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POLSKIE ARCHIWUM HYDROBIOLOGII (Pol. Arch. Hydrobiol.)	19	1	1–9	1972

S. RAKUSA-SUSZCZEWSKI

WINTER HYDROLOGICAL OBSERVATIONS IN ALASHEYEV BIGHT, EASTERN ANTARCTIC

Department of Bioenergetics and Bioproductivity, Nencki Institute of Experimental Biology, Pasteura 3, Warsaw, Poland

ABSTRACT

Hydrological observations were carried out in the coastal region of Alasheyev Bight, near the station Molodezhnaya. Measurements and analyses of water were performed at 10 days intervals from June to October 1969 on 8 horizons from the surface to the depth of 137 m by the bottom. Changes of temperatures, as well as of oxygen and silica contents in water were recorded. They are periodic in character. Hydrological conditions in the Bight were compared with those prevailing in other coastal regions of the Antarctic.

1. INTRODUCTION

Winter hydrological observations in the coastal regions of the Antarctic continent were carried out only sporadically, mainly in the neighbourhood of the stations McMurdo (Littlepage 1965 and others), Mawson (Bunt 1960) and Mirny (Chikovskiy 1969). Continuous observations establishing hydrological changes during the winter season have been lacking for Alasheyev Bight. Researches by Ledenev (1965, 1967) covered only the period of Antarctic summer in this region. According to the latter author, the main mass of water of Alasheyev Bight has the temperature from —1.4 to —1.8°C. Salinity of water ranges from 34.2 to 34.6‰, the amount of oxygen from 8.2 to 7.0 ml/l.

It was the aim of the present paper to contribute to the knowledge of hydrological conditions prevailing in the coastal waters of the Bight, as these may have a decisive influence upon the biological aggregates of the pelagic and sub-glacial zones.

Measurements of temperature and of oxygen contents in water were taken. The collected samples also allowed for a rough estimation of the silica contents.

2. TERRAIN DESCRIPTION AND METHODS

Alasheyev Bight is situated in Eastern Antarctic at the coast of Enderby Land (Fig. 1). The eastern coast of the Bight forms the Tang Peninsula, and its southern coast is the Antarctic continent. From NW to SE the Bight is crossed by a trench with depths down to 1000 m at the shore.

In greater depths there are deposits of warmer and more salined waters (Botnikov 1967) with lesser oxygen contents (Ledenev 1967), inflowing from the open sea. The directions of the inflow and the patterns of circulation of water are not quite clear, since the existence of a confluence and contact of waters of Alasheyev and Lena Bights under the Tang Peninsula (Vaigachev 1963) is not definitely established. Alasheyev Bight is covered with ice from the middle of May through March (Yeskin 1969). The thickness of ice in the littoral zone reaches

140-150 cm. Climatic conditions in the region are illustrated by the data of the meteo station Molodezhnaya (cf. Table I).

Observations were performed on the Bight at the point situated about 900 m north from Thala Hills (67°39′ S, 45°50′ E, Fig. 1 B). Temperature was measured and water samples were drawn at about ten days intervals from June 13 to October 9, 1969. All the works were carried out inside a tent providing a shelter against the weather conditions. Each time two overlapping holes were bored in the ice, 30 cm in diameter each. A Cherepanov's (1965) bore was used. Bathometers and plankton nets 0.5 m in diameter were lowered down into the hole. A hand winch with two cranks was used. The depth at the investigated spot was 140 m. Temperatures were measured successively at the horizons of 1, 10, 25, 50, 75, 100, 125 and 137 m by means of reversible thermometers allowing for a reading exact to 0.01°C. At the same time samples of water were taken by means of bathometers. Water from the bathometers was poured into glass bottles for oxygen content analysis. After the bottle was over-filled a couple of times, it was closed with a glass cork cut to fit and it was submerged without any fixing in a thermos with sea water. The analyses were performed a few hours later in the station house. Oxygen contents was determined by the Winkler's method. In the samples of water transported to the country in April 1970, Cl and Si contents were determined. The

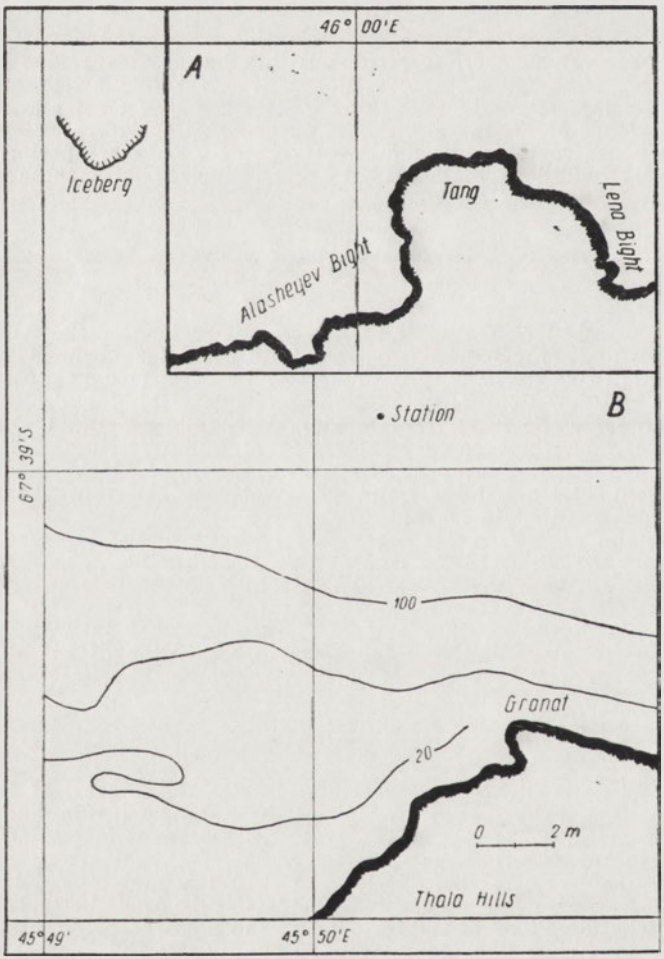

Fig. 1. Map of the investigated region (the Antarctic). A — Alasheyev Bight, B — location of the station for hydrological researches

Table I. Some meteorological data for the Thala Hills Area, Enderby Land, Antarctic, according to the observations of the Soviet Station Molodezhnaya (67°40.3′ S, 45°50.3′ E, 39 m a.s.l.)

Month	Mean air temperature (°C)		Mean velocity of wind (m/sec)		Mean air pressure (mb)		Mean air pressure for decade (mb)		
	1964-1968	1969	1964-1968	1969	1964-1968	1969	1969		
I	—0.6	0.0	5.6	6.7	987.6	991.1	986.9	991.6	994.3
II	—4.6	—2.4	7.7	8.2	988.7	986.6	988.2	988.2	982.7
III	—7.8	—7.4	11.9	13.0	982.4	979.8	983.3	978.3	978.2
IV	—11.2	—11.2	14.3	12.8	980.2	986.3	990.4	988.7	980.1
V	—13.0	—14.2	13.8	14.0	983.9	982.9	973.4	981.2	993.1
VI	—16.2	—14.5	13.0	14.7	987.1	993.2	997.3	1001.3	980.9
VII	—18.6	—18.3	10.9	9.6	986.0	975.1	975.4	970.0	979.4
VIII	—18.0	—21.9	10.5	9.7	978.1	974.6	975.2	976.7	972.2
IX	—18.4	—18.6	10.1	7.4	976.0	977.1	970.3	980.1	980.9
X	—14.1	—13.2	9.8	10.1	975.4	984.8	989.5	983.0	982.6
XI	—6.7	—6.6	8.3	8.6	981.8	980.8	985.3	982.5	974.6
XII	—1.5	—1.0	6.2	5.6	985.4	983.0	—	—	—
Mean	—10.9	—10.8	10.2	10.0	982.6	983.0	—	—	—

Table II. Results of hydrological observations performed in Alasheyev Bight during winter 1969 (67°39′ S, 45°50′ E)

Depth (m)	T (°C)	O_2 (ml/l)	Si (μg-at/l)	T (°C)	O_2 (ml/l)	Si (μg-at/l)	T (°C)	O_2 (ml/l)	Si (μg-at/l)	T (°C)	O_2 (ml/l)	Si (μg-at/l)
	13 June, 9.30 a.m. — 12.30 p.m.			24 June, 10.30 a.m. — 1.15 p.m.			4 July, 10.50 a.m. — 12.45 p.m.			14 July, 10.30 a.m. — 12.45 p.m.		
1	—	7.59	—	—1.81	7.72	52.8	—1.80	7.64	52.6	—1.80	7.59	61.7
10	—1.82	8.17	—	—1.81	7.42	55.9	—1.82	7.38	53.9	—1.81	7.42	53.4
25	—	7.37	—	—1.81	7.52	57.4	—1.82	7.42	59.7	—1.82	7.53	47.5
50	—1.81	7.22	—	—1.81	—	53.6	—1.83	7.41	59.2	—1.81	—	58.4
75	—1.81	7.33	—	—1.81	7.52	—	—1.77	7.32	—	—1.81	7.29	58.4
100	—1.80	7.44	—	—1.82	7.47	54.4	—1.79	7.35	61.7	—1.78	7.36	61.5
125	—1.80	7.30	—	—1.81	7.33	—	—1.78	7.31	61.2	—1.74	7.23	61.2
137	—	—	—	—1.82	7.36	—	—1.81	7.34	58.7	—1.72	7.13	61.2
Mean	—1.81	7.49	—	—1.81	7.48	54.1	—1.80	7.40	58.1	—1.79	7.36	57.9
	26 July, 11.30 a.m. — 1.30 p.m.			5 Aug., 10.50 a.m. — 12.45 p.m.			16 Aug., 10.45 a.m. — 12.45 p.m.			25 Aug., 11.15 a.m. — 1.10 p.m.		
1	—1.81	7.58	54.9	—1.81	7.32	58.2	—1.82	7.43	54.4	—1.83	7.46	58.2
10	—1.82	7.00	55.1	—1.81	7.30	54.1	—1.82	7.31	52.1	—1.81	7.26	58.2
25	—1.81	7.31	56.9	—1.82	7.25	51.6	—1.81	7.26	55.4	—1.82	7.32	57.4
50	—1.78	7.26	57.7	—1.82	7.37	—	—1.82	7.22	52.3	—1.80	7.22	57.9
75	—1.76	7.26	55.9	—1.82	7.27	56.2	—1.81	7.21	49.8	—1.76	7.19	58.7
100	—1.77	7.12	58.2	—1.82	7.19	53.1	—1.82	7.14	53.1	—1.74	7.01	58.4
125	—1.74	7.24	60.0	—1.82	7.22	52.8	—1.80	7.18	52.6	—1.65	6.81	62.8
137	—1.74	7.06	54.9	—1.81	7.20	57.9	—1.82	7.19	55.6	—1.63	6.77	59.5
Mean	—1.78	7.23	56.6	—1.82	7.27	54.8	—1.82	7.24	53.1	—1.76	7.13	58.8

	5 Sept., 10.50 a.m. — 12.10 p.m.			15 Sept., 11.25 a.m. — 1.15 p.m.			28 Sept., 10.55 a.m. — 1.15 p.m.			9 Oct., 11.45 a.m. — 1.15 p.m.		
1	—1.83	7.39	53.1	—1.83	7.39	54.9	—1.82	7.22	53.9	—1.81	7.14	53.1
10	—1.78	6.69	55.9	—1.80	7.27	55.1	—1.83	7.22	52.3	—1.83	7.27	52.3
25	—1.78	7.30	56.4	—1.81	7.18	52.3	—1.83	7.21	53.9	—1.81	—	52.1
50	—1.72	7.18	57.4	—1.77	6.90	53.6	—1.83	7.26	52.1	—1.81	7.04	53.6
75	—1.72	7.04	57.4	—1.73	7.06	56.4	—1.83	7.12	52.9	—1.81	6.86	56.4
100	—1.67	6.83	58.2	—1.70	7.00	55.9	—1.73	6.94	54.9	—1.73	6.17	61.2
125	—1.62	6.86	59.7	—1.64	6.89	58.7	—1.71	6.81	59.5	—	—	—
137	—1.57	6.84	59.2	—1.61	6.88	56.9	—1.69	6.77	58.4	—1.66	5.95	60.2
Mean	—1.71	7.02	57.2	—1.74	7.07	55.5	—1.79	7.08	54.7	—1.78	6.90	55.5

	T (°C)			O_2 (ml/l)			Si (µg-at/l)		
	Max.	Min.	Mean	Max.	Min.	Mean	Max.	Min.	Mean
1	—1.80	—1.83	—1.82	7.72	7.22	7.46	61.7	52.6	55.3
10	—1.78	—1.83	—1.81	8.17	6.69	7.31	58.2	52.1	54.4
25	—1.78	—1.83	—1.81	7.53	7.18	7.33	59.7	47.5	54.6
50	—1.72	—1.83	—1.80	7.41	6.90	7.21	59.2	52.1	55.6
75	—1.72	—1.82	—1.79	7.52	6.86	7.21	58.7	52.9	55.8
100	—1.67	—1.82	—1.76	7.47	6.17	7.09	61.7	53.1	57.3
125	—1.62	—1.82	—1.74	7.33	6.81	7.11	62.8	52.6	58.7
137	—1.57	—1.82	—1.72	7.36	5.95	6.95	61.2	54.9	58.3

data for salinity are certainly overestimated, since water must have been evaporating from the untight containers. For the same reason the results of the Si contents analysis must be considered as rough estimations.

3. RESULTS

Changes of water temperature in the coastal region of Alasheyev Bight are presented in Table II, Fig. 2. The minimum temperature during the period of investigations was −1.83°C, it was recorded a number of

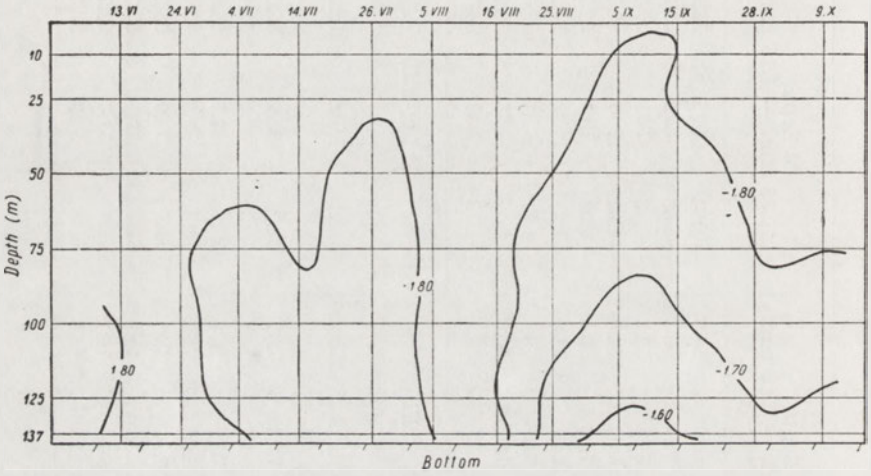

Fig. 2. Changes of water temperature in the coastal region of Alasheyev Bight during winter 1969

times up to the depth of 75 m. The maximum temperature −1.57°C was recorded at the depth of 137 m. The results of the measurements and the shape of the isotherms drafted from them are presented in Fig. 2. It can be seen that at the observed spot warmer waters raised from the bottom of the Bight appeared twice. For the first time the phenomenon was observed in July, and for the second time at the end of August and at the beginning of September. During the intermittent period between the inflows of warmer waters to the coastal region the temperature of water decreased. In the first decade of October the close-to-bottom waters were warmed up a little again.

The changes in oxygen contents are presented in Table II, Fig. 3. The maximum oxygen content was 8.17 ml/l and it was recorded at the depth of 10 m. The minimum oxygen content was 5.95 ml/l and it was recorded in the near-to-bottom layer. From June to October (Fig. 3) the amount of oxygen in water has been gradually decreasing. The oxygen decrease was somewhat accelerated during the raising of warmer profundal waters in the Bight.

The changes of silica contents are presented in Table II, Fig. 4. The

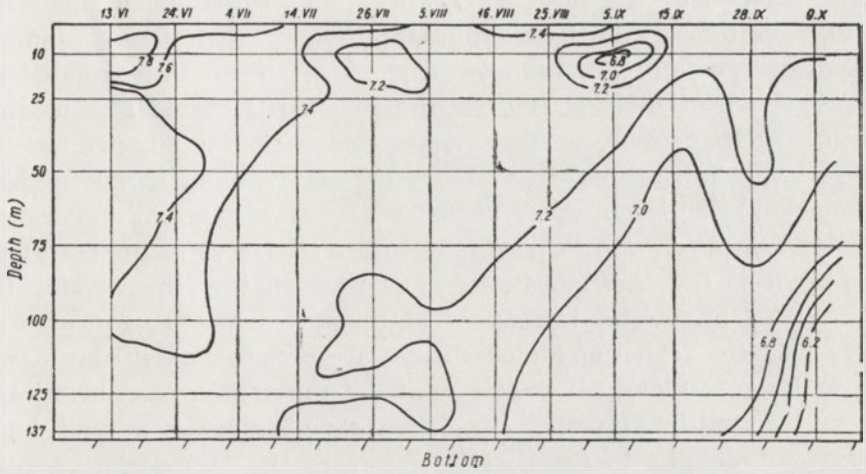

Fig. 3. Changes of oxygen contents in coastal waters of Alasheyev Bight during winter 1969

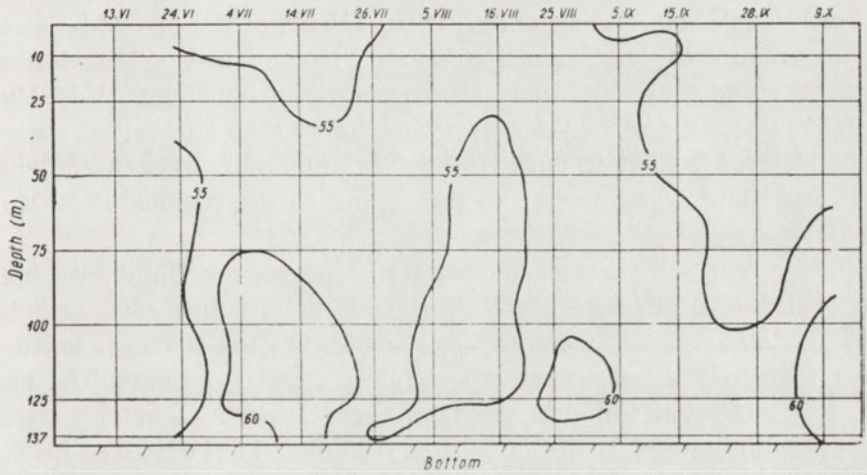

Fig. 4. Changes of silica contents in coastal waters of Alasheyev Bight during winter 1969

minimum amount of silica recorded in the investigated region was 47.5 μg-at/l at the depth of 25 m. The maximum value 62.8 μg-at/l was found out at the depth of 125 m. During the observed influx of waters from the deeper zones of the Bight which were warmer and less saturated with oxygen, the amount of silica in the whole column has been remarkably increasing (cf. Fig. 4).

4. DISCUSSION

According to the measurements, water temperatures in the coastal region of Alasheyev Bight reveal only minor oscillations from June to

October, caused by the raising of water from the profundal zone rather than by air temperatures, steadily decreasing to their yearly minimum in August. The raising of the profundal waters seems to be related with the periodical intensive activity of the cyclons (cf. Table I — mean air pressure for a decade), as the investigated region is situated on their routes. The temperature −1.57°C, recorded at 137 m of depth, points to the possible raising of water of that temperature reposing in Alasheyev Bight at 300 m (cf. Ledenev 1965). Bunt (1960) in his research in the region of the Mawson station suggested that warmer water from other zones might be introduced. Minimum temperatures of water observed in the region of Molodezhnaya are higher than in the Mawson region (Bunt 1960). Maximum winter temperatures are identical in both regions but in Alasheyev Bight they are observed at greater depths.

Oxygen contents in the coastal waters of the Molodezhnaya region had been decreasing during the whole period of research. The difference between the amount of oxygen in the surface and close-to-bottom layers has been steady and increasing during the raising of the profundal waters. The maximum observed values of soluted oxygen in the Molodezhnaya region exceeded those observed in the waters neighbouring with McMurdo (cf. Littlepage 1965), but they were lower than the values observed in the Mawson region (Bunt 1960). The minimum oxygen content in Alasheyev Bight was lower from that found in the regions of McMurdo and Mawson.

Silica contents in the coastal waters of Alasheyev Bight was highly changeable. The differences between the surface and close-to-bottom layers in silica contents were the greatest during the rising of profundal waters with higher temperatures and lower oxygen contents. The maximum and minimum contents of silica were higher in coastal waters of Alasheyev Bight than in the McMurdo region (Littlepage 1965).

A comparison of the results of measurements of temperature, oxygen and silica contents in water clearly reveals the existence of local differences of hydrological conditions at various coasts of the Antarctic continent. The periodical raising of profundal waters characteristic for Alasheyev Bight may be the cause of the large variety of plankton species found in this region (cf. Zvereva 1969). The warmer waters raising from the greater depths can make up for the overcooling of subsurface waters and prevent the formation of ice below the surface, thereby significantly influencing the sub-fast ice community.

Acknowledgements

I wish to thank the chief of the station, Mr H. G. Bunjak, and our Soviet colleagues, for helping us in our work. I also wish to thank Mr K. Opaliński, Msc., for his collaboration and aid.

5. SUMMARY

Hydrological researches were carried out in the coastal region of Alasheyev Bight. From June 13 to October 9, 1969, measurements of temperatures, oxygen and silica contents in water were taken at about 10 days intervals. Measurements were made, and samples were drawn, at the depths of 1, 10, 25, 50, 75, 100, 125, and 137 m close to the bottom. During the whole period of research the temperatures ranged from —1.83 to —1.57°C, the oxygen contents was from 8.17 to 5.95 ml/l, and the silica contents, estimated for the samples transported to Poland, were from 47.5 to 62.8 μg-at/l. The factor responsible for the changes and pattern of temperature, oxygen and silica contents in the coastal waters of the investigated region is the periodical raising of profundal waters brought about by the activity of cyclons. The conditions prevailing locally in Alasheyev Bight are different from other investigated and described coastal regions of the Antarctic.

6. STRESZCZENIE

Punkt, na którym prowadzono badania hydrologiczne, położony był w przybrzeżnym rejonie Zalewu Alasheyeva. W okresie od 13 czerwca do 9 października 1969 r. w odstępach ok. 10 dniowych prowadzono pomiary temperatury, zawartości tlenu i krzemionki w wodzie. Pomiary i próby wody brano z głębokości 1, 10, 25, 50, 75, 100, 125 i 137 m przy dnie. W ciągu całego badanego okresu temperatury wahały się od —1.83 do —1.57°C, zawartość tlenu od 8.17 do 5.95 ml/l, a zawartość krzemionki, jak wykazały analizy z prób przywiezionych do kraju, wahała się od 47.5 do 62.8 μg-at/l. Przyczyną decydującą o zmienności i stratyfikacji temperatury, tlenu i krzemionki w przybrzeżnych wodach badanego obszaru jest okresowe podnoszenie się wód głębinowych wywołane działaniem cyklonów. Warunki panujące w Zalewie Alasheyeva lokalnie różnią się od innych badanych i znanych w literaturze obszarów przybrzeżnych Antarktydy.

7. REFERENCES

[Botnikov, V. N.] Ботников, В. Н. 1967. Океанографические работы в прибрежных водах Антарктиды [Oceanographic observations in coastal waters of Antarctica]. *Trudy sov. antarkt. Eksped.*, 51, 174–183.

Bunt, J. S. 1960. Oceanography, hydrology. Introductory studies: hydrology and plankton, Mawson, June 1956-February 1957. *A. N. A. R. E. Rep., Ser. B*, 1-35.

[Cherepanov, N. V.] Черепанов, Н. В. 1969. Новый кольцевой ледовый бур [The new type of an ice ring-drill]. *Problemy Arkt. Antarkt.*, 32, 122-125.

[Chikovskiy, S. S.] Чиковский, С. С. 1969. Прибрежные гидрологические исследования в море Дейвиса в 1965/66 г. [Inshore hydrological researches in the Davis Sea, 1965/66]. *Trudy sov. antarkt. Eksped.*, 49, 346-354.

[Ledenev, V. G.] Леденев, В. Г. 1965. Структура и циркуляция вод залива Алашеева (в море Космонавтов) [Structure and water circulation of Alasheyev Bay (in the Cosmonaut Sea)]. *Inf. Byull. sov. antarkt. Eksped.*, 53, 24-26.

[Ledenev, V. G.] Леденев, В. Г. 1967. Морские океанографические работы [Marine oceanographic observations]. *Trudy sov. antarkt. Eksped.*, 51, 17-91.

Littlepage, J. L. 1965. Oceanographic investigations in McMurdo Sound, Antarctica. *Antarctic Res. Ser.*, 5, 1-38.

[Vaigachev, A. Z.] Вайгачев, А. З. 1963. Из опыта плавания д/э „Обь" в заливе Алашеева [From the experience of the d/e ship "Ob" sailing in Alasheyev Bight]. *Inf. Byull. sov. antarkt. Eksped.*, 39, 24-28.

[Yeskin, L. I.] Ескин, Л. И. 1969. Морские льды Южного Океана [Sea ice of the Southern Ocean]. *Problemy Arkt. Antarkt.*, 31, 24-30.

[Zvereva, Z. A.] Зверева, Ж. А. 1969. Предварительная характеристика сезонных сборов планктона на станции Молодежной [Preliminary characteristic of seasonal plankton collections in the Alasheev Bay]. *Trudy sov. antarkt. Eksped.*, 49, 464-467.

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S. RAKUSA-SUSZCZEWSKI

THE BIOLOGY OF *PARAMOERA WALKERI* STEBBING (AMPHIPODA) AND THE ANTARCTIC SUB-FAST ICE COMMUNITY

Department of Bioenergetics and Bioproductivity, Nencki Institute of Experimental Biology, Pasteura 3, Warszawa, Poland

ABSTRACT

Investigations were carried out at the coast of Alasheyev Bight[1] from May to December, 1969. *Paramoera walkeri* lives on the shallow sandy bottom, and when the sea freezes, it moves beneath the ice. The process is associated with maturation, the laying of eggs observed by the end of May, and the hatching of the new generation starting at the beginning of October. The growth of *P. walkeri* varies during its more than two years long life cycle, but it remains close to the isometric value. *P. walkeri* is an omnivorous animal. The investigated Amphipoda, fish and microflora developing on the reverse side of ice constitute a characteristic community, significant for the coastal waters of the Antarctic.

1. INTRODUCTION

In recent years much attention was devoted to the flora and fauna living upon, or related with, the reverse side of marine ice. A new field of hydrobiology has emerged, named marine cryobiology (Andriashev 1970). Bunt (1960, 1963, 1964, 1965, 1966), Bunt, Wood (1963), Burkholder, Mandelli (1965), Littlepage (1965) and others started investigations on species composition and production of the sub- and inside-fast ice communities at the coasts of the Antarctic. Peckham (1964) and Ray (1966) found Amphipoda and fish larvae beneath the ice. Russian investigations in the Davis Sea during the summer seasons (Gruzov et al. 1967, 1969) confirmed the existence of the specific community of plants and animals associated with the reverse side of ice. Production of the sub-fast ice community is an important link in food chains of the Antarctic waters. It can be a source of food for the rich sublittoral benthos fauna (Andriashev 1967), or for fish shoals which are very abundant close to the shore, while some of their species are dependent on the sub-ice community. In summer, penguins, seals and whales feed on it.

According to the present findings, in the coastal region of the Molodezhnaya station the most numerous crustaceans were *Paramoera walkeri* Stebbing (Amphipoda). Up to now, this species has been found in the region of the Ross Sea, South Shetlands and South Georgia, either in the littoral or on the beach (Stebbing 1906, Barnard 1932). Individual specimens were found as deep as 180-250 m, on the bottom and among the plankton (Barnard 1930). In the region of the Mirny station, *P. walkeri* was observed in a small amount beside *Orchomenopsis sp.*, Amphipoda predominating in the sub-fast ice community of that region (cf. *Bovallia walkeri* in Gruzov et al. 1967, 1969, which is identical with *Paramoera walkeri*

[1] Geographical names according to the *Official Name Decisions*, the United States Board of Geographic Names, Washington 1966.

in Andriashev 1967). The presence of *P. walkeri* in Alasheyev Bight may reflect its circumpolar distribution in the Antarctic.

The biology of this species has remained unknown. Observations on the biology of other Antarctic Amphipoda are also rather scanty. A few informations on reproduction of *Orchomenella proxima* and on the growth, life cycle and fertility of *Bovallia gigantea* can be found in Pearse (1963) and Thurston (1968, 1970). The aim of the present work was to solve some selected problems related with the biology of *Paramoera walkeri*, as this species plays an important role in the formation and development of the sub-fast ice community in the coastal region of Alasheyev Bight.

2. TERRAIN DESCRIPTION

The investigations were carried out in Alasheyev Bight, the site of the Soviet station Molodezhnaya (67°40′ S, 45°50′ E, Thala Hills, Enderby Land). Samples were drawn in a small bay (Fig. 1). The shore consists of an ice barrier not exceeding

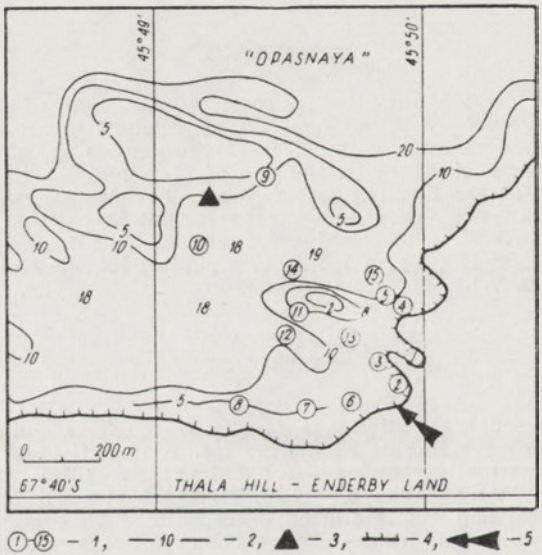

Fig. 1. A chart of the region of investigations. 1 — sampling stations, 2 — isobates (depth in m), 3 — icebergs, 4 — ice barrier, 5 — water outlet from Lake Glubokoye

5 m of height and in the central part there is a short stretch of a flat and rocky coast. The bottom of the bay is varied (Maltsev 1963, Koblents 1968); near the shore it is covered with sand, in the deeper part there are organic sediments. At some spots there are large agglomerations of plants on rocks.

The thickness and duration of ice is changeable in various years. The ice thaws by the end of February or the beginning of March, and it sets up by the middle of May (Yeskin 1969 quotes observations of six years). In the season 1969-1970 the respective dates were May 15-February 22. One of the factors making the ice less stable and more easily disintegrating are Diatomea developing inside it and on its reverse side (Baranov et al. 1968, Gordienko et al. 1960). On Alasheyev Bight, up to 800 m from the shore, the thickness of ice attained the maximum of 110 to 140 cm. 20 m from the shore it exceeded 150 cm (Yevseev 1969). In opposition to the Davis Sea, there was no record of ice formation in the depth of water which would float up under fast ice so as to make it thicker (Baranov et al. 1968, Treshnikov 1963). However, anchor ice formation was observed in the littoral zone of Alasheyev Bight, reaching as deep as 10 m (Kornilov, a personal communication). On May 9, 1969, Amphipoda frozen in anchor ice were observed during the sampling of the bottom.

After the steady ice cover was established, tide cracks appeared in the littoral zone. Tides are not huge in Alasheyev Bight (148 to 170 cm according to Shamont'yev 1963), but they are the main cause of the strong hummocking of the littoral. By the end of November, single hummocks were as tall as a man. At small depths, the surface of the bottom is doubtless exposed to strong mechanical attrition. At deeper spots, as by the steep banks or the ice barrier, no hummocking was observed (Fig. 2).

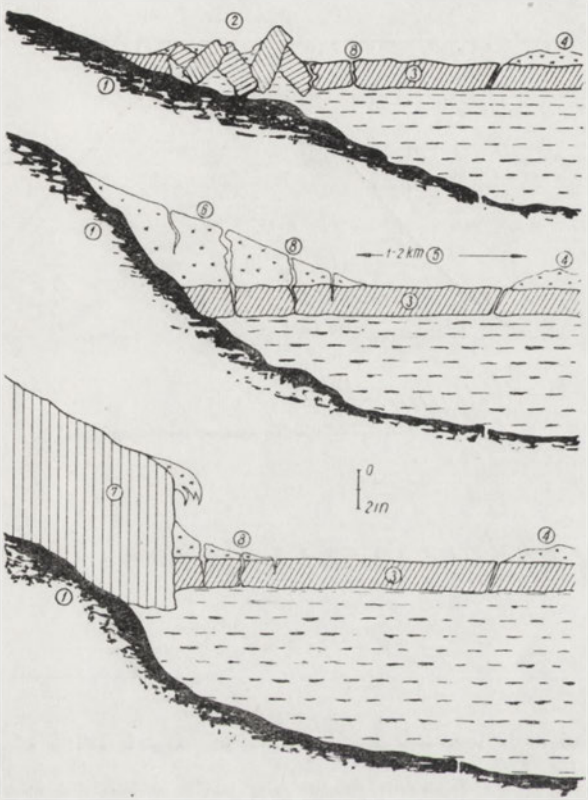

Fig. 2. Characteristic types of shore in the investigated region of Thala Hills. 1 — rocks, 2 — hummocks, 3 — fast ice, 4 — snow covered ice, 5 — bare ice, 6 — snow drift, 7 — ice barrier, 8 — tide cracks

The strip of ice up to 2 km from the shore was free of snow because of strong winds, blowing mainly from S and SE in that region. In the littoral zone, the ice was covered with sand and gravel brought from the oasis and being a result of intensive denudative processes (Simonov 1968). The shape of the valley and its rocky bedding made for an intensive heating in summer and the consequent melting of ice and snow, in its turn producing water which runs down to the bay. Before the present research started, there had been a rapid outflow of water from the Lake Glubokoye. Between January 18 and January 22, 1969, as much as 2.7 millions of cubic meters of fresh water flew to the bay (Klokov 1970).

During summer only fragmentary measurements of littoral water temperature and salinity in the Molodezhnaya region were taken (Fig. 3, according to Chikovskiy's unpublished data). In January water temperature never exceeded —0.7°C; in winter it was about —1.8 to —1.9°C. This was confirmed by our own data (Rakusa-Suszczewski 1971 a). According to Chikovskiy's data, the lowest salinity in the littoral region of the Molodezhnaya station was 18.53‰ (February 3, 1968); data for December are lacking. Bunt (1960) gives data concerning the changes of water temperature and salinity in the littoral zone of

Mawson station during summer. Extremal oscillations of water temperatures were 3.65°C (cf. Fig. 3). The maximal surface temperature of water was +1.43°C and it was recorded at the end of December. In winter a fairly steady temperature of about —1.9°C is maintained. The salinity of water under the ice decreases to 1.05–4.65‰ during December and January. During the rest of the year it is kept relatively steady at the level of 33–34‰. Observations by Chikovskiy (1969), carried out near the station Mirny, revealed a fall of salinity down to 3–6‰ imme-

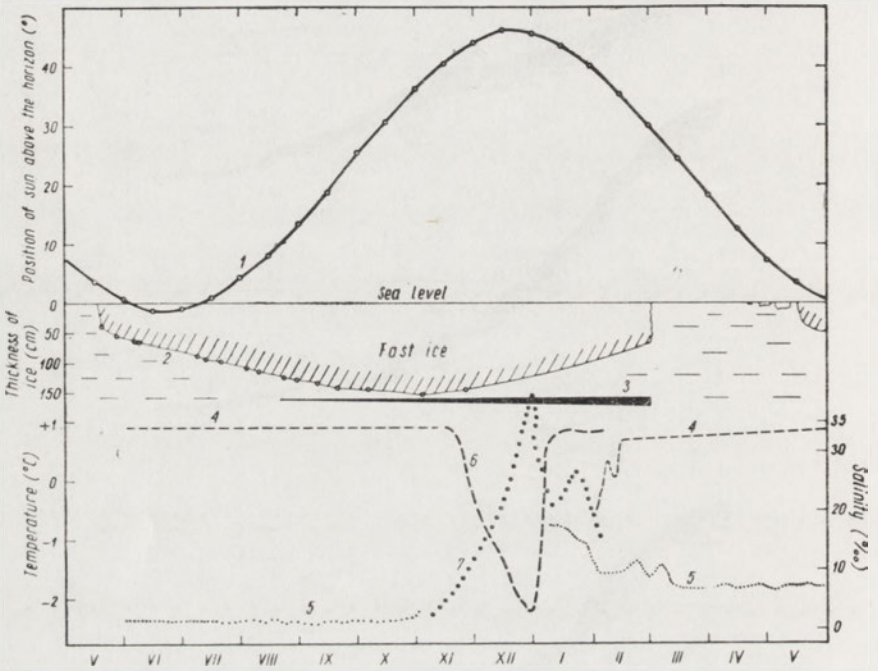

Fig. 3. Glacial and hydrological conditions in the coastal region of Alasheyev Bight. 1 — position of the sun above the horizon at 67°40′ S, 45°50′ E, 2 — thickness of ice as recorded; average duration of the ice cover according to Yeskin (1969), 3 — period of development of sub-fast ice microflora, 4 — salinity (Chikovskiy — unpublished), 5 — water temperature (Chikovskiy — unpublished), 6 — salinity of water in the Mawson Station region (Bunt 1960), 7 — water temperature in the Mawson Station region (Bunt 1960)

diately beneath the ice as a result of the melting of ice and an inflow of fresh water from the land. After the ice had disappeared, the salinity was raised up again to 32–33‰, and during winter and spring it was maintained at the level of 34.4‰.

It can be expected that similar thermic and salinity conditions prevail in the littoral region near Molodezhnaya. In general, there are short and huge oscillations of salinity in summer, as well as small oscillations of temperature. In winter, both temperature and salinity are kept fairly steady.

3. METHODS AND MATERIALS

The investigations were made from May 5 to December 4, 1969, during the Antarctic winter, spring and summer. Samples were drawn from the bottom of the bay from May 5 to July 12 (Fig. 1, Table I). Ekman's dipper with the surface of 250 cm² was used. When the sea was covered with ice, the dipper was submerged

through two overlapping holes, 30 cm in diameter each. A drill described in Cherepanov (1969) was used to make the holes. Sub-ice samples were drawn from May 18 to December 4 (Fig. 1, Table II). To obtain material from the reverse side

Table I. Distribution of *P. walkeri* on the bottom of the coastal region of Alasheyev Bight (1969)

Sample No.	No. of samples drawn with Ekman dipper	Date	Station No.(Fig.1)	Depth (m)	Type of bottom	No. of ind./m²	Notes
1	5	5.V	1	2-3	sand	1728	1 mature female (12 mm)
2	5	9.V	1	4-5	sand, mud	8456	1 female with eggs (13.5 mm)
3	5	18.V	1	4-5	sand, rocks	2136	no females
4	8	19.V	1	4	sand	30	—
5	6	20.V	1	2.5	sand	1260	—
6	6	28.V	2	3	rocks, plants	0	—
7	8	28.V	3	5	rocks	0	—
8	4	30.V	4	3	rocks, plants	1	egzuvium
9	5	30.V	5	10	mud	3	egzuvium
10	6	31.V	6	4	rocks, plants	1	juvenile
11	1	31.V	7	5-6	rocks	1	—
12	9	6.VI	8	4.5	rocks	1	juvenile
13	8	7.VI	9	5-6	rocks	0	—
14	5	12.VII	10	21	sand	0	—

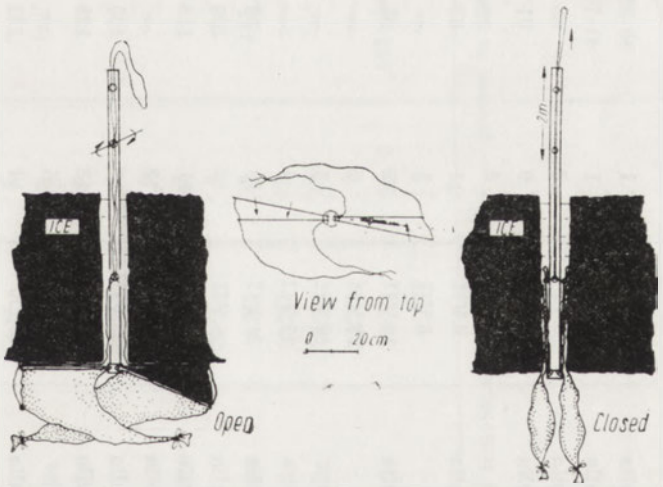

Fig. 4. The construction and principle of operation of umbrella

of ice, a device called an "umbrella" was contrived (Fig. 4). The closed umbrella was inserted into a hole in ice, 12 cm in diameter. A circular motion of the gadget scratched whatever was sitting or floating beneath and under ice. The samples thus drawn are not quantitative. Material collected into the both nets of the umbrella was transported in a vacuum flask, partly filled with sea water. At home, after the ice melted, the material was sipped into a plastic bottle and it was condensed. Amphipoda were also caught in an ice hole near the shore where a mareograph was installed (station 5). A small net on a stick was employed.

The length of Amphipoda was measured from a rostrum to the end of a telston

Table II. Distribution of *P. walkeri* under the ice in the coastal region of Alasheyev Bight (1969)

Sample No.	Means of sampling	Date	Station No. (Fig. 1)	Thickness of ice (cm)	Number of caught individuals				
					juv. adolesc.	ovigorous	bearing eggs	with juv. in brood pouch	freshly hatched juv.
15	3 × umbrella	18.V	1	39-55	57	11	0	0	0
16	3 × umbrella	27.V	1	41-70	14	4	4	0	0
17	3 × umbrella	6.VI	8	63	1	3	3	0	0
18	2 × umbrella	7.VI	9	61	0	0	0	0	0
19	net	1.VII	8	—	2	9	9	0	0
20	2 × umbrella	8.VII	11	87	1	0	0	0	0
21	net	8.VII	5	—	19	2	2	0	0
22	2 × umbrella	12.VII	12	93	0	0	0	0	0
23	net	13.VII	5	—	2	1	1	0	0
24	net	16.VII	5	—	49	13	13	0	0
25	net	17.VII	5	—	42	6	6	0	0
26	2 × umbrella	21.VII	13	98	2	0	0	0	0
27	2 × umbrella	4.VIII	13	109	146	28	28	0	0
28	2 × umbrella	10.VIII	11	115	0	14	14	0	0
29	3 × umbrella	20.VIII	13	—	572	35	35	0	0
30	3 × umbrella	23.VIII	13	125	407	27	27	0	0
31	2 × umbrella	29.VIII	13	129	many	25	25	0	0
32	net	8.IX	5	—	many	+	+	0	0
33	2 × umbrella	10.IX	14	133	6	0	0	0	0
34	net	12.IX	5	—	many	120	120	0	0
35	net	14.IX	5	—	many	85	85	0	0
36	4 × umbrella	20.IX	13, 15	142	131	39	39	0	0

37	net	29.IX	15	—	0	4	4	0	0
38	2 × umbrella	3.X	13	—	many	11	11	+	0
39	net	4.X	5	—	0	11	11	+	0
40	2 × umbrella	6.X	13	144	0	15	15	+	0
41	2 × umbrella	10.X	13	—	25	3	3	+	0
42	net	11.X	5	—	95	18	18	+	+
43	net	15.X	5	—	0	58	58	23	+
44	2 × umbrella	20.X	13	—	131	5	5	+	+
45	net	29.X	5	—	138	139	139	+	+
46	2 × umbrella	4.XI	13	153	18	2	2	+	+
47	2 × umbrella	10.XI	13	—	41	0	0	0	+
48	3 × umbrella	16.XI	13	—	226	29	29	+	+
49	net	23.XI	5	—	0	9	0	0	+
50	3 × umbrella	28.XI	13, 5	143—148	215	33	1	3	+
51	net	4.XII	5	—	0	22	0	3	+

many — more than 500 individuals, — — no data, + — present in the sample but no counted.

exact to 0.5 mm. Wet weight was determined after drying on a blotting-paper exact to 0.5 mg. Dry weight was assessed by sorting out the collected individuals into several classes of length and drying them separately at 105°C. To measure the size of eggs it was necessary to keep them in salt sea water, since they swelled up when kept in melted ice water even for a short time. Eggs from one female were counted in vivo since the females treated with formalin dropped their eggs.

A part of the collected material was used for studies of metabolism and for liofilization. The results will be discussed in a separate paper.

4. RESULTS

DISTRIBUTION AND BEHAVIOUR OF *P. WALKERI*

In the investigated region, *P. walkeri* appeared in great number near the bottom at station 1 (Table I). They were found immediately beneath the ice by the end of May, after the ice cover had set in. Females constituted a large percentage in proportion to the number of the caught animals. During the successive winter months, in June, July and August, the number of *P. walkeri* caught beneath the ice was increasing. It was found in the sub-ice zone at stations 5, 13, 14, 15, i.e. at greater distances from the shore. It can be seen that its range became more extensive. The shallow bottom welcoming large agglomerations of *P. walkeri* before the sea had frozen, became inaccessible in winter because of the tall ice hummocks covering it. For the last time observations were made by the end of November and in December, when the ice began to thaw. During that period mature females which had produced their off-spring, immature individuals and newly hatched ones were found in the littoral sub-ice zone.

Thus, during the period when there was no ice, *P. walkeri* lived in the narrow strip of sandy bottom near the shore. In winter the whole population moved under the ice and it widened its range in effect of tides and of its own activity, but still it did not leave the littoral zone. Probably the animals returned to the bottom before or during the retreat of ice.

Behaviour of *P. walkeri* was observed in an ice hole near the mareograph (station 5) and in experimental environments. *P. walkeri* is a skillful but not persistent swimmer; it requires a slightly rough surface for rest. Very numerous agglomerations of *P. walkeri* were observed on the walls of the ice hole many times, but there were days when they appeared only sporadically. A marked negative phototropism was noted in females. Newly hatched individuals showed positive phototropism. When sea water was freezing, the activity of the animals decreased, partly because they were impeded by the developing crystals of ice.

MATURATION, EGGS AND FERTILITY OF FEMALES

The first mature female of *P. walkeri* with a bristle oostegites was observed on May 5. On May 9 one female with eggs in the marsupium

was caught. The material had been drawn from the bottom before the sea froze down. On May 18, 11 mature females without eggs in their marsupia were collected immediately beneath the ice. Among them 3 individuals were 13.0 mm in length, other 3 measured 13.5 mm, and the remaining measured 12.0, 15.0, 15.5, 16.0, and 16.5 mm. In relation to the number of females in the several classes of length, it seems that it is the bigger individuals which mature first. By the end of May and beginning of June females with eggs appeared.

Eggs of *P. walkeri* are large, olive in colour, oval in shape. Their length to breadth ratio is 1.23 in the initial period. During the development an egg assumes the shape of a pear as the embryo deforms it. The dimensions of eggs change, too (Table III). Wet weight of *P. walkeri* eggs 0.6 mm in length is 0.09 mg (evaluation based on nomograms by Tshyslenko 1968). The eggs swell strongly if they are kept in dissoluted sea water, and their transparent covering coats expand.

Table III. Changes of dimensions of eggs of *P. walkeri* during embryo development (1969)

Sample No.	Date	Average length (mm)	No. of measured eggs
16	27.V	0.60	44
30	23.VIII	0.63	14
31	29.VIII	0.61	10
32	8.IX	0.66	10
34	12.IX	0.67	10
39	4.X	0.71	18

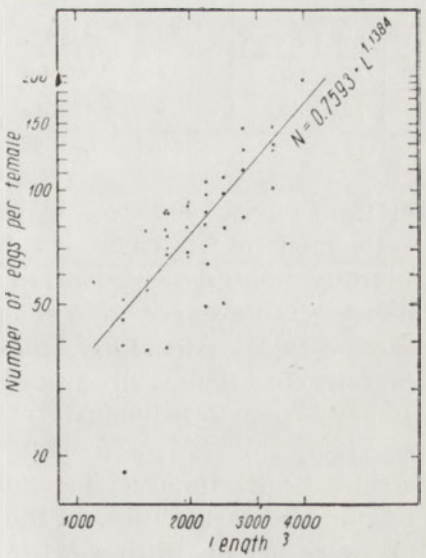

Fig. 5. Relationship between body size (cubed length) and number of eggs in marsupium in *P. walkeri*

Measurements of 11 such eggs gave medium length of 0.98 mm and width of 0.72 mm, i.e. their volume was 3.5 times greater than normal. However, the embryos were not damaged.

During the period from August to October, eggs were counted in 47 females. The eggs were produced by females measuring from 10.5 to 17.0 mm in length. The relationship between length and number of eggs found in a marsupium of a single female is a function of the volume of the female (or of the cube of its length). The data are presented in Fig. 5.

Analysis of marsupia revealed that some eggs were turbid, reddish, villous, obviously blocked in their development. Their amount in a marsupium of a single female was from 1 to 58%. In average, in 18% of females the eggs were partly damaged. On surfaces of the injured eggs Ciliata were found.

EMBRYO DEVELOPMENT AND HATCHING

The females of *P. walkeri* collected under the ice at the end of May and at the beginning of June have got eggs in their marsupia. Individual newly hatched animals were found in marsupia of females on October 3 (Table II). The embryo development of *P. walkeri* is illustrated in Fig. 6.

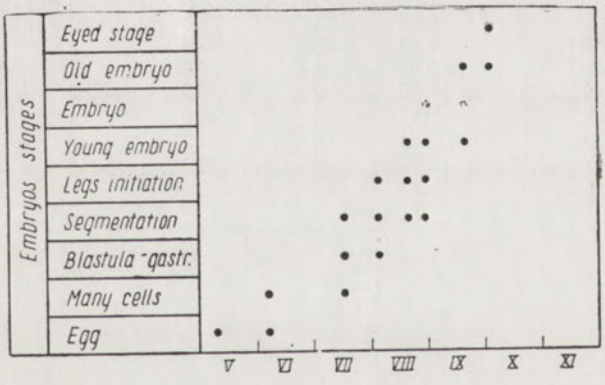

Fig. 6. Stages of development of eggs in *P. walkeri* females

For the analysis conserved material was used. The successive stages of development of an embryo were assumed after Vlasblom (1969). According to his observations, in steady temperature the periods between the consecutive stages were about equal. In the sample drawn on October 28, a full or partial hatching occurred in 28% of the caught females. The following figures illustrate the number and length of females with hatched young: 4 individuals — 11 mm of length, 4 — 11.5, 2 — 12.0, 4 — 13.0, 4 — 13.5, 3 — 14.0, 1 — 14.5, 1 — 16.0. It seems that the hatching begins in larger individuals first, considering the amount of all the animals bearing eggs. In the samples collected on November 23, the bulk were females with a bristle oostegites, but without juvenile forms

in marsupia. It was an evidence that the incubation of the new generation had finished. Young animals are incubated by their mothers after the hatching, but we failed to determine the period of incubation.

Thus, the embryo development of *P. walkeri* lasts for about 4.5 months during winter in temperature −1.8-−1.9°C and at about 34‰ of salinity. The period of incubation of the new generation lasts for about 40 to 50 days.

