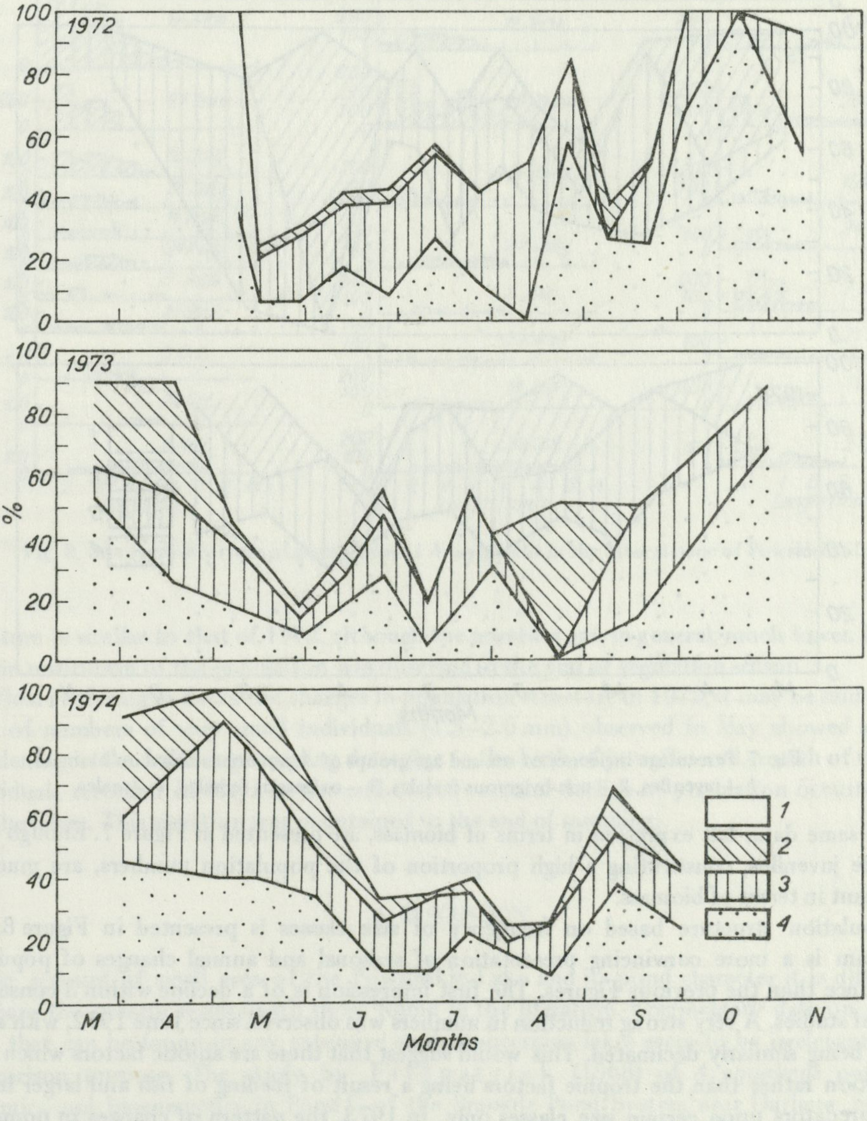

Fig. 6. Percentage incidence of sex and age groups of *A. aquaticus* based on numbers
1 – juveniles, 2 – non-ovigerous females, 3 – ovigerous females, 4 – males

