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PRIMARY PRODUCTION AND CHLOROPHYLL CONTENT IN THE
BALTIC SEA. PART II. CHLOROPHYLL-A DISTRIBUTIONSea Fisheries Institute, Department of Oceanography, Al. Zjednoczenia 1, Gdynia,
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ABSTRACT

The present paper shows the results of measurements of chlorophyll concentrations in the Baltic waters in the periods from May 20 to June 19, and from September 7 to October 1, 1971, and also the results of monthly measurements of chlorophyll content in the Gdańsk Deep. In the spring season the average chlorophyll concentrations in the euphotic layer in the Baltic were of about 1.5 mg/m³. In September the average chlorophyll concentrations there exceeded 2 mg/m³. In both the above-mentioned periods the greatest quantities of chlorophyll were found in the water of the Gdańsk Bay and the Pomeranian Bay. At the time of phytoplankton bloom in April, 1971, the chlorophyll concentration measured in the Gdańsk Deep was of 20.5 mg/m³ of the surface water. The other phytoplankton bloom that year in the Gdańsk Deep was recorded in November.

1. INTRODUCTION

Studies on the Baltic phytoplankton in respect of its composition had been carried on for scores of years. A detailed description of species composition of the Baltic phytoplankton in dependence on hydrological conditions was given by Ringer (1970, 1971) and other authors. An attempt to estimate the phytoplankton productivity in relation to nutrient concentrations was made by Buch (1954), yet the data on the phytoplankton biomass in the Baltic are relatively very scarce. It may be emphasized, however, that the knowledge of the phytoplankton biomass is of great importance both for the fishery and for possibility of estimating the Baltic biological productivity. Especially, in the face of the increasing eutrophication of the Baltic Sea estimation of the plankton biomass is nowadays playing a role of the first rank. The simplest and most frequently used method for evaluation of phytoplankton biomass consists in determination of chlorophyll-a obtained by extraction from phytoplankton filtered out of the sea water. The first attempts at evaluation of the chlorophyll content in the Baltic plankton were made by Krey (1939, 1952). Using the chlorophyll method, Gillbricht (1952), Banse (1957), Wellershaus (1964) and Zeitschell (1965) estimated the phytoplankton biomass in various regions of the Baltic Sea. Nevertheless, even a rough estimate of the chlorophyll distribution in the Baltic based on the above-mentioned papers is very difficult because of the following reasons:

1. Insufficient frequency of observations made hitherto as against the relatively great seasonal changes (Buch, Gripenberg 1938), short-term changes (Niemi 1971), and diurnal changes (Renk, Torbicki 1972).
2. Too small number of observations, as against great differences in fertility of each particular region of the Baltic (Krey, Szekiolda 1966).
3. The results of the chlorophyll content determinations given in the literature were obtained by various, thus not comparable, analytical methods.

Since 1965 a uniform method has been used for determination of chlorophyll

content, as recommended by the SCOR-UNESCO Working Group (1966). Notwithstanding the use of the standardized method of measurements there is always a possibility of some divergence or inaccuracy in determination of this pigment in consequence of an unsatisfactory apparatus used, e.g. spectrophotometer (Nehring et al. 1969). Some recent studies by Nehring, Francke (1971) provide information on chlorophyll distribution in the Baltic Sea in the spring and autumn seasons of 1969 and 1970.

The chlorophyll distribution in waters of the southern Baltic deeps in some months of 1970 and 1971 was described by Renk (1971, 1972a). In the present study the author intends to present the pattern of the chlorophyll distribution all over the southern Baltic, and to discuss the annual cycle of changes in chlorophyll concentration, in the latter case basing on the observations conducted at only one "example station" of the Gdańsk Deep.

2. MATERIAL AND METHODS

In order to work out the scheme of chlorophyll distribution, measurements were carried out during two cruises of the research vessel "Hydromet" belonging to the State Hydro-Meteorological Institute at Gdynia in the periods of May 20–June 19, and September 7–October 1, 1971. A complete list of the stations where the determinations of chlorophyll content were carried on during those two cruises, is presented in Table I. A portion of the material, in particular that one which is put down in Table III, was collected during the cruises of the research vessel "Birkut" belonging to the Sea Fisheries Institute at Gdynia. These cruises were made at several times of the year (practically every month) in the southern area of the Baltic Sea and once a year (September–October) in the North Sea. On board the "Birkut", samples of water for determination of chlorophyll content were taken, each time, half an hour before the sunrise, while on board the "Hydromet" they were collected at different times of the day. Chlorophyll was determined in the water at 0.5, 5 and 10 m depth, and, where the bottom

Table I. The list of the stations where chlorophyll concentrations were measured in May–June and September–October of 1971

Station	Position		Station	Position		Station	Position	
	E	N		E	N		E	N
ZN 1	18°54'	54°22'	G ₂	19°20'	54°50'	BY 22	25°36'	59°55'
ZN 3	19°01'	54°22'	P 2	18°00'	55°17'	BY 25	23°18'	59°35'
ZN 4	18°50'	54°40'	P 3	17°04'	55°13'	BY 31	18°14'	58°35'
ZN 5	20°37'	55°42'	P 5	15°59'	55°15'	BY 37	17°05.5'	57°44'
ZN 6	20°30.5'	56°30'	P 7	14°05'	55°00'	BY 38	17°40'	57°07'
ZN 7	21°36'	58°04'	P 8	15°03'	56°06'	BY 39	16°32'	56°07'
ZN 8	22°20'	59°15'	P 16	16°48'	54°38'	15	17°06'	55°27'
ZN 9	21°22'	59°32.7'	P 21	14°15'	55°28'	16	17°05'	55°23'
ZN 10	18°38'	59°43'	P 25	19°30'	55°12.5'	17	17°04'	55°19'
ZN 11	18°00'	56°15'	P 37	13°18'	55°00'	29	15°47'	54°49.5'
ZN 12	12°33'	55°28'	P 39	15°15'	54°42'	Gt ₁	18°28'	55°40'
ZN 13	11°15'	54°36.5'	P 40	18°36'	55°38'	J	18°46'	54°36'
ZN 14	10°20'	54°39'	P 41	19°10'	56°05'	A ₁	14°02'	55°02'
ZN 15	10°56'	55°24.5'	P 44	20°03'	57°20'	B ₂	14°24'	55°17'
ZN 16	11°00'	56°10'	P 45	19°54'	58°00'	34	15°00'	55°33'
ZN 17	10°46'	56°52'	P 46	20°19'	58°53'	B ₄	16°33'	55°18'
ZN 18	11°07'	57°43'	L 7	17°32.1'	54°50'	B ₁	15°45'	55°20'
ZN 19	12°03'	57°01'	K 6	15°32'	54°15.4'	B ₂	17°02'	55°13'
ZN 20	12°08'	56°22'	B 13	14°15'	54°04'	B ₃	18°00'	55°20'
ZN 21	24°25'	59°45'	B 15	14°41.5'	54°04'	NS*	2°00'	54°00'
ZN 22	19°00'	59°00'						

was deep enough, the water samples for chlorophyll determinations were taken at 20, 30, 40 and 50 m depth, especially in the spring season in waters of the Central Baltic, and all over the year in the area of the southern Baltic. At each depth 1.5 or 2 l of water were taken and filtered through H. A. "Millipore" membrane filters.

Chlorophyll content was determined using the method generally accepted in oceanography, recommended by the SCOR-UNESCO Working Group (1966), and described in detail by Strickland, Parson (1968). Coefficients of light absorption were calculated basing on measurements of penetration of natural light into the water (Holmes 1968). Measurements were made between 10 and 11 a. m. by means of the Model 420 underwater photometer, "Hydro-Products" (USA).

In several cases at the G_2 , G_{t1} , and B_1 stations, in the spring of 1970, the vertical distribution of phytoplankton was determined by the radioisotope method, described in detail by Sorokin (1957). To this purpose samples of water, taken at the same depths as those used for determination of chlorophyll concentrations, were poured into bottles, then 10 μ Ci of radio-carbon was added to each bottle in form of 1 ml of the sodium carbonate solution (Renk et al. 1972). After a five-hour incubation of bottles in the sea at 0.5 m depth the content of bottles was filtered off through membrane filters. The ratio of the radioactivity of the filter with the plankton from the bottle containing the water taken at a given depth to the radioactivity of the filter with the plankton from the surface water was considered the relative biomass of living plankton at a given depth (Sorokin 1960).

3. RESULTS

VERTICAL DISTRIBUTION OF CHLOROPHYLL-A

The amount of phytoplankton at a given station varied with depth in a manner depending on the season. The vertical distribution of chlorophyll at the G_2 station in the Gdańsk Deep is shown in Fig. 1.

In spring and summer chlorophyll concentrations of the euphotic

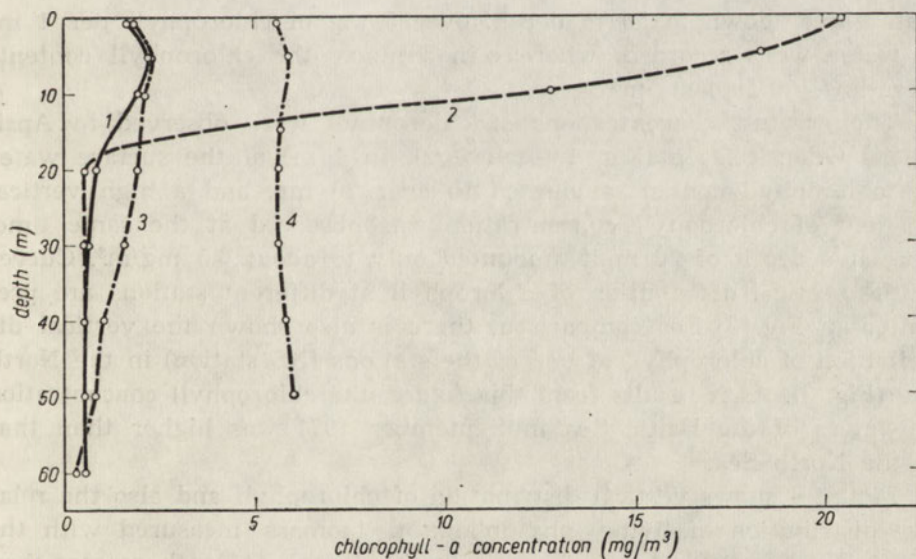


Fig. 1. Vertical distribution of chlorophyll-a concentrations in G_2 station (Gdańsk Deep) in 1971. 1—March 28, 2—April 7, 3—July 19, 4—November 20

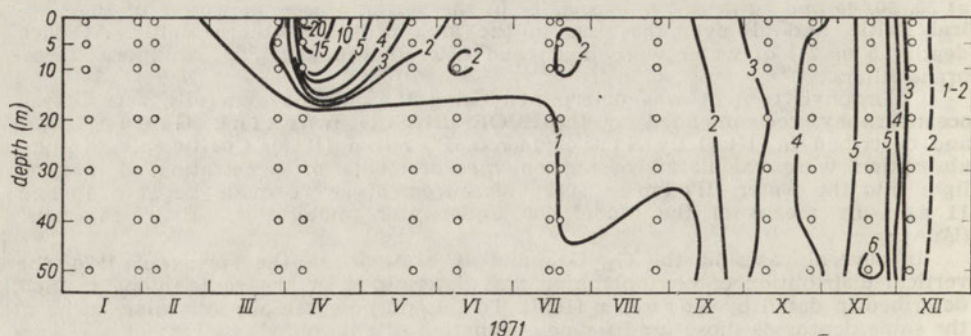


Fig. 2. Changes of chlorophyll concentrations in water depths in G_2 station during a year

layer are distinctly higher than those of the deeper water layers. It should be taken into account that the thickness of the euphotic zone in the Baltic Sea is of about 20 m (Dera 1971, Renk 1972 b).

Curve 1 in Fig. 1 presents the chlorophyll concentration in spring. Dependence of chlorophyll concentration on the depth during the whole summer time is similar to that presented by curve 3. The isopleths of chlorophyll content of the Gdańsk Deep (G_2 station in Fig. 2) illustrate the fact that in the spring and summer of 1971 the surface waters (down to 30 m depth) exhibited greater chlorophyll concentrations than those of the deeper layers. In the autumn and winter no greater differences were found in chlorophyll concentration at all different depths. There were, however, great seasonal differences, viz., in November, in the whole water layer down to 50 m depth, over 5 mg of chlorophyll per 1 m^3 of water were recorded, whereas in January the chlorophyll contents were lower than 1 mg/m^3 .

The greatest concentrations of chlorophyll were observed in April in the Gdańsk Deep (Fig. 1—curve 2). In 1 m^3 of the surface water the chlorophyll content amounted to over 20 mg, and a high vertical gradient of chlorophyll concentration was observed at the same time, thus at a depth of 20 m it amounted only to about 0.5 mg/m^3 . Curves of the vertical distribution of chlorophyll at different stations are presented in Fig. 3. For comparison, there is also shown the vertical distribution of chlorophyll at one of the stations (NS station) in the North Sea (Fig. 3). As it results from this figure, the chlorophyll concentration in waters of the Baltic Sea in September 1971 was higher than that in the North Sea.

Figure 4 shows vertical distribution of chlorophyll and also the relative distribution of living phytoplankton biomass measured with the radioisotope method. As can be seen in this figure, at depth greater than 20 m there is a decrease in the amount of living phytoplankton per unit of the water volume. There is also a decrease in chlorophyll concentra-

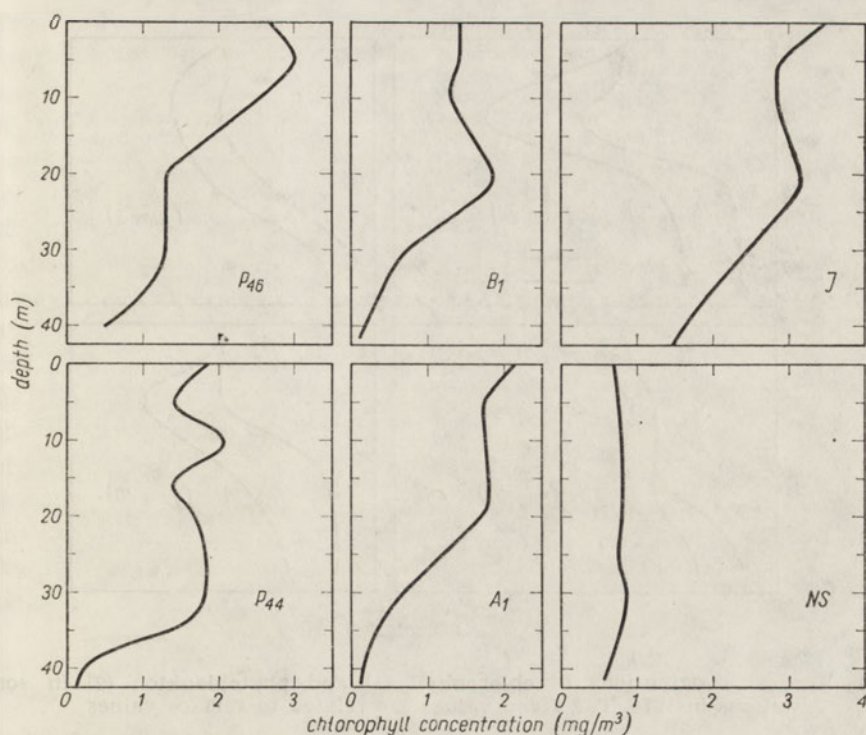


Fig. 3. Vertical distributions of chlorophyll concentration in water depths of different regions in 1971. P_{46} —Gotland Deep (Sept. 30), P_{44} —Gotland Deep (Oct. 1), B_1 —Bornholm Deep (Sept. 6), A_1 —Arkona Deep (Sept. 5), J —Puck Bay (Sept. 1), NS —North Sea (Sept. 23)

tion of water, although in three cases it is less distinct than that in the phytoplankton biomass. This last fact implies that at depths of more than 20 m a portion of the measured chlorophyll consists of chlorophyll decay products¹.

ANNUAL CYCLE OF VARIATIONS IN THE CHLOROPHYLL CONCENTRATION

Figure 2 illustrates the changes in the chlorophyll concentration at the G_2 station in 1971. The annual cycle of variations in the mean value of the chlorophyll concentration in the euphotic zone at the G_2 station is presented in Fig. 5.

It can be assumed from the present observations that the pattern shown in Fig. 5 is typical for the whole Baltic Sea. In the winter chlorophyll concentrations in the Baltic Sea are of an order of 0.5 mg/m^3 .

¹ With the method used for chlorophyll determinations not only chlorophyll itself but also some of its decay products are registered (Strickland, Parsons 1968).

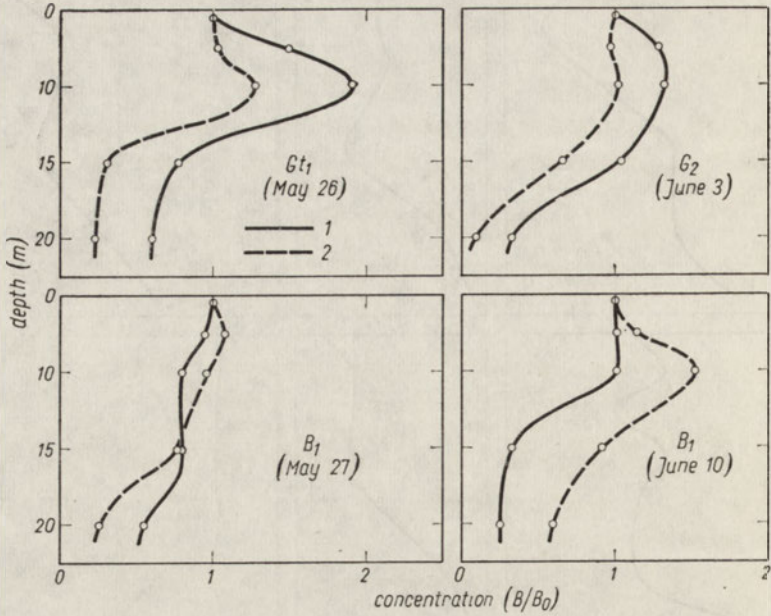


Fig. 4. Vertical distributions of chlorophyll (1) and phytoplankton (2) in some stations in 1970. The given values are related to surface values

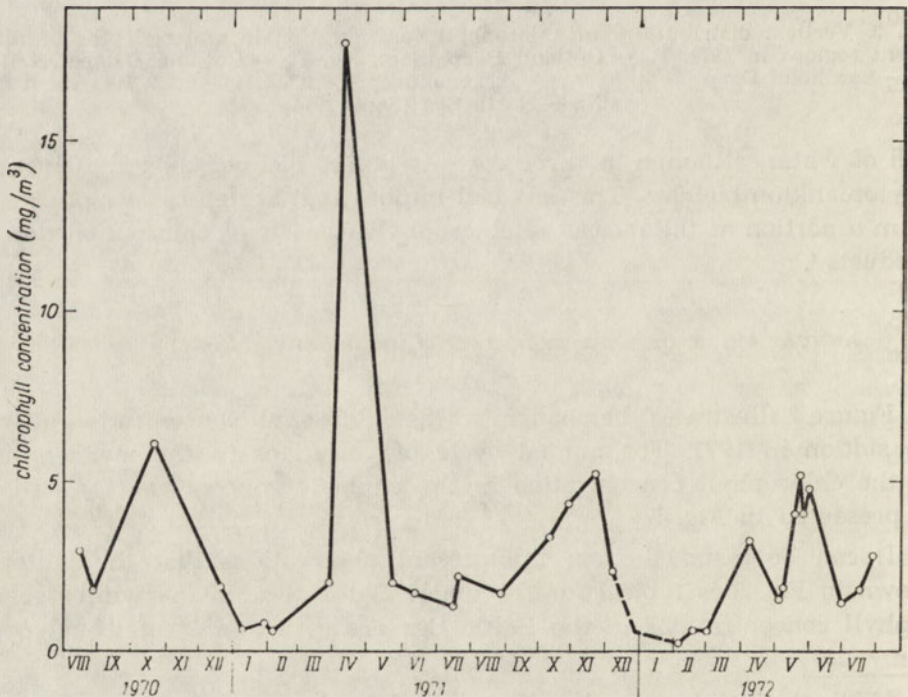


Fig. 5. Changes of mean chlorophyll concentration in a top water layer (0-10 m) in G_2 station during two years

From first days of the springtime the amount of phytoplankton starts increasing. The greatest increase in the chlorophyll concentration of the euphotic layer appeared to be in the period between March 28 and April 7, 1971 (phytoplankton bloom). Measurements carried out in other years have never shown such a rich bloom of phytoplankton as that in 1971. This was probably due to the low frequency of measurements of the chlorophyll concentration and to the relatively short duration of the phytoplankton blooming time. In the summer chlorophyll concentrations are of an order of 2 mg/m^3 . The low concentration of chlorophyll at that time, despite the high rate of phytoplankton production, was probably brought about by grazing of phytoplankton by zooplankton. In the autumn the chlorophyll concentration increased anew reaching the maximum values at the end of October or in early November. The chlorophyll content in the water column under 1 m^2 from the surface down to 50 m depth amounted in November up to 286 mg, whereas at the spring blooming time 266 mg were found in the same volume of water. In December a decrease in the chlorophyll concentration was observed.

HORIZONTAL DISTRIBUTION OF CHLOROPHYLL

To illustrate the horizontal distribution of chlorophyll in both the seasons discussed at present (May 20–June 19 and September 7–October 1, 1971) the maps were made showing the chlorophyll distribution in the waters of the euphotic layer of the Baltic Sea. Figures 6 and 8 present the distribution of chlorophyll in the surface water (samples from the 0.5 m depth), while Fig. 7 and 9 show the mean values of chlorophyll concentration in the 10 m layer of the surface water. In the spring season of 1971 the greatest concentrations of chlorophyll were found in the estuaries of the Vistula and Oder rivers; at the same time in the Pomeranian Bay waters with high chlorophyll concentration were spreading over as far as the Arkona and Bornholm Deeps. A relatively great chlorophyll content was also noted in the Gulf of Finland. On the other hand, low concentrations of chlorophyll were observed in the spring time of 1971 in the Transition Area (Kattegat and the Belt Sea), as well as in the area of the Middle Bank and Słupsk Bank. In September, just as in the spring time, the lowest chlorophyll contents were found in the Transition Area, whereas the greatest ones in the Gdańsk Bay, the Pomeranian Bay, and in the Gulf of Finland. The distribution of chlorophyll along the section through the Gdańsk Bay is shown in Fig. 10. It can be seen there that with the increasing distance from the Vistula estuary the chlorophyll concentrations were decreasing.

Presentation of the chlorophyll distribution in the form of maps suggest distribution in the water to have been constant during the time of

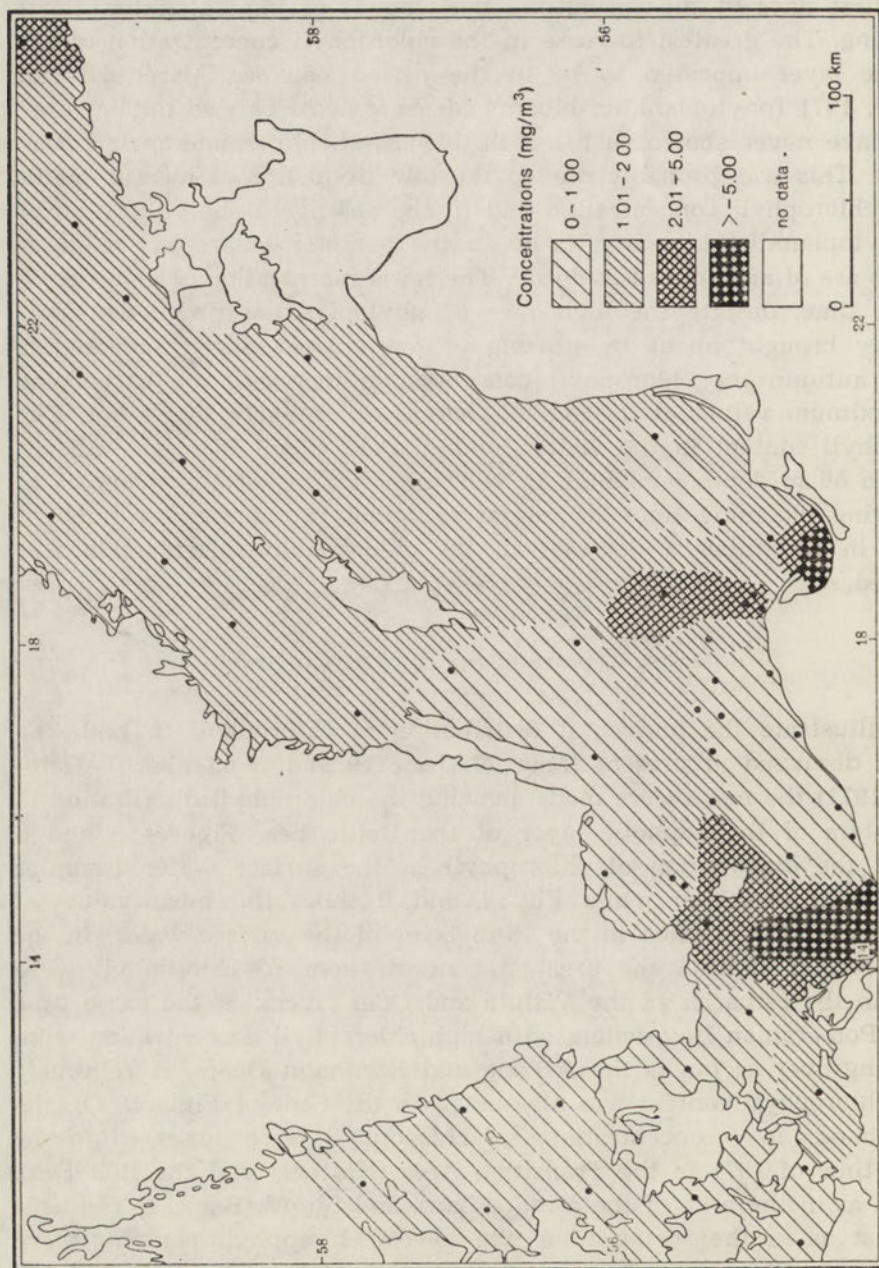


Fig. 6. Distribution of chlorophyll-a concentrations at a depth of 0.5 m in the Baltic Sea in the period of May 20 - June 19, 1971

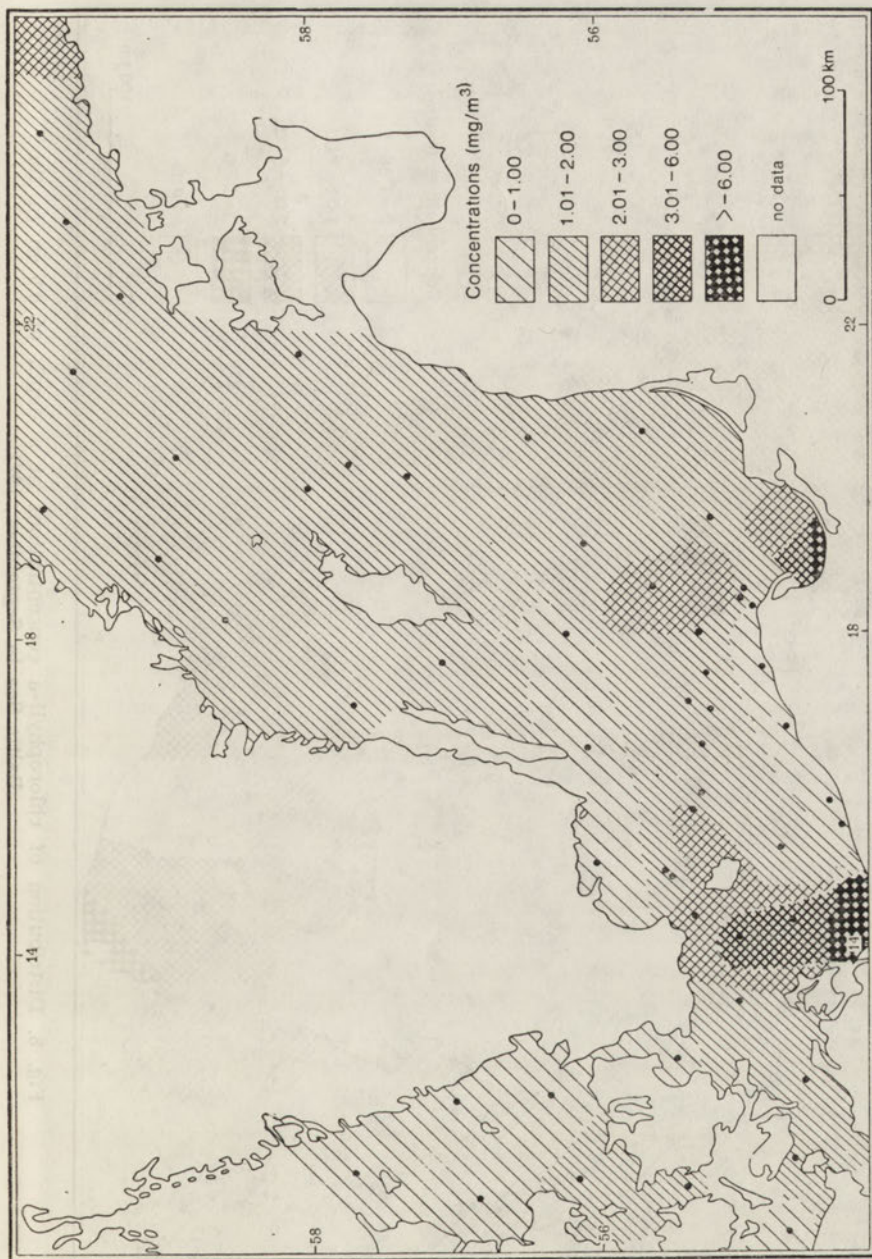


Fig. 7. The mean chlorophyll-a concentrations in a top water layer (0-10 m) in the Baltic Sea in the period of May 20 - June 19, 1971

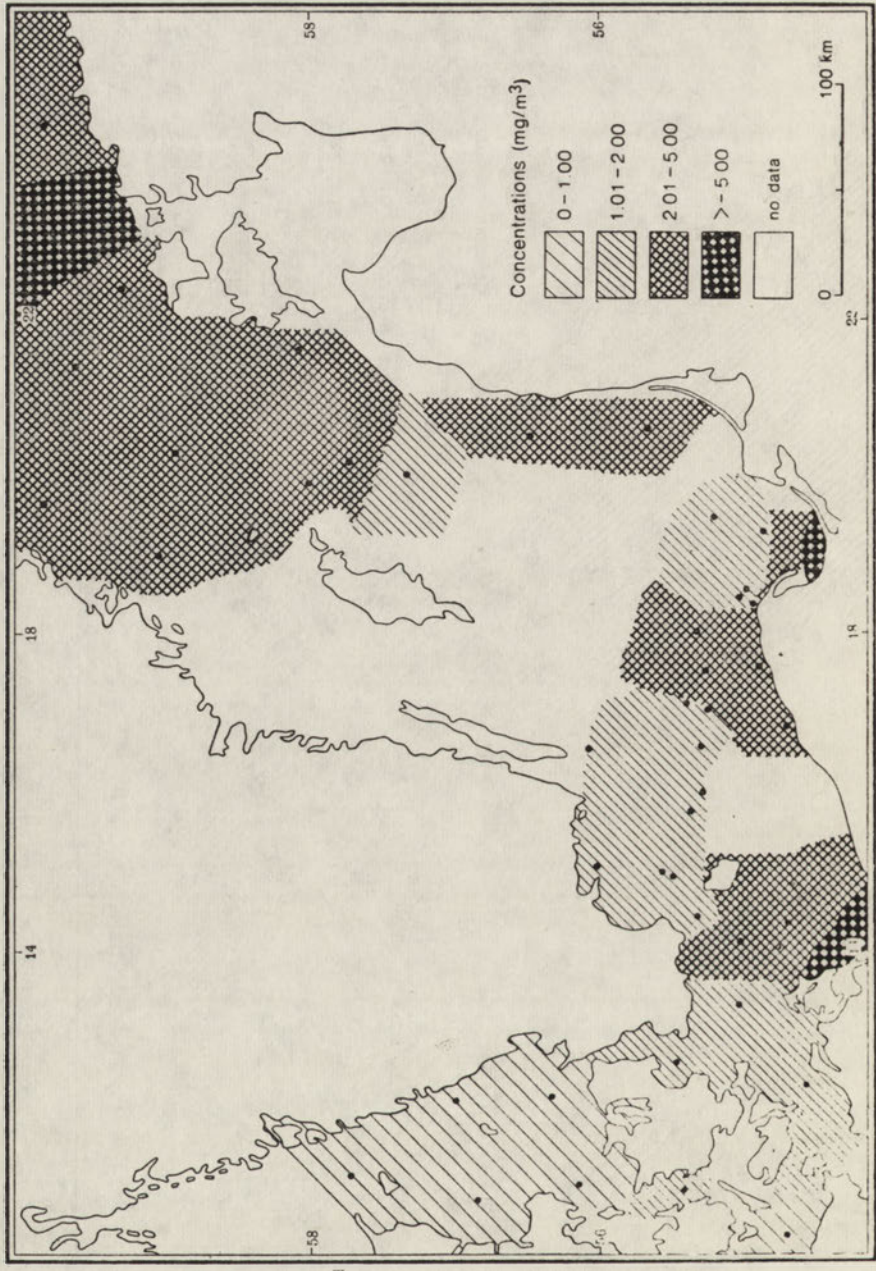


Fig. 8. Distribution of chlorophyll-a concentrations at a depth of 0.5 m in the Baltic Sea in September, 1971

