Food consumption and energy transformations by fish populations in two small lowland rivers in Poland

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Food consumption and energy transformations by fish populations in two small lowland rivers in Poland

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Abstract

The food consumption of all fish species was estimated at nine sites in two lowland rivers. The fish populations, whose diet consisted chiefly of invertebrates (88%), used on the average 9.88 (7.14–13.3) kg of invertebrates for the production of 1 kg of fish flesh. This number of invertebrates corresponds to 39.35 ± 7.34 MJ ($\bar{x} \pm$ S.D.). In estimating the effective use of consumed (K_1) and assimilated (K_2) food for growth, it was found that the predominance of food of animal origin over plant of detrital food resulted in a decrease in the living cost (maintenance ration) of fish.

Introduction

Information on the efficiency with which food is converted into fish flesh within a wild population is fundamental for proper comprehension of the role played by fish in an ecosystem. Assessment of food consumption is essential for calculation of energy flow within fish populations and for judging whether the ecological factors and abiotic conditions may effectively influence this value.

There are two basic approaches to estimating food consumption (Mann, 1978). One is to collect field data on stomach contents. The other is to calculate food requirements in a laboratory. The latter method involves laboratory experiments on feeding (direct measurements) and/or indirect empirical techniques in which an estimation of consumption is based on nitrogen or energy budget.

Participation in such research is difficult for an ecologist because of the following reasons: 1) it is time-consuming to estimate the diet of a few species at a number of sites (especially in the case of Cyprinidae fish which smash their prey with pharyngal teeth), and 2) it is difficult to measure precisely the four basic parameters influencing the density of populations (birth, mortality, immigration, emigration). The degree of difficulty is still greater when the objects of the research are less stable ecosystems (Andrewartha, 1972; Krebs, 1978). Rivers undoubtedly belong to such ecosystems (Vannote *et al.*, 1980).

Therefore, in order to gather experience, the researches were started in small lowland rivers using fish as the zoological group. The population density and structure have been described previously (Penczak *et al.*, 1981; Zalewski Penczak, 1981) and the production of the dominant species has also been estimated (Penczak, 1981). Owing to the knowledge of the above-mentioned parameter the estimation of consumed food seems to be more real.

The aim of this work is as follows: 1) to estimate the food energy taken by fish populations in two small lowland rivers, 2) to assess the quantities of energy used for growth and metabolism processes during a year, and 3) to investigate relations between the amounts of consumed food types (invertebrates, fish, vegetation and detritus) required to produce 1 kg of fish.

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Material and methods

Fish were caught at 6 sites on the Utrata River (a tributary of the Bzura River in the Vistula drainage basin) and at 3 sites on the Zalewka Brook (a tributary of the Ner River in the Warta drainage basin). The maps showing the localities of both rivers and the sites as well as the tables with physical and chemical characteristics of the sites were included in earlier papers (Penczak, 1981; Penczak *et al.*, 1981; Zalewski & Penczak, 1981). The methods of fish capture, the estimation of density and all information necessary for production estimating at the time of annulus formation were included in the abovementioned papers.

The consumption of food energy (Cons.) was estimated from Winberg's equation (1956): Cons. = 1.25 (2R + Prod.). The total monthly production of the species was counted separately for each age-group according to the equation proposed by Mann (1969) (1):

$$\text{Prod.} = \int_{d}^{d+1/12} N_t d\bar{w}_t \tag{1}$$

N = number of individuals at time t.
$d\bar{w}_t$ = mean weight increase at time t.

The production of the other species (rare, additional) was estimated from their mean biomass ($\bar{B}$) and the ($P/\bar{B}$) ratio for dominant species (Penczak, 1981). To convert mass units (kg) into energy units (MJ) the caloric body content was estimated for separate species (taking into account age and seasons).

The monthly energy of routine metabolism (Winberg, 1956) was counted according to the equation proposed by Mann (1969) (2):

$$R = \int_{d}^{d+1/12} N_t(A\bar{w}_t)^{0.813} \tag{2}$$

A = constant determined by temperature according to Krogh's curve,
$\bar{w}$ = mean weight of the individual at time t.