LENGTH DISTRIBUTION

The extreme lengthes of *P. walkeri* in the investigated material ranged from 1.75 to 17.0 mm. All individuals of the investigated population clearly fell into one of the three classes of size (Fig. 7). The first

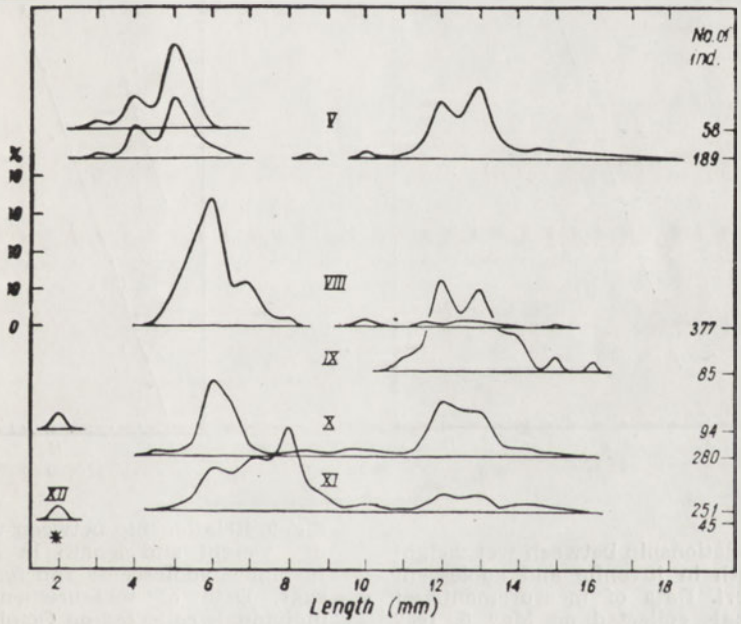

Fig. 7. Length distribution of *P. walkeri*. * — individuals measured after conservation in formaline

group consisted of newly hatched individuals measuring from 1.75 to 2.3 mm. In this group no growth was observed from October to December. The second group were juvenile and immature individuals from 2.5 to 10.0 mm. They grow up markedly during winter and spring. The third group consisted of females from 10.0 to 17.0 mm. No growth was observed in this group during winter and spring. In the distribution of length of the second and third groups there was a marked bimodality. The difference between the peaks of length distribution was 1 mm in

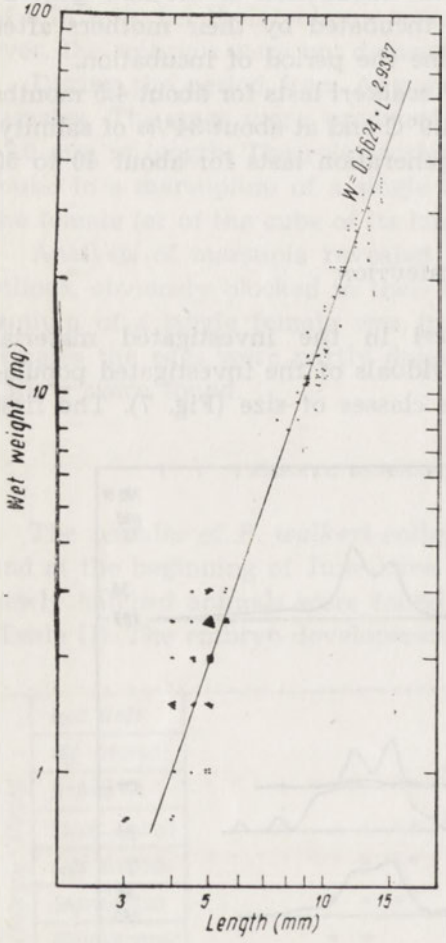

Fig. 8. Relationship between wet weight and length in juvenile and adolescent *P. walkeri*. Data of measurements of 137 animals collected on May 5, 1969

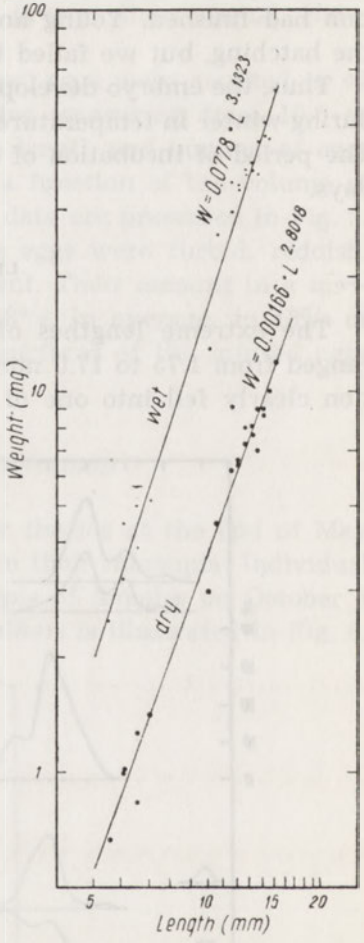

Fig. 9. Relationship between wet weight, dry weight and length in *P. walkeri* juveniles, adolescents and females with eggs. Data of measurements of 280 individuals collected on October 29, 1969

both groups. Considering the slow rate of growth at the beginning of life, this difference is relatively large. Perhaps it is an evidence of a heterogeneity of the collected material; it can be suspected that there were two cohorts overlapping in time.

LENGTH AND WET WEIGHT RELATIONSHIP

In the investigated material the extreme wet weight of individuals belonging to the second and third length class was from 0.5 to 90.0 mg.

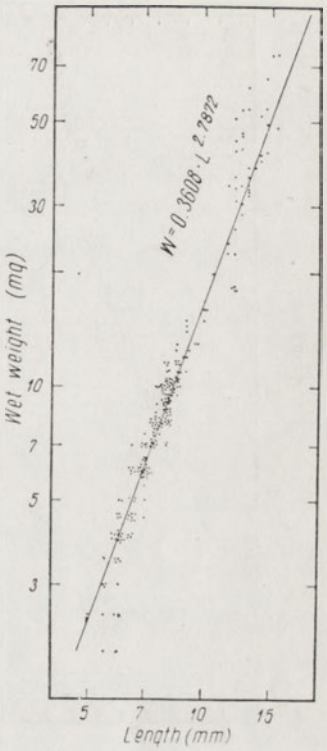

Fig. 10. Relationship between wet weight and length of *P. walkeri* juveniles, adolescents, females with eggs and females without eggs. Data of measurements of 251 individuals collected on November 28, 1969

We failed to weigh individuals belonging to the first group of length. The relationship between wet weight and length for *P. walkeri* is presented in Fig. 8, 9, 10, depending on the general formula $w = aL^b$, where w stands for wet weight, while a and b are constants. In general, the increase of weight in relation to length is close to isometric (b = about 3), but there are seasonal changes.

The relationship between wet weight and length in immature females without eggs (Fig. 11) and in females with eggs (Fig. 12) was analysed separately. In both cases the coefficient b was lower than 3. The increase of weight in relation to length was greater in females with eggs than in those without. This was caused not only by the production of eggs but also by the increasing weight of water filling the space between the eggs in the marsupium. This water accounted for 14% of wet weight in females with eggs measuring 13.5 mm in average. There was less of it in smaller individuals and more in bigger ones. Water filling the marsupium during a measurement in vivo influenced the value of the coefficient b. Hence, it was possible to draw the third line on Fig. 13 representing the actual increase of wet weight of egg-producing females, based on the correlation between the length of females and the number of eggs, and on the value of weight of a single egg. When the young incubate and leave the marsupia, the weight of females decreases.

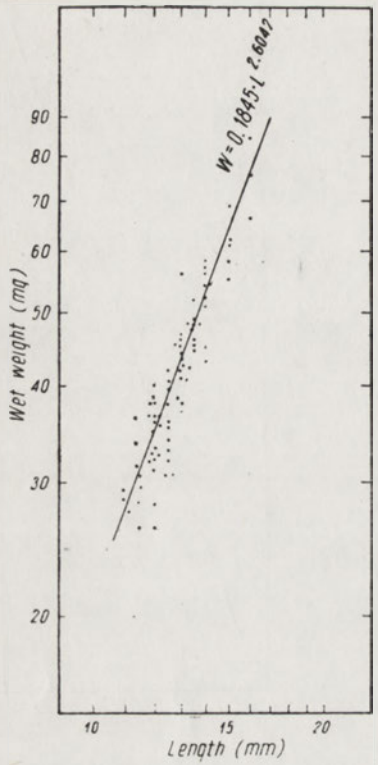

Fig. 11. Relationship between wet weight and length of *P. walkeri* females without eggs in marsupium. Data of measurements of 117 individuals of more than 10 mm, collected on May 20, 1969

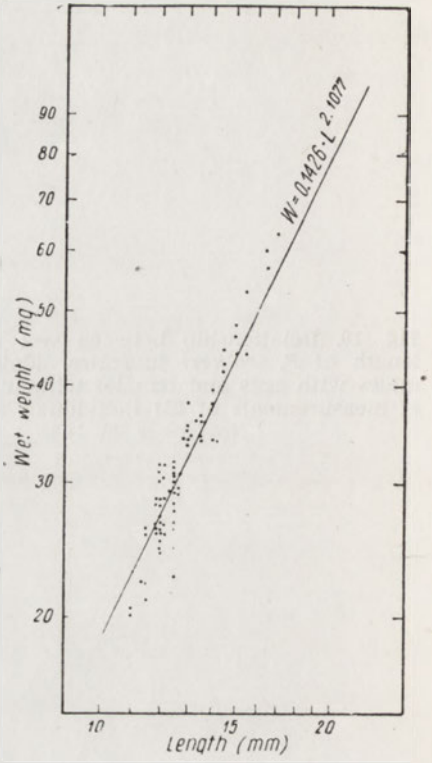

Fig. 12. Relationship between wet weight and length of *P. walkeri* females with eggs in marsupium. Data of measurements of 20 individuals collected on August 20, 1969 and of 83 individuals collected on September 14, 1969

The shape of the regression line wet weight/length is also influenced by seasonal changes of weight of the animals. This was confirmed by a statistical analysis of individuals collected in the middle of winter (August 20) and in summer (November 28). In both cases individuals 6.0 mm long were taken into consideration. Average weights were 3.15 ± 0.21 mg ($n = 60$) and 3.78 ± 0.28 mg ($n = 27$) respectively, at 95% confidence interval. The changes of weight are related with feeding conditions in the environment. In general, the animals lose weight in winter and assume it during spring and summer.

WET-WEIGHT AND DRY-WEIGHT RELATIONSHIP

This relationship was analysed once in summer (Fig. 9). Dry weight of *P. walkeri* females with eggs is about 20% of their wet weight. How-

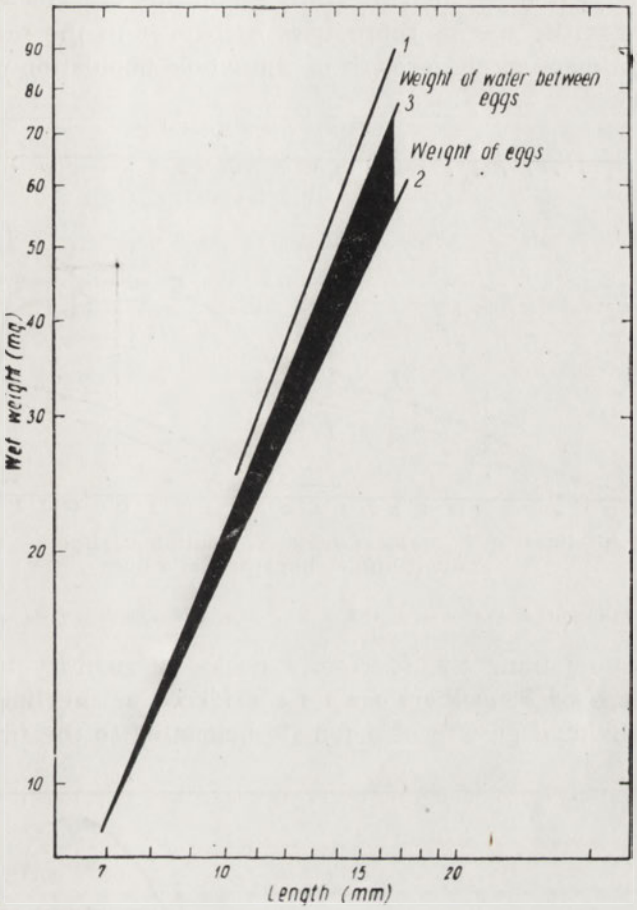

Fig. 13. A comparison of wet weight of *P. walkeri* females. 1 — with eggs and water in marsupium (cf. Fig. 12), 2 — no eggs and no water in marsupium (cf. Fig. 11), 3 — wet weight of females with eggs, water in marsupium discounted (values computed)

ever, if we account for water filling the space between the eggs in the marsupium which amounts to 14% in average, dry weight of females with eggs is actually about 23% of their wet weight. Dry weight of juvenile and immature individuals is about 27% of their wet weight. It can be seen that there is a significant difference between water content in mature egg bearing females and in juvenile and immature individuals.

LIFE CYCLE AND GROWTH

A hypothetical individual growth during a life cycle of *P. walkeri* is represented in Fig. 14, based on the measurements of length of the species (Fig. 7). The first of the three groups of size discerned in the population

was set one year back, and the third group one year forward, assuming of course that the species reproduces each year in the same season. As a result, an image of the growth of the whole population during the life cycle emerged.

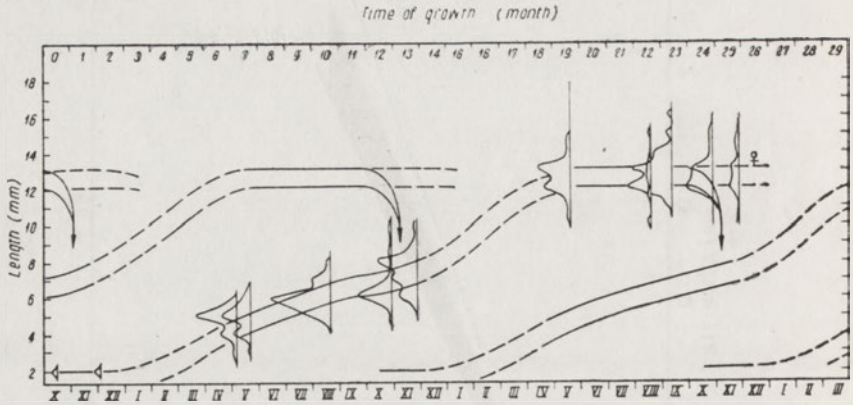

Fig. 14. Growth lines of *P. walkeri* females. Continuous line — observed values, dotted line — hypothetical values

The curve joining the successive peaks of quantity in each of the length groups of *P. walkeri* can be considered as the line of individual growth. Individual growth of a female belonging to the first cohort (not

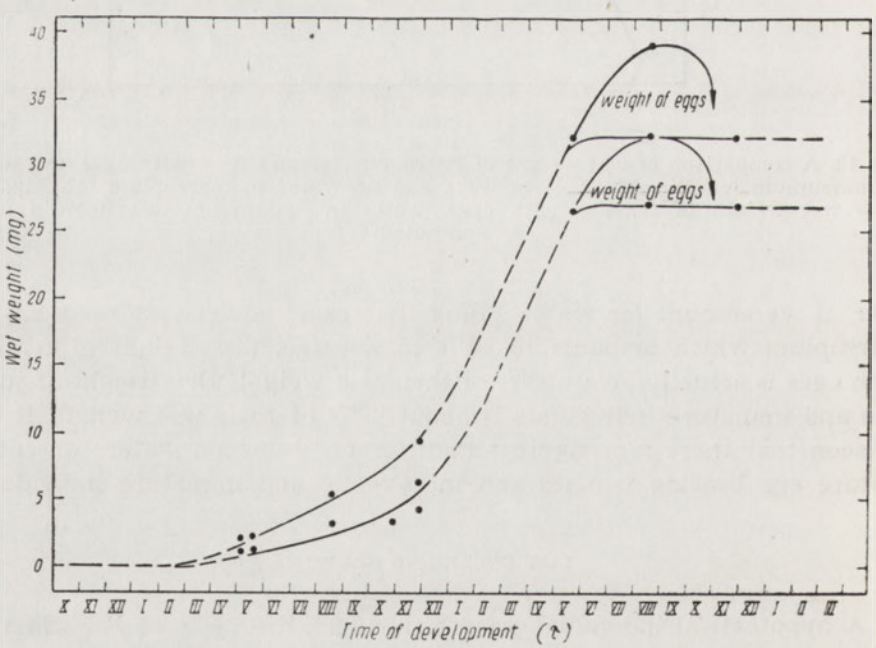

Fig. 15. Growth of wet weight of *P. walkeri* females. Continuous line — observed values, dotted line — hypothetical values

enough males have been found) began at the moment of incubations observed in October and ended in May, after 19 months. Next, a plateau appeared in the growth curve. The lines assumed a similar S-shape, with a characteristic slow down of the growth rate during winter.

Figure 15 presents the increase of wet weight of females along their development. The draft is based on the curves of individual growth of females (Fig. 15), with due account for the relationships between length and wet weight, and between length and egg production. Both wet-weight increase curves reveal a characteristic S-shape. In both cases a high share of the wet weight of the produced eggs in relation to the total body wet weight is remarkable.

A NOTE ON FOOD

Alimentary canals of *P. walkeri* were analysed a number of times during winter and spring. In winter, highly macerated plant remnants with fragments of crusts of Diatomea encountered on the bottom were found in the intestines. Remnants of Copepoda were also recorded. In spring (October 4, 1969), detritus with spicula of sponges was found in the intestines of a female caught beneath the ice. In the same sample remnants of Copepoda of the genus *Oithona sp.* were found in the intestines of two individuals 7 mm in length. However, during that period the bulk of food were remnants of filiform algae developing on the reverse side of ice. It can be seen that *P. walkeri* is an omnivorous species, feeding near the bottom and in the sub-ice zone.

Trophozoites of Eugregarinaria, probably of the Rotundula genus, were found in alimentary canals of *P. walkeri* (cf. Rakusa-Suszczewski 1971b).

THE SUB-FAST ICE COMMUNITY

The composition and formation of the littoral sub-fast ice community has been observed since the ice cover was established in the investigated region; at the same time the bottom was sampled. In all stations, except station 1 where *P. walkeri* appeared in large number, extreme poverty of fauna was observed. It was represented by scanty individuals belonging to the following groups of animals: Nemertini, Molusca, Polychaeta, Isopoda, Harpacticoida, Ophiurioidea, Ostracoda, Decapoda, Amphipoda. On station 1, besides *P. walkeri*, one individual of the *Orchomenella sp.* (Amphipoda) and one Isopoda were found.

Sub-fast ice samples revealed a somewhat different composition of fauna than the bottom samples. Plankton forms were found, represented by Pteropoda, Coelentherata, Calanoida, Cyclopoida, Amphipoda — Hy-

periidae. Bottom and over-bottom forms were represented by Ostracoda, Polychaeta, Decapoda, Harpacticoida. Probably they went under fast-ice with anchor ice floating in and their presence in small amounts was rather accidental. It was only the motion of *P. walkeri* from the bottom zone under the ice which was an active process, related with the biology of the species. Since the ice has established in the littoral, large agglomerations of fish were found, mainly belonging to the species *Trematomus borchgrevinki* and *T. newnesi* (cf. Rakusa-Suszczewski 1971 c); a few times *T. penelli* and young *Gymnodraco acuticeps* and *Dissostichius mawsoni* were caught. *T. bernacchii* were caught in the bottom zone.

At the beginning of the polar winter and night, when sub-fast ice microflora has not yet developed, the main components of the littoral sub-fast ice community are Amphipoda *P. walkeri* and fish feeding on them, *T. borchgrevinki* and *T. newnesi*. The other groups appear in small amounts, but some of them may provide food for the main components of the community. In the littoral zone of the investigated region, microflora begins to develop on the reverse side of ice during the third decade of August. Its development is very intensive during spring and summer. It is also in spring that the most numerous sub-ice Amphipoda, *P. walkeri*, breed their offspring. Thus a number of animal groups, both plankton and bottom inhabitating, as well as fish and their larvae, can find food and shelter under the ice, forming the specific sub-fast ice community.

Floating Euphausiacea, Ctenophora and Hyperiidae were observed in ice cracks twice, in December 1968 and 1969, near Drygalski Island on the Davis Sea and for the second time about 90 km north of the Molodezhnaya station. This is certainly another community, with different timing of formation and different biology of its component species, but similarly as in the littoral zone, the plant production of the sub-fast ice zone is its basic resource.

5. DISCUSSION

Vertical movements of littoral Amphipoda species related with their reproduction is a common phenomenon (Watkin 1939, Segerstråle 1950, Fincham 1970). Observations on *P. walkeri* confirmed that it occurs in littoral waters of the Antarctic continent, too. The shallow zone of sandy bottom, where *P. walkeri* appears in mass, is an area where anchor ice forms, and after the sea is definitely frozen, intensive hummocking occurs there, likely to destroy bottom animal communities (Knox 1968, 1970). Thus the movement of *P. walkeri* under the ice, where it can find favourable conditions for its reproduction, food, shelter and space, is a biologically sound process. According to the observations,

it is in the sub-fast ice zone that the maturation and egg-laying of *P. walkeri* take place.

The eggs of *P. walkeri* are large, which is typical for animals living in cool polar waters (Thorson 1950, MacGinitle 1955, Chia 1970). The size of eggs in proportion to the size of females is larger than Thurston (1970) observed in *Bovallia gigantea*. *P. walkeri* eggs are deformed during their development, which is typical for Amphipoda (Hynes 1954, Sheader, Chia 1970, Thurston 1970). The swelling of the covering coat in diluted sea water without any damage to the embryo may be one of the mechanisms protecting the eggs against extensive oscillations of salinity occurring beneath the ice (cf. Fig. 3, curve 6). The amount of eggs produced by a female of *P. walkeri* is proportional to its volume considered as the cube of its length (cf. Jensen 1958); a similar relationship was found by Thurston (1970) for *Bovallia gigantea*, but the number of eggs produced by the latter is smaller, and the increase of egg production along with the increase of length is lesser in comparison with *P. walkeri*. The number of eggs and their production by *P. walkeri* females is one of the highest ever observed in Amphipoda of similar size (Kinne 1961, Vlasblom 1969, Steele, Steele 1970). High percentage of destroyed eggs observed in *P. walkeri* is analogous to the situation recorded in littoral Amphipoda living in polluted zones with high oscillations of salinity (Sheader, Chia 1970). The cause of destruction is not clear; an infection by Ciliata or a freezing of eggs may be involved.

Embryo development of *P. walkeri* continues for 4.5 months and it is notably shorter than in *Bovallia gigantea* which develops 7 months (Thurston 1970). *B. gigantea* begins to incubate by the end of September and beginning of October, i.e. somewhat earlier than *P. walkeri*, but the former was investigated under a lower geographical latitude, where light and food conditions favour the earlier development of *B. gigantea* population. A comparison of the period of embryo development with a few other Amphipoda species whose rate of development was observed in higher temperatures (Fig. 16) suggests that after a transition to very low temperatures and below zero degrees, the time of development no longer remains a simple function of temperature (cf. Winberg 1968, Forrester, Alderdice 1965). For *P. walkeri* which lives in temperatures below zero, even a slight warming up may shorten very markedly the time of embryo development (cf. Fig. 16).

The size of *P. walkeri*, considering that the biggest caught individual measured 17.0 mm, is relatively small, but there appear three distinct and "discreet" (Golikov 1970) length and weight groups in the population. This is typical for populations marked by a slow growth and a long life cycle.

The growth of weight with length in the whole population of *P. walkeri* is typical for the crustaceans ($b = 3$) (Winberg 1966). In *P. walkeri* females, weight and length increase is also typical for Amphipoda during maturation, the laying of eggs and the incubation of young.

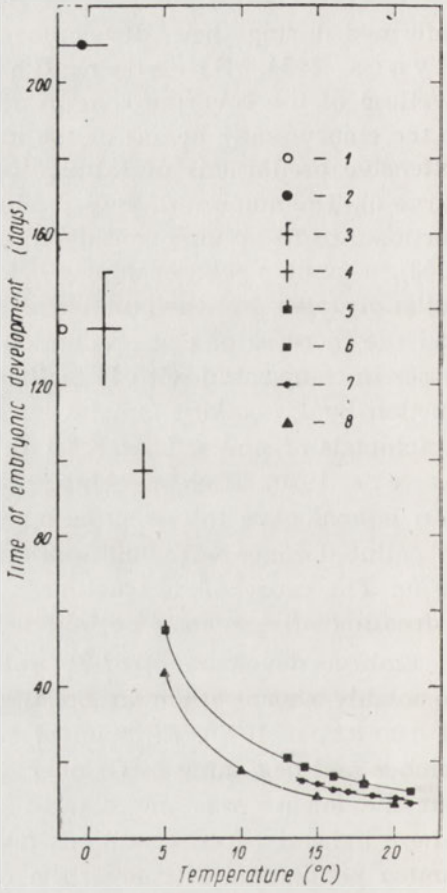

Fig. 16. A comparison of periods of embryo development of Amphipoda in various temperatures. 1 — *Paramoera walkeri*, 2 — *Bovallia gigantea* (Thurston 1970), 3 — *Pantoporeia affinis* (Segerstråle 1950), 4 — *Pantoporeia affinis* (Mathisen 1953), 5 — *Gammarus duebeni* (Hynes 1954), 6 — *Gammarus duebeni* (Kinne 1953), 7 — *Gammarus salinus* (Kinne 1960), 8 — *Marinogammarus salinus* (Vlasblom 1969)

Dry weight content in *P. walkeri* is quite similar to that of *Euphausia superba*, in which dry weight of females is 23.4% in summer, while in juvenile forms it is in average 25% of the body weight (Shevtsov, Makarov 1969).

The life cycle of *P. walkeri* differs from what has been observed in other Antarctic Amphipoda both with respect to its period of incubation (cf. Pearse 1963, Thurston 1968) and the character of its growth which is less uniform and continues for a shorter period than in *B. gigantea* (Thurston 1970). Remarkable for *P. walkeri* is the slow down of its rate of growth during winter, which may be related with the scantiness of food during the polar night. The curve of the increase of

body weight during the life cycle assumes an S-shape, in accordance with the general pattern of growth for crustaceans as stated by Winberg (1966).

An analysis of food contents of *P. walkeri* proved that they are no exception among the omnivorous Pontogeneiidae (cf. Thurston 1970 p. 291). Omnivorous behaviour of the species may be important for its survival in the sub-fast ice zone before microflora can develop there.

During its life cycle *P. walkeri* is bound with the sub-ice zone during both its first and second year of life and it spends more time there than near the bottom. It can be thus considered as the main and steady component of the sub-fast ice community.

The presence of a number of representants of bottom and near-to-bottom fauna beneath the ice, dragged there with anchor ice arising from the bottom, was also observed by Peckham (1964) and Dayton et al. (1970). They found sea-urchins, starfish, nemertini, isopoda and fish on the reverse side of ice in the McMurdo region. The process of transporting of organisms under the ice is important with regard to diminishing the density of sublittoral bottom communities, but the groups so transported are accidental. Scanty bottom fauna in the sublittoral zone in the region of Molodezhnaya station was observed by Gruzov, Pushkin (1970); this finding is also confirmed by the present observations, though numerous agglomerations of *P. walkeri* on the shallow sandy bottom before the freezing of the sea were also observed. Transportation of communities or of their fragments may be important for the development of sub-fast ice microflora whose spore forms begin to develop more quickly under ice because of the favourable lighting conditions. In the investigated region microflora began to develop in the third decade of August, i.e. almost a month earlier than it was observed by Littlepage (1965) in the McMurdo region further to the south. It is remarkable that the sub-ice microflora begins to develop at various latitudes in periods when the position of the sun over the horizon is about the same. Perhaps similar lighting conditions prevail under the ice then.

The rocky coasts of the Antarctic constitute only 8% of its coastal line (Markov et al. 1968). If the coastal sub-fast ice community appears in this area only, then it occupies only a minor percentage of the surface of ice covering the sea around the continent. However, it is in that area that colonies of penguins, birds and seals are usually crowding, and whales come in during summer to feed on what the coastal sub-ice community had produced. Possibly there are local differences in composition and timing of the coastal sub-fast ice communities, as it is suggested by a comparison with observations by Gruzov et al. (1967, 1969) carried out in the Mirny region. It was another species of Amphipoda, *Orchomenopsis sp.*, which predominated in quantity there. The open sea sub-fast

ice community also seems to have a different composition and a different significance in the circulation of organic matter in Antarctic waters. Those problems require further investigations and they promise interesting results in the new field of marine cryobiology, so labelled by Andriashev (1970). A number of related phenomena discovered and observed in high Northern and Southern latitudes (Golikov — a personal communication) turn out to have their correlates in the moderate climate, too, as those observed by Hickel (1969) on the Baltic Sea.

Acknowledgements

I thank the management of the Molodezhnaya station for their technical help in our work. I also thank my companion K. Opaliński, M. Sc., for his toil and assistance.

6. SUMMARY

Investigations were made in the coastal region of Alasheyev Bight from May 5 to December 4, 1969, operating from the Soviet Antarctic base Molodezhnaya (67°40′ S, 45°50′ E, Enderby Land). The Amphipoda, *Paramoera walkeri* Stebbing was observed. It appears on the sandy bottom when there is no ice. After the sea freezes down, it moves beneath the ice. *P. walkeri* is a motile animal, a good but not persistent swimmer. Females mature in the depth of water, in the sub-fast ice zone. By the end of May and the beginning of June the females lay eggs into their marsupia. Eggs are 0.6 mm in diameter and they are produced by females 10.5-17.0 mm in length. The number of eggs produced by a single individual can be expressed by the formula $N = 0.7593 \cdot L^{1.138}$ and it is proportionate to the cube of length. Embryo development continues for about 4.5 months in water, at —1.8—1.9°C of temperature and about 34‰ of salinity. The hatching starts at the beginning of October and it ends by the end of November. The length of *P. walkeri* is from 1.75 to 17.0 mm. There are three distinct length and weight groups in the population. The increase of weight as related to length is close to isometric. The relationship between wet weight (mm) and length (mm) in the beginning of May is expressed by the formula $w = 0.5624 \cdot L^{2.9337}$, and by the end of October it assumes the form $w = 0.778 \cdot L^{3.1323}$, and for the dry weight it is $w = 0.00166 \cdot L^{2.8018}$. By the end of November the relationship between wet weight and length is expressed by the formula $w = 0.3608 \cdot L^{2.7872}$. Among the egg-producing females the relationship of wet weight to length is given by the formula $w = 0.1426 \cdot L^{2.1077}$ before the laying of eggs to the marsupium, and $w = 0.1845 \cdot L^{2.6042}$ after the eggs are laid. The life cycle of the species takes more than two years. After 19 months since the hatching, a plateau of growth sets in for the females. It is in this phase that maturation and laying of eggs occurs. The growth of females during their lifetime is represented by an S-shaped curve, typical for the growth of crustaceans. *P. walkeri* is an omnivorous animal, it feeds on plant remnants on the bottom, sub-fast ice microflora and Copepoda. *P. walkeri* is a steady and most numerous crustacean component of the coastal sub-fast ice community. It comprises also sub-ice microflora and fish. There is also a number of more or less accidental animal forms under the ice. The composition and timing of the formation of the community suggests local differences between the coastal parts of the Antarctic continent. There are reasons to suppose that the coastal community differs from that living under the ice in the zone more remote from the coast. The sub-fast ice community is an important one, as penguins, seals and whales feed on it in summer.

7. STRESZCZENIE

Badania prowadzono w przybrzeżnym obszarze Zalewu Alasheyeva od 5 maja do 4 grudnia 1969 r. w oparciu o radziecką stację antarktyczną Molodezhnaya

(67°40′ S, 45°50′ E, Enderby Land). Obiektem badań były Amphipoda — *Paramoera walkeri* Stebbing. W okresie kiedy nie ma lodu występuje na dnie piaszczystym. Po zamarznięciu morza przenosi się pod lód. *P. walkeri* jest formą ruchliwą, dobrze lecz krótko pływającą. Dojrzewanie samic następuje w toni wodnej w strefie podlodowej. W końcu maja — początku czerwca samice składają jaja do marsupium. Jaja mają średnicę 0,6 mm i produkowane są przez samice w wymiarach 10,5-17,0 mm. Ilość jaj wyprodukowanych przez osobnika macierzystego wyrazić można wzorem $N = 0{,}7593 \cdot L^{1{,}138}$ i jest ona proporcjonalna do sześcianu długości. Rozwój embrionalny trwa około 4,5 miesiąca w temperaturze wody —1,8—1,9°C i zasoleniu około 34‰. Wylęg rozpoczyna się w początkach października i kończy w końcu listopada. Długość *P. walkeri* wynosi od 1,75 do 17,0 mm. W rozkładzie długości populacji wyraźnie występują trzy grupy wymiarowo-wagowe. Wzrost masy z długością ma charakter zbliżony do izometrycznego. Zależność pomiędzy mokrą masą (mg) i długością (mm) w początkach maja przedstawia wzór $w = 0{,}5624 \cdot L^{2{,}9337}$, a w końcu października przybiera postać $w = 0{,}778 \cdot L^{3{,}1323}$, dla suchej masy zaś $w = 0{,}00166 \cdot L^{2{,}8018}$. Z końcem listopada zależność pomiędzy mokrą masą i długością wyraża wzór $w = 0{,}3608 \cdot L^{2{,}7872}$. W przedziale długości samic produkujących jaja, zależność mokrej masy i długości przed złożeniem jaj do marsupium wyraża wzór $w = 0{,}1426 \cdot L^{2{,}1077}$, po złożeniu jaj przybiera postać $w = 0{,}1845 \cdot L^{2{,}6042}$. Cykl życiowy gatunku trwa ponad 2 lata. Po 19 miesiącach od wylęgu, następuje faza stacjonarna wzrostu samic. W fazie tej zachodzi dojrzewanie i składanie jaj. Wzrost samic w cyklu życiowym przebiega według krzywej S-owatej typowej dla wzrostu skorupiaków. *P. walkeri* jest organizmem wszystkożernym, pokarm jego stanowią szczątki roślinne z dna, mikroflora podlodowa i Copepoda. *P. walkeri* jest trwałym i najliczniejszym z fauny skorupiaków komponentem przybrzeżnego zespołu podlodowego. W skład tego zespołu wchodzi również mikroflora podlodowa i ryby. Pod lodem występuje również szereg grup zwierzęcych, których obecność ma często charakter przypadkowy. Skład zespołu i czas jego formowania się wykazuje lokalne różnice w przybrzeżnej części kontynentu Antarktydy. Istnieją podstawy do przypuszczenia, że przybrzeżny zespół różni się od podlodowego w strefie odległej od brzegu. Zespół podlodowy ma duże znaczenie, gdyż latem czerpią tu pokarm również pingwiny, foki i wieloryby.

8. REFERENCES

[Andriashev, A. P.] Андрияшев, А. П. 1967. О микрофлоре и фауне, связанной с антарктическим припайным льдом [Microflora and fauna associated with the antractic fast ice]. *Zool. Ż., Mosk.*, 46. 1585-1593, [Engl. summ.].

Andriashev, A. P. [Андрияшев, А. П.] 1970. Cryopelagic fishes of the Arctic and Antarctic and their significance in polar ecosystems. In: M. W. Holdgate [Ed] *Antarctic ecology*, 1, 297-304, London, Academic Press.

[Baranov, G. I., Nazintzev, L., Cherepanov, N. V.] Баранов, Г. И., Назинцев, Л., Черепанов, Н. В. 1968. Условия формирования и некоторые своиства морских антарктических льдов (по наблудениям в 1963 году) [Conditions of formation of the Antarctic sea ice and its properties (according to the observations in 1963)]. *Trudy sov. antarkt. Eksped.*, 38, 77-89.

Barnard, K. H. 1930. Crustacea. Part XI-Amphipoda. British Antarctic (Terra Nova) Expedition 1910. *Natural History Rep., Zoology.* 8, 307-454.

Barnard, K. H. 1932. Amphipoda. *Discovery Rep.*, 5, 1-326.

Bunt, J. S. 1960. Oceanography, hydrology. Introductory studies: hydrology, and plankton, Mawson, June 1956-February 1957. *A. N. A. R. E. Rep., Ser. b*, 3, 1-35.

Bunt, J. S. 1963. Diatoms of antarctic sea ice as agents of primary production. *Nature, Lond.*, 199, 1255-1257.

Bunt, J. S. 1964. Primary productivity under sea ice in antarctic water. *Antarctic Res. Ser.*, 1, 13-26.

Bunt, J. S. 1965. Measurements of photosynthesis and respiration in a marine diatom with the mase spectrometer and aith carbon 14. *Nature Lond.*, 207, 1373-1375.

Bunt, J. S. 1966. Microalgae of the antarctic pack ice zone. SCAR Symposium on antarctic oceanography. Santiago de Chile [mimeographed copy].

Bunt, J. S., Wood, E. J. F. 1963. Microalgae and antarctic sea ice. *Nature, Lond.*, 199, 1254.

Burkholder, P. R., Mandelli, E. F. 1965. Productivity of microalgae in antarctic sea ice. *Science*, 149, 872-874.

[Cherepanov, N. V.] Черепанов, Н. В. 1969. Новый кольцевой ледовый бур [The new type of an ice ring-drill]. *Problemy Arkt. Antarkt.*, 32, 122-125.
Chia, F. S. 1970. Reproduction of arctic marine invertebrates. *Mar. Poll. Bull.*, 1 (NS), 78-79.
[Chikovskiy, S. S.] Чиковский, С. С. 1969. Прибрежные гидрологические исследования в море Дейвиса в 1965/66 г. [Inshore hydrobiological researches in the Davis Sea, 1965/66]. *Trudy sov. antarkt. Eksped.*, 49, 346-354.
Dayton, P. K., Robilliard, G. A., Paine, R. T. 1970. Benthic faunal zonation as a result of anchor ice at McMurdo Sound, Antarctica. In: M. W. Holdgate [Ed] *Antarctic ecology*, 1, 244-258, London, Academic Press.
Fincham, A. A. 1970. Amphipods in the surf plankton. *J. mar. biol. Ass. U. K.*, 50, 177-198.
Forrester, C. R., Alderdice, D. F. 1965. Effects of salinity and temperature on embryonic developments of the pacific Cod (*Gadus macrocephalus*). *J. fish. Res. Bd Can.*, 23, 319-340.
[Golikov, A. N.] Голиков, А. Н. 1970. Метод определения продукционных свойств популяций по размерной структуре и численности [The method of determining productive properties of populations according to size and quantity]. *Dokl. Akad. Nauk* S.S.S.R., 193, 730-733.
[Gordienko, P. A., Fedotov, V. I., Šil'hikov, V. I.] Гордиенко, П. А., Федотов, В. И., Шильников, В. И. 1960. Ледяной покров прибрежных вод восточной Антарктиды [Ice cover of the Antarctic coastal waters]. *Trudy sov. antarkt. Eksped.*, 11, 1-118.
Gruzov, Ye. N., Pushkin, A. F. [Грузов, Е. Н., Пушкин, А. Ф.] 1970. Bottom communities of the upper sublittoral of Enderby Land and the South Shetland Islands. In: M. W. Holdgate [Ed] *Antarctic ecology*, 1, 235-238, London, Academic Press.
[Gruzov, Ye. N., Propp, M. V., Pushkin, A. F.] Грузов, Е. Н., Пропп, М. В., Пушкин, А. Ф. 1967. Биологические сообщества прибрежных районов моря Дейвиса (по результатам водолазных наблюдений) [Biological communities of the inshore areas of the Davis Sea (from data of diving observations)]. *Inf. Byull. sov. antarkt. Eksped.*, 65, 124-140.
[Gruzov, Ye. N., Propp, M. V., Pushkin, A. F.] Грузов, Е. Н., Пропп, М. В., Пушкин, А. Ф. 1969. Гидробиологические наблудения [Hydrobiological studies]. *Trudy sov. antarkt. Eksped.*, 50, 99-111.
Hickel, W. 1969. Planktonische und hydrographisch-chemische Untersuchungen in der Eckernförder Bucht (Westliche Ostsee) während und nach der Vereisung im extrem kalten Winter 1962/63. *Helgoländer wiss. Meeresunters.*, 19, 318-331.
Hynes, H. B. N. 1954. The ecology of *Gammarus duebeni* Lilljeborg and its occurrence in fresh water in Western Britain. *J. Anim. Ecol.*, 23, 38-84.
[Jakubowski, M.] Якубовски, М. 1970. Особенности морфологии системы органов боковой линии представителей антарктического рода Trematomus Boul. (Nototheniidae, Pisces) [The morphological characteristics of the lateral line organs in fishes belonging to the Antarctic genus Trematomus Boul. (Nototheniidae, Pisces)]. *Vop. ihtiol.*, 10, 385-390.
Jensen, J. P. 1958. The relation between body size and number of eggs in marine malakostrakes. *Meddr. Dan. Fisk.-og Havunders*, NS(II), 19, 1-25.
Kinne, O. 1953. Zur Biologie und Physiologie von *Gammarus dubeni* Lillj. *Z. wiss. Zool.*, 157, 427-491.
Kinne, O. 1960. *Gammarus salinus*-einige Daten über dem Umwelteinfluss auf Wachstum, Hautungsfolge, Herzfrequenz und Eientwicklungsdauer. *Crustaceana*, 1, 208-217.
Kinne, O. 1961. Growth, molting frequency, heart beat, number of eggs and incubation time in *Gammarus zaddachi* exposed to different environments. *Crustaceana*, 2, 26-36.
[Klokov, V. D.] Клоков, В. Д. 1970. Прорыв вод из озера Глубокого на станции Молодежной [Water flush from the Lake Glubokoe at Molodezhnaya Station]. *Inf. Byull. sov. antarkt. Eksped.*, 77, 96-99.
Knox, G. A. 1968. Tides and intertidal zones. In: *Symposium on Antarctic Oceanography*. 131-146, Cambridge, Scott Polar Res. Inst.
Knox, G. A. 1970. Antarctic marine ecosystems. In: M. W. Holdgate [Ed] *Antarctic ecology*, 1, 69-96, London, Academic Press.
[Koblents, Ya. P.] Кобленц, Я. П. 1968. Топографические и гидрографические работы в райное станции Молодежной [Hydrographic and topographic survey in the Molodeznaya Station area]. *Inf. Byull. sov. antarkt. Eksped.*, 67, 65-71.

Littlepage, J. L. 1965. Oceanographic investigations in McMurdo Sound, Antarctica. *Antarctic Res. Ser.*, 5, 1-38.

MacGinitle, G. E. 1955. Distribution and ecology of the marine invertebrates of Point Barrow Alaska 1955. *Smithson. musc. Collns*, No. 9, 1-201.

[Maltsev, V. N.] Мальцев, В. Н. 1963. Гидрографическое обследование района станции Молодежной [Hydrogrophic observations of the area of Molodezhnaya Station]. *Inf. Byull. sov. antarkt. Eksped.*, 44, 17-21.

[Markov, K. K., Bardin, V. I., Lebedev, V. L., Orlov, A. I., Suetova, I. A.] Марков, К. К., Бардин, В. И., Лебедев, В. Л., Орлов, А. И., Суетова, И. А. 1968. География Антарктиды [Antarctic geography]. Moskva, Izdat. „Mysl".

Mathisen, O. A. 1953. Some investigations of the relict Crustaceans in Norway with special reference to *Pontoporeia affinis* Lindstrom and *Pallasea quadrispinosa* G. O. Sars. *Nytt Mag. Zool.*, 1, 49-86.

Pearse, J. S. 1963. Marine reproductive periodicity in Polar seas: A study on two invertebrates at McMurdo Sound. *Bull. ecol. Soc. Am.*, 44, part 2, 43-

Peckham, V. 1964. Year-round SCUBA in the Antarctic. *Polar. Rec.*, 12, No. 77, 143-146.

Rakusa-Suszczewski, S. 1971 a. Preliminary report of work of Polish hydrobiologists during the antarctic expedition 1968-1970. *Oceanologia*, 2, 00-00.

Rakusa-Suszczewski, S. 1971 b. Biology of *Paramoera walkeri* Stebbing (Amphipoda) as a component of sub-fast-ice community in the antarctic coastal region. (Preliminary information). *Oceanologia*, 2, 00-00.

[Rakusa-Suszczewski, S.] Ракуса-Сущевски, С. 1971c. Видовой состав и некоторые своиства популаций рыбы ловленной зимой у берега залива Алашеева (Enderby Land) [Species composition and some features of fish population caught in winter near the shores of Alasheyev Bight (Enderby Land). *Inf. Byull. sov. antarkt. Eksped.*, 83, 000-000.

Ray, C. 1966. Stalking seals under Antarctic ice. *Geogr. Mag., Lond.*, 129, 54-65.

Segerstråle, S. C. 1950. The amphipoda on the coasts of Finland — some facts and problems. *Commentat. Biol.*, 10, No. 14, 1-28.

[Shamont'yev, V. A.] Шамонтьев, В. А. 1963. Приливы в заливе Алашеева [Tides in Zaliv Alasheyeva]. *Inform. Byull. sov. antarkt. Eksped.*, 43, 31-32.

Sheader, M., Chia, F. S. 1970. Development, fecundity and brooding behaviour of the Amphipod, *Marinogammarus obtusatus. J. mar. biol. Ass. U. K.*, 50, 1079-1099.

[Shevtsov, V. V., Makarov, P. P.] Шевцов, В. В., Макаров, П. П. 1969. К биологии антарктического крила [On the biology of krill]. *Trudy vses. naučno-isled. Inst. morsk. ryb. hoz. okeanogr. (VNIRO)*, 66, 177-206.

[Simonov, I. M.] Симонов, И. М. 1968. Физио-географическия характеристика оазиса Молодежная [Physico-geographical characteristic of Meledezhnayal]. *Trudy sov. antarkt. Eksped.*, 38, 6-21.

Stebbing, T. R. A. 1906. Crustacea. Amphipoda, Gammaridea. *Das Tierreich. Lief.* 21, 1-39, Berlin.

Steele, V. J., Steele, D. H. 1970. The biology of Gammarus (Crustacea, Amphipoda) in the Northwestern Atlantic. II- *Gammarus setosus* Dementieva. *Can. J. Zool.*, 48, 659-671.

Teissier, G. 1960. Relative growth. In: T. H. Waterman [Ed] *The physiology of crustacea*, 1, 537-560, New York, Academic Press.

Thorson, G. 1950. Reproductive and larval ecology of marine bottom invertebrates. *Biol. Rev.*, 25, 1-45.

Thurston, M. H. 1968. Notes on the life history of *Bovallia gigantea* (Pfeffer) Crustacea, Amphipoda. *Br. Antarct. Surv. Bull.*, 16, 57-64.

Thurston, M. H. 1970. Growth in *Bovallia gigantea* (Pfeffer) Crustacea, Amphipoda. In: M. W. Holdgate [Ed] *Antarctic ecology*. 1, 269-278, London, Academic Press.

[Treshnikov, A. F.] Трешников, А. Ф. 1963. Особенности ледового режима Южного Ледовитого океана [The characteristics of ice structure of Southern Ocean]. *Trudy sov. antarkt. Eksped.*, 21, 1-237.

[Tshyslenko, L. L.] Численко, Л. Л. 1968. Номограммы для определения веса водных организмов по размерам и форме тела (морской мезобентос и планктон) [The nomograms for weight estimation of aquatic organisms dealing with their body's size and shape (marine mesobenthos and plankton)]. Leningrad, Izdat. „Nauka".

Vlasblom, A. G. 1969. A study of a population of *Marinogammarus marinus* (Leach) in the Oosterschelde. *Neth. J. Sea Res.*, 4, 317-338.
Watkin, E. E. 1939. The pelagic phase in the life history of the amphipod genus Bathyporeia. *J. mar. biol. Ass. U. K.*, 23, 467-481.
[Winberg, G. G.] Винберг, Г. Г. 1966. Скорость роста и интенсивность обмена у животных [The rate of growth and intensity of metabolism in animals]. *Usp. sovrem. Biol.*, 61, 274-293.
[Winberg, G. G.] Винберг, Г. Г. [Ed.] 1968. Методы определения продукции водных животных [The methods for the estimation of production of aquatic animals]. Minsk, Izdat. „Vyšejšaja Škola".
[Yeskin, L. I.] Ескин, Л. И. 1969. Морские льды Южного Океана [Sea ice of the Southern Ocean]. *Problemy Arkt. Antarkt.*, 31, 24-30.
[Yevseev, V. V] Евсеев, В. В. 1969. Ледовые условия в заливе Алашеева [The ice conditions in the Alasheev Bay]. *Trudy sov. antarkt. Eksped.*, 49, 460-463.

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E. FISCHER

SEASONAL CHANGES OF THE NUMBER OF NITROGEN CYCLE BACTERIA IN BOTTOM SEDIMENTS OF A POOL

Department of Bioenergetics and Bioproductivity, Nencki Institute of Experimental Biology, Pasteura 3, Warszawa 22, Poland

ABSTRACT

The seasonal changes of the total number of bacteria were investigated as well as those of bacterial groups taking part in the conversions of nitrogen compounds in the surface layers of bottom sediments in a pool of the Kampinos Forest. All groups of bacteria respond to factors affecting the whole community, but in different ways. Their densities in particular seasons of the year are different.

1. INTRODUCTION

The aim of this work was to characterize the seasonal changes of the total number of bacteria as well as of the bacteria of selected physiological groups taking part in the conversions of nitrogen compounds in bottom sediments. These groups were selected in view of their role in the nitrogen cycle of the pool. Owing to processes of mineralization of dead animal and plant material these bacteria convert nitrogen into the form available to animals and plants and to other microorganisms, which in turn may constitute the food for aquatic animals (ZoBell, Feltham 1938, ZoBell, Grant 1943, ZoBell 1946, Rodina 1949a, 1949b, Żukova 1954, Nauwerck 1963).

2. MATERIAL AND METHODS

The study on bottom sediments was carried out in a small pool in the Kampinos Forest. This pool was easily affected by climatic influences because of its small size and therefore was a good object for this kind of investigations.

The investigations lasted from January 1961 to January 1962. The pool is bordered by meadows and marshes and situated at some distance from fields and a mixed forest. The pool has no flow, but at high water level it joins another pool by a ditch, which is dry in summer. The distance of the pool from the nearest buildings is about 200 m. The pool is an oval basin, 8×15 m about. During the year its maximum depth fluctuates from 70 to 180 cm. In summer, near the shore of the pool, *Scirpus silvaticus* occurs sparsely; *Juncus effusus* and *Equisetum limosum* dominate among the emergent vegetation. The bottom of the pool is in 50% overgrown with *Elodea canadensis*.

The bottom of the pool is formed on sandy substratum and has a layer of bottom sediments of several cm. The bottom layers of sampling stations are as follows: 1 — semi-liquid detritus (about 3 cm), 2 — detritus with fine-grained sand (about 5 cm), 3 — pale fine-grained sand (4–5 cm), 4 — coarse-grained gravel (the deep reaching layer). The colour of bottom sediments is black-grey in the top layer and deeper it is grey and grey-yellow, what points to its organic character in the top layer and a mixed, siliceous-organic character in deeper layers.

The concentrations of biogenic substances (phosphates, nitrates and nitrites) in water are low (Table I). The pH was close to 7. The temperature of water and of the top sediment layer was measured using the thermometer described by Paschalski (1967). The water temperature strongly fluctuates during the year. In

Table I. Some results of physical and chemical analysis of water and bottom sediments of the investigated pool (10.I.1961-3.I.1962)

Date	Water										Sediment	
	PO_4^{---} (mg/l)	SO_4^{--} (mg/l)	NH_4^{+} (mg/l)	NO_2^{-} (mg/l)	NO_3^{-} (mg/l)	H_2S (mg/l)	O_2 (mg/l)	CO_2 (mg/l)	pH	Temp. (°C)	Temp. (°C)	CO_2 (mg/l)
10.I	0.5	28.1	2.3	T	—	+	0.9	48.2	6.6	3.8	4.2	348
24.I	0.6	39.0	1.3	T	—	+	1.1	45.1	7.1	3.8	3.8	340
9.II	0.4	37.8	0.2	T	—	0	0.8	89.1	6.8	1.6	3.5	483
22.II	0.5	45.1	0.2	0.01	—	0	1.2	49.2	6.8	1.7	2.7	219
8.III	0.2	42.3	0.1	0	—	0	9.5	43.1	6.9	5.3	5.4	608
23.III	0.1	40.2	0.1	0	—	0	9.0	43.1	6.9	4.5	4.8	—
5.IV	0.1	50.6	0.1	0	0.1	0	11.2	45.6	6.8	6.0	5.7	—
22.IV	0.03	47.3	0.1	0	0.1	0	8.3	42.0	7.0	5.9	5.7	527
12.V	0.01	38.3	0.1	0	0.1	0	6.5	35.2	6.9	12.1	10.5	—
6.VI	T	43.3	0.14	0	0.12	0	7.35	32.5	7.3	19.0	18.3	—
12.VI	0.01	34.2	0.1	0	0.1	0	6.7	38.0	7.1	21.0	19.9	307
12.VII	0	24.2	0.1	T	0.1	0	2.3	42.0	6.8	23.0	22.9	457
20.VII	0.01	24.0	0.11	0.001	0.2	0	3.6	41.0	6.7	20.1	18.0	—
19.VIII	T	22.6	1.2	0	0.06	0	6.97	43.5	6.4	16.3	16.0	322
1.IX	T	27.6	0.08	T	0.06	0	7.6	26.7	6.9	16.8	16.0	—
6.IX	0.1	35.2	0.05	0	0.06	0	6.8	33.3	7.1	15.0	14.5	586
17.X	0.15	30.0	0.12	0	0.06	0	3.2	21.5	7.0	12.5	13.0	816
7.XI	0.12	37.0	0.1	T	0.08	0	2.5	18.2	7.1	3.2	3.4	439
5.XII	0.1	40.3	0.02	0	0.06	+	2.3	16.7	7.0	5.7	5.8	622
3.I	0.6	19.7	3.6	0.012	0.2	+	0	33.0	6.8	0.3	4.2	402

0 — not found, + — found, T — traces, — — no measurements was made.

the upper 20 cm of water layer the annual fluctuations were from 0.3 to 23°C, and in the top sediment layer (Fig. 1) from 1.2 to 22.9°C. The ice cover during the period

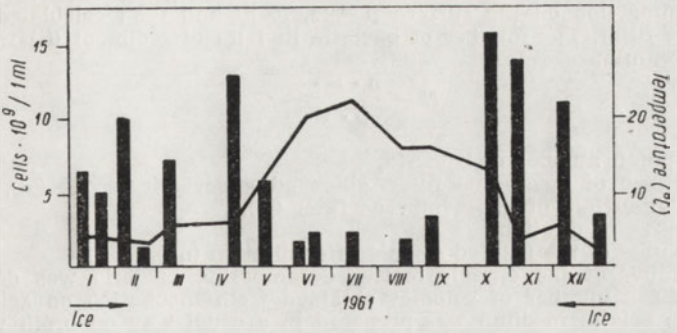

Fig. 1. Seasonal changes of temperature in the top layer of sediment (line) and of total number of bacteria cells per 1 ml of bottom sediment (black columns)

of investigations lasted from the first days of January to the third decade of February, and then from mid-December till the end of investigations. The presence of hydrogen sulphide in water was found during the time when the pool was covered with ice.

In spite of the variability of small pools (P a s c h a l s k i 1958, 1959) the sampling of material was limited to once a month. More frequent sampling might have caused too great disturbance in such a small biotope. Samples were taken from one place, from a foot bridge, 3 m off the bank, using a sterile sounder 35 cm long and of the opening diameter 3.5 cm. The bottom part of the sounder has been wedge shaped to make easier the entering into the sediment. After the sounder had been drawn ashore the heavy head placed on the top was lifted out and the sediment was pushed upwards by means of a piston. The top layer, about 3 cm thick, of a 30 ml volume, was taken from each sampling. In order to collect one sample the sounder was submerged three times, less than 20 cm apart, with the interval between samplings from 3 to 5 minutes. This interval was necessary to enable the settlement of the stirred part of semi-liquid detritus.

Such a slime sample was transferred to the laboratory in a sterile vacuum flask. The time between sampling and the further treatment of the sample did not exceed 2 hours.