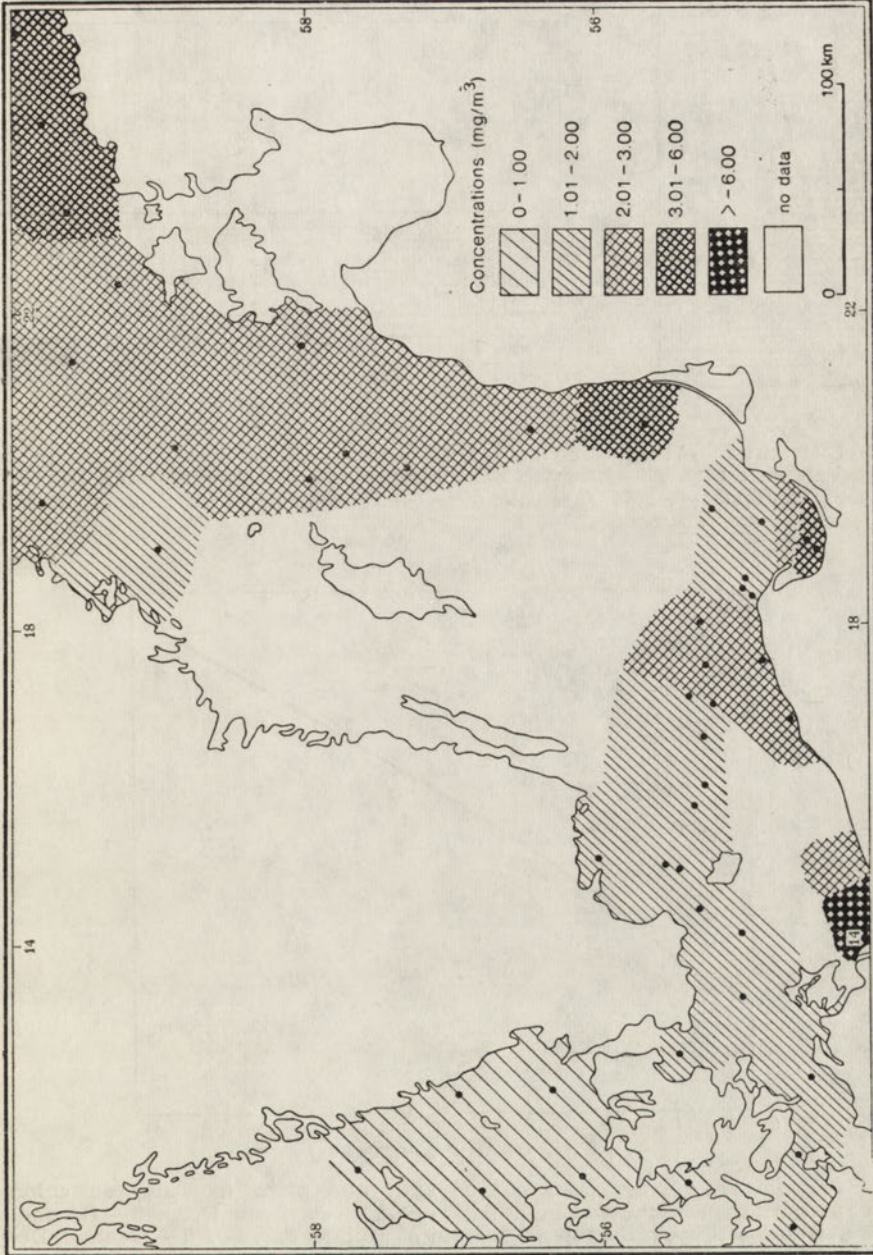


Fig. 9. The mean chlorophyll-a concentrations in a top water layer (0-10 m) in the Baltic Sea in September, 1971

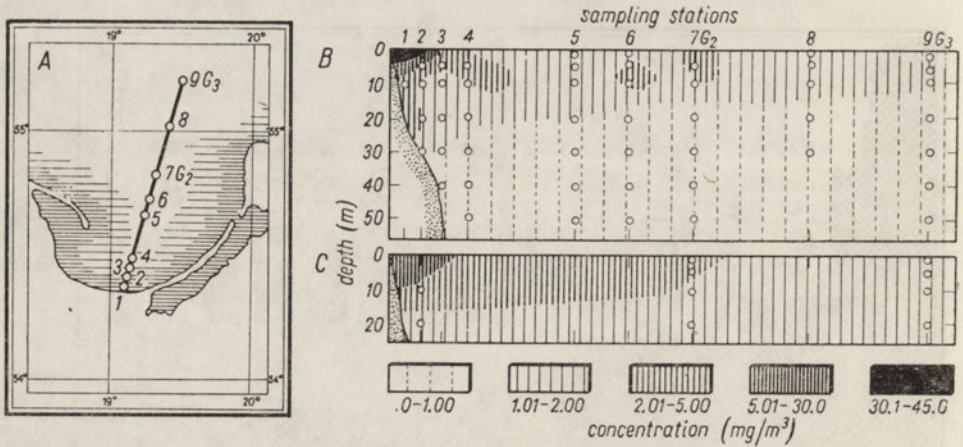


Fig. 10. Distribution of chlorophyll-a concentrations in water depths, along the section of Gdańsk Bay. A — situation of sampling stations, B — chlorophyll-a concentrations in June 1–9, 1971, C — chlorophyll-a concentrations in September, 1971

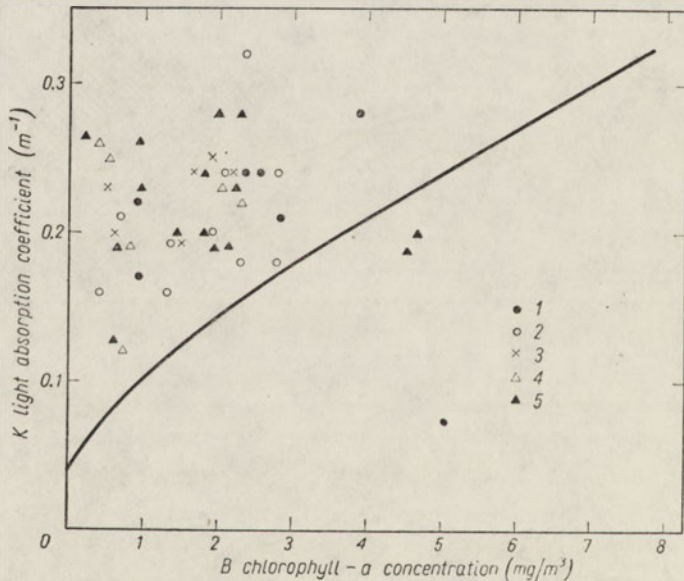


Fig. 11. Dependence of the coefficient of light absorption in water on chlorophyll-a concentration in the southern Baltic Sea. 1 — Arkona Deep, 2 — Bornholm Deep, 3 — western Slupsk Furrow, 4 — eastern Slupsk Furrow, 5 — Gdańsk Deep

collecting information for a given map. In reality such an assumption may be accepted on the basis of Fig. 2 and 5 which do not indicate great temporary changes in chlorophyll concentration in the Baltic surface waters for May–June and September of 1971. However, it may be taken into consideration that the daily differences in the chlorophyll con-

centrations may amount up to 30%. Therefore in order to have a full picture of the matter the whole of the investigation results are given in Tables II and III.

Transparency of the sea water depends, among others, on the seston content of water. For pure waters, devoid of inorganic seston, the Riley's relation (Yentsch 1963) can be applied. It expresses the relationships between the chlorophyll concentration and the coefficient of light absorption by the following equation:

$$k = 0.04 \pm 0.088B + 0.054B^{\frac{2}{3}}$$

where k — the light absorption coefficient (m^{-1}), B — chlorophyll concentration of water (mg/m^3).

In Figure 9 a curve expressing graphically the Riley's relationship is plotted and the points expressing chlorophyll concentration together with the corresponding coefficients of light absorption in the waters of the southern Baltic are given. It is evident from Fig. 9 that the light absorption in the Baltic Sea waters is usually considerably stronger than it could be expected from the phytoplankton content, and this in turn can be taken as evidence of a high inorganic seston content of the Baltic surface waters.

4. DISCUSSION

The observations on chlorophyll distribution in the Baltic waters have enabled us to formulate some regularities. The course of variations in the concentration of chlorophyll in an annual cycle, which is presented in Fig. 5, will probably be (with but slight differences) the same in the whole area of the Baltic Sea, i.e., after a period of low chlorophyll concentrations in winter, when the surface waters get rich in nutrients, there occurs a prompt increase in the phytoplankton content (Buch, Gripenberg 1938, Hickel 1967).

It has probably not been possible until now to register either the duration of the phytoplankton bloom or the maximum concentrations of chlorophyll during the blooming time in the open Baltic waters. At the phytoplankton blooming time in the Gdańsk Deep 20 mg/m^3 of chlorophyll were recorded on April 7, 1971, whereas Nehring, Francke (1971) noted 12 mg/m^3 of chlorophyll during the phytoplankton bloom in the Gottland Deep in May 1970. From these data it follows that the maximum chlorophyll concentrations at the blooming time of phytoplankton happen to be different and likewise the time of blooming start happens to be dependent on climate-and-weather conditions. For instance, in the Gulf of Finland and the Gulf of Bothnia the phytoplankton bloom is likely to start later (Bage, Niemi 1971, Nehring et al. 1969).

Table II. Chlorophyll-a concentrations (mg/m³) at different depths measured in May—June and September—October, 1971

Station	May — June						September — October								
	Date	hr	Depth (m)			30	Date	hr	Depth (m)			10			
			0.5	5	10				20	30	0.5		5	10	
ZN 1	21 M	9 ⁰⁰	9.42	4.10	3.74	—	—	—	—	—	—	—	—	—	—
ZN 3	21 M	11 ³⁰	34 ⁵⁰	7.73	7.79	—	—	—	—	—	—	—	—	—	—
ZN 4	22 M	2 ⁰⁰	1.46	1.84	1.70	0.73	0.83	—	—	—	—	—	—	—	—
ZN 5	9 J	13 ⁰⁰	0.89	3.21	0.94	0.48	0.42	—	—	—	—	—	—	—	—
ZN 6	12 J	18 ⁰⁰	1.50	1.50	1.56	0.47	1.15	—	—	—	—	—	—	—	—
ZN 7	14 J	6 ⁰⁰	1.30	1.21	1.28	0.34	0.30	—	—	—	—	—	—	—	—
ZN 8	14 J	17 ⁰⁵	1.50	1.06	0.53	0.36	0.27	—	—	—	—	—	—	—	—
ZN 9	16 J	6 ⁰⁰	1.65	1.92	1.35	0.85	0.69	—	—	—	—	—	—	—	—
ZN 10	16 J	15 ⁰⁰	1.32	1.23	1.20	1.12	0.97	—	—	—	—	—	—	—	—
ZN 11	8 J	22 ³⁰	0.38	0.49	1.23	1.60	0.48	—	—	—	—	—	—	—	—
ZN 12	7 J	17 ³⁰	0.32	0.48	1.12	—	—	—	—	—	—	—	—	—	—
ZN 13	5 J	1 ⁰⁰	0.61	1.18	1.26	0.66	—	—	—	—	—	—	—	—	—
ZN 14	5 J	5 ³⁰	0.39	0.59	0.79	1.06	—	—	—	—	—	—	—	—	—
ZN 15	5 J	14 ⁰⁰	0.78	0.83	1.65	0.76	—	—	—	—	—	—	—	—	—
ZN 16	5 J	23 ⁰⁰	0.50	0.61	2.48	1.04	—	—	—	—	—	—	—	—	—
ZN 17	6 J	6 ³⁰	0.50	0.41	0.49	—	—	—	—	—	—	—	—	—	—
ZN 18	6 J	15 ³⁰	0.59	0.76	0.80	2.41	7.59	—	—	—	—	—	—	—	—
ZN 19	7 J	1 ⁰⁰	0.55	0.52	1.38	1.20	0.39	—	—	—	—	—	—	—	—
ZN 20	7 J	7 ⁰⁰	0.46	0.48	0.68	2.96	0.79	—	—	—	—	—	—	—	—
ZN 21	15 J	7 ³⁰	1.94	1.58	1.77	0.96	0.68	—	—	—	—	—	—	—	—
ZN 22	17 J	1 ⁰⁰	1.29	1.42	1.25	1.05	0.51	—	—	—	—	—	—	—	—
G ₂	10 J	8 ³⁰	1.00	1.25	1.46	0.52	0.21	—	—	—	—	—	—	—	—
P ₂	22 M	11 ³⁰	1.66	1.77	1.76	0.66	0.66	—	—	—	—	—	—	—	—
P ₃	22 M	17 ⁰⁰	0.93	1.02	1.17	0.86	0.74	—	—	—	—	—	—	—	—
P ₅	23 M	8 ³⁰	1.53	1.94	1.54	1.40	0.58	—	—	—	—	—	—	—	—
P ₇	26 M	18 ⁰⁰	7.66	5.97	2.14	—	0.56	—	—	—	—	—	—	—	—
P ₈	27 M	6 ⁰⁰	0.59	0.72	0.60	0.65	—	—	—	—	—	—	—	—	—
P ₁₆	3 J	16 ⁰⁰	0.50	0.63	0.99	—	—	—	—	—	—	—	—	—	—
P ₂₁	27 M	9 ³⁰	1.73	1.50	0.79	0.58	0.14	—	—	—	—	—	—	—	—
P ₂₅	9 J	20 ⁰⁰	0.75	0.97	1.72	0.32	0.31	—	—	—	—	—	—	—	—
P ₃₆	4 J	18 ⁰⁰	1.50	1.65	2.10	0.98	—	—	—	—	—	—	—	—	—
P ₃₇	8 J	9 ³⁰	0.85	0.98	1.51	1.88	0.93	—	—	—	—	—	—	—	—
P ₃₉	26 M	11 ⁰⁰	0.34	1.87	0.93	0.64	0.56	—	—	—	—	—	—	—	—
P ₄₀	18 J	16 ⁰⁰	2.06	2.03	3.15	2.72	1.17	—	—	—	—	—	—	—	—
P ₄₁	9 J	5 ⁰⁰	1.21	1.08	2.02	1.46	0.89	—	—	—	—	—	—	—	—

P ₄₄	13 J	2 ⁰⁰	1.71	1.76	1.70	0.74	0.24	1 O	4 ⁰⁰	2.02	1.93	2.04
P ₄₅	13 J	10 ³⁰	1.27	1.50	1.40	1.31	—	30 S	21 ⁰⁰	2.18	2.32	1.69
P ₄₆	13 J	21 ⁰⁰	1.60	1.70	1.42	0.97	0.85	30 S	4 ⁰⁰	2.72	3.02	2.50
L ₇	3 J	10 ³⁰	0.33	0.30	0.56	0.60	—	13 S	6 ⁰⁰	3.41	3.76	3.21
K ₆	3 J	22 ³⁰	0.61	0.40	0.56	—	—	—	—	—	—	—
B ₁₃	4 J	6 ⁰⁰	9.60	4.89	7.88	—	—	12 S	9 ³⁰	7.49	7.27	6.81
B ₁₅	—	—	—	—	—	—	—	12 S	12 ³⁰	2.74	2.66	2.64
BY ₂₂	15 J	14 ⁰⁰	2.87	2.82	2.10	1.46	1.70	28 S	0 ⁰⁰	2.83	3.44	3.35
BY ₂₅	14 J	0 ⁰⁰	1.59	0.94	0.87	0.47	0.42	28 S	15 ⁰⁰	5.09	4.66	2.46
BY ₃₁	17 J	10 ³⁰	1.24	1.03	1.05	0.91	0.53	—	—	—	—	—
BY ₃₇	17 J	22 ⁰⁰	1.02	1.15	1.22	1.10	0.75	—	—	—	—	—
BY ₃₈	18 J	4 ³⁰	0.96	1.27	0.96	1.13	0.44	—	—	—	—	—
BY ₃₉	27 M	13 ³⁰	0.78	0.90	1.01	0.91	0.78	—	—	—	—	—
15	3 J	19 ²⁰	0.52	0.73	1.79	1.77	1.95	—	—	—	—	—
16	3 J	20 ²⁰	1.51	1.06	0.83	0.92	0.62	—	—	—	—	—
17	4 J	8 ³⁰	0.99	3.16	1.66	0.92	0.62	—	—	—	—	—
29	6 J	11 ⁰⁰	1.41	1.23	1.20	0.84	0.48	—	—	—	—	—
Gt ₁	23 M	8 ³⁰	2.80	2.84	2.87	0.97	0.97	—	—	—	—	—
J	—	—	—	—	—	—	—	—	—	—	—	—
A ₁	27 M	3 ⁰⁰	2.83	3.89	2.54	1.15	0.82	5 S	7 ³⁰	3.54	3.54	3.38
B ₆	26 M	17 ³⁰	3.46	2.63	2.14	1.16	1.15	5 S	5 ⁰⁰	2.10	1.73	1.76
34	26 M	12 ⁰⁰	1.58	2.02	2.21	1.83	0.77	5 S	10 ⁰⁰	1.19	1.39	1.35
B ₄	28 M	19 ³⁰	1.76	1.88	1.47	1.68	1.65	6 S	15 ⁰⁰	1.55	1.43	1.37
									18 ⁰⁰	1.44	1.60	1.63

Table III. The coefficients of light absorption k (m^{-1}) in water of the Baltic sea and the chlorophyll-a concentrations B (mg/m^3) at the different depths as well as the depths h which are reached by 1% of the sunlight falling on the sea surface

Station	Date 1971	Depth (m)										h (m)
		0.5		5		10		20		h	B	
		k	B	k	B	k	B	k	B			
B_2	6.I	0.27	0.52	0.23	0.50	0.20	0.60	0.14	0.72	19	0.72	
G_2	9.I	0.28	0.63	0.19	0.62	0.19	0.62	0.13	0.52	21	0.52	
B_3	29.I	0.29	0.46	0.26	0.38	0.26	0.55	0.14	0.54	21	0.54	
G_2	30.I	—	0.87	0.26	0.85	0.23	0.95	0.14	0.70	17	0.70	
Gt_1	10.II	0.20	0.38	0.17	0.40	0.13	0.36	0.13	0.41	25	0.41	
B_3	11.II	0.21	0.70	0.19	0.77	0.12	0.73	0.16	0.70	25	0.70	
B_1	21.II	—	0.58	0.21	0.68	0.16	0.39	0.25	0.58	25	0.58	
A_1	23.II	0.25	0.98	0.22	0.89	0.17	0.87	0.15	0.51	23	0.51	
G_2	28.III	0.26	1.86	0.19	2.13	0.19	1.96	0.26	0.80	22	0.80	
B_1	29.III	—	1.30	0.19	1.35	0.16	1.30	0.11	1.17	23	1.17	
B_2	1.IV	0.26	1.49	0.19	1.49	0.19	1.49	0.26	1.41	23	1.41	
G_2	25.V	0.38	2.30	0.24	2.29	0.23	1.78	0.19	0.90	16	0.90	
A_1	27.V	0.36	3.10	0.28	3.89	0.24	2.54	0.20	1.15	16	1.15	
B_1	28.V	0.35	2.76	0.24	2.78	0.18	2.28	—	0.76	21	0.76	
G_2	19.VII	0.34	1.81	0.28	2.28	0.28	2.01	0.22	1.95	17.5	1.95	
G_2	27.VIII	—	1.72	0.24	1.77	0.20	1.41	0.14	1.69	18	1.69	
B_1	6.IX	—	1.40	0.19	1.37	0.15	1.28	—	1.86	18	1.86	
B_2	7.IX	—	1.86	0.25	1.90	0.24	1.66	—	1.86	18	1.86	
B_3	8.IX	—	2.12	0.22	2.30	0.23	2.06	—	1.68	15.5	1.68	
B_1	11.XI	—	2.09	0.32	2.36	0.24	2.09	0.37	2.41	16	2.41	
A_1	13.XI	—	2.60	0.21	2.84	0.24	2.34	0.21	2.61	22	2.61	

In consequence of the warming up of waters in the spring season there is an increase in quantity of zooplankton. The largest losses of chlorophyll in summer, when the phytoplankton production is high, may be ascribed to the grazing of phytoplankton by zooplankton (Schmidt-Ries 1939, Schneise 1971).

Another regularity worth mentioning is the characteristic distribution of chlorophyll observed in the Gdańsk Deep in late spring, summer and autumn. Starting from the estuary of the Vistula River towards the Gdańsk Deep, a progressive decrease in the chlorophyll concentration is observed. A similar phenomenon seems to occur also in the Pomeranian Bay (Nehring, Francke 1971). Great chlorophyll concentrations in the areas of river estuaries may be explained by the fertilizing effect of the pollutions brought in by the rivers (Andrulewicz et al. 1972, Majewski et al. 1972). The concentrations of chlorophyll in the Gulf of Finland greater than the average for the open Baltic Sea seem also to be the result of waste waters inflowing from the nearby large urban agglomerations (Bagge, Lehmusluoto 1971).

Apart from the phytoplankton blooming time which most frequently takes place in spring and autumn, the characteristic chlorophyll concentration values for the open waters of the proper Baltic Sea in the previous years were probably approximate to those presented in this study. This seems also to be confirmed by the sporadic measurements carried out by Nehring et al. (1971) and Lessing, Niemi (1971).

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5. SUMMARY

The vertical distribution of chlorophyll in waters of the Baltic Sea varied within the annual cycle. During the spring and summer time the chlorophyll content of the euphotic layer was higher than that of the deeper waters, whereas in autumn and winter no essential differences in chlorophyll concentrations were found at any of the various depths within the investigated water layer down to 50 m depth. In the Gdańsk Deep seasonal differences in chlorophyll concentrations were observed which in 1971 were caused by two phytoplankton blooms, the one in April, the other in November. During the two cruises to the Baltic, May 20–June 19, and September 7–October 1, 1971, the following statements were made:

In the area of the southern Baltic, the regions from the Bornholm Deep in west, through the Słupsk Furrow to the Gdańsk Deep in east were characterized by chlorophyll concentrations amounting to 2 mg/m³ in spring.

The inshore waters of the western Baltic situated far away of estuaries were in the spring season of 1971 characterized by lower chlorophyll concentrations than the off-shore waters.

In close vicinity of the estuaries of large rivers high concentrations of chlorophyll were observed which gradually decreased toward the open sea.

Also in the Gulf of Finland the chlorophyll concentrations were higher than the mean for the open Baltic Sea.

At the end of the spring the most of the central Baltic area showed the chlorophyll concentrations to be nearly uniform and amounting to about 1.5 mg/m³.

In September 1971, the surface waters of the northern part of the Gotland Deep had chlorophyll concentrations ranging from 2 to 3 mg/m³.

6. STRESZCZENIE

Rozmieszczenie pionowe chlorofilu w wodach Bałtyku zmieniało się w cyklu rocznym. W okresie wiosny i lata obserwowano w strefie eufotycznej większe ilości chlorofilu aniżeli w głębszych warstwach wody, natomiast jesienią i zimą w przebadanej warstwie wody do 50 m nie stwierdzono istotnych różnic koncentracji chlorofilu na poszczególnych głębokościach. W Głębi Gdańskiej zaobserwowano różnice sezonowe koncentracji chlorofilu, które w 1971 r. były spowodowane dwoma zakwitami fitoplanktonu, w kwietniu i listopadzie. W czasie dwóch rejsów na obszarze Bałtyku w okresach 20.V–19.VI.1971 i 7.IX–1.X.1971, stwierdzono, że:

Na obszarze południowego Bałtyku, rejonu od Głębi Bornholmskiej poprzez Rynną Słupską do Głębi Gdańskiej, w okresie wiosny, charakteryzowały się koncentracjami chlorofilu wynoszącymi 2 mg/m³.

Akweny przybrzeżne zachodniego Bałtyku oddalone od ujść rzecznych charakteryzowały się wiosną 1971 r. mniejszymi koncentracjami chlorofilu aniżeli obszary otwarte Bałtyku.

W bezpośrednim sąsiedztwie ujść dużych rzek notowano duże koncentracje chlorofilu, które malały w miarę oddalania się od ujść rzek w kierunku pełnego morza.

Większe od przeciętnych na Bałtyku koncentracje obserwowano również w Zatoce Fińskiej.

Większa część środkowego Bałtyku w końcowym okresie wiosny posiadała w przybliżeniu jednakowe koncentracje chlorofilu, ok. 1,5 mg/m³.

W wrześniu 1971 r. wody powierzchniowe północnej części Głębi Gotlandzkiej zawierały koncentracje chlorofilu od 2 do 3 mg/m³.

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F. SZAJNOWSKI

RELATIONSHIP BETWEEN LEAF AREA INDEX AND SHOOT PRODUCTION OF *PHRAGMITES COMMUNIS* TRIN.

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ABSTRACT

Relationship between LAI and shoot production value was studied. Plant material was sampled in 1969 during a period of the maximum biomass (August 15 – September 15) in 49 stations in ten lakes of the Mazurian Lakeland. 233 samples were analysed in total. It was stated that shoot production increases with the increase in LAI value. This dependence was found to be significant and in the first approximation — rectilinear. The reed-belts situated at the wooded shores were less productive than the others. The ratio of shoot production to LAI was not stable and decreased as LAI value increased.

1. INTRODUCTION

In the recent years, attention has been given to the research on productivity of natural plant communities. One of the ecosystems investigated within the International Biological Programme is *Phragmites communis* Trin. communities.

Reed belonging to helophytes from an ecological point of view, is a predominating species in littoral of the Mazurian lakes. In the Lake Śniardwy, reed constituted 80% of biomass of emergent plants, and its productivity was 4.3 t dry weight per ha of a reed-belt (Bernatowicz et al. 1968). In the Mikołajskie Lake, it occupied 82.4% of the area overgrown by helophytes, and its productivity was 6.7 t dry weight per ha (Kowalczewski, Wasilewski 1966).

One of the most important morphological adaptations of the vascular plants to gas exchange and photosynthesis, is the enlargement of their surface area by formation of leaves flattened strongly. In most plants, surface area of 1 cm² of leaves is between 30 cm² (*Picea*) and 200 cm² (*Prenathes*) (Strebeiko 1970).

The aim of the present paper is to investigate the interdependence between the leaf area index (LAI) and the shoot production of reed (*Phragmites communis* Trin.).

2. MATERIALS AND METHODS

The investigations were made at 49 stations in 10 lakes of Mazurian Lakeland (Fig. 1, Table I). Only those reed stations were investigated in which other plants were not more than 5% of the total biomass. Plant material was sampled from pure reed-belts of an area not less than 100 m² (Project *Phragmites* 1969).

Biometrical characteristics of the cross-section of a reed-belt point to close dependence between the level of water surface and the stalk length, as well

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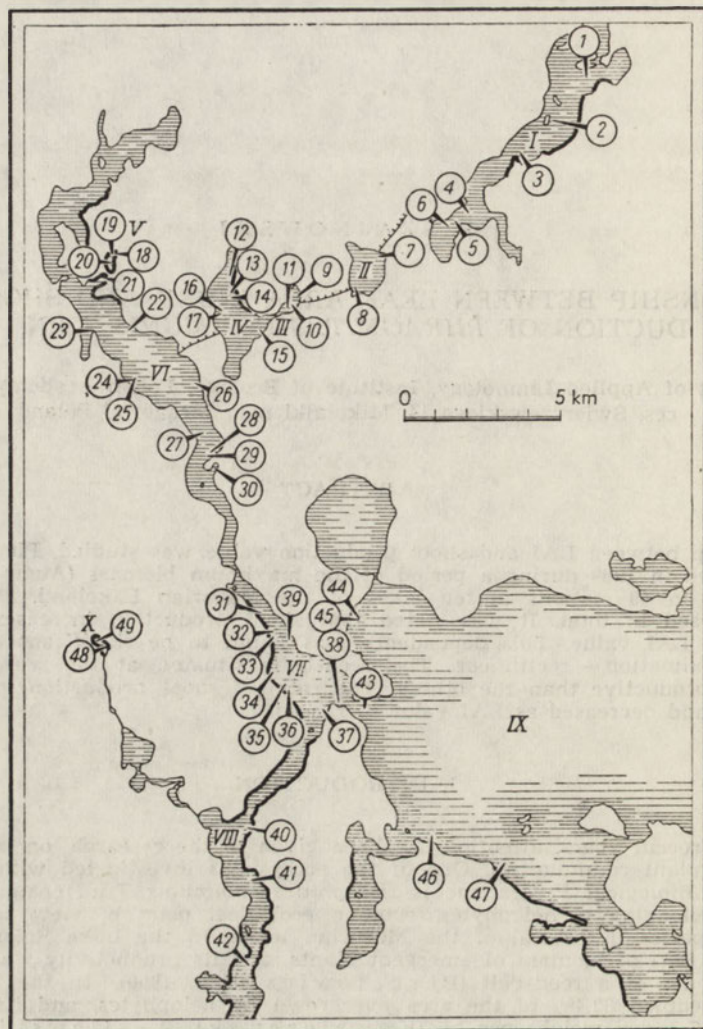


Fig. 1. Distribution of the sampling stations. Thickened shoreline — wooded shores, arabic numerals — station numbers, Roman numerals — lake numbers (cf. Table I)

as between the level of water surface and the size of assimilating area of reed (Geisslhofer, Burian 1970). Gorham, Pearsall (1956) found that plant mass is also in close connection with the level of water surface. To make the material comparable, all the samples were taken from the same depth (0.5 m).

Plant material was sampled in the period of maximum biomass (Aug. 15–Sept. 15, 1969). According to Project *Phragmites* (1969), it was assumed that a reed-belt was sufficiently represented by 5 plant samples, each drawn from the area of 1 m². Plant material was taken with 0.25 m² frame used for estimation of helophyte density. Material taken fourfold by the frame (1 m²) was considered as one sample. Reed stalks were cut at the bottom. Immediately after cutting, length of particular stalks was measured. Stalk length was defined as a distance between the bottom end of a plant and the base of panicle, or, if no panicle, the uppest leaf.

For further investigations, a representative subsample was prepared consisting in 10% of the material sampled from 1 m². A subsample was arranged in

Table I. Characteristics of the lakes under investigations

Lake		Station No.	Limnological type	Area (ha) (acc. to Olszewski, Paschal-ski 1959)
No. (cf. fig. 1)	Name			
I	Jagodne	1—6	eutrophic, holomictic	936.0
II	Szymon	7—8	eutrophic, polymictic	181.1
III	Kotek	9—11	eutrophic, polymictic	42.2
IV	Tałtowisko	12—17	mesotrophic, holomictic	323.5
V	Skonał	18—20	eutrophic, holomictic	20.0
VI	Tały	21—30	eutrophic, holomictic	1162.0
VII	Mikołajskie	31—39	eutrophic, holomictic	460.0
VIII	Beldany	40—42	eutrophic, holomictic	780.0
IX	Śniardwy	43—47	eutrophic, polymictic	10,588.4
X	Lisunie	48—49	eutrophic, polymictic	14.8

the following way: all the sampled plants were set in order of increasing length and then each tenth plant was taken out; attention was paid to leave the same number of the shortest and the longest stalks. Before a subsample was brought to the laboratory, leaf blades were separated from their sheaths. To avoid leaves getting dry before their area had been measured, stalks were kept in foil bags with some water.

Leaf area was estimated according to Szczepański (unpublished) using the formula:

$$p = 0.57 \cdot l \cdot d$$

where: p — leaf area, 0.57 — coefficient of difference between the area of a respective rectangle and the practical leaf area, l — maximum leaf length, d — maximum leaf breadth.

Only those leaves were measured, of which green area was more than 50% of the total area. For estimation of the leaf area index, leaf surfaces were recalculated per area unit of a reed-belt (1 m²).

Before weighing, plant material was dried at 85°C to constant weight. Leaf biomass and stalk biomass were measured separately for particular subsamples. The sum of biomasses of leaves and stalks with panicles and sheaths per area unit of a reed-belt (1 m²) was assumed as shoot production. Confidence half-intervals for correlation coefficients, regression coefficients and mean values were calculated at $p = 0.95$ level. Using χ^2 consistence test by Pearson, it was estimated whether distributions of particular parameters were different from the normal distribution or not. Distributions of investigated parameters were compared according to method of Kolmogorov, Smirnov (Perkal 1967).

3. RESULTS

LEAF AREA INDEX (LAI)

No significant difference was found between theoretical (normal) and empirical (presented) distributions of LAI (Fig. 2 A).

Leaf area per 1 m² of a reed-belt (LAI) from 233 samples was on the average $\bar{x} = 227 \pm 13$ dcm² (confidence half-interval). The least value, 18 dcm²/m², was found in station 14 (Lake Śniardwy), and the highest one, 521 dcm²/m², in station 10 (Lake Kotek). The standard deviation of LAI was $S_x = 103$ dcm²/m², thus 45% of the mean value.