For the additional species consumption was estimated by dividing their production into ratio Prod./Cons. (= K_1) calculated for dominant species (Penczak *et al.*, 1982b); their total metabolism energy (2R) was estimated in a similar way.

Population density and the mean weight of an individual for each age-group in consecutive months were calculated from the exponential equations (3, 4):

$$N_t = N_0 e^{Zt} \tag{3}$$

$$\bar{w}_t = \bar{w}_0 e^{Gt} \tag{4}$$

Z and G were computed from Ricker's (1975) equations.

The detailed procedure of estimating Prod., Cons., and R for a chosen age-group of rainbow trout at monthly intervals, using the above equations, is given by Penczak *et al.* (1982a).

For dominant species, the total food content in a fish's guts was measured gravimetrically to establish one year's food spectrum. The food components were divided volumetrically, assuming that their wet mass is not different as far as weight is concerned. Then dry mass (Winberg, 1956) as well as the caloric body content of the isolated food components were estimated using pills made from homogenated of the whole animals (Penczak *et al.*, 1976, 1977). In the case of invertebrates and plants, samples for estimating the dry mass and coloric content were also prepared on the basis of fresh material directly from the river, Knowing the percentage of water content in tissues, and the caloric content of the dry mass of the examined food components, the caloric content of their mass was established. The caloric content of fresh mass and the prepared food spectrum enabled us to divide consumption energy (from Winberg's equation) into food eaten by fish (Penczak *et al.*, 1982b).

The efficiency of enery flow through fish populations was analysed using the coefficients of ecological effectiveness (Grodziński *et al.*, 1975):

$$U^{-1} = \frac{A}{\text{Cons.}},\ K_1 = \frac{\text{Prod.}}{\text{Cons.}},\ K_2 = \frac{\text{Prod.}}{A},\ \frac{2R}{\text{Cons.}},$$

(A = Prod. + 2R).

The caloric content of fish body, invertebrates and plants was measured with the help of non-adiabatic micro-bomb (Klewkowski & Beczkowski, 1973). The scale of the register was tested using Prus's method (1975).

Results

The caloric content of the body, examined directly for dominant species, indicates changeability both in dry and in wet fish mass (Table 1). The energy content in dry mass decreases with age, although for some species as late as from the second or even from the third age-group. A contrary situation was noticed in the case of wet mass, and this results from a greater water content in younger fish in which larger departures from the above-mentioned regularities were found. Extreme values of the caloric body content changed with age in the majority of species (χ^2 test: $p > 0.05$ and even $p > 0.01$); hence data from Table 1 were used for changing total production values to the energy units in the various age-groups.

Total production and food consumption (MJ ha^{-1} a^{-1}) and indicators of ecological efficiency were represented separately for the various gudgeon age-

Table 1. Percentages of dry weight and energy content of fish body in dry and wet weight. Averages for summer and autumn seasons. Each result is based on 5 ÷ 10 repetitions.

Species	Age	Dry weight (%)	Energy content (J g^{-1} dry wt)	Energy content (J g^{-1} wet wt)
Loach	0+	22.76	22169.9	5045.9
	1+	25.47	21767.6	5544.2
	2+	25.52	21365.2	5452.4
	3+	26.16	20967.5	5485.1
	4+	26.68	20573.9	5489.1
	Mean	25.32	21368.8	5403.3
Gudgeon	0+	23.08	23487.8	5420.0
	1+	24.10	24321.1	5861.4
	2+	24.67	24739.8	6103.3
	3+	24.57	23875.2	5866.1
	4+	27.02	22619.2	6111.7
	Mean	24.69	23808.6	5872.5
Three-spined stickleback	0+	20.55	22857.0	4697.1
	1+	24.23	23737.5	5751.6
	2+	29.84	23763.0	7090.9
	Mean	24.87	23452.5	5846.5
Nine-spined stickleback	0+	21.05	23175.2	4878.4
	1+	24.25	24012.6	5823.0
	Mean	22.65	23593.9	5350.7
Sunbleak	0+	19.58	22210.9	4349.0
	1+	20.27	23467.8	4756.9
	Mean	19.92	22839.4	4553.0
Roach	0+	24.10	22607.9	5448.5
	1+	26.52	21522.7	5707.8
	2+	26.01	21939.2	5706.4
	3+	27.85	20113.4	5601.6
	4+	28.04	17721.9	4909.0
	5+	27.70	16884.5	4677.0
	Mean	26.70	20131.6	5341.7
Mean for all species		24.03	22532.47	5394.6