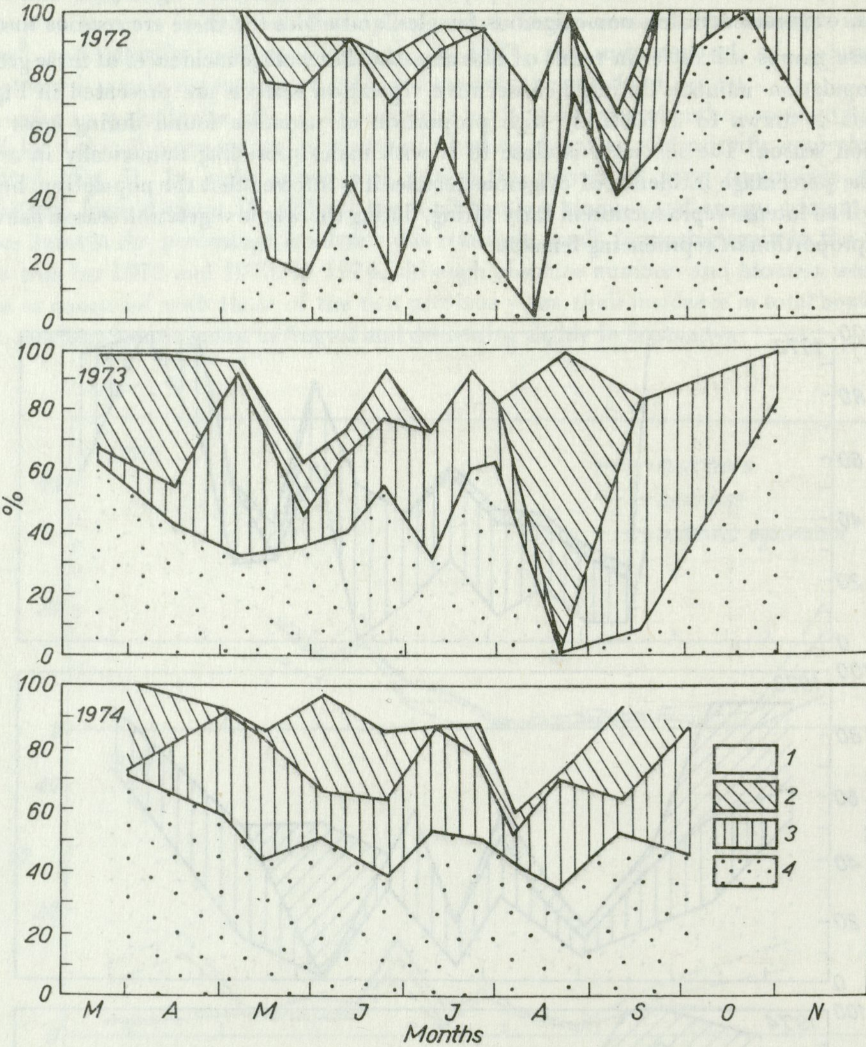

Fig. 7. Percentage incidence of sex and age groups of *A. aquaticus* based on biomass
1 – juveniles, *2* – non-ovigerous females, *3* – ovigerous females, *4* – males

The same data, but expressed in terms of biomass, are presented in Figure 7. Enough to say that the juveniles, constituting a high proportion of the population numbers, are much less significant in terms of biomass.

Population structure based on frequency of size classes is presented in Figure 8. This histogram is a more convincing presentation of seasonal and annual changes of population occurrence than the previous Figures. The first impression is of a decline within 3 consecutive years of studies. A very strong reduction in numbers was observed since June 1972, with all size classes being similarly decimated. This would suggest that these are abiotic factors which affect population rather than the trophic factors being a result of feeding of fish and larger invertebrate predators upon certain size classes only. In 1973, the pattern of changes in population