It was not comprised in the aim of the present paper to estimate whether the investigated material has been representative for homoge-

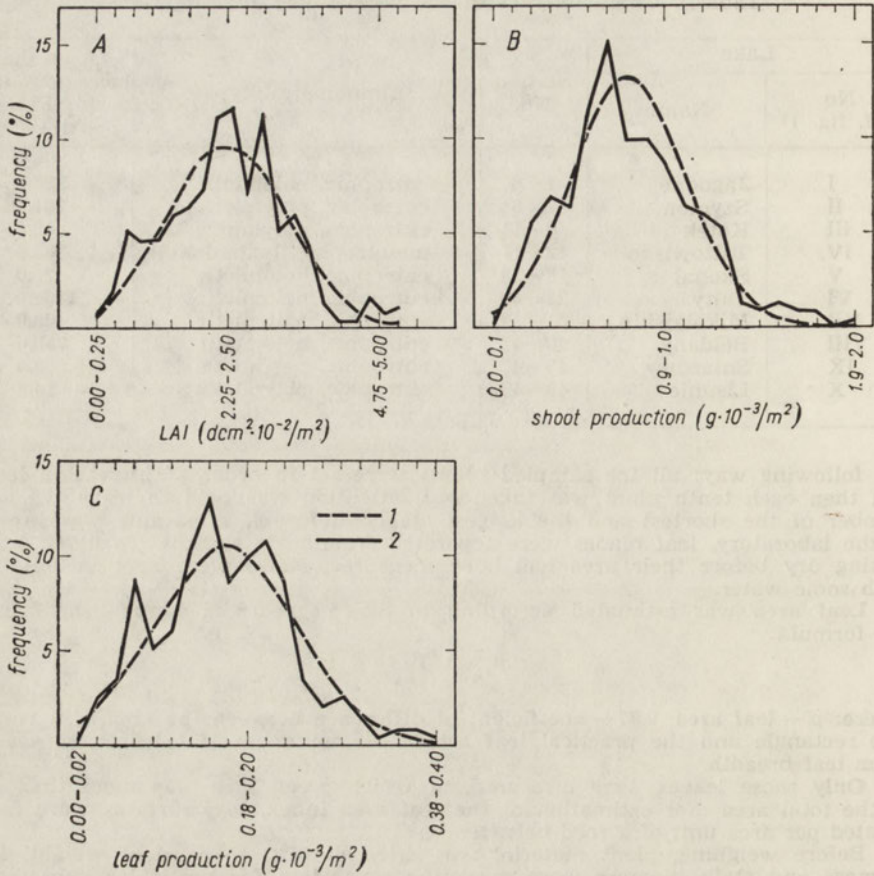


Fig. 2. Frequency distribution of leaf area index (A), shoot production (B) and leaf production (C). 1— theoretical distribution, 2— empirical distribution

nous population; however, it was found that LAI value was lower in reed-belts situated at the shores overgrown with coniferous forests than in the other reed-belts. Mean LAI value for 103 samples from reed-belts adjoining forests was $\bar{x} = 208 \pm 20$ dcm²/m², while for other 130 samples $\bar{x} = 242 \pm 18$ dcm²/m². The significant difference for these values was at $p = 0.95$ level. Comparison of LAI distributions for both groups showed the significant difference (Fig. 3 A). Standard deviations for both groups were nearly the same: $S_x = 102$ and $S_x = 101$ dcm²/m², respectively. LAI for stations adjoining forests were more diversified; coefficient of variability was $v = (S_x \cdot 100/\bar{x}) : \bar{x} = 49\%$, while for the others $v = 42\%$.

Mean LAI values in particular stations were less diversified than those in the samples. Standard deviation of mean LAI values for 49 stations was $S_x = 86$ dcm²/m² and coefficient of variability $v = 38\%$. The lowest mean LAI value, $\bar{x} = 37$ dcm²/m², was found in station 48 (Lake Lisunie). This station was localized in a reed-belt situated in a distance

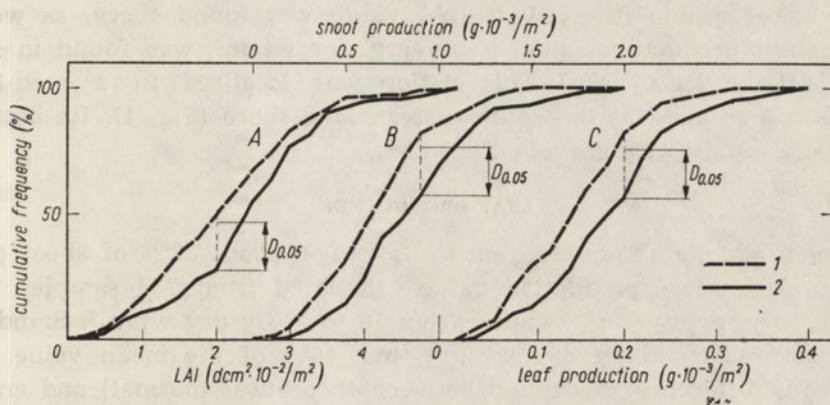


Fig. 3. Cumulative frequencies of leaf area index (A), shoot production (B) and leaf production (C). 1—the stations at the wooded shores, 2—the other stations. $D_{0.05}$ —maximum difference at confidence $w=0.05$

of 100 m from the west shore, in a central part of the lake (Fig. 1). Its bottom sediment consisted in about 90% of calcium carbonate (Planter unpublished). The highest mean LAI value, $\bar{x}=410$ dcm^2/m^2 , was found in station 32 (Mikołajskie Lake). This station was localized in the 50×20 m reed-belt, situated at the west shore of the lake (Fig. 1). Its bottom was dense, sandy with small amount of reed detritus.

SHOOT PRODUCTION

No significant difference was found between theoretical (normal) and empirical (presented) distributions of shoot production values (Fig. 2 B).

Mean shoot production value calculated from 233 samples was $\bar{y}=759 \pm 45$ g dry wt./ m^2 , and ranged from 58 to 1998 g dry wt./ m^2 . Standard deviation was $S_y=306$ g dry wt./ m^2 , thus 45% of the mean value.

Significant difference was found between distributions of shoot production values in reed from reed-belts adjoining forests and that from the other reed-belts (Fig. 3 B). Mean values for both groups were also significantly different: $\bar{y}=659 \pm 60$ and $\bar{y}=838 \pm 62$ g dry wt./ m^2 , respectively. Standard deviations were $S_y=306$ and $S_y=354$ g dry wt./ m^2 , respectively. Shoot production of reed growing at wooded shores was more diversified: coefficient of variability was $v=46\%$, while for the other reed-belts $v=42\%$.

Mean shoot production values in particular stations were less diversified than those in the samples. Standard deviation of mean shoot production values for 49 stations was $S_y=250$ g dry wt./ m^2 , and coefficient of variability $v=33\%$.

The least production value, $\bar{y}=119$ g dry wt./ m^2 , was found in station

18 in Lake Lisunie (the lowest LAI value was found there, as well). The highest production value, $\bar{y}=1477$ g dry wt./m², was found in station 15 (Lake Tałtowisko). This station was localized in a reed-belt 30×200 m, situated at the south-eastern lake shore (Fig. 1). Its bottom was dense, sandy with gravel admixtures.

LEAF PRODUCTION

Leaf production amounted, on the average, about 22% of shoot production. Mean leaf production value calculated from 233 samples was $\bar{y}=167 \pm 10$ g dry wt./m², ranging from 18 to 513 g dry wt./m². Standard deviation was $S_y=76$ g dry wt./m², thus 46% of the mean value. No significant difference was found between theoretical (normal) and empirical (presented) distributions of leaf production values (Fig. 2 C).

Significant difference was found between distributions of leaf production values in reed from reed-belts adjoining wooded shores and that from the other reed-belts (Fig. 3 C). Mean values for both groups were also significantly different: $\bar{y}=144 \pm 12$ and $\bar{y}=186 \pm 14$ g dry wt./m², respectively. Standard deviations were $S_y=64$ and $S_y=80$ g dry wt./m², respectively. Coefficients of variability were nearly the same: $v=44\%$ and $v=43\%$, respectively.

Standard deviation of mean leaf production values for particular stations was $S_y=65$ g dry wt./m², and coefficient of variability was $v=39\%$. The lowest production, $\bar{y}=29$ g dry wt./m², was found in station 48 (Lake Lisunie). The highest value, $\bar{y}=350$ g dry wt./m², was found in station 24 (Tały Lake) which was situated on the land, at 5 m from the water level (Fig. 1). Its bottom was soft with a lot of reed detritus.

4. DISCUSSION

Shoot production values for particular lakes were similar to those found by other authors. Bernatowicz, Pieczyńska (1965) gave mean value of 915 g dry wt./m² for central parts of reed-belts in Lake Tałtowisko for 1962–1963, and in the present investigations it was 844 ± 15 g dry wt./m². Kowalczewski, Wasilewski (1966) found that in 1963 mean shoot production in the central part of reed-belts in Mikołajskie Lake was 690 g dry wt./m². In the present investigations it was 732 ± 87 g dry wt./m².

In 1969, shoot production value was 759 ± 45 g dry wt./m² (the mean of all the sampled reed-belts). Shoot production value of Swedish lakes in 1961–1964 calculated from data by Björk (1967), was similar (707 ± 182 g dry wt./m²). Somewhat higher production value (943 g dry wt./m²) was found in Kazakstan (Demidovskaya et al. 1964). The highest shoot production values were given by Rudescu et al. (1965) for Danube Delta — about 1400 g dry wt./m² and by Dykyjová (1971) for littoral of a fishpond — 1481 g dry wt./m².

The mean LAI value for all the sampled reed-belts was found to be 227 ± 13 dcm^2/m^2 . Recalculation of Björk (1967) data gave somewhat higher value of 238 ± 63 dcm^2/m^2 for the Swedish lakes in 1961–1964. The difference between both values is insignificant statistically.

The significant, in the first approximation, rectilinear dependence was stated between green leaves' area and shoot production of reed

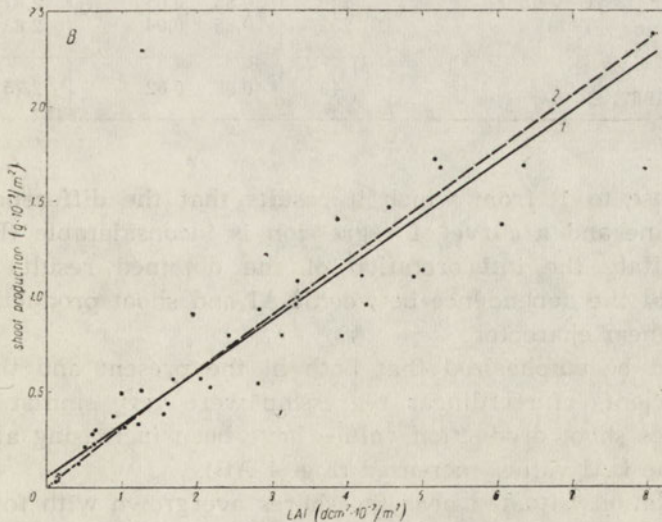
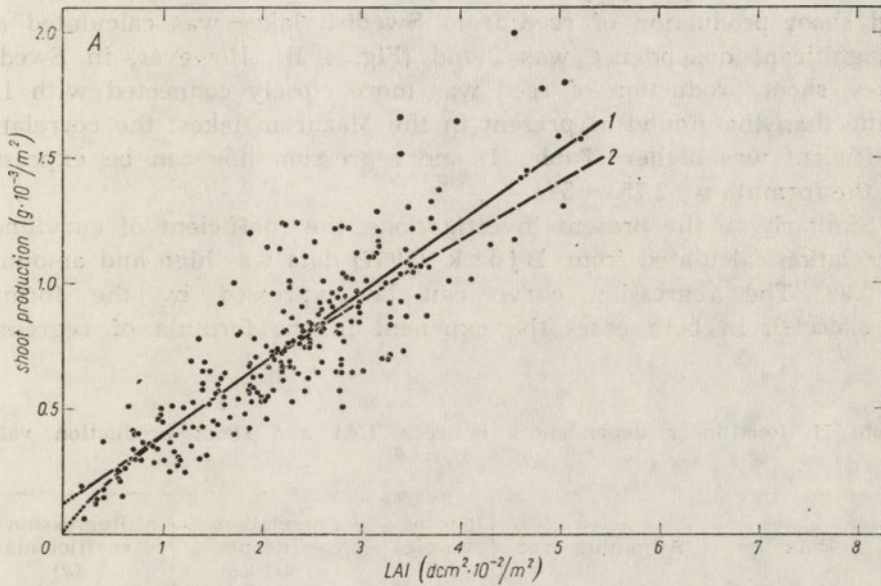


Fig. 4. Relationship between leaf area index (LAI) and shoot production. A — the present paper, B — recalculated from Björk (1967). 1 — rectilinear regression, 2 — curvilinear regression

(Fig. 4 A). Correlation coefficient r was 0.85 ± 0.04 and regression line can be expressed by the formula $y = (2.83 \pm 0.23)x + 116$. However, distribution of measurement points in Fig. 4 A shows a rather curvilinear dependence. Statistical analysis confirmed this assumption. Coefficient of curvilinear correlation ($r=0.88$) was higher than that of rectilinear correlation and regression curve can be expressed by the formula $y = 9.73x^{0.8}$. Basing on Björk (1967) data, the correlation between LAI and shoot production of reed from Swedish lakes was calculated and a significant dependence was found (Fig. 4 B). However, in Swedish lakes, shoot production of reed was more closely connected with LAI value than that found at present in the Mazurian lakes; the correlation coefficient was higher (Table II) and regression line can be expressed by the formula $y = 2.75x + 52$.

Similarly to the present investigations, the coefficient of curvilinear correlation calculated from Björk (1967) data was high and amounted $r=0.99$. The regression curve can be expressed by the formula $y = 3.59x^{0.97}$. In both cases the exponent in the formula of regression

Table II. Rectilinear dependences between LAI and shoot production values of reed

Data	Adjoining area	No. of samples (<i>n</i>)	Correlation coefficients (<i>r</i>)	Regression coefficients (<i>a</i>)
Present paper	Wooded	103	0.84 ± 0.06	2.52 ± 0.50
	Unwooded	130	0.85 ± 0.05	2.97 ± 0.52
	Total	233	0.85 ± 0.04	2.83 ± 0.23
Recalculated from Björk (1967)		48	0.96 ± 0.02	2.75 ± 0.25

curve is close to 1, from which it results that the difference between a straight-line and a curve of regression is inconsiderable (Fig. 4 AB).

To facilitate the interpretation of the obtained results it can be assumed that the dependence between LAI and shoot production of reed has a rectilinear character.

It should be emphasized that both in the present and the Swedish data, coefficients of rectilinear regression were very similar (Table II). In both cases shoot production values have been increasing almost identically as the LAI values increased (Fig. 4 AB).

In the stations situated near the shores overgrown with forests, shoot production values were somewhat less correlated with LAI than in the others, and there were lower regression coefficients (Table II). Production increment, with the LAI increase, is considerably lower in these

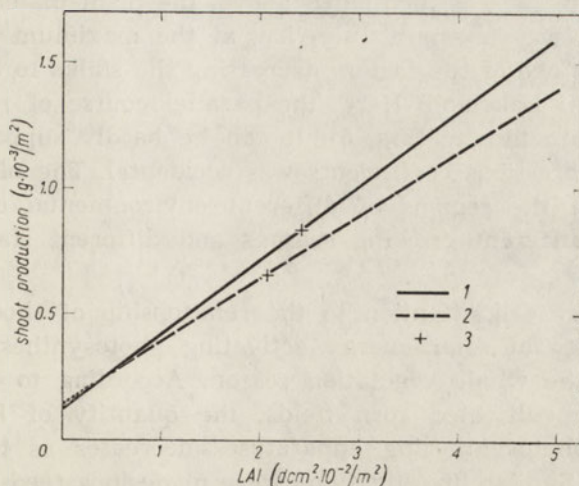


Fig. 5. Relationship between leaf area index and shoot production (rectilinear regressions). 1—the stations at the wooded shores, 2—the other stations, 3—mean values.

stations than in the others (Fig. 5). For example, LAI equal to 200 dcm²/m² corresponded to the shoot production value of about 640 g dry wt./m² in the stations of the wooded shores, whereas in the other stations—714 g dry wt./m². The LAI value higher by 100%, i.e. 400 dcm²/m² corresponded to 1144 and 1308 g dry wt./m², respectively. Thus in this case the 100% increase of LAI caused shoot production increment by 78.8 and 83.2%, respectively.

The course of rectilinear regressions between LAI and shoot production testifies to unstable production/LAI ratio. The highest ratio was in reed-belts with low LAI and low shoot production values. For example, at LAI equal to 100 dcm²/m² it was about 3.99 g of biomass per 1 dcm² of leaf surface area. At fivefold higher LAI, 500 dcm²/m², biomass of underground parts of reed falling to 1 dcm² of leaf area decreased to 3.06 g dry wt./m².

Similarly the weight ratio of stalks to leaves has changed. Coefficient of rectilinear correlation was $r=0.25$ and rectilinear regression can be expressed by the formula $y=-0.0032x+4.19$. For comparative purposes, data of Szczepańska (1973) were recalculated to find out the dependence between stalk and leaf biomasses. (Plant material was sampled in Suwalki Lakeland in 1967). Correlation coefficient was $r=0.40$, and rectilinear regression can be expressed by the formula $y=-0.0033x+2.84$. In both cases, these dependences were significant in spite of low correlation coefficients. It results from investigations of Szczepański (unpublished) carried out in a reed-belt of Mikołajskie Lake that maximum leaf biomass per area unit of a reed-belt is reached already about July 20, while maximum biomass of underground parts—only

about August 28. As was mentioned above, the plant material from Suwalki Lakeland was taken in July, i. e. at the maximum leaf biomass. Probably it was one of the factors decreasing the stalks to leaves weight ratio in Suwalki Lakeland. Here, the parallel course of rectilinear regressions is characteristic (Fig. 6). It can be hardly supposed that the similarity of regressions coefficients was accidental. The plant materials originated from the regions of different environmental conditions, as well as from different growing seasons and different stages of development.

Many authors call attention to the relationship of shoot production and the quantity of solar energy activating photosynthesis (PhAR) in plants during the whole vegetation season. According to Ničiporovič (1970), in cultivated corn fields, the quantity of PhAR energy reaching the photosynthesizing apparatuses decreases as the total leaf area increases. Similar investigations were made in a reed-belt by Dykyjová et al. (1970). It was found that the quantity of reaching energy decreases from upper to lower parts of a plant.

Leaves are one of the factors limiting the PhAR quantity reaching the photosynthesizing apparatus and therefore the more they are abundant the less is the production value per area or weight unit of leaves. Certainly, the absolute shoot production value was higher in the stations with great number of leaves since the lower leaves were also assimilating in spite of less quantity of the reaching PhAR energy. In the stations situated at the wooded shores, quantity of reaching PhAR energy during a vegetation season was probably lower than in the other stations on account of the additionally shading role of forest. The results obtained in the present paper are in accordance with the observations by Bittman (1953), who has found that reed was developing poorly in the shade of inshore trees.

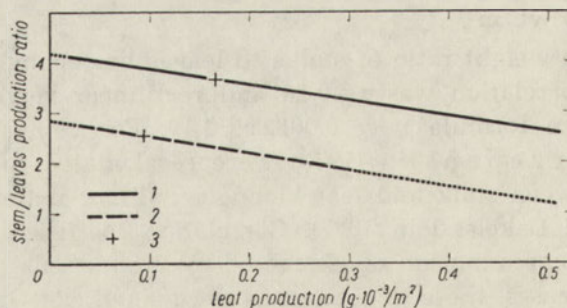


Fig. 6. Relationship between stem to leaves weight ratio and leaf production. 1— the present data, 2— recalculated from Szczepańska (1973), 3— mean values

However, the shade was probably not the only factor limiting the shoot production in the stations of wooded shores. It is known that lands unsuitable for agriculture have been afforested. Thus reed growing in the neighbourhood of such a forest has rather poor soil to its disposal.

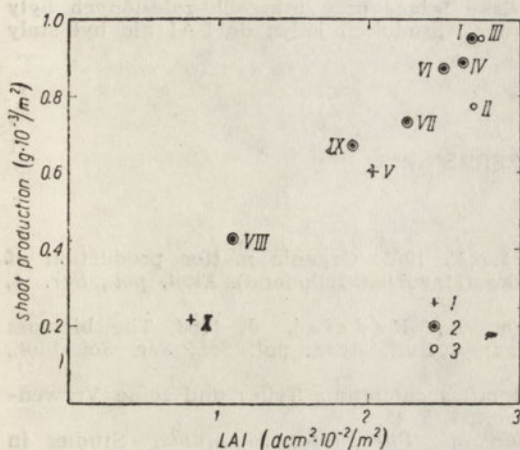


Fig. 7. Relationship between leaf area index and shoot production (mean values for particular lakes). 1—small eutrophic lakes influenced by surrounding forests, 2—great lakes (more than 200 ha), 3—other lakes. Roman numerals—lake numbers according to Table I

The present investigations were carried out only in few lakes and therefore it cannot be stated whether there is a significant relationship between the trophic type of a lake and the shoot production. However the general tendencies can be observed. Considerably lower shoot production was recorded in the stations of small eutrophic lakes influenced by a surrounding forest (Fig. 7). Mean shoot production in these lakes was $\bar{y}=457 \pm 109$ g dry wt./m². In the stations of small eutrophic lakes, not wooded, shoot production values were nearly twice as high ($\bar{y}=846 \pm 130$ g dry wt./m²). In these lakes, shoot production was similar to that of the great eutrophic lakes ($\bar{y}=786 \pm 50$ g dry wt./m²). The above results confirm the negative influence of forests on shoot production value in the reed-belts.

5. SUMMARY

Relationship between LAI and shoot production value was studied. Plant material was sampled in 1969 during a period of the maximum biomass (August 15–September 15) in 49 stations in ten lakes of the Mazurian Lakeland. 233 samples were analysed in total. It was stated that shoot production increases with the increase in LAI value. This dependence was found to be significant and in the first approximation—rectilinear.

The correlation coefficient was $r=0.85 \pm 0.04$ and straight-line of regression can be expressed by the formula $y=(2.83 \pm 0.23)x+116$. The reed-belts situated at the wooded shores were less productive than the others. The ratio of shoot production to LAI was not stable and decreased as LAI value increased.

6. STRESZCZENIE

Przeprowadzono badania nad związkiem LAI z produkcją trzciny. Materiał roślinny do badań zebrano w 1969 r. w okresie maksimum biomasy (15.VIII–15.IX) z 49 stanowisk leżących w trzcinowiskach 10 jezior Pojezierza Mazurskiego. Łącznie objęto analizą 233 próbki. Stwierdzono, że ze wzrostem LAI wzrasta produkcja łądy. Zależność ta okazała się istotna, w pierwszym przybliżeniu prostoliniowa. Wskaźnik korelacji wynosił $r=0,85\pm 0,04$, a prosta regresji wyrażała się wzorem $y=(2,83\pm 0,23)x+116$. Trzcinowiska leżące przy brzegach zalesionych były mniej produktywne niż pozostałe. Stosunek produkcji łądy do LAI nie był stały i malał ze wzrostem LAI.

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A. GRABOWSKI

THE BIOMASS, ORGANIC MATTER CONTENTS AND CALORIFIC VALUES OF MACROPHYTES IN THE LAKES OF THE SZESZUPA DRAINAGE AREA

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ABSTRACT

The biomass, organic matter content and calorific values were measured in macrophytes living in the littoral of the lakes of the Szeszupa drainage area (the Suwałki-Augustów Lakeland). Both the macrophyte biomass and their calorific values per an area unit of the littoral were estimated, as well as organic matter contents and their calorific values in the particular macrophyte species.

1. INTRODUCTION

Intense investigations on energy flow through aquatic environment have made it necessary to learn the energetic value of plant and animal organisms living there.

In all the lowland lakes, especially small and very shallow, littoral macrophytes are the main producers of organic matter (Bernatowicz, Radziej 1960). A considerable part of them reaches littoral and even profundal sediments when dying and is decomposed there with the participation of bacteria. Some of the macrophytes, especially emergent and floating species, are the food of animals. Thus the role of macrophytes in energy transfer in water bodies is very important.

For estimation of energetic values of macrophytes, it is necessary to know the data on their biological production and organic matter content beside their calorificity (Westlake 1965).

Percentage contents of proteins, fat and carbohydrates in organic matter of water plants changes within a wide range and their shares depend on species, cell physiology, environmental conditions, and other factors. Therefore the calorific value of each plant species is different, and even particular organs of the same plant can differ in this respect (Barashkov 1963).

The aim of the present paper is to estimate the biomass, organic matter content and calorific values of some macrophyte species and ecological plant groups living in the littoral of the studied lakes, as well as to calculate the calorific value per an area unit of the littoral.

2. TERRAIN DESCRIPTION AND MATERIAL

The Suwałki-Augustów Lakeland is situated in the zone of the recent Baltic glaciation; thus it is an area of the glacial accumulation. The region is composed of sediments originating in the frontal moraine. It is strongly undulated, its soils are loamy and a relative small area is overgrown with forests.

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Close neighbourhood of fields under cultivation and wet meadows as well as confluence of many lakes by the numerous rivers and streams are the reasons of trophic similarity of the lakes (Stangenberg 1937, Sobotka 1967).

14 lakes of the Szeszupa drainage area were investigated (Table I, Fig. 1). They are situated in the area of Suwałki district, between 22°52.6' and 22°58.3'E and between 54°13.7' and 54°52.6'N, and they are numbered among Kleszczowieckie Lakes of the Suwałki Lakeland (Stangenberg 1937).

Three among the investigated lakes were deep and temperate eutrophic lakes, nine—eutrophic pond-like lakes, and two—a-mesotrophic lakes (Table I). The trophic types of the investigated lakes are given according to Stangenberg (1937) and to unpublished data of the Laboratory of Ecological Chemistry at Mikołajki.

Water plants are abundant in these lakes due to their mostly eutrophic type, relatively small areas and well developed shore-lines. The lakes are surrounded by a belt of littoral macrophytes of great density, 5–15 m wide, where *Phragmites communis* Trin. is a predominating species.

Two types of substrata were observed in the stations on the investigated lakes: one—soft, muddy with a great quantity of plant detritus and the other—hard, sandy with a small quantity of organic detritus (Table I).

The following plant groups were recorded in the sampling stations: emergent plants, submerged plants, submerged with floating leaves and floating plants.

The following species were investigated in the particular plant groups: emergent plants—*Phragmites communis* Trin., *Carex rostrata* Stokes, *Typha angustifolia* L., *Schoenoplectus lacustris* (L) Palla, *Sparganium ramosum* Huds., *Ranunculus lingua* L., *Acorus calamus* L., *Equisetum limosum* L.; submerged plants with floating leaves—*Nymphaea alba* L., *Nuphar luteum* (L) Sm., *Potamogeton natans* L., *Sagittaria sagittifolia* L.; submerged plants—*Potamogeton lucens* L., *Elodea canadensis* Rich., *Lemna trisulca* L., *Myriophyllum spicatum* L., *Fontinalis* sp., *Hippuris vulgaris* L., *Chara* sp.; floating plants—*Hydrocharis morsus-ranae* L., *Stratiotes aloides* L., *Utricularia vulgaris* L.

3. METHODS

Plant materials were sampled between 6th and 27th July of 1967; in this period most of the species were in a stage of full development.

Table I. Trophic characteristics of lakes and characteristics of bottoms of the investigated stations

Bottom	Lake	Trophic type	Detritus	
			Plant	Plant and animal
muddy	Gulbin	eutrophic, pond-like	++	
	Kamendul		+	
	Łopuszek			+
	Płamszyn			++
	Okrażle			++
	Okrażłek		+++	
	Potopy		++	
Przechodnie	++			
Udziejek	++			
sandy	Jegłówek	deep, temperate eutrophic		+
	Kopane	deep, temperate eutrophic		+
	Pobondzie	deep, temperate eutrophic		+
	Jaczo	a-mesotrophic		+
	Szurpiły	a-mesotrophic		+

+ small quantity, ++ great quantity, +++ very great quantity

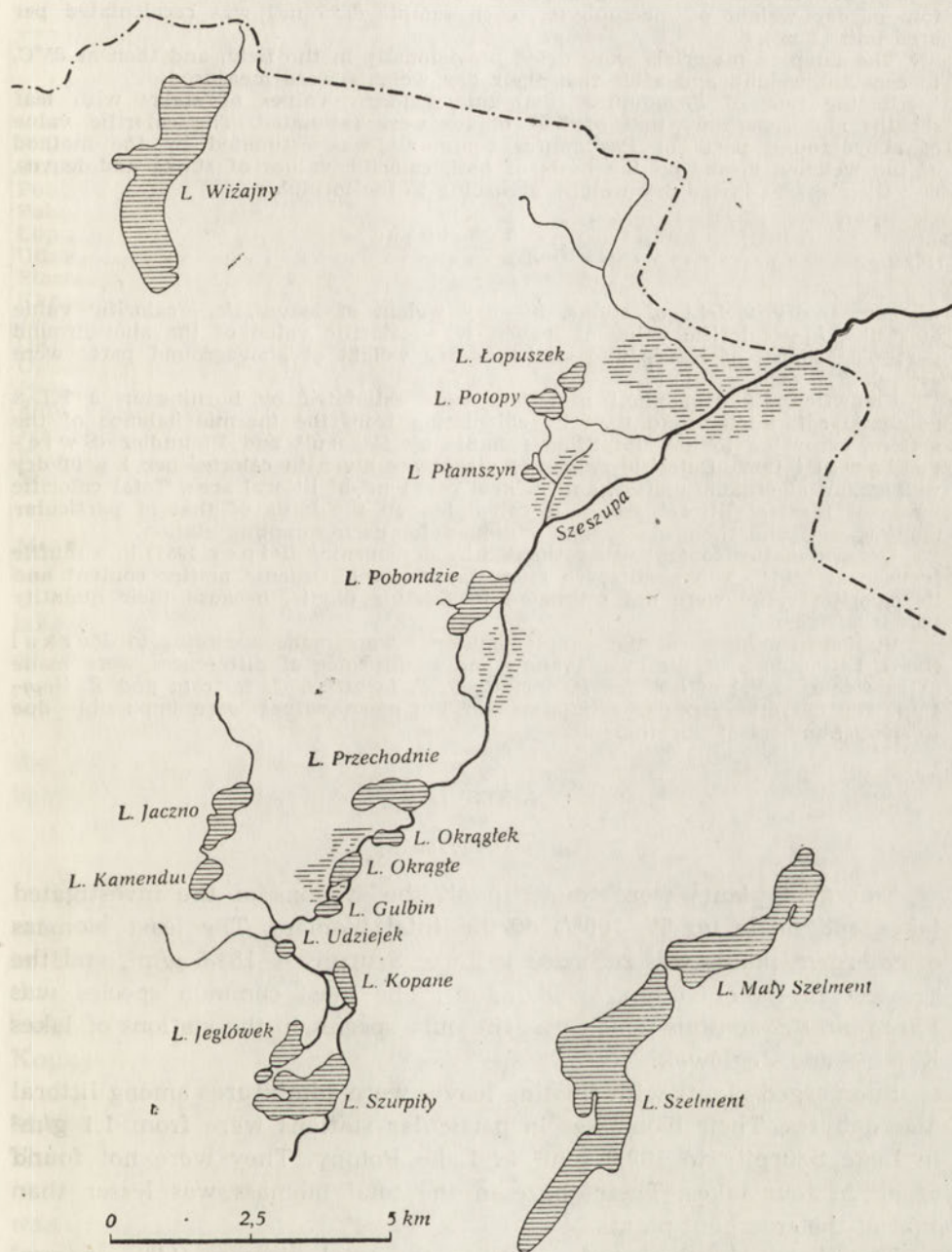


Fig. 1. The map of the Szeszupa drainage area

Only one belt of macrophytes was investigated in each lake. It was assumed that species composition in the whole littoral zone of a given lake was similar.

A sample consisted of all the plants taken from an area of 0.25 m², each time from the same depth of 0.5 m, with the use of a wooden frame. 3 samples from neighbouring areas were taken from each lake, and a mean value for

a lake was calculated. 42 samples were taken from all the lakes. For an estimation of dry weight of macrophytes, each sample (0.25 m²) was recalculated per area unit (1 m²).

The sampled materials were dried provisionally in the field, and then at 85°C, to constant weight, and after that their dry weights were measured.

In the case of *Phragmites communis*, calorific values of stalks with leaf sheaths and separately that of leaf blades were estimated. The calorific value of aboveground parts of *Phragmites communis* was estimated by the method of the weighed means on the basis of both calorific values of stalks and leaves, and their shares in the dry weight, according to the formula:

$$K_a = \frac{a \cdot K_s + b \cdot k_l}{a + b}$$

where: *a*—dry weight of stalks, *b*—dry weight of leaves, *k_s*—calorific value of stalks, *k_l*—calorific value of leaves, *K_a*—calorific value of the aboveground part. The shares of leaves and stalks in dry weight of aboveground parts were estimated in each sample.

Calorific values of plant materials were estimated by burning in a KL-3 adiabatic calorimeter, and then by calculating from the thermic balance of the system, according to the simplified formula by Regnault and Pfaundler (Świętosiłowski 1952). Calorific values of plants are given in calories per 1 g of dry weight and of organic matter, and in kcal per 1 m² of littoral area. Total calorific value of 1 m² of littoral area was calculated on the basis of that of particular plant species and their dry weight obtained for each sampling station.

Organic matter content was estimated by dry burning (Piper 1957) in a muffle furnace at 550°C. The results are given in per cent. Organic matter content and its calorific value were not estimated in floating plants, because their quantity was insufficient.

Statistical analyses of the sampled material were made according to Perkal (1967). Estimations of the mean values and significance of differences were made at confidence level of 0.95 for *P. communis*, *S. lacustris*, *C. rostrata* and *E. limosum*. For the other species estimations of the mean values were impossible due to small numbers of burnings.

4. RESULTS

BIOMASS (Table II)

Emergent plants were found in all the stations of the investigated lakes and made up 57–100% of the total biomass. The least biomass of emergent plants was recorded in Lake Szurpiły—184.6 g/m², and the greatest in Lake Gulbin—968.0 g/m². The most common species was *Phragmites communis* which was the only species in the stations of lakes Kopane and Jegłówek.

Submerged plants with floating leaves were admixtures among littoral macrophytes. Their biomasses in particular stations were from 1.1 g/m² in Lake Szurpiły to 139.0 g/m² in Lake Potopy. They were not found at all in four lakes. Their share in the total biomass was lesser than that of the emergent plants.

The share of submerged plants in the total biomass (14% on average) was higher than that of the submerged plants; they were also an admixture among littoral macrophytes. They were found in nine of the investigated lakes and their biomasses were from 0.4 g/m² in Lake Jaczno to 140 g/m² in Lake Szurpiły.