groups from all sites (Table 2); production is also presented in mass units to facilitate further calculations. We wanted to show that, in the case of species living for several years, the values of the following parameters and indicators change with age in spite of different fish diversity at sites which also differ in hydrographical construction of the bed and in the physical and chemical proprieties of their water (Penczak, 1981). The value of the indicator U^{-1} calculated as 80% indicates that the calculations are correct in all cases, apart from information about the quantity of the assimilated food (Mann, 1969, 1978).

At all sites the efficiency of using the eaten and the assimilated food by gudgeon at growth decreased with age. But the amount of assimilated energy which is lost in metabolic processes increased with age (Table 2).

Table 2. Total production kg ha^{-1} a^{-1} and MJ ha^{-1} a^{-1}, food consumption MJ ha^{-1} a^{-1} and coefficients of ecological efficiencies for gudgeon from the sites of Utrata River and Zalewka Brook. The 365-day intervals between successive annuli are distinguished.

Sites	Age	Prod. (kg)	Prod. (MJ)	Cons. (MJ)	U^{-1} (%)	K_1 (%)	K_2 (%)	$\frac{2R}{Cons}$ (%)	$\frac{P}{\bar{B}}$
U_2	0–1	15.81	85.69	248.98	80.00	34.42	43.02	45.59	8.07[b]
	1–2	21.39	125.36	977.94	79.99	12.82	16.02	67.18	1.48
	2–3	10.64	64.91	694.40	80.00	9.35	11.68	70.65	0.86
	3–4	5.56	32.61	359.14	79.99	9.08	11.35	70.92	0.75
Total or mean		53.40	308.57	2280.46	79.99[a]	16.42[a]	20.52[a]	63.58[a]	1.47[c]
U_3	0–1	118.71	643.42	1273.52	79.99	50.52	63.15	29.48	8.53[b]
	1–2	54.05	316.83	4395.45	79.99	7.21	9.01	72.79	0.84
	2–3	35.02	213.77	2466.34	79.99	8.67	10.83	71.33	0.75
	3–4	23.34	136.90	1809.21	80.00	7.57	9.46	72.43	0.66
	4–5	6.02	36.82	557.84	79.99	6.60	8.25	73.40	0.57
Total or Mean		237.14	1347.74	10502.36	79.99[a]	16.11[a]	20.14[a]	63.89[a]	1.39[c]
U_4	0–1	10.89	59.00	185.60	80.00	31.79	39.74	48.21	8.18[b]
	1–2	10.55	61.84	748.30	80.00	8.26	10.33	71.74	0.90
	2–3	12.11	73.94	837.66	80.00	8.83	11.03	71.17	0.80
	3–4	6.85	40.19	571.35	80.00	7.03	8.79	72.97	0.68
Total or mean		40.40	234.97	2342.91	80.00[a]	13.97[a]	17.47[a]	66.02[a]	1.05[c]
U_6	0–1	18.60	100.79	273.43	79.99	36.86	46.08	43.14	8.56[b]
	1–2	10.45	61.27	873.56	79.99	7.01	8.77	72.98	0.78
	2–3	7.04	42.97	538.28	80.00	7.98	9.98	72.02	0.76
	3–4	2.77	16.24	281.20	80.00	5.77	7.22	74.22	0.50
	4–5	1.44	8.81	136.70	80.00	6.44	8.06	73.56	0.50
Total or Mean		40.30	230.08	2103.17	79.99[a]	12.81[a]	16.02[a]	67.18[a]	1.21[c]
L_2	0–1	9.02	48.86	156.67	80.00	31.19	38.98	48.82	7.47[b]
	1–2	12.15	71.23	724.23	79.99	9.83	12.29	70.16	1.21
	2–3	13.40	81.81	802.41	80.00	10.20	12.74	69.80	0.99
	3–4	12.34	72.39	833.37	79.99	8.69	10.86	71.31	0.74
	4–5	4.31	26.36	515.61	80.00	5.11	6.39	74.89	0.44
Total or Mean		51.22	300.65	3032.29	79.99[a]	13.00[a]	16.25[a]	67.00[a]	1.00[c]