The number of bacterial cells was determined in 1 ml of top layer of the bottom sediments, after the following pattern:

1. directly counted cells,
2. saprophytic ones growing on gelatin,
3. denitrifying bacteria,
4. free living, molecular nitrogen fixing bacteria,
5. bacteria oxidizing ammonium compounds to nitrites,
6. bacteria oxidizing nitrites to nitrates.

Besides, the strains isolated from the cultures were identified.

The total number of bacterial cells inhabiting the sediment was determined by the method of direct counting of cells on membrane filters (Co-5, Göttingen). In order to open the pores in the filters, they were boiled three times for at least 5 minutes in distilled water.

The number of bacteria was expressed in relation to 1 ml of sediment. A volume of 10 ml of sediment diluted with sterile saline in a proportion 1 : 10, was shaken for 10 minutes on a shaker in order to separate the bacterial cells from sediment particles, and then successively diluted. After the sediment particles settled at the bottom of the flask, 10 ml of the suspension was taken from the suitable dilution and filtered. Most frequently three dilutions were chosen and from each one the material was filtered through three to five membrane filters Each membrane filter was immediately placed on filter paper soaked with 4% formalin solution to prevent formation of microcolonies on the membrane filter. Then the membrane filters were stained with 5% erythrosine solution in phenol 5% aqueous solution (S o r o k i n 1954). The staining time of 24 hrs was chosen by the author's own practice. Subsequently the membrane filters were discoloured by

transferring them several times onto a filter paper soaked with distilled water. The bacterial cells preserved their bright red colour. Two strips were cut out of the dried filter, of the total surface about 2 cm², on which the bacteria were counted under oil immersion on the surface $p = 12{,}870$ μ² and then calculated per surface of the entire filter. The number of bacteria in 1 ml of sediment (N) was calculated using the formula:

$$N = \frac{n \cdot P \cdot s}{p \cdot V}$$

where:

n — counted number of bacteria,
p — surface of membrane filter, observed under microscope (μ²),
P — total surface of the membrane filter (μ²),
s — degree of dilution,
V — volume of the filtered sample after dilution (ml).

The number of the organic matter decomposing bacteria was determined on the basis of the number of colonies obtained from incubation on gelatin medium at 20°C. The gelatin medium was prepared in a usual way on broth with addition of 30% gelatin, its pH was 7.4. Sterilization was made by pasteurization. The medium after pouring it on Petri dishes was kept at 20°C during 48 hrs in order to check its sterility. The inoculations were made out of 4 or more dilutions, pouring 0.5 ml of bacterial suspension on the dish with the medium. Out of each dilution inoculations were made on 5 dishes. The dishes were incubated at 20°C during 48 hrs and afterwards all colonies were counted. Apart from that the protease excreting colonies were counted, that was deduced from gelatin liquefaction around them. The colonies differing from one another as to their size, structure, character of margin and of the surface were inoculated onto agar medium in order to multiply the strain for its further identification.

The bacterial cells were counted using the formula:

$$N = \frac{n \cdot s}{v}$$

where:

N — number of bacteria in 1 ml of bottom sediment,
n — number of colonies found on the dish,
v — volume of the diluted sediment suspension poured onto the dish (ml),
s — degree of dilution.

It was assumed in the calculations, that each colony originated from a single cell. The isolated strains were determined according to Breed et al. (1952).

The determination of the number of denitrifying bacteria was made as above, using the culture medium after Fiodorov (1952):

Seignette salt — 20.0 g, KNO_3 — 2.0 g, K_2HPO_4 — 0.5 g, $MgSO_4$ — 0.2 g, redistilled water — 1000 ml.

The filters were placed on sponges which were soaked with this culture medium. The inoculations were incubated 3 days at 25°C, then the colonies were counted. Their macro- and microscopical appearance was described. The colonies of differing strains were isolated on slant agar with the above described medium for the sake of identification. Moreover each of the isolated strains was inoculated on two liquid media, one with nitrates and another with nitrites. The inoculations were incubated together with the control (medium not inoculated) for 6 days at 25°C and then their nitrate, nitrite and ammonia content was determined after Just, Hermanowicz (1955). The colonies which gave a positive result in reduction of nitrates or nitrites were considered as denitrifying ones. The strains thus selected were counted and identified.

The molecular nitrogen fixing bacteria were cultivated on a medium containing mannitol (Fiodorov 1952): mannitol — 20.0 g, K_2HPO_4 — 0.2 g, $MgSO_4$ — 0.2 g, NaCl — 0.2 g, K_2SO_4 — 0.1 g, $CaCO_3$ — 5.0 g, crystal violet — 0.1 g, redistilled water — 1000 ml.

The culture was incubated at 25°C for 5 days. Investigations of the group of nitrifying bacteria consisted in the determination of the number of their colonies grown from bottom sediments as well as in establishing of morphological and physiological features of strains isolated from the culture for the sake of identification.

Both groups of nitrifying bacteria (oxidizing ammonium compounds into nitrites and oxidizing nitrites into nitrates) were cultivated on mineral liquid medium. The sampled bottom sediment was diluted with water from the pool, free of bacteria, in a proportion 1 : 10, 1 : 10^2, 1 : 10^3 and so on. Out of 3-4 successive dilutions of the

sediment, 10 ml were sampled and filtered through membrane filters (Co-5, Göttingen). Of each dilution 5 filtrations were made.

The liquid mineral medium was prepared after Fiodorov (1952) with which synthetic sponges were soaked. For the bacteria oxidizing ammonium compounds into nitrites (group I) the medium composition was: $(NH_4)_2SO_4$ — 0.2%, K_2HPO_4 — 0.1%, $MgSO_4$ — 0.05%, NaCl — 0.2%, $FeSO_4$ — 0.04%, $CaCO_3$ — 0.5%, redistilled water ad 100%.

For the bacteria oxidizing nitrites into nitrates (group II) the composition was: $NaNO_2$ — 0.1%, Na_2CO_3 — 0.1%, NaCl — 0.05%, K_2HPO_4 — 0.05%, $MgSO_4$ — 0.05%, $FeSO_4$ — 0.04%, $CaCO_3$ — 0.5%, redistilled water ad 100%.

The sponges and media were sterilized in the autoclave (1.5 atm., 0.5 hr). The filters placed on sponges were incubated for 6 days at 25°C. After incubation the colonies were inoculated on an enrichment medium for the sake of identification and their nitrifying properties were checked, also the number of bacteria was counted. The ability to oxidize ammonium compounds into nitrites was found by placing the filters with bacteria on filter paper soaked with the Griess reagent (Just, Hermanowicz 1955). Colonies oxidizing ammonium compounds into nitrites became red.

Colonies grown on the selective medium for the II group of nitrifying bacteria were inoculated on an identical liquid medium in which the content of nitrites and nitrates was determined quantitatively. An inoculated medium and the control one (not inoculated) were incubated at 25°C for 10 days and after that period the analysis of the nitrate and nitrite content was made again. Disappearance of nitrites and appearance of nitrates in the culture pointed to the oxidizing intensity from nitrites into nitrates exhibited by the bacteria in the sample.

The colonies were counted twice under a magnifying glass (×5) before and after staining with 5% erythrosine in phenol 5% aqueous solution, as described above.

In order to identify the cultivated strains, the colonies exhibiting an autotrophic character were chosen. This character was checked by a negative result of inoculation on broth.

3. RESULTS

The total number of bacteria in the bottom sediment of the investigated water body is presented on Fig. 1. The seasonal character of the quantitative occurrence of bacterial flora is evident.

1. Winter period (December–February) is characterized by great variations of the number of microorganisms, from $1.2 \cdot 10^9$ to $10.9 \cdot 10^9$ cells in 1 ml. It seems interesting, that both in the sample taken before the freezing over of the water body and in the sample taken before the thawing, the greatest numbers of bacteria (about $10 \cdot 10^9$) for the winter period were found, and then in both instances the maximum number of bacteria is followed by a decrease.

2. Spring period (March–May) shows greater number of bacteria, than in winter. The highest value for the spring period occurred in April — $13.2 \cdot 10^9$ cells/ml.

3. The summer period (June–August) is characteristic with smallest numbers of bacteria, $1.6 \cdot 10^9$ to $2.4 \cdot 10^9$ cells/ml. This is a period of abundant plant vegetation and of appearance of a large amount of aquatic organisms feeding on bacteria.

4. In the autumn period (mainly October, November) the highest numbers of bacteria are met in the bottom sediment, up to $15.9 \cdot 10^9$ cells/ml in October.

The number of saprophytes grown on gelatin is presented on Fig. 2. The number of grown bacteria varied greatly within the year — $3 \cdot 10^3$

to 85 · 10³ cells/ml of sediment and rapid changes in number were often observed (e.g. in June 3718 · 10³, in July 3.3 · 10³, in November 85 · 10³, in December 628 · 10³ cells/ml). Each season of the year showed distinct features of quantitative occurrence of saprophytes, able to grow on

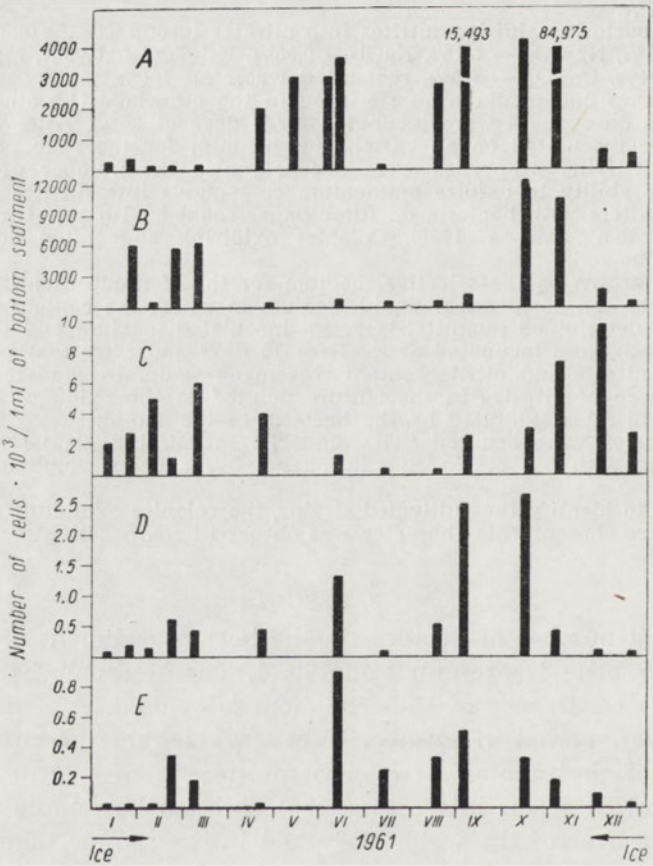

Fig. 2. Seasonal changes of number of cultivated bacteria cells per 1 ml of bottom sediment. A — saprophytic bacteria cultivated on gelatine, B — denitrifying bacteria, C — bacteria fixing atmospheric nitrogen, D — nitrifying bacteria ($NH_4^+ \rightarrow NO_2^-$), E — nitrifying bacteria ($NO_2^- \rightarrow NO_3^-$)

gelatin. The winter period was characterized by low and rather level number of bacteria (138 · 10³–520 · 10³ cells/ml of sediment). During the spring period great changes occurred in the number, but in an increasing order, as the spring passed into the summer (from 92 · 10³ to 3114 · 10³ cells/ml of sediment). In summer also great variations were noticed, in the middle of summer (July) there was very little of bacteria. In autumn the highest numbers of bacteria were found, thousand times higher than the minimum ones. Just before the freezing over of the water body the number of bacteria decreased rapidly.

The bacteria showing high proteolytic activity were found in cultures all year round. The percentage of colonies liquefying gelatin was various

in particular seasons of the year. Proteolytic saprophytes occurred most numerously in winter. Their number reached up to 95% of grown colonies, whereas in spring and summer only 3–17% and in autumn 20–40%. During the summer the liquefaction of gelatin usually took place on the second day of incubation, when in autumn it took place frequently before the first day passed.

Among the growing microorganisms fairly numerous colonies of pigmented bacteria were distinguished, yellow in various shades and pink. Exceptionally many colonies of pigmented bacteria were observed in October (about 90%), in September and November (60–80%). It is possible that, since the consumption of bacteria by aquatic animals is greater in summer, the bacteria containing dyes of carotene type, as rich in A provitamin, were more intensely destroyed than other cells.

The identification of isolated strains showed the presence of microorganisms belonging to genera: Pseudomonas, Aerobacter, Flavobacterium, Escherichia, Sarcina, Proteus, Spirillum.

The results of estimations of the number of denitrifying bacteria are also presented on Fig. 2. This was, beside the saprophytes growing on gelatin, the most numerous group of nitrogen cycle bacteria in the bottom sediment of the investigated water body. One ml of sediment contained $158 \cdot 10^3$-$12{,}500 \cdot 10^3$ cells. The most numerous denitrifying bacteria were found in autumn (October, November). Considerably lower numbers of denitrifying cells were found from March to September, $158 \cdot 10^3$–$807 \cdot 10^3$ bacteria in 1 ml of sediment. However these are high values as compared with the numbers of bacteria of other nitrogen groups. The identification of the isolated strains showed the predominance of Pseudomonas genus. Furthermore the following organisms were found: *B. vulgaris, B. coli, B. coli aerogenes, B. denitrificans, Micrococcus denitrificans.*

The studies on the group of free nitrogen fixing bacteria included only the aerobic, free living one. The number of colonies grown from bottom sediment samples were determined and the genus of the isolated strains was identified. The number of bacteria fixing the molecular nitrogen falls under the range 275–10,000 cells/ml of sediment sample (Fig. 2).

The genera Azotobacter and Azotomonas were distinguished among the cultivated microorganisms. During the autumn period the cultures were frequently contaminated with a microorganism not belonging to Azotobacter. It formed fine, flat, dry, colourless colonies, containing single coccoid or diplococcoid cells, Gram negative, characterized by Brown motion. These colonies were not included in calculations and detailed identification.

The results obtained (Fig. 2) show a relatively small difference between respective samples. Thousands of cells were found in 1 ml of sediment in all samples, with the exception of two summer months (July,

August), when hundreds of bacteria specimens occurred in 1 ml. A regularity in the annual dynamics of the number of molecular nitrogen fixing bacteria was observed. During the winter, when the ice began to thaw, the number of bacteria gradually increased. As the ice melted away, their number rapidly decreased. However already in March the number of bacteria increased again, but since then a decrease of their number was observed, which lasted during the summer till autumn, when it increased again.

The nitrifying bacteria, oxidizing NH_4^+ to NO_2^- were found during the year in an amount 25–2800 cells/ml of sediment. The lowest values were obtained in winter months (December–February) and in July, when the numbers in almost all the investigated physiological groups, and also the density of the whole community, were at the lowest level.

In the group of bacteria oxidizing NO_2^- to NO_3^- the variations in number were greater than in the previous group. In 1 ml of bottom sediment 4-900 cells were found. Also in this group a decrease in number was observed in winter months. The density of both groups of nitrifying bacteria show changes, that are irregular and not connected with the seasons. The strains of the genus Nitrosomonas were identified as nitrifying bacteria oxidizing ammonium salts into nitrites. They formed fine, colourless colonies, from 0.3 to 0.6 mm in diameter, smooth, glossy, slightly convex. The cells were oval-shaped, measuring about 0.5–1.3 μ, motile, without capsules, nonspore-forming, Gram negative. The staining of cilia did not allow to establish their position, as they were found detached from the cells.

Bacteria oxidizing nitrites into nitrates were reckonned among the genus Nitrobacter on the basis of the estimations of their morphological and physiological features.

4. DISCUSSION

The number of bacteria in bottom sediments of the investigated water body shows periodical variations. This results both directly from the astatic character of the abiotic habitat of the pool (Table I, Fig. 1), and also from the seasonal changes of biological relations. Thus, for example the change in chemical composition of the water of the pool (e.g. O_2, CO_2 content) during freezing and thawing and the disturbance of the biological balance connected with it may be the reason for rapid change of the number of bacteria in that period (Fig. 1).

On the other hand the reasons for the small number of bacteria established in the bottom sediments in summer may be found either in low production activity of bacteria, probably caused by unfavourable development conditions (e.g. competition of algae in the utilization of biogenic substances), or, probably, in the bacteriostatic action of some

algae on bacteria. It seems, however, that the dominant role in maintaining the low number of bacteria in summer should be attributed to other factors, e.g. consumption by zooplankton. The evidence is supplied by estimations of the daily production of bacteria carried out on the same material by the isotopic method. The calculated factor of production activity of bacteria was the highest in summer.

The occurrence of abundant microflora during the autumn (Fig. 1) may be the result of copious food base for bacteria formed on the bottom of the pool consisting of the remains of dead plants and animals. Simultaneously, in that period, the consumption of bacterial population by zooplankton decreases.

Summing up the results of estimations of the number of bacteria in the bottom sediments during the year, it may be stated, that the numbers obtained are high and approximate to the numbers of bacteria in soil ($10 \cdot 10^9$ in 1 g of soil — Fiodorov 1952 a). These numbers are also approximate to those given by Kuznecov (1938) for therapeutic muds ($38 \cdot 10^6$ in 1 mg of dry mud weight), whereas the recounted present results showed from $3 \cdot 10^6$–$48 \cdot 10^6$ bacteria in 1 mg of dry weight. In seas and great lakes, the number of microorganisms in bottom sediments is approximate to the present results. And so, according to Kuznecov (1952) these values for lakes are $7.9 \cdot 10^6$–$54.2 \cdot 10^6$/mg of dry mud weight; after Isačenko (1937) for Kara Sea: $11 \cdot 10^6$/mg of dry weight; Hartuari (1937) found for Kosino Lake: $1 \cdot 10^6$–$3 \cdot 10^6$/mg of dry weight, similarly Rubenčik, Goiherman (1940) for Lake Repno: $2.6 \cdot 10^6$/mg of fresh mud weight.

The quoted data show that the range of the number of bacteria in bottom sediments of various reservoirs is considerable and that the investigated water body is rich in bacterial flora.

The majority of quoted papers does not provide information about the period, during which the authors took the samples, which makes the estimation of the number of bacteria in different seasons of the year more difficult. Therefore, the paper by Nikitina (1955) on the seasonal changes in the occurrence of microorganisms on the bottom of littoral of Barents Sea deserves greater attention. The numbers obtained by Nikitina are low as compared with the present data (Fig. 3). The ratio of the greatest number of bacteria found by Nikitina to the lowest one is 3.1, whereas in the pool under investigation it was 12.9. Moreover Nikitina observed the highest numbers of bacteria in summer, whereas in this season in the investigated pool the minimum of bacteria density was found. According to Melchiorri-Santolini (1966), this can be explained by different dynamics of the zooplankton feeding on bacteria.

The low number of saprophytes in summer is probably the result of plant development (e.g. antagonistic effect of plants on bacterial flora,

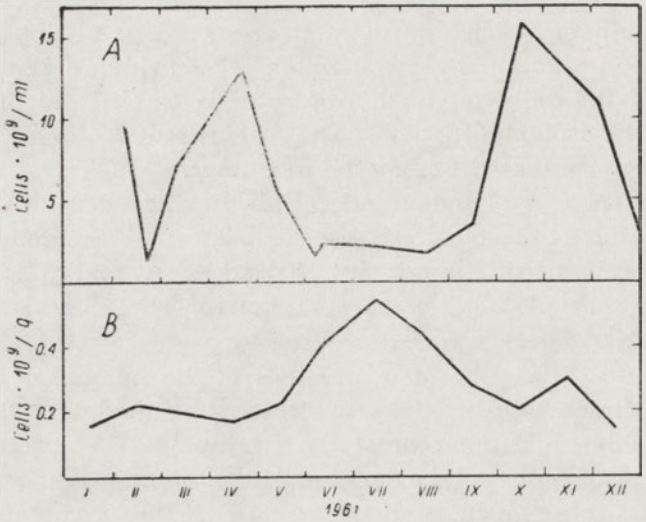

Fig. 3. Seasonal changes of number of bacteria cells in the top of bottom sediment. A — present data, B — littoral of Barents Sea (Nikitina 1955)

Matusiak 1954) and the great abundance of organisms feeding on bacteria. The high number of saprophytes in autumn is connected with the accumulation of organic matter in the water body. The slowing down of life processes in winter and greater stability of vegetation conditions result in an even and low number of saprophytic bacteria.

According to Melchiorri-Santolini (1966) many authors consider the per cent of heterotrophic bacteria in the total number of bacteria as the measure of the reservoir's trophy. This value varies from 10% for eutrophic lakes to 0.1% for seas having a very low productivity level. Analogous recounting of the present results is given in Table II. The share of saprophytic bacteria does not exceed 1% of the total number of bacteria. This is a lower percentage than that mentioned previously. The share of these bacteria in the bacterial community colonizing the

Table II. Saprophytic bacteria as promille of total number of bacteria (10.I.1961—3.I.1962)

Date	10.I	24.I	9.II	22.II	8.III	22.IV	12.V	6.VI
‰	0.033	0.080	0.014	0.075	0.017	0.153	0.540	1.900

Date	12.VI	12.VII	19.VIII	6.IX	17.X	7.XI	5.XII	3.I
‰	0.001	1.400	1.620	1.660	0.270	6.100	0.057	0.156

bottom sediments of the investigated pool varies frequently and considerably throughout the year. It is characterized by low values during winter and spring (up to 0.54‰) and by a considerable increase during summer and autumn (1.4–6.1‰). Samples taken in July and October are an exception. It might have been supposed that during the sampling period the factors destroying this group of bacteria acted particularly intensely in the pool. In July it was probably the intensive consumption of saprophytic bacteria by abundant zooplankton, or the harmful action of algae. In October such effect might have originated from large amounts of pigmented bacteria (about 90% of grown colonies) that appeared in this time. According to Bezborodov, Dobromyslov (1955) these bacteria produce substances harmful to numerous putrefactive bacteria.

The number of saprophytes found in the bottom sediments by other authors differ considerably. Potter (1963) found $990 \cdot 10^3$–$98{,}000 \cdot 10^3$ cells in 1 g of sediment in a number of pools in Montana, which were as shallow as the investigated one. Since the period of those investigations is not indicated, these results can be hardly compared with the present ones. However almost all the present results for summer and autumn are within the range of results presented by that author.

It is of interest that the estimations of saprophytes made by Potter for the same period for great oligotrophic lakes are close to lower limit of range of saprophyte number found in the pool under investigation ($780 \cdot 10^3$ in Flathead Lake and $1490 \cdot 10^3$ in Swan Lake).

Henrici, McCoy (1938) also obtained a relatively low number of saprophytes in the lake bottom sediments. In the surface layer of sediment of Lakes Alexander, Mendota and Brezelle (Minnesota and Wisconsin) $123 \cdot 10^3$–$148 \cdot 10^3$ cells in 1 ml of sediment were found. Also considerable differences were observed in the density of saprophytic bacteria in the bottom sediments in seas. For example Sorokin (1962) while investigating the bottom sediments of Black Sea, obtained $800 \cdot 10^3$–$980 \cdot 10^3$ colonies growing on agar, out of 1 g of sediment. ZoBell, Anderson (1936) found in bottom sediments of Mexico Bay $74 \cdot 10^6$ cells per 1 g.

The denitrifying bacteria occur most numerously in the investigated water body during autumn (Fig. 2). The conditions are suitable at that time, since the organic matter being accumulated in summer forms an ample food source. Intensive decomposition of organic matter undoubtedly causes a considerable oxygen depletion, which may result in the microspheres of mineralization processes in an advanced oxygen deficit that favours the reduction of nitrates and nitrites.

The present results of quantitative examination of denitrifying bacteria as compared with the results of other authors are relatively high (Table III). Both the present data and those of other authors indicate great variations in the number of denitrifying bacteria. Nikitina

Table III. Comparison of denitrifying bacteria in bottom sediments of different water bodies

Paper	Water body	Month	No. of bacteria · 10^3/g
Kuznecov 1952	Lake: eutrophic	—	up to 3000
	Lake: mesotrophic	—	60
	Lake: oligotrophic	—	10
	Lake: dystrophic	—	not found
Rubenčik 1948	Saline therapeutic muds	—	100–10,000
Fiodorov 1952	Lake	—	10,000
Nikitina 1955	Barents Sea (littoral)	XI	6.2
		XII	2.2
		I	0.03
		II	0.02
		IV	0.05
		V	5.5
		VI	172.0
		VII	218.0
		VIII	85.0
		IX	7.0
		X	0.4
		XI	3.53
		XII	0.37
			$NO_3^- — NO_2^-$ / $NO_3^- — N_2$
ZoBell 1946	Pacific Ocean depth (m) 780	—	100 / 0.1
	Pacific Ocean depth (m) 505	—	10,000 / 10
	Pacific Ocean depth (m) 1322	—	10 / 10
Present paper	Pool	whole year	150–1250/ml

(1955) in the course of investigations in an annual cycle of the bottom sediments of the littoral of Barents Sea found 20–218,000 denitrifying bacteria cells in 1 g of sediment. She observed the greatest densities of these microorganisms in samples taken in June and July. Kuznecov (1952) also noticed seasonal changes in number of denitrifying bacteria in lakes.

The results concerning the number of bacteria fixing molecular nitrogen are relatively more equal. In all samples thousands of cells were found in 1 ml of sediment (Fig. 2). This is probably due to the facility of Azotobacter to use various sources of carbon, nitrogen and phosphorus (Nowotny-Mieczyńska, Gołębiowska 1960). Low density of Azotobacter in summer months seems to prove the correlation with the small number of denitrifying bacteria in that time and also the fact,

that Azotobacter cells are devoured by aquatic organisms. The high protein content, up to 70% (Nowotny-Mieczyńska, Gołębiowska 1960) and of vitamins (Gebgart 1961), make them a desirable food for many organisms. The lack of rapid changes in the number of Azotobacter cells in particular sediment samples points to the facility of this species to adapt to the variable conditions of a pool. Azotobacter was found by many authors in water and bottom sediments of seas and oceans, in lakes, rivers and ponds. Very few quantitative examinations show that the density of bacteria fixing molecular nitrogen in water is small. They occur as single cells in 1 ml of water (Kuznecov 1952), whereas the bottom sediments contain from thousands to dozens of thousands of cells in 1 g of wet mud (Gambarian 1958, Rubenčik 1948).

These observations are confirmed by the present results. Seasonal investigations on the occurrence of Azotobacter in the mud of a lake, carried out by Gambarian, showed that the lowest number of positive results of inoculations of a suspension in water of plant and mud particles was found in July (0–18%) and the highest result was in winter (50–100%) and autumn (34–47%). Despite of the lack of absolute results, these results illustrate the relative density of Azotobacter in mud, the lowest one in July, which is also in agreement with the present results.

Great irregularities in the number of nitrifying bacteria (Fig. 2) may be explained by high sensitivity of these organisms to the presence of organic matter, the pH value, oxygen level and so on. The physiology of these microorganisms is well known in conditions of artificial culture (Fry 1955); despite of their sensitivity to the action of inhibiting factors, they possess the ability to adapt to a fairly wide range of conditions [1]. The high sensitivity to the environmental conditions and considerable adaptation ability of nitrifying bacteria make more difficult the finding of the reasons for their appearance or disappearance in the sediment of the astatic reservoir.

The literature on quantitative investigations on nitrifying bacteria in bottom sediments of water bodies is not very comprehensive. The majority of papers are discussing the investigations on sea sediments, and only few of them deal with lakes. Usually the authors limit their information as to state the presence or lack of nitrifying bacteria in the examined bottom sediments, or after finding nitrifying properties of the mud, conclude on the presence of nitrifying bacteria in it.

Among the few papers discussing the quantitative occurrence of nitrifying bacteria in bottom sediments, the papers of Rubenčik

[1] Fry (1955) stated that the pH optimum for the culture of nitrifying bacteria is not a constant value, but it depends on the pH of the environment out of which the nitrifying bacteria were isolated. Moreover some inhibitors such as peptone act on them differently in dependence upon the character of the environment, e.g. they are less harmful in the presence of sand than in liquid cultures.

(1948) and Nikitina (1955) deserve attention. Rubenčik found in saline reservoirs $0.01 \cdot 10^3$–$10 \cdot 10^3$ nitrifying bacteria in 1 g of sediment (in the present investigation up to 2800 cells/ml). The investigations of Nikitina on the littoral of Barents Sea were carried out in an annual cycle. The author found the lowest number of nitrifying bacteria in December, January, February and April, whereas in June and July about million cells/1 g of sediment of bacteria belonging to this group were present. These great variations in the annual cycle were very similar to our results: 25–2800 in the first group of nitrifying bacteria and 4–900 in the second one.

5. SUMMARY

The paper aimed at studying the seasonal changes of the total number of bacteria (using the method of direct count) and of several groups of bacteria taking part in the conversions of nitrogen compounds (incubation method) in the surface layer of the bottom sediments of a small pool of the Kampinos Forest.

The following groups were distinguished: bacteria cultivated on broth-gelatin medium and bacteria cultivated on membrane filters soaked with selective media for the nitrogen cycle bacteria, that is denitrifying, oxidizing ammonium compounds into nitrites, oxidizing nitrites into nitrates and free living ones, fixing molecular nitrogen.

Although all the investigated bacterial groups respond to factors acting on the entire bacterial community, the reaction of particular groups to these factors is different, that is shown by different dynamics of their number in particular seasons of the year.

The total number of bacteria and the number of free nitrogen fixing bacteria show relatively explicit changes in the annual cycle: the least of them occur in summer and the most in autumn. The remaining groups (with the exception of bacteria oxidizing nitrites into nitrates), although most numerous in autumn, do not seem to have their decrease in number connected with a particular season of the year; however almost in all examined physiological groups the number of bacteria was very low in July.

6. STRESZCZENIE

Celem pracy było zbadanie sezonowych zmian całkowitej liczby bakterii (metodą bezpośredniego liczenia) oraz szeregu grup bakterii, biorących udział w przemianach związków azotowych (metodą inkubacji), w wierzchniej warstwie osadu dennego małego zbiornika Puszczy Kampinoskiej.

Były to grupy bakterii hodowane na podłożu bulionowo-żelatynowym oraz bakterie hodowane na filtrach membranowych nasyconych pożywkami selektywnymi dla bakterii denitryfikujących, utleniających związki amonowe do azotynów, utleniających azotyny do azotanów. i wolnożyjących asymilujących azot cząsteczkowy.

Stwierdzono, że mimo iż wszystkie badane grupy bakterii podlegają czynnikom działającym na całą populację bakteryjną, to sposób reagowania poszczególnych grup na te czynniki jest odmienny, co objawia się inną dynamiką ich liczebności w poszczególnych porach roku.

Całkowita liczba bakterii oraz liczba bakterii asymilujących wolny azot wykazują stosunkowo wyraźne zmiany w poszczególnych porach roku: jest ich najmniej w okresie letnim, najwięcej w jesiennym. Liczebność pozostałych grup (z wyjątkiem bakterii utleniających azotyny do azotanów), była również najwyższa jesienią, lecz wyraźniejsze spadki nie wydają się być powiązane z określoną porą roku. Jednak w lipcu stwierdzono bardzo niskie ilości bakterii prawie wszystkich badanych grup fizjologicznych.

7. REFERENCES

[Bezborodov, A. M., Dobromyslov, V. V.] Безбородов, А. М., Добромыслов, В. В. 1955. Антибактериальное действие некоторых каротиноидов микробного происхождения [The antibacterial activity of some carotenoids of microbial origin]. *Mikrobiologija*, 24, 697-699.

Breed, R. S., Murray, E. G. D., Smith, N. R. 1952. *Bergey's manual of determinative bacteriology*. 7th ed., London, Baillière, Tindall and Cox.

Fiodorov, M 1952. *Ćwiczenia praktyczne z mikrobiologii* [Course of practical microbiology]. Warszawa, PWRiL.

Fiodorov, M. 1952 a. *Mikrobiologia* [Microbiology]. Warszawa, PWRiL.

Fry, B. A. 1955. *The nitrogen metabolism of micro-organisms*. London, Methuen.

[Gambarian, M. E.] Гамбарян, М. Е. 1958. Ассимиляция молекулярного азота в воде и грунтах озера Саван [Assimilation of molecular nitrogen in the water and grounds of the Sevan Lake]. *Mikrobiologija*, 27, 366-370 [Engl. summ.].

[Gebgart, A. G.] Гебгарт, А. Г. 1961. Роль микроорганизмов в накоплении их в растениях [The role of microorganisms in accumulation of them in plants]. *Mikrobiologija*, 11, 292-301.

[Hartuari, E. M.] Хартуари, Е. М. 1937. Бактериологические исследования в связи с вопросом газа [Bacterial investigations in relation to gaseous problem]. I Sessija Limnol. Sta Kosino.

Henrici, A. T., McCoy, E. 1938. The distribution of heterotrophic bacteria in the bottom deposit of some lakes. *Trans. Wis. Acad. Sci. Arts Lett.*, 31, 323-361.

[Isačenko, B. L.] Исаченко, Б. Л. 1937. Микробиологическая характеристика грунтов и воды Карского моря [Microbiological characteristics of soil and water of Karskoje Sea]. *Trudy vses. arkt. Inst.*, 82, 7.

Just, J., Hermanowicz, W. 1955. *Fizyczne i chemiczne badanie wody do picia i potrzeb gospodarczych* [Physical and chemical studies of the tap water and for economical purpose]. Warszawa, PZWL.

[Kuznecov, S. I.] Кузнецов, С. И. 1938. Количественный учет микрофлоры в связи с разроботкой микрозонального показателя грязей [Quantative studies of microflora in relation to elaboration of microzone indicator of pollution]. *Mikrobiologija*, 7, 36-49.

[Kuznecov, S. I.] Кузнецов, С. И. 1952. Роль микроорганизмов в круговороте веществ в озерах [Role of microorganisms in turnover of matter in lakes. Moskva, Izdat. Akad. Nauk S.S.S.R.

Matusiak, K. 1954. Badania mikrobiologiczne stawów doświadczalnych w Landeku i Gołyszu [Microbiological studies on experimental ponds in Landek and Gołysz]. *Ekol. pol.*, 2, 247-270 [Engl. summ.].

Melchiorri-Santolini, U. 1966. Pelagic heterotrophic bacteria in the Ligurian Sea and Lago Maggiore. *Memorie Ist. ital. Idrobiol.*, 20, 261-287.

Nauwerck, A. 1963. Die Beziehungen zwischen Zooplankton und Phytoplankton im See Erken. *Symb. bot. ujsal.*, 17, 1-163.

[Nikitina, N. S.] Никитина, Н. С. 1955. Сезонные изменения бактериального состава грунтов литорали восточного Мурмана [Seasonal variations of bacterial composition of littoral grounds of east Murman]. *Mikrobiologija*, 24, 580-588.

Nowotny-Mieczyńska, A. Gołębiowska, J. 1960. *Krążenie azotu w przyrodzie* [Circulation of nitrogen in nature]. Warszawa, PWRiL.

Paschalski, J. 1958. Zmiany obrazu chemicznego drobnych zbiorników wodnych [Changes of chemical properties of the small waterbodies]. 4 Zjazd Pol. Tow. Hydrobiol., Kraków, Streszcz. ref., 119-120.

Paschalski, J. 1959. Obserwacje warunków środowiskowych drobnych zbiorników wodnych okolic Warszawy [Observations of environment conditions in small ponds in the Warsaw district]. *Ekol. pol., Ser. A*, 7, 1-20 [Engl. summ.].

Paschalski, J. 1967. A modified water sampler with thermometer and sounding thermometer. *Pol. Arch. Hydrobiol.*, 14 (2), 43-59.

Potter, L. F. 1963. Planktonic and benthic bacteria of lakes and ponds. In: H. Heukelekian, N. C. Dondero [Eds]. *Principles and applications in aquatic microbiology*. 148-166, New York, J. Wiley.

[Rodina, A. G.] Родина, А. Г. 1949 a. Роль бактерий в питании личинок тендипедид [Role of bacteria in feeding of Tendipedidae larvae]. *Dokl. Akad. Nauk S.S.S.R.*, 67, 1121-1123.

[Rodina, A. G.] Родина, А. Г. 1949 b. Бактерии как пища пресноводных моллюсков [Bacteria as food for freshwater mollusc]. *Mikrobiologija*, 17, 232-239.

[Rubenčik, L. I.] Рубенчик, Л. И. 1948. Микроорганизмы и микробные процессы в соланых водоемах УССР [Microorganisms and microbial processes in brackish water of USSR]. Kiev, Izdat. Akad. Nauk U.S.S.R.

[Rubenčik, L. I., Geiherman, D. G.] Рубенчик, Л. И., Гоихерман, Д. Г. 1940. Вертикальное распространение бактерии в донных отлошениях Репного озера [Vertical distribution of bacteria in bottom deposits of Repno Lake]. *Mikrobiologija*, 9, 39-44.

[Sorokin, Ju. I.] Сорокин, Ю. И. 1954. К методике окраски слабокрасящихся бактерий [Method of staining bacteria which attain poorly]. *Trudy biol. Sta. Borok*, 2, 414-415.

[Sorokin, Ju. I.] Сорокин, Ю. И. 1962. Микрофлора грунтов Черного моря [Microflora of the Black Sea grounds]. *Mikrobiologija*, 31, 899-903 [Engl. summ.].

ZoBell, C. E. 1946. *Marine microbiology. A monograph on hydrobacteriology.* Waltham, Mass., Publ. the Chronica Botanica.

ZoBell, C. E., Anderson, D. Q. 1936. Vertical distribution of bacteria in marine sediments. *Bull. Am. Ass. Petrol. Geol.*, 20, 258-269.

ZoBell, C. E., Feltham, C. B. 1938. Bacteria as food for certain marine invertebrates. *J. mar. Res.*, 1, 312-327.

ZoBell, C. E., Grant, C. W. 1943. Bacterial utilization of organic matter. *J. Bact.*, 45, 555-564.

[Žukova, A. I.] Жукова, А. И. 1954. Значение микроорганизмов в питании *Nereis succinea* Каспийского моря [Significance of microorganisms in feeding by *Nereis succinea* in Caspian Sea]. *Mikrobiologija*, 23, 46-48.

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E. STYCZYŃSKA-JUREWICZ

OSMOTIC PROPERTIES OF CAPSULAR FLUID IN EGGS OF SOME SNAILS FROM FRESH AND BRACKISH WATERS

Department of Bioenergetics and Bioproductivity, Nencki Institute of Experimental Biology, Pasteura 3, Warszawa 22, Poland

ABSTRACT

Using a microcryoscope the freezing-point depression was measured of the capsular fluid in egg capsules of *Physa acuta* Drap. and some other snails. Osmotic concentration of the capsular fluid oscillates in relation to the stage of embryonic development and salinity of the medium. Both in fresh and in brackish water medium a hyperosmotic surplus of about 0.1 Δ°C over the concentration of external medium is demonstrated in capsular fluid. The biological significance of the phenomenon in mention is discussed.

1. INTRODUCTION

Many typically freshwater species occur and breed also in brackish waters up to a certain degree of salinity. Remane (1958) demonstrated a diagram of number of animal species occurring in waters of different salinity. From this diagram one can see that a rapid decrease of freshwater species entering brackish waters occurs between 5 and 8‰ of salinity. There is a clear boundary separating marine world from freshwater one; this boundary can be passed only by some euryhyaline species. Similar diagram elaborated by Johanson for Mollusca (Remane 1958) positions this boundary near 5‰. However other authors (Jaeckel 1960, Schermer 1938, Soszka 1968), have reported on occurrence of many freshwater snails also at higher salinities, up to 8‰, and of *Theodoxus fluviatilis* even up to 10‰.

It is known that eggs and early embryonic stages are most sensitive to any change of osmotic concentration (Kinne 1964). The chance to survive by a species at changed salinity depends from its resistance and adaptability. Freshwater animals had to adapt to embryonic development occurring in hypoosmotic medium; their hyperosmotic embryos as regards fresh water have to be secured from superfluous hydration by a system of covers with appropriate permeability and probably by less investigated mechanisms of an active osmotic regulation. A question arises what a character can take osmoregulation in eggs of freshwater animals in the case of reverse direction of adaptation to live and develop in brackish environment. In such environment the embryo must defence against dehydration and any damage caused by an excess of ions penetrating inside through the covers. One should expect then, that chances of embryonic development in brackish medium will depend on changes brought about in structures that shelter the egg.

The subject of this paper is description of osmotic changes in such sheltering layer of snail eggs and embryos, namely, in capsular fluid of *Physa acuta* Drap. during the development occurring both in freshwater and brackish media up to 8‰.

The eggs of freshwater snails of Pulmonata and Prosobranchia develop in hyaline capsules glued by a polysaccharide jelly in an egg mass. The capsule holds perivitellary (capsular) fluid which forms a direct medium for the embryo as well as the source of food during embryogenesis (Wilbur, Yonge 1964, Raven 1966). This fluid is complex chemically and it holds carbohydrate compound — ga-

lactogen, typical for snails (Horstmann 1956, Horstmann, Geldmacher-Malinckrodt 1961, Jansen — unpublished data acc. to Raven 1966). This compound is energy material for the developing embryo. The fluid contains also proteins used as building materials (Raven 1946, 1966, Morrill 1964), water and calcium (Morrill et al. 1964). The developing embryo takes nutritional substances from the fluid by means of pinocytosis, which starts at the stage of 40 cells (Elbers, Bluemink 1960). The pinocytosis is clearly visible at the stage of gastrula (Morrill 1964, Bluemink 1967). Thus one should expect that with following embryonic development the osmotic concentration of capsular fluid can undergo changes due to the loss of food substances and the appearance of embryo waste products. Therefore larger changes should be expected in a brackish medium.

2. MATERIAL AND METHODS

Main data were obtained by investigating the eggs of *Physa acuta* Drap.; supplementary data concern *Limnaea stagnalis* L., *Radix limosa f. baltica* Nilss. and a brackish population of *Theodoxus fluviatilis* L.

Physa acuta is a thermophylous species originating from South Europe, commonly encountered in aquaria and breeding in them during the whole year. The snails were cultured in small glass aquaria, 8×8×8 cm with a layer of sand on the bottom, water (conditioned tap water) being changed every 3-6 days.

Fresh lettuce was used as food with fine powdered dry daphnids. Such conditions brought about fairly high reproduction at optimum temperature for reproduction found to be 18-20°C. The snails laid commonly eggs on belts of transparent thin polyethylene foil placed in aquaria. Application of the foil was very useful on account of easy collection of egg masses and securing against damage during checking in vivo egg development. In these experiments only those egg masses were used which were attached to the foil without separating them from foil, although control experiments showed no difference in the development of egg masses separated from the substratum, e.g. walls of aquarium. The embryonic stages were defined acc. to the description by Wierzejski (1905) and Raven (1966).

The eggs of *L. stagnalis* were collected from the individuals kept continuously in aquaria. The brackish populations of *R. limosa f. baltica*, collected in Dead Vistula estuary and *T. fluviatilis* from Lake Sinoe (Danube estuary) were transferred to the laboratory with water of their natural environment and they were laying in it eggs which were later used for experiments. The experiments were run in several series. In the first series intact egg masses were exposed to diluted artificial sea-water, prepared acc. to the formula by Hale (1960) and diluted by conditioned tap water to concentration of 2, 5 and 8‰.

Since the highest salinity that resulted in hatches of parrallelly bred *Physa acuta* was 5‰, it was accepted as being still within the tolerance limit. However salinity of 8‰ is critical one. Incubation was run for 20 hr at temperature of 5 ± 0.5°C. Such low temperature causes a considerable retardation, practically stop of embryonic development. In the second series incubation lasted also 20 hr at temperature of 25 ± 1°C, which ensured a rapid development of the embryo.

The eggs were placed to the experimental media at the stage of freshly laid egg, that is before cleavage, at the stage of gastrula and trochophore. After 20 hr of incubation the egg masses slightly dried of external water by filter paper, were placed in paraffin oil where the capsules were removed from jelly and from each capsule a drop of capsular fluid was taken under the paraffin screen. Puncturing the capsule was done by means of preparatory needles made of cactus spikes (Klekowski, Domurat 1967). The osmotic concentration of the fluid was measured by means of microcryoscope of Ramsay type (Ramsay 1949, Ramsay, Brown 1955) modified by Klekowski (1963). In the last reference one can find a detailed description of the procedure of measurement. The accuracy in the present experiment was about 0.010 Δ°C. The capsular fluid of snails is transparent and homogeneous which enables an accurate measurement with this method. The degree of salinity of the natural and artificial medium was always checked by cryoscope. The mean concentration of the capsular fluid was based usually on 25 individual measurements.

In the third series of experiments osmotic concentration of the capsular fluid was measured in the case of longer incubation (4 and 8 days) in critical salinity of 8‰, in the fourth series — concentration was measured of the fluid in eggs

freshly laid and placed into oceanic water (34.3‰) at a temperature of 25°C for various periods, from 10 minutes to 20 hrs.

The changes of osmotic concentration of the capsular fluid were also measured in the sequence of developmental stages within the whole embryonic development of *Physa acuta* under natural conditions i.e, in fresh water at ambient temperature of 20°C. Control measurements were also made to check the effect of incubation temperature on concentration of the capsular fluid (5, 20 and 25°C) in fresh water for an egg, gastrula, and trochophore. Since in all temperatures identical results were obtained for each stage (n=6), the data concerning normal conditions of development (n=25) were accepted as controls in the remaining experiments.

3. RESULTS

STUDIES ON EGGS OF *PHYSA ACUTA* DRAP.

I. Osmotic concentration of capsular fluid during normal course of embryonic development in fresh water (Fig. 1)

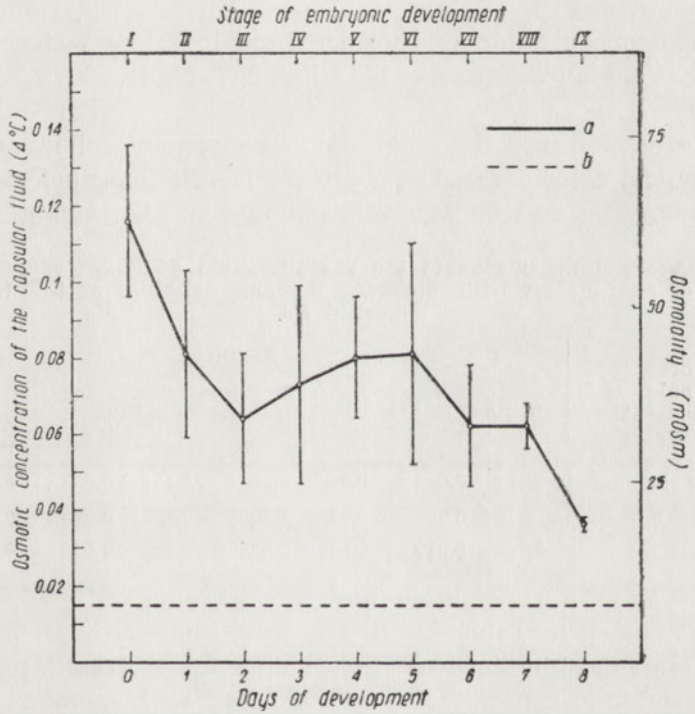

Fig. 1. Osmotic concentration of capsular fluid during normal embryonic development of *Physa acuta* Drap. in fresh water, 20°C. a — concentration of the capsular fluid, b — contentration of the external medium. I-IX — stages of embryonic development. I — egg before cleavage, II — gastrula, III — young trochophore, IV — old trochophore, V — young veliger, VI — old veliger, VII — hippo, VIII — young snail possessing the shell, IX — young snail near to hatching. Means ± st. dev., n=25

The embryonic development of *P. acuta* at room temperature of 20°C from the moment of laying the egg to the moment of hatching lasted 9 days, and at temperature of 25°C — 7 days. During this development the osmotic pressure of capsular fluid surrounding the embryo maintain-

ed always a higher level than that of the osmotic pressure of water surrounding the egg mass and in jelly gluing the capsules together. The jelly is isoosmotic as compared with external environment (or slightly hyperosmotic $\Delta°C=0.015$). This means that substances forming the capsular fluid are osmotically active and that the capsule membrane is unpermeable to them. As the embryonic development follows, the osmotic concentration of the fluid decreases, reaching at the stage of trochophore the level twice as low as that at the beginning of development. At the stage of veliger it rises slightly to decrease again at the stage of hippo. This decreasing tendency is expressed in young snails ready to hatch by osmotic concentration 3 times lower than that in the freshly laid egg. The differences between the stages are statistically significant (Student test, $P=0.01$).

II. Osmotic concentration of capsular fluid in saline water after incubation at low temperature of 5°C (Fig. 2, Table I)

In this temperature the embryonic development follows slowly that practically can be considered as stopped since the morphological changes in the embryo become unperceivable at in vivo observation.

Table I. Hyperosmotic surplus of the capsular fluid of *Physa acuta* after 20 hr treatment of egg masses with different medium salinities at 5°C ($n = 25$; $\Delta°C$, mean ± S.D.)

Stage of embryonic development	Salinity			
	0.03‰	2‰	5‰	8‰
Egg before cleavage	0.111 ± 0.020	0.150 ± 0.052	0.175 ± 0.083	0.118 ± 0.071
Gastrula	0.076 ± 0.022	0.123 ± 0.070	0.160 ± 0.075	0.110 ± 0.065
Trochophore	0.059 ± 0.017	0.102 ± 0.020	0.183 ± 0.058	0.225 ± 0.219

As it is shown in Table I and Figure 2, the capsular fluid shows always, at all combinations of embryonic stage and salinity, a certain surplus of osmotic concentration as compared with medium concentration. Its value ranges from 0.12 to 0.18 $\Delta°C$ and it increases in such range at the increase of salinity of the medium up to 5‰ in the range tolerated by the snails (cf. Introduction). After exceeding the physiological tolerance limits for snails, at salinity of 8‰ the capsules holding older embryos, trochophores, show large individual differences in the concentration of capsular fluid. The coefficient of variation which does not exceed 50% in the remaining cases, here increases almost to 100%, covering the capsules of a very high hyperosmosis (hyperosmotic surplus up to 0.590 $\Delta°C$) as well as several cases of hypoosmotic concentration of capsular fluid.

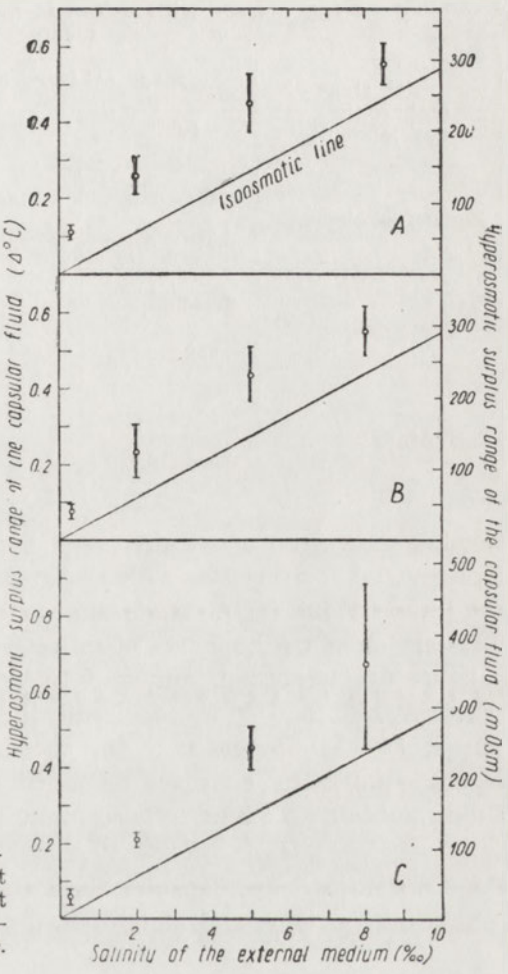

Fig. 2. Osmotic concentration of capsular fluid of *Physa acuta* at different salinities after 20 hours of treatment at 5°C. A — egg before cleavage, B — gastrula stage, C — trochophore stage. Means ± st. dev., $n=25$

It is obvious that in saline medium, which evokes some osmotic stress, there is higher deviation of individual measurements, which causes that the permanent differences between hyperosmotic surpluses for 3 embryonic stages that were investigated are insignificant statistically. Significant differences were only found between the means for eggs and trochophores at a salinity of 5‰ with $P=0.05$, and at salinity of 8‰ between means for trochophores and younger stages ($P=0.01$).

III. Concentration of capsular fluid in relation to salinity at temperature of 25°C (Table II)

At this temperature the embryonic development occurs rapidly; in fresh water the stage of trochophore is reached on the third day, and at salinity of 5‰ — as early as on the second day. The hyperosmotic

Table II. Hyperosmotic surplus of the capsular fluid of *Physa acuta* after 20 hr treatment of egg masses with different medium salinities at 25°C ($n = 25$; Δ°C, mean ± S.D.)

Initial stage of embryonic development	Stage achieved after the treatment with salinity:			
	0.03‰	2‰	5‰	8‰
Egg before cleavage	Gastrula 0.076 ± 0.022	Gastrula 0.095 ± 0.025	Trochophore 0.056 ± 0.012	Egg non-developed 0.143 ± 0.054
Gastrula	Trochophore 0.059 ± 0.017	Old trochophore 0.080 ± 0.025	Old trochophore 0.147 ± 0.025	Trochophore 0.081 ± 0.045
Trochophore	Old trochophore 0.068 ± 0.026	Veliger 0.061 ± 0.015	Veliger 0.060 ± 0.015	Old trochophore 0.025 ± 0.020

surplus shows the above discussed dependence from the stage of development, i.e. it decreases with embryonic development going on, reaching the lowest value in the stage of trochophore and veliger. Certain exceptions are older trochophores at salinity of 5‰ where a high hyperosmotic surplus was recorded, almost 0.15 Δ°C. It can be also observed that salinities of 2 and 5‰ accelerate the embryonic development and salinity of 8‰ — hinders it to the speed observed in fresh water. At the latter salinity the eggs are damaged and do not develop, but capsular fluid maintain still high hyperosmotic surplus.