The floating plants were found in the littoral of the four investigated

Table II. Dry weight of macrophytes of the investigated lakes

Lake	Total biomass (g/m ²)	Emergent		Submerged with floating leaves		Submerged		Floating	
		g/m ²	%	g/m ²	%	g/m ²	%	g/m ²	%
Gulbin	979.0	968.0	98.99	11.0	1.11	0	0	0	0
Potopy	925.0	709.0	76.65	139.0	15.00	76.9	8.30	0.1	0.02
Pobondzie	661.2	644.0	97.40	17.2	2.60	0	0	0	0
Łopuszek	648.9	584.8	90.13	47.2	7.30	2.1	0.32	14.8	2.25
Udziejek	644.8	643.1	99.90	0	0	1.7	0.10	0	0
Pląmszyn	626.8	534.0	85.18	9.3	1.82	83.5	13.00	0	0
Kamendul	574.5	528.0	91.90	0	0	46.4	8.10	0	0
Jacžno	508.1	497.7	98.00	10.0	1.88	0.4	0.12	0	0
Okragłek	431.0	314.4	72.94	10.8	2.51	104.1	24.00	1.7	0.55
Okragłe	399.0	372.2	93.30	26.8	6.70	0	0	0	0
Przecho-dnie	394.1	272.0	68.90	6.8	1.70	115.3	29.40	0	0
Jeglówek	333.6	333.6	100.00	0	0	0	0	0	0
Kopane	332.0	332.0	100.00	0	0	0	0	0	0
Szurpiły	326.5	184.6	56.60	1.1	0.40	140.5	42.90	0.3	0.10
Mean	556.0	494.0	87.80	27.9	4.10	63.43	14.00	4.2	0.70

lakes and their shares in the total biomass were insignificant (0.7% on average). The highest share of floating plants in the total biomass was recorded in the station of Lake Łopuszek.

The least total biomass was found in Lake Szurpiły — 326.5 g/m², the highest one — 979 g/m² — in Lake Gulbin. The mean value of total biomass calculated from the values for particular stations was 556 g/m².

ORGANIC MATTER

In *Phragmites communis*, organic matter content was measured separately in leaves and stalks (Table III). In stalks it was from 93.6% in Lake Okragłek to 97.3% in Lake Jeglówek. It was lesser in leaves than in stalks by 5.8% on the average. In the aboveground part, organic matter content was from 91.3% in Lake Okragłek to 96.1% in Lake Kopane.

In the other emergent plants, organic matter contents were between 84.8% (*Equisetum limosum*) and 93.2% (*Typha angustifolia*) (Table IV). The average value for all the investigated emergent species was 90.2%.

In submerged plants with floating leaves, organic matter content was lesser than that of emergent plants — 83.2% on the average. It was from 80.7% in *Potamogeton natans* to 87.1% in *Nuphar luteum* (Table IV).

The least organic matter content was found in submerged plants (61.2% on the average). Among them the least value was recorded in *Hippuris vulgaris* — 39.9%, and the highest one in *Myriophyllum spicatum* — 70.6% (Table IV).

Table III. Organic matter contents in *Phragmites communis*

Lake	Leaves (%)	Stems (%)	Aboveground part (%)
Gulbin	89.9	95.4	94.5
Jaczno	89.4	95.5	94.2
Jeglówek	90.0	97.3	95.5
Kamenduł	91.4	95.6	94.5
Kopane	94.6	96.5	96.1
Łopuszek	88.2	94.5	92.8
Okragłe	90.6	95.7	94.2
Okragłek	88.7	93.6	91.3
Płamszyn	87.3	95.3	92.5
Pobondzie	87.8	95.8	93.5
Potopy	89.0	95.8	93.9
Przechodnie	87.8	94.2	92.6
Szurpiły	90.7	94.7	93.9
Udziejek	87.4	94.0	91.5
Mean	89.5	95.3	93.6

CALORIFIC VALUE OF THE DRY WEIGHT

In *Phragmites communis*, the calorific values of dry weight of leaves and stalks were similar (Table V). The mean calorific value of leaves estimated from 121 burnings was $\bar{x}=3947 \pm 50.8$ (confidence half-interval) cal/g; and the coefficient of variability c.v. was 7.1%. The mean calorific value of stalks estimated from 121 burnings was $\bar{x}=4005 \pm 34.9$ (confidence half-interval) cal/g and c.v. was 4.9%. Both the highest and the least calorific values of dry weight of leaves were found in the pond-like eutrophic lakes. The mean calorific value of aboveground parts was $\bar{x}=3988 \pm 33.1$ (confidence half-interval) cal/g, c.v.=4.5%.

In *Schoenoplectus lacustris*, the mean calorific value of the dry weight estimated from 66 burnings was $\bar{x}=3797 \pm 95.5$ cal/g, and in *Carex rostrata* (33 burnings) $\bar{x}=3690 \pm 77.1$ cal/g. C.v. were 22.0% and 6.0%, respectively. In *Equisetum limosum* (45 burnings) it was $\bar{x}=3152 \pm 61.3$ cal/g and c.v.=6.4%.

Thus the highest calorific value among the four species was that of *Phragmites communis*, and the least one — that of *Equisetum limosum*. The differences between *P. communis* and the others and between *E. limosum* and the others are statistically significant. However, the differences between calorific values of *Schoenoplectus lacustris* and *Carex rostrata* (the second and the third place in order of decreasing value) are insignificant.

In the other emergent plants, calorific values of dry weight were

Table IV. Calorific values and organic matter contents of macrophytes in the investigated lakes (\pm confidence half-interval)

Group of plants	Species	Calorific value (cal/g dry wt.)		Organic matter (%)
		Total	Organic	
Emergent	<i>Phragmites communis</i>	3988 \pm 33	4281 \pm 74	93.6
	<i>Sparganium ramosum</i>	3751	4281	87.7
	<i>Schoenoplectus lacustris</i>	3797 \pm 96	4112 \pm 70	91.3
	<i>Typha angustifolia</i>	3836	4107	93.2
	<i>Carex rostrata</i>	3690 \pm 77	4010 \pm 88	90.5
	<i>Ranunculus linqua</i>	3517	3951	89.0
	<i>Acorus calamus</i>	3250	3548	91.6
	<i>Equisetum limosum</i>	3152 \pm 61	3757 \pm 76	84.8
Submerged with floating leaves	<i>Nymphaea alba</i>	3247	3967	83.5
	<i>Nuphar luteum</i>	3207	3647	87.1
	<i>Potamogeton natans</i>	3069	3762	80.7
	<i>Sagittaria sagittifolia</i>	3037	3376	81.5
Submerged	<i>Potamogeton lucens</i>	2747	—	—
	<i>Elodea canadensis</i>	2054	3091	67.9
	<i>Lemna trisulca</i>	1999	3018	67.9
	<i>Fontinalis</i> sp.	1855	2982	64.7
	<i>Myriophyllum spicatum</i>	1706	3274	70.6
	<i>Hippuris vulgaris</i>	980	2454	39.9
	<i>Chara</i> sp.	628	1164	55.8
Floating	<i>Hydrocharis morsus-ranea</i>	1619	—	—
	<i>Stratiotes aloides</i>	1544	—	—
	<i>Utricularia vulgaris</i>	1416	—	—

— no data.

Table V. Calorific values of leaves and stalks of *Phragmites communis*

Lake	Calorific value (cal/g dry wt.)					
	Leaves		Stalks		Aboveground part	
	Total	Organic	Total	Organic	Total	Organic
Gulbin	4062	4515	3958	4150	4019	4364
Jacznó	4053	4576	3974	4166	3983	4176
Jęglówek	4014	4458	4031	4142	4028	4214
Kamendul	3909	4275	4044	4242	4019	4256
Kopane	4145	4380	4137	4288	4139	4348
Lopuszek	4030	4568	3863	4012	3897	4196
Okragłe	3471	3830	3932	4112	3798	4032
Okragłek	3808	4124	4267	4268	4095	4129
Płamszyn	4012	4474	3874	4063	3900	4212
Pobondzie	3864	4279	4182	4364	4134	4322
Potopy	3933	4418	4010	4188	4003	4341
Przechodnie	4129	4704	3773	4007	3882	4194
Szurpiły	3979	4412	4068	4224	4008	4241
Udziejek	3855	4412	3968	4216	3926	4270

from 3250 cal/g in *Acorus calamus* to 3836 cal/g in *Typha angustifolia* (Table IV).

The mean calorific value of the emergent plants was the highest when compared with the other plant groups — 3621 cal/g dry weight (Fig. 2).

In the submerged plants with floating leaves, calorific values were from 3037 cal/g in *Sagittaria sagittifolia* to 3247 cal/g in *Nymphaea alba*. The mean value in this group was 3140 cal/g, thus it was lower than that for the emergent plants (Fig. 2).

In the seven submerged plants found out, the calorific values were from 628 cal/g in *Chara* sp. to 2747 cal/g in *Potamogeton lucens*. The

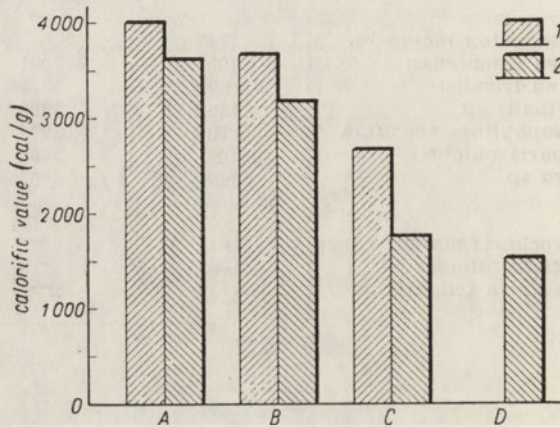


Fig. 2. Calorific values of the ecological groups of macrophytes. 1 — organic matter, 2 — dry matter. A — emergent plants, B — submerged plants with floating leaves, C — submerged plants, D — floating plants

mean value for this group was 1710 cal/g, thus lower than that for the two above groups.

The floating plants were found very rarely and in small amounts. The calorific values of particular species of this group were similar to that of submerged plants (Table IV). The mean calorific value of this plant group was 1526 cal/g, thus the lowest among the four groups (Fig. 2).

GENERAL NUMBER OF KCAL PER 1 M² OF LITTORAL

The general number of kcal per 1 m² of the littoral area of the investigated lakes was determined on the basis of measurements of both the dry weight of macrophytes and their calorific value. It was from 992 kcal/m² in Lake Szurpiły to 3762 kcal/m² in Lake Gulbin (Table VI).

Table VI. General number of kcal per 1 m² of littoral in the investigated lakes

Lake	Total calorific value	Group of plants			
		Emergent	Submerged with floating leaves	Submerged	Floating
Gulbin	3762	3758	4	0	0
Potopy	3396	2753	459	183	1
Pobondzie	2635	2573	62	0	0
Udziejek	2523	2521	0	0	2
Łopuszek	2333	2277	37	17	2
Kamenduł	2216	2126	0	90	0
Płamszyn	2204	2054	26	124	0
Jaczno	1731	1703	27	1	0
Okrażę	1486	1237	249	0	0
Okrażętek	1484	1230	33	215	6
Przechodnie	1320	1041	18	261	0
Jeglówek	1289	1289	0	0	0
Kopane	1119	1119	0	0	0
Szurpiły	992	694	3	294	1

The highest value was that for the emergent plants, and the least — that for the floating plants.

CALORIFIC VALUE OF THE ORGANIC MATTER

The calorific values of the organic matter were different in leaves and in stalks of *Phragmites communis* (Table V). The mean value for leaves calculated from 120 burnings was $\bar{y}=4377 \pm 79.1$ (confidence half-interval) cal/g, c.v.=12.0%. That for stalks (118 burnings) was $\bar{y}=4165 \pm 77.4$ (confidence half-interval) cal/g, c.v.=11.0%, thus being lesser than that of leaves by 212 cal/g. The mean value for aboveground parts of *Phragmites communis* was $\bar{y}=4281 \pm 74.3$ (confidence half-interval) cal/g, c.v.=10.0%.

The respective values for other emergent plants were: for *Schoenoplectus lacustris* (63 burnings) $\bar{y}=4112 \pm 69.9$ cal/g, c.v.=7.0%, for *Carex rostrata* (33 burnings) $\bar{y}=4010 \pm 88.4$ cal/g, c.v.=6.0%, and for *Equisetum limosum* $\bar{y}=3757 \pm 75.5$ cal/g, c.v.=7.0%.

Thus the highest value among the four species was that of *Phragmites communis*, and the least one — that of *Equisetum limosum*. The differences between *E. limosum* and the others and between *P. communis* and *Carex rostrata* are statistically significant. However, the differences between *S. lacustris* and *P. communis* or *C. rostrata* are insignificant.

In the other emergent plants, the calorific values of organic matter

were from 3548 cal/g in *Acorus calamus* to 4281 cal/g in *Sparganium ramosum*. The mean value for all the investigated emergent plants was 4006 cal/g, thus being the highest among all the plant groups (Fig. 2).

In the submerged plants with floating leaves, these values were from 3376 cal/g in *Sagittaria sagittifolia* to 3967 cal/g in *Nymphaea alba*. The mean value for the group amounting to 3688 cal/g (Fig. 2) was lesser than that for the emergent plants.

In the submerged plants, the mean values were from 1164 cal/g in *Chara sp.* to 3091 cal/g in *Elodea canadensis*. The mean value for the group was 2664 cal/g, thus being the least among all the plant groups (Table IV, Fig. 2).

5. DISCUSSION

It is necessary to estimate the calorific values of plant and animal organisms living in the water biocenoses, when the energy flow through such a biocenosis is studied. The following aquatic materials were hitherto investigated as to their calorific value: algae (e.g. Bartošova, Koniček 1967), plankton (e.g. Ostapeniya et al. 1967), macrophytes (e.g. Straškraba 1968), periphyton (e.g. Szczepański 1968, Szczepańska 1970), bottom sediments (e.g. Rybak 1969), animals (e.g. Prus 1970). Many authors give the calorific values calculated from the chemical composition using certain coefficients, which is a reason of considerable differences in the obtained results (Szczepański 1970). The more precise method of estimation of calorific value, used in the present investigations, is the burning of organic material in a calorimetric bomb.

The calorific value of dry weight of aboveground parts of *Phragmites communis* found in the present investigations (mean value 3988 ± 33 (confidence half-interval) cal/g) is similar to that found by Straškraba (1968) — 3870–4200 cal/g. Golley (1969) gave the value of 4220 cal/g for the high mountain forests of tropical zone, and Górecki (1965) — 4194 cal/g for lichens of coniferous forests of the taiga. The comparison of the three given values show their close energetic similarity, although the plant materials came from unlike environments. Mean calorific value of dry weight of *Carex rostrata* (3690 ± 77 cal/g) is similar to that of *Schoenoplectus lacustris* (3797 ± 96 cal/g) and to that given by Kaishio et al. (1961) for some species of meadow grasses (3500–3781 cal/g).

Organic matter content (85%) and calorific value of dry weight (3152 ± 61 cal/g) in *Equisetum limosum* are similar to that for the submerged plants with floating leaves (Table IV). The latter value is lesser than that given by Straškraba (1968) for *Equisetum* by about 500 cal/g.

The least calorific values of dry weight among the investigated species were that for *Chara sp.* (628 cal/g) and *Hippuris vulgaris* (980 cal/g). Straškraba (1968) gave markedly higher value for *Chara sp.* (1930–2080 cal/g) and also for *Lemna trisulca*. The differences have been probably caused by the presence of incrustations on the plants which cannot be removed without damages in tissue structure.

The ecological groups of macrophytes are discussed separately due to the found differences in their calorific values (Table IV). The calorific differences between the ecological groups were discussed in the papers by Straškraba (1968) and Szczepański (1970). Straškraba (1968) gave the following calorific values of dry weight: submerged plants — 3620 cal/g, emergent plants — 3950 cal/g, and submerged plants with floating leaves — 4010 cal/g (no data for floating plants).

The values found in the present investigation are different from that of Straškraba (1968): floating plants — 1526 cal/g, submerged plants — 1723 cal/g, submerged plants with floating leaves — 3140 cal/g, and emergent plants — 3621 cal/g. The differences in calorific values of dry weight between the ecological macrophyte groups can be caused by differences in shares of proteins, carbohydrates and fat in particular plant species, by dissimilarities in cell physiology related to environmental conditions, by differences in ash contents, etc. (Barashkov 1963).

The emergent plants were the main component of the total macrophyte biomass in the littoral of the investigated lakes (Table II). Their mean share in the total biomass amounted to 88%, and sometimes it was equal to 100% (e.g. lakes Jeglówek and Kopane). In the case of lower share of emergent plants (Lake Szurpily — 57%), the total biomass in the station was the least (327 g/m²). The shares of the other plant groups in the total biomass in the investigated stations were distinctly lower (0.7% — floating plants, 4% — submerged plants with floating leaves, 14% — submerged plants). It is because the littoral zone is not a typical environment for submerged and floating plants.

When arranging the list of values of the total biomass per 1 m² of littoral in a decreasing order (Table II), four groups of lakes can be distinguished, irrespective of their trophic type, with the following biomass values: 925.0–979.0, 574.4–661.2, 394.1–508.1, and 326.5–333.6 g dry wt./m².

However, the characteristics of water plants in a water body using a value of biomass per area unit of littoral is insufficient. The more complete characteristics of the role of a given group of organisms in the energy flow through water biocenosis can be obtained by a determination of the calorific value of biomass (Lieth 1968). In the case of macrophytes, the calorific value should be given per area unit of littoral (1 m²). It can be seen from the results given in Table VI that the highest

values are those for eutrophic pond-like lakes (Gulbin, Potopy), in which high values of the biomass of macrophytes (especially emergent plants) were found. In the other lakes, the calorific values per 1 m² are similar, with the exception of a-mesotrophic Lake Szurpiły (992 kcal/m²). They were emergent plants which effected the calorific values per 1 m² due to their great biomass and higher calorific value than in the other plant groups.

Organic matter content in the aboveground parts of *Phragmites communis* (94%) is the same as that given by Bernatowicz (1969) for reed of Mazurian Lakeland. The leaves of *P. communis* contain by about 6% less organic matter than the stalks (Table III), the difference being probably due to different physiological functions of these organs. The highest organic matter contents were found in *Phragmites communis* from monospecies stations in lakes Jęglówek and Kopane (deep and temperate eutrophic ones).

The organic matter contents in the particular species of emergent, submerged with floating leaves and submerged plants are similar to those given by Bernatowicz (1969).

In submerged with floating leaves and submerged plants, the organic matter contents are lesser than that in emergent plants (Table IV). The least values were found in submerged plants, and especially in *Chara sp.* (55.8%) and *Hippuris vulgaris* (39.6%), which can be due to the periphyton with great content of calcium carbonate, settled on the plants.

The dependence of calorific value on organic matter content is discussed in the papers by Ostapeniya et al. (1967), Lieth (1968), and Szczepański (1970).

The calorific value of organic matter in the particular macrophyte species were different. The highest value was found in emergent plants — 4006 cal/g on the average. Organic matter contents in *Phragmites communis* amounted to 89.5% on the average in leaves and 95.3% in stalks, while its calorific values were 4377 ± 79.1 cal/g in leaves and 4165 ± 77.4 cal/g in stalks. Thus the contents of organic matter is higher in stalks (by 5.8%) and the calorific value is higher in leaves (by about 212 cal/g).

The analyses of material coming from the Mazurian Lakeland carried out in our laboratory showed that there was about 7 times more of organic nitrogen in leaves of *Phragmites communis* than in stalks (Mikołajskie Lake — stalks 0.3%, leaves 2.25%, Lisunie Lake — 0.38% and 2.12%, respectively). Thus it results from the presented data that there is a qualitative difference in organic matter contents of leaves and stalks of *Phragmites communis*.

Among the emergent plants, it is only *Equisetum limosum* in which the organic matter content and calorific value are similar to those of submerged plants with floating leaves. The lowest calorific values of

organic matter were found in submerged plants and especially in *Chara sp.* and *Hippuris vulgaris* (Table IV).

The comparison of calorific values of organic matter in ecological macrophyte groups found in the present investigations with those of Straškraba (1968) is as follows:

	The present paper	Straškraba (1968) (cal/g)
Emergent plants	4006	4480
Submerged plants with floating leaves	3688	4770
Submerged plants	2664	4580

It can be seen that the values found in the lakes of the Szeszupa drainage area are lower than that given by Straškraba (1968) for Blatná fishpond system, S. Moravia. The differences are probably caused by different environmental and climatic conditions in both regions.

The results obtained in the present investigations allow to state the differences in calorific values of dry weight, organic matter contents and its calorific values between the particular macrophyte species, as well as ecological plant groups living in the lake littoral.

6. SUMMARY

The biomass, organic matter content and calorific values were measured in macrophytes living in the littoral of the lakes of the Szeszupa drainage area (the Suwałki-Augustów Lakeland). 14 lakes of different trophic types were investigated. It was found that macrophyte biomass per 1 m² of the littoral area in the investigated lakes was from 326.5 to 979.0 g/m². The highest share in the total biomass was that of emergent plants—87.8% on the average, and the lowest one—that of floating plants—0.7%.

The highest organic matter content was that of emergent plants—90.2% on the average, and the lowest one—of submerged plants (61.2%). The particular ecological plant groups were of different calorific value: emergent plants—3621 cal/g, submerged plants with floating leaves—3140 cal/g, submerged plants—1710 cal/g, and floating plants—1526 cal/g dry weight.

On the basis of the obtained results, calorific values of organic matter were calculated for the particular macrophyte species as well as for the ecological plant groups. The calorific value per area unit of the littoral was also estimated.

7. STRESZCZENIE

Określano biomasę, zawartość materii organicznej oraz kaloryczność makrofitów zasiedlających litoral jezior dorzecza Szeszupy. Badaniami objęto czternaście jezior o różnej trofii z terenu Pojezierza Suwalsko-Augustowskiego.

Stwierdzono, że biomasa makrofitów przypadająca na 1 m² stanowiska w badanych jeziorach wynosiła od 326,5 do 979,0 g. Największy udział w ogólnej biomacie badanych stanowisk miały helofity—średnio 87,8%, a najniższy rośliny pleustonowe—0,7%.

Najwyższą zawartość materii organicznej posiadały helofity—średnio 90,2%, natomiast najniższą elodeidy—61,2%. Poszczególne grupy ekologiczne posiadały

różną kaloryczność: helofity 3621, nympheidy 3140, elodeidy 1710 oraz rośliny pleustonowe 1526 cal/g suchej masy.

Na podstawie przeprowadzonych analiz określono również kaloryczność materii organicznej poszczególnych gatunków makrofitów i grup ekologicznych. Określono także ilość kilokalorii na jednostkę powierzchni litoralu, zawartych w zasiedlających go makrofitach.

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QUANTITATIVE CORRELATION OF TEMPERATURE AND RESPIRATORY RATE IN POIKILOTHERMIC ANIMALS

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ABSTRACT

The dependence of metabolism on temperature has been examined using five Black Sea species which had been previously acclimated to each temperature. In all cases this dependence can be described by the formula of Vant-Hoff and Arrhenius. The influence of temperature was stated to be increasing the respiratory rate and is characterized by coefficient μ ranging from 13 to 16 (mean 14) kcal · mol⁻¹. Q_{10} values, calculated for five degree intervals, decreased from 2.5 to 2.0 as the temperature arises. The literature data showed that there are differences in respiratory rates of animals living in the broad range of temperatures under natural conditions and these differences are within the limits foreseen by Vant-Hoff and Arrhenius' law. Basing on the results obtained, it can be stated that animals acclimate themselves to the life in low temperatures without increasing energy losses for cost of maintenance.

1. INTRODUCTION

In the past years, many works have been written about the influence of temperature on the metabolism of poikilothermic animals. In these investigations, the determination of the metabolic rate was limited to data obtained immediately after a change in the temperature conditions without any significant preliminary acclimation of the experimental animals. At the same time, as shown earlier (Ivleva 1972), the results of such measurements in most cases are of little use for a quantitative description of a temperature dependence of metabolic intensity, which is stipulated by the following reasons.

Changes in temperature cause corresponding changes in the rates of metabolic processes. The increase of metabolic intensity with an increase in temperature or the decrease with a fall in temperature reach maximum at the moment when conditions change, and the more the final temperature differs from the initial, the more significant they prove, as shown in Fig. 1. The initial period of acclimation is as a rule extremely unstable and the metabolic rates of animals undergo many rises and falls which gradually smooth during the completion of the adaptation process. More or less stable levels, which have been established at a high temperature prove lower in comparison with the indications during the first hours; at low temperatures—the initial depression is deeper as compares with the next.

The duration of the period of acclimation at each given temperature is extremely changeable and is determined by the physiological peculiarities of the type and the previous conditions of life. The temperature interval, in the bounds of which the measurements are conducted, is also of importance. In the region of high temperatures the acclimation ends quite fast, usually in a few hours time. At a low temperature the process is prolonged for many days as in these conditions all the life functions in the organism proceed with the least intensity.

It is thus obvious that the dependence of the metabolic rates on temperature,

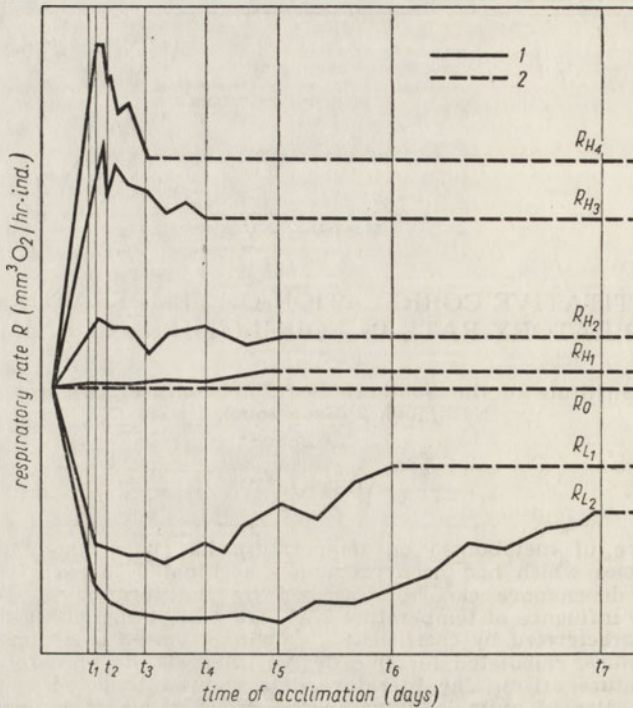


Fig. 1. A scheme of the changes of respiratory rate (R) in the process of acclimation of animals to different temperatures. 1 — the acclimation period, 2 — the post-acclimation period. R_0 — respiratory rate at the initial temperature, R_{H_1} – R_{H_4} — respiratory rates at the higher temperatures than the initial one, R_{L_1} – R_{L_2} — respiratory rates at the lower temperatures than the initial one.

established in the gradient of temperatures on the animals with an unfinished acclimation will each time be substantially different, depending in which moment of the acclimation process (t_1 – t_7 , see Fig. 1) the readings are taken.

The second reason why the use of acute or sub-acute experiments does not allow for an objective evaluation of the existing relation between the metabolic rate and the temperature is that the basic principle of correct analysis is upset (the principle of the comparison of equivalent values). The metabolic rates of animals, measured in the temperature gradient, are not comparable until at each given temperature exactly the same stage of an "established level" is not attained.

Based on these considerations, methods used in most of the published works (a survey of them is given in the works of Ivleva, Popenkina 1968, Ivleva 1972) can scarcely be considered correct and sufficiently reliable while determining the dependence of metabolism upon temperature.

The question of the influence of temperature on the rate of energetic metabolism of aquatic poikilothermic animals, presenting a large theoretical interest, is at the moment also exploited for practical purposes. For calculations of biological production in aquatic reservoirs of different geographical regions and in seasonal aspect it is necessary to learn rather about the true rates, characteristic for animals living in different temperature conditions and not about periodic oscillations of metabolic rates at an abrupt temperature change.

The aim of the present work was to analyse the temperature relations of metabolic rates of poikilothermic sea animals, under the following conditions:

1. The investigations were conducted in a wide range of temperatures in the bounds of the biokinetical zone;
2. The animals were fully acclimated to each temperature of the experiments;
3. The animals of equal sizes were used in the experiments;
4. The measurements were repeated several times in order to obtain a reliable average value and evaluate it statistically.

2. MATERIAL AND METHODS

The work was conducted in 1966–1970. It was based upon materials obtained from the shores of the Crimean peninsula in the region of Sevastopol. As an object of the investigations served five common species of Black Sea invertebrates which are also widely distributed beyond the bounds of the Black Sea: *Actinia equina* L., *Nereis diversicolor* O. F. Müller, *Modiola adriatica* Lamarck, *Palaemon adspersus* Rathke, *Branchiostoma lanceolata* L.

M. adriatica and *B. lanceolata* were collected in the autumn at a depth of 20–25 m and at a water temperature of 14–15°C. *A. equina* and *N. diversicolor* were collected at the surface of the water at a temperature close to 17°C. Also the individuals of the winter population of *Nereis diversicolor* were examined. They were obtained from bottom deposits taken from a depth of 0.7–1.2 m at a temperature of 6.5–7.0°C. *P. adspersus* was collected in the beginning of summer at a depth of 5–8 m and a water temperature of 15–18°C.

The collected animals were strictly classified according to size. For each type, any size group (represented in the collection by the largest number of individuals) was chosen and this group later took part in the experiments.

Before beginning the measurements of metabolism, the animals were kept at the temperature of the experiment until the moment of completion of the acclimation process. The acclimation of *A. equina* and *N. diversicolor* took place in thermostat chambers, where the fluctuations of the chosen temperature did not exceed 0.5°C. The animals were placed into glass vessels, the bottoms of which were covered by a thin layer of gravel and sea water. Apart from this, for the nereids, short glass tubes were placed in the vessels. The worms crawled eagerly into the tubes, using them as burrows. The water in the crystalizers was changed everyday. Fresh sea water flowed through a siphon from tanks set in each chamber and consequently, having the same temperature at which the acclimation of the animals proceeded.

Up to the time of the experiment, *P. adspersus*, *M. adriatica* and *B. lanceolata* were kept in flowing water in aquariums with a thermoregulating mechanism, allowing the maintaining the chosen temperature with an accuracy of 0.5°C.

In most cases the acclimation was conducted at five temperatures 5, 10, 15, 20, 25°C. For *N. diversicolor* measurements were additionally conducted at 27°C and for *P. adspersus* — at 28 and 30°C.

The period of acclimation was determined in correspondence with the data obtained in the previous investigations (Ivleva, Popenkina 1968, Ivleva 1972). At a temperature of 25–30°C the measurements of metabolism were begun 1–2 days after acclimation started. In low temperature the animals were kept in experimental conditions for not less than 5 days for *N. adriatica* and nearly two to three weeks for all the remaining species. The preliminary acclimation of *N. diversicolor* of the winter population at all temperatures lasted for 20–25 days.

During the whole period of observation, *A. equina*, *N. diversicolor* and *P. adspersus* were regularly fed with live *Enchytraeus albidus* and with gonads of *Mytilus*. *M. adriatica* and *B. lanceolata* consumed plankton, which entered the aquariums with water.

The measurements of standard respiratory rate were conducted by the method of closed respirometers. The volume of the respirometer was chosen according to the size of the animal. The respirometers were filled with filtered, aerated water of the same temperature, at which the acclimation had proceeded. One animal was placed into each respirometer. The exposure time was changed depending on the temperature of the experiment: at 25–30°C it was equal to 1.5–2 hr, at 5°C it lasted 16 hr. The water after exposure contained 30–40% less oxygen than the water before exposure. The oxygen content was determined by Winkler method. The oxygen consumption was calculated using the oxygen content in experimental and control respirometers. Dry weight of animals (at 105°C) was determined after each experiment.

The experiments were conducted in thermostat-controlled conditions. During the time of exposure the fluctuations of the temperature did not exceed 0.1°C.

The measurements of respiration were repeated 5–20 times at each temperature. The respiration values are given in mm³ per hour per one individual.

3. RESULTS

WEIGHT OF ANIMALS

It is known that the respiration rate of animals is a function of their body weight. So it is important to conduct all the measurements of metabolism using material with the highest possible conformity of weight. It is not always easy to select animals of equal weight, even from between individuals of one species. For this reason, a visual selection of animals of approximately one size, conducted before the experiment, was corrected by determining the exact dry weight after it ended.

Respiratory data, referring to a strictly determined weight group were selected from the total results: *A. equina* with a dry body weight from 250 to 280 mg, *N. diversicolor* — from 40 to 50 mg, *M. adriatica* with a dry weight of soft body parts from 50 to 70 mg, and *B. lanceolata* — from 10 to 15 mg. The dry weights of the animals used in the experiments, are characterized in Table I.

RESPIRATORY RATES AT DIFFERENT TEMPERATURES

The respiratory rates at different temperatures were determined by averaging the several parallel measurements. The parameters of the samples are shown in Table II.

The overall results include the data of measurements conducted at the initial water temperature of the sea at the time when the animals were collected. In this case the adaptation of the animals to the corresponding conditions took place in a natural situation; for *N. diversicolor* at 6.5 and 16.5°C, *M. adriatica* at 14°C and *P. adspersus* at 15°C.

Irrespective to the comparatively small weight variations for each species, the variation of respiratory results was rather high. A similar situation is not exceptional and has been noticed by most investigators, studying the respiration of invertebrates.

The dispersion of respiratory rates for individuals, adapted to temperature of the habitat, is lower than that of individuals acclimated in the laboratory. This points to a significant individual variability of the adaptational features of the animals, which increases the already large oscillations in metabolic rates.

A considerable dispersion in the respiratory rates was sometimes caused by a large dispersion of body weight, as can be seen while comparing the data of Table I and II.

A graphical presentation of the results of respiratory rate measurements in the temperature gradient gives a definite notion about the functional dependence of the studied values (Fig. 2–6).