[a] These are mean values.

[b] Values calculated on the basis of a mortality curve (Penczak, 1981).

[c] $\frac{\Sigma P}{\Sigma \bar{B}}$

The turnover ratio ($P/\bar{B}$) changed for gudgeon according to the locality, but the changes of its values seem to be conditioned mainly by age. A high value for this ratio was noticed for the first age-group at all five localities (Table 2). The discussed regularities concerning the changeability of ecological indicators confirm the results obtained for the remaining dominant species in both rivers (Table 3). While preparing Table 3 it was found that it makes sense to count the mean values of the examined ecological indicators only for age-groups, but mean values for species, because of the wide variation observed especially for K_1 and K_2 ($\bar{x} \leqslant$ S.D.), cannot have practical meaning.

The combined values of total production and food consumption for all dominant species at all sites are presented in Table 4, together with values for other species calculated indirectly, in order to

Table 3. Coefficient of ecological efficiencies for dominant species from all sites of Utrata River and Zalewka Brook $\bar{x}$ or $\bar{x} \pm$ S.D.

Ecological coefficients	Species	Age intervals				
		0–1	1–2	2–3	3–4	4–5
K_1	Loach	47.70 ± 6.48	11.32 ± 3.84	7.36 ± 1.72	4.71	
	Gudgeon	36.96 ± 7.91	9.02 ± 2.40	9.00 ± 0.83	7.63 ± 1.33	6.05 ± 0.82
	Roach	31.73	14.35	12.28	9.92	7.63
	Three-spined stickleback	33.54 ± 2.36	5.04 ± 0.20			
	Nine-spined stickleback	26.49 ± 3.07	3.36 ± 0.39			
	Sunbleak	36.07	5.92			
	Mean	35.41 ± 7.08	8.17 ± 4.17	9.54 ± 2.51	7.42 ± 2.61	6.84 ± 1.12
K_2	Loach	59.63 ± 8.11	14.16 ± 4.80	9.19 ± 2.16	5.21	
	Gudgeon	46.19 ± 9.89	11.28 ± 2.99	11.25 ± 1.03	9.54 ± 1.66	7.57 ± 1.02
	Roach	39.70	17.94	15.36	12.41	9.54
	Three-spined stickleback	41.92 ± 2.94	6.30 ± 0.24			
	Nine-spined stickleback	33.12 ± 3.84	4.20 ± 0.48			
	Sunbleak	45.09	7.40			
	Mean	44.27 ± 8.84	10.21 ± 5.21	11.93 ± 3.14	9.05 ± 3.62	8.56 ± 1.39
$\frac{2R}{Cons.}$	Loach	32.20 ± 6.48	68.68 ± 3.84	72.64 ± 1.73	75.83	
	Gudgeon	43.05 ± 7.91	70.97 ± 2.40	71.00 ± 0.83	72.32 ± 1.40	73.95 ± 0.82
	Roach	48.19	65.65	67.72	70.08	72.37
	Three-spined stickleback	46.46 ± 2.35	69.68 ± 7.64			
	Nine-spined stickleback	54.22 ± 2.75	76.64 ± 0.39			
	Sunbleak	44.95	74.08			
	Mean	44.86 ± 7.24	70.95 ± 3.93	70.45 ± 2.51	72.74 ± 2.90	73.16 ± 1.12
$\frac{P}{\bar{B}}$	Loach	8.78 ± 0.36	1.32 ± 0.38	0.80 ± 0.21	0.40	
	Gudgeon	8.16 ± 0.44	1.04 ± 0.29	0.83 ± 0.10	0.67 ± 0.10	0.50 ± 0.06
	Roach	8.51	1.32	0.93	0.66	0.51
	Three-spined stickleback	8.34 ± 0.33	4.67 ± 0.43			
	Nine-spined stickleback	8.26 ± 0.17	0.51 ± 0.06			
	Sunbleak	8.86	0.95			
	Mean	8.48 ± 0.28	1.63 ± 1.51	0.85 ± 0.07	0.58 ± 0.15	0.51 ± 0.01