IV. Concentration of capsular fluid after a longer incubation at a critical salinity of 8‰ and at temperature of 25°C (Fig. 3)

In this series of experiments the time of exposure to the critical salinity was prolonged from 20 hrs to 4 and 8 days. The hyperosmotic surplus of the capsular fluid showed a characteristic variation with the embryonic stage, at which the capsules were placed into experimental medium, with the stage in which they were investigated later, and with the duration of incubation. This latter dependence was found in freshly laid eggs, which lost the ability of development and underwent disintegration at salinity of 8‰. One observe in them the decrease of osmotic concentration of capsular fluid with time down to the state of isoosmosis as compared with to the medium after 8 days (Fig. 3A). It should be stressed that more advanced embryonic stages (gastrula and trochophore) do not loose the ability of development at this salinity although the development is delayed as compared with normal development in fresh water, and embryos of the same egg mass being developed nonuniformly and showing some morphological abnormalities. In this series the tro-

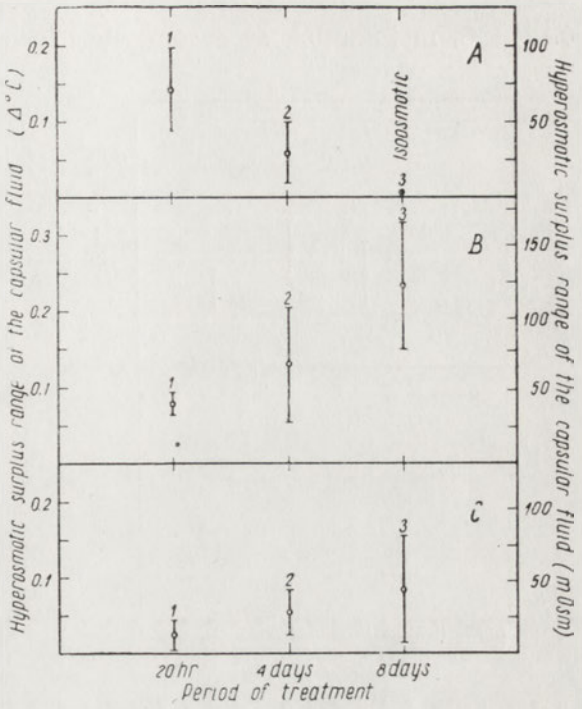

Fig. 3. — Hyperosmosis of capsular fluid of *Physa acuta* after prolonged treatment with the salinity of 8‰ at 25°C. A — initial stage: egg before cleavage. 1, 2, 3 — state after the treatment; 1 — non developed eggs, 2, 3 — disintegrated eggs, B — initial stage: gastrula. Stage achieved after the treatment: 1 — trochophore, 2 — young veliger, 3 — old veliger. C — initial stage: trochophore. Stage achieved after the treatment: 1 — young veliger, 2 — old veliger, 3 — hippo. Means ± ± st. dev., n=25

chophores also had the lowest concentration of the capsular fluid out of all three first stages. Besides, when the eggs at the stage of trochophore were exposed to extreme salinity the decreased concentration of capsular fluid was maintained in the stages of veliger and hippo (cf. Fig. 3 C).

V. Concentration of capsular fluid in oceanic water of 34.3‰ (Fig. 4)

The permanent maintenance of hyperosmotic surplus of capsular fluid even at critical salinity of 8‰ was an encouragement to investigate the osmotic properties of the fluid in even more concentrated medium: in oceanic water of salinity of 34.3‰. Such high concentration of ions quickly penetrating inside the capsule caused immediately irreversible changes in the cortex layer of the egg, unabling its further development.

The concentration of capsular fluid was tested after 10 minutes, 1 hour, 3, and 20 hrs from the moment of placing the egg masses with freshly laid eggs to oceanic water. After 10 minutes all capsules showed still concentration lower than that of the medium. Probably by chance this hypoosmotic shortage as compared to the state of isoosmosis with the environment amounted at the moment of investigation to about 0.1 Δ°C, thus it equaled to the average hyperosmotic surplus. However, after 1 hour the hyperosmosis of capsular fluid settled in over the

medium with characteristic average value of hyperosmotic surplus 0.15 Δ°C, maintaining at a somewhat lower level even after 20 hrs.

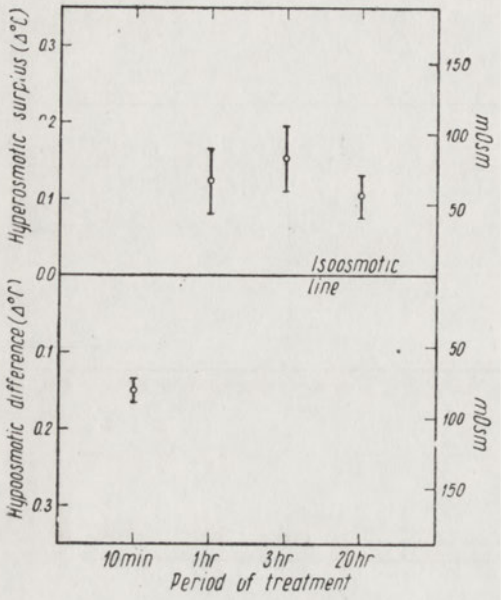

Fig. 4. Passing from hypo to hyperosmotic concentration of capsular fluid in *Physa acuta* egg masses treated with oceanic water (salinity 34.3‰) at 25°C. Means ± st. dev., n=25

OSMOTIC CONCENTRATION OF CAPSULAR FLUID OF OTHER SNAILS (TABLE III)

The hyperosmotic surplus of capsular fluid in *Limnaea stagnalis* had a similar values and showed a similar variation as in *Physa acuta*, both in fresh and brackish waters (only 2‰ salinity was investigated).

Table III. Hyperosmosis of the capsular fluid in some embryonic stages of other snail species from habitats of different salinity

Species	Embryonic stage	No. of capsules	Salinity of the habitat (‰)	Hyperosmotic surplus of the fluid (Δ° C, mean ± S.D.)
Limnaea stagnalis L.	Egg before cleavage	30	fresh	0.085 ± 0.022
	Young trochophore	31	fresh	0.053 ± 0.009
	Young trochophore	31	2	0.036 ± 0.02
	Young snail with the shell	22	fresh	0.062 ± 0.002
Radix limosa f. baltica Nilss.	Egg before cleavage	19	6.4	0.140 ± 0.073
	Egg before cleavage	17	5.7	0.097 ± 0.044
	Young trochophore	20	6.6	0.052 ± 0.019
	Hippo	7	6.6	0.137 ± 0.024
Theodoxus fluviatilis L.	Young snail with the shell	14	9.8	0.128 ± 0.007

In eggs of snails from natural brackish habitats there is always observed a hyperosmotic surplus of capsular fluid with a similar range of values, i.e. 0.05-0.14 Δ°C, depending on the stage of embryonic development. Thus, it is a natural phenomenon and not caused by action of artificial experimental conditions.

4. DISCUSSION

Summarizing the results of the experiments, it can be said that perivitellary fluid in egg capsules of freshwater snails living in fresh and in brackish waters has the following properties:

1. Ability to maintain the osmotic concentration surplus as compared with external environment within the whole embryonic development.

2. This ability depends on the presence and the physiological stage of the embryo. In those capsules whose eggs were killed it disappeared within several days.

3. The value of hyperosmotic surplus amounting on the average to about 0.1 Δ°C changes depending on the stage of embryonic development, on salinity of the egzocapsular medium, and on the duration of the presence of egg masses in this medium.

The perivitellary fluid is a direct medium for the development of embryo through which the latter contact the external environment. It can be considered as a special protective layer which changes the osmotic stimuli coming from the external environment into the shape which does not threaten homeostasis of the embryo needed for its normal development. The literature data on the osmotic properties of the previtellary fluid in eggs of aquatic animals are very rare, probably on account of technical difficulties. The oldest data are given by Svetlov (1928, 1929), who reported on the fact that perivitellary fluid in eggs of salmonid fish had osmotic concentration of 0.02 Δ°C, maintained within the whole embryonic development. He considered that fluid is isoosmotic as compared with external aquatic environment, however, detailed microcryoscopic measurements (Klekowski, Domurat 1967) revealed that in eggs of *Salmo trutta* the fluid is slightly hyperosmotic as related to external environment and considerably hypoosmotic as compared with yolk. If the eggs of trout developed in the medium void of water (paraffin oil) then osmotic concentration of perivitellary fluid, which normally shows inconsiderable oscillations, increases considerably within the embryonic development (the difference was 0.03 Δ°C in water to 0.25 Δ°C in oil for the same developmental stage) probably on account of agglomeration in it the waste products of the embryo, usually excreted from perivitellary fluid to water.

These reports of the above mentioned authors allow to suppose about the biological role of the hyperosmotic state of the capsular fluid in snails of the brackish water. Even small positive difference in the osmotic

pressure between perivitellary fluid and egzocapsular environment allows to remove harmful waste products of the embryo by simple diffusion, without engaging energetically expensive (and probably non--existing in the capsular fluid) mechanisms of active transportation.

It is not clear yet why the capsular fluid obtains and maintains such positive hyperosmosis. One can only suppose that it is maintained without expenditure for transportation due to the fact that organic molecules arise perhaps ion-organic complexes for which the capsule membrane is not permeable. Such hypothesis was put forward in the first publication in mention of the author (Styczyńska-Jurewicz 1970). Since the embryo and its developmental stage affects the value of hyperosmotic surplus, one can also suspect the existence of some enzymatic factor, responsible for the presence and maintenance at a proper level of this surplus.

The presence of such regulatory factor is also suggested by exceptionally large oscillation of osmotic concentration of capsular fluid, observed in the stage of trochophore at salinity of 8‰ (Fig. 2 C). It is also sugested by the states of both exceptionally high hyperosmosis (Δ°C=0.59) and several cases of hypoosmosis of the fluid. Apparently at salinity above the tolerance limits some disturbances occur of factors which control the osmotic pressure of the perivitellary fluid. A gradual disappearance of osmoregulatory ability can be observed in capsular fluid, in egg masses placed at salinity of 8‰ at the stage of freshly laid egg, since the eggs undergo disintegration (Fig. 3 A). This fact proves the dependence of ability to hyperosmotic regulation in capsular fluid on the presence, thus on biological functions, of a living embryo.

5. SUMMARY

1. By means of measurement of osmotic concentration in a microcryoscope of Ramsay type (modified by Klekowski, 1963) the osmotic properties of capsular fluid in eggs of *Physa acuta* Drap. were investigated for different stages of embryonic development in fresh water.

2. It was found that the capsular fluid showed a surplus over the osmotic pressure of egzocapsular environment (Δ°C about 0.1), this surplus diminishes with development at various intensity down to reaching about 1/3 of the initial value just at the moment of hatching.

3. Similar hyperosmotic surplus was found in the capsular fluid after placing the egg masses in the medium of diluted artificial sea water of the salinity of 2, 5 and 8‰, and also in the full sea water (34.3‰). This proves that the capsular fluid shows an ability to hyperosmotic regulation only.

4. Analogous osmotic properties of capsular fluid were found for other snails: *Limnea stagnalis*, *Radix limosa f. baltica* and *Theodoxus fluviatilis*, the two latter coming from brackish waters.

5. A discussion is given of biological significance of these properties of capsular fluid, as enabling removal of waste products of the embryo even in the environment of higher osmotic concentration.

6. STRESZCZENIE

1. Drogą pomiarów koncentracji osmotycznej w mikrokrioskopie typu Ramsaya (modyfikacja Klekowskiego, 1963) badano własności osmotyczne płynu

kapsularnego w jajach *Physa acuta* Drap. na różnych stadiach rozwoju zarodkowego w wodzie słodkiej.

2. Stwierdzono, że płyn kapsularny wykazuje nadwyżkę nad ciśnieniem osmotycznym środowiska egzokapsularnego (Δ°C ok. 0,1), malejącą w miarę postępującego rozwoju z różnym nasileniem aż do osiągnięcia około 1/3 wartości początkowej tuż przed momentem wylęgu.

3. Podobna nadwyżka hyperosmotyczna występuje w płynie kapsularnym po umieszczeniu kokonów w środowisku rozcieńczonej sztucznej wody morskiej o zasoleniu 2, 5 oraz 8‰, a także w wodzie oceanicznej (34,3‰). Dowodzi to, że płyn kapsularny wykazuje zdolność do regulacji tylko hyperosmotycznej.

4. Analogiczne własności osmotyczne płynu kapsularnego stwierdzono u innych gatunków ślimaków: *Limnea stagnalis* oraz pochodzących z naturalnych środowisk słonawych *Radix limosa f. baltica* i *Theodoxus fluviatilis*.

5. Omawia się biologiczne znaczenie tych własności płynu kapsularnego, jako umożliwiające usuwanie produktów przemiany materii zarodka nawet w środowisku o podwyższonej koncentracji osmotycznej.

7. REFERENCES

Bluemink, J. G. 1967. The subcellular structure of the blastula of *Limnaea stagnalis* L. (Mollusca) and the mobilization of the nutrient reserve. Ph D. Thesis, Univ. Utrecht.

Elbers, P. F., Bluemink, J. G. 1960. Pinocytosis in the developing egg of *Limnaea stagnalis* L. *Expl Cell Res.*, 21, 619-622.

Hale, L. J. 1960. *Biological laboratory data.* London, Methuen.

Horstmann, H. J. 1956. Der Galaktogengehalt der Eier von *Lymnaea stagnalis* L. während der Embryonalentwicklung. *Biochem. Z.*, 328, 342-347.

Horstmann, H. J., Geldmacher-Malinckrodt, M. 1961. Untersuchungen zum Stoffwechsel der Lungenschnecken. III. Das Galaktogen der Eier von *Lymnaea stagnalis* L. *Hoppe-Seylers Z. physiol. Chem.*, 325, 251-259.

Jaeckel, S. 1960. Zur Molluskenfauna der Binnensalzstellen von Bad Oldesloe. *Schr. natur. Ver. Schl.*, 30, 39-45.

Kinne, O. 1964. The effects of temperature and salinity on marine and brackish water animals. II. Salinity and temperature-salinity combinations. *Oceanogr. and mar. Biol.*, 2, 281-339.

Klekowski, R. Z. 1963. Water balance and osmoregulation in the snail *Coretus corneus* (L.) under conditions of desiccaton and in diluted sea water. *Pol. Arch. Hydrobiol.*, 11, 219-240.

Klekowski, R. Z., Domurat, J. 1967. The osmotic pressure of eggs from Lake Wdzydze trout (*Salmo trutta m. lacustris L.*) developing in water or paraffin oil. *Pol. Arch. Hydrobiol.*, 14, 19-27.

Morrill, J. B. 1964. Protein content and dipeptidase activiy of normal and cobalt treated embryos of *Limnaea palustris. Acta Embryol. Morph. exp.*, 7, 131-142.

Morrill, J. B., Norris, E., Smith, S. D. 1964. Electro-and immunoelectrophoretic patterns of egg albumen of the pond snail *Limnaea palustris. Acta Embryol. Morph. exp.*, 7, 155-166.

Ramsay, J. A. 1949. A new method of freezing point determination for small quantities. *J. exp. Biol.*, 26, 57-64.

Ramsay, J. A., Brown, R. H. J. 1955. A simplified apparatus and procedure for freezing-point determination upon small volumes of fluid. *J. Scient. Instrum.*, 32, 327-375.

Raven, C. P. 1946. The development of the egg of *Limnaea stagnalis* L. from the first cleavage till the trochophore stage, with special reference to its "chemical embryology". *Arch. neerl. Zool.*, 7, 353-434.

Raven, C. P. 1966. *Morphogenesis. The analysis of molluscan development.* New Yok, Pergamon Press.

Remane, A. 1958. Okologie des Brackwassers. II A. In: Remane A., Schlieper C. *Die Biologie des Brackwassers.* 18-28, Stuttgart, E. Schweitzerbatsche Verl.

Schermer, E. 1938. Süsswassermollusken im Brackwasser der Ostseeküste der Nordmark. *Heimat, Kiel*, 48, 21-25.

Soszka, G. 1968. Selected problems of the ecology of molluscs (Mollusca) of the braskish Lake Łebsko. *Ekol. pol., Ser. A*, 16, 729-753.
[Svetlov, P. G.] Светлов, П. Г. 1928. К вопросу об осмотическом давлении и проникаемости яиц форели [On the osmotic pressure and permeability in the trout eggs]. *Dokl. Akad. Nauk S.S.S.R., Ser. A*, 24, 504-508.
Svetlov, P. 1929. Entwicklungsphysiologische Beobachtungen an Forelleneiern. *Roux Arch. Entw. Mech. Organ.*, 114, 504-508.
Wierzejski, A. 1905. Embryologie von *Physa fontinalis* L. *Z. wiss. Zool.*, 83, 502-699.
Wilbur, K. M., Yonge, C. M. 1964. *Physiology of Mollusca*. New York, Academic Press.

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Z. FISCHER

THE ELEMENTS OF ENERGY BALANCE IN GRASS CARP (*CTENOPHARYNGODON IDELLA* VAL.) PART II. FISH FED WITH ANIMAL FOOD

Department of Bioenergetics and Bioproductivity, Nencki Institute of Experimental Biology, Pasteura 3, Warszawa, Poland

ABSTRACT

Comparison of energy budgets of grass carp fed with exclusively plant and exclusively animal food was made. Grass carp bred under laboratory conditions is omnivorous, its growth rate is smaller when fed with exclusively plant food than with animal one.

1. INTRODUCTION

Grass carp, *Ctenopharyngodon idella* Val., is an Asiatic ciprinid fish, of Leuciscinae subfamily. It has been bred for many years in the Soviet Union, and since 1964 in Poland. Recently there is a great interest in this fish in many European countries. This interest arises from the fact that the grass carp is commonly considered as a plant-feeder. Grass carp being a plant-feeder does not compete with other fish bred in pond cultures, which makes this species most interesting for the studies. The advantage of this species is not only usefulness of it as commercial fish resulting from the rapid body growth but also the ability of this fish to consume hard vascular plants which overgrow aquatic bodies and by this are a nuisance for fishermen. It is foreseen that this species will have a great importance both in pond management which recently shows interest in poly-species culturing (Opuszyński 1969), and also as a biological factor useful for controlling the overgrowth of water bodies. Recently, however, the herbivorousness of grass carp becomes more and more controversial. Basing on findings of Chinese studies, Nikolskij (1956) reports that this fish is omnivorous in the region of its natural geographic occurrence. Krupauer (1967) states that grass carp cannot live without admixture of animal food. Scheer et al. (1967) are of the opinion that grass carp shifts from animal to plant food depending on the temperature of its habitat. At temperature up to 15°C it feeds on zooplankton, above this temperature — on plants.

With such a diversity of views on the feeding by grass carp it seems interesting to trace the ability of this species to feed exclusively on plant or animal food under laboratory conditions. Investigations of energy budget are especially important, i.e. the amount of energy bound in the food eaten by grass carp, the energy incidence in the body growth, respiration, and excretion. Studies on energy budget parameters of grass carp fed with plant food were reported in part I, Fischer (1970b). The present part (part II) will include the same elements and the energy budget for fish kept on animal food. The energy budgets for fish fed with plant and animal food will be compared.

It seems also interesting to trace the pathways of basic organic compounds: proteins, lipids, and carbohydrates consumed in food as well as the degree of their utilization and excretion. This last problem will be presented in part III (Fischer 1972).

2. MATERIAL AND METHODS

The experiments were carried out of one-year-old fish (fingerlings) 40–120 g in weight, brought from the fish ponds of Field Station of Inland Fisheries Institute at Zabieniec near Warsaw. The fish had been acclimated for 2–3 months to experimental conditions before the 6-month experiments were started. Aiming at establishing the optimal conditions during the experiments, a temperature of 22°C has been chosen (Stroganov 1955). During both periods of acclimation and experiment, the fish were kept individually in well-aerated water contained in 10 l bottles submerged in a water-bath. The water was changed daily. The fish were fed with Tubificidae supplied in excess. This food has been chosen on account of the finding by Babajan (1962) that the representatives of the bottom fauna, mainly Chironomidae are the items of animal food found in intestines of grass carp. Thus, tubificids are similar to natural food, and are rather easy to obtain in the laboratory.

Gaseous exchange measurements

Gaseous exchange (O_2 consumption and CO_2 production) was measured in a flowing respirometer, which has been described in detail elsewhere (Fischer 1970 b). The oxygen uptake was measured by Winkler method modified by Carrit, Carpenter (1966), Just, Hermanowicz (1964). The measurements were run simultaneously with eight individuals for a month (a total of 96 measurements). The oxygen consumption by each individual was measured from 11 a.m. to 2 p.m. In order to test whether the respiration during the remaining of 24 hrs cycle corresponds to that of the time tested, a series of 24-hr measurement was carried out with records being taken every one and a half hour. These time intervals were considered frequent enough on account of papers by Winberg (Winberg, Beljackaja-Potaenko 1963) and on account of own results Fischer (1970 a). Parallel to oxygen consumption, carbon dioxide production was measured from the flowing respirometer. CO_2 content was measured by Van Slyke method, modified by Rodier (1960). Measurements were run on eight fish (a total of 125 measurements), a series of 24 hr measurement was also carried out, with records being taken every 3 hrs. Respiratory quotient was calculated for each fish basing on the almost simultaneous measurements of oxygen consumed and carbon dioxide produced as well as on 24-hr measurements by summing up the amount of oxygen used and carbon dioxide produced within 24 hrs.

Measurements of ammonium nitrogen

Ammonium nitrogen was defined by Prochaskova (1964) method. The samples of nitrogen excreted by fish were taken in two ways: either identically with the collection of gaseous samples i.e., at the outflow of water from the respiration chamber, inside of which there was a fish and its food, or directly from the respiration chamber which has contained the fish and its food for 24 hrs (a total of 125 samples). In the control chamber the ammonium nitrogen excreted only by food (Tubificidae) was defined. When comparing the both ways of sampling, no difference was found in the obtained results.

In spite of numerous trials the quantitative measurement of urea by means of urease was unsuccessful. Therefore the data by Smith (1929) were accepted according to which the uretic nitrogen in ciprinid fish is 15% of ammonium nitrogen. His results were supplemented with several orientative samples done by Kjeldahl method with assumption that non-protein nitrogen defined with this method is the uretic nitrogen.

Measurement of consumption rate

The consumption rate was measured by weight method, described in earlier paper (Fischer 1970 b). It was ascertained from the difference between the weight of food given and of its remains. Each time the calorific value of food was defined by burning a desiccated sample of food in Phillipson (1964) microbomb-calorimeter. From the product of calorific value (cal/mg) and the amount of food

eaten during 24 hrs (mg dry weight), the daily consumption rate was calculated. A total of 85 measurements was taken.

Measurement of the body growth of fish

These measurements were obtained by weighing the fish every two weeks. The detailed description of this method is given in the paper dealing with bioenergetics of grass carp fed with plant food (Fischer 1970 b). The calorific value of fish was obtained by burning several samples of each fish in the Phillipson microbomb-calorimeter.

Measurement of faeces production

The amount of faeces was obtained by centrifugation of the water in which the fish together with its food had been presented for 24 hrs. The flowing centrifuge was used with the rotation speed of 10,000/min, adjusted for centrifuging large quantities of water (10 l per 2 hrs).

After removing the uneaten food, the faeces present in 10 l of water were centrifuged, homogenized, and made up to 20 ml with distilled water. A precisely measured part of this sample was dried at 60°C to a constant weight and burned in the Phillipson microbomb calorimeter in order to obtain the calorific value of faeces. The ash content in faeces was also measured. The control sample was the water from a container holding food but no fish.

The control analysis of the supernatant remaining after centrifugation were also made. The samples proved that when the plant food was supplied the calorific value of supernatant was so low that it was within the error of the method (Fischer 1970 b). However when the animal food was given, a certain fraction of proteins remained in the supernatant. The amount of this fraction was checked by evaporation to 20 ml and then by Kjeldahl method. This fraction of proteins constituted 8% of the total protein content excreted by fish in faeces. This correction was taken into account in further calculations.

Control samples were carried out in order to find out whether during several months of the experiment there were any changes in calorific value of the fish body. Such control depended on parallel cultures under identical temperature and food conditions. From these cultures the fish (3 fish at each time) were taken 3 times during the whole experiment (6 months), killed and burned for finding the calorific value. There were no changes observed in the calorific values between subsequent samples.

Calculation of the energy budget

The energy budget was based on equation in which the amount of energy coming to an individual or other ecological unit equals to the sum of energy used for growth, metabolism, and rejecta.

$$C=P+R+F+U$$

where: C — consumption rate, P — increase in body weight, R — metabolism, F — faeces, U — excreted matter. (These symbols were accepted by International Biological Programme — *IBP-News* No. 19). All these parameters were expressed in the same units viz., calories per 24 hrs. The budget was based on differentiation (Klekowski 1970). The results were calculated individually for each fish, basing on the averages of food consumption, metabolism, and body growth obtained for each individual.

3. RESULTS

The consumption rate denoted as the amount of food eaten (cal) by a fish within unit time (24 hrs). The calorific value of tubificids was obtained from 14 burnings. The differences between samples were so inconspicuous that for further calculations an average value was used. The calorific value of 1 mg dry weight of tubificids amounted to $5.307 \pm \pm 0.037$ (S.E.) cal.

During the development a considerable differentiation of weights of fish was observed, therefore the body growth was presented as functions

and regression lines of the body weight. The equation for the dependence of fish body growth from fish weight is as follows:

$$P = 1.92 \cdot W^{1.18}$$

where: W is the live weight of fish (g), P is body weight in cal/24 hrs. The regression line on Fig. 1 is a graphical presentation of this depen-

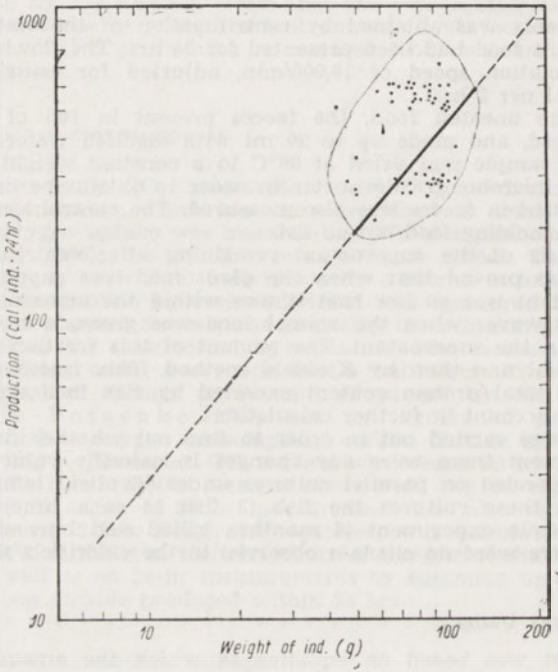

Fig. 1. Dependence of body growth from body weight in fish fed with Tubificidae ($P = 1.918 \cdot W^{1.183}$)

dence. The calorific value of fish fed with animal food ranged from 5.4523 to 6.4696 cal/mg dry weight.

The oxygen consumption was also expressed as a function of body weight of fish:

$$R_{O_2} = 300 \cdot W^{0.82}$$

where W is the life weight of fish (g), R_{O_2} — the oxygen consumption (µl O_2/ind. · hr). This regression is presented in Fig. 2.

The dependence of CO_2 output from the body weight of fish is presented as function:

$$R_{CO_2} = 456.6 \cdot W^{0.64}$$

where W is the live weight of fish (g), R_{CO_2} — carbon dioxide output (µl CO_2/ind. · hr).

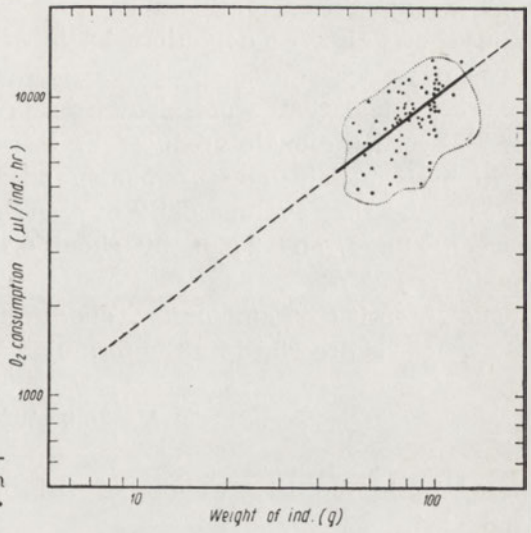

Fig. 2. Dependence of oxygen consumption from body weight in fish fed with Tubificidae ($R_{O_2} = 300.1 \cdot W^{0.768}$)

In order to find out whether the carbon dioxide output and oxygen input by fish during 11a.m.–2p.m. differs from that during 24-hr cycles, continuous 24-hr measurements were carried out. These results are shown in Fig. 3. The figure comprises averages obtained for given time of a 24-hr cycle as well as their standard errors. The range of standard error is rather broad, especially for CO_2 measurements, on account of a few samples which could be done simultaneously. It seems that the results presented in Fig. 3 — depicting the trend of respiration within 24 hrs — are rather typical ones. There is a decrease in respiration at night followed by an increase. It can be, thus, supposed that the hours chosen for measure-

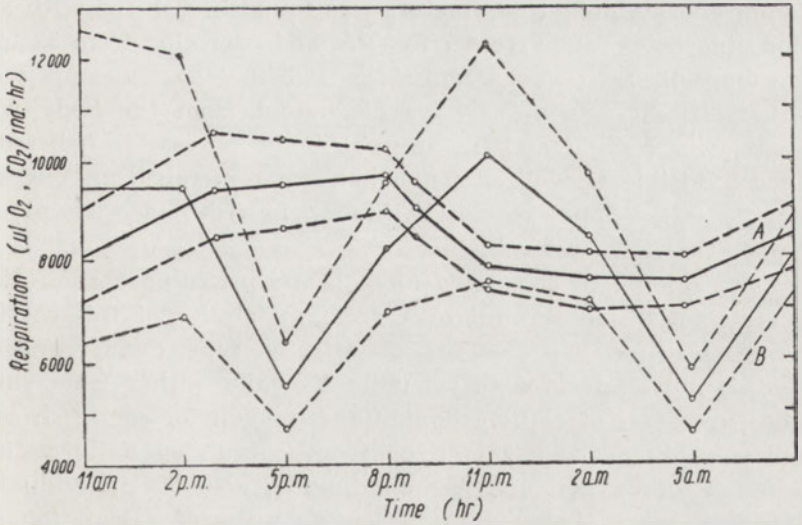

Fig. 3. Diurnal changes in respiration of fish (averages ± standard error). A — O_2 consumption, B — CO_2 production

ments do not differ considerably from 24-hr cycle. The curve for CO_2 output shows also two depletions in the afternoon (4-6 p.m.) and at night (2–4 a.m.).

Direct calculations were also made, i.e. the amount of oxygen consumed and carbon dioxide produced by a fish within 24 hrs was calculated on the basis of daily measurements, and averages per hr were obtained. It was found that average daily oxygen consumption is lower from that between 11 a.m. and 2 p.m. by about 0.7% and in the case of carbon dioxide by 17.7%.

The intensity of ammonium and uretic nitrogen excretions against body weight is described by the formula:

$$N = 36.9 \cdot W^{0.49}$$

where: W is the live weight of fish, N — nitrogen excretion (μg N/ind. · hr).

Basing on the obtained results the amounts of excreted ammonium and uretic nitrogen were obtained, and later, from multiplication by a coefficient of 6.25, the amount of proteins burned by fish was ascertained. By knowing the amount of excreted ammonia and urea and their calorific values, the excreted matter was expressed in terms of calories. In this way the remaining parameters were obtained: $F+U$, both for experiments with animal and plant food. Energy balances of all fish fed with plant and animal food are shown in Table I and II respectively. Each budget is based on about ten measurements of every parameter. These Tables illustrate a considerable individual differences between fish, irrespective to the type of food and the body weight. Especially high variation of energy budget parameters was found in fish fed with animal food. Body increases range from 7 to 37%, and excretion from 32 to 83% (the consumption rate was accepted as 100%). The consumption rate differed greatly, it was not always dependent from the body weight. When comparing Table I and II, the small body increase in fish fed with plant food is visible as well as somewhat lower metabolism. The excretion, on the other hand, is clearly higher in fish fed with plants as compared to that fed with animal food.

From the amount of consumed oxygen and produced carbon dioxide, RQ was calculated. On account of a great instability of this coefficient (it depended on time of a day, fish activity, on type, quality and quantity of food) it was decided to calculate its value either from simultaneous measurements of carbon dioxide and oxygen for each fish separately between 11 a.m. and 1 p.m., or from cumulated daily values of measurements of oxygen and carbon dioxide, also for individual fish. No differences were observed in these two ways of calculation. From 86 calculations the average RQ value of 0.86 ± 0.029 (S.E.) was accepted

Table I. Energy budgets of fish fed with *Lactuca sativa* ($C = P+R+F+U$)

Mean body weight (g)	Unit	C	P	R	F	U	Difference between C_{exp} and $C_{calc.}$ (%)
19.6	cal	3000	39	414	1872	103	
(19-20)	%	100	1	14	62	3	20
28.5	cal	3550	69	599	2852	85	
(24-30)	%	100	2	17	80	2	1
29.5	cal	2927	53	601	2343	50	
(29-30)	%	100	2	20	80	2	6
30.4	cal	3816	57	609	2908	77	
(28-32)	%	100	1	16	76	2	5
31.0	cal	5215	132	535	3315	69	
(30-32)	%	100	2	10	64	1	23
34.5	cal	4013	85	398	3114	75	
(31-36)	%	100	2	10	78	2	8
35.1	cal	5683	129	504	3578	89	
(34-36)	%	100	2	9	63	1	25
35.4	cal	3455	126	580	2496	74	
(32-40)	%	100	4	17	72	2	5
39.7	cal	4605	171	572	3545	85	
(38-41)	%	100	4	12	77	2	5
49.1	cal	4163	182	528	3238	83	
(48-51)	%	100	4	13	78	2	3
49.5	cal	3347	55	658	2254	64	
(49-50)	%	100	2	20	67	2	9
55.0	cal	4697	56	872	3357	70	
(54-56)	%	100	1	18	71	1	9

Table II. Energy budgets of fish fed with Tubificidae ($C = P+R+F+U$)

Mean body weight (g)	Unit	C	P	R	F	U	Difference between C_{exp} and $C_{calc.}$ (%)
86.0	cal	4184	751	1084	1566	79	
(81-91)	%	100	18	26	37	2	17
87.5	cal	3660	585	1566	1813	52	
(86-90)	%	100	16	43	49	1	9
88.0	cal	8627	673	1385	6537	85	
(75-98)	%	100	8	16	76	1	1
92.0	cal	2810	1055	834	900	95	
(89-95)	%	100	37	30	32	3	—
95.5	cal	10,753	1494	1858	7480	67	
(77-114)	%	100	14	17	69	1	1
103.0	cal	7515	890	1132	6298	63	
(100-105)	%	100	12	15	84	1	12
107.0	cal	10,069	1044	1859	6847	72	
(96-114)	%	100	10	18	68	1	3
107.5	cal	5087	761	1063	2590	91	
(102-119)	%	100	15	21	51	2	11

for fish fed with animal food. For fish fed exclusively with plants this value amounted to 0.96 ± 0.076 (S.E.) (Fischer 1970 b).

Basing on the measurements of gaseous exchange and of ammonium and urea nitrogen excretion the amount of energy used for metabolism was calculated by means of indirect calorimetry. For these calculations the averages of oxygen consumption, carbon dioxide production and nitrogen excretion by fish 86-107 g in live weight fed with animal food were used. The comparison of thus obtained data with the data published in previous paper concerning the fish fed exclusively with plant food is presented in Table III. Table IV comprises the same data calculated per gram of fish body in order to make them more comparable with the literature data. One should remember, however, that these data concern only fish of a certain body weights, given in the Table.

From the elements of energy budget it is possible to calculate the indices of energy transformation efficiency for the investigated fish and

Table III. Consumptions of proteins, carbohydrates and lipids for metabolism per 1 hr (indirect calorimetry)

Consumption	Food					
	Tubificidae (Fish: 95.8 (86-107) g, non-protein RQ=0.81)			*Lactuca sativa* (Fish: 35 (20-50) g, non-protein RQ=0.91)		
	mg	cal	%	mg	cal	%
Carbohydrates	3.9	16.4	29.5	3.1	13.0	58.3
Lipids	3.1	29.4	52.8	0.3	2.8	12.6
Proteins	2.3	9.9	17.7	1.5	6.5	29.1
Energy expenditure		55.7	100.0		22.3	100.0

Table IV. Consumptions of proteins, carbohydrates and lipids for metabolism per 1 g per 1 hr (indirect calorimetry)

Consumption	Food					
	Tubificidae (Fish: 95.8 (86-107) g, non-protein RQ=0.91)			*Lactuca sativa* (Fish: 35 (20-50) g, non-protein RQ=0.91)		
	mg	cal	%	mg	cal	%
Carbohydrates	0.040	0.171	29.5	0.011	0.371	58.3
Lipids	0.032	0.307	52.8	0.008	0.080	12.6
Proteins	0.024	0.103	17.7	0.043	0.185	29.1
Energy expenditure		0.581	100.0		0.636	100.0

to compare them with those found for fish fed exclusively with plant food. These indices for both groups differ entirely between the both groups. K_1 index, i.e. the ratio of body growth to consumption rate, expressed in per cent, is in both cases low, and for plant food extremally low:

animal food: $K_1 = 12.5 \pm 3.5\%$,
plant food: $K_1 = 2.2 \pm 1.0\%$

K_2 index, i.e. the ratio of body growth to the assimilated food is also low:

animal food: $K_2 = 40.4 \pm 3.0\%$,
plant food: $K_2 = 14.4 \pm 2.0\%$

It is also possible to calculate the assimilation in 3 ways for both groups of fish.

1. from formula: $A = P + R$, where: P — body growth, R — respiration, C — consumption,
2. from formula: $A = C - FU$, where C — consumption, FU — rejecta,
3. from Conover's (1966) formula:

$$A\,\% = \frac{F - E}{1 - EF} \cdot 100,$$

where: F is the ratio of dry weight of organic matter in food to dry weight of food; E is the ratio of dry weight of organic matter in faeces to dry weight of faeces. Using this method one assumes that inorganic substances (ash) are in dynamic equilibrium.

The data calculated according to the above given formulae concerning the assimilation as well as the indices of energy transformation efficiency are given in Table V.

Table V. Mean values of bioenergetic parameters (%)

Food	Parameter				
	U^{-1}			K_1	K_2
	$\frac{P+R}{C}$	$\frac{C-FU}{C}$	Conover's method		
Tubificidae	39.50 ± 5.4	40.10 ± 7.2	41.82 ± 5.5	12.53 ± 3.5	40.40 ± 3.0
Lactuca sativa	17.20 ± 1.2	24.81 ± 2.0	20.72 ± 2.1	2.22 ± 0.9	14.47 ± 2.0

4. DISCUSSION

In spite of the fact that grass carp is generally considered as plant-feeding fish (Boruckij 1952, Pavlovskij 1966, Scheer et al.

1967, Verigin 1961, Nakamura 1958, Cjan-I-chun et al. 1963, Opuszyński 1967). The results of Chinese papers quoted by Nikolskij (1966) as well as Stroganov's (1955) papers point to a broad feeding ability of this fish. Besides many vascular plant species the grass carp consumes also Chironomidae, and when fed artificially it consumes also oats, leaves, grass, many cerales, bread, and others.

As it appears from the above data, such a principal problem as that of the diet of grass carp is not fully elucidated. There is scarse information on the amount of energy consumed by this fish and the fact whether grass carp is herbivorous, carnivorous, or omnivorous is still controvercial. That is why the elucidation of herbivorousness of grass carp seems to be most interesting.

The results of the present paper allow to suppose that the grass carp does not belong to typical herbivores. The body growth of this fish when fed exclusively with plant food is strikingly low, almost null, however it grows and develops much faster when kept on animal food. The growth rates given in Fig. 4 speak in favour of omnivorousness of this fish. The

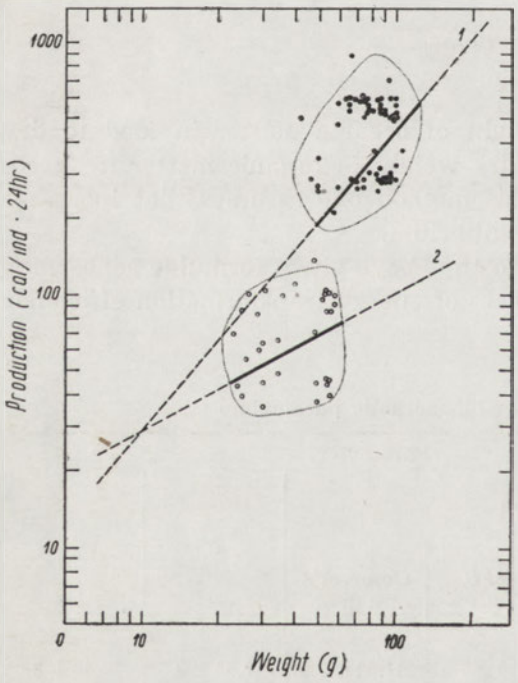

Fig. 4. Dependence of body growth from body weight. 1 — fish fed with animal food ($P=1.918 \cdot W^{1.183}$), 2 — fish fed with plant food ($P=11.51 \cdot W^{0.456}$)

results comprising 8 months of experiments of feeding by grass carp presented in this paper are incongruent with data by Opuszyński (1967).

There is a conspicuous difference between the results concerning growth of fish investigated by Opuszyński at 22°C and fed exclu-

sively with plant food, and those of the present experiments. The growth rates of fish fed with plant food in experiments by Opuszyński were similar to that in present paper to fish fed with animal food. But growth rates of fish kept exclusively on plant food in the present paper were very small: within 10 days an average growth of one fish amounted to about 0.5 g whereas that of fish fed with animal food about 7 g — i.e. 14 times more. The results of experiments by Opuszyński, showing such a considerable growth rate were probably caused by the duration of his experiments (10 days). It is possible that in such a short time the organism did not shift yet fully to plant food and did not suffer yet from the lack of minimum factors, e.g. vitamins or certain animal proteins which were necessary for growth.

Paper by Krupauer (1967) supports our results concerning the growth rate of grass carp fed with lattuce. This author found that there was no growth of fish fed with plant food and drew a conclusion that the exclusively plant food must lead in a short time to death of the fish. However in our experiments no death was observed. It is possible that the phenomenon observed by Krupauer is connected with so-called "biological uselessness of food" (Karzinkin 1952). Another factor connected with plant protein properties can be involved. In many cases the supply of plant proteins alone without even small amount of animal proteins will cause retardation of the growth.

In the light of results discussed earlier, it seems that grass carp can live on exclusively animal food. Thus it is difficult to consider it as exclusive herbivore. Thus it seems reasonable to compare the consumption rate of grass carp with that of omnivorous fish.

Ivlev (1939) in his paper pays great attention to consumption of carp. The fish he has studied were taken from a natural habitat. There is a great similarity in consumption index of carp (7.28%) and of grass carp fed in the present experiment with animal food (7%). Consumption index is calculated as ratio of energy bound in food consumed daily to the energy bound in animals body, in per cent. A considerable difference is found, however, when comparing the consumption index of grass carp kept on plant food (16%) and that of carp (6.38%).

Winberg (1956), basing on results of various authors studying different fish species — mainly carnivores, gives tables of consumption rates. The consumption rates considered by him are in full agreement with present results obtained for animal food but different for plant food. Results of Winberg's papers seem to speak in favour of the conclusion coming from present experiment, i.e. about omnivorousness of grass carp.

Oxygen consumption values agree with data obtained by other authors who studied gaseous exchange of carp or Carassus (Privolnev

1945, Strelcova 1951, Ivlev 1954, Fry 1957, Fry, Hart 1948, Stroganov 1949, Gerking 1967).

The oxygen consumption-weight dependence has been broadly studied in fish. Winberg (1961) gives a formula for all the fish species $Q = 0.307 \cdot W^{0.81}$, where W — live weight (g), Q — O_2 consumption (ml/ind. · hr). Winberg (1961) gives also following formula for grass carp and white carp, quoted by Chinese autors: $Q = 0.152 \cdot W^{0.84}$. Unfortunately I could not reach the original of this paper quoted by Winberg. One does not know what age were the fish examined, were they taken from the natural environment, or were they bred in laboratory conditions, what food they have been given? Regressions obtained in present experiments for grass carp deviate greatly from those obtained by Chinese authors and quoted by Winberg. In experiments of the present paper (after recalculation in units used by Winberg) the following regression was obtained for fish fed with animal food: $Q = 0.300 \cdot W^{0.768}$, and for fish fed with plant food: $Q = 0.487 \cdot W^{0.614}$. Yeh Ye Tsu (1959) gives data concerned with grass carp, 1.1 and 9.6 g in weight. From the above mentioned formulae it is possible to calculate theoretical oxygen consumptions by fish 1.1 and 9.6 g in weight and compare them with the experimental data obtained by Yeh Ye Tsu. The comparison of those data is as follows:

Weight of fish (g)	Yeh Ye Tsu (1959)	Winberg 1961		Present work	
		Chinese data	General formula	fed with Tubificidae	fed with *Lactuca sativa*
		$0.152 \cdot W^{0.84}$	$0.307 \cdot W^{0.81}$	$0.300 \cdot W^{0.76}$	$0.487 \cdot W^{0.614}$
1.1	416.?	165.9	332.0	323.0	520.0
9.6	2658.3	1016.0	1920.0	1705.0	1950.0

Thus respiration of grass carp obtained in present experiments (especially when fish were fed with Tubificidae) does not deviate from the general formula for all fish given by Winberg (1961). Some deviations from his formula must occur, as he states broady himself, since respiration is dependent on the ecological characteristics of the species. These deviations, however, both for grass carp and other species, do not seem to have essential importance in bioenergetic studies.

The values of carbon dioxide production obtained in the present paper are similar to those given by Yeh Ye Tsu (1959) for grass carp. Having in disposal data of carbon dioxide production and oxygen consumption RQ was calculated. This quotient is unstable and it changes not only with the food diet, but also with quantity of food, and with temperature, fish body weight, and even with diurnal cycle. According to Yeh Ye Tsu (1959) RQ in grass carp ranges from 0.88 to 0.91

depending on the fish age. This author accepted an average value of 0.91. This value differs from that obtained in the present experiments, both for animal and plant food. *RQ* for grass carp kept on animal food amounts to 0.80, thus it is relatively low and results from the type of food, which comprises small amounts of carbohydrates. Opposite situation was observed with exclusively plant food, when due to an increased transformation of carbohydrates *RQ* is high and amounts to 0.96. The variation of this quotient with body weight is discussed in detail in previous paper (Fischer 1970 b).

5. ENERGY BUDGET

Calculation of energy budgets aims at characterizing the species investigated as converters of energy supplied in food into energy bound in the animal body. Present budgets are of differentiated type (Klekowski 1970) and they describe only energy transformation in grass carp and its role in bodies by transferring energy to other links of the trophic chain.

Detailed energy budgets are presented in Tables I and II. When comparing only calories of consumption, irrespective to the quality of food, one should say that the amounts of energy consumed are rather large. Comparing them with data by Ivlev (1939), it appears that after adequate recalculation grass carp consumes a considerable amount of calories, exceeding greatly values given both by Ivlev (1939), and by Karzinkin (1952). From this fact one can draw a conclusion that the grass carp faced with abundance of food, can be a potential consumer both of animals and plants.

The body growth of fish fed with animal food when expressed in calories exceeds the growth of fish fed with plant food about ten times. The amount of faeces is large in both cases. Index U^{-1} says about energy assimilated. This index can be calculated in 3 ways which have been discussed above (Table V). Elaboration of the data including 3 ways of ascerting assimilation was only possible due to rather rare situation where all the budget parameters were defined experimentally. Differences between various ways of calculation were inconsiderable (Table V). The assimilation efficiency by fish fed with animal food calculated with different ways amounts to about 48%. This value is close to assimilation efficiency in predatory, inactive animals, such as larvae of *Lestes sponsa* (Fischer 1967), Actinia (Ivleva 1964), where the assimilation index amounts to 35%, and to 65% in its atmost (Fischer 1970 b). It seems that the grass carp under present experimental conditions and fed with animal food can be classified as inactive carnivore. This inactivity can results from the imprisoning of grass carp in the respiration chamber. Under natural conditions, when activity of the fish is not

restricted, the assimilation should be probably a little higher. The excess of food can also affect the assimilation in present experiments. Davies (1964) obtained decreasing assimilation with increasing consumption rate, as reported in his paper on bioenergetic of Carassius.

In the fish fed with plants assimilability of food amounts to about 20%. Such low efficiency occurs also in filtrators (Richman 1958, Monakov, Sorokin 1961) or in detritus-feeders (*Asellus aquaticus* — Klekowski et al. 1971, *Tubifex tubifex* — Ivlev 1939 a). Both groups mentioned feed on plant food, fresh or decaying. A conclusion can be drawn that assimilation is closely dependent on the type of food consumed and that the same organism swiching from one item of food to another can shift also assimilation efficiency. However, the assimilation efficiencies in fish fed with plant food, as calculated by different ways are less consequent than the assimilation efficiencies of grass carp fed with animal food. The differences in assimilation efficiency obtained by direct methods in grass carp fed with plant food are the following: $\frac{P+R}{C} = 17.5\%$ and $\frac{C-FU}{C} = 24.8\%$. These differences point to some error in the measurement of one of the energy budget parameters. The body growth and/or respiration were underestimated, or rejecta were overestimated. The latter possibility is quite probable since complete distinguishing of faeces from the plant remains of the food is almost impossible. When centrifuging faeces, the food remains are carefully collected. However, it is most probable that small particles of cut and spat plants will remain and be considered as faeces.

A trial was made to estimate assimilation efficiency by means of Conover's method (Conover 1966), based on assumption that there is an equilibrium of mineral substances supplied to the organism and egested. This method evoked a considerable discussion. Pavljutin's (1970) paper proves from studies of different species how this method can be erroneous. Results reported by Prus (gathered in paper by Klekowski et al. 1971) concerning *Asellus aquaticus* are the proof how one has to be careful when applying this method. Studying the assimilation efficiency by direct $\left(\frac{P+R}{C} \text{ and } \frac{C-FU}{C}\right)$ and indirect (Conover's) method, he obtained a high incongruency of results. Inconsiderable differences obtained in the present experiments on grass carp under natural condition with direct and indirect methods, are difficult to be explained (Table V). Pavljutin (1970) has obtained the smallest errors when he calculated by the Conover's method, the assimilation efficiency for molluscs fed with plants. Perhaps plant food has some decisive role here. In the present experiments, the fish were fed with very monotonous food, either Tubificidae alone or *Lactuca*

sativa alone. This probably effected the equilibrium of mineral substances in the organism.

However, in spite of the results obtained by the Conover's method it is possible to state that grass carp has an ability to assimilate both type of food and that animal food is better assimilated that the plant food.

Index K_1 defines this part of food consumed which is being used for growth. This index for fish fed with animal food amounts on the average to 12.5%, and with plant food to 2.2%. These value are smaller than those obtained by Ivlev (1939) for carp and by Karzinkin (1952) for other fish. In fish fed with plants K_1 is somewhat similar to that of such animals as *Simocephalus vetulus* (Klekowski, Shushkina 1966), *Lestes sponsa* (Fischer 1967). It seems that this congruency is a good example of advantages resulting from calculation of cumulative budgets of these species. These budgets allowed to trace precisely the course of energetic efficiencies of the animals studied during their developmental stages.

The budgets for fish can only describe the energy transformation at a given period of life. That is why it is difficult to compare the present results with other data on energy transformation in fish. For example, the comparison with Davies' paper (1967) is not possible. His values concerned with consumption rate used for growth are so large (54%) that they can be explained only by a study of a special period of life of Carassius. Such result can be not typical for other fish or other periods of their life.

K_1 index for grass carp is astonishingly low. Similar value was only found in *Asellus aquaticus* (Klekowski et al. 1971) where this index amounted to 5.3%. K_2 index which reflects what part of assimilated food is used for growth of fish fed with plants is also low and amounts to 14.5%. Similar values were obtained by Prus for *Asellus aquaticus*: 17.6%. Klekowski, Duncan (in print) also report on similar data for some long-living poikilotherms. K_2 index obtained for grass carp fed with animal food is similar to that obtained by Ivlev (1939) for carp and it amounts to 40%. This value is close to commonly obtained for aquatic poikilotherms (Klekowski, Duncan in print).

By and large, one can suppose that grass carp fed with animal food has bioenergetic processes similar to carp which assimilates animal food in average degree and is characterized by large growth and a vast food diet. However, grass carp fed with plant food, assimilates it in inconsiderable degree and is characterized by a small growth rate. Feeding of grass carp on vascular plants in natural habitat should be supposingly explained by the fact that these plants are a "free" food supply, unused by other animals and the fish does not meet any competition in using this food.

6. SUMMARY

The studies aimed at comparison of energy budgets of grass carp fed with exclusively plant and exclusively animal food. These detailed studies concerned the body growth efficiency. The following findings were ascertained:

1. Grass carp bred under laboratory conditions is omnivorous.

2. Growth rate of grass carp fed with exclusively plant food is smaller than when fed with exclusively animal food. The dependences of body growth from body weight are as follows:

animal food: $P = 1.92 \cdot W^{1.18}$,
plant food: $P = 11.51 \cdot W^{0.46}$.

3. Food assimilability by grass carp fed exclusively with animal food was about 40% and that of fish fed exclusively with plant food about 20%.