On a semi-logarithmic coordinate graph, when the reverse temperature values, expressed in degrees of the Kelvin scale, are plotted on the abscissa and the logarithms of the metabolic rates are plotted on the

Table I. Variation of dry weights of five animal species used in respiration experiments

Temp. (°C)	n	Mean dry wt. (mg) \bar{w}	Standard error (mg) $s_{\bar{w}}$	95% confidence limits $t_{0.05} \cdot s_{\bar{w}}$	Coefficient of variation (%)
<i>Actinia equina</i>					
5	6	259.87	3.77	9.68	3.55
10	8	272.14	3.02	7.13	3.14
15	6	268.54	2.51	6.46	2.29
20	6	266.86	2.18	5.59	1.99
25	5	277.02	2.52	6.94	1.82
<i>Nereis diversicolor</i>					
5	12	44.58	0.92	2.03	7.14
6.5	7	45.43	1.15	2.81	6.68
10	14	43.25	0.53	1.17	4.62
16.5	13	46.57	0.53	1.15	4.10
20	14	44.46	0.66	1.43	5.55
25	11	43.93	0.62	1.38	4.69
27	5	45.75	1.55	4.30	7.58
<i>Modiola adriatica</i>					
5	16	59.48	1.23	2.61	8.28
10	18	58.70	1.53	3.21	11.05
14	16	59.34	1.30	2.77	8.78
15	5	60.22	1.83	5.08	6.79
20	25	57.31	1.03	2.12	8.96
25	12	60.77	1.83	3.92	11.64
<i>Palaemon adspersus</i>					
5	6	93.85	3.07	5.90	8.01
10	15	91.03	1.53	3.22	7.11
15	6	89.57	4.79	12.32	13.11
20	11	89.46	1.86	4.15	6.91
25	10	87.38	1.97	4.46	7.15
28	5	92.95	3.41	8.78	8.99
30	6	94.01	2.49	6.40	7.03
<i>Branchiostoma lanceolata</i>					
5	13	12.71	0.60	1.31	16.90
10	13	13.01	0.40	0.86	10.97
15	12	12.36	0.53	1.21	14.72
20	16	12.66	0.47	1.00	14.70
25	7	13.00	0.43	1.06	8.80

ordinate, the dependence of metabolism upon temperature can be satisfactorily represented by a straight line. This means that the functional dependence between the respiratory rate and temperature agrees with the law of Vant-Hoff and Arrhenius and can be approximated by the equation:

$$V = V_0 \cdot e^{-\frac{\mu}{R} \cdot \frac{1}{T}}$$

where: V — the respiratory rate, R — gas constant = 1.986 cal · mol · degree⁻¹, T — absolute temperature (°K), V_0 — coefficient having the same

Table II. Variation of the respiratory rates at different temperatures in five animal species

Temp. (°C)	n	Mean respiratory rate (mm ³ /hr · ind.) $\frac{R}{R}$	Standard error s_R	95% confidence limits $t_{0.05} \cdot s_R$	Coefficient of variation (%)
<i>Actinia equina</i>					
5	6	18.79	1.14	2.94	14.90
10	8	29.69	2.73	6.45	25.97
15	6	49.72	5.78	14.85	28.45
20	6	78.38	6.18	15.89	19.31
25	5	97.11	6.99	19.41	16.10
<i>Nereis diversicolor</i>					
5	12	8.93	0.49	1.08	19.08
6.5	7	11.02	0.37	0.92	8.87
10	14	14.65	0.92	2.00	23.59
16.5	13	25.36	1.17	2.55	16.72
20	14	34.97	1.96	4.24	21.00
25	11	47.80	1.19	2.65	8.24
27	5	57.41	2.27	6.30	8.85
<i>Modiola adriatica</i>					
5	16	4.83	0.32	0.69	26.71
10	18	7.47	0.59	1.24	33.41
14	16	11.21	0.72	1.55	25.84
15	5	12.94	1.90	5.26	32.78
20	25	22.21	1.07	2.22	24.12
25	12	30.83	2.99	6.44	37.57
<i>Palaemon adspersus</i>					
5	6	32.88	2.94	7.57	21.91
10	15	51.85	2.87	6.05	23.47
15	6	89.57	4.79	12.32	13.11
20	11	115.69	8.10	18.05	23.22
25	10	153.03	11.25	25.45	23.25
28	5	221.39	15.60	40.11	17.26
30	6	231.33	18.57	45.44	24.24
<i>Branchiostoma lanceolata</i>					
5	13	1.51	0.20	0.43	47.53
10	13	2.74	0.27	0.59	35.85
15	12	4.06	0.39	0.84	32.97
20	16	6.43	0.68	1.45	42.28
25	7	9.50	1.27	3.12	35.50

measure as V , μ — „temperature characteristic”, i.e., the coefficient determining the slope of the straight line and quantitatively expressing the accelerative influence of temperature.

Numerical value of coefficients V_0 and μ (Table III) obtained by the least squares method were used for the calculation of each curve.

In Figures 2–6 showing the Arrhenius scale experimental points lie sufficiently near along the calculated curve and small deviations which occur in some cases are reflected in Table III by the index S_0^2 (the index S_0^2 after Nalimov 1960).

The accelerating influence of temperature transmitted by the coeffi-

coefficient μ has proved sufficiently near for all species: the value of μ changed within the bounds of 13–16 kcal · mol⁻¹. These values served as basis for quantitative evaluation of Q_{10} —the coefficient temperature more convenient for practical purposes.

Fig. 2. The change of respiratory rate in relation to temperature in *Actinia equina* with a dry body weight of 250–280 mg. The abscissa—Arrhenius' scale—the inverse value of temperature, counted from absolute zero

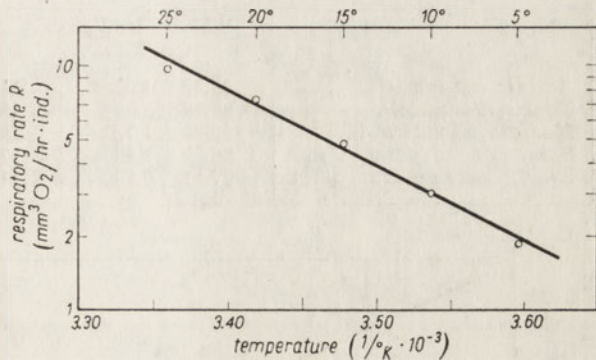


Fig. 3. The change of respiratory rate in relation to temperature in *Nereis diversicolor* with a dry body weight of 40–50 mg. The abscissa as in Fig. 2

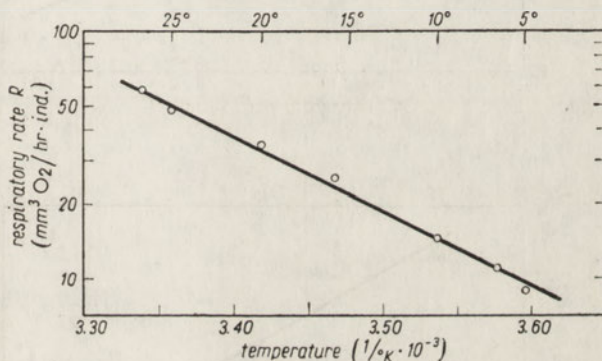


Fig. 4. The change of respiratory rate in relation to temperature in *Modiola adriatica* with a dry body weight of 50–70 mg. The abscissa as in Fig. 2

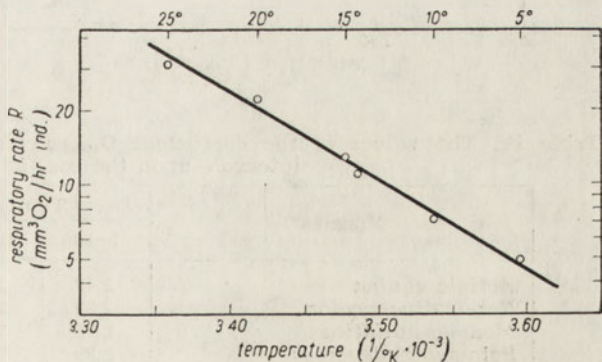


Table III. The values of the coefficients $\ln V_0$ and μ in the equation expressing the connection between respiration and temperature in five animal species. S_0^2 —unbiased estimation of S. D. of measurement points from the approximated curve

Species	Mean \pm S. E.	Mean \pm S. E.	S_0^2
	$\ln V_0 \pm s_{\ln V_0}$	$\mu \pm s_\mu$	
<i>Actinia equina</i>	28.89 \pm 1.92	14.222 \pm 1.098	0.011
<i>Nereis diversicolor</i>	26.08 \pm 2.99	13.156 \pm 1.726	0.054
<i>Modiola adriatica</i>	30.00 \pm 1.73	15.818 \pm 0.998	0.009
<i>Palaemon adspersus</i>	26.97 \pm 1.72	12.943 \pm 1.006	0.019
<i>Branchiostoma lanceolata</i>	27.11 \pm 0.59	14.778 \pm 0.338	0.001

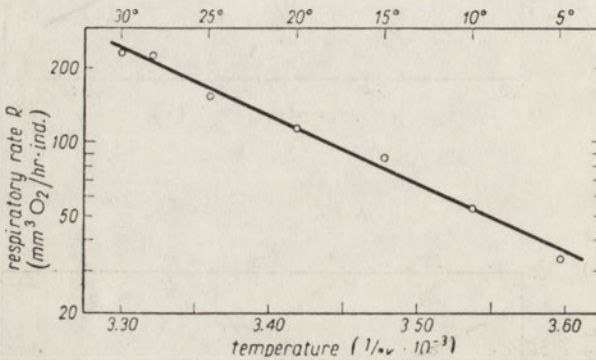


Fig. 5. The change of respiratory rate in relation to temperature in *Palaemon adspersus* with a dry body weight of 80–100 mg. The abscissa as in Fig. 2

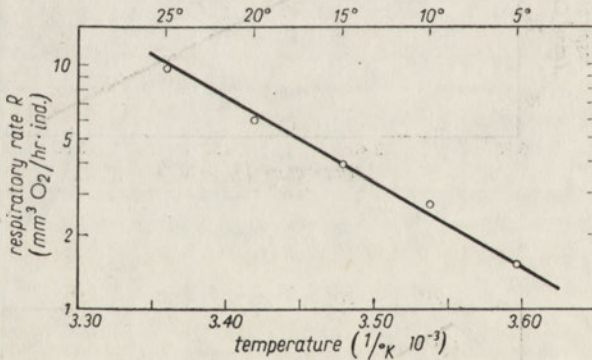


Fig. 6. The change of respiratory rate in relation to temperature in *Branchiostoma lanceolata* with a dry body weight of 10–15 mg. The abscissa as in Fig. 2

Table IV. The values of the coefficient Q_{10} calculated for different temperature intervals upon the coefficient μ

Species	Temperature range (°C)			
	5-10	10-15	15-20	20-25
<i>Actinia equina</i>	2.49	2.41	2.34	2.27
<i>Nereis diversicolor</i>	2.32	2.25	2.19	2.14
<i>Modiola adriatica</i>	2.75	2.66	2.57	2.49
<i>Palameon adspersus</i>	2.29	2.23	2.17	2.11
<i>Branchiostoma lanceolata</i>	2.58	2.49	2.42	2.35

The change from parameter μ to Q_{10} is carried out according to equation:

$$\log Q_{10} = 2.187 \frac{\mu}{T_1 \cdot T_2}$$

The results of calculations carried out for five degree intervals are compiled in Table IV.

According to Vant-Hoff and Arrhenius coefficient Q_{10} in all cases changed within limits of 2–3 and this value systematically diminished as temperature increased.

The values of the coefficient Q_{10} for the species examined in the same temperature intervals proved sufficiently close and this allowed to obtain data to calculate the average value of the coefficient μ and the average values of Q_{10} (Table V).

Table V. Variations of coefficient values μ and Q_{10}

Coefficient		\bar{X}	$s_{\bar{X}}$	$t_{0.05} \cdot s_{\bar{X}}$	Coefficient of variation (%)
$\bar{\mu}$		14.183	0.530	1.517	8.30
\bar{Q}_{10}	5-10	2.49	0.09	0.236	7.63
	10-15	2.41	0.08	0.222	7.39
	15-20	2.34	0.07	0.205	7.11
	20-25	2.27	0.07	0.197	6.87

4. DISCUSSION

At present the opinion prevailing in literature is that temperature changes of the respiratory rates of poikilotherms cannot be described by Arrhenius' function since in the majority of works an unstable character of these changes is shown.

Without analysing the reasons determining this situation many authors consider it more reliable to select new mathematical expressions which, from the point of view of each author, show more precisely the relation between respiration and temperature. In this relation the studies of Bělehrádek (1930, 1935, 1957), Heintzen (1958), Krüger (1961, 1963, 1964), Mc Laren (1963) and others are well known. Krogh's "normal curve" had the greatest recognition (Krogh 1914, 1916). The possibility of using it for practical purposes has been substantiated by Winberg (1956, 1968) and then by Sushchenya (1969) who analysed the influence of temperature upon the respiratory rate of fish and crustaceans only on the basis of data to be found in the literature. As the overwhelming majority of this data was obtained from animals that had not undergone preliminary

acclimation to the temperatures of measurement it is obvious that the results proved to be similar to Krogh's generalized "normal curve" which was also established on the basis of the results of acute experiments.

If studying the influence of temperature upon the respiratory rate of poikilotherms one uses another method and in each case measures the metabolism of animals after the process of acclimation has been accomplished, one can see that in the limits of the biokinetical zone, the dependence of metabolism on temperature is subject to the law of Vant-Hoff and Arrhenius and can be quantitatively analysed with sufficient accuracy.

The methodical approach to this problem had been presented earlier (Ivleva, Popenkina 1968, Ivleva 1972) and had been shortly explained at the beginning of the present paper. Now we again tried to appraise from the point of view of our notions the examples reported in literature and to examine how the conducted observations relate to the problem of temperature adaptations of poikilotherms.

Looking for data in literature for this purpose one has to state with regret that the enormous quantity of accumulated material is useless for the appropriate analysis. In spite of the fact that the measurements of metabolism were basically conducted in acute or near to acute observations, the respiratory rate of animals is determined at 2-3 temperatures, which certainly is not sufficient for establishing the quantitative regularity of kinetics of the metabolism process. Often this data cannot be supplemented or compared with data of other authors obtained on the same or similar species at other temperatures, as the authors do not indicate the exact weight of experimental animals but confine themselves to presenting the relative respiratory rates (R/W). In many cases the comparisons are done on the basis of single measurements and on animals which considerably differ in sizes. Finally in published works all the results are given in graphs and the necessary readings can be obtained only very approximately.

Among investigations in question it is necessary to mention the results of measurements of respiratory rates of Cladocera and Copepoda carried out by Shcherbakov (1935) and Marshall et al. (1935). Though their studies were conducted without any special control of the degree of completion of the acclimation process, the dependence of the metabolic rates on temperature can be satisfactorily presented by the function of Vant-Hoff and Arrhenius (Fig. 7 and 8, in both cases semi-logarithmic coordinates were used) possibly because this group of animals is adapted to great range of temperatures as in natural conditions they show considerable vertical migrations.

According to data of the authors mentioned, coefficients μ and Q_{10} are calculated for description of the curves. The results of the calcu-

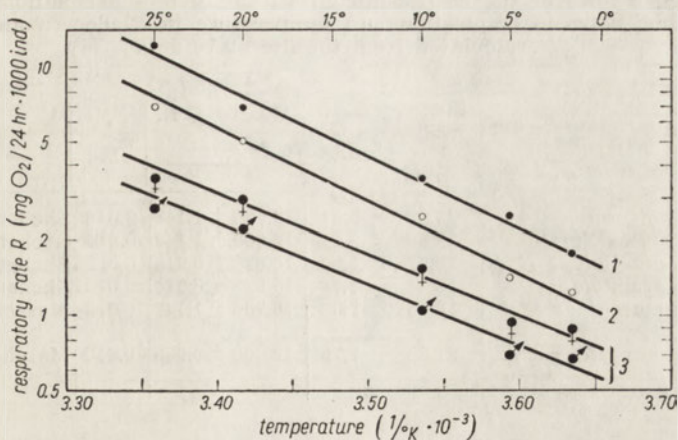


Fig. 7. The change of respiratory rate in relation to temperature in *Cyclops strenuus* (1), *Daphnia longispina* (2), and male and female *Diaptomus graciloides* (3). The abscissa as in Fig. 2. (after Shcherbakov 1935)

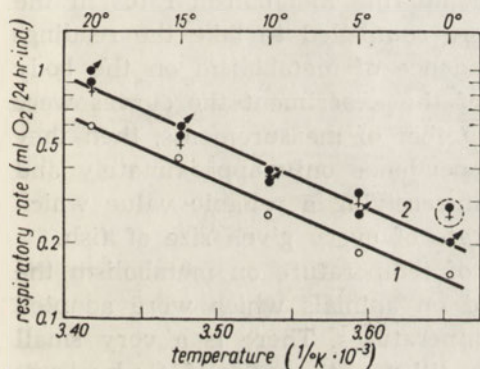


Fig. 8. The change of respiratory rate in relation to temperature in copepodites (1) and male and female *Calanus finmarchicus* (2). The abscissa as in Fig 2 (after Marshall et al. 1935)

lations (Table VI) show that value of coefficient μ was changing from 11 to 13 kcal · mol⁻¹ and in general was proved quite near to the one determined during our experiments. 95% confidence limits of the average value μ deduced for nine species of animals according to Tables III and VI is equal to 12.750 ± 1.193 kcal · mol⁻¹.

Quite satisfactory results were obtained in the case of the analysis of the materials of Taliev, Koryakov (1947) who had studied the respiratory rates of Baikal Cottoidei (*Cottocomephorus grewingki* and *Batrachocottus baicalensis*) with the gradual increase of temperature (Fig. 9). In spite of the limited range of temperatures (0–10°C) these data are also of interest and can be used for finding the coefficients when characterizing the curves, because they are based on the measurements taken at 6–8 different temperatures.

Table VI. The values of the coefficients in V_0 and μ in the equations expressing the connections between respiration and temperature in Cladocera and Copepoda calculated from the literature data

Species	Mean \pm S. E. $\ln V_0 \pm s_{\ln V_0}$	Mean \pm S. E. $\mu \pm s_{\mu}$	S_0^2	Paper
<i>Daphnia longispina</i>	23.00 \pm 2.01	12.536 \pm 1.148	0.018	Shcherbakov 1935
<i>Cyclops strenuus</i> ♀♀	22.50 \pm 2.01	12.000 \pm 1.144	0.018	Shcherbakov 1935
<i>Diaptomus graciloides</i> ♂♂	18.87 \pm 1.60	10.628 \pm 0.913	0.012	Shcherbakov 1935
<i>Diaptomus graciloides</i> ♀♀	19.14 \pm 1.48	10.622 \pm 0.844	0.010	Shcherbakov 1935
<i>Calanus finmarchicus</i> ♀♂	18.15 \pm 1.02	10.750 \pm 1.142	0.013	Marshall et al. 1935
<i>Calanus finmarchicus</i> c. v.	21.35 \pm 1.75	12.900 \pm 0.988	0.010	Marshall et al. 1935

There is no doubt that the investigations of collaborators of prof. F. Fry (Fry, Hart 1948, Job 1955, Beamish 1964) who always conducted the measurements on the acclimated material, should represent great value for establishing the temperature dependence of metabolism of fish. However fish used in the experiments were of different size and for the purpose of comparing metabolism rates in the temperature gradient the authors were compelled to take the readings from the curves reflecting the dependence of metabolism on the body weight. Since at every temperature of the experiment the curves were established on the basis of a small number of measurements, then they reflect the general aspect of this dependence only approximately and could not be used for the purpose of receiving a reliable value which characterizes the average metabolic rate of every given size of fish.

For the analysis of the influence of temperature on metabolism the most important are studies conducted on animals which were adapted in natural conditions to different temperatures. There is a very small number of such research works and up till now the work of Schlander et al. (1953) seems to be the only example of a serious approach to solve this problem.

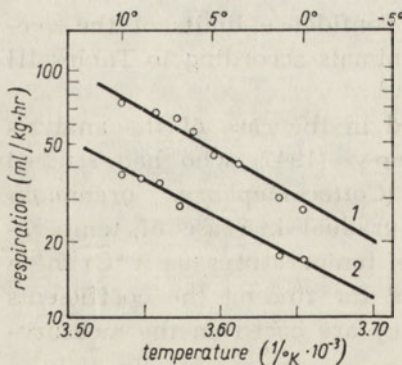


Fig. 9. The change of respiratory rate in relation to temperature in *Cottocomephorus grewingki* (1) and *Batrachocottus baicalensis* (2). The abscissa as in Fig. 2 (after Taliev, Koriakov 1947)

After having done a great number of measurements of respiration rates of animals that live all the time in arctic and tropical regions, these authors obtained very important data showing that at 0°C the level of metabolism of arctic animals is roughly 10 times lower than the metabolism of tropical species living at 30°C. This difference has proved to be exactly the same as that supposed by the Vant-Hoff and Arrhenius law. It should be here stressed that the same difference (10.7 times) is obtained if for the purpose of calculations the coefficient μ equal 13–14 kcal · mol⁻¹ is used; this coefficient has been established in the present paper experimentally.

Scholander et al. (1953) did not pay enough attention to the results obtained by them and they continued further discussions on the basis of calculations done according to the Krogh's "normal curve". In this way the hypothetical level of metabolism has been established, which could have been revealed by tropical animals if they were kept in water of 0°C. If temperature was lowered from 30 to 0°C their metabolism should diminish 43 times. As in reality it diminished only 10 times the authors found it possible to explain this difference by the ability of poikilotherms to compensate the unfavourable influence of low temperatures by the increase of the metabolism level.

The data given by Scholander et al. (1953) were discussed in many works and survey (Rao, Bullock 1954, Bullock 1955, Precht et al. 1955, Prosser 1955, 1958, Winberg 1956, 1968, Fry 1958, Wolvekamp, Waterman 1960, Prosser, Brown 1962) but in no single case was there any doubt shown concerning the correctness of the conclusion drawn, perhaps for this reason that long before the works of Scholander et al. (1953) this view was supported by Krogh (1916), Zeuthen (1947) and other authors who thought that the active life of poikilotherms in low temperatures are caused only by a higher level of their metabolism.

The experiments of Scholander et al. (1953) were repeated by Ikeda (1970). The author examined the respiratory rate of plankton animals living in different regions of the Pacific Ocean. Ikeda (1970), unlike Scholander et al. (1953), did not concentrate his attention on definite taxonomic groups which in different conditions of temperature are represented by closely related species but he measured metabolism of these animals which had fallen in his plankton net. As the results of this, about 100 tests were conducted on 77 species which belong to 15 higher taxonomic categories. In this way there were 1–2 measurements for each species and if we take into consideration that experimental animals in different regions of the ocean differed as regards their body weight it becomes clear how complicated it was in this case to draw conclusions on the effect of the differences of temperatures on the levels of metabolism. Ikeda (1970) put the animals

of all taxonomic groups together and obtained a general dependence of metabolism on the body weight for each temperature (8, 17 and 29°C). In spite of the fact that all the figures were calculated in relation to the dry weights and even in relation to the quantity of ash in the dry substance of body, the dispersion of points in each case proved to be so large and the slope of curves so diverse that it was impossible to make any proper comparison. For this reason we turn again to the experiments of Scholander et al. (1953) to appraise the facts obtained in our experiment and indirectly in natural conditions. These facts show that there is no increase of the level of energy metabolism when the animals adapt themselves to cold. The measurements of metabolism rate in low temperatures agree with the calculations according to Vant-Hoff and Arrhenius. This means that they are the respiratory rates, characteristic for animals under natural conditions (or after the acclimation of animals in a laboratory), which should be taken into account when qualitatively determining the dependences between temperature and respiratory rates. Only those mathematical formulae describing the dependences in question can be used which are in accordance with the mentioned regularity, i.e. they reflect factual relationships in natural conditions.

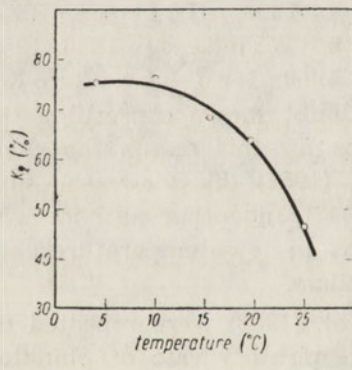


Fig. 10. The degree of usage of the assimilated food for growth (K_2) in *Nereis diversicolor* at different temperatures (see also Table VII)

At present the thesis that all animals are well adapted to the conditions in which they exist and particularly to the surrounding temperature does not raise any doubt. The question how this adaptation proceeded appears however to be controversial. On the basis of the above given considerations it should be assumed that the adaptation of animals to the life in low temperatures took place without increasing losses of energy for respiration.

If life in cold climate proved to be possible under the condition that the animals had acquired the ability to increase the rate of energy metabolism, then this increase must have affected the general balance of energy and was inevitably connected with the decrease of "plastic

Table VII. The mean values of coefficient K_2 in *Nereis diversicolor* cultivated at different temperatures

Temp. (°C)	n	$K_2 \pm s_{K_2}$	Coefficient of variation (%)
4.1	3	75.3 ± 0.8	1.8
10.3	3	76.2 ± 2.1	4.7
15.7	3	68.5 ± 2.7	6.7
19.6	3	63.8 ± 2.4	6.6
25.0	3	46.5 ± 3.1	11.6

metabolism", e.g. growth. Together with this, the advantage of animals which adapted themselves to life at constantly low temperatures consists in their ability to grow and multiply in unfavourable conditions. Consequently the adaptation to the cold should have proceeded by increasing the expenditures of energy upon these processes.

This assumption is proved experimentally. When studying temperature changes of the parameters of the energy balance of *N. diversicolor*, which normally lives in a broad range of temperatures it was ascertained (Ivleva 1970, 1971) that the relation between the losses of energy for cost of maintenance and growth does not remain constant.

The value of the coefficient K_2 (‰) ($K_2 = P / (P + R)$) where P — production, R — cost of maintenance), which shows the degree of utilizing of the assimilated food for growth proves to be the highest in low temperatures (Fig. 10, Table VII).

The increase of temperature stimulated in greater degree the katabolic processes and in a lesser degree the anabolic processes as a result of which the utilization of energy for growth steadily diminished and proved to reach minimum at 25°C.

Further development of investigations in this direction will help to understand the specific character of metabolism of poikilothermic animals stipulating the possibility of their existence in extreme temperature conditions.

Acknowledgements

The author is very grateful to the senior laboratory assistant, M. I. Popenkina for her skilled assistance.

5. SUMMARY

The dependence of metabolism on temperature has been examined using Black Sea *Actinina equina* L., *Nereis diversicolor* O. F. Müller, *Modiola adriatica* Lamarck, *Palaemon adspersus* Rathke and *Branchiostoma lanceolata* L., which had been beforehand acclimated to each temperature.

In all cases the functional dependence of metabolism rates on temperature

was subordinated to Vant-Hoff and Arrhenius' law and could be expressed quantitatively. The accelerating influence of temperature, characterized by coefficient μ varied with different species of animals from 13 to 16 kcal·mol⁻¹ and on the average was equal to 14 kcal·mol⁻¹. The value of temperature coefficients (Q_{10}), calculated for five degree intervals regularly decreased from 2.5 to 2.0 according to the increase of temperature. The literature data analysed by the author have shown that the differences in metabolism rates of animals living in natural conditions at different temperatures are also within the limits foreseen by Vant-Hoff and Arrhenius' law. It has been noted that the opinion firmly established in the last years according to which poikilothermic animals show certain temperature independence of functioning by increasing or lowering metabolism, cannot be regarded as well-founded, as it is based on data which describe the initial reaction of animals at the moment of change of their temperature conditions.

The facts which have been obtained during experiments and in natural conditions show that the adaptation of animals to life at low temperatures took place without increased energy losses for cost of maintenance.

6. РЕЗЮМЕ

Исследована температурная зависимость обмена у черноморских *Actinia equina* L., *Nereis diversicolor* O. F. Müller, *Modiola adriatica* Lamarck, *Palaemon adspersus* Rathke и *Branchiostoma lanceolata* L., предварительно акклиматизированных к каждой температуре.

Во всех случаях функциональная зависимость скоростей обмена от температуры подчинялась закону Вант-Гоффа и Аррениуса и могла быть выражена количественно. Ускоряющее влияние температуры, характеризуемое коэффициентом μ у разных видов животных изменялось от 13 до 16 тыс. кал. моль⁻¹ и в среднем равнялось 14 тыс. кал. моль⁻¹. Величина температурных коэффициентов (Q_{10}), рассчитанная для пятиградусных интервалов, по мере увеличения температуры закономерно снижалась от 2,5 до 2,0. При анализе литературных данных показано, что различия в скоростях обмена у животных, существующих в природных условиях при разной температуре, также лежат в пределах, предусмотренных законом Вант-Гоффа и Аррениуса. Отмечено, что утвердившееся в последние годы мнение о способности пойкилотермных животных проявлять определенную температурную независимость функционирования путем повышения или снижения обмена, не может считаться обоснованным, поскольку базируется на данных, характеризующих первичную реакцию животных в момент изменения температурных условий. Факты, полученные в экспериментальных исследованиях и природной обстановке, свидетельствуют о том, что адаптация животных к жизни при низких температурах проходила без повышения трат энергии на окислительный метаболизм.

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RESPIRATION OF ANTARCTIC AMPHIPODA *PARAMOERA WALKERI* STEBBING DURING THE WINTER SEASON

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ABSTRACT

Respiration of Antarctic Amphipoda *Paramoera walkeri* Stebbing belonging to the sub-fast ice community in the coastal zone of Antarctica was investigated. Measurements of oxygen consumption by *Paramoera walkeri* were carried out in constant-pressure volumetric respirometers at temperatures of -1.9 , 0.0 and 2.0°C . Increase of temperature causes rapid raise of oxygen demand: Q_{10} values for temperature ranges of $-1.9-0.0$, $0.0-2.0$ and $-1.9-2.0^{\circ}\text{C}$ were 15.9 , 4.6 and 8.6 , respectively. Dependence of oxygen consumption R on body weight W in *Paramoera walkeri* can be expressed by regression $R_{(-1.9^{\circ}\text{C})} = 0.99 \cdot W^{0.71}$. The value of the regression exponent decreases as temperature increases.

1. INTRODUCTION

A question of dependence of metabolism of poikilothermic animals on environmental temperature has an abundant literature (Bělehrádek 1930, Precht 1958, Vernberg, Vernberg 1969, Ivleva 1972, and others). However, such dependence in animals living in extremal thermic conditions, i.e. in polar regions, is relatively less known.

Most studies on influence of low temperatures on metabolism of poikilothermic animals were carried out on arctic species (Scholander et al. 1953 a, b, 1957, Krog 1954, Kanwisher 1959, and others). Similar papers for Antarctica are less numerous (Wohlschlag 1960, Armitage 1962, McWhinnie 1964). Armitage (1962) investigated the effect of temperature on oxygen demand in Amphipoda *Orchomonella chilensis* (Heller) during Antarctic summer. This effect, in the range of survival temperatures of that species, was rather low: the value of Q_{10} coefficient amounted to less than 2.

It seems to be interesting which is the influence of changes of environment temperature on animal metabolism during Antarctic winter, i.e. when an organism has been exposed to low and constant temperature (ca. -1.8°C) for a long time (more than half a year).

For such studies a suitable object is Amphipod *Paramoera walkeri* Stebbing (Pontogeneidea). It is a circumpolar species, inhabiting the coastal zone of Antarctic seas; its biology was described in details in Rakusa-Suszczewski (1972).

2. MATERIAL AND METHODS

Studies on the influence of temperature on oxygen demand in *Paramoera walkeri* Stebbing were carried out in the Soviet Antarctic station Molodezhnaya ($67^{\circ}40'\text{S}$, $45^{\circ}50'\text{E}$, Enderby Land, Eastern Antarctica) during the works of the

First Polish Scientific Group in Antarctica within the project of the XIVth Soviet Antarctic Expedition in 1968–1970.

Experimental animals were caught near the station, at the coasts of Alasheyev Bight, ca. 50 m from the shore, at 45°49'47"E, 67°39'45"S; water depth was ca. 5 m, and the bottom was sandy.

Animals were caught from October 3 to November 11, 1969. By then an ice-cover was ca. 1.5 m, mean water temperature about -1.8°C and mean salinity about 34‰.

The catches were made mostly by means of an "umbrella"—an apparatus enabling to scrape the biocenosis from under the lower surface of the ice-cover, through a small hole in ice, ca. 16 cm in diameter. Detailed description of an "umbrella" is given in Rakusa-Suszczewski (1972). After draught the animals were placed in a vacuum flask and then, in the laboratory, they were transferred into the respiratory chambers where they were acclimated for 18–24 hr to the thermic conditions of the experiment. During the period of acclimation and experiments no food was administered.

Measurements were made in two age-size groups of animals; the first one was composed of juvenile and adolescent individuals (2–16 mg fresh weight) and the other of ovigerous females with eggs (25–65 mg fresh weight).

Oxygen consumption by animals was measured in constant-pressure volumetric respirometers modified by Klekowski (1968). Respiration chambers of 35 ml capacity were used; animals were placed into 10 ml of sea water taken from the draught place. 5 individuals of the first group or 3 individuals of the other were put into one respirometer chamber where a small flock of cotton wool was added in order to arrange a substratum similar to the natural one.

Readings of oxygen consumption were made every 10 min during 3–4 hr of the experiment.

Experiments were made at three temperatures: -1.9 , 0.0 and 2.0°C . Temperature in the thermostat was kept with an accuracy of 0.05°C . Numbers of measurements made and of the animals used are presented in Table I. Dependence of oxygen consumption on body weight was calculated using the least squares method according to formula $R = a \cdot W^b$, where R —oxygen consumption ($\mu\text{l O}_2/\text{ind.} \cdot \text{hr}$), W —fresh weight of an individual (mg), a and b —coefficients.