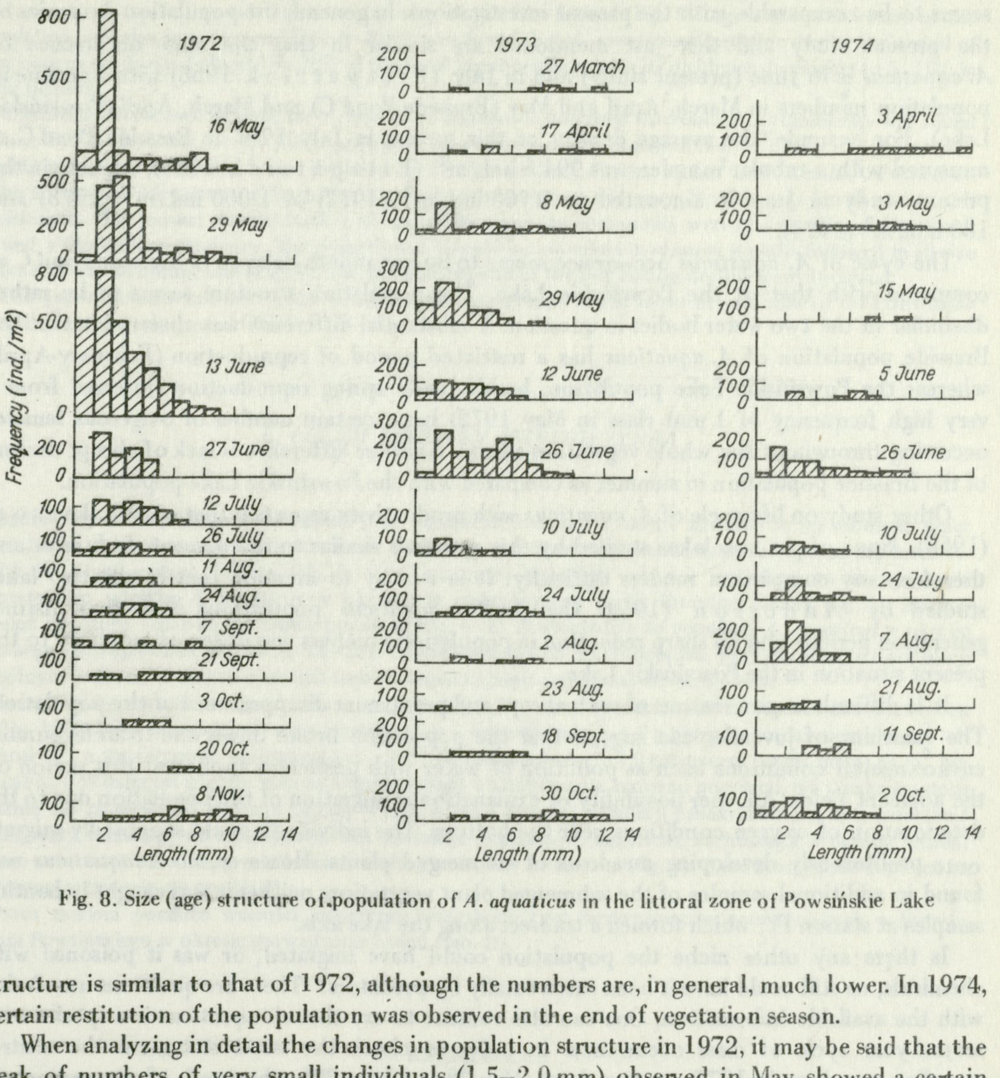

Fig. 8. Size (age) structure of population of *A. aquaticus* in the littoral zone of Powsińskie Lake

structure is similar to that of 1972, although the numbers are, in general, much lower. In 1974, certain restitution of the population was observed in the end of vegetation season.

When analyzing in detail the changes in population structure in 1972, it may be said that the peak of numbers of very small individuals (1.5–2.0 mm) observed in May showed a certain broadening in the following sampling dates due to the birth of juveniles and growth of the small individuals recorded in May. In the end of June a total decline of population occurred in all length classes. This situation was maintained to the end of sampling.

4. DISCUSSION

On account of small area of the Powsińskie Lake and its pond character it is difficult to compare the present results with those found in the literature. Fragmentary data on *A. aquaticus* that can be found in any extensive study concerning lakes seem to be irrelevant for the comparison purpose. The study by Fitzpatrick (1968) of *A. aquaticus* population dynamics and bioenergetics in Pond C of the Brasside Pond System near Durham, Scotland, seems to be comparable with the present investigations. In general, the population dynamics of the present study and that just mentioned are similar in that the mass occurrence of *A. aquaticus* is in June (present study) and in July (F i t z p a t r i c k 1968) with a decline in population numbers in March, April and May (Brasside Pond C) and March, April (Powsińskie Lake). For example, the average density of this species in July 1967 in Brasside Pond C as measured with a tubular sampler, was 994.6 ind./m^2 (F i t z p a t r i c k 1968), whereas in the present study in June it amounted to 2,700 ind./m^2 (1972) or 1,000 ind./m^2 (1973) and 180 ind./m^2 (1974).