4. Energy transformation efficiency indices for grass carp on animal food are: $K_1 = 12.5\%$, $K_2 = 40.4\%$, but on plant food: $K_1 = 2.2\%$, $K_2 = 14.5\%$.

5. In grass carp 95.8 g in weight, fed with animal food exclusively, non-protein *RQ* amounted to 0.81. In the process of respiration, lipids are burned at 53%, carbohydrates at 30% and proteins at 18%.

6. In grass carp 35.0 g in weight, fed with plant food exclusively, non-protein *RQ* was 0.91. At the process of respiration carbohydrates are being burned at 58.3%, proteins at 29.1% and lipids at 12.6%.

7. STRESZCZENIE

Badania miały na celu porównanie bilansów energetycznych białego amura przy stosowaniu pokarmu wyłącznie roślinnego i wyłącznie zwierzęcego. Szczególnie badania te dotyczyły wydajności wykorzystania energii tych pokarmów na przyrost ryb. Stwierdzono:

1. Biały amur hodowany w warunkach laboratoryjnych ma cechy ryb wszystkożernych.

2. Wzrost amura żywionego pokarmem wyłącznie roślinnym jest mniejszy, niż żywionego pokarmem wyłącznie zwierzęcym. Zależności przyrostów od wagi ryb przedstawiają się następująco:

pokarm zwierzęcy: $P = 1,92 \cdot W^{1,18}$
pokarm roślinny: $P = 11,51 \cdot W^{0,46}$

3. Przyswajalność pokarmu białego amura żywionego pokarmem wyłącznie zwierzęcym wynosi około 40%, a żywionego pokarmem wyłącznie roślinnym około 20%.

4. Wskaźniki wydajności energetycznej białego amura żywionego pokarmem wyłącznie zwierzęcym wynoszą: $K_1 = 12,5\%$, $K_2 = 40,4\%$, natomiast te same wskaźniki dla amura żywionego pokarmem wyłącznie roślinnym wynoszą: $K_1 = 2,2\%$, $K_2 = 14,5\%$.

5. U amura o średniej wadze 95.8 g żywionego pokarmem wyłącznie zwierzęcym *RQ* niebiałkowe wynosi średnio 0,81. Przy oddychaniu lipidy spalane są w 53%, węglowodany w 30%, a białka w 18%.

6. U amura o średniej wadze 35,0 g karmionego wyłącznie roślinami *RQ* niebiałkowe wynosi średnio 0,91. Przy oddychaniu węglowodany spalane są w 58,3%, białka w 29.1% a lipidy w 12,6%.

8. REFERENCES

[Babajan, K. E.] Бабаян, К. Е. 1962. Некоторые результаты рыбохозяйственного освоения растительноядных рыб в водоемах С.С.С.Р. [Some results of acclimation of plant-feeding fish to fish-farm conditions in reservoirs of USSR]. *Ryb. Hoz.*, vyp. 12, 23-27.

[Boruckij, E. V.] Боруцкий, Е. В. 1952. Материалы по питанию белого амура (*Ctenopharyngodon idella* Val.) и мелкочешуйчатого желтотера (*Plagiognathops microlepis* Bl.) в бассейне Амура [Materials on feeding of grass carp (*Ctenopharyngodon idella* Val.) and *Plagiognathops microlepis* Bl. in the basin of Amur river]. *Trudy Amursk. ihtiol. Eksped.*, 1945-1949, T. 3.

Carrit, D. A., Carpenter, J. H. 1966. Comparison and evaluation of currently employed modifications of the Winkler method for determination dissolved oxygen in sea water. *J. mar. Res.*, 24, 286-318.

[Cjan I-chun, Djan Djit-Sa, Chen Si-Tao] Цян И-чун, Чжан Цзить-Ся, Чень Си-Тао. 1963. Исследование питания и корма белого амура [Investigations on feeding and food of grass carp]. Dokl. na 7 plenume meždunarodnoj komissii po izučeniju zapadnoj časti Tihogo Okeana. Manuscript at the Library M.G.U. [Transl. from Chinese].

Conover, R. J. 1966. Assimilation of organic matter by zooplankton. *Limnol. Oceanogr.*, 11, 338-346.

Davies, P. M. C. 1964. The energy relations of *Carassus auratus* L. I- Food input and energy extraction efficiency at two experimental temperatures. *Comp. Biochem. Physiol.*, 12, 67-69.

Davies, P. M. C. 1967. The energy relations of *Carassus auratus* L. III- Growth and the overall balance of energy. *Comp. Biochem. Physiol.*, 23, 59-63.

Fischer, Z. 1967. The energy budget of *Lestes sponsa during* its larval development. In: *IBP Meeting "Methods of assessment of secondary production in fresh waters"*. Prague [Mimeographed copy].

Fischer, Z. 1970 a. Some remarks about the food ration. *Pol. Arch. Hydrobiol.*, 17, 177-182.

Fischer, Z. 1970 b. The elements of energy balance in grass carp (*Ctenopharyngodon idella* Val.). Part I. *Pol. Arch. Hydrobiol.*, 17, 421-434.

Fischer, Z. 1972. The elements of energy balance in grass carp (*Ctenopharyngodon idella* Val.). Part III. Assimilability of proteins, carbohydrates, and lipids by fish fed with plant and animal food. *Pol. Arch. Hydrobiol.*, 19, 83-95.

Fry, F. E. 1957. The aquatic respiration of fish. In: M. E. Brown [Ed.] *The physiology of fishes*. I, 1-63, New York, Academic Press.

Fry, F. E. J., Hart, J. S. 1948. Cruising speed of goldfish in relation to water temperature. *J. Fish. Res. Bd Can.*, 7, 169-175.

Gerking, S. D. [Ed.] 1967. *The biological basis of freshwater fish production*. Oxford, Blackwell.

[Ivlev, V. S.] Ивлев, В. С. 1939. Энергетический баланс карпов [Energy balance of carp]. *Zool. Ż., Mosk.*, 18, 303-318.

Ivlev, V. S. 1939 a. Transformation of energy by aquatic animals. Coefficient of energy consumption by *Tubifex tubifex* (Oligochaeta). *Int. Rev. ges. Hydrobiol. Hydrograph.*, 38, 449-458.

[Ivlev, V. S.] Ивлев, В. С. 1954. Зависимость интенсивности обмена от веса их тела [Dependence of metabolism on body weight of fish]. *Fiziol. Ż., S.S.S.R.*, 40, 717-721.

[Ivleva, I. V.] Ивлева, И. В. 1964. Элементы энергетического баланса актиний [Elements of energy balance in Actinia]. *Trudy sevastopol. biol. Sta*, 15, 410-428.

Just, J., Hermanowicz, W. 1964. *Fizyczne i chemiczne badania wody do picia i potrzeb gospodarczych* [Physical and chemical studies of the tap water and for economical purpose]. Warszawa, PZWL.

[Karzinkin, G. S.] Карзинкин, Г. С. 1952. Основы биологической продуктивности водоемов [Principles of biological productivity of water bodies]. Moskva, Piščepromizdat.

Klekowski, R. Z. 1970. Bioenergetic budgets and their application for estimation of production efficiency. *Pol. Arch. Hydrobiol.*, 17, 55-80.

Klekowski, R. Z., Duncan, A. [in print] Parameters of energy budget. In: *Methods of ecological bioenergetics*. IBP Handbook. Oxford, Blackwell.

Klekowski, R. Z., Fischer, E., Fischer, Z., Ivanova, M. B., Prus, T., Shushkina, E. A., Stachurska, T., Stępień, Z., Żyromska-Rudzka, H. 1971. Energy budget and energy transformation efficiency of several animal species of different feeding types. In: Z. Kajak, A. Hillbricht-Ilkowska [Eds] *Productivity problems of freshwaters*. 00-00. Warszawa-Kraków.

Klekowski, R. Z., Shushkina, E. A. 1966. Ernährung, Atmung, Wachstum und Energie-Umformung in *Macrocyclops albidus* (Jurine). *Verh. int. Ver. Limnol.*, 16, 399-418.

Krupauer, V. 1967. Vyberost v potrave u dvouletych bilnych amru. *Buletin vyzk. Ust. Ryb. Vodnany*, 3, 7-17.

[Monakov, A. V., Sorokin, Ju. I.] Монаков, А. В., Сорокин, Ю. И. 1961. Количественные данные о питании дафний [Quantitative data on the feeding of Daphnids]. *Trudy Inst. biol. Vodohran.*, 4, 251-261.

[Nakamura, I.] Накамура, И. 1958. Выращивание белого амура в водохранилищах Суйсан Сиген [Culturing of grass carp in dam reservoir Sujsan Sigen]. No 2. Manuscript at the Library of M.G.U. [Transl. from Japanese].

[Nikolskij, G. V.] Никольский, Г. В. 1956. Рыбы бассейна Амура [Fish of the basin of Amur river]. Moskva, Izdat. „Nauka".

Opuszyński, K. 1967. Odżywianie się białego amura (*Ctenopharyngodon idella* Val.) roślinami wodnymi w warunkach akwaryjnych [Feeding of *Ctenopharyngodon idella* Val. on aquatic plants under aquarium conditions]. *Roczn. Nauk roln., Ser. H*, 90, 453-462 [Engl. summ.].

Opuszyński, K. 1969. Produkcja ryb roślinożernych (*Ctenopharyngodon idella* Val. i *Hypophthalmichthys molitrix* Val.) w stawach karpiowych [Production of plant-feeding fish (*Ctenopharyngodon idella* Val. and *Hypophthalmichthys molitrix* Val.) in carp ponds]. *Roczn. Nauk roln., Ser. H*, 91, 221-309 [Engl. summ.].

[Pavljutin, A. P.] Павлютин, А. П. 1970. К методам определения усвояемости пищи у водных животных [On the methods of calculation of assimilation of food in aquatic animals]. *Zool. Ż., Mosk.*, 49, 288-293.

[Pavlovskij, E. H.] Павловский, Е. Х. 1966. Рыбохозяйственное освоение растительноядных рыб [Acclimation of plant feeding-fish to fish-farm conditions]. Moskva, Izdat. „Nauka".

Phillipson, J. 1964. A miniature bomb calorimeter for small biological samples. *Oikos*, 15, 130-139.

[Privolnev, G. I.] Привольнев, Г. И. 1945. Кожное дыхание у карасиа *Carassus carassus* [Skin-breathing in *Carassus carassus*]. *Dokl. Akad. Nauk S.S.S.R.*, 48, 623-625.

Prochaskova, L. 1964. Spectrophotometric determination of ammonia as rubazoic acid with bispyrazolone reagent. *Analyt. Chem.*, 36, 865-871.

Richman, S. 1958. The transformation of energy by *Daphnia pulex*. *Ecol. Monogr.*, 28, 273-291.

Rodier, J. 1960. Determination de l'acide carbonique. In: J. Rodier [Ed.] L'analyse chimique et physicochimique de l'eau. 94-102, Paris, Dunod.

Scheer, D., Jahnichen, H., Grahl, K. 1967. Beobachtungen bei der Haltung von ein- und zweisömmigen Graskarpfen (*Ctenopharyngodon idella*) in kleinen Teichen im Gebiet von Karl-Marx-Stadt. *Dt. Fisch. Ztg., Radebeul*, 14, 141-146.

Smith, H. W. 1929. The excretion of ammonia and urea by the gills of fish. *J. biol. Chem.*, 81, 727-742.

[Strelcova, S. V.] Стрельцова, С. В. 1951. Кожное дыхание рыб [Skin-breathing in fish]. *Dokl. Akad. Nauk S.S.S.R.*, 76, 157-160.

[Stroganov, N. S.] Строганов, Н. С. 1949. Зависимость дыхания рыб от скорости течения воды [Dependence of fish respiration from the speed of water flow]. *Vestn. Moskovsk. Univ.*, 2, 145-154.

[Stroganov, N. S.] Строганов, Н. С. 1955. Подкармливание осетров и амуров в прудах [Feeding up of sturgeon and grass carp in ponds]. *Ryb. Hoz.*, vyp. 10, 36-39.

[Verigin, B. V.] Веригин, Б. В. 1961. Итоги работы по аклиматизации дальневосточных растительноядных рыб и мероприятия по их дальнейшему освоению и изучению в новых районах [Results of work in the sphere of acclimatization of Far-East herbivorous fish and measures aimed at their study in new areas]. *Vop. Ihtiol.*, 1 (18), 640-649.

[Winberg, G. G.] Винберг, Г. Г. 1956. Интенсивность обмена и пищевые потребности рыб [Rate of metabolism and food requirements of fish]. Minsk, Belgosuniversit. im. V. L. Lenina.

[Winberg, G. G.] Винберг, Г. Г. 1961. Новые данные об интенсивности обмена у рыб [New data on intensity of metabolism in fish]. *Vop. Ihtiol.*, 1 (18), 157–166.

[Winberg, G. G., Beljackaja-Potaenko, Ju. S.] Винберг, Г. Г., Беляцкая-Потаенко, Ю. С. 1963. Суточный ход интенсивности газообмена у пойкилотермных животных [Diurnal course of gas exchange intensity in poikylothermal animals]. *Zool. Ż., Mosk.*, 42, 1593-1600, [Engl. summ.].

Yeh Ye Tsu 1959. [A preliminary report on the oxygen consumption, energy requirement as phyxation point and respiratory quotient of the fish dry and young fish]. *Acta zool. Sinica*, 11, 117-137, [in Chinese].

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Z. FISCHER

THE ELEMENTS OF ENERGY BALANCE IN GRASS CARP (*CTENOPHARYNGODON IDELLA* VAL.). PART III. ASSIMILABILITY OF PROTEINS, CARBOHYDRATES, AND LIPIDS BY FISH FED WITH PLANT AND ANIMAL FOOD

Department of Bioenergetics and Bioproductivity, Nencki Institute of Experimental Biology, Pasteura 3, Warszawa, Poland

ABSTRACT

Analysis was made of main organic compounds: proteins, carbohydrates and lipids consumed by grass carp in food, of the degree of their utilization and excretion. The fish were fed with animal and plant food. Trials were made to balance the above mentioned compounds.

1. INTRODUCTION

In previous papers all elements of energy budgets of grass carp fed either exclusively with plant food (Fischer 1970) of exclusively with animal food (Fischer 1972) were given, supplemented with a trial of energy budget when both items of food were supplied simultaneously (Fischer 1972). The present paper aims at tracing the chances of basic organic compounds — proteins, carbohydrates and lipids consumed with food by grass carp; the degree of their assimilation and excretion. The trials of the budget of these components, when applying either plant or animal food, have been also carried out.

2. MATERIAL AND METHODS

The experiments were carried out on one-year-old fish (fingerlings) which were the same as those studied earlier by Fischer (1970, 1972), with weight range from 40 to 120 g, derived from fish ponds. Before the 6-month experiment started, the fish had been acclimated for 2–3 months to experimental conditions at the same temperature and at the same food conditions as used during the experiments. The experiments, similarly as previous ones, have been run at temperature of 22°C and with food excess.

Samples were taken of food, faeces and body of fish for analyses of chemical composition of basic organic components. The proteins were defined by Kjeldahl method, carbohydrates — by anthrone method (Trevelyan, Harrison 1952), lipids by Stern, Shapiro (1953) method. The content of cellulose was not measured. When analysing plant food and faeces of fish kept on plant food cellulose was defined as the "remaining part" i.e., by knowing the weight incidence of lipids, proteins, hydrolytic carbohydrates and inorganic matter the remaining part was considered as cellulose. Measurements of consumption rate, faeces production, biomass growth, and ammonium nitrogen excretion were done according to methods described in details by Fischer (1970, 1971).

Consumption rate was measured by weighing method from the difference

between food supplied and remaining. The body growth was measured by weighing the fish every two weeks. The faeces production was measured by centrifugation of water in which the fish and its food have been present for 24 hrs.

Knowing the amount of lipids and carbohydrates supplied to the fish in the form of food consumed as well as the amounts bound in the fish body as body growth and those excreted in faeces, a trial was made to balance the organic compounds. The balance of proteins was estimated from the balance of nitrogen (by accepting 1 mg N corresponding to 6.25 mg proteins). The amount of burned lipids, carbohydrates, and proteins in the process of metabolism was estimated by the method of indirect calorimetry. The calculations were given in part II (Fischer 1972).

3. RESULTS

The utilization of food components for body growth, metabolism, and their excretion by fish is as follows.

The protein content of fish body, as calculated from dry weight of fish fed with animal food, amounts to 56.5%, in fish fed with plants — 63.5%. The protein content in animal food is 51.6%, in plant food — 15.3%, and that in faeces produced from animal food is 48.9%, and from plant food 8.3%.

From the data concerned with excreted urea nitrogen (Fischer 1970, 1972) it is also possible to compare the amount of proteins supplied to the organism and used for the body growth, metabolism, and excretion. These results are presented in Tables I and II. The tables comprise individual data of each fish; values of consumption (C), growth (P), respiration (R), and excreted matter (F) are averages of about 10 measurements taken for each individual.

The content of lipids was investigated in the food, faeces and in the fish body. These values for a fish fed with plant food amounted in the fish body to 5% on the average, to 16.7% when the fish were fed with animal food. There was 20% of lipids in animal food, 5.8% in plant food, 15.3% in faeces when the fish were fed with animal food and 17% when they were fed with plant food. Basing on these data it is possible to compare the amount of lipids which enter the organism as food, with the amount which has been used for growth and metabolism (indirect calorimetry — Fischer 1970, 1972), and that which has been excreted. These balances for individual fish are presented in Tables III and IV. They illustrate differences between the amounts of consumed lipids in the food eaten and the amount obtained by summing up the data of growth, metabolism and excretion. This difference in per cent is higher with plant food (25.3% on the average) but in weight units it amounts only to 1.7 mg (Table V). When animal food is supplied the amount of lipids entering the organism is on the average lower by 44.7 mg than the amount obtained by summation of growth, respiration and excretion, but it forms only 16% (Table VI).

Hydrolytic carbohydrates were investigated in fish body, in faeces and

Table I. Protein budgets in fish fed with animal food ($C = P+R+F$)

Mean body weight (g)	Unit	C	P	R	F	Difference between C_{exp} and $C_{calc.}$ (%)
86.0	mg	406	74	57	158	
(81-91)	%	100	18	14	39	29
87.5	mg	356	54	19	199	
(86-90)	%	100	15	5	56	24
88.0	mg	839	61	62	598	
(75-98)	%	100	7	7	71	15
92.0	mg	272	101	69	119	
(89-95)	%	100	37	25	43	5
95.5	mg	1361	143	49	687	
(77-114)	%	100	13	5	65	17
103.0	mg	852	78	45	571	
(100-105)	%	100	9	5	67	19
107.0	mg	1225	103	52	804	
(96-114)	%	100	8	4	66	22
107.5	mg	494	79	66	262	
(102-119)	%	100	16	13	53	18

Table II. Protein budgets in fish fed with plant food ($C = P+R+F$)

Mean body weight (g)	Unit	C	P	R	F	Difference between C_{exp} and $C_{calc.}$ (%)
19.6	mg	134	4	95	74	
(19-20)	%	100	3	71	55	29
28.5	mg	135	8	62	80	
(24-30)	%	100	6	45	59	10
29.5	mg	117	5	36	55	
(29-30)	%	100	4	31	47	18
30.4	mg	167	7	56	58	
(28-32)	%	100	4	33	35	28
31.0	mg	199	15	81	50	
(30-32)	%	100	8	41	25	26
34.5	mg	168	10	54	44	
(31-36)	%	100	6	32	26	36
35.1	mg	173	15	64	106	
(34-36)	%	100	9	37	62	8
35.4	mg	149	15	54	73	
(32-40)	%	100	10	36	48	6
39.7	mg	231	20	61	115	
(38-41)	%	100	8	27	50	15
49.1	mg	194	22	60	88	
(48-51)	%	100	11	30	45	14
49.5	mg	125	5	46	79	
(49-50)	%	100	4	37	63	4
55.0	mg	175	5	51	105	
(54-56)	%	100	3	29	60	8

Table III. Lipid budgets in fish fed with plant food ($C = P+R+F$)

Mean body weight (g)	Unit	C	P	R	F	Difference between C_{exp} and $C_{calc.}$ (%)
19.6	mg	5.1	0.65	0.79	4.69	20
	%	100	13	15	92	
28.5	mg	5.1	1.08	1.29	2.65	2
	%	100	21	25	52	
29.5	mg	6.2	0.67	1.80	8.24	73
	%	100	11	29	133	
30.4	mg	6.3	0.96	0.90	4.41	—
	%	100	15	14	71	
31.0	mg	7.6	2.94	0.05	3.01	20
	%	100	39	1	40	
34.5	mg	6.4	1.42	1.20	2.37	22
	%	100	22	19	37	
35.1	mg	6.6	2.17	1.20	7.64	67
	%	100	33	18	116	
35.4	mg	5.7	2.12	1.20	4.00	28
	%	100	37	21	70	
39.7	mg	8.8	1.20	3.19	2.94	13
	%	100	14	36	33	
49.1	mg	7.4	3.05	1.49	7.27	59
	%	100	41	20	98	
49.5	mg	6.6	0.53	1.40	5.78	16
	%	100	8	21	88	
55.0	mg	9.2	0.45	1.45	8.41	13
	%	100	5	16	92	

Table IV. Lipid budgets in fish fed with animal food ($C = P+R+F$)

Mean body weight (g)	Unit	C	P	R	F	Difference between C_{exp} and $C_{calc.}$ (%)
86.0	mg	157.9	40.6	62.4	69.5	9
	%	100	26	39	44	
87.5	mg	138.3	19.5	67.2	54.2	2
	%	100	14	49	39	
88.0	mg	326.2	32.5	67.2	337.7	34
	%	100	10	21	103	
92.0	mg	106.1	32.6	67.2	32.5	25
	%	100	31	63	31	
95.5	mg	529.3	42.1	72.0	411.2	—
	%	100	8	14	78	
103.0	mg	331.4	25.2	74.4	274.6	13
	%	100	8	22	83	
107.0	mg	457.7	29.5	81.6	183.7	36
	%	100	6	18	40	
107.5	mg	192.1	19.9	81.6	130.4	21
	%	100	10	43	68	

Table V. The share of proteins, carbohydrates and lipids in matter budget in fish fed with Tubificidae

Parameter		Proteins	Lipids	Carbohydrates
Fish (%)		56.5	16.7	2.6
Food (%)		51.6	20.0	3.8
Faeces (%)		48.9	15.3	9.8
U^{-1}		26.1 ± 5.5	44.3 ± 7.1	92.3 ± 1.3
K_1		15.2 ± 3.4	13.9 ± 3.2	0.32 ± 0.002
K_2		60.1 ± 2.4	30.1 ± 2.7	0.32 ± 0.003
Difference between C_{exp} and $C_{calc.}$	%	16.0 ± 3.1	16.0 ± 4.3	148.8 ± 4.8
	mg	115.7	44.7	80.4

Table VI. The share of proteins, carbohydrates and lipids in matter budget in fish with *Lactuca sativa*

Parameter		Proteins	Lipids	Carbohydrates glucose	cellulose
Fish (%)		63.5	5.0	3.1	—
Food (%)		15.3	5.8	6.3	53.4
Faeces (%)		8.3	17.0	3.3	48.4
U^{-1}		41.0 ± 2.4	36.6 ± 4.4	75.4 ± 2.1	
K_1		6.5 ± 1.5	23.8 ± 3.8	0.003 ± 0.0006	
K_2		15.9 ± 2.0	39.2 ± 9.2	0.003 ± 0.0004	
Difference between C_{exp} and $C_{calc.}$	%	16.5 ± 3.4	25.3 ± 5.7	63.3 ± 1.3	
	mg	26.9	1.7	41.5	

in food. Experiments with animal food (Table VI) showed that there is 2.6% of hydrolytic carbohydrates in body tissues, and with plant food (Table VI) — 3.1%. In the animal food there was 3.8% of carbohydrates and 6.3% in plant food, faeces from animal food comprised 9.8% and from plant food — 3.3% of carbohydrates. According to the method previously described, the value of 53.4% was accepted as percentages incidence of cellulose in dry plant matter. Similarly in faeces produced of plant food there was 48.4% of cellulose in dry matter of faeces. The balances of hydrolytic carbohydrates as well as the remaining carbohydrates for each fish are presented in Table VII and VIII. In both cases i.e., with plant and animal food there is no balance of hydrolytic carbohydrates, i.e. the amount of carbohydrates supplied to an organism do not cover the animal's requirement (respiration). The cellulose balance showed small difference between the amount of supplied cellulose and that excreted in faeces.

When analysing the incidence of proteins, lipids and carbohydrates used by fish, it was intended to explain which organic compounds are mainly being used for growth of fish. That is why the energy transfor-

Table VII. Carbohydrate budgets in fish fed with plant food ($C = P+R+F$)

Mean body weight (g)	Unit	Hydrolysing carbohydrates				Difference between C_{exp} and $C_{calc.}$ (%)	Cellulose		Difference between C_{exp} and $C_{calc.}$ (%)
		C	*P*	*R*	*F*		*C* (mg)	*F* (mg)	
19.6	mg	55.3	0.08	60.0	29.9	62	513	193	62
	%	100	0	108	54				
28.5	mg	55.9	0.08	67.2	33.9	81	518	546	5
	%	100	0	120	61				
29.5	mg	40.0	0.33	72.0	22.3	137	455	414	10
	%	100	1	180	56				
30.4	mg	69.4	0.11	72.0	25.8	41	637	554	13
	%	100	0	104	37				
31.0	mg	82.2	0.09	72.0	24.8	18	762	708	8
	%	100	0	88	30				
34.5	mg	69.2	0.17	76.8	19.1	39	641	544	15
	%	100	0	111	28				
35.1	mg	71.3	0.27	76.8	37.8	60	661	622	6
	%	100	0	107	53				
35.4	mg	61.7	0.26	72.0	11.4	36	572	429	25
	%	100	0	117	19				
39.7	mg	99.2	0.19	84.0	21.7	7	887	504	43
	%	100	0	85	22				
49.1	mg	80.1	0.37	96.0	27.2	54	743	615	17
	%	100	0	120	34				
49.5	mg	42.6	0.35	96.0	16.1	165	485	465	4
	%	100	1	226	38				
55.0	mg	59.6	0.36	64.8	30.7	62	674	653	3
	%	100	1	109	52				

Table VIII. Carbohydrate budgets in fish fed with animal food ($C = P+R+F$)

Mean body weight (g)	Unit	*C*	*P*	*R*	*F*	Difference between C_{exp} and $C_{calc.}$ (%)
86.0	mg	30.4	0.34	98.4	3.4	236
	%	100	1	324	11	
87.5	mg	26.6	0.25	98.4	3.7	285
	%	100	1	370	14	
88.0	mg	62.8	0.28	100.8	30.2	108
	%	100	0	160	48	
92.0	mg	20.4	0.32	100.8	1.8	405
	%	100	2	494	9	
95.5	mg	101.9	0.53	105.6	14.7	19
	%	100	1	104	14	
103.0	mg	63.8	0.35	110.4	12.3	93
	%	100	1	173	19	
107.0	mg	91.7	0.34	120.0	13.9	46
	%	100	0	131	15	
107.5	mg	36.9	0.36	117.6	5.6	232
	%	100	1	316	15	

mation indices were calculated as percentage of consumption: K_1 — the ratio of growth to consumption $\frac{P}{C}$, K_2 — the ratio of growth to assimilated food $\frac{P}{A}$, and assimilation efficiency $U^{-1} = \frac{A}{C}$ for the discussed proteins, lipids, and carbohydrates. The compilations of the incidence of these organic substances in energy transformation in grass carp fed with plant and animal food are presented in Tables V and VI. It is clear that with plant food the lipids are more utilized for growth although their assimilability is not especially high, but the best assimilated are hydrolytic carbohydrates, which do not affect practically the growth of fish. With animal food proteins are best utilized for growth, although their assimilability is smallest. Carbohydrates, in spite of the highest assimilability, are almost not used for growth of fish.

4. DISCUSSION

Balances of nitrogen, carbohydrates, and lipids aimed at orientative analysis of the role of this substances in the fish body. That is why one should not pay much attention to absolute values obtained in this paper, but the results should be considered as enabling a comparison of main pathways of utilization of this substances by fish fed with the two types of food.

The results obtained in this work concerning the nitrogen balance for the fish fed with animal and plant food deviate considerably from the literature data. Ivlev (1939) has reported on the nitrogen balance for carp, the fish that best compares with grass carp. His balance was calculated basing on ascertion of nitrogen in faeces, liquid excretions, and in the fish body. On the contrary to the present experiments, Ivlev's investigations were carried out under natural conditions. When comparing Ivlev's results obtained for carp 79 g in weight with the present data obtained for fish with weights close to 79 g (Table I and II) the following picture is obtained (Table IX).

The differences are clearly visible. The results differ mainly in different values of assimilation. From the paper by Ivlev (1939) as well as from that by Karzinkin (1952) dealing with pike, perch, and other fish and carried out in identical way as the former work it results that proteins are ingested in 90% of the average. The reason of such incongruency of their and the present results can be explained by a further experimentation; at present it is only possible to put forward several hypotheses.

One of them can be the difference in the amount of food supplied. In the present experiments the fish were fed in excess. It is known that the

Table IX. Comparison of nitrogen balance obtained by Ivlev (1939) for carp with that of the present paper for grass carp

Parameter	Unit	Ivlev (1939) carp	Present paper grass carp	
			animal food	plant food
Consumption	mg N/24 hr/ind.	147.4	406	175
Faeces	mg N/24 hr/ind.	17.7	158	105
Growth	mg N/24 hr/ind.	65.0	74	5
Liquid excretion	mg N/24 hr/ind.	64.7	57	51
U^{-1}	%	88.0	32.3	32.0
K_1	%	44.1	18.3	2.9
K_2	%	50.1	57.0	9.1

superfluous food diminishes assimilation (Klekowski, Shushkina 1966, Monakov, Sorokin 1961, Richman 1958). It does not explain, however, such a large diminishing of protein assimilability. Ivlev reports that in carp studied under natural conditions it amounts on the average to 89%; in present experiments with animal food it amounted only to 26% (Table VI). Comparing the elements of nitrogen balance for carp and grass carp (Table IX) the difference can be found only between this component excreted in faeces, and consequently in consumption rate calculated by Ivlev as a sum of growth, faeces and liquid excretion. In grass carp studied in present work and fed with animal food the consumption exceeded over 3 times that in carp, and excretion is ten times higher.

The second hypothesis is based on assumption that poor ingestion of proteins is a specific feature of grass carp. It appears, however, that the fish fed with food in excess have such an abundance of proteins that at normal growth and respiration rates even small assimilability of proteins is sufficient to cover the energy requirements (Table VI). The balance for grass carp fed with plant food differs also from that obtained by Ivlev for carp. Excretion in grass carp fed with lettuce is five times higher than the Ivlev's data calculated for carp. However this excretion is lower than in grass carp fed exclusively with animal food. The assimilability of proteins by grass carp fed with plant food is the same as that in grass carp fed with animal food when one compares individual results (Table IX), however it is somewhat higher when one compares the averages (Table V, U^{-1} equals 41%). On the other hand, the utilization of proteins is at its minimum (Table V and VI — K_1 for proteins amounts only to 6.5% and K_2 to 15.9%). Incongruent amount of proteins supplied with food and that ascertained in growth, respiration and excretion is in both cases close to 16% and it results probably from the errors in measuring the energy budget parameters. It can possibly result from the methodological error or from the measurement in Kjeldahl apparatus (for example incomplete burning of proteins found in faeces).

By and large, one can suppose that the plant proteins taken by fish can be used for respiration process but to a lesser extent used for growth (Table V). For the normal growth the animal proteins are necessary. From this work it appears that at the shortage of animal proteins and low values of plant proteins, both the amount and assimilability of proteins are increasing. However it is not sufficient for normal development of fish. These results are incongruent with the Penzes, Tölg (1966) thesis that the presence of animal proteins is not necessary for the growth of grass carp.

When considering the role of protein metabolism in total metabolism one should draw attention to the fact that these results are in accordance with data given by Ivlev (1939) and Karzinkin (1952), however, they are far apart from results obtained by Chalupova and Blažka (1960). In grass carp fed in the present experiment exclusively with plants this incidence amounts only to 29%, and with animal food — to 17%. Chalupova and Blažka reported that the resting protein metabolism in carp amounts to 65% of total metabolism and with increasing activity of fish, the protein transformation also increases, but it covers a lower percentage of total metabolism. Our results do not support this thesis.

Carbohydrate balances obtained in present work for fish fed with both types of food are presented in Tables VII and VIII. When analysing the incidence of carbohydrates in growth, metabolism and excretion by fish fed with animal food it is characteristic that metabolism takes unproportionally large amount of carbohydrates as compared to the process of growth and excretion. The amount of combusted carbohydrates in the process of metabolism exceeds the amount of carbohydrates taken in food. At the same time excretion is very small. This causes that the incongruency between the amount of carbohydrates supplied to the organism and that used for growth, metabolism and excretion is very large and amounts to 148.8% on the average (Table VI). The reason for such small amount of carbohydrates supplied to the organism is their minimal incidence in the food. The data on contents of carbohydrates in fish body and in Tubificidae body, as given in Table VI support the literature data (Stroganov 1962, Blažka 1966). It appears that in the fish fed exclusively with animal food glikoneogenesis must occur.

Attention should be drawn to a high assimilability of carbohydrates by fish fed exclusively with animal food. This assimilability amounts to $U_c^{-1}=92.3\%$ (Table VI). This value exceeds other values of assimilability of carbohydrates given by Blaxter (1963) for mammals. It may be supposed that the shortage of carbohydrates in the animal food causes an economic utilization of these compounds. Somewhat different is the incidence of carbohydrates in growth, metabolism, and excretion in the fish fed exclusively with plants which comprise large amounts of carbo-

hydrates. In this case the assimilability decreases and amounts to 75.4% (Table V), approaching the values given by Blaxter.

The incidence of carbohydrates in growth of the fish fed with plants is small. Similar to the fish fed with animal food the largest part of carbohydrates is being used for metabolism. The difference between the amount of carbohydrates supplied to the fish in consumed food and that used for growth, metabolism and excretion is in the fish fed with plants smaller and it equals to 63.3% ($C_{exp} < C_{P+R+F}$) (Table V).

However excretion of carbohydrates is relatively high and many times larger than in the fish fed with animal food. In the balance of carbohydrates for fish fed with plants one should also consider the group of carbohydrates of cellulose fraction. The difference between the amount of cellulose taken and excreted by the organism is small and amounts to 17.7% (data calculated from Table VII — last column). By this per cent the amount of cellulose given is higher than that excreted. When considering previous fraction of non-cellulose carbohydrates, the amount of carbohydrates was smaller in consumed food than in growth, metabolism and excretion. The preliminary results on calculating the cellulose--decomposing bacteria from the content of the grass carp intestine did not give any evidence of their presence. However, it is possible that in these fish a small amount of supplied cellulose is being decomposed to simpler carbohydrates, which can be used for metabolism in further processes of decompositions.

Such hypothesis could explain the difference between the amount of hydrolytic carbohydrates supplied to the organism and their amounts used for growth, metabolism and excretion. ($C_{exp} < C_{P+R+F}$, Table V). To counterbalance this difference 111 mg cellulose (calculated as dry matter/mg) would be sufficient for an individual per 24 hrs, which would diminish the incongruency of cellulose balance from 17 to 9%.

The lipid contents in the fish fed exclusively with animal food is large and congruent with data by Okoniewska, Okoniewski (1969). They have studied the fish collected from the same fish ponds, and they analysed the fish muscles. The present work was done on the whole tissues of the fish. From the comparison of their data with present experiments it results that the fish fed with animal food have a higher lipid content than the fish cultured under natural conditions. However, the content of lipids in the body of fish fed with plants exclusively is 3 times lower than that in the fish cultured under natural conditions.

The lipid balances obtained for both groups of fish in present experiments in spite of percentageous accordance (Table V and VI), differ considerably in quantities (Table III and IV). Assimilability of lipids in fish of the both groups is similar (36.6 and 44.3%), however, excretion of lipids by the fish fed exclusively with plant food ranges from 2 to 8 mg per 24 hrs per individual. When exclusively animal food is supplied

this value ranges from 32 mg to 411 mg. Similar difference was found between the amount of lipids supplied to the organism and that used for growth metabolism, and excretion. This value is 16% ($C_{exp} > C_{P+R+F}$) in the fish fed exclusively with animal food, which amounts to 14.7 mg per fish per 24 hrs, and when fish were fed exclusively with plant food — 25.3%, which amounts only to 1.7 mg. Lipids are being used to a greater extent for growth in fish fed exclusively with plant food. It is reasonable because of a lesser usefulness of plant proteins in the growth of fish. Usage of lipids for growth of the fish fed exclusively with animal food is somewhat lower in term of per cent (plant food: $K_1=13.9\%$, $K_2=30.1\%$, animal food: $K_1=23.8\%$, $K_2=39.2\%$) but in terms of weight it is much higher (Table V and VI). In both groups assimilability of lipids is similar to the values given by Blaxter (1963) for all the animals where they amount 45 to 55%. The difference between the amounts of lipids supplied to the organism and that used for growth metabolism and excretion can result from excretion of epithelium and bile by an organism.

If this difference depended on excretion of bile, it would be understandable that larger amounts were excreted when larger amounts of lipids were digested i.e. in the fish fed with animal food, when this difference amounted to 44.7 mg on the average, than in the fish digesting plant food with a small incidence of lipids (where this difference was about 2 mg).

It seems that when taking into account the present results as well as the results of other authors, one can state that incidence of proteins, carbohydrates and lipids in growth, metabolism, and excretion by grass carp, differs in the fish fed with plants. When exclusively animal food is supplied, the growth of fish is mostly covered by proteins ($K_{2P}=60.1\%$) and to a greater extent by lipids ($K_{2P}=30.1\%$). Carbohydrates are to certain degree produced by means of glikogenesis and used almost completely for metabolism. In the fish fed exclusively with plants the growth is almost exclusively covered by lipids. Because of a small content of lipids in plant food it is obvious that growth is very small. Proteins are being used in its prepondering part for metabolism, and also for excretion. Carbohydrates are used for metabolism in the similar degree.

By analysing the same data from the aspect of particular components in metabolism (Fischer 1972) one can state that the metabolism in the fish fed with plants is covered mainly by combusting carbohydrates in 58.3%, proteins in 29.1%, and lipids only in 12.62%. As it has beer said, small amounts of lipids which are in the disposal of the fish fed with plants are being used mainly for growth.

In cultures of fish fed with animal food, the fish have in their disposal such large amounts of lipids that they cover not only the greater part

of growth but also metabolism (52.82%). The proteins are being combusted in the metabolic processes to a smaller degree — only in 17.7%.

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5. SUMMARY

The investigations aimed at tracing the pathways of main organic compounds: proteins, carbohydrates, and lipids taken by grass carp in food, the degree of their usage and excretions. Two different types of food were supplied: animal food (Tubificidae) and plant food (*Lactuca sativa*). The food was always supplied in excess. The fish examined were 40 to 120 g in weight, fingerlings taken from fish ponds. Samples of the above mentioned components were carried out.

It was found that grass carp fed exclusively with plant food uses for growth only small percentage of proteins (K_{1P}=6.5%, K_{2P}=15.92%). For growth lipids are mostly used (K_{1L}=23.8%, K_{2L}=39.2%).

On the other hand, grass carp fed with animal food uses for growth mainly proteins (K_{1P}=15.2%, K_{2P}=60.1%).

6. STRESZCZENIE

Badania miały na celu prześledzenie losów podstawowych związków organicznych — białek, węglowodanów i tłuszczy, pobieranych przez amura w pożywieniu, stopnia ich zużycia i ich wydalania. Doświadczenia były prowadzone na dwóch różnych typach pokarmu: mięsnym (Tubificidae) i roślinnym (*Lactuca sativa*). Pokarm podawano zawsze w nadmiarze. Doświadczeniom poddawano ryby o wadze od 40 do 120 g — palczaki, pochodzące ze stawów rybnych. Wykonane zostały próby bilansów wymienionych składników organicznych.

Stwierdzono, że: amur żywiony wyłącznie pokarmem roślinnym wykorzystuje na wzrost pobrane białka jedynie w słabym procencie (K_{1P}=6.5%, K_{2P}=15.9%). Na wzrost wykorzystywane są w głównej mierze lipidy (K_{1L}=23.8%, K_{2L}=39.2%). Natomiast amur żywiony pokarmem zwierzęcym wykorzystuje na wzrost w głównej mierze białka (K_{1P}=15.2%, K_{2P}=60.1%).

7. REFERENCES

Blažka, P. 1966. The ratio of amide proteins, glycogen, and fat in the individual steps at the production chain. *Hydrobiol. Stud.*, 1, 395-404.

Blaxter, J. H. S. 1963. The feeding of herring larvae and their ecology in relation to feeding. California Cooperative Oceanic Fisheries Investigations, Reports 10 July 1962-June 1962, 73-88.

Chalupowa, Z., Blažka, P. 1960. Metabolismus bilkovin u ryb. *Babak's Collection*, 16, 139-142.

Fischer, Z. 1970. The elements of energy balance in grass carp (*Ctenopharyngodon idella* Val.). Part I. *Pol. Arch. Hydrobiol.*, 17, 421-434.

Fischer, Z. 1872. The elements of energy balance in grass carp (*Ctenopharyngodon idella* Val.). Part II. Fish fed with animal food. *Pol. Arch. Hydrobiol.*, 19, 65-82.

[Ivlev, V. S.] Ивлев, В. С. 1939. Энергетический баланс карпов. [Energy balance of carp]. *Zool. Ż., Mosk.*, 18, 303-318.

[Karzinkin, G. S.] Карзинкин, Г. С. 1952. Основы биологической продуктивности водоемов [Principles of biological productivity of water bodies]. Moskva, Piscepromizdat.

Klekowski, R. Z., Shushkina, E. A. 1966. Ernährung, Atmung, Wachstum und Energie-Umformung in *Macrocyclops albidus* Jurine. *Verh. int. Ver. Limnol.*, 16, 399-418.

[Monakov, A. V., Sorokin, Ju. I.] Монаков, А. В., Сорокин, Ю. И. 1961. Количественные данные о питании дафний [Quantitative data on the feeding of Daphnids]. *Trudy Inst. biol. Vodohran.*, 4, 251-261.

Okoniewska, Z., Okoniewski, Z. 1969. Wyniki wstępnych badań ciężaru części użytkowych i składu chemicznego ciała ryb roślinożernych i karpia [Preliminary results of investigations on the weight commercially useful body parts and chemical composition of plant-feeding fish and carp]. *Roczn. Nauk roln., Ser. H*, 91, 385-401 [Engl. summ.].

Penzes, B., Tölg, I. 1966. Aquaristische Untersuchung des Pflanzenverbrauches des Graskarpfen (*Ctenopharyngodon idella* Cuv. et Val.). *Z. Fischerei, N. F.*, 14, 131-137.

Richman, S. 1958. The transformation of energy by *Daphnia pulex*. *Ecol. Monogr.*, 28, 273-291.

Stern, I., Shapiro, B. 1953. Rapid and simple method for the determination of esterified fatty acids and for total fatty acids in blood. *J. clin. Pathol.*, 6, 158-160.

[Stroganov, N. S.] Строганов, Н. С. 1962. Экологическая физиология рыб [Ecological physiology of fish]. Vol. I. Moskva, Izdat. Moskovskogo Univ.

Trevelyan, W. E., Harrison, J. S. 1952. Studies on yeast metabolism I.-Fractionation and microdetermination of cell carbohydrates. *Biochem. J.*, 50, 298-303.

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T. PRUS

ENERGY REQUIREMENT, EXPENDITURE, AND TRANSFORMATION EFFICIENCY DURING DEVELOPMENT OF *ASELLUS AQUATICUS* L. (CRUSTACEA, ISOPODA)

Department of Bioenergetics and Bioproductivity, Nencki Institute of Experimental Biology, Pasteura 3, Warszawa 22, Poland

ABSTRACT

A complete energy budget, based on measurements of production, respiration and on assumed assimilation efficiency which has been ascertained in previous work (Prus 1971) is given for a considerable part of developmental cycle. Daily and cumulative budgets were calculated. The cumulative amount of energy of each budget parameter as well as production efficiencies were presented as functions of body weight. Using body weight-length dependence these equations were transformed to the functions of body length.

1. INTRODUCTION

A freshwater isopod, *Asellus aquaticus*, feeds mainly on dead organic matter of innate or allochthonous origin. Thus it brings about retention of some amount of energy from the decaying material and transfers it to a higher trophic level. The energy accumulated in its body is being used either by predacious invertebrates, or by the highest trophic level which in an aquatic reservoir is represented by fish. On the other hand, by mechanical breaking of dead plant debris the species accelerates desintegration of this material, making non-assimilated energy more available to bacteria. This process accelerates the rotation of energy in the water body preventing it from rapid eutrophization. In spite of a high dispersion of energy when it passes from one trophic level to another, and irrespective to the efficiency of energy transformation, *Asellus aquaticus* recuperates its considerable part since it shortens the food chain.

In general, the learning about energy requirement and its expenditure and also about efficiencies of energy transformation in *A. aquaticus* seems to be most interesting on account of the recuperative role of this species in the energy flow through an aquatic reservoir.

The energy budget was based on the following equations proposed by Ivlev (1938):

$$C=P+R+F, \quad A=P+R$$

where C — the energy consumed as food (consumption), P — the energy which has been incorporated in animal body (production), R — the energy used for respiratory processes (respiration), F — the unassimilated energy (rejecta), and A — the energy assimilated by the organism (assimilation).

The efficiency of an organism as the energy converter is well described by the index of net production efficiency: $K_2=\frac{P}{A}$, and gross production efficiency: $K_1=\frac{P}{C}$, as well as by the index of assimilation efficiency: $U^{-1}=\frac{A}{C}$.

Elaboration of a full energy budget of *A. aquaticus* at the individual level was the aim of this paper. The budget parameters were either measured or calculated for a considerable part of the developmental cycle. Proportions between these parameters were also considered in order to characterize the efficiencies of the species in energy conversion. Further aim of this paper was the calculation of cumulative energy budget sensu Klekowski et al. (1967), Klekowski (1970), basing on daily energy budgets for the investigated period of development. Such cumulative form of the budget permits to define a total amount of energy which went through an individual, or was retained in its body from the moment of leaving by it the brood pouch of a female to the moment when it has reached a given weight or a given body length. The cumulative budget parameters were expressed by equations which were functions of weight or body length; they will allow to estimate the cumulative amount of energy that was available to any individual during its life.

2. MATERIAL AND METHODS

The material used for the experiment was collected from a small pond situated in the Kampinos Forest, near Warsaw. A continuous experiment was set up, i.e., the measurements were carried on with the same individuals for about 4 months (from 16 Oct. 1967 to 15 Feb. 1968). Ten animals of a similar size with an average wet weight of 1.58 mg were placed each in a container holding 50 ml of tap water, which had been conditioned in the room for several days. To each animal a decaying leaf of alder tree, *Alnus glutinosa* Gertn. (about 300 mg wet weight) was given as food. The leaves were taken from a storage that had been gathered from the bottom of the pond while collecting the animals for the experiment, thus they were natural food for this species. They were stored in the tap water at the ambient temperature, so they were at the process of decomposition. The food has been changed every 7 days, the water — every 3 or 4 days, by transferring the individual to another container. The cultures were run at ambient temperature of about 21–23°C.

Twice a week, every 3 or 4 days alternately, each individual was weighed in order to assess its wet body weight. Daily production was calculated from the increases in body weight between two subsequent weighings. The results obtained in wet weight per individual per 24 hrs were later expressed as dry weight and finally as calories, by taking into account the wet weight/dry weight ratio and the calorific value of dry matter of the body tissue.

The respiratory rate was measured once a week in volumetric respirometers (Klekowski 1968). The same animals which had been used for the production assessment were tested. Measurements were run individually for about 4 hrs at 23 ± 0.1°C. The obtained results were related to standard conditions of temperature and pressure (0°C and 760 mm Hg). Then the O_2 consumption values obtained as μl O_2/ind. · hr were expressed in calories. For this calculation *RQ* of 0.82 was assumed which corresponds to oxy-calorific coefficient of 4.825 cal/ml O_2 according to Harrow, Mazur (1966).

The respired energy was calculated in two ways: (1) from a general equation of wet weight — O_2 consumption regression, based on all the measurements that were carried out during this long-term experiment, and (2) from direct calculation when the average O_2 consumption rate per mg body weight of the animals used in a given measurement was multiplied by an average body weight of all the experimental individuals at this time. For the first type of calculation the general equation has been transformed in order to allow a direct calculation of respired energy in calories per ind. · 24 hrs. For the second type of calculation the intermediate values between two subsequent measurements were interpolated. Both ways of calculation were compared and the second way of calculation was accepted for the budget.

Consumption (*C*) and faeces production (*F*) were also measured every 3–4 days (Prus unpubl.); however, on account of inadequate method used for these measurements, as it was proved by other studies on assimilation efficiency in this species (Prus 1971) these results were considered erroneous and therefore not included in the present paper. Values *C* and *F* were calculated from value *A* ascertained in this work as the sum of *P* and *R*, using assimilation efficiency index, $U^{-1}=30.28\%$, defined in other work (Prus 1971).

The content of dry matter in wet matter as well as ash content in dry matter of animal body were ascertained. The calorific value of *A. aquaticus* was measured in non-adiabatic microbomb calorimeter of Phillipson type (Phillipson 1964, Prus 1968 a), using the material derived from the same stock as that used in setting up the cultures.

In order to describe the dependence between body wet weight and body length, 80 males and 80 females of various size were weighed and measured. Measurements were taken under binocular microscope using calibrated ocular. When measuring, the animals were placed in water and covered with microscope glass in order to straighten their bodies. The distance between base of antennae and the distal part of telson were accepted as length measure. The weights were ascertained by means of Sartorius balance, with accuracy of 0.0002 g.

All instantaneous budget parameters were expressed as calories per an average individual per 24 hrs. Further elaboration of the results involved moving averages of 3 subsequent measurements. These averages are presented in some figures. The equations of regression lines were calculated with the method of least squares.

3. RESULTS

The dry matter content in wet matter of animal body was defined in two series each containing 15 individuals. The average wet weight of animals was 9.23 mg and the dry matter content amounted to 21.25 ± 2.5 (S.E.) %.

The calorific values, based on 4 combustions amounted to 2.9575 ± 0.0644 (S.E.) kcal/g dry weight of animal body.

These both data were used for calculation of production in terms of calories.

CHANGES IN WET WEIGHT OF A GROWING INDIVIDUAL

The changes of wet weight against the developmental time are shown in Fig. 1. They pertain to the average weight range of an individual from 1.58 mg at the beginning of the experiment to 22.53 mg wet weight at the end of the experiment.

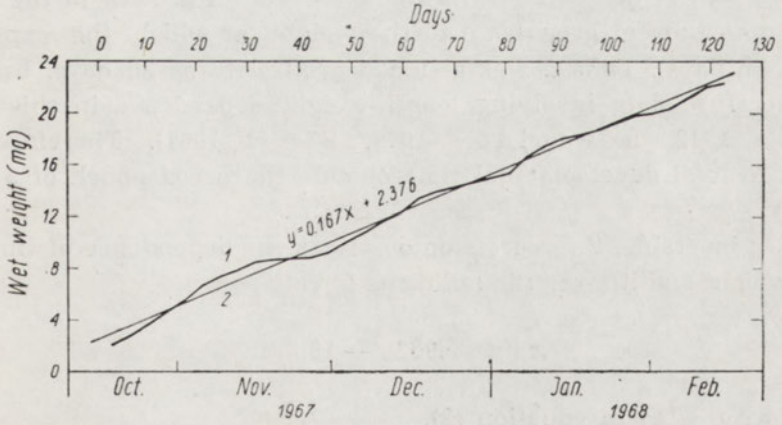

Fig. 1. Changes in wet body weight of an average individual against time. 1 — the moving average, 2 — the regression line

In spite of the fact that S-shaped curve is characteristic for growth of the vast majority of species (Bertalanffy 1957, Sushchenya 1968, Winberg 1968) the life span studied here showed colinear growth. The linear function is its best approximation. Thus, the dependence of wet body weight from developmental time was expressed by the equation:

$$y=0.167x+2.376 \quad (1)$$

where: y — wet body weight in mg, x — time of growth during the experiment in days. Value 2.376 denotes the initial weight (mg) at the beginning of the experiment. This is theoretic value resulting from equation (1); weight of 2.12 mg presented in Fig. 1 results from calculation of the moving average, and actually the experiment was started with animals weighing 1.58 mg on the average.

The straight line plotted on Fig. 1 and described by equation (1) converges to a greater degree with the real changes in body weight of an average individual. Somewhat larger deviation of the latter from theoretic line was caused by certain retardation of growth for about two weeks in animals of 8.5–9.0 mg in weight. This retardation was preceded by slightly more intense growth rate. These both facts resulted in a larger deviation of the experimental curve from the theoretic one.

When taking into account the initial period of growth from the moment of leaving by the animal the brood pouch to the initial weight in the experiment, the dependence of body weight from the time of development can be described by the following equation:

$$y=0.167\ (x+a) \quad (2)$$

where y — wet body weight in mg, x — time of growth in the experiment, a — time of growth up to the weight at which the experiment began (in days). Time a was assumed arbitrarily as 30 days, basing on the literature data involving length-weight dependence in this species (Allee 1912, Levanidov 1949, Steel 1961). Therefore $x+a$ equals to total developmental time outside the brood pouch of a female (in days).

After inversing, the regression describes the dependence of time from body weight and it takes the following form:

$$x+a=5.962y-13.901 \quad (3)$$

where x, a, y as in equation (2).

Equation (3) permits to calculate the developmental time (age) of an animal from its known body weight.