3. RESULTS

In both age-size groups of *Paramoera walkeri*, oxygen consumption increased as temperature rose. Females with eggs used much more oxygen than juvenile and adolescent individuals, e.g. about five times as much at -1.9°C (cf. Table I). When regarding body weight of individuals from both groups (i.e. after recalculation of oxygen consumption per unit of body weight), the situation was reverse—juvenile and adolescent individuals used 2–3 times more oxygen per 1 g fresh weight than females. These proportions are somewhat different when recalculating the values per dry body weight on account of various water contents in the bodies of juvenile and adolescent individuals (73% on average) and females (80% on average).

Q_{10} values calculated from data of Table I are quite high, and those for juveniles and adolescents are always considerably higher than that for females (Table II). As temperature increased, Q_{10} values were considerably lower.

Regressions of dependence of oxygen consumption on fresh body weight of *Paramoera walkeri* are presented in Fig. 1. Similar dependences on dry body weight were as follows: $R_{(-1.9^{\circ}\text{C})} = 0.24 \cdot W^{0.80}$;

Table I. Body weight and oxygen consumption in *Paramoera walkeri* Stebbing. A — juveniles and adolescents, B — females with eggs

Temp. (°C)	Age group	No. of ind.	Body weight (mg) Mean \pm S. E.		No. of experiments	Oxygen consumption (μ l O ₂ /hr) Mean \pm S. E.		
			Fresh	Dry		per ind.	per g fresh wt.	per g dry wt.
-1.9	A	35	3.8 \pm 0.39	1.0 \pm 0.10	7	0.24 \pm 0.02	67.0 \pm 7.59	251.8 \pm 7.31
	B	24	37.1 \pm 2.10	7.4 \pm 0.41	8	1.20 \pm 0.07	33.0 \pm 1.32	162.6 \pm 5.02
	Mean	59	20.5 \pm 3.73	4.2 \pm 0.86	15	0.72 \pm 0.13	50.0 \pm 5.70	207.2 \pm 16.84
0.0	A	95	6.0 \pm 0.79	1.6 \pm 0.68	19	0.57 \pm 0.06	97.0 \pm 4.91	386.1 \pm 24.9
	B	39	35.0 \pm 2.21	8.2 \pm 1.63	13	1.88 \pm 0.13	46.3 \pm 11.03	234.0 \pm 18.9
	Mean	134	20.5 \pm 2.76	4.9 \pm 2.02	32	1.22 \pm 0.13	71.6 \pm 5.81	310.0 \pm 20.4
2.0	A	70	7.4 \pm 0.87	2.0 \pm 0.23	14	0.89 \pm 0.08	141.8 \pm 13.42	507.3 \pm 51.28
	B	54	33.5 \pm 1.96	8.4 \pm 0.44	18	2.44 \pm 0.14	59.3 \pm 4.34	302.7 \pm 22.87
	Mean	124	20.5 \pm 2.89	5.2 \pm 0.63	32	1.66 \pm 0.16	100.5 \pm 11.16	405.0 \pm 31.75

$R_{(0.0^{\circ}\text{C})} = 0.40 \cdot W^{0.74}$; and $R_{(2.0^{\circ}\text{C})} = 0.62 \cdot W^{0.60}$. As temperature increased, a values increased but b values decreased.

Table II. Q_{10} values for *Paramoera walkeri* Stebbing

Age group	Temperature interval ($^{\circ}\text{C}$)		
	-1.9-0.0	0.0-2.0	-1.9-2.0
Juveniles and adolescens	71.4	12.2	28.7
Females with eggs	10.7	8.7	6.0
Average for both groups	15.9	4.6	8.6

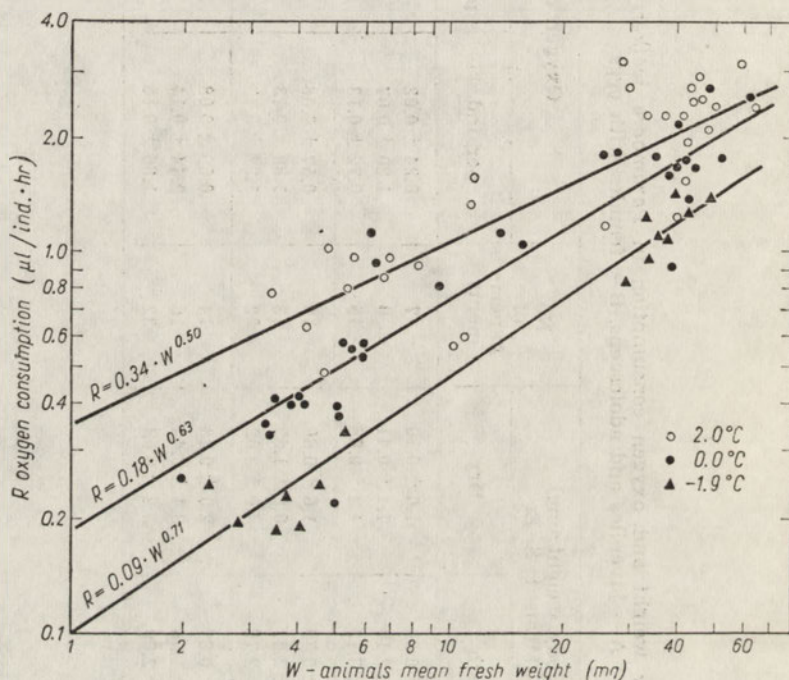


Fig. 1. Size and temperature dependence of respiratory rate of *Paramoera walkeri* Stebbing

4. DISCUSSION

Oxygen consumption by *Paramoera walkeri* Stebbing recalculated per weight unit is similar to that by other Amphipoda living at temperatures lower than 0°C , e.g. by Antarctic species *Orchomonella chilensis* (Heller) (Armitage 1962), arctic species *Pseudalibrotus littoralis* (Kroyer) (Scholander et al. 1953 a), and by other freshwater arctic Amphipoda *Gammarus limnaeus* (Smith) (Krog 1954). Similar values of oxygen consumption can be obtained for *Gammarus pulex* L. (tempe-

rate zone) by extrapolation of data by Wolvekamp, Waterman (1960) to 0°C (cf. Fig. 2).

The curve of dependence of respiratory rate on temperature (R-T curve) is more steep for *P. walkeri* than for other Amphipoda living in cold zone (Fig. 2).

The other way of presentation of the dependence of respiratory rate on temperature is Q_{10} coefficient. Its values for *P. walkeri* are quite high (Table II). Similarly high Q_{10} values for animals living at temperatures of about or below 0°C were obtained by Scholander et al. (1953 b) for Chironomidae larvae from arctic lakes, by Kanwisher (1959) for *Littorina littorea* L. and by Scholander et al. (1953 a) for some poikilothermic aquatic animals from Arctica (cf. Fig. 3).

High Q_{10} values for temperatures about 0°C obtained for *P. walkeri* and other animals living in cold zone confirm the finding that Q_{10} value increases within the range of low temperatures (cf. Bělehrádek 1930, Grainger 1958, Precht 1958). However, Q_{10} value for *Orchomonella chilensis* calculated from data by Armitage (1962) is considerably different, which seems to testify to the presence of metabolism compensation in this species.

According to Ivleva (1972, 1973), high Q_{10} values are the results of too short period of acclimation of animals to the thermic conditions of the experiment. Quite often, especially at low temperatures, at least several weeks' acclimation is necessary for full adaptation of an organism to a new temperature (Ivleva 1973). Also the phenomenon of metabolism compensation at low temperatures is considered by this author to be an artefact occurring as a result of a too short period of acclima-

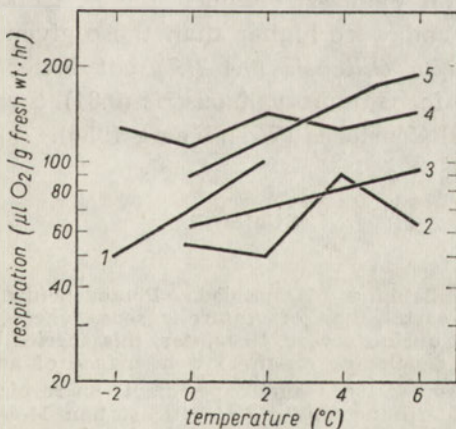


Fig. 2. Dependence of oxygen consumption on temperature (R-T curve) in some Amphipoda species. 1—*Paramoera walkeri* Stebbing (Antractica, the present paper), 2—*Gammarus limnaeus* (Smith) (Arctica, Krogh 1954), 3—*Gammarus pulex* L. (temperate zone, from extrapolation of data by Wolvekamp, Waterman 1960), 4—*Orchomonella chilensis* (Heller) (Antractica, Armitage 1962), 5—*Pseudalibrotus littoralis* (Kroyer) (Arctica, Scholander et al. 1953 a)

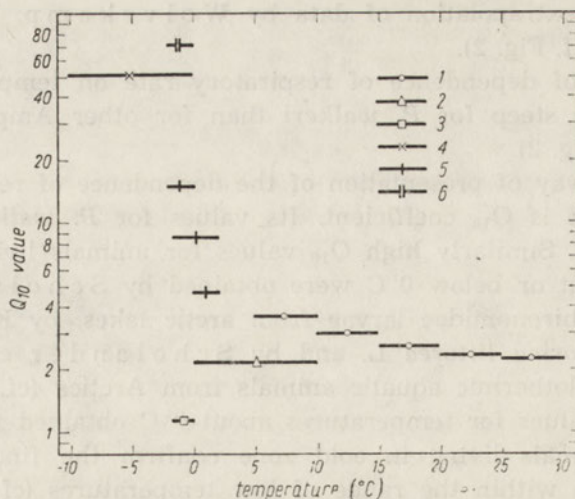


Fig. 3. Q_{10} values in the various temperature ranges (horizontal lines indicate the studied temperature range). 1 — various animals (Winberg 1956, 1968), 2 — *Gammarus limnaeus* (Smith) (Krog 1954), 3 — *Orchomonella chilensis* (Heller) (Armitage 1962), 4 — *Littorina littorea* L. (Kanwisher 1959) and Chironomida larvae (Scholander et al. 1953 b), 5 — *Paramoera walkeri* Stebbing, mean for juveniles, adolescens and females with eggs (the present paper), 6 — *Paramoera walkeri* Stebbing, the juvenile and adolescent individuals only (the present paper)

tion of the experimental animals. On the other hand, however, too long acclimation can provoke several changes in an organism (e.g. attaining a new "steady state"—cf. Grainger 1956), which blur the direct influence of temperature on an organism.

Values of regression exponent b defining the dependence of oxygen consumption on animal biomass, obtained for *P. walkeri*, ranged from 0.5 to 0.7 (cf. Fig. 1) and were higher than those given by Armitage (1962) for *Orchomonella chilensis* (0.4–0.7) but lower than that given by Winberg (1956) for *Gammarus lacustris* (0.81). b value equal to 0.81 is characteristic for all Crustacea (Winberg 1956).

5. SUMMARY

Paramoera walkeri Stebbing (Amphipoda, Pontogeneidae) is a circumpolar species inhabiting the coastal zone of Antarctic seas, where water temperature is never higher than 0°C during a year. In winter, this species belongs to so-called sub-fast ice community developing on the lower surface of an ice-cover.

In October and November 1969, some experiments on respiration of *Paramoera walkeri* were carried out in the Soviet Antarctic station Molodezhnaya in Thala Hills casis (Enderby Land, Eastern Antarctica). Animals were caught from under the ice at Alasheyev Bight. Measurements of oxygen consumption were made in constant-pressure volumetric respirometers modified by Klekowski (1968) at -1.9, 0.0, and 2.0°C. Before the measurements, 18–24 hr acclimation of animals to the thermic conditions of the experiments was made.

Oxygen demand of *Paramoera walkeri* is similar to that of other Amphipoda species living at temperatures below 0°C (Table I, Fig. 2).

Increase of environment temperature caused a faster increase of respiratory rate in juvenile and adolescent individuals than in ovigerous females with eggs in marsupia. Q_{10} values calculated for temperature ranges $-1.9-0.0^{\circ}\text{C}$, $0.0-2.0^{\circ}\text{C}$ and $-1.0-2.0^{\circ}\text{C}$ are 10.7, 8.7 and 6.0 for the females and 71.4, 12.2 and 28.7 for the juveniles, respectively. Such high Q_{10} values occur only in animals living at temperatures about or below 0°C .

Dependence of oxygen consumption on body weight of *P. walkeri* can be presented by the exponential formulae: $R_{(-1.9^{\circ}\text{C})} = 0.34 \cdot W^{0.50}$; $R_{(0.0^{\circ}\text{C})} = 0.18 \cdot W^{0.63}$ and $R_{(2.0^{\circ}\text{C})} = 0.09 \cdot W^{0.71}$. b values of regression exponents are close to 0.66, which confirm the dependence of oxygen consumption on the surface of animal body.

6. STRESZCZENIE

Paramoera walkeri Stebbing (Amphipoda, Pontogeniidae) jest gatunkiem circumpolarnym, występującym w przybrzeżnej strefie mórz antarktycznych, gdzie temperatura wody w cyklu rocznym nie przekracza 0°C . Zimą gatunek ten wchodzi w skład tzw. zespołu podlodowego rozwijającego się na spodniej stronie lodu morskiego.

W październiku i listopadzie 1969 r. na radzieckiej stacji antarktycznej Molo-dezhnaya leżącej w oazie Thala Hills (Ziemia Enderby, Antarktyda Wschodnia), przeprowadzono szereg eksperymentów nad oddychaniem *Paramoera walkeri*. Zwierzęta łowiono spod lodu w Zatoce Alasheyeva. Pomiary zużycia tlenu prowadzono w stałościennieniowych respirometrach wolumetrycznych w modyfikacji Klekowskiego (1968) w temperaturach -1.9 , 0.0 i 2.0°C . Pomiary poprzedzono 18-24 godz. aklimatyzacją zwierząt do warunków termicznych eksperymentu.

Zapotrzebowanie tlenowe *Paramoera walkeri* jest zbliżone do zapotrzebowania tlenowego innych gatunków Amphipoda żyjących w temperaturach poniżej 0°C (Tabl. I, Fig. 2).

Podwyższenie temperatury środowiska powoduje szybszy wzrost tempa metabolizmu u osobników niedojrzałych płciowo i młodocianych niż u dojrzałych samic z jajami w marsupium. Wartości współczynnika Q_{10} obliczone dla przedziału temperatur $-1.9-0.0^{\circ}\text{C}$, $0.0-2.0^{\circ}\text{C}$ i $-1.9-2.0^{\circ}\text{C}$ dla dojrzałych samic wynoszą 10,7, 8,7 i 6,0, a dla osobników młodocianych, odpowiednio 71,4, 12,2 i 28,7. Tak wysokie wartości współczynnika Q_{10} spotykane są tylko u zwierząt żyjących w temperaturach w pobliżu i poniżej 0°C .

Zależność zużycia tlenu od masy ciała *Paramoera walkeri* ilustrują równania wykładnicze: $R_{-1.9^{\circ}\text{C}} = 0.34 \cdot W^{0.50}$; $R_{(0.0^{\circ}\text{C})} = 0.18 \cdot W^{0.63}$ i $R_{2.0^{\circ}\text{C}} = 0.09 \cdot W^{0.71}$. Wartości wykładników regresji b zbliżone są do 0,66, co odpowiada zależności zużycia tlenu od powierzchni ciała zwierzęcia.

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Z. FISCHER

THE ELEMENTS OF ENERGY BALANCE IN GRASS CARP
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ABSTRACT

The consumption rate of grass carp, 20 to 400 g in weight, was measured with an excess of animal, plant, and mixed (animal+plant) food. A series of measurements involved also the feeding with an excess of animal food at diminishing amount of plant food and vice versa, i. e. with an excess of plant food at diminishing amount of animal food. It was found that grass carp bred under laboratory conditions at the excess of plant and animal food consumed about 75.7% of animal food, the remaining 24.3% being the plant food. However a complete lack of plant food caused almost twofold diminishing the amount of animal food consumed.

1. INTRODUCTION

Grass carp, an Asiatic fish of the Cyprinid family, has recently evolved a broad interest in many countries both of Europe and of America. This interest results from the view that the grass carp is herbivorous fish which permits to forebode a great future for this species in pond management.

However the herbivorousness of grass carp becomes a controversial problem. It is thought more often that the grass carp is an omnivorous fish. That is why a trial was made to trace, in general aspect, the energy transformation by grass carp kept on different food. The energy transformations by grass carp kept on either plant or animal food were described in the 3 recent parts of this paper (Fischer 1970, 1972 a, b). Those papers showed that the grass carp consumed and assimilated not only plant food but also animal food. When fed on animal food, the grass carp grows faster than fed on exclusively plant food. Basing on this finding studies were started on tracing one of main elements of energy budget viz. consumption rate at mixed food conditions.

The consumption rate by young fish (0.5-3 years old) of different weights (20-450 g) was investigated when the fish were given 3 experimental series of food: 1. plants only, 2. animals only, 3. mixed: plants and animals. Besides this two short series were performed with fish of about 100 g in weight when the animal food was in excess and the amount of plant food varied and vice versa, when the plant food was in excess and the animal food varied.

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2. MATERIAL AND METHODS

The experiments were carried out on the fish obtained from the fish ponds of the Institute of Inland Fisheries, Zabieniec, Poland. They were one year old (fingerlings) of about 20 g of weight. Further culturing was run in aquarium and the final weight of the fish reached over 400 g. The plant food consisted of lettuce, *Lactuca sativa*, and the animal food — of Tubificidae. This choice of food resulted from the studies which showed a clear preference of grass carp to these two items of food (Stroganov 1955, Babayan 1962, Penzes, Tölg 1966, Jachnichen 1967, Fischer 1968).

Depending on the series of experiments the food was either rationed or in excess. The excess of food when feeding on Tubificidae was such amount of food that was double (by weight) portion of the food eaten. In the series of experiments with lettuce this principle had to be abandoned on account of too large volume of supplied plant leaves, exceeding the volume of 10 l aquaria. This was the reason why the excess of food was considered when at least one gram of wet weight of plants remained, i. e. two leaves of an average size after the exposure of lettuce to the fish.

The consumption rate was determined by exposing to the fish a known amount of food (plant, animal, or mixed) for 24 hrs. After this time non-eaten food was removed from the aquarium and dried to a constant weight at 60°C. Simultaneously a control sample of food was weighed and dried, in order to calculate the dry matter content. The dry weight of food consumed was calculated by difference between dry weight of food given and that of food remaining. From the dried remains a subsample was taken each time and it was burned in Phillipson (1964) microbomb-calorimeter in order to assess its calorific value (3 combinations were made of each subsample). The ash content in the food was also determined by burning the food at a temperature of 550°C.

In order to check whether calorific value of plant food does not undergo any change within 24 hrs of exposure in water, the lettuce used for the experiment was divided into two portions and calorific value of one portion was determined before placing it into water and of another portion after 24 hrs exposure in a control vessel with water but with no fish. No difference was found in calorific value before and after exposure.

From the product of calorific value of food (calories per mg dry wt.) and the amount of food eaten (mg dry wt./24 hrs) the calorific content of diel food consumption was determined.

The general design of the experiments is given in Table I.

Table I. Design of experiment

Type of experiment		No. of samples	No. of fish	Range of fish weights (g)
Food	Quantity			
Plant	Excess	246	27	15—450
Animal	Excess	114	14	70—300
	Both in excess	103	14	30—300
Mixed food	Animal in excess + plant food (g):	21	7	122—288
	10			
	5			
	2.5			
	Plant in excess, + animal food (g):	27	9	72—122 97—152 99—157 104—164
	10			
	5			
	2.5			
	1.0			

The experiments with the food excess (3 first series in Table I) were run for several months. Before each experiment was started, the fish had been acclimated to a given food for about one month. On the other hand the experiments with mixed food lasted for a short period. After 3 days of habituation to the rationed food only 3 replications were made, and the average calculated.

3. RESULTS

The food consumption rate was considered as amount of food eaten within 24 hrs, and expressed in calories. The calorific value of 1 mg of animal food was calculated from 14 combustions of Tubificidae. The differences in subsequent combustions were so small that for further calculations an average was used. The calorific value of 1 mg dry weight of Tubificidae amounted to 5.307 ± 0.037 (S. E.) cal. The calorific value of lettuce varied with season, thus it was measured for each experiment; it ranged from 3.054 to 5.021 cal/mg dry wt.

The results of consumption rate experiments at the plant food in excess and at mixed food are presented as dependence on weight of fish, expressed in the form of regression equation ($C = a \cdot W^b$). Such approach was not possible when supplying exclusively animal food since such dependence was non-existing. On the other hand, the dependence of consumption rate with mixed food on body weight of fish is presented in Fig. 1 and can be described as $C = 1.06 \cdot W^{0.49}$, where the consumption rate is expressed in Kilocalories and weight of fish in g. The regression is significant at the 99% confidence level.

For plant consumption rates (Fig. 2) this dependence is $C = 0.30 \cdot W^{0.80}$

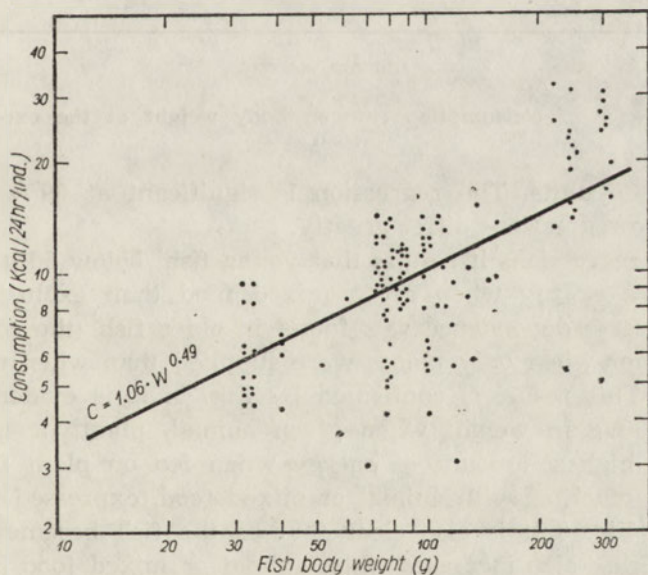


Fig. 1. Dependence of consumption rate on body weight at the excess of plant+animal food

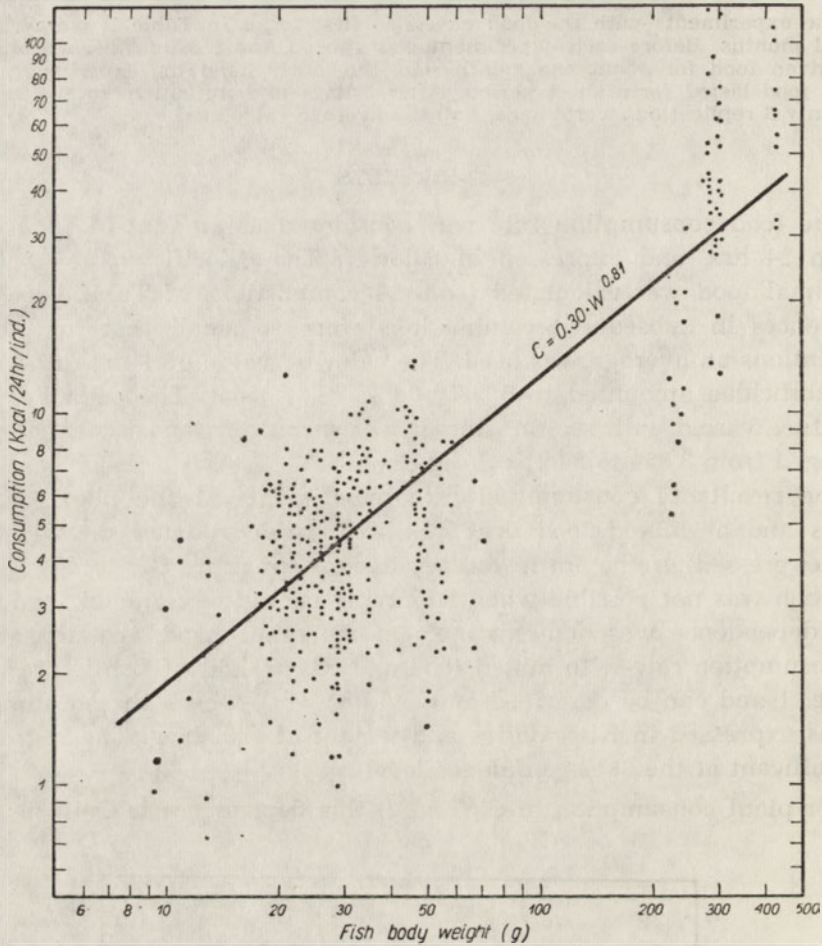


Fig. 2. Dependence of consumption rate on body weight at the excess of plant food

using the same units. The regression is significant at 99% confidence level. The two regressions differ greatly.

For these regressions it results that young fish, below 60 g in weight, consume more energy when given mixed food than exclusively plant food. The reverse dependence was found in older fish (the consumption rate was higher when only plants were supplied than when mixed food was given). This result is confirmed by Fig. 3. It is evident that the fish about 300 g in weight when given animal, plant, or mixed food consume the highest amount of energy when fed on plant food (about two times as much as with animal or mixed food, expressed in calorific units). From Fig. 3 it is also clear that as the fish become older, the consumption rate also increases when animal or mixed food is supplied. When supplying plant food exclusively, this increase is astonishingly high.

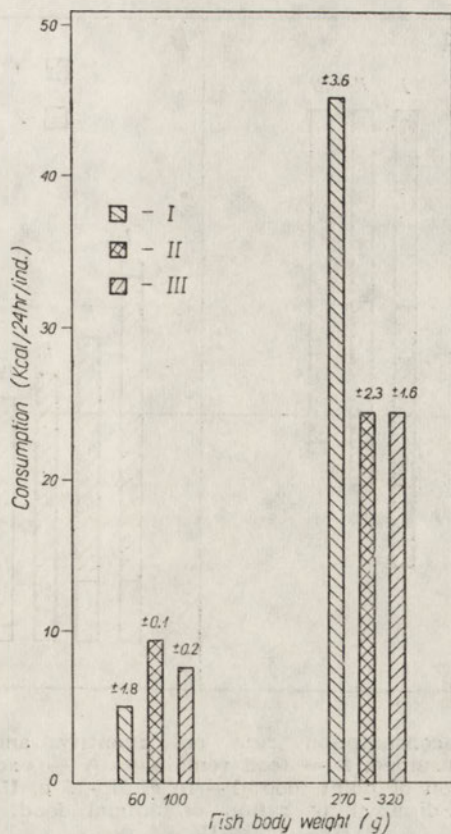


Fig. 3. Dependence of consumption rate on the type of food supplied. I—excess of plant food, II— excess of plant+animal food, III—excess of animal food

Besides the experiments discussed above short-lasting experiments were carried out when one item of food was supplied in excess and the remaining in decreasing amounts. These results are presented in Fig. 4. The fish faced with an excess of animal food (Fig. 4 A) do not consume it in a constant rate. In the two first series (I and II— 10 and 5 g plant food) when the food supply seemed to be sufficient since the fish does not consume it wholly the amounts of eaten Tubificidae were similar. On the other hand, when availability of plants was diminished to 25 g (Fig. 4 A— III) the fish consumed clearly less animals (about 4 g = =3.7 Kcal).

In the experiments where the plant food was given in excess and the animal food was given in diminishing portions (Fig. 4 B) the consumption of food did not show the same tendency. The plant food (given in excess) was more and more consumed when the supply of animal food was diminishing. However, when converted to calories the differences are small and range from 4 to 4.5 Kcal. The rations of food 5, 2.5 and 1 g (Fig. 4 B— II, III, IV) were consumed entirely. This experiment sug-

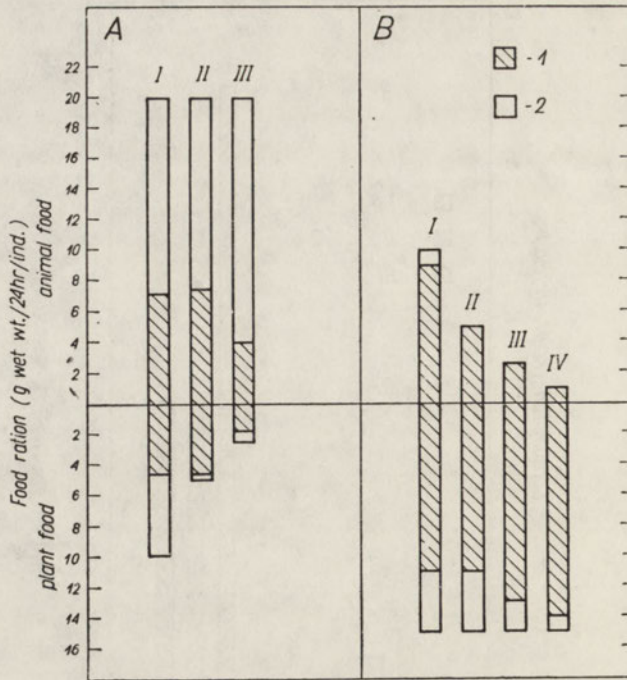


Fig. 4. Dependence of consumption rate on quantity and quality of food supplied. 1 — food consumed, 2 — food remained. A — excess of animal food (20 g)+diminishing ration of plant food: I—10 g, II—5 g, III—2.5 g; B—excess of plant food (15 g)+diminishing ration of animal food: I—10 g, II—5 g, III—2.5 g, IV—1 g

gests that a relatively constant amount of plant food is consumed, irrespective to the amount of animal food eaten. Both in case when the fish have consumed about 8.5 Kcal of animal food, and in the case when they consumed 4.5 Kcal, the energy of plant origin amounted to 4 Kcal (Fig. 4B—I, II). When diminishing the amount of Tubificidae eaten to 0.9 Kcal (Fig. 4 B—IV) the amount of lettuce eaten increases from 4 Kcal only to about only 4.5 Kcal.

4. DISCUSSION

Investigations on the energy and matter budgets in grass carp have proved that this fish can feed both on exclusively plant or exclusively animal food. From a theoretical calculation it is known that:

$$C = P + R + FU$$

in other terms:

$$C = A + FU$$

where:

$$A = P + R$$

then:

$$P = A - R$$

Thus, if we have in disposal such data as C , R , and A , we can estimate the expected amount of growth of the fish. The results of such calculations for three exemplifying groups of fish of different weights are presented in Table II. It includes the results of experiments with different types of food. The values of consumption are obtained experi-

Table II. Elements of energy balance of grass carp fed with different types of food, based on data by Fischer (1972 a, b)

Mean weight (g)	Balance parameter (Kcal)	Food		
		Animal	Mixed	Plant
74	C	7.8	9.5	5.0
	A	3.1	3.4	1.0
	R	0.9	0.9	0.8
	$P=A-R$	2.1	2.5	0.2
235	C	20.5	23.8	16.0
	A	8.2	8.0	3.2
	R	2.3	2.0	1.7
	$P=A-R$	5.8	6.0	1.5
295	C	24.5	24.4	45.0
	A	9.8	10.7	9.0
	R	2.6	2.4	1.9
	$P=A-R$	7.1	8.3	7.0

mentally in this paper, but such elements of the budget as assimilation, respiration and growth (A , R , P), are based on the data obtained previously (Fischer 1970, 1972 a, b). For these calculations the following were accepted: the assimilation efficiency of animal food = 40%, the respiration rate calculated from the regression equation $RO_2 = 300 \cdot W^{0.83}$, the oxycaloric coefficient being 4.83; and of plant food: the assimilation efficiency = 20%, the respiration rate calculated from the equation $RO_2 = 487 \cdot W^{0.64}$, the oxycaloric coefficient being 5.031.

The values given in Table II were approximated. From this Table it results that growth (P), obtained by subtraction of the calories burned in the respiration process from the assimilated calories is similar both when applying animal and mixed food. It can be thus supposed that when the fish are given mixed food these are Tubificidae that are mainly eaten. The average of all measurements shows that with the excess of animal + plant food the animal food constitutes 75.76% of the whole consumption with standard error of 0.27%, and standard deviation of 2.74%.

The increasing consumption rate with the increase in weight of fish at the excess of animal and mixed food follows more or less similarly

(Table II). However, when plant food was given exclusively there was a large increase in consumption rate at increasing fish weight from about 240 to 300 g. Within these relatively small differences in weight the consumption rate increased by about 3 times (Table II, from 16 to 45 Kcal). Assuming a constant assimilation efficiency of plant food (20% — Fischer 1972 a, b), it would result that the grass carp ca. 300 g in weight when feeding exclusively on plants utilizes about 7 Kcal for growth. Thus, the increment of its body should be similar to that of grass carp fed with animal food. This statement is not true. Within 10 days the fish (five experimental individuals) fed exclusively with plants lost their weight by about 2.2% of its initial weight (minimum 1.2%, maximum 3.38%). At the same time other fish of a similar weight fed exclusively with animal food gained weight by 3.9%, on the average (minimum 2.04%, maximum 6.82%). Thus, since the fish are losing their weight, one should assume that when fed with plant food they either increase rapidly their respiration (which is less probable) or diminish their assimilation efficiency. This latter explanation seems to be most probable. It is possible that when reaching 300 g in weight the fish undergo a strong lack of "minimum" factor (e. g., some of egzogenic aminoacids), so that the food consumption rate increases rapidly. It is also possible that lack of this factor in the food brings about a cessation of growth. It is probable on account of inconspicuous amount of some aminoacids in plant food, such as leucine, isoleucine, valine (Phillips 1969).