The cycle of *A. aquaticus* occurrence seems to be one month delayed in Brasside Pond C as compared with that of the Powsińskie Lake. The population structure seems to be rather dissimilar in the two water bodies in question. A substantial difference was observed in that the Brasside population of *A. aquaticus* has a restricted period of reproduction (February-April) whereas the Powsińskie Lake population, besides early spring reproduction (inferred from a very high frequency of 1 mm class in May 1972) has a certain number of ovigerous females occurring throughout the whole vegetation season. Another difference is lack of abrupt decline of the Brasside population in summer as compared with the Powsińskie Lake population.

Other study on life cycle of *A. aquaticus* with productivity aspects is that of A n d e r s o n (1969). None of the two lakes studied by this author is similar to the present study area and therefore any comparison renders difficulty. It is worthy to mention that in the two lakes studied by A n d e r s o n (1969) the *Asellus aquaticus* populations have two distinct generation periods and no sharp reduction in population numbers was observed, contrary to the present situation in the Powsińskie Lake.

It is difficult to give reasons of such abrupt and permanent disappearance of the population. The vanishing of juveniles can suggest that the population broke down due to unfavourable environmental conditions such as pollution of water with pesticides applied at this period on the adjacent fields. Another possibility of explanation is migration of the population due to the deterioration of oxygen conditions near the bottom. The individuals could supposedly migrate onto proliferously developing meadows of submerged plants. However, no *A. aquaticus* was found in additional samples of the submerged plant vegetation; neither it was caught in benthic samples at station IV, which formed a transect along the lake axis.

Is there any other niche the population could have migrated, or was it poisoned with chemicals, or still could have it been eaten totally by predators? These are questions unsolvable with the available information. One can also venture to say that *A. aquaticus* is a species with several-year cycle of mass occurrence. In order to check the latter statement the control sampling was done in 1975, on two dates (May 28 and June 20), when peak of occurrence was expected to occur. The fact that density of *A. aquaticus* in this period was 859.0 ind./m^2 thus approaching the peak of occurrence in 1972 is self-explaining. Therefore it was concluded that the observed annual changes in occurrence of *A. aquaticus* are probably a natural pattern of population existence and it is unnecessary to tray to explain them with any sort of environmental catastrophy.

5. SUMMARY

The dynamics of population numbers, biomass, and calorific content were studied during 3 vegetation seasons as confronted with changes in total macrobenthos occurrence (except *Mollusca*) in the littoral zone of a small lake (Figs. 3, 4). The importance of the species studied was inferred from the percentage incidence

of *A. aquaticus* in the macrobenthos community of the lake littoral (Fig. 5). Age and sex structure of the population was also investigated (Figs. 6–8). It was found that *A. aquaticus* population during the period of mass occurrence formed about 10–20% of the total macrobenthos, with its incidence decreasing to 5–10% in other periods.

Maximum occurrence of both the *A. aquaticus* population and total macrobenthos community was found in June 1972, when the former was represented by a density of 2.7 thousand ind./m^2, 1.7 g of biomass (dry weight) per m^2 or 4.5 kcal/m^2, and the latter by 18 thousand/m^2, 7 g dry wt /m^2 or 35 kcal/m^2. Further on in the season the occurrence of both the *A. aquaticus* population and macrobenthos was found to diminish considerably. The annual changes both in the population and the community were of a significant degree and showed a diminishing tendency. The reduction of population observed in summer months followed in all size classes and was an abrupt one (Fig. 8). The possible reasons of the population decline were discussed.