DAILY PARAMETERS OF THE BUDGET

Production. Changes in daily production (P) together with the remaining parameters, expressed in cal/ind. · 24 hrs, are presented in Fig. 2. During the initial span of growth, two periods of decreased production were observed: the first between 35th and 42nd day of the experiment, when the animals had an average wet weight of about 9.0 mg, and the second after 91st day to the end of the experiment with an average wet weight from 18.0 to 22.5 mg.

Respiration. Oxygen consumption was the second parameter measured directly in the experiment (Fig. 3). The equation for O_2 con-

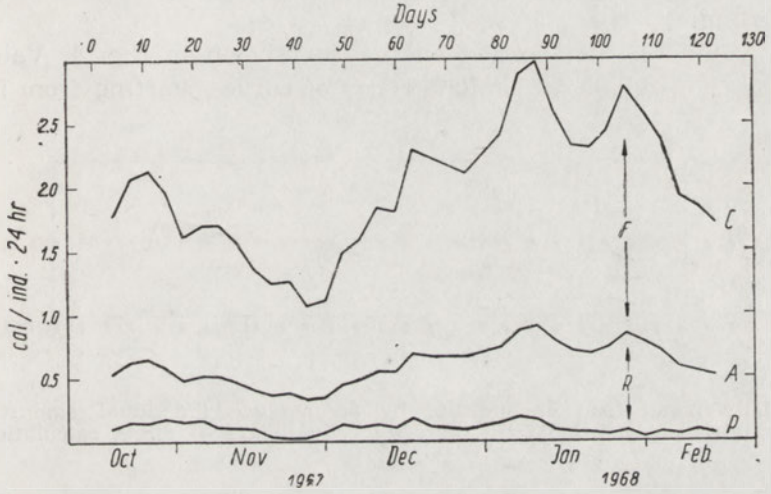

Fig. 2. Daily values of production (P), assimilation (A), and consumption (C) against time. Respiration (R) and faeces (F) are the distances between the lines

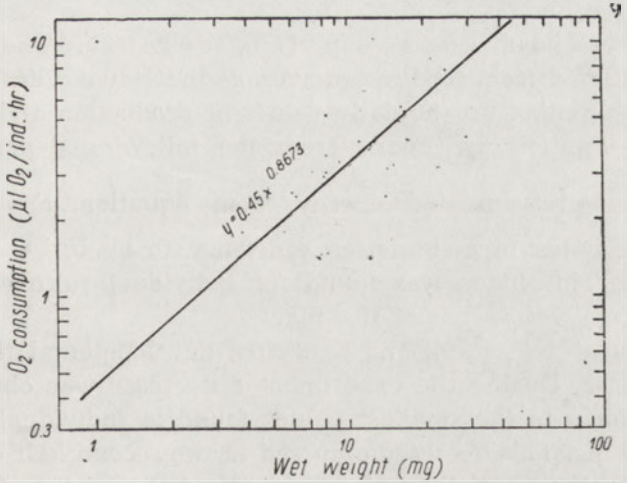

Fig. 3. Oxygen consumption against wet body weight

sumption-wet weight dependence, based on 60 measurements, was found graphically:

$$y = 0.45x^{0.867}, \text{ or } \lg y = 0.867 \lg x - 0.3448 \quad (4)$$

where: y — oxygen consumed by one individual per hr in µl, x — wet weight of animal in mg.

In order to obtain metabolized energy in cal/ind. · 24 hrs, equation (4) was transformed into:

$$y = 0.05211x^{0.867}, \text{ or } \lg y = 0.867 \lg x - 1.2831 \quad (5),$$

where y — metabolized energy in cal/ind. · 24 hrs, x — wet weight of animal in mg.

Daily values of metabolized energy are shown in Fig. 4. Values R defined by two ways have similar trends of curves, starting from indivi-

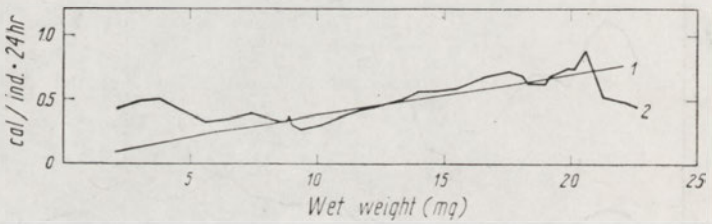

Fig. 4. Daily metabolism expenditure by an average individual against time. 1 — indirect calculation from regression equation, 2 — direct calculation

duals with average weight of 9.5 mg. The smaller individuals show higher values calculated directly from measurements than analogous values obtained from regression equation. The values calculated directly were included in the budget.

Assimilation, consumption, rejecta. The amount of energy assimilated from food by an average individual within 24 hrs was obtained by summing up the daily values of production and metabolized energy. Consumption was found from the following dependence: $C = \frac{1}{U^{-1}} \cdot A$ and non-assimilated energy from equation: $F = \frac{1}{1-U^{-1}} \cdot A$, assuming the index of assimilation efficiency to be $U^{-1} = 0.3028$ (after Prus 1971). This index was found for individual cultures of animals with an average wet weight of 10.8 mg.

Daily values of P, R, A, and C against developmental time are presented in Fig. 2. During the experiment a decrease was observed in all parameters down to the smallest values found in individuals of average weight of 9.0 mg. This decrease occurred in the second half of November and at the beginning of December and was followed by an increase in

all the values. It is possible that this decrease was related with a general diminished activity, which may reflect seasonal changes of environmental factors; this diminished activity could occur even in the animals kept in the laboratory.

Production efficiency indices. Daily net production efficiency index (K_2) and gross production efficiency index (K_1) are shown in Fig. 5. Due to changeable production and varying other budget

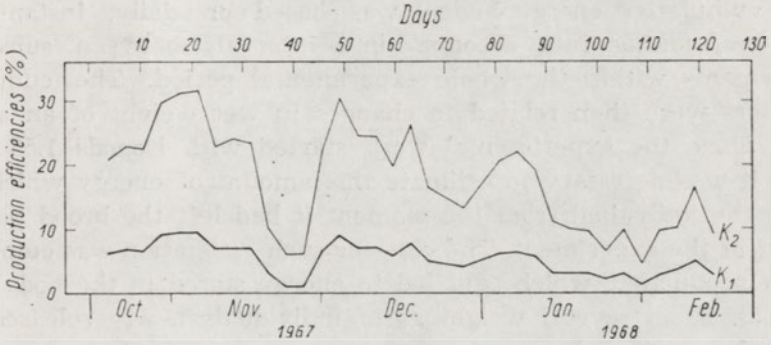

Fig. 5. Daily net (K_2) and gross (K_1) production efficiency indices against time

parameters the two indices show a considerable oscillation during the growth of animals. K_2, denoting what part of assimilated energy is stored in the organism as chemical energy, varies from 4.69 to 31.77%. K_1, denoting what part of ingested energy is assimilated, ranges from 1.42 to 9.62%. For an individual of average weight of 12.81 mg (the mean for the whole range of experimental weights) these indices are the following: $K_2 = 17.58\%$, $K_1 = 5.32\%$.

Daily energy budget. The energy budget of an individual of 12.81 mg in weight based on the average values of daily parameters for the whole experimental period expressed in calories is the following:

$$C = P + R + F$$
$$1.9801 = 0.1054 + 0.4942 + 1.3805$$
$$A = 0.5996$$

Out of about 2 cal consumed daily as food by the individual of 12.81 mg in weight, about 0.6 cal is assimilated, whereas the remaining amount of energy, about 1.4 cal is excreted. Only 0.1 cal of the assimilated energy is incorporated in body tissues and 0.5 cal is used for respiration. The percentageous presentation of the budget in relation to consumption (C) is as follows:

$$C = P + R + F$$
$$100 = 5.32 + 24.96 + 69.72$$
$$A = 30.28$$

Thus, 30.3% of energy consumed is assimilated, out of which 5.3% is incorporated in animal body and 25% is used for respiration. Out of energy assimilated 17.6% forms production and 82.4% — respiration.

CUMULATIVE BUDGET

Budget parameters against body weight. Calculation of cumulative energy budget was based on daily, instantaneous parameters, taking into account time intervals between subsequent measurements within the whole experimental period. The cumulative parameters were then related to changes in wet weight of an average animal. Since the experimental work started with isopods 1.58 mg in weight, it was necessary to estimate this amount of energy which went through the individual from the moment it had left the brood pouch to the start of the experiment. The clue for such estimation was cumulative value of production, which equalled to energy stored in the body of the individual. From several weighings of individuals newly released from the brood pouch, their average weight was ascertained. It equalled to 0.05 mg on the average. From the difference between initial weight in the experiment and the weight of individuals that had left the brood pouch of a female the cumulative production was calculated: $P_c = 1.53$ mg which corresponds to 0.9928 cal. Assuming K_2 equal to 0.261 (the average of 8 first measurements in the experiment), cumulative assimilation was calculated from the formula: $A = \frac{P_c}{K_2} = 3.8038$ cal, and assuming $U^{-1} = 0.3028$, cumulative consumption was obtained: $C_c = \frac{A_c}{U^{-1}} = 12.5621$ cal. The values of respiration $R_c = 2.8110$ cal and faeces production $F_c = 8.7583$ cal were calculated from formulae $R = A - P$ and $F = C - A$, respectively. Thus estimated values of budget parameters for the initial stage of development were then added to further parameters, so that cumulative parameters covered the whole development from the time the animals had left the brood pouches to a given moment of life or to a given body weight.

It is possible that the estimated values for the initial period of growth which was not covered by the experiment can involve a certain error since they are based on indices obtained for somewhat larger animals or even on those accepted for the whole development. Nevertheless, they are comparatively small, so that they should not affect essentially the total cumulative budget.

Cumulative parameters of energy budget against the individual weight are presented in Fig. 6, and the production efficiency indices (K_{1c} and K_{2c}) in Fig. 7.

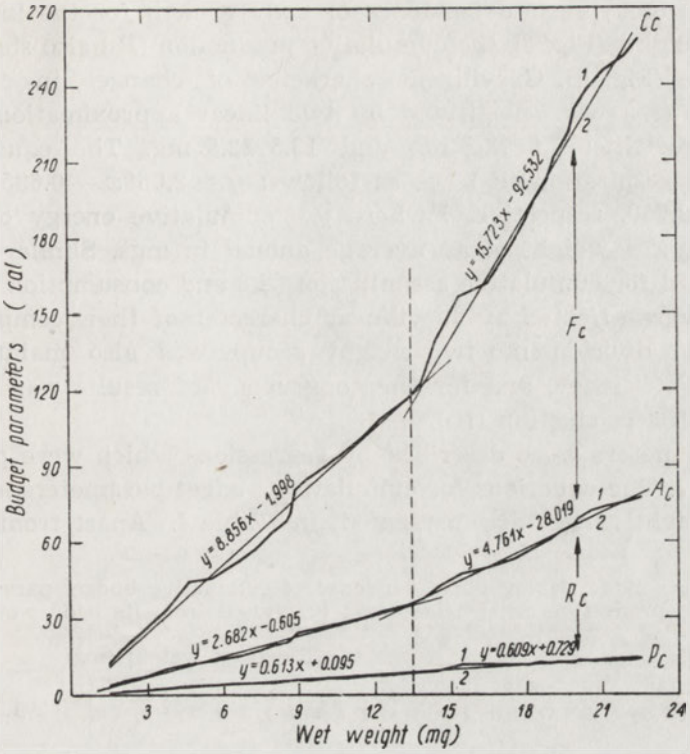

Fig. 6. Cumulative production (P_c), assimilation (A_c), and consumption (C_c) against body weight for two weight groups. Cumulative values R_c and F_c are the distances between the lines. 1 — the moving averages, 2 — the regression lines

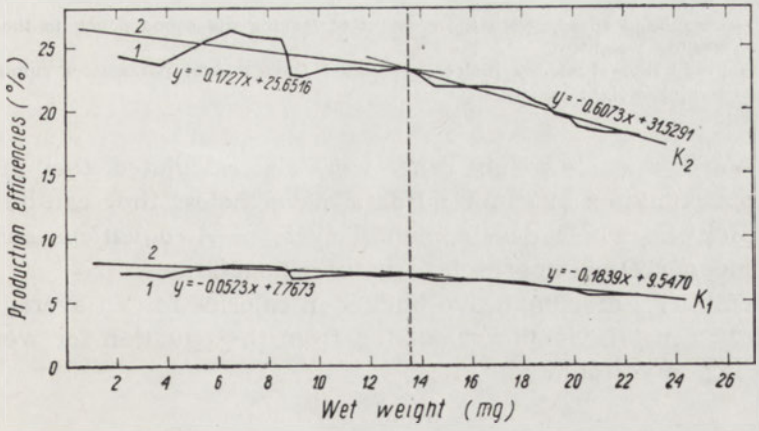

Fig. 7. Cumulative net (K_2) and gross (K_1) production efficiency indices against body weight for two weight groups. 1 — the moving averages, 2 — the regression lines

Because of a linear dependence of body growth for the investigated range of weights (Fig. 1), the cumulative production (P_c) also shows linear dependence (Fig. 6). Curvilinear character of changes in cumulative respiration (R_c) was substituted by two linear approximations for the ranges of weights: 1.5–13.5 mg and 13.5–22.5 mg. The equations for cumulative respiration (R_c) are as follows: $y = 2.068x - 0.695$ and $y = 4.152x - 28.750$, respectively, where y = cumulative energy of respiration in cal, x = weight of an average animal in mgs. Similar approach was accepted for cumulative assimilation (A_c) and consumption (C_c), both of which were affected by curvilinear character of their component, R_c (Fig. 6). The division into two weight groups was also maintained for production efficiency, and for the congruency of results was also back calculated for production (P_c).

All parameters were described by regressions which were plotted on Fig. 6 and 7. The equations for cumulative budget parameters, calculated for two weight ranges are presented in Table I. Apart from this, the

Table I. Equations describing the dependence of cumulative budget parameters and cumulative production efficiencies of an individual from its body wet weight

Parameter	Unit	Range of weight (mg)		
		1.5–13.5	13.5–22.5	1.5–22.5
Production P_c	cal/ind.	$y=0.613x+0.095$	$y=0.609x+0.729$	$y=0.652x-0.146$
Respiration R_c		$y=2.068x-0.695$	$y=4.152x-28.750$	$y=2.969x-7.197$
Assimilation A_c		$y=2.682x-0.605$	$y=4.761x-28.019$	$y=3.621x-7.342$
Consumption C_c		$y=8.856x-1.998$	$y=15.723x-92.532$	$y=11.959x-24.253$
Gross efficiency K_{1c}	%	$y=-0.0523x+7.7673$	$y=-0.1839x+9.5470$	$y=-0.1086x+8.1740$
Net efficiency K_{2c}		$y=-0.1727x+25.6516$	$y=-0.6073x+31.5291$	$y=-0.3587x+26.9947$

x — wet body weight (mg),
y (cal/ind.) — cumulated energy from the moment of leaving the brood pouch to the moment of reaching weight x,
y (%) — the production efficiency indices calculated from budget parameters cumulated up to reaching weight x.

equations for the whole weight range were also calculated; they give less precise approximation of empirical data, nevertheless they can be representative for the whole developmental cycle of *A. aquaticus* and later used for bioenergetical approach to natural populations.

To exemplify, the cumulative budget in calories for an average individual of 22.0 mg in weight, calculated from the equation for weight of 13.5–22.5 mg is as follows:

$$C_c = P_c + R_c + F_c$$
$$253.4 = 14.2 + 62.6 + 176.6$$
$$A_c = 76.8$$

The production efficiency indices based on cumulative parameters for this weight are: $K_{2c} = 18.17\%$ and $K_{1c} = 5.50\%$. The range and direction of changes in cumulative production efficiences within the development and growth of animals are as follows: K_{2c} diminishes from 25.31% for 2 mg of weight to 18.17% for 22.0 mg in weight, and K_{1c} from 7.66 to 5.50%, respectively.

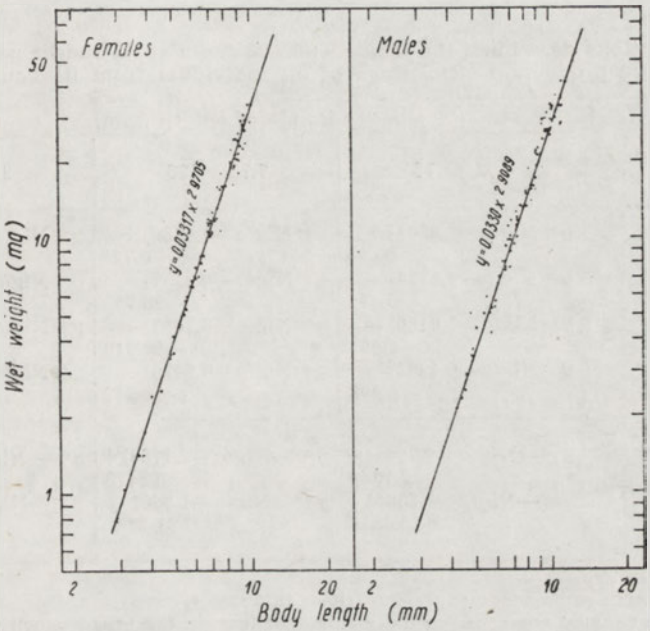

Fig. 8. Dependences of body length from body wet weight

Body weight-length dependence. The dependences of body weight from the body length are presented in Fig. 8. These dependences are described by the equations:
for females:

$$y = 0.03317x^{2.9705}, \text{ or } \lg y = 2.9705 \lg x - 1.4794,$$

and for males:

$$y = 0.03300x^{2.9089}, \text{ or } \lg y = 2.9089 \lg x - 1.4815,$$

and for mixed sexes (50% females and 50% males):

$$y = 0.03602x^{2.8972}, \text{ or } \lg y = 2.8972 \lg x - 1.4435 \quad (6),$$

where y = body wet weight in mg, x = body length in mm.

Males measuring the same length as females are somewhat lighter. and power is close to 3 in both sexes.

Budget parameters against body length. The possibility of cumulation of the parameters for the given life span of an individual only from the final body length is very important on account of methodology. It is much easier to obtain the measure of body length than

that of wet weight, especially in aquatic animals. Substituting x value denoting body weight in equations gathered in Table I by right side of equation (6) which expresses body weight in terms of length one obtains equations or dependence of cumulative budget parameters from body length. After simplification and partial logarithming one obtains equations presented in Table II. They allow to estimate P_c, R_c, A_c, C_c, and also K_{1c} and K_{2c} from the known length of animals.

Table II. Equations describing the dependence of cumulative budget parameters and cumulative production efficiencies of an individual from its body length

Parameter	Unit	Range of length (mm)		
		3.62–7.73	7.73–9.23	3.62–9.23
Production P_c	cal/ind.	$y=\mathrm{Nlg}(a-1.6561)+0.095$	$y=\mathrm{Nlg}(a-1.6588)+0.729$	$y=\mathrm{Nlg}(a-1.6291)-0.146$
Respiration R_c	cal/ind.	$y=\mathrm{Nlg}(a-1.1279)-0.695$	$y=\mathrm{Nlg}(a-0.8251)-28.750$	$y=\mathrm{Nlg}(a-0.9710)-7.197$
Assimilation A_c	cal/ind.	$y=\mathrm{Nlg}(a-1.0150)-0.605$	$y=\mathrm{Nlg}(a-0.7657)-28.019$	$y=\mathrm{Nlg}(a-0.8847)-7.342$
Consumption C_c	cal/ind.	$y=\mathrm{Nlg}(a-0.4962)-1.998$	$y=\mathrm{Nlg}(a-0.2470)-92.532$	$y=\mathrm{Nlg}(a-0.3657)-24.253$
Gross efficiency K_{1c}	%	$y=-\mathrm{Nlg}(a-2.7249)+7.7249$	$y=-\mathrm{Nlg}(a-2.1788)+9.5470$	$y=-\mathrm{Nlg}(a-2.4076)+8.1740$
Net efficiency K_{2c}	%	$y=-\mathrm{Nlg}(a-2.2061)+25.6516$	$y=-\mathrm{Nlg}(a-1.6601)+31.5291$	$y=-\mathrm{Nlg}(a-1.8887)+31.5291$

The range of length corresponds to weights given in Table I.
y (cal/ind.) — cumulated energy from the moment of leaving the brood pouch to the moment of reaching length L,
$a = 2.8972\ \mathrm{lg}L$ (L(mm) — body length),
y (%) — the production efficiency indices calculated from budget parameters cumulated up to reaching length L.

4. DISCUSSION

Some explanation is needed for certain constants accepted for the whole development in this paper. They are: the dry matter/wet matter ratio, the calorific value of animal body, the oxy-calorific coefficient and the percentage assimilation. The dry matter/wet matter ratio was considered as representative for the whole development, basing on Fitzpatrick's data (1968). This author found no statistical differences of this ratio in females and males as well as in summer and winter individuals. He reports an average value of 0.217, thus very close to that found in the present work — 0.213. He also investigated calorific value sorting the animals into size classes, but each sex characterized by a separate, average value. Making an average for mixed group of males and females (50% each) gives 3.035 cal/mg dry matter, which is very close to that obtained in this work — 2.9575.

The percentage assimilation which has been accepted in this paper was measured for animals kept at 10°C (Prus 1971). In the light of White's paper (1968) on the effect of temperature on energy budget of terrestrial isopod, *Tracheoniscus rathkei* Brandt, the assimilation was found to diminish in this species from 41 to 27% of consumption with increasing temperature from 10 to 25°C. Basing on these data, the earlier defined percentage assimilation of 40.2% for an average individual of *A. aquaticus* of 10.80 mg in weight, obtained for New Hinksey stream population (England) was diminished by about 10%, obtaining thus 30.28%.

The main data obtained in this work are rather congruent with those which can be found in literature (Levanidov 1949, Fitzpatrick 1968). Daily values of production, respiration and assimilation reported by Levanidov (1949) for an individual of 20 mg in weight at temperature of 14–19°C ($P = 0.09$ cal, $R = 0.42$ cal, $A = 0.51$ cal) are very close to these obtained in this work. Incongruence was found only between values of consumption and resulting from this assimilation efficiency and gross production efficiency. This incongruence stems probably from methodological errors (for explanation see Prus 1971).

The essential part of the cumulative budget is calculation of the total amount of energy which went through an organism from its birth to a given moment of life. Such way of calculation was proposed by Klekowski et al. (1967) in a paper dealing with bioenergetics of flour beetle, *Tribolium castaneum* Hbst. This approach was developed later in studies of energy budgets of other species (Fischer 1967, Klekowski, Ivanova in prep., Klekowski, Stępień in prep.). The review of these studies can be found in a compilation paper (Klekowski et al. 1971). Klekowski (1970) has supplemented the review of daily and cumulative budgets with cumulative forms of budgets calculated by him from other paper (Richman 1958, Klekowski, Shushkina 1966, Khmeleva 1967, Phillipson 1967 and unpublished data, Shushkina et al. 1968). Prus (1968 b) described the way of calculation of cumulative budget exemplifying it with Tribolium study.

The type of cumulative budget depends to a greater extent on the degree of complexity of the developmental cycle. In the case of an insect with complete metamorphosis the energy cumulation is rather uneven. In the development cycle there are two periods of an intense energy agglomeration, during larval development and in the period of reproduction (oviposition). In pupal stage there is no energy input, but cumulated energy is spent for respiration and methamorphosis processes. This situation is clearly reflected in the course of cumulative budget parameters and net production efficiency index (Klekowski et al. 1967).

Similarly in an acarine, *Rhisoglyphus echinopus* F. et R. there are

several periods of intense growth and energy accumulation, alternately with periods of non-feeding, resting stages (K l e k o w s k i, S t ę p i e ń in prep.). This intermittent course of development is clearly expressed by the step-like form of the budget parameter curves.

In hemimetabolic insects the cumulation of energy is rather uniform within the whole larval development. In *Lestes sponsa* L. the cumulated energy budget parameters revealed almost straight line courses (F i s c h e r 1967). Similarly uniform trends are found in planktonic filtrator, *Simocephalus vetulus* O.F. Müller (K l e k o w s k i, I v a n o v a in prep.).

In a representative of Isopoda, *A. aquaticus*, the cumulative budget has also very uniform course. Besides short, reoccurring non-feeding periods connected with moults, the animals feed continuously during its life. That is why cumulated parameters of energy budget have a colinear character. This made it possible to describe them with linear functions. By defining the dependence of energy budget parameters from the body weight, and later using the weight-length dependence, also from the body length, it made it possible to obtain a cumulative value of any parameter for an individual of a given weight or length. From the dependence between body weight and development time one can also define approximately the time during which this energy went through or became incorporated in the body of any given individual.

It seems that this way of calculation of energy flow at the individual level can be used for estimation of energy flow of a population of this species.

5. SUMMARY

A complete energy budget of *A. aquaticus* was elaborated for 4 months of development with weights of animals ranging from 1.5 to 22.5 mg. Production and respiration were measured continously in the experiment, and assimilation was calculated by summation. The remaining elements of energy budget, i.e. consumption and non-assimilated energy were obtained by assuming the percentage assimilation to be similar to that obtained in another experiment (P r u s 1971).

The daily energy budget based on average values of daily parameters for the whole investigated period of development, i.e., for an animal of average weight of 12.81 mg, is as follows: Out of 2 cal consumed daily as food, about 0.6 cal is assimilated by the organism and remaining 1.4 cal is not assimilated and returned to the environment. Only 0.1 cal of assimilated energy is incorporated in the body (production) and 0.5 cal is used for respiration. Thus about 30% of energy consumed is assimilated out of which 5% is incorporated in body tissues and 25% is used for respiration. When energy assimilated is considered as 100% about 18% is production and 82% — respiration.

Cumulative energy budget for the period investigated was also calculated. A linear character was found for dependences of animal weight and budget parameters (Fig. 6) and for production efficiency indices (Fig. 7). These dependences were described by regressions as functions of body weight (Table I) and of body length (Table II), basing the latter on ascertained dependence of body weight from body length. The dependence of body weight from time of development was also described by mathematical function.

The calculated equations will allow to estimate the total amount of energy that went through an animal from the moment of leaving by it the brood pouch up to obtaining a given weight or a given body length. They will also allow to trace the distribution of this energy.

6. STRESZCZENIE

Podano pełny bilans energii *A. aquaticus* dla czteromiesięcznego okresu rozwoju obejmującego zakres ciężarów zwierząt od 1,5 do 22,5 mg. W eksperymencie ciągłym mierzono produkcję i respirację zwierząt, otrzymując wielkość asymilacji. Pozostałe elementy bilansu, konsumpcję i energię nieprzyswojoną, wyznaczono przyjmując wcześniej zbadaną wydajność asymilacji (Prus 1971).

Bilans dobowy energii oparty o średnie wartości dobowe parametrów za okres doświadczenia dla osobnika o średnim ciężarze ciała 12,81 mg wyrażony w kaloriach jest następujący: z blisko 2 cal pobieranych w pokarmie dziennie, ok. 0,6 cal jest asymilowane przez osobnika, reszta, tj. 1,4 cal energii, zostaje nie przyswojona i wraca do środowiska. Tylko ok. 0,1 cal energii przyswojonej zostaje wbudowane w ciało zwierzęcia (produkcja), natomiast ok. 0,5 cal jest zużywane na procesy oddechowe. Tak więc ok. 30% energii pobranej jest asymilowane, z czego ok. 5% zostaje wbudowane w ciało zwierzęcia, a 25% jest zużywane na procesy oddechowe. Z energii asymilowanej ok. 18% stanowi produkcja, a 82% respiracja.

Opracowano również bilans kumulatywny dla badanego okresu rozwoju. Uzyskano liniowy charakter zależności parametrów bilansu kumulatywnego od ciężaru zwierząt (Fig. 6) oraz wskaźników wydajności produkcji (Fig. 7). Zależności te opisano równaniami prostych regresji jako funkcji ciężaru ciała zwierząt (Tab. I) oraz jako funkcji długości zwierząt (Tab. II) w oparciu o wyznaczoną wcześniej zależność ciężaru ciała od długości osobnika. Wyznaczono również matematyczną zależność ciężaru ciała zwierzęcia od długości czasu rozwoju.

Podane równania pozwalają oszacować całkowitą ilość energii, jaką rozporządzał osobnik od momentu opuszczenia komory lęgowej do momentu osiągnięcia danego ciężaru ciała bądź długości ciała, jak też określić losy tej energii.

7. REFERENCES

Allee, W. C. 1912. An experimental analysis of the relation between physiological states and rheotaxis in Isopoda. *J. exp. Zool.*, 13, 269-344.

Bertalanffy, L. 1957. Quantitative laws in metabolism and growth. *Quart. Rev. Biol.*, 32, 217-231.

Fischer, Z. 1967. The energy budget of *Lestes sponsa* during its larval development. In: IBP Meeting "Methods of assessment of secondary production in freshwaters". Prague [mimeographed copy].

Fitzpatrick, C. M. 1968. The population dynamics and bioenergetics of the isopod *Asellus aquaticus* L. in a small freshwater pond. M. Sci. Dissertation, University of Durham.

Harrow, B., Mazur, A. 1966. *Textbook of biochemistry*. Ed. 9th, London, W. B. Saunders.

[Ivlev, V. S.] Ивлев, В. С. 1938. О превращении энергии при росте беспозвоночных [Sur la transformation de l'énergie pendant la croissance des invertébrés]. *Byull. Mosk. Obshch. Ispyt. Prir.*, 47, 267-277 [French summ.].

[Khmeleva, N. N.] Хмелева, Н. Н. 1967. Трансформация энергии у *Artemia salina* L.]. *Dokl. Akad. Nauk S.S.S.R.*, 175, 934-937.

Klekowski, R. Z. 1968. Constant-pressure microrespirometer for terrestrial invertebrates. In: W. Grodziński, R. Z. Klekowski [Eds] *Methods of ecological bioenergetics*. 67-68, Warszawa-Kraków, PWN.

Klekowski, R. Z. 1970. Bioenergetic budgets and their application for estimation of production efficiency. *Pol. Arch. Hydrobiol.*, 17, 55-80.

Klekowski, R. Z., Fischer, E., Fischer, Z., Ivanova, M. B., Prus, T. Shushkina, E. A., Stachurska, T., Stępień, Z., Żyromska-Rudzka H. 1971. Energy budget and energy transformation efficiency of several animal species of different feeding types. In: Z. Kajak., A. Hillbricht-Ilkowska [Eds] *Productivity problems of freshwaters*. 00-00. Warszawa-Kraków.

Klekowski, R. Z., Ivanova, M. B. [in prep.]. Elements of energy budget of *Simocephalus vetulus*.

Klekowski, R. Z., Prus, T., Żyromska-Rudzka, H. 1967. Elements of energy budget of *Tribolium castaneum* Hbst in its developmental cycle. In: K. Petrusewicz [Ed.] *Secondary productivity of terrestrial ecosystems*. 2, 859-879. Warszawa-Kraków, PWN.

Klekowski, R. Z., Shushkina, E. A. 1966. Ernährung, Atmung, Wachstum

und Energie-Umformung in *Macrocyclops albidus* (Jurine). *Verh. int. Ver. Limnol.*, 16, 399-418.
Klekowski, R. Z., Stępień, Z. [in prep.]. Elements of energy budget of *Rhisoglyphus echinopus* (Acarina).
[Levanidov, V. I.] Леванидов, В. И. 1949. Значение аллохтонного материала как пищевого ресурса в водоеме на примере питания водяного ослика *Asellus aquaticus* [Role of allochthonous material as food resource in water body, exemplified by feeding of water hog-louse, *Asellus aquaticus*]. *Trudy vsesojuz. gidrobiol. Obščestva*, 1, 100-117.
Phillipson, J. 1964. A miniature bomb calorimeter for small biological samples. *Oikos*, 15, 130-139.
Phillipson, J. 1967. Secondary productivity in invertebrates reproducing more than once in a life-time. In: K. Petrusewicz [Ed.] *Secondary productivity of terrestrial ecosystems*. 2, 459-475. Warszawa-Kraków, PWN.
Prus, T. 1968 a. Measurements of calorific value using Phillipson microbomb calorimeter. In: W. Grodziński, R. Z. Klekowski [Eds] Methods of ecological bioenergetics. 15-32, Warszawa-Kraków, PAN.
Prus, T. 1968 b. Computation of energy budgets using all stages of Tribolium. In: W. Grodziński, R. Z. Klekowski [Eds] Methods of ecological bioenergetics. 99-116, Warszawa-Kraków, PAN.
Prus, T. 1971. The assimilation efficiency of *Asellus aquaticus* L. (Crustacea, Isopoda). *J. Freshwat. Biol.*, 1, 287-305.
Prus, T. [unpublished data] delivered as a report at XIV Conference on studies of freshwater reservoirs of countries bordering with Baltic, Riga, June 1968.
Richman, S. 1958. The transformation of energy by *Daphnia pulex*. *Ecol. Monogr.*, 28, 275-291.
Shushkina, E. A., Anisimov, S. I. Klekowski, R. Z. 1968. Calculation of production efficiency in planktonic copepods. *Pol. Arch. Hydrobiol.*, 15, 251-261.
[Sushchenya, L. M.] Сущения, Л. М. 1968. Элементы энергетического баланса амфибионтного бокоплава *Orchestia bottae* M.-EDW (Amphipoda, Talitropoda Talitroidea) [The elements of energy balance of *Orchestia bottae* M.-EDW (Amphipoda, Talitropoda, Talitroidea)]. *Biologija morja*, 15, 52-70 [Engl. summ.].
Steel, E. A. 1961. Some observations on the life history of *Asellus aquaticus* (L.) and *Asellus meridianus* Rakovitza (Crustacea, Isopoda). *Proc. zool. Soc. Lond.*, 137, 71-87.
White, J. J. 1968. Bioenergetics of the woodlice *Tracheoniscus rathkei* Brandt in relation to litter decomposition in a deciduous forest. *Ecology*, 49, 694-704.
Winberg, G. G. [Ed.] Винберг, Г. Г. [Ред.] 1968. Методы определения продукции водных животных [The methods for estimation of production of aquatic animals]. Minsk, Vysejšaja Škola.

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F. B. TRAMA

TRANSFORMATION OF ENERGY BY AN AQUATIC HERBIVORE (*STENONEMA PULCHELLUM*) EPHEMEROPTERA [1]

Department of Zoology, Rutgers University, New Brunswick, New Jersey 08903, U. S. A.

ABSTRACT

A laboratory study of the energy budget for mayfly nymphs, *Stenonema pulchellum*, was made using a cultured diatom, *Navicula minima*, as the sole source of nutrition. Calorific equivalents were determined with an oxygen semi-microbomb, and food intake was estimated by a radiophosphorus tagging technique. The 33-day energy budget representing a 1 mm increase in body length was computed for individuals ranging from 4 to 7 mm in length. In this study, the calories expended via respiration were approximately three times those stored as growth.

1. INTRODUCTION

Detailed analyses of energy budgets for individual organisms or populations have limited value in assessing energy flow in an ecosystem. This is especially true when measurements are made under laboratory conditions. While the ultimate and most useful goal is the analysis and understanding of ecosystem energetics, detailed information on individuals and populations can be instrumental in discovering principles and mechanisms or simply used to indicate correct orders of magnitude.

Present knowledge of energy flow for herbivorous freshwater invertebrates is based upon data from few studies (Phillipson 1966). Prior to the studies by Richman (1958) on a cladoceran and Trama (1957) on a mayfly, the work of Ivlev (1939) on the bioenergetics of *Tubifex tubifex* represented all that was known for this trophic level in fresh water. Furthermore, because Tubifex is a detritus feeder its characterization as an herbivore is questionable.

Odum (1957 and Teal (1957) reported on energy flow studies in freshwater ecosystems, and their findings have been widely cited. Their work, along with that of others, has been summarized in several ecology textbooks (Odum 1959, Phillipson 1966, Kormondy 1969, Whittaker 1970). These broad studies at the ecosystem level, while valuable, do indicate a need for more detailed studies on the individual and population level in order to define the fundamental laws governing ecological energetics.

2. METHODS

Culturing Techniques

Nymphs of the mayfly, *Stenonema pulchellum*, are a common inhabitant of freshwater streams in eastern North America (Burks 1953) and were abundant

[1] This paper originated from a portion of a thesis submitted in partial fulfillment of a Ph. D. at the University of Michigan. Assistance and guidance rendered by Dr. David C. Chandler is greatfully acknowledged.

in riffle areas of the Huron River, Washtenaw County, Michigan. Specimens were hand picked from rocks and transported to the laboratory where they were kept in aerated river water at 20°C. Physical and chemical data were not taken routinely at times of collection, but river water temperatures ranged from near zero in winter to about 25°C in late summer. The diatom, *Navicula minima*[2] was isolated from its natural habitat, and a clone was cultured in a modified Chu No. 10 medium (Chu 1942).

A special procedure was devised to permit quantitative manipulation of the source of food-energy, Navicula. A series of sterile, preweighed (±10 μg) circular coverslips were arranged in a circle inside a 15 cm petri dish containing sterile culture medium. They remained immobile once they were firmly pressed onto the bottom plate. A coverslip, bearing a heavy growth of diatoms was then placed in the center of the circle. Diatoms grew outward from this "inoculum" covering the bottom of the petri dish and the coverslips in a fairly uniform layer. In this fashion coverslips were covered on one side only and were easily manipulated with clean, fine-tip forceps. Growth on the petri dish bottom was harvested and used to determine the calorific content.

Biomass and Calorific Values

Nymphs were placed in size classes and held without food for 96 hours. The live weight, dry weight and organic content (loss-on-ignition) of size groupings were determined as outlined by Welch (1948).

Navicula biomass was estimated by oven drying at 60°C for 24 hours and reweighing ten preweighed coverslips covered with a heavy growth of the diatoms. Coverslips were then ignited in a muffle furnace at 600°C for 30 min and reweighed to determine the organic fraction.

Oxygen microbombs were not commercially available as they are today, and a semi-microbomb (70 ml) was utilized. Samples varying from 11 to 80 mg were mixed with sufficient benzoic acid (206–258 mg) to produce a temperature change of 1.5°C. This method was suggested by Dr. Shelby D. Gerking (personal communication) and has been detailed by Richman (1958).

Oxygen Consumption

Oxygen consumed by non-fasting mayflies was determined by the unmodified Winkler technique using 250 ml glass, stoppered bottles. Tests were conducted over a 24 hr period, at 15, 20 and 25°C and in the dark; a sufficient number of organisms (never more than ten) was used to produce a decrease of one to two milligrams oxygen per liter. Temperature was controlled to within ±1°C in all experiments. All bottles were gently agitated at 12 and 24 hours.

A single control bottle was run with each series, and the oxygen consumed was calculated by subtracting oxygen content of the blank from that of the experimental bottle at the end of 24 hours.

Ingestion Rate and Growth

Preweighed coverslips covered by a rich growth of Navicula were transferred to culture medium spiked with radioactive phosphorus (< 10 μCi P-32). The diatoms were effectively tagged after 30 minutes' exposure under a light source. Clean coverslips were used as controls but rarely showed radioactivities above background.

A coverslip bearing labeled diatoms was presented to isolated nymphs that had been held for 24 hours in the dark with a surplus of Navicula. Feeding rates were measured over a 12 hr period, at 20°C, and in the dark; the time period was empirically determined to allow adequate ingestion of radioactive food and to leave about 50% uneaten. Mayflies with surgically removed mouthparts served as controls and their radioactivity was substracted from the experimentals.

Oven-dried samples were assayed using a thin end-window GM detector and decade scaler. To covert corrected radioactivity of the consumer into terms of

[2] More precisely identified as *N. minima* var. *atomoides* (Grun.) Cl by Dr. Ruth Patrick, Curator of Limnology, Academy of Natural Sciences of Philadelphia.

diatom biomass ingested, it was necessary to weigh the diatom residue remaining on the coverslip upon which the nymph had been feeding.

Conditions for determining rate of growth were identical to those employed in measuring ingestion rates but the diatoms were not made radioactive. Every seven days body length was measured, number of molts noted, and the water renewed. Surplus food was always present.

3. RESULTS

Food Intake

Based on six determinations, the mean calorific value of Navicula was 3218 cal/g dry weight (S.E. ± 82). This was equivalent to 4963 cal/g organic matter since the ash-free weight was 63.5% of total dry weight.

The estimated quantity of food ingested by the nymphs in a 12 hr period is presented in Table I; calorific equivalents are also given. Values

Table I. Food ingested by various size classes of *S. pulchellum* in 12 hours at 20° C

Length (mm)	No. of measurements	Food (mean ± S.E.)	
		µg dry wt.	cal.
4	15	54.5 ± 2.4	0.176 ± 0.008
5	17	73.2 ± 3.3	0.233 ± 0.011
6	10	125.6 ± 4.5	0.403 ± 0.014
7	10	135.2 ± 5.2	0.432 ± 0.017

ranged from 54.5 to 135.2 µg ingested per 12 hours depending upon size of the animal. The relation between length and quantity of food ingested is non-linear and possibly sigmoidal. Due to the rather large variance associated with each mean value (Table I) a definite relationship between size and calories ingested was not evident. Nevertheless, mean calorific equivalents were used in formulating the energy budget.

Oxygen Consumption

Mean oxygen consumption by non-fasting nymphs (4–7 mm) was

Table II. Oxygen consumed by various size naiads of *S. pulchellum* at various temperatures (number of measurements given in parentheses)

Length (mm)	Oxygen Consumption (mean±S.E.) (µl/mg/hr)		
	15°C	20°C	25°C
4	1.20 ± 0.06 (4)	1.78 ± 0.05 (6)	2.56 ± 0.11 (5)
5	1.33 ± 0.09 (6)	1.69 ± 0.05 (6)	2.68 ± 0.09 (8)
6	1.22 ± 0.05 (4)	1.70 ± 0.06 (6)	2.67 ± 0.08 (4)
7	1.28 ± 0.04 (4)	1.78 ± 0.11 (5)	2.60 ± 0.06 (5)
Mean	1.26 ± 0.04 (18)	1.74 ± 0.03 (23)	2.63 ± 0.04 (22)

Table III. Growth and number of molts for *S. pulchellum* at 20°C over an eight-week period

No. of nymphs	Mean length of nymphs in succesive weeks									Total growth in 8 weeks	Mean growth per week	Total No. of molts	Molts/nymphs in 8 weeks	Mean growth per molt
	0	1	2	3	4	5	6	7	8					
5	3.0	—	3.5	3.5	3.8	4.0	4.2	4.4	5.1	2.1	0.26	39	7.8	0.27
6	3.2	—	3.6	3.8	4.0	4.3	4.5	4.7	5.0	1.8	0.23	37	6.1	0.30
10	3.5	—	3.9	4.0	4.3	4.6	4.8	5.0	5.3	1.8	0.23	65	6.5	0.28
6	3.6	3.8	3.8	3.9	4.1	4.4	4.5	4.6	4.9	1.3	0.16	26	4.3	0.30
10	3.8	4.0	4.3	4.6	4.8	5.0	5.2	5.5	5.6	1.8	0.23	68	6.8	0.26
20	4.0	4.2	4.5	4.7	4.7	4.9	5.1	5.2	5.3	1.3	0.16	98	4.9	0.27
20	4.5	4.8	5.0	5.2	5.2	5.5	5.7	5.8	6.1	1.6	0.20	115	5.8	0.28
20	5.0	5.3	5.5	5.7	6.0	6.2	6.4	6.6	6.8	1.8	0.23	127	6.4	0.28
									Mean	1.7	0.21		6.1	0.28

Dash (—) indicates no data available.

1.26, 1.74, and 2.63 microliters per milligram dry weight per hour at 15°C, 20°C and 25°C, respectively. These mayflies apparently consumed oxygen in direct proportion to their mass (Table II) and have an oxygen Q_{10} value of about 2.1. An oxy-calorific equivalent of 5 cal/ml oxygen (Ivlev 1934, Swift, French 1954) was used to convert oxygen consumed into calories expended.

Growth

Nymphs ranging in size from 3 to 5 mm grew linearly at approximately 0.21 mm per week over an 8 week period (Table III). Interestingly, the average increase in length per molt was fairly constant (Table III), and could theoretically have been used to measure growth indirectly. To increase their body length 1.0 mm these nymphs required an estimated 33 days.

The calorific value per unit weight increased as the *S. pulchellum* nymphs increased in length and dry weight (Table IV, Fig. 1). This

Table IV. Mean weights and calorific values ± S.E. of various size nymphs of *S. pulchellum*

Length (mm)	Weight (mg)		Calorific equivalent	
	Live	Dry	cal/dry gram	cal/nymph
4	2.45	0.51	5295 ± 116	2.70
5	4.62	0.96	5396 ± 44	5.18
6	7.24	1.29	5552 ± 53	7.16
7	10.06	2.01	5710 ± 37	11.48
8	—	—	5975 ± 29	—

Dash (—) indicates no data available.

increase in calorific value could be associated with an increased lipid synthesis since gonad development was evident in nymphs greater than 6 mm in length. No measurements of lipid content were made, however. The difference in calories per nymph between any two size classes was assumed to be growth or net production.

Energy Budget

A 33 day energy budget was constructed from data collected at 20°C and is summarized in Table V. This budget represents a 1.0 mm increase in length. Because ingestion rate and oxygen consumption were measured on specific size classes, it was expedient to assume a linear relationship between successive size classes. For example, the average daily ingestion rate over 33 days was simply the mean of the measured ingestion rates for nymphs of succesive size classes.

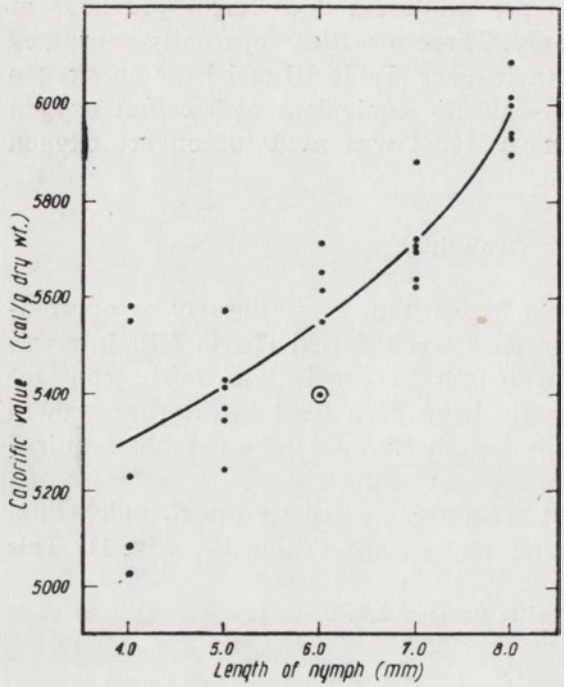

Fig. 1. Calorific values of various size classes of *S. pulchellum* nymphs. Each point represents a single measurement made on a composite sample. The circled point indicates two observations of equal value. Curve is drawn through the arithmetic mean of observations

Mean efficiency of growth was 14.5% and metabolic expenditure amounted to 38.6%. By difference, the energy lost through egestion was estimated to be 46.9% (Table V).

Table V. Energy budget for *S. pulchellum* at 20°C. Budget based on the mean growth rate of 1 mm per 33 days

Initial length of nymphs (mm)	Caloric Intake (cal)	Metabolic Loss		Growth		Egestion	
		Cal.	%	Cal.	%	Cal.	%
4.0	13.53	5.08	37.6	2.48	18.3	5.97	44.1
5.0	21.02	7.76	37.0	1.98	9.4	11.28	53.6
6.0	27.56	11.37	41.2	4.32	15.7	11.87	43.1
Mean	20.70	8.07	38.6	2.93	14.5	9.71	46.9

4. DISCUSSION

Ivlev (1945) and others have utilized the following equation to describe transfer paths of energy in an organism:

$$Q = Q' + Q_r + Q_t + Q_v + Q_w \qquad (1)$$

where, Q — the gross energy of consumed food, Q' — the energy accu-

mulated as growth, Q_r — unassimilated energy of food, Q_t — the energy of primary heat, Q_v — the energy of external work, and Q_w — the energy of internal work. Ricker (1946) indicated that $Q_t+Q_v+Q_w$ could be combined and treated as a single factor, respiration, thereby simplifying computations:

$$Q=Q'+Q_r+Q_m \tag{2}$$

where, $Q_m=Q_t+Q_v+Q_w$=total metabolic expenditure of energy estimated by respiration. Calories assimilated from the energy intake (Q) can be determined from the relationship:

$$\text{assimilation} = \text{growth} + \text{respiration} \tag{3}$$

used by Lindeman (1942) and Slobodkin (1962).

Using equation (3) the mean assimilation was 53.1% for the mayfly nymphs used in this study. This agreed with a mean of 50.35% for *Tubifex tubifex* (Ivlev 1939) but was more than twice the maximum assimilation percentage reported by Richman (1958) for pre-adult Daphnia. According to Richman, percentage of calorific intake assimilated by daphnia was inversely related to the concentration of food available per day. Herbivorous mammals assimilate in the order of 50% of their calorific intake (Kleiber 1961) which is low in comparison with carnivores.

The gross efficiency of growth may be defined as:

$$\frac{\text{calories accumulated}}{\text{calories consumed}} \tag{4}$$

where calories accumulated includes all products of storage — protoplasm, cellulose, keratin, reproductive bodies, etc. As Brody (1945) and Ivlev (1945) pointed out, in accordance with Rubner's law the gross efficiency in initial stages of biological growth is fairly constant and approximates 35%. With increasing age, however, this efficiency declines and regularly reaches zero in organisms with determinant growth patterns. Brody (1945) estimated an efficiency of 35% for early post-natal growth in cattle with a rapid decline to only 5% at the end of two years.

Nymphs from 4 to 7 mm in length exhibited a mean gross efficiency of 14.5% (Table V) which can be taken as representative for a major portion of their life span since nymphs normally attain a maximum length of 9 mm. It must be noted that stages younger than those studied may have average efficiencies between 14.5 and 35% while later stages (8–9 mm) could be less than 14.5%. Richman (1958) found that gross

efficiencies of growth in pre-adult Daphnia decreased from 13.22 to 3.87% as the food supply was increased. For adults he found that essentially all growth was transformed into production of young and gross efficiency for producing young was from 16.52 to 10.02%, depending upon food supply.

The energy expenditure required for normal animal activities (= respiration) is of considerable interest in analysing energy budgets for individuals, populations or trophic levels. Those individuals or species populations that have a rapid metabolism and turnover will utilize a greater share of the energy flow. Since a significant portion of the energy lost at each trophic transfer can be attributed to respiration, the relationship between calories stored as growth and calories lost via respiration will have a direct bearing on the rate at which food is being produced for the next trophic level. If assimilation is assumed to be fixed, it follows from equation (3) that any increase in respiration must be accompanied by a decrease in growth or, in other words, net productivity.

From this study it appears that *S. pulchellum* nymphs have a high metabolic demand. The mean metabolic loss amounted to 8.07 cal while only 2.93 cal were stored as growth (Table V). The mean ratio of respiration to growth (8.07/2.93) was 2.76. This same ratio computed for Tubifex (Ivlev 1939) was 0.62; for Daphnia 0.79 to 0.37, depending upon food supply (Richman 1958); and for Microtus 0.68 (Golley 1960), which could be typical for small, herbivorous mammals. Production of mayfly biomass, if one were to generalize from this study, is consequently an expensive process in terms of calories expended to calories stored.

The relationship between gross efficiency of growth and gross ecological efficiency (Slobodkin 1962, Phillipson 1966) though somewhat similar is far from analogous. Slobodkin (1962) has given an excellent summarization of the relevance of energy studies in ecology and the significance of ecosystem efficiencies. He concluded that ecological efficiencies are of the order 5 to 20% (10% most probable) and assimilation percentages for most organisms generally of the order of 20 to 40%. Consequently, percentage of consumed energy transmitted from prey to predator cannot exceed the maximum assimilated.

5. SUMMARY

Few detailed energy budgets for herbivorous freshwater invertebrates have been reported. More such data are needed in order to generalize and hypothesize further on energy flow in populations and communities under more or less natural conditions.

Nymphal forms of *S. pulchellum* ranging in size from 4 to 7 mm ingested the equivalent of 0.176 to 0.432 cal in a 12 hr period at 20°C. Oxygen consumption did not vary significantly over the entire range of sizes tested, and nymphs had a mean consumption of 1.74 µl/mg per hour at 20°C. Growth measurements revealed

that each molt resulted in a body length increase of about 0.28 mm regardless of the size of the nymph. Growth rate was approximately constant during the eight week period of observation and amounted to 0.21 mm per week or 1.0 mm per 33 days.

A mean gross efficiency of growth of 14.5% can be accepted as representative for a major portion of the life cycle in this case. It was in good agreement with the findings of others working with Tubifex and Daphnia. However, Stenonema lost through respiration roughly three times as many calories relative to those stored as growth. The ratio of 2.76 implied high metabolic demand in these aquatic insects as opposed to a ratio of about 0.7 for Tubifex and Daphnia.

6. REFERENCES

Brody, S. 1945. *Bioenergetics and growth.* New York, Reinhold Publ.

Burks, B. D. 1953. The mayflies, or Ephemeroptera, of Illinois. *Bull. nat. Hist. Surv. Div.*, 26, 1-216.

Chu, S. P. 1942. The influence of the mineral composition of medium on the growth of planktonic algae. Part I. Methods and culture media. *J. Ecol.*, 30, 284-325.

Golley, F. B. 1960. Energy dynamics of a food chain of an old-field community. *Ecol. Monogr.*, 30, 187-206.

Ivlev, V. S. 1934. Eine Mikromethode zur Bestimmung des Kaloriengehalts von Nährstoffen. *Biochem. Z.*, 275, 49-55.

Ivlev, V. S. 1939. Transformation of energy by aquatic animals. *Int. Revue ges. Hydrobiol. Hydrogr.*, 38, 449-458.