Thus, it results that the most optimal diet for grass carp should include about 75% of animal food, which would ensure the growth of the fish, and the remaining 25% of plant food, which would supply with necessary vitamins and large amounts of carbohydrates utilized mostly for respiration (Fischer 1972 a, b). Basing on this statement the results of experiments when the grass carp was fed with different rations of animal and plant food become very interesting (Fig. 4). From Fig. 4 it is clear that limitation of the amount of animal food, irrespective to the fact that it is less than 1 Kcal or 8 Kcal, with a simultaneous excess of plant food does not affect the amount of plants eaten. The differences in extremal cases amount only 0.5 Kcal, but with reversely designed experiments when the animal food is given in excess and plant food is limited, the consumption of animal food is decreased by almost half at the limitation of plants supplied to 0.5 Kcal. Thus, it is concluded that the grass carp needs some minimum amount of plants, which would facilitate ingestion and digestion of large quantities of animal food which, in turn, ensures high increment of body weight. It follows that both animal and plant food holds some components necessary for a normal growth of this species. In such situation the herbivorousness of grass carp should be considered not as an ability to consume plants, exclusi-

vely, but as an ability to consume also plant food besides animal food. The amount of plant food under optimum conditions should amount to about 25%. However, the availability of food for grass carp should be considered somewhat different than for other fish. It is most probable that the grass carp has some difficulty in obtaining most of all animal food. It is not able to dig in the bottom, as does carp, it is also unable to hunt for larger aquatic invertebrates, neither it has filtrating ability. One can infer that the grass carp has a broader physiological food spectrum than ecological one — the one it encounters in the field. Because of lack of ecological adaptations for consuming the animal food, it feeds on plants. It seems that when faced with the choice of food, the grass carp depends mostly on availability of food. This was confirmed by the results of earlier experiments on the food preference of this species (Fischer 1968). Those experiments were as a matter of fact carried out almost exclusively on plant foodstuffs, but they proved that the availability of food decides foremost upon its choice. Thus it seems very probable that when given the choice of animal and plant food, the grass carp depends also on its availability. However it is unable to get enough animal food. It is most probable that if there is a shortage of animal food, and nolens volens grass carp feeds on plants; this brings about the diminished growth rate of this fish.

Thus, grass carp plays a role of an omnivorous consumer in aquatic reservoirs. One should expect that depending on the composition of flora and fauna in the reservoir, that is food supply and competitors, the grass carp can change the diet and adapt to any trophic situation in the reservoir. However, this fitness should be considered as amelioration or deterioration of trophic conditions that affect gratefully the growth of the fish.

Acknowledgements

The author wishes to acknowledge Prof. Dr. R. Z. Klekowski, head of the Department of Bioenergetics and Bioproductivity, Nencki Institute of Experimental Biology, for guidance and assistance throughout the study.

5. SUMMARY

The study aimed at defining the consumption rate by grass carp fed mainly with plant and animal food simultaneously. It was found that under such trophic conditions in the laboratory, the animal food constitutes about 75% of the total amount of food eaten. In order to get a broader comparison the consumption rate was also studied in fish 30–300 g in weight fed with plant and animal food separately. A series of experiments pertained also to the situation when the fish were given an excess of animal food and a diminishing rations of plant food and vice versa i.e. an excess of plant food and a diminishing rations of animal food. The latter experiments proved that the lack of plant food or its diminished amount (about 0.5 Kcal) brings about a diminishing quantity of animal food eaten, even that it is supplied *ad libitum*.

6. STRESZCZENIE

Badania miały na celu określenie racji pokarmowej białego amura żywno-
nego przede wszystkim równocześnie nadmiarem pokarmu roślinnego i zwierzę-
cego. Stwierdzono, że w takich warunkach pokarmowych w laboratorium pokarm
zwierzęcy stanowi ok. 75% całości zjedzonego pokarmu. Celem uzyskania szersze-
go porównania przebadano również rację pokarmową amura, w granicach wag
od ok. 30 do ok. 300 g, żywnoego wyłącznie pokarmem roślinnym i wyłącznie po-
karmem zwierzęcym. Wykonano również serię doświadczeń przy stosowaniu po-
karmu zwierzęcego podawanego w nadmiarze, w różnej, coraz mniejszej ilości
pokarmu roślinnego i odwrotnie — przy stosowaniu pokarmu roślinnego w nad-
miarze, a zmniejszającej się ilości pokarmu zwierzęcego. Doświadczenia te wy-
kazały, że brak pokarmu roślinnego lub jego małe ilości (ok. 0,5 Kcal) powodują
zmniejszenie ilości zjadanego pokarmu zwierzęcego, który jest podawany w nad-
miarze.

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INVESTIGATION OF A METHOD FOR COMPARING THE EFFICIENCY OF ELECTRICAL FISHING MACHINES¹

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ABSTRACT

Five electrical fishing machines, four of which were portable, producing different currents and using several fishing techniques, were tested to determine their efficiencies. There were great differences of efficiency between the machines, which were apparent in the first fishing (*P* efficiency) as well as in the third (*Q* efficiency). In the light of the results, modifications are proposed to improve the experimental method.

1. INTRODUCTION

At the Symposium on Electrical Fishing at Belgrade (1966), a working party was set up for the purpose of developing an objective method of measuring the efficiency of an electrical fishing machine or a type of current, the efficiency being defined as the relationship between the number of fish caught and the number present in the water under consideration. The report of the Symposium appeared in two publications (Vibert 1967, 1968). It emerged from the discussion at Belgrade that in different countries, or for different scientific considerations, different types of current and different methods of fishing were used in similar conditions, without any comparison which would allow the best to be recognized. It therefore appeared appropriate to assemble a group of experts to demonstrate electrical fishing in the same body of water, where each could arrange in his own way to obtain the best efficiency.

In the first instance the experts were asked to submit plans for methods of efficiency testing complying with two requirements: objectivity and reproducibility. It was agreed to confine the tests to relatively simple conditions, with portable fishing machine in a trout stream.

Two methods were proposed: one by R. Cuinat (1969, "Assessment of the efficacy of electric fishing gear in a trout stream", unpubl.) and the other by P. Lamarque (1969, "Projet d'elaboration d'une methode de tests d'efficacite de peche a l'electricite", unpubl.). Cuinat's method recommended the conduct of the tests in a channel or a section of a water course previously emptied of native fish, into which a known number of fish was introduced, while in the method of Lamarque the tests would be carried out in a natural stream on the native fish. For practical reasons obtaining in the local conditions, the method selected was that of Cuinat.

¹ Technical report of the EIFAC Working Party on Electrical Fishing held at Giżycko, Poland, October 1969. <http://rcin.org.pl>

It was further suggested that the efficiency tests should be completed by tests of fatigue and mortality, carried out with each machine in simulated fishing conditions (Chmielewski et al. 1973).

W. Dembiński (Poland) kindly agreed to organize the international meeting and all the tests. In the conduct of the tests he had a very effective cooperation of A. Korycki, K. Krasowski and J. Waluga (all of Poland). Besides the above, the other experts participating in the meeting were: A. Chmielewski (Poland), R. Cuinat (France), E. Halsband (Federal Republic of Germany), G. Hartley (United Kingdom), P. Lamarque (France) and P. Sharkey (Eire).

Four portable fishing machines were supplied by the following countries: Eire, France, Federal Republic of Germany and the United Kingdom. The machine used for clearing the section between tests was Polish.

2. MATERIAL AND METHODS

A stretch of the river Drwęca, near the farm of the Polish Angling Association at Czarci Jar (Northern Poland), was chosen as the site for the tests (Fig. 1). The characteristics of the stretch were as follows: length — 100 m, width — 2 to 4 m, depth — 0 to 0.9 m, conductivity — 333 $\mu\text{S}/\text{cm}$, temperature — 7°C, flow speed — 0.18 m/sec, bottom — sand and mud, emergent vegetation — *Acorus calamus*.

The experimental stretch was isolated by traps at both ends (Fig. 2), and all the native fish were removed electrically before the tests; these comprised rainbow trout which had escaped from the fish farm, tench, carp, and pike.

In the present investigations two species were used: rainbow trout (*Salmo gairdneri* Richardson) and common eel (*Anguilla anguilla* L.)

The fish had been marked with plastic tags 5×10 mm attached anterior to the pectoral fins (Fig. 3). Each tag was numbered according to the batch used for a test. Three colours were used for the tags to distinguish size classes.



Fig. 1. General view of the experimental stretch of the River Drwęca

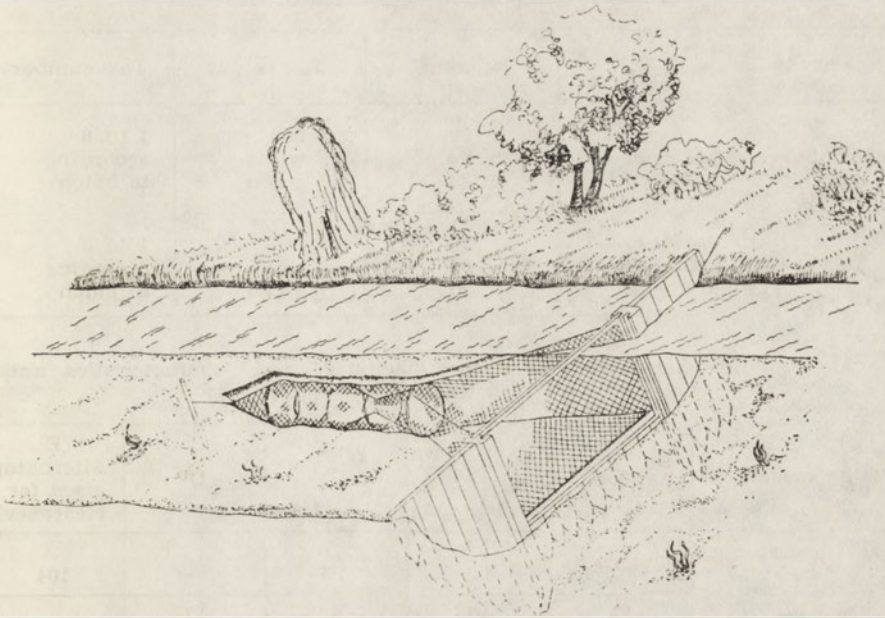


Fig. 2. Diagram of the upstream trap

The composition of each batch of fish is shown in Table I. It was intended to use fish in numbers and sizes appropriate to a trout stream. The batches of fish had been prepared and held before the start of the tests at the fish farm at Czarci Jar. A reserve supply of fish had been arranged for every batch in case of sickness or death occurring before the tests. Every care had been taken over aerating the travelling tanks and expediting their transport in order that the fish might reach the experimental sector in perfect condition.

The machines intended to be tested and the one used for clearance have been respectively designated by the letters A, B, C, D, and E; their characte-

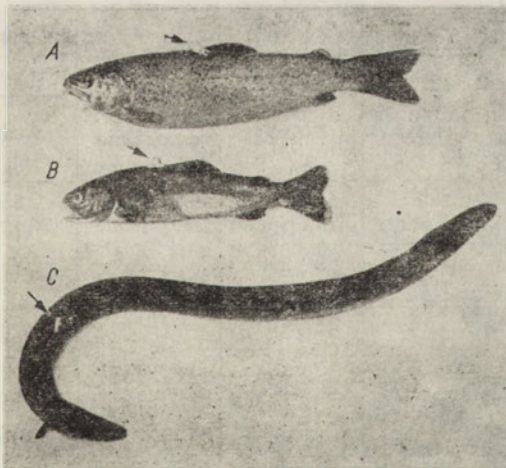


Fig. 3. Fish tagged. A and B — trout, C — eel. Plastic tags indicated with arrows

Table I. Composition of a batch of fish

Species	Length (cm)	Number	Tag colour	Tag numbers
Trout	5-10	80	red	1 to 8 according to batch
	10-20	60	white	
	20-30	20	green	
Eels	20-30	20	red	1 to 8 according to batch
	30-40	20	white	
	40-50	20	green	

Table II. General characteristics of the machines and characteristics under tests

Fishing machines	A	B	C	D	E (Alternator used for clearance)
Weight without battery (kG)	3.2	4.5	1.5	—	104
Voltage (V)	12	12	6	12	Alternator
Battery Capacity (Ah)	—	9	7	10	
Weight (kG)	7.3	5	5	—	
Duration under fishing conditions (hr)	—	5	5	6	Alternator
Maximum power (W)	—	100	80	80	2 kVA 1425 W
Power used (W)	36.7	34.6	5.0	32.2	
Portable on back	yes	yes	no	yes	no
Actually carried	no	yes	no	yes	no
shape	triangular	circular	Y-shaped	square	circular
Anode area (cm ²)	—	700	—	600	plate
shape	see text	see text	see text	see text	see text
Cathode area (cm ²)	—	1600	—	300	1600
Safety switch	yes	yes	—	yes	see text
Type of current	Condenser discharge	Pulses	Condenser discharge	Pulses	Rectified AC smoothed
Voltage range (V)	350	150-300	300-450	350	220-280
Pulse voltage used (V)	350+peak	150+peak	350+peak	220+peak	250±30
Frequency range (Hz)	10-150	2-200	34.5	20-66	100
Frequency used (Hz)	118	64.5	34.5	36	100
Range of pulse width (ms)	—	0.5-400	—	1-10	Rectified AC smoothed
Pulse width used (ms)	RC=0.3	5	RC=0.1	2	
Inter-electrode resistance during test (ohm)	70.5	61.3	40.2	97.6	43.2

— no data available.

istics are shown in Table II. The interelectrode resistances were measured in the condition of use by the relationship U/I , when coupled to the alternator E. The diagrams showing pulse shapes of the various machines were produced subsequently, from the oscillograph traces supplied by each expert with his apparatus working into the interelectrode resistance determined on site (Fig. 4).

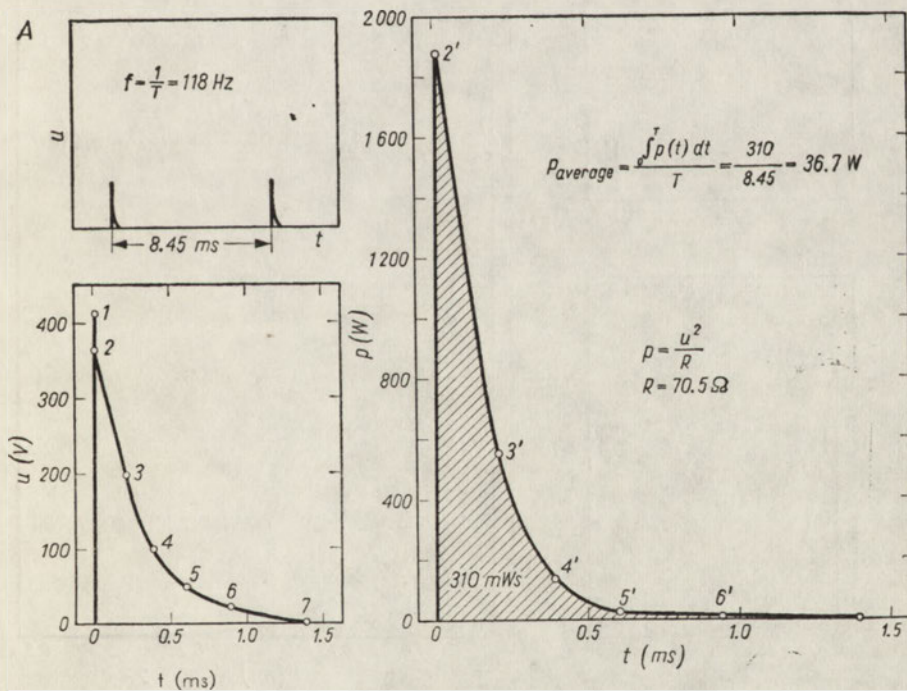
Certain machines possessed peculiarities which are worth mentioning.

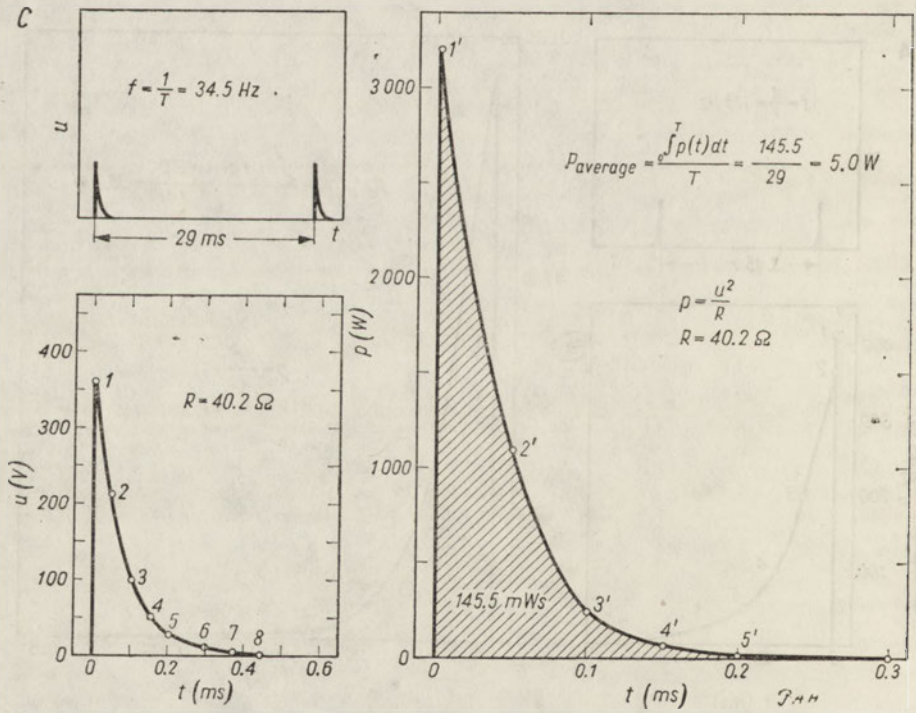
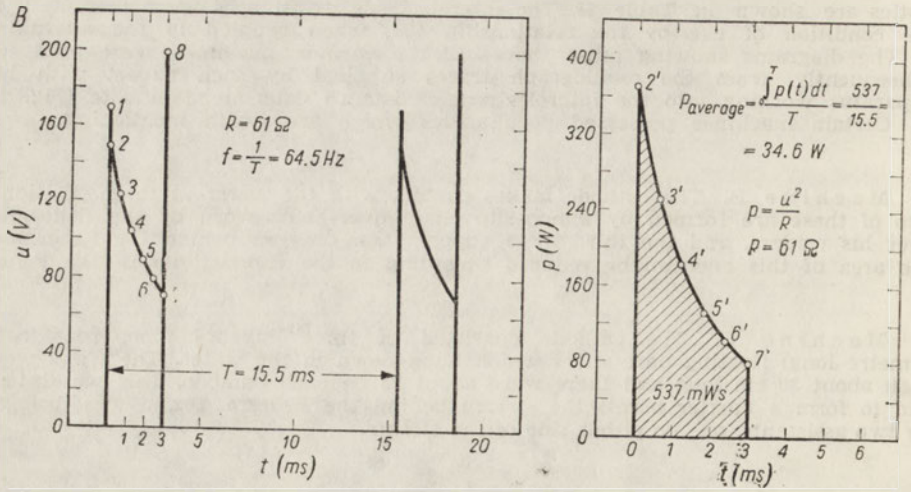
Machine B. The cathode makes contact with the water at three positions; two of these are formed by a non-slip chain over-boots worn by the fisherman over his waders, and the third by a copper strip dragged behind the fisherman; the area of this one can be reduced according to the conductivity of the water.

Machine C. The cathode consisted of three linked bamboo rods (each a metre long) floating bare wires which hung down in the water. The wires were each about 30 cm long and there were about 13 on each bamboo. This was intended to form a barrier across the stream behind the fisherman, and was dragged by two assistants, one on either side of the stream.

Machine D. The cathode consisted of a copper tube about 30 cm long and 4 cm in diameter pushed onto the end of a staff. This type of cathode is meant to be used as a wading staff and can be also used to drive fish out of shelter.

Machine E. An electronic safety device automatically reduces the voltage from the working value of 220–280 volts, to 12 volts, the safety voltage when the anode is out of the water; when the anode is again immersed, the working voltage is re-established. This obviates accidents should the anode touch a fisherman.





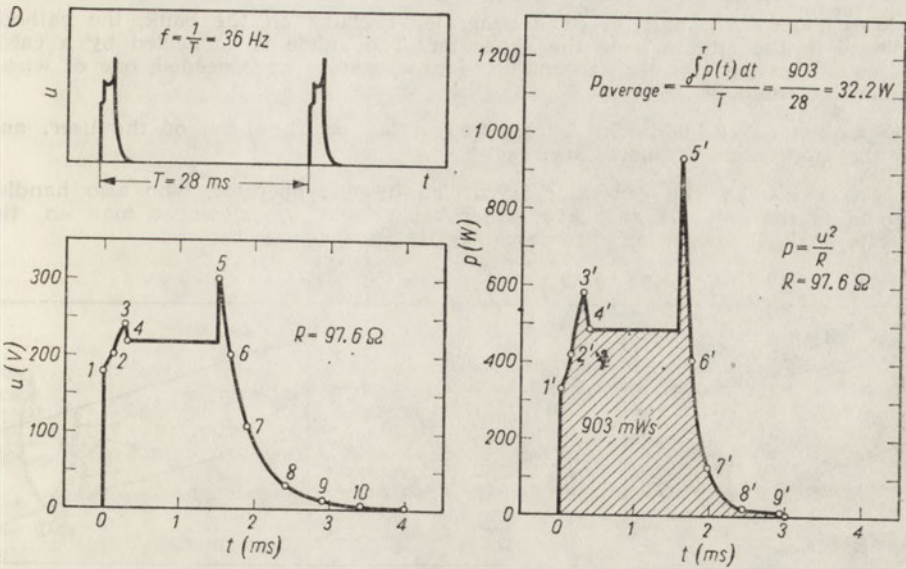


Fig. 4. Pulse course $u = u(t)$ and graphical calculation of the mean power for machines A, B, C, D and E

Fishing techniques are shown diagrammatically in Fig 5.

Machines A and E. The generator remains on the bank, the cathode is placed in the stream near the generator. The anode is connected by a cable of adequate length. In this technique, four operators were needed, one of whom handled the cable.

Machines B and D. These are carried on the back of the user, and only three operators are necessary.

Machine C. The generator is carried by one operator, who also handles one end of the cathode "raft", the other being held by a second man on the opposite bank. Five operators are necessary.

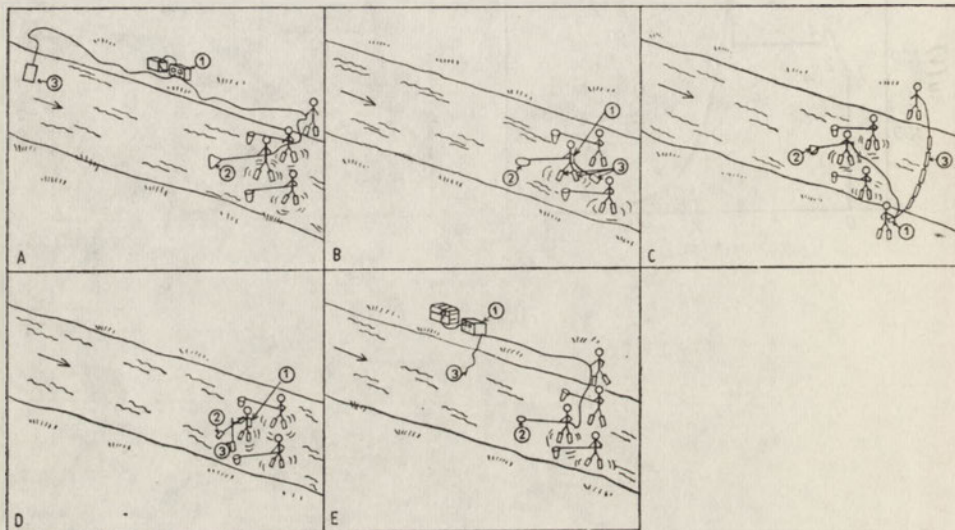


Fig. 5. Fishing techniques. A-E—machines. 1—electrical fishing machine, 2—active electrode, 3—passive electrode

For each test the operations were as follows: decanting the batch of fish, and distributing them throughout the test sector; waiting ten minutes to allow the fish to settle down and take shelter; fishing with the machine under the test, which took twenty minutes; the sector was worked from the lower to the upper end, in order to keep the water clear for the fisherman; lifting the traps at both ends of the sector; clearing the sector by fishing with machine E.

These operations occupied 1 hr 30 min. The fish caught in the course of each test were immediately carried to a bench where a special team identified and counted them. The tests took place in the order and at the times and dates shown in the Table III.

Test No. 1 was considered as a "blank", and used to determine the fishing time. Tests 1, 2 and 7 on the one hand, and 3 and 6 on the other, carried out with the same machines, allowed the variation in the results for a single machine to be studied. Finally, test 8 concerns the machine used for clearing the channel of fish; it was meant to compare the results with those obtained with other machines.

All the tests, except the 6th, were carried by the same team of technicians, who were familiar with practical electric fishing from long experience.

Several factors conspired to disturb the course of operation: An excessive stocking with fish from the reserve in the course of one of the first three trials; it appears from the analysis that the results of test 2 are affected; An escape of fish from the sector past the traps, which had been undermined by the water flow; analysis of the results suggests that these escapes were parti-

Table III. Dates, times and order of the tests

Date	Starting time for test (hr)	Test number	Machine
1.X.1969	12.40	1	A
	14.03	2	A
	15.39	3	B
2.X.1969	8.50	4	C
	10.14	5	D
	11.40	6	B
	13.10	7	A
	14.35	8	E

cularly large during test 7; A breakdown owing to the contact failure in the case of machine B during test 6, at the upper end of the sector, at the time when the trout should have been concentrated between the trap and the fishermen; The intermittent rain and occasional lightning which to some extent hampered the fishermen during some of the tests.

Originally it had been intended to measure fishing efficiency only in the case of fish which had not been electrically fished previously. However, as the clearance fishings were incomplete, fish belonging to earlier batches accumulated in the stream, and this had permitted two categories of efficiency to be determined for each machine: the efficiency which we designate P (P_t for trout, P_e for eel), which applies to fish liberated for the particular test; the Q efficiency (Q_t and Q_e), applying to fish remaining in the river after having escaped both the machine under test and the subsequent clearance; it therefore represents the efficiency of the third fishing.

Reference to the Tables IV and V, containing all the results, will show these efficiencies calculated thus:

Efficiency P^2 :

$$\text{For test 1} \quad \frac{\text{Batch 1, column 6 total}}{\text{Batch 1, column 4 total}} \times 100$$

$$\text{For test 2} \quad \frac{\text{Batch 2, column 11 total}}{\text{Batch 2, column 4 total}} \times 100$$

and similarly for succeeding tests.

Efficiency Q^2 :

Inapplicable to test 1.

$$\text{For test 2} \quad \frac{(\text{Batch 1, column 11 total}) \times 100}{(\text{Batch 1, column 4 total}) - (\text{batch 1, column 10 total})}$$

$$\text{For test 3} \quad \frac{(\text{Batch 2, column 16 total}) \times 100}{(\text{Batch 2, column 4 total}) - (\text{batch 2, column 15 total})}$$

etc.

3. RESULTS

Distribution of recaptures is shown in Table IV for trout and Table V for eel.

² These so calculated efficiencies concern the whole batch of fish; to calculate the efficiencies by class of length, it is necessary to refer to the corresponding columns.

Table IV.

		No of trout before the bests			Test 1					Test 2					Test 3					Test 4				
1	2				3	4	5	6	7	8	9	10	11	12	13	14	15	16	17	18	19	20	21	22
Batch No.	Size class (cm)	Relict	Released	Total	Test 1	U. t.	D. t.	Clearance	Total	Test 2	U. t.	D. t.	Clearance	Total	Test 3	U. t.	D. t.	Clearance	Total	Test 4	U. t.	D. t.	Clearance	Total
1	5-10		80	80	11	—	—	25	36	3	—	—	13	16	5	—	—	3	8	—	—	—	3	3
	10-20		60	60	19	—	—	13	32	—	—	—	6	6	5	—	—	2	6	—	—	—	—	—
	20-30		20	20	6	—	—	7	13	1	—	—	2	3	—	—	—	—	—	—	—	—	—	—
2	5-10	44	80	124						11	—	—	33	44	5	—	—	5	10	—	—	—	6	6
	10-20	28	60	88						19	—	1	25	45	4	—	—	3	7	—	—	—	1	1
	20-30	7	20	27						10	—	5	4	19	—	—	—	—	—	—	—	—	—	—
3	5-10	64	80	144											36	—	—	1	37	—	—	—	12	12
	10-20	37	60	97											30	—	—	9	39	—	—	—	—	—
	20-30	5	20	25											16	—	—	1	17	—	—	—	—	—
4	5-10	89	80	169																44	—	—	1	45
	10-20	45	60	105																1	—	—	17	18
	20-30	8	20	28																2	—	—	8	10
5	5-10	103	80	183																				
	10-20	87	60	147																				
	20-30	17	20	37																				
6	5-10	131	80	211																				
	10-20	114	60	174																				
	20-30	29	20	49																				
7	5-10	152	80	232																				
	10-20	139	60	199																				
	20-30	33	20	59																				
8	5-10	175	80	255																				
	10-20	180	60	240																				
	20-30	51	20	71																				
Total			1280																					

U. t. — upstream trap, d. t. — downstream trap

Recaptures of trout (unworked data)

Numbers of trout recaptured																				Machine					
Test 5					Test 6					Test 7					Test 8						Total				
26	27	28	29	30	31	32	33	34	35	36	37	38	39	40	41	42	43	44	45		46	47	48	49	50
Test 5	U. t.	D. t.	Clearance	Total	Test 6	U. t.	D. t.	Clearance	Total	Test 7	U. t.	D. t.	Clearance	Total	Test 8	U. t.	D. t.	Clearance	Total	Tests	U. t.	D. t.	Clearance	Total	
—	—	—	—	—	2	—	—	—	2	1	—	—	1	2	—	—	—	—	—	22	—	—	45	67	A
—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	23	—	—	21	47	
—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	7	—	—	9	16	
1	—	—	1	2	—	—	—	—	—	2	—	—	—	2	2	—	—	1	3	21	—	—	46	67	A
—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	23	—	1	29	53	
—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	1	—	—	—	—	11	—	5	4	20	
1	—	1	7	9	2	—	—	—	2	3	—	—	—	3	1	—	—	2	3	33	—	1	32	66	B
—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	30	—	—	9	39	
—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	16	—	—	1	17	
2	—	1	8	11	3	—	—	3	6	—	—	—	1	1	2	—	—	—	2	11	—	1	53	65	C
2	—	—	7	9	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	3	—	—	24	27	
—	—	—	—	—	1	—	—	—	1	—	—	—	—	—	—	—	—	—	—	3	—	—	3	11	
9	—	—	21	30	3	—	1	6	10	4	—	—	8	12	3	—	—	1	4	19	—	1	36	56	D
7	—	—	17	24	5	—	—	2	7	1	—	—	1	2	1	—	—	1	2	14	—	—	21	35	
4	—	—	4	8	1	—	—	—	1	1	—	—	—	1	—	—	—	—	—	6	—	—	4	10	
					24	—	—	15	39	6	—	—	3	9	4	—	—	5	9	34	—	—	23	57	B
					16	—	1	11	28	1	—	—	1	2	1	—	—	1	2	18	—	1	13	32	
					8	—	—	1	9	—	—	—	—	—	—	—	—	—	—	8	—	—	1	9	
										16	—	—	12	28	8	—	—	4	12	24	—	—	16	40	A
										6	—	—	9	15	3	—	—	1	4	9	—	—	10	19	
										2	—	—	4	6	2	—	—	—	2	4	—	—	4	8	
															40	—	—	10	50						E
															47	—	—	7	54						
															18	—	—	1	19						
239																						—	10	409	758

Table V.