The paper includes calorific values of all invertebrate groups found in the littoral zone of the Powsińskie Lake during the study period (Table II).

6. POLISH SUMMARY (STRESZCZENIE)

Badano dynamikę liczebności populacji *A. aquaticus*, biomasy i energii zawartej w jej biomasie przez okres trzech sezonów wegetacyjnych na tle ogólnych zmian występowania bentosu (oprócz *Mollusca*) w strefie litoralnej małego jeziora (fig. 3, 4). O znaczeniu badanego gatunku wnioskowano na podstawie procentowego udziału *A. aquaticus* w biocenozie makrobentosu strefy litoralnej jeziora (fig. 5). Badano również strukturę wiekową i płciową populacji (fig. 6–8). Stwierdzono, że populacja *A. aquaticus* w okresie masowego występowania stanowiła 10–20% ogólnej liczebności makrobentosu, przy czym udział populacji w ogólnym bentosie w innych okresach sezonu wegetacyjnego zmniejszał się do 5–10%.

Szczyt występowania zarówno badanej populacji jak i biocenozy makrobentosu zanotowano w czerwcu 1972 r., kiedy populacja osiągała zagęszczenie 2,7 tys. osobników/m^2, 1,7 g biomasy (sucha masa) na m^2 lub 4,5 kcal/m^2, a zagęszczenie makrobentosu – 1,8 tys. osobników/m^2, 7,0 g biomasy (sucha masa) na m^2 lub 35 kcal/m^2. W dalszym okresie sezonu wegetacyjnego występowanie zarówno populacji, jak i makrobentosu znacznie się zmniejszało. Roczne zmiany występowania badanej populacji i makrobentosu były znaczne i wykazywały tendencję do zmniejszania się. Redukcja populacji *A. aquaticus*, zachodząca w okresie letnim, obejmowała wszystkie klasy wielkości i miała gwałtowny charakter (fig. 8). Omówiono prawdopodobne przyczyny załamania się populacji.

Praca zawiera ponadto wartości kaloryczne wszystkich grup bezkręgowców występujących w litoralu Jeziora Powsińskiego w okresie prowadzenia badań (tab. II).

7. REFERENCES

1. Anderson E. 1969 – Life-cycle and growth of *Asellus aquaticus* (L.) with special reference to the effects of temperature – Rep. Inst. Freshwat. Res. Drottingholm, 49: 5–26.
2. Fitzpatrick C. H. 1968 – The population dynamics and bioenergetics of the isopod, *Asellus aquaticus* L., in a small freshwater pond – M.Sc. Thesis, University of Durham.
3. Just J., Hermanowicz W. 1964 – Fizyczne i chemiczne badanie wody do picia i potrzeb gospodarczych – Państwowe Zakłady Wydawnictw Lekarskich, Warszawa, 311 pp.
4. Klekowski R. Z., Bęczkowski J. 1973 – A new modification of microbomb calorimeter – Ekol. pol. 21: 229–238.
5. Phillipson J. 1964 – A miniature bomb calorimeter for small biological samples – Oikos, 15: 130–139.
6. Prus T. 1971 – The assimilation efficiency of *Asellus aquaticus* L. (*Crustacea, Isopoda*) – Freshwat. Biol. 1: 287–305.

7. Prus T. 1972 – Energy requirement, expenditure and transformation efficiency during development of *Asellus aquaticus* L. (*Crustacea, Isopoda*) – Pol. Arch. Hydrobiol. 19: 97–112.

8. Prus T. 1976 – Experimental and field studies on ecological energetics of *Asellus aquaticus* L. (*Isopoda*). II. Respiration at various temperatures as an element of energy budget – Ekol. pol. 24: 607–621.

Paper prepared by H. Dominas

AUTHOR'S ADDRESS:
Dr Tadeusz Prus
Zakład Bioenergetyki Ekologicznej
Instytut Ekologii PAN
Dziekanów Leśny k. Warszawy
05–150 Łomianki
Poland.