[Ivlev, V. S.] Ивлев, В. С. 1945. Биологическая продуктивность водоемов [The biological productivity of waters]. *Usp. sovrem. Biol.*, 19, 98-120, [Engl. transl. by W. E. Ricker: *J. Fish. Res. Bd Can.*, 23, 1966, 1727-1759].

Kleiber, M. 1961. *The fire of life.* An introduction to animal energetics. New York, J. Wiley.

Kormondy, E. J. 1969. *Concepts of ecology.* Eaglewood Cliffs, Prentice-Hall.

Lindeman, R. L. 1942. The trophic dynamic aspect of ecology. *Ecology*, 23, 399-418.

Odum, E. P. 1959. *Fundamentals of ecology.* Philadelphia, W. B. Saunders.

Odum, H. T. 1957. Trophic structure and productivity of Silver Springs, Florida. *Ecol. Mongr.*, 27, 55-112.

Phillipson, J. 1966. *Ecological energetics.* London, Clowes and Sons.

Richman, S. 1958. The transformation of energy by *Daphnia pulex*. *Ecol. Monogr.*, 28, 273-291.

Ricker, W. E. 1946. Production and utilization of fish populations. *Ecol. Monogr.*, 16, 373-391.

Slobodkin, L. B. 1962. Energy in animal ecology. *Adv. ecol. Res.*, 1, 69-101.

Swift, R. W., French, C. E. 1954. *Energy metabolism and nutrition.* New York, Scarecrow Press.

Teal, J. M. 1957. Community metabolism in a temperate cold spring. *Ecol. Monogr.*, 23, 41-78.

Trama, F. B. 1957. The transformation of energy by an aquatic herbivore *Stenonema pulchellum* (Ephemeropthera). Ph D. Thesis, Univ. Michigan.

Welch, P. S. 1948. *Limnological methods.* Philadelphia, Blakiston.

Whittaker, R. H. 1970. *Communities and ecosystems.* London, MacMillan.

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D. H. H. Kühlmann

DIE BEWERTUNG KLEINER GEWÄSSER ALS FUNKTIONELLE ÖKOLOGISCHE EINHEITEN UND SICH DARAUS ERGEBENDE KONSEQUENZEN HINSICHTLICH DER ÖKOLOGISCHE TERMINOLOGIE

Museum für Naturkunde an der Humboldt-Universität, 104 Berlin, Invalidenstrasse 43, D. D. R.

ABSTRACT

A new terminology for discussing ecosystems is introduced and illustrated by complex data from three different temporary pools. Cycles of oxygen, carbon dioxide and nitrogen, as well as food webs networks have been taken as criteria. A conclusion emerges that the widely used term „ecosystem" is not quite precise. A new terminology is suggested, referring to the close or open character of the cycle of metabolism in a reservoir.

INHALT

1. DIE STELLUNG DER KLEINGEWÄSSER IM KOMPLEX DER ÖKOLOGISCHEN PROBLEMATIK

Zu den Kleingewässern zählt Thienemann (1925) alle periodischen, temporären und ephemeren Gewässer, z. B. Schmelzwassertümpel, Tümpel in Überschwemmungsgebieten der Flüsse, Regenpfützen, Konservendosen und Schneckengehäuse, sowie Behältnisse bildende Pflanzen, wie Nepenthes-Kannen oder die Blattachseln von Bromeliaceen. Kreuzer (1940) charakterisiert die Kleingewässer als „stehende Gewässer ohne ständige Zuflüsse; ihr Wasser ist meteorischen Ursprungs und gelangt durch Grundwasseranstieg ins Becken (Kleingewässer mit dauernder Wasserfüllung aus dem Erdboden und Abfluss sind nicht hierher zu stellen, sie sind Tümpelquellen, Limnokrenen). Auch Kleingewässer mit ständigem Graben-oder Bachzufluss sollen nicht hierher gestellt werden". Das alleinige Heranziehen dieses einen Merkmals, des Ursprungs der Wasserführung, genügt jedoch nicht, um zu entscheiden, ob ein Gewässer der Gruppe der Kleingewässer zuzuordnen ist oder nicht. Es existieren durchaus kleine Gewässer mit überwiegend perennierendem Charakter — z. B. in Wiesen gelegene kleine Becken, die nicht mit Wasser meteorischen Ursprungs bespannt, sondern von einem fast ständig Wasser führenden Graben gespeist werden — deren Milieubedingungen in charakteristischer Weise so stark schwanken, dass auch sie der Gruppe der Kleingewässer zuzuordnen sind. Und wohin sollen die hinsichtlich ihrer physikochemischen Faktoren noch stärkeren Schwankungen unterliegenden Fluttümpel und Bran-

dungslachen gestellt werden, deren Wasser in der Regel vom Meer herrührt, also ebenfalls nicht meteorischen Ursprungs ist, wenn nicht zu den Kleingewässern? „Für den Ablauf der Lebensvorgänge in den stehenden Binnengewässern ist von grosser Bedeutung die grössere oder geringere Konstanz der Milieubedingungen. Je mehr man in der Reihe „See — Weiher — Sumpf — Moor — Tümpel — Kleingewässer" nach der „See"-Seite geht, um so konstanter sind sie im allgemeinen, ...je mehr es sich um ausgesprochene Kleingewässer handelt, um so weniger konstant ist das Milieu" (Thienemann 1925).

So sind es die durch exogene wie endogene Einflüsse hervorgerufenen hohen Amplituden der physikochemischen Faktoren sowie Herkunft und Aspektfolge der Organismenwelt, die dem Kleingewässer das Gepräge verleihen und es als solches charakterisieren. „Nicht die Herkunft des Wassers entscheidet über die Frage ob Kleingewässer oder nicht, sondern die starken Schwankungen, die Astasie der inneren Faktoren" (Kühlmann 1960 a). Die in Kleingewässern herrschende aussergewöhnlich hohe Dynamik lässt die Beziehungen der verschiedenen Faktoren zueinander, ihre gegenseitige Beeinflussung und ihre Bedingtheit des einen durch den anderen, innerhalb kurzer Zeit besonders deutlich hervortreten und die Kleingewässer selbst zu interessanten Forschungsobjekten werden. Wegen ihrer geringen praktischen Bedeutung wurden sie bislang nur wenig beachtet, obwohl sie wegen ihrer relativ leichten Überschaubarkeit einerseits und ihrer hohen Dynamik andererseits prädestiniert sind, grundlegende Erkenntnisse hinsichtlich des ökologischen Geschehens in Gewässern zu liefern.

Es erhebt sich die Frage, ob die durch ihre hohe Dynamik und Astasie charakterisierten, zum Teil nur sehr kurzlebigen Kleingewässer als Lebensraum und Lebensgemeinschaft mit geschlossenem Beziehungskreisläufen aufgefasst werden können oder nicht?

Innerhalb der von Organismen besiedelten Oberfläche unserer Erde sind bekanntlich in sich mehr oder weniger abgegrenzte funktionelle Einheiten charakteristisch, die als "Microcosmos" (Forbes 1887), "Ecosystem" (Tansley 1923), „Holocön" (Friedrichs 1930), „Biosystem" (Thienemann 1939) oder "Geobiocoenose" (Sukačev 1957) bezeichnet worden sind. "In einem Ökosystem muss jedes Element auf der Erde, das in das Lebensgeschehen einbezogen wird, Stufen des Aufbaus und Abbaus durchlaufen. Es ist aber nicht nur der Stoffkreislauf, sondern auch der Energieumsatz, der alle Lebewesen in gegenseitige Abhängigkeit bringt (Tischler 1955). Nach Kühnelt (1965) könnten Ökosysteme „verschiedenen Umfang haben, müssen aber immer natürliche Einheiten sein, die aus lebenden und nicht lebenden Teilen aufgebaut sind, durch deren Wechselwirkung ein stationäres System entshteht, in dem Kreisprozesse ablaufen".

Wurde die anorganische Komponente eines Ökosystems als Biotop (Dahl 1908) bezeichnet, prägt Möbius (1877) für den die Organismen umfassenden lebenden Teil den Ausdruck Biocönose. Eine Lebensgemeinschaft oder Biocönose ist das gemeinsame Vorkommen von Pflanzen und Tieren. Sie ist weitgehend regulationsfähig, besitzt eine relative Stabilität und befindet sich in einem gewissen Gleichgewicht (Dotterweich 1940, Kühnelt 1965, Tischler 1965).

Die zur Regulationsfähigkeit und Stabilität notwendigen, in jedem Ökosystem stattfindenden "Kreisprozesse" beziehen sich vorzugsweise auf den Stoffumsatz, wobei den Kreisläufen des Kohlenstoffs, Sauerstoffs und Stickstoffs eine besondere Bedeutung für die Lebewesen zukommt (Tischler 1955). Sie können in verschiedener Weise ablaufen. Kühnelt (1965) macht auf die Haupttypen der am Stoffumsatz beteiligten Organismen — Produzenten, Konsumenten und Reduzenten — aufmerksam. „Sind alle drei Gruppen in entsprechenden Mengen vorhanden, so ist der Stoffkreislauf innerhalb des Systems geschlossen. Fälle, wo die Konsumenten fehlen, wären zwar denkbar, sind aber meines Wissens nicht verwirklicht. Dagegen können die Reduzenten fehlen oder stark zurücktreten, dann wird die gebildete organische Substanz angehäuft. Geringe Entwicklung der Konsumenten steigert diesen Prozess noch beträchtlich, z.B. in Mooren. Fehlen die Produzenten so ist das System nicht autark, und es muss organische Nahrung von aussen her eingebracht werden (z.B. in der Tiefsee)". Er kennzeichnet das Ökosystem weiter als „nur auf die Zufuhr von Sonnenenergie angewiesen. In ihm spielen sich „biogene Kreisprozesse" ab, die die lebenswichtigen Stoffe immer wieder umlagern". Wie der Ablauf der Kreisprozesse zum Ausdruck bringt, handelt es sich im Falle des Ökosystems im allgemeinen um geschlossene Systeme, nicht vollkommen geschlossene, sondern, da Inputs und Outputs von Stoff und Energie wirksam sind (Ovington 1962), schliesslich aus dem Ökosystem hinausführende (vgl. Schmalhausen 1961).

Den Biocönosen der Ökosysteme werden die auf „Kleinbiotope" oder "Habitate"

beschränkten Synusien als kleinste, regelmässig in der Natur vorhandene Gesellschaftseinheiten gegenübergestellt (nicht im Sinne von Davis 1960). Sie sind „zeitlich durch bestimmte Kleinklima-, Wetter- oder Nahrungsbedingungen beschränkt. Sie sind die kleinsten Gesellschaftseinheiten, die man regelmässig in der Natur antrifft. Bei der Differenzierung von Habitaten kann ausserordentlich weit gegangen werden" (Kühnelt 1965). In der terrestrischen Tierökologie werden vornehmlich unterschieden:

a. Biochorien als horizontal differenzierte Bezirke eines Biotops, die ausserhalb desselben infolge fehlender Regulationsfähigkeit das Gleichgewicht einbüssen. Die hier lebenden Organismengesellschaften werden als Choriocönosen bezeichnet.

b. Strata als vertikal differenzierte Bezirke, "Stockwerke" eines Biotops, die auch unabhängig voneinander auftreten können. Die hier lebenden Organismengesellschaften nennt man Stratocönosen.

c. Strukturteile als Teilbezirke innerhalb der Biochorien und Straten und ihnen zugehörig. Die dazu gehörigen Gesellschaften von Lebewesen führen die Bezeichnung Merocönosen (Tischler 1949).

Eine Gegenüberstellung der funktionellen ökologischen Einheiten „Biotop plus Biocönose" und „Habitat plus Synusie" ergibt folgende Differenzierung:

a. Biotop plus Biocönose sind weitestgehend selbständige natürliche Einheiten, deren Existenzen von der Zufuhr von Sonnenenergie und Sauerstoff abhängen. Der in ihnen stattfindende Stoffumsatz verläuft in Form geschlossener Kreisprozesse. Die Biocönose ist regulationsfähing und befindet sich im sogenannten „biologischen Gleichgewicht". Derartige biologische Einheiten werden als Ökosysteme bezeichnet. Jedoch sind auch sie ständigen Veränderungen unterworfen.

b. Habitat plus Synusie sind die kleinsten, überall in der Natur auftretenden ökologischen Einheiten. Ihre Existenz ist — neben der Zufuhr von Sonnenenergie und Sauerstoff — abhängig von dem Vorhandensein der Biotope, in die sie eingebettet sind. Zeitlich werden sie durch bestimmte Kleinklima-, Wetter- und Nahrungsbedingungen eingeschränkt und sind somit abhängig von dem Auftreten einer Vielzahl von Umweltfaktoren. Andererseits aber ist es möglich, dass sich die Existenzbedingungen einer Synusie nur sehr langsam ändern. Eine zusammenfassende Bezeichnung für diese ökologische Einheit wurde bisher m. W. nicht verwandt.

Trotz aller bisher gewonnenen Erkenntnisse werden daraus harvorgegangene generalisierende Formulierungen und definierte Begriffe noch heute teilweise falsch angewandt. So ist es nicht vertretbar, dass eine Tiergruppe, auch wenn sie zahlenmässig stark überwiegt, eine Biocönose bilden soll, und es kann mithin nicht von „kompakten Mysiden-Biocönosen" gesprochen werden (Busnita 1966). Eine Vielzahl weiterer Beispiele falscher oder unsicherer Verwendung ökologischer termini technici nennt Udvardy (1959). Weiter erwächst aus den natürlichen Gegebenheiten, die nicht alle ohne weiteres in das bestehende Schema zu passen scheinen, manche Unsicherheit. Das wird dadurch, dass Ökosystems Veränderungen unterworfen sind, noch verstärkt. Die Entscheidung zu treffen, ob es sich bei einer Lebensgemeinschaft um eine Biocönose oder eine Synusie handelt, fällt deshalb nicht immer leicht. Es muss jedoch angezweifelt werden, ob zur Charakterisierung der Habitate und Synusien deren Kleinheit und Kurzlebigkeit herangezogen werden darf, obwohl diese Umstände eine Entscheidung herbeiführen können. Jedoch setzt eine solche Feststellung eingehende Untersuchungen voraus. Es liegt in der Natur der Sache, dass eine Biocönose meist einen grösseren Lebensraum bewohnt und einen grösseren Umfang hat als eine Synusie, und, da die Begriffe Raum und Zeit untrennbar miteinander verknüpft sind, sowie ein grosses funktionelles System im allgemeinen stabiler als ein kleines ist, sich eine Synusie als kurzlebiger als eine Biocönose erweist.

Deshalb werden die Fragestellungen „Biocönose oder Habitat?" und „Biocönose oder Synusie?" an Hand einiger schwer entscheidbarer Beispiele aus der Gruppe kleiner Gewässer näher betrachtet. Hierbei sollen die in den einzelnen ökologischen Einheiten auftretenden Strukturen ihrer Systeme, die darin eventuell ablaufenden Kreisprozesse und im Zusammenhang damit die Frage nach ihrer Autarkie als Kriterien dienen, wobei unter Wahrung der Einheit von Organismus und Umwelt (Tansley 1935, Lindeman 1942, Löther 1966), zur leichteren Überschaubarkeit derselben ihre Zuordnung zu materiallen Systemen versucht wird.

2. DIE UNTERSUCHUNGSBEISPIELE

Die drei Untersuchungsbeispiele sind dem Verfasser von eigenen, teilweise veröffentlichten Untersuchungen her bekannt (Kühlmann 1958, 1959, 1960 a, 1960 b,

1960 c, 1961, 1962, 1963). Sie weisen einen jeweils unterschiedlichen Charakter auf. Es handelt sich um:

1. einen auf einer Wiese gelegenen Grabenweiher bei Leipzig,
2. einen Auwaldtümpel daselbst,
3. Brandungslachen an der rumänischen Schwarzmeerküste.

Das auf der Wiese gelegene Kleingewässer hatte eine Abmessung von 40 mal 11 m und ist je nach dem Wasserstand 35 cm bis 90 cm tief. Der Südrand wurde von einem kleinen unterholzreichen Baumbestand gesäumt. Das von diesem stammende Fallaub wirkte düngend. Das Gewässer wurde von einem Graben durchflossen und deshalb als Grabenweiher bezeichnet. Es führte demzufolge das ganze Jahr hindurch Wasser. Der Durchfluss sorgte für klares, relativ sauerstoffreiches Wasser und liess nur die Ablagerung einer geringen Schlammschicht zu. Das Bild änderte sich sofort, wenn der Durchfluss — etwa durch Ausfrieren des Grabens — unterbrochen wurde. Dann trat Schwefelwasserstoff auf. Die Durchschnittstemperaturen schwankten während eines Jahres zwischen 0 und 20°C und konnten auch während eines Tages an der Wasseroberfläche Amplituden bis 10°C aufweisen.

Der Auwaldtümpel wurde rings von Erlen umgeben, deren abfallende Blätter ihn reichlich düngten (vgl. Paschalski 1959). Seine langovale Form wies bei ziemlich hohem Wasserstand eine Abmessung von etwa 50 mal 10 m und eine Tiefe von 50 cm auf. Während zweier Monate im Jahr, im Juni und Oktober, trocknete er aus. Bei den Hochsommerlichen und herbstlichen Regenfällen wurde er von dem in unmittelbarer Nähe befindlichen blinden Arm eines Flüsschens her bespannt. Sein Wasser war relativ sauerstoffreich. Bei Stagnation (unter Eis) konnte Schwefelwasserstoff auftreten. Der umstehende Wald vermittelte eine ausgeglichene Temperatur, so dass die Schwankungen derselben geringer als im oben beschriebenen Grabenweiher waren.

Die auf den Kalksteinklippen gelegenen untersuchten Brandungslachen hatten entweder die Form schmaller Rinnen oder flacher Teller. Ihre Oberfläche betrug zwischen 1 und 8 m². Sie entstanden durch überkommende Brecher oder Brandungsspritzer und trockneten bei ruhiger See sehr bald wieder aus. Insgesamt gesehen waren sie etwa die Hälfte des Jahres, aber meist jeweils nur für wenige Tage, bespannt, in den windstilleren Monaten, wie Juli und August, weniger. Die Schwankungen der physikalischen und chemischen Faktoren waren erheblich. So konnte die Temperaturamplitude innerhalb von 24 Studen 13°C umfassen, wobei sie bis auf 32°C anzusteigen vermochte. Lag die durchschnittliche Salinität des vom Meer in die Becken geschlagenen Wassers zwischen 14,5 und 16‰, so konnte diese durch heftige Regenfälle auf unter 1‰ herabgedrückt werden, andererseits aber durch Verdunstung auf über 25‰ ansteigen. Die Wasserstoffionenkonzentration betrug gewöhnlich zwischen pH 8 bis 10, konnte aber unter dem Einfluss einer auftretenden Schwefelwasserstoffentwicklung auf pH 6 absinken. Bei starker Assimilation der autotropfen Pflanzen konnte die aktuelle Sauerstoffkonzentration über 17 mg O_2/l erreichen, unter der reduzierenden Wirkung von Fäulnisprozessen jedoch völlig zurückgehen. Innerhalb eines Tages wurden Sauerstoffschwankungen, die mehr als 14 mg O_2/l ausmachten, beobachtet. Die Brandungslachen stellten also wegen der in ihnen herrschenden dauernden starken Schwankungen aller Milieufaktoren einen den Organismen nur schwer zugänglichen Lebensraum dar.

Bei oberflächlicher Betrachtung könnte man zu der Entscheidung gelangen, dass von den angeführten Gewässern der Grabenweiher auf Grund seiner ständigen Wasserführung den Kriterien eines Biotops am ehesten entsprechen müsste. Jedoch wird die Beantwortung der Frage problematisch, sobald der Systemcharakter dieser ökologischen Einheiten genauer studiert wird. Es ist deshalb notwendig, zunächst die hauptsächlichsten Organismen der Gewässer, untergliedert nach der ökologischen Rolle, die sie im Haushalt derselben verwirklichen, zu erfassen. Hierbei müssen Sukzessionswechsel und Aspektfolgen im Rahmen dieser Arbeit unberücksichtigt bleiben. Sie beeinflussen das ökologische Gesamtgeschehen in den Gewässerbeispielen — wenn nicht ausdrücklich anders erwähnt — nicht entscheidend.

Der Grabenweiher war hinsichtlich seiner Besiedlung durch die Organismen folgendermassen charakterisiert: Es hatten eine ganze Anzahl autotropher Pflanzen, vor allem planktische Flagellaten (Trachelomonas, Phacus, Pandorina, Anthophysia u.a.), Diatomeen (Melosira, Synedra, Nitschia, Gomphonema, Gyrosigma u.a.), einige Cyanophyceen (Oscillatoria, Cylindrospermum), diverse Algen (Spirogyra, Mougeotia, Stigeoclonium, Closterium, Cladophora u.a.) und auch höhere submerse Pflanzen (Ranunculus, Myriophyllum, Callitriche, Potamogeton, *Lemna trisulca* L. u.a.) hier eine Lebensmöglichkeit gefunden, so dass reichlich Produzenten vorhanden waren, die im Verein mit den abiotischen günstigen Lebensbedingungen

einer zahl- und artenreichen Gesellschaft von Konsumenten als Lebensgrundlage dienten.

Es überrascht deshalb nicht, dass viele Pflanzenfresser in dem Gewässer festzustellen waren, die nahezu allen in Binnengewässern vorkommenden zoologischen Taxa von den Protozoen bis zu den Vertebraten angehörten. So traten viele Rhizopoden (Difflugia-Arten und Verwandte, Cyphoderia, Arcella, Actinophrys) Ciliaten (vor allem Chilodon, Strobilidium und Holosticha), Rotatorien (Lepadella, Notholca, Rotaria, Proales, Mytilina, Synchaeta u.a.), der Gastrotriche *Chaetonotus hystrix* M. die Anneliden Chaetogaster und Stylaria und die Cladoceren Daphnia, Simocephalus und Macrothrix auf. Das Heer der Insekten war durch die Coleopteren Peltodytes, Haliplus, Hydrophilus, Laccobius, Hydrobius u.a., sowie durch zahlreiche Larven von Trichopteren (Polycentropidae, Limnophlidae u.a.), Ephemeropteren (Cloëon und Caenis) und die Dipteren (Chironomus, Paradixa, Polypedilum, Pentaneura u.a.) vertreten. Von den Gastropoden fanden sich *Lymnaea stagnalis* L. und *Galba pallustris* Müll. besonders häufig, und selbst Fische waren in Form einer kleinen Schule von *A. alburnus* L. vorhanden.

Wo Pflanzenfresser in solcher Mannigfaltigkeit lebten, fanden auch Fleischfresser ein reiches Nahrungsangebot. Hier ist abermals der Allesfresser *Actinophrys sol* Ehrenbg. zu nennen, weiter die Ciliaten Coleps, Spathidium, Lacrimaria, der Süsswasserpolyp Chlorohydra, Turbellarien der Gattung Planaria und Dendrocoelum. Anneliden verschiedener Gruppen (Stylaria, Haemopis Herpobdella), Hydracarinen (Hydrachna, Elais, Hydrophantes, Piona), die Wasserspinne, Argyroneta, im und die Wolfsspinne, Pirata, auf dem Wasser. Gross war die Zahl räuberischer Wasserwanzen (Notonecta, Naucoris, Nepa, Gerris, Hydrometra) und Wasserkäfer (Dytiscus, Hygrotus, Colymbetes, Agabus, Acilius, Graptodytes, Hydaticus, Cyrinus u.a.), sowie räuberische Larven von Odonaten (Lestes), Heteropteren (wie oben) Coleopteren (z. B. Dytiscinen und Hydrophiliden) und Megalopteren (Sialis).

Von abgestorbenen Pflanzenteilen (vor allem dem Buschrand entstammenden Fallaub) und Tieren ernährten sich Vegetabilien- und Aasfresser. Neben einigen Ciliaten (z. B. Stylonychia), Rotatorien (Dissotrocha), Gastrotrichen (Chaetonotus) und Nematoden (vgl. Chodorowska 1961) dominierten eine Anzahl Schnecken (Viviparus, Bithynia, Coretus, Planorbis, Hippeutis u.a.), Copepoden der Gattungen Cyclops und Canthocamptus und die sehr häufigen Wasserasseln, *Asellus aquaticus* L. Der Coleoptere *Helochares lividus* Forst, die Köcherfliegenlarven aus den Familien der Polycentropiden und Limnophiliden und Mückenlarven aus der Pentaneura- Costalis- und Procladius- Psilotanypus-Gruppe sind hier ebenfalls zu nennen.

Von den nicht näher untersuchten Parasiten wurden hier nur die Egel *Hemiclepsis marginata* (O. F. Müll.) und *Piscicola geometra* (L.) festgestellt. Auf Grund des Vorkommens bestimmter Tierarten wäre jedoch das Vorhandensein weiterer Parasiten möglich. So schmarotzen bekanntlich *Castradella granea* (M. Braun) in Asellus, *Diphyllobothrium latum* (L.) und *Depranidotaenia lanceolata* in Cyclops. Nach Styczyńska-Jurewicz (1966) wurden in derartigen Gewässern auch verschiedene Schistosoma-Arten, *Fasciola hepatica* L. und *Plagiorchis elegans*, beobachtet.

Verwessungs- und Mineralisationsprozesse nahmen in dem Grabenweiher einen normalen Verlauf, das beweist, dass auch die Bakterienflora (vgl. Fischer 1966) reichlich vertreten war, die ihrerseits wieder den Bakterienfressern aus dem Reich der Protozoen den Tisch deckten. Unter ihnen befanden sich sowohl einige bereits unter den Pflanzenfressern genannte Arten (Difflugia, Actinophrys, Chilodon), als auch Spezialisten (*Colpoda cucullus* O. F. Müll., *Halteria grandinella* (O. F. Müll.), *Euplotes patella* Ehrenbg., Vorticella- und Rhabdostyla-Arten u.a.).

Zweifellos schuf zum grossen Teil der das Kleingewässer fast ständig durchfliessende Graben die guten Bedingungen für eine so reiche Organismengesellschaft, wie sie hier angedeutet werden konnte. Er sorgte für sauerstoffreiches Wasser, für den Abtransport von Fäulnisstoffen, für den An- und Abtransport von wichtigen Nährstoffen für die Produzenten. Er sorgte auch für den Antransport neuer Organismen, die in dem Kleingewässer günstige Umweltfaktoren vorfanden sich in ihm entwickelten und fortpflanzten. Somit erfolgte auch nach Zeiten mit schlechten Bedingungen stets eine Neubesiedlung.

Im Auwaldtümpel war die Artenzahl der hier auftretenden Organismen wesentlich kleiner, wobei aber die Arten selbst in manchen Fällen massenhaft vorkamen. So konnten innerhalb der Gruppe autotropher Pflanzen die Flagellaten *Synura uvella* Ehrenbg., *Gymnodium aeroginosum* Stein, *Pandorina morum* O. F. Müll. und *Euglena proxima* Dang, als zeitweise „massenhaft auftretend" festgestellt werden. Neben anderen Flagellaten fanden sich Oscillatorien und Nodularia von den Cyanophyceen, nur wenige Diatomeen (*Fragilaria hanissoni* W. Smith und sel-

tener *Gyrosigma acumniatum* (Kütz.) Rabh., an Algen Closterium, Mougeotia, Spirogyra und Vaucheria, an Gefässpflanzen *Rorippa amphibia* Bess., die mit dem Fallen des Wasserstandes mehr und mehr ihre Landform ausbildete, und *Lemna minor* L., der im Verein mit *Vaucheria sessilis* Decandolle die hohe ökologische Bedeutung zukam, nach dem Abfallen des Wassers bis zum Grund auf diesem eine dichte, feuchte Decke zu bilden und den Grund so vor dem völligen Austrocknen zu bewahren. Hierbei fungierten freilich auch die umstehenden belaubten Bäume als Verdunstungsschutz.

Auch die Gruppe der Pflanzenfresser war, wenngleich verhältnismässig artenreich, doch längst nicht so vielgestaltig wie im Grabenweiher. Es zeigten sich Difflugia- und der Gattung nahestehende Arten, Arcella, Actinophrys aus der Klasse Rhizopoda, kaum Ciliaten, einige Rotatorien (Colurella, Testudinella, Lepadella u.a.), die Anneliden *Stylaria lacustris* (L.) und *Nais variabilis* Pig. und die Cladoceren *Chydorus sphaericus* (O. F. Müll.) und die sehr häufige *Daphnia pulex* Geer. Von den Insekten waren hinsichtlich der Artenzahl wieder die fluggewandten Käfer die Überlegenen (Haliplus, Helophorus, Ichthebius, Limnoxenus, Hydrobius, Laccobius, Anacaena). Von den Wasserwanzen traten *Hesperocorixa sahlbergi* Fieb. und. *S. striata* L. auf. An Larven fanden sich vor allem Cloeon sowie Paradixa, Culicini, insbes. Aedes (vgl. Chodorowski 1958b) und Chironomus von den Dipteren und Limnophilidenlarven von den Trichopteren. Die Schnecke *Galba palustris* Müll. war häufig.

Für die Fleischfresser galt dasselbe wie für die Pflanzenfresser: Die Artenzahl war geringer als im Grabenweiher. Einige Arten aber traten wieder sehr häufig bis massenhaft auf. Von den Protozoen sollen Actinophrys, Lacrimaria und Coleps genannt werden. Von den Turbellarien war *Planaria torva* (O. F. Müll.) vertreten, daneben *Dendrocoelum lacteum* (O. F. Müll.) und *Mesostoma productum* O. Schm. Auch die Anneliden Stylaria (s.o.) und Chaetogaster waren nicht selten. In grosser Zahl bevölkerten Hydracarinen den Tümpel, vor allem *Hydrophantes ruber* (Geer), *Piona nedata* (Müll.) und *P. uncata* (Koenike). An Wasserwanzen wurden Nepa, Gerris-Arten und Hydrometra festgestellt. Von den zahlreichen räuberischen Wasserkäfern traten *Hydroporus palustris* L. massenhaft und *Acilius sulcatus* L. häufig auf. An Coleopterenlarven waren die von Ilybius und Hydroporus am stärksten vertreten. Die räuberische Mückenlarve Chaoborus war ebenfalls nicht selten. Genannt werden müssen auch die zahlreichen grossen Stichlinge (*Gasterosteus aculeatus* L.) die im Frühjahr mit dem aus dem blinden Arm übertretenden Wasser in das Tümpelgebiet einwanderten, hier zur Brut schritten, dann aber samt ihrer Nachkommenschaft während der frühsommerlichen Trockenphase zugrunde gingen und wesentlich zur Düngung des Beckens beitrugen.

Von den Vegetabilien- und Aasfressern fanden sich vor allem der Annelide *Lumbriculus variegatus* (Müll.), der Copepode *Megacyclops viridis* (Jur.) (seltener *Cyclops strenuus* s. lat.), die Wasserassel *Asellus aquaticus*, die Collembolen *Podura aquatica* L. und *Isotoma viridis* Bourl., Limnophiliden-, Chironomiden- und Tipulidenlarven sowie die Schnecken *Planorbarius corneus* L. und *Anisus leucostomus* Mllt. in grosser Zahl.

Hinsichtlich der Parasiten gilt im grossen und ganzen das gleiche wie für den Wiesentümpel. Gefunden wurde der Egel *Glossiphonia complanata* (L.).

An Bakterienfressern traten häufig Difflugia und verwandte Gattungen, Holosticha und *Aspidisca lynceus* Ehrenbg. auf. Der saprophytische Flagellat *Cryptomonas erosa* Ehrenbg. nahm hinsichtlich seiner Ernährung eine Sonderstellung ein, die jedoch ökologisch hier nicht weiter ins Gewicht fiel.

Die inmitten von Kalkfelsen gelegenen Brandungslachen waren — wie bereits dargestellt — durch die ausserordentlich starken Schwankungen ihrer physikochemischen Faktoren charakterisiert. Während auf den Felsen eine ständige Organismengesellschaft anzutreffen war, die aus Aufwuchs bildenden Algen (Colothrix, Microspora, Ulothrix, Pleurocapsa) bestand, in der sich bei Benetzung eine reiche Mikroorganismenwelt entwickelte, wiesen die flachen Brandungslachen kaum einen nennenswerten Bestand an Lebewesen auf. Schon von mittelschweren Seen wurde Wasser in die entsprechenden Vertiefungen geschlagen. Je nachdem, ob es sich dabei um sandführende Grundseen oder um Oberflächenwellen handelte, wurden die Becken mit Sand gefüllt oder ausgewaschen. Dadurch bestand für die meist zarten, feinen Meeresorganismen immer wieder die Gefahr zerrieben zu werden. Oder der Zufluss durch Regen war so stark, dass die Aussüssung die Organismen tötete. Oder die rasch erfolgende Austrocknung brachte alles aktive Leben zum Erliegen. Trotzdem konnte sich in Zeiten ruhiger, gleichmässiger Bespannung der Lachenbecken, vorwiegend an deren Rändern, durch die o.a. Algen Aufwuchs mit einer zwar nur kurzlebigen, aber doch verhältnismässig vielgestaltigen Organismen-

welt entwickeln. Hierbei traten vor allen die Produzenten — eben die genannten Algen, Flagellaten (Cryptomonaden und Eugleniden) und Diatomeen (neben zwei häufigen Achnathes-Arten noch Bacillaria, Navicula, Grammatophora, Pleurosigma, Striatella u.a.) — stark in den Vordergrund. Das den Grund bildende Kalkgestein war auch häufig von endolithisch lebenden Cyanophyceen (Microcystis, Hyella u.a.) durchsetzt, was zu seiner Aufbereitung beitrug. Die Tierwelt hingegen war arm. Zwar fanden sich noch ciliate Pflanzen- und Bakterienfresser, wie Chilodonella, Protocrucia, Keronopsis u.a., jedoch blieben höher organisierte Tiere — abgesehen von hauptsächlich Vegetabilien fressenden Nematoden — wegen der zur Ernährung fehlenden Voraussetzungen und zeitlich zu kurzen Entwicklungsmöglichkeiten aus. So konnten sich nur wenige räuberische Ciliaten, z. B. Euplotes und Diophrys, für kurze Zeit hier am Leben halten.

Hingegen brachten die Wellen oft in reicher Zahl dem freien Wasser des Meeres entstammende Organismem — Nauplien, Harpacticiden, manchmal grössere Isopoden, wie Idotea und Dynamene, oder gar kleine Grundfische, z. B. Callionymus — mit in die Brandungslachen. Algen wurden hin und wieder in grösseren Mengen eingeschwemmt. Es waren meist vom flachen Grund gerissene zartere Formen wie Ceramium, Callithammnion, Cladophora, und Enteromorpha. Aber Tiere wie Pflanzen des offenen Meeres hielten sich nicht lange im stagnierenden Wasser der Lachen. In flachen Becken fielen sie der Austrocknung anheim, in tieferen gingen sie nach dem Absterben in Fäulnis über, wodurch sich das Wasser mit Schwefelwasserstoff derart anreicherte, dass jegliches Leben höherer Organismen zusammenbrach.

3. ÖKOLOGISCHE KONNEXE INNERHALB DER UNTERSUCHTEN KLEINGEWÄSSER

Nach der Vorstellung der drei Untersuchungsbeispiele kann auf die zu Beginn der Abhandlung aufgeworfene Problemstellung zurückgekommen werden, welchen funktionellen ökologischen Einheiten Grabenweiher, Waldtümpel und Brandungslachen im einzelnen zuzuordnen sind. Handelt es sich um Biotope und bei den in ihnen lebenden Organismenansammlungen um Biocönosen, oder sind die entsprechenden Grössen als Habitate und Synusien anzusprechen? Nunmehr bekannt, müssen deshalb die angeführten Beispiele einer Betrachtung hinsichtlich ihrer Autarkie, unterzogen werden (vgl. p. 125 ff.), d. h., es ist zu untersuchen, ob die in den Kleingewässern verlaufenden Stoffumsatzprozesse dem Modell geschlossener oder offener materieller Systeme entspricht (Löther 1966, Eichhorn et al. 1967).

Diese Frage soll auf jeweils dreifache Weise Beantwortung finden, und zwar in der Untersuchung und Darstellung der Sauerstoff-Kohlenstoff-Verhältnisse, des Stickstoff-Kreislaufes und des mit diesem eng verknüpften Nahrungsnetzes. Die Funktion der drei Komplexe ist für die ökologischen Einheiten existenznotwendig,

1. die Sauerstoff-Kohlenstoff-Verhaltnisse für die Assimilation, Dissimilation, Respiration und Aufrechterhaltung des Bau und Betriebsstoffwechsels der Organismen,

2. der Stickstoff-Kreislauf zur Formierung des Stickstoffs zum Aufbau des Eiweisses und verwandter Verbindungen sowie zur Entwicklung der autotrophen Pflanzen, deren grundlegende Bedeutung als Produzenten für die Konsumenten, schliesslich,

3. in dem Nahrungsnetz zum Ausdruck kommt.

Alle drei Komplexe bilden zwar untereinander und zusammen mit

anderen, hier nicht aufgeführten Komplexen Konnexe, weisen aber andererseits eine gewisse Selbständigkeit auf. Sie werden deshalb voneinander gesondert betrachtet, wodurch die Darstellung an Übersichtlichkeit gewinnt.

Im Grabenweiher lassen sich hinsichtlich der Sauerstoff--Kohlenstoff-Varhältnisse (Abb. 1) folgende Feststellungen treffen: Die

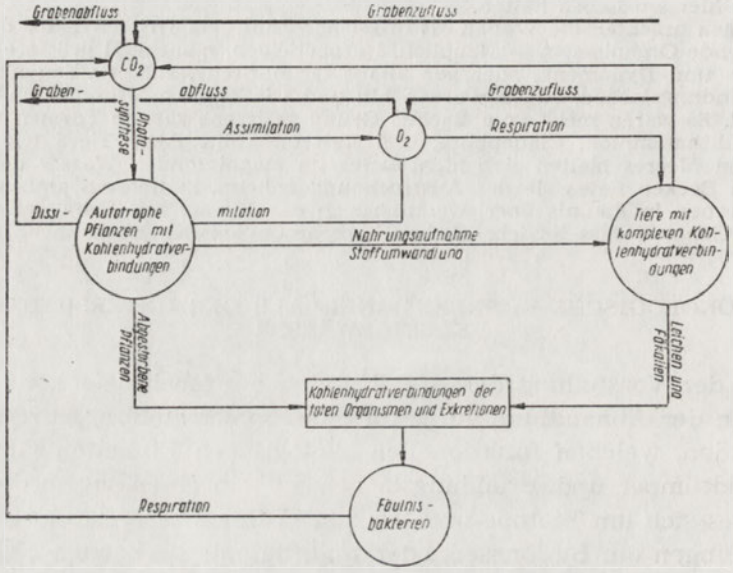

Abb. 1. Die Sauerstoff-Kohlenstoff-Verhältnisse im Grabenweiher

autotrophen Pflanzen produzieren im Zuge der Assimilation, Dissimilation und Photosynthese Sauerstoff und Kohlendioxid innerhalb einer geschlossenen Wirkungskette. Tiere und Fäulnisbakterien veratmen ebenfalls CO_2, das den autotrophen Pflanzen beim Aufbau komplexer Kohlenhydratverbindungen und danach den pflanzenfressenden Tieren bei der Nahrungsaufnahme zugute kommt. Da Pflanzen und Tiere absterben, finden Fäulnisbakterien und -pilze damit ihre Nahrungsgrundlage und bereiten die in den Tier-und Pflanzenleichen gespeicherten Kohlenhydratverbindungen wieder auf. Die Sauerstoff-Kohlenstoff-Verhältnisse würden in Form eines geschlossenen Systems vorliegen, hätte nicht der Grabenzufluss eine erhebliche Bedeutung für den Grabenweiher. Wird er gestoppt, führt die Stagnation des Wassers innerhalb kurzer Zeit zu einer derart starken Schwefelwasserstoffentwicklung, dass die meisten ursprünglich vorhandenen Organismen absterben. Das aufgehobene biocönotische Gleichgewicht stellt sich aber sofort wieder ein, wenn der Zufluss O_2-reichen Wassers durch den Graben wieder erfolgt. Der Grabenweiher erhält also vom Grabenzufluss einen Input und gibt

durch den Grabenabfluss einen Output ab. Dadurch entstehen charakteristische Randelemente die auf die Offenheit dieses ökologischen Systems hindeuten.

Bei der Betrachtung des Stickstoffkreislaufes im Grabenweiher (Abb. 2) verhalten sich die Komponenten ähnlich. Fäulnisbakterien bereiten die abgestorbenen Organismen mit von der Jahreszeit abhängigen unterschiedlichen Intensität auf (F i s c h e r 1960, 1961) und führen die mi-

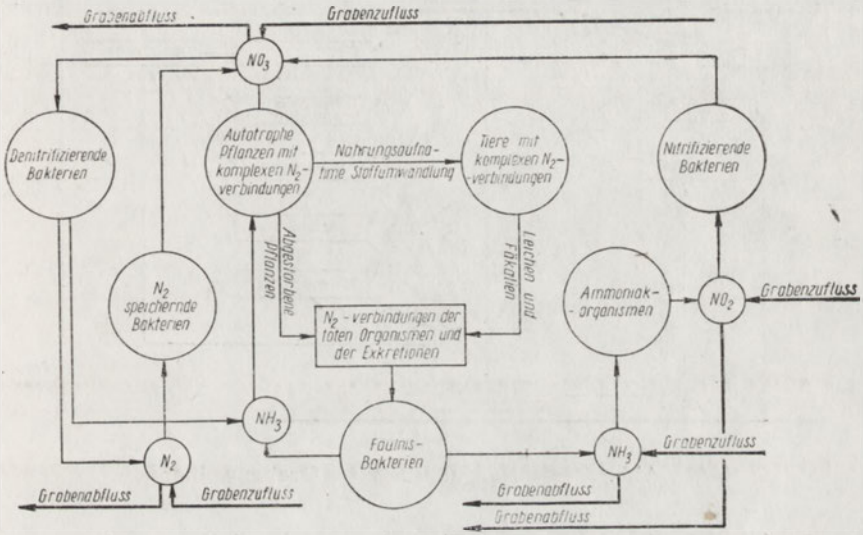

Abb. 2. Die Stickstoffverhältnisse im Grabenweiher

neralisierten Stickstoffverbindungen über teils lineare, teils geschlossene Wirkungsketten dem Verbraucher in Gestalt autotropher Pflanzen wieder zu. Diese wiederum ernähren die Tiere. Aber alle Stickstoffverbindungen werden dem Grabenweiher auch von aussen durch den Grabenzufluss zugeführt, während ein anderer Teil derselben dem Kleingewässer durch das abfliessende Wasser wieder entzogen wird. Das Schema des Stickstoffkreislaufes weist also ebenfalls eine ganze Reihe von Randelementen auf, die es aus der Geschlossenheit herausführen. Über die diesbezüglichen Einflüsse seintens des Grabens auf den Grabenweiher fehlen leider genaue Untersuchungen. Im allgemeinen aber ist es so, dass ein Fliessgewässer einemstehenden Gewässer weniger Nährstoffe (und also auch N-Verbindungen) zu-als abführt. Gemessen an den im Grabenweiher herrschenden Sauerstoff-Kohlenstoff-Verhältnissen ist wahrscheinlich auch der Stickstoffhaushalt einer massgeblichen Regulation durch den Grabenzufluss unterworfen.

Im Hinblick auf die regulatorischen Einflüsse des Grabens auf das Kleingewässer hinsichtlich seiner chemischen Faktoren überrascht es nicht, dass ein vollständiges Nahrungsnetz (Abb. 3) in ihm vorzufinden

ist. Man könnte angesichts dessen geneigt sein, von einer Biocönose zu sprechen. Jedoch weisen eingehende, einen kompletten Jahreszyklos erfassende Untersuchungen nach, dass die funktionelle ökologische Einheit "Grabenweiher" zusammenbricht, sobald der Durchfluss des Grabens

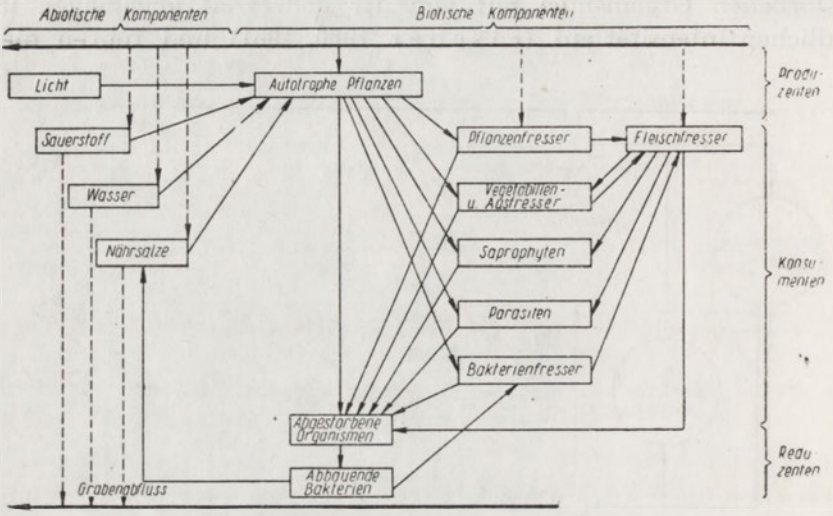

Abb. 3. Das Nahrungsnetz im Grabenweiher

gestoppt ist. Die in derartigen Situationen ebenfalls zu einem grossen Teil absterbenden Organismen werden nach dem erneuten Einsetzen eines Zuflusses durch Antransport vom Graben her und auch bei Transgression der umliegenden Wiese von dort her, in jedem Falle aber von aussen, wieder ersetzt. Da sie im Grabenweiher günstige Lebensbedingungen vorfinden, verbleiben sie dort und bilden gesunde, im Gleichgewicht befindliche Populationen, bis der Durchfluss wieder ausbleibt, womit eine erneute Krisis einhergeht. In dem Grabenweiher präsentiert sich also kein autarkes ökologisches System, sondern ein von einem autarken System abhängiges ökologisches System, dessen Existenz dem Vorhandensein eines ihm übergeordneten Ökosystems und seiner Einflussnahme unterliegt. Der Grabenweiher ist in diesem Sinne mehr zur ökologischen Einheit "Graben" zu rechnen, als umgekehrt der Graben zum ökologischen System des Grabenweihers. Somit ist der Grabenweiher als Habitat, die in ihm lebende Organismenwelt als Synusie zu klassifizieren.

Wie gestaltet sich der gleiche Sachkomplex im Auwaldtümpel? Im Prinzip folgen die Funktionsabläufe der Sauerstoff-Kohlenstoff-Verhältnisse (Abb. 4), des Stickstoffkreislaufes (Abb. 5) und im Nahrungsnetz (Abb. 6) den gleichen Schemata wie im Grabenweiher (Abb. 1 bis 3). Doch besteht ein tiefwirkender Unterschied: Dem Waldtümpel fehlt

der Durchfluss. Einmal bespannt, ist er — abgesehen von durch Luftströmungen, Regenfällen und Temperaturunterschieden hervorgerufenen Zirkulation — ein fast absolut stehendes Gewässer. Alle in ihm stattfindenden Prozesse sind in sich geschlossene Kreisläufe. So werden die Sauerstoffe und Kohlenstoffe ebenso wie die Nitratverbindungen durch Abläufe, die nur im Gewässer selbst stattfinden, regeneriert, und die innerhalb des Nahrungsnetzes agierenden Organismen entstammen dem Tümpel selbst.

Einschränkungen müssen jedoch auch hier vorgenommen werden:

1. Ohne den Zugang des von den umstehenden Bäumen stammenden Fallaubes würde der Tümpel nicht die Menge an Nährstoffen enthalten,

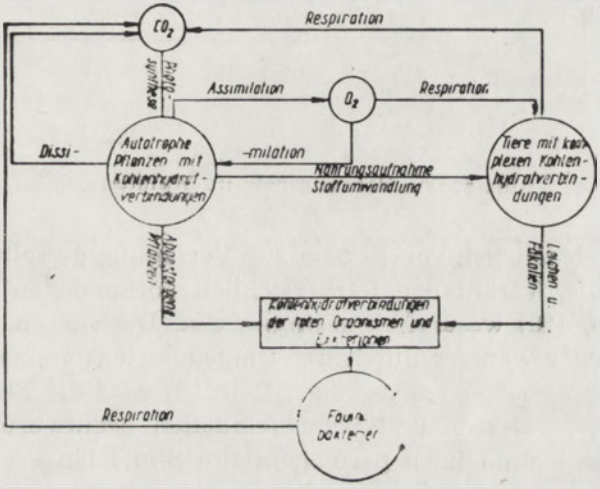

Abb. 4. Der Sauerstoff-Kohlendioxid-Kreislauf im Waldtümpel

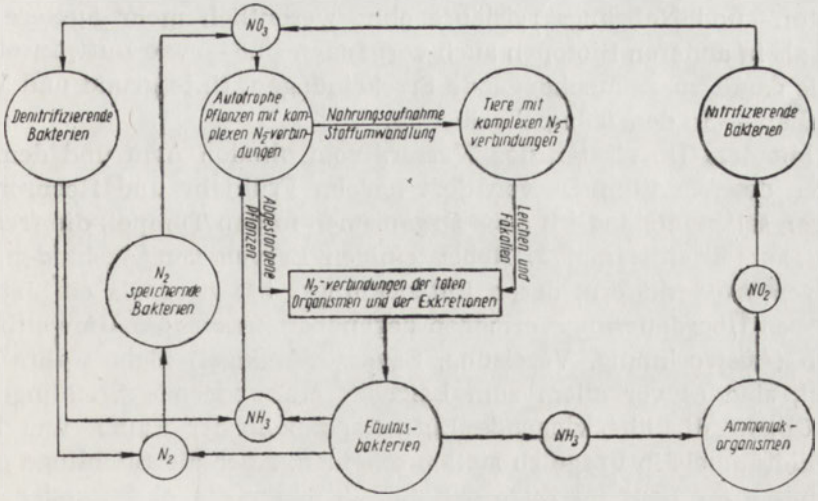

Abb. 5. Der Stickstoffkreislauf im Waldtümpel

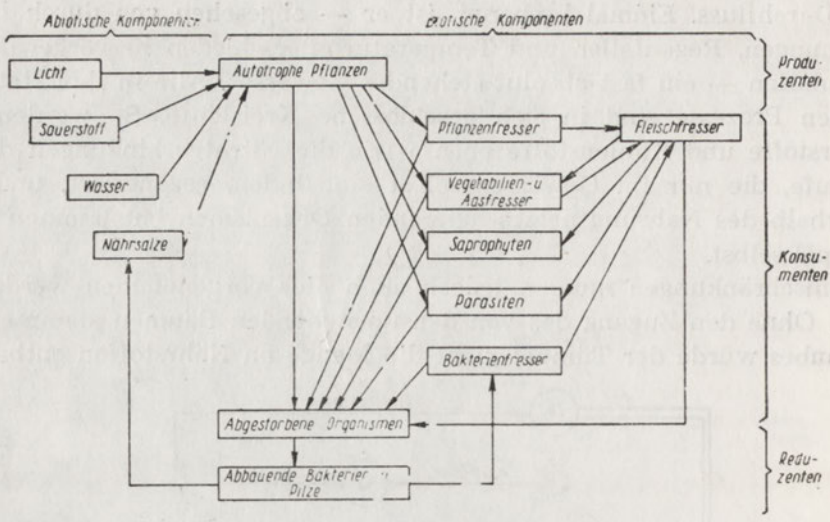

Abb. 6. Das Nahrungsnetz im Waldtümpel

die ihm dadurch jährlich von Neuem zur Verfügung gestellt wird. Sicher würde dann die Anzahl der jetzt reichlich vorhandenen Vegetabilienfresser (vgl. p. 128) wesentlich geringer sein. Doch ist nicht jedes Gewässer mehr oder weniger durch der Umgebung enstammende Faktoren in irgend einer Weise gekennzeichnet? Deutlich wird die Frage durch die Natrongewässer, Salzseen und Schwefelquellen beantwortet, mit deren aus dem Boden stammenden permanent (im Sinne längerer, aber endlicher Zeiträume) gelösten Salzen oder Gasen, mit denen das im Waldtümpel vorhandene Laub und seine Destruktion und Mineralisierung verglichen werden kann. Trotz allem aber wikkeln sich die Geschehnisse der Stoff- und Nahrungskreisläufe ohne wesentlich mehr äussere Einflüsse als in anderen Biotopen auch vorhanden sind — wie Luft, Insolation und die damit zusammenhängende Erscheinungen, Untergrund und Wasserhaushalt — in dem Tümpel selbst ab.

2. Mit dem Übertreten des Wassers vom blinden Arm und dem Bespannen des Waldtümpels von dort her im Frühjahr und Hochsommer gelangen selbstverständlich auch Organismen in den Tümpel, die fremden Lebensräumen entstammen. Neben einigen Larven von Aeshniden, und grösseren Wasserkäfern, deren Entwicklungszeit länger als ein Jahr ist und deren Überdauerungsvermögen gegenüber pessimalen Umweltbedingungen (Austrocknung, Vereisung, Sauerstoffmangel) nicht wahrscheinlich ist, sind es vor allem zum Laichakt einwandernde Stichlinge, die im Frühjahr die überwiegende Eigenständigkeit der Fauna und Flora des Waldtümpels in Frage zu stellen scheinen. Aber die Stichlinge gehen mit samt ihrer Brut im Zuge der zum Sommer hin einsetzenden Austrocknung zugrunde und bedecken dicht an dicht den Boden der Restla-

chen (Kühlmann 1963), zersetzt und mineralisiert auch ihrerseits einen Beitrag zur Düngung des temporären wiederentstehenden Gewässers liefernd.