		No. of eels before ethe tests			Test 1					Test 2					Test 3					Test 4					
1	2	3	4	5	6	7	8	9	10	11	12	13	14	15	16	17	18	19	20	21	22	23	24	25	
Batch No.	Size class (cm)	Relict	Released	Total	Test 1					Test 2					Test 3					Test 4					
					U. t.	D. t.	Clearance	Total	U. t.	D. t.	Clearance	Total	U. t.	D. t.	Clearance	Total	U. t.	D. t.	Clearance	Total					
1	20-30		20	20	4	—	1	3	8	1	—	—	6	7	—	—	—	—	—	—	—	—	—	—	
	30-40		20	20	1	—	1	3	5	4	—	—	2	6	1	—	—	—	—	1	—	—	—	1	1
	40-50		20	20	2	—	—	5	7	1	1	—	3	5	—	—	—	1	1	—	—	—	—	—	
2	20-30	12	20	32						7	—	—	1	8	1	—	—	—	1	—	—	—	—	—	
	30-40	15	20	35						4	—	—	1	5	2	—	—	—	2	—	—	—	—	—	
	40-50	13	20	33						7	—	—	—	7	—	—	—	—	—	—	—	—	—	—	
3	20-30	17	20	37											5	—	—	2	7	—	—	—	1	1	
	30-40	24	20	44											5	—	—	1	6	—	—	—	—	—	
	40-50	21	20	41											6	—	—	3	9	—	—	—	1	1	
4	20-30	29	20	49																2	—	—	4	6	
	30-40	35	20	55																6	—	—	1	7	
	40-50	31	29	51																2	—	—	4	6	
5	20-30	42	20	62																					
	30-40	47	20	67																					
	40-50	44	20	64																					
6	20-30	54	20	74																					
	30-40	54	20	74																					
	40-50	57	20	77																					
7	20-30	65	20	85																					
	30-40	59	20	79																					
	40-50	67	20	87																					
8	20-30	63	20	88																					
	30-40	65	20	85																					
	40-50	76	20	96																					
Total				480																					

Recaptures of eels (unworked data)

Number of eels recaptured																				Machine					
Test 5					Test 6					Test 7					Test 8						Total				
26	27	28	29	30	31	32	33	34	35	36	37	38	39	40	41	42	43	44	45		46	47	48	49	50
Test 5	U. t.	D. t.	Clearance	Total	Test 6	U. t.	D. t.	Clearance	Total	Test 7	U. t.	D. t.	Clearance	Total	Test 8	U. t.	D. t.	Clearance	Total	Tests	U. t.	D. t.	Clearance	Total	
—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	5	—	1	9	15	A
—	—	—	—	—	—	—	—	—	—	1	—	—	—	1	—	—	—	—	—	7	—	1	6	14	
—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	3	1	—	9	13	
—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	8	—	—	1	9	A
1	—	—	1	2	—	—	—	—	—	—	—	—	—	—	—	—	—	1	1	7	—	—	3	10	
—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	7	—	—	—	7	
—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	5	—	—	3	8	B
—	—	—	1	1	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	5	—	—	2	7	
—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	6	—	—	4	10	
—	—	—	3	3	—	—	—	—	—	—	—	—	1	1	1	—	—	—	1	3	—	—	8	11	C
1	—	—	2	3	1	—	—	1	2	1	—	—	—	1	—	—	—	—	—	9	—	—	4	13	
—	—	—	—	—	1	—	—	—	1	1	—	—	—	1	—	—	—	—	—	4	—	—	4	8	
1	—	—	4	5	2	—	—	1	3	—	—	—	—	—	1	—	—	—	1	4	—	—	5	9	D
—	—	—	7	7	3	—	—	1	4	—	—	—	—	—	—	—	—	1	1	3	—	—	9	12	
4	—	—	3	7	—	—	—	—	—	—	—	—	—	—	—	—	—	1	1	4	—	—	4	8	
—	—	—	—	—	6	—	—	—	6	2	—	—	1	3	2	—	—	—	2	10	—	—	1	11	E
—	—	—	—	—	6	—	—	3	9	3	—	—	—	3	1	—	—	—	1	10	—	—	3	13	
—	—	—	—	—	5	—	1	3	9	2	—	—	—	2	3	—	—	1	4	10	—	1	4	15	
—	—	—	—	—	—	—	—	—	—	9	—	—	4	13	2	—	—	—	2	11	—	—	4	15	A
—	—	—	—	—	—	—	—	—	—	6	—	—	3	9	2	—	—	1	3	8	—	—	4	12	
—	—	—	—	—	—	—	—	—	—	5	—	—	3	8	2	—	—	—	2	7	—	—	3	10	
—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	5	—	—	6	11	—	—	—	—	—	E
—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	12	—	—	4	16	—	—	—	—	—	
—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	10	—	—	4	14	—	—	—	—	—	
135																						—	3	91	229

Table VI shows the P and Q efficiencies for each test for each machine. Trout of all sizes were computed together. The tests are arranged in order of decreasing P_t efficiency.

Table VI. Efficiencies P_t and Q_t for trout of all sizes

Machine	Batch and test number	P_t (%)		Q_t (%)		Total number of trout recaptured*
		Test	Machine	Test	Machine	
E	8	65.63	65.63	11.72**	11.72**	123
B	3	45.00	37.50	17.31**	13.25**	122
	6	30.00**		9.19		98
A	2	25.00	20.80	5.07	6.76	140**
	1	22.50		—		127
	7	15.00		8.34		67**
D	5	12.50	12.50	4.60	4.60	101
C	4	4.40	4.40	0.00	0.00	103
General averages		27.50		8.11		

* Number of trout from particular batch (160 fish) recaptured during all the tests, the clearances and found in traps.

** Values discussed in the text.

Table VII. Efficiencies P_t by size classes for trout (‰)

Machine	Test number	Trout size (cm)					
		5-10		10-20		20-30	
		Test	Machine	Test	Machine	Test	Machine
E	8	50.00	50.00	78.30	78.30	90.00	90.00
B	3	32.50	31.25	50.00	38.30	80.00	60.00
	6	30.00		26.60		40.00	
A	2	13.70	15.80	31.60	24.40	50.00	30.00
	1	13.70		31.60		30.00	
	7	20.00		10.00		10.00	
D	5	11.20	11.20	11.60	11.60	20.00	20.00
C	4	5.00	5.00	1.60	1.60	10.00	10.00
General averages		22.00		30.00		41.00	

Table VIII. Efficiencies P_e and Q_e for eels of all sizes

Machine	Batch and test number	P_e (%)		Q_e (%)		Total number of eels recaptured*
		Test	Machine	Test	Machine	
E	8	45.00	45.00	20.00	20.00	41
B	3	26.60	27.45	7.50	9.85	25
	6	28.60		12.20		39
A	2	30.00	24.87	15.00	17.22	26
	1	11.60		—		42
	7	33.30		19.45		37
D	5	16.60	16.60	0.00	0.00	32
C	4	8.30	8.30	2.44	2.44	29
General averages		25.04		11.36		

* Number of eels from particular batch (60 fish) recaptured during all the tests, the clearances and found in traps.

Table IX. Efficiencies P_e by size classes for eels (%)

Machine	Batch and test number	Eel size (cm)					
		20—30		30—40		40—50	
		Test	Machine	Test	Machine	Test	Machine
E	8	25.00	25.00	60.00	60.00	50.00	50.00
B	3	25.00	27.50	25.00	27.50	30.00	27.50
	6	30.00		30.00		25.00	
A	2	35.00	33.33	20.00	18.33	35.00	23.33
	1	20.00		5.00		10.00	
	7	45.00		30.00		25.00	
D	5	5.00	5.00	0.00	5.00	20.00	20.00
C	4	10.00	10.00	30.00	30.00	10.00	10.00
General averages		24.31		25.00		25.62	

Table VII shows the P_t efficiencies for each test for each machine. Results for different size classes were computed separately. Q_t efficiencies by size classes are not significant owing to the small samples, and have not been shown in the Table.

Table VIII shows the P_e and Q_e efficiencies for each test for each machine. Eels of all sizes were computed together. The order in the case of P_e efficiencies is the same as that for trout. This is, however, not true for Q_e efficiencies.

Table IX shows the P_e efficiencies for each test for each machine for different size classes of eels. As in the case of the trout, the Q_e efficiencies are not shown, owing to lack of data.

4. DISCUSSION

In order to obtain a correct interpretation of the differences in efficiency between the various machines, it would be necessary to make a statistical comparison of the variability of the results, both for each machine and between the various machines. Unfortunately the factors which disturbed the course of operations, introduced into the experimental data uncertainties which preclude a statistical interpretation. We must therefore restrict ourselves merely to commenting on the results, accepting that they have only a doubtful validity.

Examination of Tables VI and VII, which both concern the trout, reveals considerable differences in efficiency between the machines. These differences could be the result of simple chance or artifacts, but possibly they may appear to be logically distributed.

Taking Table VI first of all; the results have been arranged in order of P_t decreasing efficiency values, by test. The order, taken by machine, remains the same, which goes to show the variation in the results between tests for a given machine is insufficient to affect the order of placing. This is not rigorously repeated in the case of the Q_t efficiencies, though it might have been expected analogy that a machine showing a higher P_t efficiency would probably display a higher Q_t efficiency also. Now, certain of these Q_t efficiencies appear to be dubious; these are underlined in Table VI.

The value 11.72% seems to be underestimated for machine E, which was chosen for making the clearances on account of its relatively great and constant efficiency (32.16% on average, calculated for clearances of Table IV). It is now acting with an efficiency Q_t on the fish remaining in the stream after the previous test, namely, test 7. It is seen that of batch 7 only 67 trout have been recaptured by all efforts (2 tests, 2 clearances and the traps) out of 160 trout put in³. This is by far the smallest proportion. As it has been established that trout succeeded in passing under the traps, it may be questioned whether the percentage escaping was not exceptionally high in the case of this batch. This would

³ It might be supposed that the small proportion of trout from batch 7 recaptured, and the large proportion from batch 2, were the result of the number of fishings to which they had been respectively subjected: 4 fishings for batch 7 and 12 for batch 2, including the clearances. This is not so; one of us has calculated that 95% of the fish introduced are caught in the first 3 fishings. The susceptibility to capture diminishes greatly from one fishing to the next.

therefore result in a slight underestimate for the efficiency in test 8, which would have been calculated on a theoretical number of fish greater than the true number. If this hypothesis is correct, the P_t efficiency of test 7 would also be underestimated, diminishing the variations in the results for machine A.

The value of 17.31% for test 3 appears to be an overestimate. It refers to a Q_t efficiency calculated on the fish of the batch 2. Now, in this test 140 out of 160 fish were recaptured, a proportion very great compared with the others³. It was reported above that an excessive number of trout was introduced in error in one of the three first tests; this probably occurred in test 2, and the Q_t efficiency for test 3 would then have been an overestimate. An excessive stocking for test 2 would consequently have resulted in an overestimate of the P_t efficiency for this test, and consequently a reduction in the variations between the P_t efficiency values for machine A.

There is a surprising large difference between the P_t efficiency of 45% and 30% for tests 3 and 6, both carried out with machine B. It has already been stated in the description of the course of the tests that this machine was out of action for several minutes when the electrodes were near the upstream trap, and a considerable number of large trout was collected in the space between. During the repair, these trout could have escaped downstream, which would explain why the efficiency was particularly low for large trout (Table VII).

Thus the anomalies appearing in Tables VI and VII appear to be due to known artifacts rather than variations caused by the experimental method itself.

There are additional arguments lending support to the results. Each size category can be considered as an independent batch, enabling each test to be considered to some extent on a triple basis. For the P_t efficiencies, it is obvious that the order shown for the machines in Table VII according to fish length remains the same as that for the fish irrespective of length. It is also obvious that for each machine the P_t efficiencies increase with fish size, as has been well known for a long time. In the case of Q_t efficiencies by size classes, the very small number of specimens robs the results of any significance.

In Tables VIII and IX, which both concern the eels, the tests are listed in the same order as for trout: that of decreasing P_t efficiencies. The order for the machines remains the same for eels as for trout as far as the P_e efficiencies are concerned. If however, the results are examined in detail, they appear far less homogeneous than those for trout. In particular, the order of P_e efficiencies by size classes is not the same. The efficiencies for each test do not increase with length, contrary to the case with trout. This may be explained by the range of the size

classes, 5 to 30 cm for the trout, only 20 to 50 cm for the eels, but there may be also other reasons concerned with the physiology of the animals. The great disparity of the results for eels appears to depend, among other factors, on the relatively small number of eels in each test: 60 eels as against 160 trout.

As concerns the traps, they were intended not only to prevent the escape of fish from the sector fished, but also to show the driving effect produced by any particular machine. They were only partly successful, as trout were able to pass under them. Table X shows that the proportion of fish taken by the traps is small; the results have no great significance. It can be seen, however, that the proportion of fish taken in the downstream trap is always much greater than in the upstream trap; it is possible that the downstream captures are due to drifting fish shocked during the fishing operation.

Table X. Fish caught in the traps

Machine	Test No.	Upstream trap		Downstream trap		Total by machine
		Fish from batch under test	Fish from other batches	Fish from batch under test	Fish from other batches	
B	6	—	—	1 trout + 1 eel	1 trout	3
A	2	—	1 eel	6 trout	—	9
	1	—	—	2 eels	—	
D	5	—	—	—	2 trout	2

* With other machines and tests no fish were caught in the traps.

The method tested has shown that a comparison between the efficiencies of fishing machines could be made, and apparently consistent results obtained. However, variations in the results for a single machine, probably due to the experimental artifacts mentioned above, prevent us accepting the conclusions as definite.

The tests demonstrated that fish become progressively harder to catch; the following figures show the great reduction in efficiency between the first and the third fishing:

mean efficiency P (first fishing): $P_t = 27.50\%$; $P_e = 25.04\%$
 mean efficiency Q (third fishing): $Q_t = 8.11\%$; $Q_e = 11.36\%$

In the case of the machine E, there are two successive fishings: the test fishing and the clearance, which constitutes a second fishing. These provide values of: 65.63% for the first, and 32.73% for the second fishing.

This diminution of efficiency in the course of successive fishings is

a serious factor in estimating the efficiency of a machine or an electrical regime. In fact it is likely that this diminution varies between various electrical regimes and fishing methods. In fish population estimations, which are in several countries the chief use of electrical fishing, it is important to maintain a high efficiency throughout several fishings; in fact, the widely used De Lury method (De Lury 1947) is based upon the constancy of fishing efforts over several successive fishings.

Lastly, these tests have shown that the efficiency diminished also with diminishing size among the trout; this result was expected, and it did not seem worth-while to complicate the organization with additional length categories. This does not, however, seem to be the case with eels. These are more easily stunned than trout, and thus less able to approach the anode; this phenomenon is correspondingly more marked as size increases, and it may be that efficiency is greater in the case of small eels. This must be taken into consideration at the start when selecting the correct size of eels for the test batch.

Another criticism which may be made of the method used was the low efficiency of the clearance operations (32.86% on average) compared with anticipation. The probable cause is insufficient smoothing of the current generated by the machine used. This resulted in leaving fish in the river in increasing numbers as the tests went on, and thus created circumstances more and more defavourable for successive machines. But even if the clearance machine had produced pure direct current, its efficiency would have been inadequate, as the clearance operation represented a second fishing at correspondingly reduced efficiency. For this method to be rigorously applied, it thus appears necessary that the channel be drained and totally cleared of fish after each test.

Having the experience of the above tests some recommendations could be made for future efficiency tests.

We have just seen that the channel should be drainable. It should in addition include natural features: shelters, rocks, weed, water speed, etc. If the channel is too easy to fish, there will be insufficient differences between various machines. The use of traps both upstream and downstream appears to be worth retaining; the lower one collects shocked fish washed downstream, and the upper one ensures that fish which have escaped upstream in front of the anode shall not be too easily captured, as they would if finally confined between the anode and a simple grid.

The composition of fish in terms of species and sizes depends on the object which is intended. For example, if the efficiency of a current for capturing small trout is being studied, it is useless to release larger trout into the test section. In our view it is better to simplify the sampling by using fish of the same size, and to compensate for this restriction on the information by using a great number of fish. In the matter of number, 200 fish per test appears to us a suitable number. The tests carried out

with eels were not significant because their numbers (60) were inadequate and also because the technique for catching eels is different from that for trout.

The study of the *P* efficiency must obviously be continued. It permits comparison between machines used for a single fishing (excluding population estimates), as for example a salvage operation or commercial fishing. But it is insufficient to characterize a machine making population estimates. As we have already pointed out, catchability diminishes considerably from one fishing to the next, and this diminution may be greater or less according to the machine used. In general, it seems considerably more evident with pulsed currents than with continuous direct current. It therefore appears important to measure the *Q* efficiency for a second fishing; in the tests carried out at Czarci Jar, the *Q* efficiency related to the third fishing, as the clearance was the second.

The *Q* efficiency could be measured in the following conditions: the fish caught in the first sweep should not be replaced in the water; the *Q* efficiency would be calculated so:

$$\frac{\text{Fish caught in the second fishing}}{\text{Total stocked fish less fish caught in the first fishing}}$$

This has the advantage of approximating the test to the De Lury (1947) method.

The incidents in the field trial such as faults during the test, hazards of weather, etc., make it essential that a machine should be tested several times. This is equally desirable for the statistical interpretation of the results. It seems that 3 tests per machine make an adequate number in view of the limited time available for this kind of operation.

We have seen that the emptying the channel would be an essential operation between each test and the next. Before undertaking a new test, it would seem necessary to make equated inventory of the fish caught: fish stocked = fish caught by the machine + fish collected during emptying. If in spite of the precautions taken, fish still remain in the channel after emptying — and this will probably occur with eels — it will be necessary to take account of them in the succeeding test. For this reason it would be better to mark the fish intended for each test by fin clipping.

The method used in this study requires experimental arrangements which have been thoroughly proved. If the tests carried out at Czarci Jar did not provide definite results, it was partly because the experimental arrangements had not been tested in advance. Moreover, it could only be carried out at a fish farm, where an artificial channel capable of being emptied, and a sufficient number of fish, would be found. The possibilities of its use are therefore restricted.

We will conclude by repeating that in the absence of a fish farm, it is always possible to use on a river, and in natural conditions the method proposed by Lamarque. However, it is important in this case, to be sure that the number of fish in the test river is sufficiently important to get significancy.

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5. SUMMARY

International group of experts was assembled to demonstrate their electrical fishing machines in the same trout stream. Each was asked to arrange in his own way to obtain the best efficiency. In this manner five machines, four of which were portable, producing different currents and using several fishing techniques, were tested. Their efficiencies were determined by means of the experimental method proposed by R. Cuinat. The efficiencies were worse than the ones hoped for. There were great differences of efficiency between the machines both in the first fishing (*P* efficiency) and in the third (*Q* efficiency). The tests demonstrated that in successive fishings the fish become progressively harder to catch.

It was shown that a comparison between the efficiencies of fishing machines could be made and apparently consistent results obtained.

On the grounds of the experiences earned at these tests some recommendations are made to improve the experimental method and the whole course of such tests.

6. STRESZCZENIE

Specjaliści z kilku krajów zebrali się dla zademonstrowania połowów w wybranym cieku pstrągowym przy pomocy przywiezionych przez siebie agregatów elektrycznych. Każdego proszono, aby prowadził połów w sposób, który, jego zdaniem, zapewnić może najlepszy wynik. Przebadano pięć agregatów wytwarzających różne prądy i wymagających użycia różnej techniki połowu. Cztery z tych agregatów były przenośne. Ich skuteczności połowowe określano wg metodyki zaproponowanej przez R. Cuinat. Skuteczności te okazały się gorsze niż się spodziewano. Poszczególne agregaty różniły się znacznie od siebie zarówno w skuteczności pierwszego połowu (skuteczność *P*), jak i trzeciego (skuteczność *Q*). Próby pokazały, że w następujących po sobie połowach ryby coraz trudniej poddają się połowowi.

Wykazano, że porównanie agregatów połowowych pod względem ich skuteczności jest możliwe i że osiągnane wyniki są najwyraźniej logiczne.

W oparciu o zdobyte doświadczenia sformułowane zostały zalecenia odnośnie ulepszenia metodyki tych badań i całego ich przebiegu.

7. RESUME

Des experts, réunis en un groupe international, ont expérimenté leurs appareils de pêche à l'électricité dans un même ruisseau à truites. Chacun d'eux s'est efforcé, selon sa propre méthode, d'obtenir la meilleure efficacité. C'est ainsi qu'ont été testés cinq appareils de pêche—dont quatre portables—produisant différents courants et utilisant plusieurs techniques de pêche. Leurs efficacités ont été déterminées selon la méthode expérimentale préconisée par R. Cuinat.

Ces efficacités ont été inférieures à celles que l'on espérait obtenir. De grandes différences d'efficacité sont apparues entre les appareils, à la fois dans la première pêche (efficacité P) et dans la troisième (efficacité Q). Les essais ont montré que lors de pêches successives le poisson devenait progressivement plus difficile à capturer.

Ces tests ont montré qu'il était possible de comparer, de façon valable, l'efficacité de plusieurs appareils.

Sur la base des enseignements tirés de ces tests, quelques recommandations ont été faites pour améliorer la méthode expérimentale et le déroulement de ce genre de tests.

8. REFERENCES

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FATIGUE AND MORTALITY EFFECTS IN ELECTRICAL FISHING¹

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ABSTRACT

The fish were exposed to the current supplied by the machines which had been tested for their fishing efficiency, in conditions as close as possible to those of fishing tests. The time which elapsed between the commencement of exposure and the instant at which the fish recovered was taken as the Index of Fatigue. Subsequent mortalities were also recorded. Indices of Fatigue are discussed in relation to the machine under test, distance from anode, fish length and number of exposures to the current.

1. INTRODUCTION

One of the factors which contribute to diminish the efficiency of electrical fishing is the tetanic effect of the current in the first fishing and the fatigue, which may follow in subsequent fishings. In the first instance, fish stunned in their lairs have less chance of being caught, and those which are already close to the anode are washed away before there is a time to catch them. In the second case, tired fish may not be equally catchable, and the efficiency of a second fishing may be affected by this. It is therefore important in the plan of research to determine which currents have the least possible tetanizing and fatiguing effects.

One of the qualities essential in the electric fishing compared with other methods is avoiding damage to fish. Occasionally it is observed that even in practical electric fishing, fish can be killed.

The EIFAC group of experts met at Giżycko (Northern Poland) with the objective to measure the efficiency of their electrical fishing machines in the same trout stream. The results of this experiment have been reported by Chmielewski et al. (1973). It appeared then appropriate to complement the efficiency tests with at least some simple observations on the fatigue and mortality effects caused by the machines tested. The results of such tests could have been susceptible to statistical analysis, but then the tests had to be designed specially for this. In this first experiment, it was felt preferable to organize the tests in an exploratory manner, with the object of obtaining the maximum amount of data.

The principle employed was the exposure of fish for a definite time to the current supplied by the machines which had been tested for their fishing efficiency, in conditions as close as possible to those of the fishing tests. The fish were

¹ Technical Report of the EIFAC Working Party on Electrical Fishing held at Giżycko, Poland, October 1969.

stunned for a set time, and the stunning or lass of equilibrium persisted after the current was switched off. The time which elapsed between the commencement of exposure and the instant at which the fish recovered was taken as the Index of Fatigue. Subsequent mortalities were also recorded.

2. MATERIAL AND METHODS

Each machine was tested against two batches of trout. Each batch consisted of 6 fish, one each at 10–15, 20–25, 25–30 cm, and two at 5–10 cm.

A container consisting of a wooden framework covered with plastic mesh forming an enclosure 40×40 cm, and having a plastic mesh partition dividing it across the center to form front and back compartments 40 cm wide and 20 cm thick, was used to contain both batches of fish (Fig. 1).

The anode of the machine under test was located in front of the box, 20 cm from the central partition on the first occasion and 40 cm on the second. This provides 4 combinations of distances, corresponding to the relative field intensity to which the fish were exposed: test at 20 cm—fish in compartment G and H; test at 40 cm—fish in compartment G and H.

The cathode was put in the same position relative to the anode which it occupied during the efficiency test.

The distribution of the fish in the two compartments, by number and size, can be seen from the column headings of Table I. Fish were placed in the two compartments and the anode of the machine under test was placed, as previously stated, at 20 cm from the central partition for the first test. The current was then switched on for 15 sec. The fish were timed from the start of the exposure period to the instant at which they regained their equilibrium. In order to eliminate variations in the assessment of this point, the timing was done by the same operator throughout. The time measured was taken as the Index of Fatigue. The fish were stimulated with a probe to accelerate their recovery. This method is obviously open to criticism, but in the field conditions of the tests, it was difficult to use a better one.



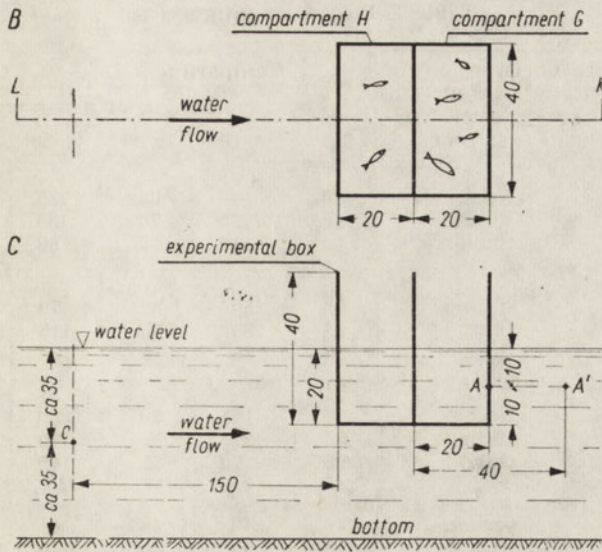


Fig. 1. Fatigue and mortality tests arrangements (dimensions in cm). A—general view, B—view from above, C—section along LK. A, A'—location of anode's centre, C—location of cathode's centre

From the commencement of this first exposure to the current, a time of five minutes was allowed to elapse before the same batch of fish was subjected to a second exposure to the current in the same conditions, and then to a third.

A second test followed with the fish of another batch, and the anode located 40 cm from the central partition. The conduct of the second test was identical with that of the first.

3. RESULTS

The results are shown in Table I. Three fish were lacking. Only a single fish was dead, which precludes interpretation of the mortality effects. On this point, the tests were insufficiently rigorous. In calculating the averages for the Indices of Fatigue, the dead fish was timed for 300 sec. This is in fact a time after which a trout which is not yet breathing has little chance of survival without an artificial breathing.

4. DISCUSSION

A matter of some interest is whether there appears any simple dependence between the Indices of Fatigue and the efficiencies. Table II shows the mean Indices of Fatigue for each machine with the corresponding first fishing efficiencies for trout. There is no obvious relationship. The following comments may, however, be made. Machine D, with a relatively low efficiency, appeared to cause more shocking; was its low efficiency due to this? Machine C, which had a particularly low effi-

Table I. Indices of fatigue (sec)

Machine	Distance of anode from central partition (cm)	Occasion of exposure to electric current	Compartment G				Compartment H	
			Length of a fish (cm)					
			5-10	5-10	15-20	25-30	10-15	20-25
A	20	first	40	40	65	235	65	25
		second	40	55	70	150	20	20
		third	40	110	55	56	35	25
	40	second	50	50	30	70	25	55
		first	35	35	30	115	35	25
		third	35	35	35	180	30	30
B	20	first	35	185	50	220	25	30
		second	35	225	95	140	25	25
		third	55	70	55	145	25	20
	40	second	40	40	45	6	25	25
		first	45	50	35	110	30	95
		third	30	30	90	145	40	25
C	20	first	35	35	35	45	25	25
		second	45	45	20	20	20	20
		third	20	20	20	20	20	20
	40	first	25	24	30	30	26	35
		second	20	20	20	20	20	20
		third	25	25	20	25	40	20
D	20	first	80	no fish	105	190	35	30
		second	41	no fish	70	65	25	25
		third	55	no fish	120	MORI*	25	25
	40	first	95	95	155	40	25	25
		second	35	40	230	60	30	45
		third	40	40	210	40	25	25
Mean			41.46	60.43	71.70	103.37	29.00	30.21

* The dead fish was timed for 300 sec.

ciency, had by far the lowest Index of Fatigue. Can this be the direct result of insufficient effect on fish?

A great variation of the values for the Index of Fatigue is obvious in Table I, to the extent which makes questionable to what point those in Table II may be considered significant. This dispersion may be due to the distance between fish and the anode at the instant of the test. The fish were in fact distributed at random in the two compartments. Those in the compartment nearer to the anode could be at any distance between 0 and 20 cm from it in one test, and between 20 and 40 in the other. In the first case, the potential gradient falls very rapidly in the

Table II. Means of indices of fatigue by machine and their first fishing efficiencies for trout

Machine	Means of Indices of fatigue (sec)	First fishing efficiency (%)
D	74	12.50
B	67	37.50
A	57	20.80
C	26	4.40

20 cm; it follows that the fish adjacent to the anode (0 cm) are subject to much more current than those at the back of the compartment (20 cm).

By taking as a reference value the distance from the centre of each compartment, four groups of distances are obtained: one of 10 cm, two of 30 cm, and one of 50 cm. By making a differential division of the length classes between the various groups, it is possible to compare them two by two: a distance of 10 cm against one distance of 30 cm; the other distance of 30 cm against a distance of 50 cm.

The comparison is given in Table III. It may be considered that even if the Index of Fatigue appears to decrease significantly between 10 and 30 cm, a difference is not recognizable between 30 and 50 cm. This result was readily predictable. The conclusion is that for future tests, there is no point in using distances over 20 cm.

Mean Indices of Fatigue given in a final line of Table I seem to suggest that fatigue increases with fish length. It is necessary for the interpretation of the results to separate the values of the compartment G from those of compartment H, since the two are at different distances from the anode. For the trout of compartment G the variations between the mean Indices of Fatigue are greater than those found in H; the greater distance diminishes the variations.

Table IV shows the distinct decrease in the Index of Fatigue with successive exposures to the current for the 20 cm distance. This appears to represent a diminished sensitivity to the electric current on the part of the fish, and might be correlated with the diminishing efficiency of successive fishings.

Therefore, in the reported tests the following phenomena have been observed: variation of Indices of Fatigue between different machines; increased value of the Indices with increasing field intensity; increased

Table III. Indices of fatigue in relation to the distance from anode for trout (sec)

Machine	Occasion of exposure to electric current	Distance from anode (cm)			
		10	30	30	50
		Number and length (cm) of fish to be compared			
		2 5—10; 1 15—20; 1 25—30		1 10—15; 1 20—25	
A	first	95	50	45	40
	second	79	54	25	30
	third	65	71	30	30
	Mean	79.66	58.39	33.33	33.33
B	first	97	46	27	25
	second	123	60	25	62
	third	81	74	22	37
	Mean	100.33	60.00	24.66	41.33
C	first	37	27	25	30
	second	32	20	20	25
	third	20	23	20	30
	Mean	29.66	23.33	21.66	28.33
D	first	125	96	32	25
	second	58	91	25	37
	third	158	82	25	25
	Mean	113.66	89.66	27.50	29.16
General mean		80.83	57.84	26.75	33.00

Table IV. Indices of fatigue (sec) in successive exposures to the current

Machine	Distance from anode to central partition (cm)								
	20			40			All distances		
	Occasion of exposure								
	first	second	third	first	second	third	first	second	third
A	78.40	61.00	53.50	46.70	45.90	64.20	62.55	53.45	58.85
B	91.00	91.00	61.00	39.00	60.00	60.00	65.00	75.50	60.50
C	33.00	28.00	20.00	28.00	21.00	20.00	31.00	24.50	23.00
D	88.00	45.00	45.00	72.00	80.00	63.00	80.00	62.50	54.00
Average	72.60	56.26	44.87	46.42	51.72	53.30	59.63	53.99	49.09

value of the Indices with increasing trout length; decreasing value of the Indices with successive exposures to current, indicating a diminishing sensitivity in the fish; virtual absence of mortality, which discounts any subsequent damage caused by the machines.

Throughout, the differences are masked where the potential gradient is insufficient.

These results were in fact easy to foresee. The advisability of carrying out such tests in the field, where conditions are variable, is debatable. It appears to us that a rigorous fatigue and mortality test ought to be made in laboratory. The test should no longer be considered in connection with the comparison of the machines themselves, but comparison of types of current. The experimental conditions should therefore be standardized in terms of following parameters: water conductivity, a standard fish length, the dimensions and characteristics of the experimental trough, the period of exposure, the determination of the Index of Fatigue or Mortality, etc.

Acknowledgements

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5. SUMMARY

In the course of testing efficiency of portable electrical fishing machines, it appeared appropriate to make some simple observations on the fatigue and mortality effects in the fish. In conditions as close as possible to those of fishing tests, the fish were exposed to the current supplied by the machines. The stunning or loss of equilibrium persisted after the current was switched off. The time which elapsed between the commencement of exposure and the instant at which the fish recovered was taken as a measure of the Index of Fatigue. Only a single fish was dead, which precluded interpretation of the mortality effects.

The following phenomena have been observed: Indices of Fatigue varied between different machines; values of the Indices increased with field intensity and fish length; in successive exposures to current the Indices decreased, indicating a diminishing sensitivity in the fish; mortality was virtually absent, which discounts any subsequent damage caused by the machines.

It is concluded that carrying out such tests in the field, where conditions are variable, is debatable. A rigorous fatigue and mortality test ought to be made in laboratory.

6. STRESZCZENIE

W trakcie badań skuteczności połowowej przenośnych agregatów elektrycznych uznano za właściwe przeprowadzenie kilku prostych prób odnośnie zmęczenia i śmiertelności u ryb. W warunkach możliwie najbliższych tym, jakie miały miejsce w badaniach skuteczności, poddawano ryby działaniu prądu elektrycznego pochodzącego z tych agregatów. Ogłuszenie lub utrata równowagi utrzymywały się jeszcze po wyłączeniu prądu. Za miarę wskaźnika zmęczenia przyjmowano czas, jaki upłynął od początku oddziaływania do chwili, w której ryba powracała do normy. Tylko jedna ryba została zabita. Fakt ten wyklucza zajmowanie się sprawą śmiertelności.

Zaobserwowano następujące zjawiska: wskaźniki zmęczenia były różne dla poszczególnych agregatów; wartości tych wskaźników wzrastały wraz z natężeniami pola i długością ryby; w następujących po sobie oddziaływaniach prądu wskaźniki malały, co wskazuje na zmniejszającą się wrażliwość u ryb; śmiertelność u ryb w zasadzie nie wystąpiła; pozwala to przyjąć, że agregaty nie czynią żadnej szkody.

Wnioskuje się, że przeprowadzanie tego rodzaju badań w terenie, gdzie warunki są zmienne, jest niecelowe. Dokładne badania zmęczenia i śmiertelności winny być wykonywane w laboratorium.

7. RESUME

Une série de tests d'efficacité d'appareils portables de pêche électrique a été réalisée par un groupe international d'experts, au cours d'une réunion en 1969 à Giżycko (Pologne). A cette occasion, il parut intéressant de faire quelques observations simples quant aux effets (fatigue, mortalité) sur des truites exposées aux courants fournis par les divers appareils, dans des conditions aussi proche que possible de celles des tests.

Les phénomènes suivants ont été observés: les indices de fatigue variaient selon les différents appareils; leurs valeurs augmentaient avec l'intensité du champ et la longueur des poissons; lors d'expositions successives au courant, les indices diminuaient, révélant ainsi une sensibilité déclinante chez les poissons; la mortalité, virtuellement inexistante, rendait négligeable tout effet dommageable causé par les appareils de pêche.

L'interprétation statistique des résultats n'a pu être faite et il est apparu que la mise en oeuvre de tests de fatigue et de mortalité donnerait des résultats plus rigoureux en laboratoire que sur le terrain, où les conditions sont variables.

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