Nach der Austrocknung stellen sich im Gebiet des Tümpels echte Waldorganismen ein. Eine ganze Anzahl von Fliegen (*Lucilia silvarum* Mg., *Sarcophaga albiceps* Mg., Dolichopodidae, Borboridae und von den Anthomyiidae vor allem *Ophyra leucostoma* Wied., *Hydrotaea dentipes* Fabr. und *Hylemya variata* Fall.) halten sich zufällig oder angelockt von den verwesenden Stichlingen im Bereich auf. An Käfern gesellen sich vorwiegend Carabiden (*Elaphrus cupreus* Dfsch., *Bembidion dentellum* Thunbg. und *B. semipunctatum* Donov., *Agonum fuliginosum* (Panz) u.a.) und Staphyliniden (*Gnypeta ripicola* Kiesw., *Philontus politus* L., *Platystethus cornutus* Grav.) hinzu, die Hymenoptere *Selandria serva* (F.) und die kleine, feuchtigkeitsliebende *Tetrix subulata* (L.) (Orthoptera) tritt auf.

Es scheint, als hätte damit die Organismengesellschaft des Waldtümpels ihr Ende gefunden. Jedoch haben all die vielen echten Tümpelorganismen, angepasst an das Leben in ephemeren Gewässern im Verlauf ihrer phylogenetischen Entwicklung irgend eine Möglichkeit des Überdauerns der Trockenzeit gefunden. Sie enzystieren, bilden Dauereier, Sporen, beenden ihre Larvenentwicklung schneller (Chodorowski 1958 a), verfallen in einen Starrezustand — bekannte Vorgänge, die hier nicht näher zu schildern sind. Aber auch Organismen, die über derartige Überdauerungsstadien nicht verfügen, vermögen als echte Bewohner ephemerer Gewässer Trockenzeiten zu überleben. Denn für sie ist der Waldtümpel gar nicht nicht mehr vorhanden. Er ist lediglich einige Zentimeter unter die Oberfläche des Tümpelgrundes gesunken. Eine dichte, feuchte Decke von *Lemna minor* und des auch an der Luft fortlebenden *Vaucheria sessilis*-Rasens verhindert im Verein mit den schattenspendenden Bäumen eine weitere Verdunstung und Austrocknung des Schlammes (vgl. p. 130). Dort hinein ziehen sich eine ganze Anzahl gegen die Austrocknung resistenter (Klekowski 1961, 1966), auch im Wasser den Grund bewohnende Organismen (Lumbriculus, Lymnaea, Tipulidenlarven) zurück: der Schlamm dient ihnen als Refugium. Die auftretenden terrestrischen Tiere des Waldes aber sind lediglich einem zeitweilig bestehenden Stratum zuzuordnen, ähnlich wie die Bewohner der aus einem Gewässer herausragenden oder auf ihm schwimmenden Pflanzen.

Ökologisch betrachtet, ist also das Funktionssystem „Tümpel" jetzt, obwohl es eine freie Wasseransammlung vermissen lässt, durchaus noch vorhanden; denn seine Lebewelt existiert, und auch die Bakterienflora hat nicht die Aufbereitung des anfallenden organischen Materials unterbrochen. Es ist lediglich in eine mehr oder weniger stark gehemmte, fast inaktive Phase eingetreten, wie sie im Winter der temperierten Zonen auch in terrestrischen Biotopen herrscht, ohne dass ernsthaft

bestritten werden könnte, dass die Wälder und Steppen Ökosysteme seien. Schon im Juli führt der Waldtümpel in der Regel durch die einsetzenden hochsommerlichen Regenfälle wieder Wasser. Im Herbst wird die aktive Phase zwar durch einen abermaligen Rückgang des freien Wassers wieder unterbrochen, jedoch ändert auch das nicht an dem kontinuierlichen Fortbestehen des Waldtümpels als selbstständige ökologische Einheit, dessen einzelne, in den Skizzen dargestellte Funktionssysteme in sich geschlossen verlaufen. Der hier dargestellte Waldtümpel ist deshalb trotz der Kleinheit als Biotop mit einer eigenständigen Biocönose anzusprechen.

Gegenteilig fällt die Beantwortung der Problemstellung im Falle der Brandungslachen aus. Zwar besteht auch hier, sind die Lachenbecken einmal mit Wasser gefüllt, zunächst ein durch biologische Stoffwechselvorgänge hervorgerufenes Sauerstoff-Kohlendioxid-Gleichgewicht (Abb. 7). Die Aufbereitung der von den abgestorbenen Organismen

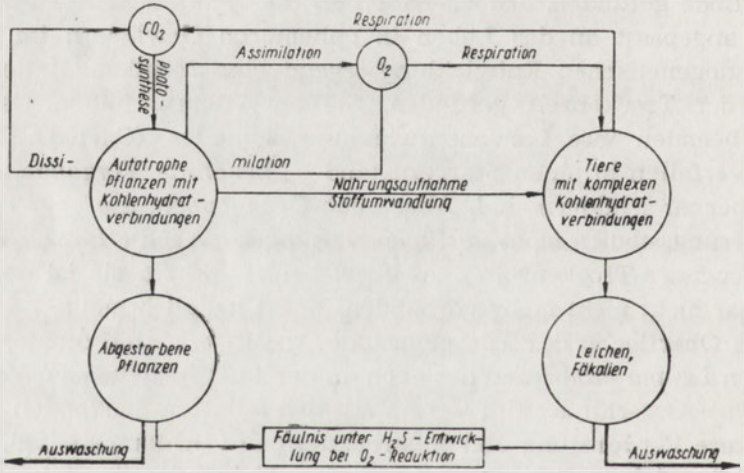

Abb. 7. Die Sauerstoff-Kohlenstoff-Verhältnisse in den Brandungslachen

herrührenden komplexen Kohlenhydratverbindungen durch Mikroorganismen jedoch bleibt aus, da entweder die Tier- oder Pflanzenleichen durch überkommende Brecher wieder ausgespült werden, oder — im Falle der flachen tellerförmigen Lachen — dieselben austrocknen, oder in den tieferen, rinnenförmigen Becken Fäulnis mit starker Bildung von Schwefelwasserstoff einsetzt, was zum Zusammenbruch wesentlicher biotischer und abiotischer Vorgänge führt. Die Aufbereitung der Kohlenhydrat- wie auch der Stickstoffverbindungen (Abb. 8) durch die Fäulnisvorgänge nimmt zwar ihren Fortgang, gelangt jedoch nicht zum Abschluss. Immer erfolgt in verhältnismässig kurzen Zeitabständen eine Auswaschung der Brandungslachen durch Brecher, so dass jegliche Zir-

kulation stets unterbrochen wird. Die Konnexe des Nahrungsnetzes demonstrieren ein gleichsinniges Schema (Abb. 9).

Alle einem autarken Ökosystem eigenen Elemente werden den Brandungslachen durch Brecher und Spritzer von aussen zugeführt und

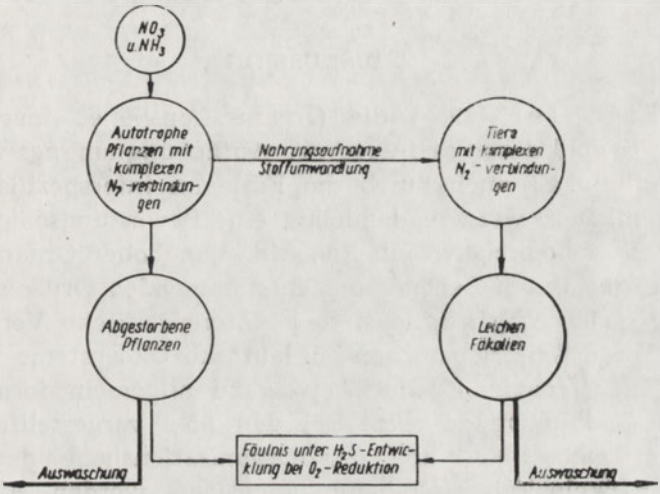

Abb. 8. Die Stickstoffverhältnisse in den Brandungslachen

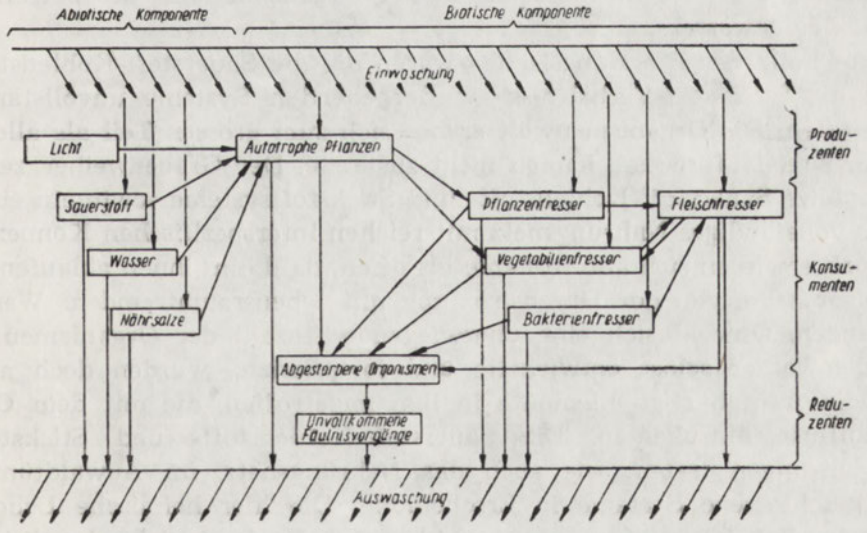

Abb. 9. Das Nahrungsnetz in den Brandungslachen

durch Auswaschungen wieder genommen. Die Brandungslachen zeigen deshalb stark reduzierte, gleichsam rudimentär wirkende, deutlich offene Funktionssysteme. Sie gehören somit als Habitate mit den in ihnen

kurzlebigen Synusien, die unter Umständen mit den Biochorien und Chorioc önosen der terrestrischen Ökologie vergleichbar (oder etwa gleichzusetzen) sind und so eventuell näher bezeichnet werden können, einem übergeordneten Ökosystem, wahrscheinlich dem eines Supralitorals, an. Genauere Untersuchungen hierüber fehlen jedoch.

4. DISKUSSION

Wenn Tischler (1965) die Organisationshöhe einer Lebensgemeinschaft "sowohl durch den Grad der Aufhebung anfangs vorhandener Zufallsbesiedlung als auch durch die Fülle an interspezifischen Verknüpfungen" misst so weist er damit auf eine Bewertungsmöglichkeit der verschiedenen ökologischen Einheiten hin. Von hoher Organisation sind hiernach die nur ihrem Lebensraum entstammenden Organismengesellschaften, die gleichzeitig möglichst viele interspezifische Verknüpfungen aufweisen. Diese Kriterien mögen für autarke Ökosysteme unter Umständen genügen, scheinen jedoch etwas zu allgemein formuliert und nicht umfassend genug zu sein. Bei den hier vorgestellten Kleingewässern soll eine Bewertung der Organisationshöhe der gesamten funktionellen ökologischen Einheiten angestrebt werden. Als Kriterien werden angesehen:

1. der Systemcharakter der abiotischen und biotischen Prozesse und,
2. der Grad der Eigenständigkeit der Organismenwelt des betreffenden Kleingewässers.

Im Falle der Brandungslachen waren die die Sauerstoff-Kohlenstoff- und die Stickstoff-Verhältnisse wiedergebenden Systeme unvollständig und offen. Die Organismenwelt erwies sich zum grossen Teil als allochthon. Kreislaufprozesse kamen nicht zustande. Der Grabenweiher zeigte komplette Sauerstoff-Kohlenstoff- und Stickstoffsysteme sowie ein ebenfalls vollständiges Nahrungsnetz mit reichen interspezifischen Konnexen. Jedoch erwiesen sich alle Systeme als offen, da die in ihnen ablaufenden Kreisprozesse von der Durchströmung mit lebensraumfremdem Wasser abhingen. Obwohl sich eine überwiegende Anzahl der Organismen im Grabenweiher selbst entwickelte und fortpflanzte, wurden doch auch ständig fremdbürtige Elemente in ihm angetroffen, die mit dem Grabenzufluss hinzukamen. Die Sauerstoff-Kohlenstoff- und Stickstoff--Umsetzungen traten, wie auch das Nahrungsnetz, im Auwaldtümpel als geschlossene Systeme in Erscheinung. Die hier heimische Lebensgemeinschaft war überwiegend autochthon. Es lässt sich also in der Reihe: Brandungslachen — Grabenweiher — Auwaldtümpel deutlich eine zunehmende Organisationshöhe der ökologischen Einheiten erkennen.

Die vielgestaltige Gruppe der Kleingewässer vereint also funktionelle ökologische Einheiten mit stark differenzierten ökologischen Grundcharakteren in sich. Es treten hier sowohl autarke als auch von einer bis

vielen Aussenbedingungen abhängige ökologische Einheiten auf. Innerhalb dieser Gruppe werden also die bezüglich der Autarkie eines Ökosystems zu erwartenden "Grenzfälle" zu suchen sein, hier vielleicht besser als „schwer erkennbare Fälle" bezeichnet, deren Erkennbarkeit mit der Erarbeitung des Systemcharakters der betreffenden ökologischen Einheit unter Zuhilfenahme einer gründlichen ökologischen Analyse möglich wird. Mit der Erarbeitung des Systemcharakters aber fällt die Entscheidung, ob es sich bei dem Untersuchungsobjekt um eine funktionelle Einheit mit in sich geschlossenem, selbständigem oder offenem und abhängigem Systemcharakter handelt. Danach bilden ökologische Einheiten mit geschlossenem Systemcharakter immer Gesamtsysteme, ökologische Einheiten mit offenem Systemcharakter hingegen immer Teilsysteme.

Hieraus ergeben sich hinsichtlich der ökologischen Terminologie bestimmte Konsequenzen, die möglicherweise als Beitrag zur Herausbildung einer einheitlichen und präzisen Wissenschaftssprache gewertet werden können, einer seit längerer Zeit aktuellen Forderung. Denn „die gesamte Biologie befindet sich terminologisch auf einem unglaublich primitiven Stadium" (Remane 1956). Ihr Mangel an eindeutigen Termini, klar definierten Begriffen und theoretischem Fundament hemmt heute bereits die Weiterentwicklung der Biologie und ihr praktisches Wirksamwerden (vgl. MacFadyen 1967, Phillipson 1967). Medwecka-Kornas (1967) stellt im Hinblick auf die Ökologie fest. "Ecosystems are units defined after the mutual relation of components. Their rank is not established and they may be considered more or less widely. In productivity studies, it is necessary to find easy and practical criteria for the definition of ecosystems in the field". Sicher beziehen diese Worte ihre Gültigkeit nicht nur auf Kosten des Mangels geeigneter Kriterien zur Definition der Ökosysteme bei Produktionsanalysen, sondern gelten für alle synökologische Forschung schlechthin. Die Notwendigkeit, die Ökosysteme mittels präziser Kriterien zu definieren, wird durch die irrigen Meinungen von Schwenke (1953, 1955), und Balogh (1958) noch hervorgehoben, die die abiotische-biotische Dualität für überflüssig erachtend nicht mehr von Biocönose, Biotop und Ökosystem sprechen wollen, sondern stellvertretend für alles nur noch von Biocönosen.

Die Gruppe der in sich geschlossenen, selbständigen ökologischen Einheiten, die Gesamtsysteme darstellen, ist — wohl charakterisiert und als "Ökosystem" bezeichnet — zu einem feststehenden Begriff geworden. Wie jedoch die weitere Einordnung der Brandungslachen und des Grabenweihers andeutete, ist im Hinblick auf die offenen and abhängigen Kleingewässersysteme — etwa analog der in der terrestrischen Ökologie gebräuchlichen Unterteilungen — zu erwarten, dass entsprechende Untersuchungen zur Aufstellung mehrerer ökologischer Grundtypen

führen werden. Zum Zweck einer besseren Übersichtlichkeit wird deshalb vorgeschlagen, zunächst den Begriff Ökosystem allen ökologischen Einheiten, gleichgültig, ob mit geschlossenem oder offenem Systemcharakter, überzuordnen. Das würde auch mit den Gedanken des Begründers diese wichtigen Grundbegriffes übereinstimmen, der äusserte: "These ecosystems, as we may call them, are of the most various kinds and sizes. They form one category of the multitudinous physical systems of the universe, which range from the universe as a whole down to the atom" (Tansley 1935).

Der Begriff Ökosystem erhält damit seinen generellen Charakter zurück und wird endlich wieder — wie von seinem Begründer gefordert — generalisierend auf alle ökologischen Einheiten angewandt. Entsprechend der Zusammensetzung eines Ökosystems aus einer abiotischen und einer biotischen Komponente, erweist sich die Anwendung der Termini „Ökotop" für die abiotische und „Ökocönose" für die biotische Komponente eines Ökosystems als folgerichtig (im Gegensatz zu Palissa (1958), der den Begriff „Ökotop" für die Umwelt des Organismus setzt). Beide Ausdrücke stellen ebenfalls generalisierende Begriffe dar und vertreten die abiotischen und biotischen Komponenten aller auftretenden funktionellen ökologischen Einheiten gleichermassen. Alle ökologischen Einheiten mit einem in sich geschlossenen, selbständigen Systemcharakter sind entsprechend ihrem Auftreten als Gesamtsysteme, als Holökosysteme, zu benennen. Diesen können nunmehr die ökologischen Einheiten, die einen offenen, abhängigen Systemcharakter aufweisen und als Teilsysteme fungieren, als Merökosysteme gegenübergestellt werden. Abgesehen von der logischen Forderung werden damit gleichzeitig der Darstellungsweise weitere Möglichkeiten eröffnet, so dass im Falle offener Systeme nicht fortwährend nur von z.B. „Habitat plus Synusie" oder von „ökologischen Einheiten" schlechthin gesprochen werden muss.

Die Ökosysteme „also overlap, interlock and interact with one another" (Tansley 1935). Mit dem Vorhandensein offener und geschlossener Ökosysteme in der Natur und der Zugehörigkeit offener zu geschlossenen Ökosystemen deutet sich eine unterschiedliche Qualität, eine bestimmte Wertstufung, eine Rangfolge, eine „enkaptische Hierarchie" innerhalb der Ökosystembegriffe an (Schellhorn 1965, 1969).

Ein Beispiel aus dem Bereich der hier angeführten Untersuchungsgewässer soll das erläutern: Auf dem Grunde des Waldtümpels sind Algenwatten häufig. Sie werden von Vaucheria, Spirogyra und Mougeotia gebildet. Die einzelnen Algenfäden zeichnen sich durch einen reichlichen Aufwuchs der hier kettenbildenden Diatomee *Melosira varians* C.A.AG. aus. Einige Protobionten zeigen gegenüber den einzelnen Algenfäden eine positive Thigmotaxis. Es sind dies Thecamöben der Difflugia-Gruppe und *Arcella hemisphaerica* Py. sowie einige holotriche Ciliaten. Im Wiesengrabenweiher traten ebenfalls Algenwatten auf, die entweder von Spiro-

gyra oder von Vaucheria gebildet wurden. Auf den Spirogyra-Fäden zeigten sich die Diatomee *Epithema turgida* (Ehrenbg.) Kütz., auf den Vaucheria-Fäden der sessile Peritriche *Vorticella convallaria* L. teilweise massenhaft als Aufwuchs. Eine Anzahl von Ciliaten und Thecamöben verhielten sich auch hier gegenüber den einzelnen Algenfäden positiv thigmotaktisch. Ähnliches konnte auch auf den kurzen Thalli der in den Brandungslachen des Schwarzen Meeres wachsenden Algen beobachtet werden und tritt praktisch überall auf, wo submerse Pflanzen gedeihen. Die einzelnen Algenfäden bilden also in ihrer Funktion als Substrat zusammen mit einer Reihe verschiedenartiger sessiler und thigmotaktisch an die Unterlage gebundener Organismen ökologische Einheiten. Sie alle verkörpern damit viele kleine Ökosysteme, die zusammen einer nächsten höheren Einheit, hier den Algenwatten, zuzuordnen sind. Ein Stoffumsatz kann im Bereich der ökologischen Einheit „Algenfaden" nicht stattfinden, da alle Stoffwechselprodukte, in das Wasser abgegeben, sofort in den Bereich der Algenwatten oder -bestände gelangen und sodann, je nach ihrer Beschaffenheit mehr oder weniger schnell, in das Kleingewässer eingehen. Es handelt sich also im Falle der Algenfäden um ein völlig offenes Ökosystem, bei dem zunächst nur die Beziehung Substrat — Lebewesen das Zustandekommen desselben vermittelt hat.

Die Algenwatten selbst werden wiederum von einer Anzahl von Organismen als Ökotop benutzt. Hier aber ist der Konnex bereits differenzierter. Einige suchen in den Algenwatten Schutz: das wäre für Closterium-Arten, die Flagellaten *Anthophysa vegetans* O. F. Müll. und *Phacus pleuronectes* (O. F. Müll.) Duj. und die Heliozoe Actinophrys denkbar. Andere halten sich wegen des günstigen Nahrungsangebotes hier auf. Die zahlreichen Cloëon- und Lestes-Larven wie die Gastropoden *Hippeutis complanatus* L. und *Anisus leucostomus* ernähren sich unmittelbar von Algenfäden. *Lumbriculus variegatus,* einige Copepoden-Arten, *Asellus aquaticus* und *Radix auricularia* L. halten sich an die reichlich entstehenden vegetabilischen Stoffe, räuberische Rotatorien an die Ciliaten, *Chlorohydra viridissima* (Pall.) an die Cyclopiden und die Larven von Agabus, Haliplus und der Hydroporus-Hygrotus-Gruppe jagen nach den pflanzenfressenden Ephemeriden- und Lestiden-Larven. Natürlich herrscht in den Algenwatten ein durch den lebhaften Stoffwechsel bedingter, vom umgebenden Milieu abweichender Chemismus, der immer neu entstehen muss, da er in das umgebende Wasser abdiffundiert, umgekehrt der Chemismus des umgebenden Wassers selbstverständlich auch die Algenwatten beeinflusst. Trotz aller Offenheit dieses Ökotops aber sind die Algenwatten als solches wohl charakterisiert. Sie wären jedoch in dieser Form nicht existent, würden sie nicht in dem Wasser des Kleingewässers schwimmen, sie gehören ihm also als dem nächst höheren Ökosystem an. Die Ökosysteme dieses Beispiels weisen somit eine bestimmte Rangfolge auf:

a. die Algenfäden, die zu,

b. den Algenwatten gehören, die wiederum,
c. dem Kleingewässer zuzuordnen sind.

In der Reihe: Algenfäden — Algenwatten — Kleingewässer drückt sich die enkaptische Hierarchie in einer Zunahme des Geschlossenseins der Ökosystemme und, damit verbunden, in einer steigenden ökologischen Stabilität aus. Vergleichbar mit den Ökosystemen der terrestrischen Ökologie wären:

a. die Algenfäden als sogenannte „Strukturteile" und der auf ihnen gedeihende Aufwuchs als Merocönose,
b. die ökotopbildenden Algenwatten als Habitat, die in ihnen lebenden Organismen als Synusie,
c. die Kleingewässer als Biotop plus Biocönose (im Falle des Waldtümpels) oder als Habitat plus Synusie (im Falle des Grabenweihers und der Brandungslachen) zu bezeichnen.

Hieraus ergeben sich weitere Probleme: Wenn in Kleingewässern mit Merökosystemcharakter Ökosysteme mit ebenfalls Merökosystemcharakter auftreten, wie die ökotopbildenden Algenkomplexe im Beispiel des Grabenweihers und der Brandungslachen, scheint die Differenzierung zunächst Verwirrungen ausgesetzt. Aber dasselbe Bild tritt ebenfalls sehr häufig bei Holökosystemen auf. So liegt der Waldtümpel mit seinen kompletten, in sich geschlossenen Wirkungskreisen als weitestgehend autarker Biotop mit einer sich in einem Nahrungsnetz als vollkommen erweisenden Biocönose inmitten eines anderen Biotops, des Auwaldes. Und beide ineinander gleichsam verschachtelte Holökosysteme (Abb. 10) zeigen eine gewisse Abhängigkeit voneinander: Der Wald, genauer gesagt, der Erlenbestand rund um den Tümpel, düngt mit seinem Fallaub das Kleingewässer, der Tümpel aber verschafft durch die stark Durchfeuchtung der Erde seines Randgebietes den Erlen, und somit einem Bestandteil des Auwaldes, die Voraussetzungen zur Existenz. Die Natur mit ihrer grossen Vielfalt an Ökosystemen lässt sich also nicht, so scheint es, in ein Schema pressen. Und doch erfordert die Einordnung natürlicher ökologischer Einheiten in das Schema der drei sich abzeichnenden ökologischen Grundeinheiten keinerlei Gewaltanwendung, wenn sowohl die Existenz gleichberechtigter, nebeneinander existierender und ineinander verschachtelter Ökosysteme erkannt wird, als auch das Vorkommen von Ökosystemen mit unterschiedlicher Rangfolge innerhalb einer einzigen ökosystematischen Grundeinheit.

Welche Verhältnisse weist diesbezüglich der Wiesengrabenweiher auf? Hier kommen eine ganze Anzahl von verschiedenen Beständen submerser Pflanzen vor: Spirogyra-Algenwatten, Vaucheria-Algenwatten, *Lemma trisulca*-Massen, kleinere Bestände von *Callitriche sp.*, *Ranunculus aquatilis* L., *Myriophyllum verticillatum* L., *Elodea canadensis* Rich., *Potamogeton crispus* L. und die flutenden Rasen der Graminee *Glyceria maxima* (Hartm.) Holmbg. Alle wirken durch ihren Stoffwechsel in

qualitativ gleicher Weise auf das Ökosystem ein. Je nach der Stärke der Lichtintensität werden Sauerstoff oder Kohlenstoff abgegeben, der pH des umgebenden Wassers wird verändert, unter besonderen Umständen finden Kalkausfällungen statt. Innerhalb des Ökosystems „Wiesengrabenweiher" bilden alle Pflanzenbestände zusammen die funktionelle ökologische Einheit „Phytal", innerhalb des Ökosystems „Phytal" wiederum treten die Spirogyra-Algenwatten, *Lemna trisulca*-Massen, Callitriche-Bestände usf. als jeweils eigene Ökosysteme auf. Unter Berücksichtigung der Stoffumsatzprozesse und des Nahrungsnetzes war festgestellt worden, dass der Grabenweiher ein Merökosystem ist. Da das Merökosystem als Ökosystem mit offenen Kreislaufsystemen definiert ist, stellen sowohl das Phytal als Gesamtheit, als die einzelnen Pflanzenbestände Merökosysteme dar, denn auch in ihnen verlaufen Stoffumsatzprozesse mit offenem Systemcharakter. Bildet also der Wiesengrabenweiher ein Merökosystem 1. Grades, ist das Phytal — wie auch jeweils das freie Wasser und der Gewässergrund (vgl. Abb. 11) — ein Merökosystem 2. Grades, in welchem nun die einzelnen Pflanzenbestände — Spirogyra-Algenwatten, Vaucheria-Algenwatten, *Lemna trisulca*-Massen, Callitriche-Bestände — als einzelne Merökosysteme 3. Grades auftreten.

Im Auwaldtümpel wird hingegen das Phytal im zeitigen Frühjahr nur von *Rorippa amphibia* und *Galium palustre* gebildet. Mit fortschreitender Jahreszeit geht der Wasserstand zurück, die amphibischen *R. amphibia* und *G. palustre* wandeln sich zu Landformen um, so dass, abgesehen von der im Frühjahr und Vorsommer nur vereinzelt vorhandenen schwimmenden *Lemna minor*, kein echtes Phytal im Tümpel mehr vorhanden ist. Nach der Juli-Regenzeit treten die beschriebenen Vaucheria-Mougeotia-Spirogyra-Algenwaten auf, und nur sie bilden jetzt das Phytal. Rorippa- und Galium-Bestände sowie die Algenwatten sind sowohl hinsichtlich ihrer Einwirkung auf das Ökosystem als hinsichtlich ihrer Ausdehnung, also in ihrer qualitativen und quantitativen Funktion, den einzelnen Pflanzenbeständen des Wiesengrabenweihers durchaus ähnlich und mit ihnen vergleichbar. Trotzdem aber bilden die Rorippa- und Galium-Bestände im Frühjahr und die Vaucheria-Mougeotia-Spirogyra-Algenwatten im Hochsommer in dem Holökosystem Auwaldtümpel Merökosysteme:

1. Grades, während die qualitativ wie quantitativ mehr oder weniger gleichen ökologischen Einheiten im Wiesengrabenweiher als Merökosystem 3. Grades in Erscheinung treten.

Denkbar wäre auch der Fall, dass in einem beliebigen in einer temperierten Zone gelegenen Holökosystem „Tümpel" im zeitigen Frühjahr ein submerser amphibischer Kormophyten-Bestand gleichzeitig mit Algenwatten auftritt. Beide zusammen bilden das Phytal und sind als ein Merökosystem 1. Grades anzusprechen, während der sub-

merse amphibische Kormophytenbestand ebenso wie die Algenwatten im einzelnen Merökosysteme 2. Grades bilden. Im Verlaufe des Jahres zwingt der Rückgang des Wasserstandes die amphibischen Kormophyten ihre Landform auszubilden, und sie scheiden aus dem Phytal aus. Jetzt vertreten die Algenwatten allein das Phytal und werden zu einem Merökosystem 1. Grades.

Rückblickend kann deshalb festgestellt werden: Die bisher niedrigste ökologische Einheit ist „Strukturteil plus Merocönose" (vgl. p. 125). „Merocönose", übersetzt Teillebensgemeinschaft, trifft dem Wortsinn nach eher die Synusie. Es wird deshalb vorgeschlagen, das griechische Wort „paraios", übersetzbar mit „Glied", als charakterisierenden Wortstamm für diese ökologische Einheit zu benutzen. Dadurch lässt sich der im deutschen Sprachgebrauch bisher als „Strukturteil" bezeichnete Terminus durch das international verständlichere Wort „Paratop", das Wort „Merocönose" durch „Paracönose" ersetzen und das Ökosystem, zu dem sich Paratop und Paracönose vereinen, als Parökosystem benennen. Man entgeht so auch der Gefahr des Auftretens von Verwirrungen, die bei gleichzeitigem Gebrauch von „Merocönose" und „Merökosystem" bei Ökosystemen verschiedener Ordnungen gegeben sein dürften.

Eine aus dem Voraufgegangenen abzuleitende Rangfolge der Ökosysteme (vgl. Zavadskij 1966, Berman et al. 1967) und zugeordneter Begriffe stellt sich in Verbindung mit den neu vorgeschlagenen Termini technici als enkaptische Hierarchie dar (Abb. 10 und 11) und beinhaltet gleichzeitig die drei Grundtypen funktioneller ökologischer Einheiten:

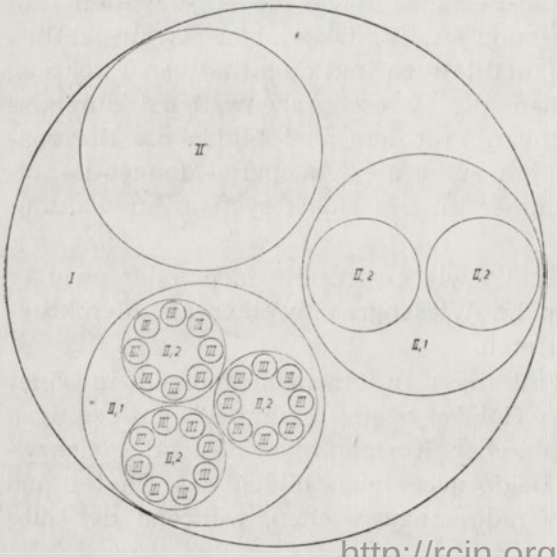

Abb. 10. Modell eines Holökosystems (I), das sich aus graduell verschiedenen Merökosystemen (II,1 und II,2) und Parökosystemen (III) in Form einer enkaptischen Hierarchie zusammensetzt. Die Ziffern sind Ausdruck der Qualität der kreisförmig dargestellten Ökosysteme. Grösse und Vielzahl der Kreise deuten die Quantität derselben an

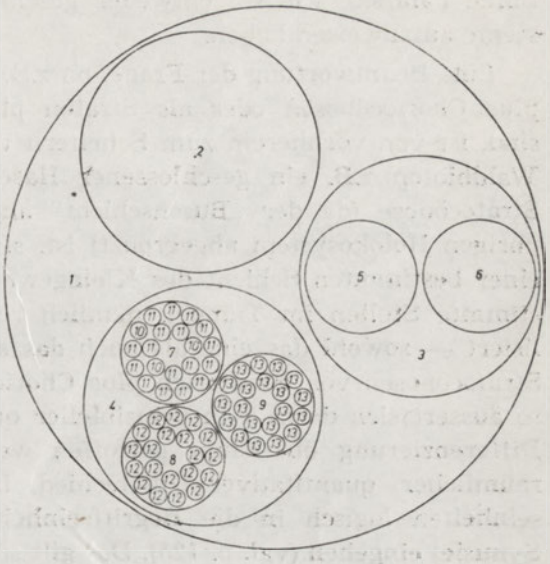

Abb. 11. Anwendungsmuster des in Abb. 10 dargestellten Modells (dortige analoge Ökosysteme durch römische Zahlen bezeichnet) am Beispiel eines beliebigen autarken Gewässers

II,1	II,2	III
1 — Gewässer I	5 — Schlamm	10 — Myriophyllum-Stengel
2 — Pelagial	6 — Fallaub	11 — Myriophyllum-Blätter
3 — Benthal	7 — Myriophyllum-Bestände	12 — Chara-Thalli
4 — Phytal	8 — Chara-Wiesen	13 — Algenfäden
	9 — Algenwatten	

Rangfolge	Ökotop + Ökocönose	= Ökosystem
Ökosysteme I. Ordnung:	Biotop + Biocönose	= Holökosystem
Ökosysteme II. Ordnung:	Paratop + Synusie	= Merökosystem
Ökosysteme III. Ordnung:	Habitat + Paracönose	= Parökosystem

Es genügt also nicht, Holökosysteme als geschlossene Ökosysteme von den offenen Merökosystemen zu scheiden, sondern es müssen von den Merökosystemen noch die von ihnen qualitativ verschiedenen Parökosysteme getrennt werden.

Ein Holökosystem ist ohne Mer- und Parökosystem existenzfähig, ein Merökosystem kann ohne Parökosystem bestehen (Schlammgrund eines Gewässers). Umkehrungen sind nicht denkbar. Die Zuordnung eines Ökosystems zu einem Ökosystem gleicher Ordnung ist räumlich und zeitlich bedingt. Sie befindet sich damit gleichzeitig über die aufeinander bezogene Rangfolge, ausgedrückt durch den Terminus „Grad", der somit quantitativen und relativen Charakter trägt. Hingegen ist die Rangfolge der ökologischen Grundeinheiten ausgedrückt als „Ordnung", qualitativ begründet und absolut. Graduelle quantitative Unterschiede gibt es nur innerhalb der Merökosysteme, da Holökosysteme und Parökosysteme (s.u.) einen im ökologischen Sinne „absoluten" Charakter besitzen in dem

Sinne nämlich, wie sie entweder geschlossene oder keine Kreislaufsysteme aufzuweisen haben.

Eine Beantwortung der Frage, ob z.B. die Algenwatten als Biochorien plus Choriocönosen oder als Straten plus Stratocönosen anzusprechen sind, ist von vornherein zum Scheitern verurteilt. Ebenso, wie in einem Waldbiotop z.B. ein geschlossener Haselbestand sowohl Stratum plus Stratocönose (da der „Buschschicht" angehörend auch horizontal vom übrigen Holökosystem abgegrenzt) ist, sind auch die Algenwatten — in einer bestimmten Schicht des Kleingewässers vorkommend und auf bestimmte Stellen im Tümpel, nämlich reichlich insolierte Stellen lokalisiert — sowohl das eine als auch das andere. Wenn also Straten plus Stratocönosen von Biochorien plus Choriocönosen unterschieden werden, so äussert sich darin kein prinzipieller qualitativer, sondern — falls die Differenzierung überhaupt getroffen werden kann oder muss — ein räumlicher, quantitativer Unterschied. Insofern können beide Begriffseinheiten logisch in die Begriffseinheit Merökosystem (Habitat plus Synusie) eingehen (vgl. p. 125). Das gilt sinngemäss auch für alle anderen nach äusseren Merkmalen unterschiedenen „Typen" von Ökosystemen.

Aus der voraufgegangenen Diskussion lassen sich für die einzelnen Ökosysteme folgende Definitionen ableiten:

Ein Holökosystem ist eine funktionelle ökologische Einheit I. Ordnung mit weitestgehend selbständigem Charakter. Seine Existenz ist von dem Vorhandensein bestimmter Faktoren — wie Nährsubstanzen, Wasser, Sonnenenergie und Sauerstoff — abhängig. Die abiotischen Faktoren des Gesamtsystems sind konstant und normalerweise nur im Verlaufe längerer Zeiträume veränderlich. Die in einem Holökosystem stattifindenden Stoffumsatzprozesse verlaufen in Form geschlossener Kreislaufsysteme. Die Umwelt wird als Biotop, die darin lebende Organismengesellschaft als Biocönose bezeichnet. Die Biocönose ist dem Prinzip nach autochthon. Biotop und Biocönose sind regulationsfähig, und befinden sich im Gleichgewicht, es sei, sie werden durch einen Eingriff seitens des Menschen oder seitens einer „Naturkatastrophe" gestört.

Ein Merökosystem ist als funktionelle ökologische Einheit II. Ordnung einem Holökosystem zugeordnet und als Bestandteil desselben von ihm abhängig. Schon zeitweilige Veränderungen eines oder mehrerer abiotischer oder biotischer Faktoren im Holökosystem können zum Zusammenbruch eines Merökosystems führen, ohne dass das Holökosystem aus dem Gleichgewicht gerät. Die in einem Merökosystem verlaufenden Stoffumsatzprozesse verlaufen in Form offener Systeme und sind inkomplett. Ihre Umwelt wird als Habitat, ihre Organismengesellschaft als Synusie bezeichnet. Eine Synusie kann sich sowohl aus autochthonen wie aus allochthonen Bestandteilen zusammensetzen. Habitat und Synusie sind in sich selbst nicht regulationsfähig.

Ein Parökosystem ist als funktionelle ökologische Einheit III. Ordnung einem Merökosystem zugeordnet und als Bestandteil desselben von ihm abhängig. Veränderungen im Merökosystem oder Eingriffe von aussen können zum Zusammenbruch eines Parökosystems führen, ohne dass das Merökosystem vernichtet wird. In einem Parökosystem finden keine Stoffumsatzprozesse statt. Die Umwelt wird hier als Paratop, die Organismengesellschaft als Parocönose bezeichnet. Die Paracönose ist stets allochthon.

Der Begriff „Ökosystem" aber ist den bisher bekannten drei ökologischen Grundeinheiten übergeordnet. Unter dem Begriff Ökosystem werden alle funktionellen ökologischen Einheiten vereint, gleichgültig, welche Eigenschaften sie besitzen. Der Begriff Ökosystem bringt des weiteren den Konnex zwischen den belebten und unbelebten Faktoren und die sich wechselseitig vollziehende Beeinflussung des einen durch den anderen zum Ausdruck. Hierbei wird die abiotische Umwelt als Ökotop, die Organismengesellschaft als Ökocönose bezeichnet.

Die Auftellung der drei ökologischen Grundeinheiten erscheint geeignet, der Ökosystemforschung mehr Übersichtlichkeit zu verleihen, ohne einer hinsichtlich der ökologischen Systematik zu Recht geforderten Flexibilität (Müller 1970) entgegenzustehen. Die Erkenntnis von Rangfolge und Systemcharakter der funktionellen ökologischen Einheiten hat ebenfalls eine unmittelbare praktische Bedeutung für den Menschen. Er vermag mit ihrer Hilfe die Folgen seiner Eingriffe in die Natur besser vorauszusehen und abzuwägen, um die im Zuge der Umgestaltung der Natur zum „Nutzen" des Menschen bisher häufig aufgetretenen, nicht wieder gutzumachenden späteren Schadwirkungen, die meist in keinem vernünftigen Verhältnis zu dem augenblicklichen Nutzen stehen, zu vermeiden. Betrifft ein Eingriff in ein Ökosystem nur Strukturteile oder kleinere Merökosysteme und bleibt in seiner Auswirkung auf diese beschränkt, so ist kein Zusammenbruch des Holökosystems zu befürchten. Wirkt sich ein Eingriff jedoch auf das gesamte Holökosystem aus, muss mit seinem Zusammenbruch und häufig auch mit einer negativen Beeinflussung benachbarter Ökosysteme gerechnet werden. Unter diesem Aspekt stellt die vorliegende Arbeit eine Ergänzung zu den wichtigen und grundlegenden Ausführungen von Odum (1969) über die Entwicklung der Ökosysteme dar. Der empirische Erfahrungsschatz ist bei manchen Holökosystem-Typen heute bereits gross genug, um entsprechende prognostische Aussagen zuzulassen, zumal es sich stets um biokybernetische Systeme handelt (vgl. Klaus 1963, Stiehler 1967, Wünsch 1968) die sich mit Hilfe der Kybernetik erfassen und auswerten lassen (Margalef 1957, Patten 1959, Laue 1968). Die meisten ökologischen Einheiten (z.B. alle marinen) bedürfen jedoch weiterer gründlicher Bearbeitung, um dieses notwendige Ziel gültiger Prognosen noch rechtzeitig zu erreichen.

5. ZUSAMMENFASSUNG

Das Ansprechen ökologischer Einheiten als Biotope + Biocönosen einerseits und Habitate + Synusien andererseits ist oft heikel und schwierig. Als entscheidende Kriterien dürfen Sauerstoff-Kohlenstoff- und Stickstoffsysteme und Nahrungsnetze gelten, deren Verhalten am Beispiel kleiner Gewässer während längerer Zeit geprüft wurde. Unter Verwendung der Modelle materieller Systeme betrachtet, zeigt ein in einem Auwald gelegener Waldtümpel trotz wiederholten Austrocknens geschlossene Kreisläufe. Ein von einem Graben durchflossenes, ständig bespanntes und in einer Wiese gelegenes Kleingewässer sowie am Meeresufer gelegene Brandungslachen, gestalten sich als offene Systeme. Somit ist die ökologische Einheit „Waldtümpel" als Biotop mit einer Biocönose anzusprechen, das von einem Graben durchflossene Kleingewässer und die Brandungslachen hingegen sind als Habitate, die darin lebenden Organismengesellschaften als Synusien zu bezeichnen.

Abgeleitet von den Untersuchungsergebnissen werden drei funktionelle ökologische Ordnungen als Grundeinheiten definiert und als

Holökosystem = Biotop + Biocönose,
Merökosystem = Habitat + Synusie und
Parökosystem = Paratop + Paracönose

benannt, während unter dem bisher für die Holökosysteme verwandten Begriff „Ökosystem" = Ökotop + Ökocönose alle funktionellen ökologischen Einheiten vereint werden.

6. LITERATUR

Balogh, J. 1958. *Lebensgemeinschaft der Landtiere.* Budapest, Verlag der Ungarischen Akademie der Wissenschaften.

[Berman, Z. I., Zavadskij, K. M., Zelikman, A. L., Paramonov, A. A., Poljanskij, Ju. I.] Берман, З. И., Завадский, К. М., Зеликман, А. Л., Парамонов, А. А., Полянский, Ю. И. 1967. Современные проблемы теории [Contemporary problems of evolution theory]. Leningrad, Izdat. „Nauka".

Busnita, T. 1966. Die Rolle der Weichtiere und Boden-Krebstiere im Leben und Produktivität der Gewässer der Überschwemmungszone und des Donaudeltas. *Verh. int. Ver. Limnol.*, 16, 655-662.

Chodorowska, W. 1961. Free-living nematoda fauna in small pools of the Kompinos Forest. *Pol. Arch. Hydrobiol.*, 9, 265-285.

Chodorowski, A. 1958 a. Wpływ wysychania zbiorników okresowych na tempo rozwoju larw komarów z rodzaju Aedes [Influence of the drying-up of temporarily-formed pools on the rate of development of mosquito larvae of the Aedes genus]. *Ekol. pol., Ser. B*, 4, 35-39 [Engl. summ.].

Chodorowski, A. 1958 b. Badania nad zmiennością układów biocenotycznych w okresowych zbiornikach wodnych Puszczy Kampinoskiej [Examination of the mutability of biocenotic systems in the periodical pools of the Kampinos Forest]. *Ekol. pol., Ser. B*, 4, 237-241, [Engl. summ.].

Dahl, F. 1908. Grundsätze und Grundbegriffe der biozönotischen Forschung. *Zool. Anz.*, 33, 349-353.

Davis, J. H. 1960. Proposals concerning the concept of habitat and a classification of types. *Ecology*, 41, 537-541.

Dotterweich, H. 1940. *Das biologische Gleichgewicht.* Jena, G. Fischer Verlag.

Eichhorn, W. Klaus, G., Kröber, G. 1967. Der Systemcharakter der objektiven Realität. In: *Marxistische Philosophie*, 207-263, Berlin.

Fischer, E. 1960. Niektóre bakteryjne przemiany związków azotowych w drobnych zbiornikach wodnych okolic Warszawy [Some types of bacteria metabolism of nitrogen compounds in small bodies of water in the Warsaw district]. *Pol. Arch. Hydrobiol.*, 7, 103-123 [Engl. summ.].

Fischer, E. 1961. Próba charakterystyki mikrobiologicznej jednego z drobnych zbiorników okolic Warszawy w okresie zimowym [Attempt of the microbiological characteristic of a small pond in Warsaw environs in winter season.]. *Pol. Arch. Hydrobiol.*, 9, 319-347 [Engl. summ.].

Fischer, E. 1966. Dynamics of autotrophic bacterial production in the bottom sediment of astatic pools. *Verh. int. Ver. Limnol.*, 16, 539-542.

Forbes, S. A. 1887. The lake as a microcosmos. *Bull. Soc. A. Peoria*, 1887, 77-87.
Friedrichs, K. 1930. *Die Grundfragen und Gesetzmässigkeiten der land- und forstwirtschaftlichen Zoologie, insbesondere der Entomologie.* Bd. 1-2, Berlin, P. Parey.
Klaus, G. 1963. *Kybernetik in philosophischer Sicht.* Berlin.
Klekowski, R. Z. 1961. Die Resistenz gegen Austrocknung bei einigen Wirbellosen aus astatischen Gawässern. *Verh. int. Ver. Limnol.*, 14, 1023-1028.
Klekowski, R. Z. 1966 Einige physiologische Mechanismen der Adaption der Wassertiere zu dem astatischen Milieu. *Verh. int. Ver. Limnol.*, 16, 492-506.
Kreuzer, R. 1940. Limnologisch-ökologische Untersuchungen an holsteinischen Kleingewässern. *Arch. Hydrobiol.*, Suppl. 10, 359-572.
Kühlmann, D. H. H. 1958. Freilandbeobachtungen an *Isotoma viridis* Bourlet (Collembola: Isotomidae). *Beitr. Ent.*, 8, 375-377.
Kühlmann, D. H. H. 1959. Über die Wirkung des Eises auf Organismen und das Phänomen der Aspektfolge in Infusionen. *Forschn Fortschr.*, 33, 74-78.
Kühlmann, D. H. H. 1960 a. Wasserführung und Eisverhältnisse zweier Kleingewässer. *Acta Hydrophys.*, 6, 97-126.
Kühlmann, D. H. H. 1960 b. Die Temperaturverhältnisse in zwei Kleingewässern verschiedener landschaftlicher Exposition. *Acta Hydrophys.*, 6, 191-267.
Kühlmann, D. H. H. 1960 c. Zur Frage der raumlichen und zeitlichen Verteilung von Sauerstoff und anderen chemischen Faktoren in kleinen Gewässern. *Gerlands Beitr. Geophys.*, 69, 294-319.
Kühlmann, D. H. H. 1961. Thermodynamische Untersuchungen in Kleingewässern verschiedener landschaftlicher Exposition. *Verh. int. Ver. Limnol.*, 14, 87-94.
Kühlmann, D. H. H. 1962. Hydrographische, mikroklimatische und chemische Untersuchungen auf überspültem Fels und in Brandungslachen des Supralitorals der rumänischen Schwarzmeerküste. *Acta Hydrophys.*, 7, 5-66
Kühlmann, D. H. H. 1963. Beobachtungen zur Biologie von *Gasterosteus aculeatus* L. und Gedanken zu seiner Bekämpfung als Schädling. *Z. Fisch.*, N.F., 11, 301-309.
Kühnelt, W. 1965. *Grundriss der Ökologie.* Jena, G. Fischer Verl.
Laue, R. 1958 Die Beschreibung offener Systeme durch bewertete Graphen. Biokybernetik, 1, 117-119.
Lindeman, R. L. 1942. The trophic-dynamic aspect of ecology. *Ecology*, 23, 399-418.
Löther, R. 1966. Philosophische Probleme der Biologie. *Dt. Z. Phil.*, 14, H.3.
MacFadyen, A. 1967. Methods of investigation of productivity of invertebrates in terrestrial ecosystems. In: K. Petrusewicz [Ed.] *Secondary productivity of terrestrial ecosystems*, 383-412. Warszawa, PWN.
Margalef, R. 1957. La teoria de lat informacion en ecologia. *Mems R. Acad. Cient. Artes, Barcelona*, 32, 373-449.
Medwecka-Kornas, A. 1967. Estimation of primary production as a basis for studies of secondary production. In: K. Petrusewicz [Ed.] *Secondary productivity of terrestrial ecosystems.* 83-95, Warszawa, PWN.
Möbius, K. 1877. *Die Auster und die Austernwirtschaft.* Berlin, P. Parey.
Müller, H. J. 1970. Stellung und Aufgaben der Ökologie in der modernen Biologie. *Biol. Rundsch.*, 8, 65-76.
Odum, E. P. 1969. The strategy of ecosystem development. *Science*, 164, 262-270.
Ovington, J. D. 1962. Quantitative ecology and the woodland ecosystem concept. *Adv. Ecol. Res.*, 1, 103-192.
Palissa, A. 1958. Zur gegenwärtigen Lage in der Biozönotik. *Forschn. Fortschr.*, 32, H.10/11.
Paschalski, J. 1959. Obserwacje warunków środowiskowych drobnych zbiorników wodnych okolic Warszawy [Observations of environmental conditions in small ponds in the Warsaw district]. *Ekol. pol., Ser. A*, 7, 1-20. [Engl. summ.].
Patten, B. C. 1959. An introduction to the cybernetics of the ecosystem: the trophic-dynamic aspect. *Ecology*, 40, 221-231.
Phillipson, J. 1967. Secondary productivity in invertebrates reproducing more than once in a lifetime. In: K. Petrusewicz [Ed.] *Secondary productivity of terrestrial ecosystems.* 459-475, Warszawa, PWN.
Remane, A. 1956. *Die Grundlagen des natürlichen Systems, der vergleichenden Anatomie und der Phylogenetik.* Leipzig.
[Zavadskij, K. M.] Завадский, К. М. 1966. Основные формы организации живого и их подразделения [Basic forms of life organization and their subdivi-

sions]. In: *Filozofskie problemy sovremennoj biologii.* 29-47, Moskva, Izdat. „Nauka".
Schellhorn, M. 1965. Struktur, Organisation und Evolution lebender Systeme. Dissertation, Humboldt-Univ., Berlin.
Schellhorn, M. 1969. *Probleme der Struktur, Organisation und Evolution biologischer Systeme.* Jena.
[Schmalhausen, I. I.] Шмальгаузен, И. И. 1961. Интеграция биологических систем и их саморегуляция [The intergation of biological systems and their regulation]. *Byull. Mosk. Obshch. Ispyt. Prir., Otd. Biol.*, 66, (2), 104-134, [Engl. summ.]. [See also: *Sowietwissenschaft, Naturwiss. Abt.*, 1961, H. 11, 1127-1155].
Schwenke, W. 1953. Biozönotik und angewandte Entomologie. *Beitr. Ent., Sonderheft,* 3, 86-162.
Schwenke, W. 1955. Ergebnisse und Aufgaben der ökologischen und biocönologischen Entomologie. Ber. 7, *Wandersammlung Dtsch. Ent.*, 1954, 62-80.
Stiehler, G. 1967. *Der dialektische Widerspruch.* Berlin.
Styczyńska-Jurewicz, E. 1966. Astatic water bodies as a characteristic habitat of some parasites of men and animals. *Verh. int. Ver. Limnol.*, 16, 604-611.
[Sukačev, V. N.] Сукачещ, В. Н. 1957. Основы теории биогеоценологи [Theoretical principles of biogeocenology]. Moskva, Izdat. „Nauka".
Tansley, A. 1923. *Practical plant ecology.* London, Allen and Unwin.
Tansley, A. 1935. The use and abuse of vegetational concepts and terms. *Ecology,* 16, 284-307.
Thienemann, A. 1925. Die Binnengewässer Mitteleuropas. Die Binnengewässer, 1. Stuttgart, E. Schweizerbart'sche Verl.
Thienemann, A. 1939. Grundzüge einer allgemeinen Ökologie. *Arch. Hydrobiol.*, 35, 267-285.
Tischler, W. 1949. *Grundzüge der terrestrischen Tierökologie. Braunschweig,* Vieweg.
Tischler, W. 1955. *Synökologie der Landtiere.* Stuttgart, G. Fischer-Verlag.
Tischler, W. 1965. *Agrarökologie.* Jena, G. Fischer Verlag.
Udvardy, M. F. D. 1959. Notes on the ecological concepts of habitat, biotope and niche. *Ecology,* 40, 725-728.
Wünsch, Z. 1968. Ein Beitrag zum Problem der Entstehung biokybernetischer systeme, *Biokybernetik,* 1, 256-259.

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CONTENTS

Pol. Arch. Hydrob. T. 19, nr 1, s. 1—150. Warszawa 1972. Indeks 37335