Table 4. The estimated production (kg wet wt ha^{-1} a^{-1} and MJ ha^{-1} a^{-1}) and food consumption (MJ ha^{-1} a^{-1}) for all species at each site. The value 5394.6 J g^{-1} wet wt (Table 1, average for all species) was used for the change of production of 'other species' form mass units to energy unit.

Species and parameters		Sites								
		U_1	U_2	U_3	U_4	U_5	U_6	L_1	L_2	L_3
Loach	Prod. (kg)	743.31	134.68	70.02	81.04	–	17.77	–	–	–
	Prod. (MJ)	4016.10	727.39	376.92	428.17	–	95.15	–	–	–
	Cons. (MJ)	20417.39	4499.95	1838.63	3086.48	–	860.50	–	–	–
Gudgeon	Prod. (kg)	–	53.40	237.14	40.40	–	40.30	–	51.22	–
	Prod. (MJ)	–	308.57	1347.74	234.97	–	230.08	–	300.65	–
	Cons. (MJ)	–	2280.46	10502.36	2342.91	–	2103.17	–	3032.29	–
Three-spined stickleband	Prod. (kg)	30.96	–	0.77	4.13	2.61	4.95	12.60	6.67	–
	Prod. (MJ)	152.39	–	3.64	19.42	12.24	23.24	73.67	33.43	–
	Cons. (MJ)	1079.31	–	10.62	58.76	33.04	67.79	293.39	307.79	–
Nine-spined stickleband	Prod. (kg)	–	–	–	21.53	0.70	85.83	–	–	–
	Prod. (MJ)	–	–	–	107.88	3.52	425.17	–	–	–
	Cons. (MJ)	–	–	–	752.66	34.20	2721.32	–	–	–
Sunbleak	Prod. (kg)	–	–	–	–	–	–	–	2.73	–
	Prod. (MJ)	–	–	–	–	–	–	–	12.31	–
	Cons. (MJ)	–	–	–	–	–	–	–	93.79	–
Roach	Prod. (kg)	–	–	–	–	–	–	–	–	27.72
	Prod. (MJ)	–	–	–	–	–	–	–	–	152.12
	Cons. (MJ)	–	–	–	–	–	–	–	–	1375.56
Other species	Prod. (kg)	32.00	42.20	22.80	21.10	54.30	0.04	41.90	15.30	2.10
	Prod. (MJ)	172.63	227.65	123.00[a]	113.83[a]	292.93[a]	0.22[a]	226.03[b]	82.54	11.30
	Cons. (MJ)	893.99	1177.70	672.33	618.31	2207.46	1.32	1525.17	481.84	74.64
Total	Prod. (kg)	806.30	230.28	330.98	168.20	57.61	148.89	54.50	75.92	29.82
	Prod. (MJ)	4341.12	1263.61	1851.30	904.27	308.69	773.86	299.70	428.93	163.45
	Cons. (MJ)	22390.69	7958.11	13023.74	6859.12	2274.70	5754.10	1818.56	3915.71	1450.20

[a] K_1 for Three-spined Stickleback was included for calculation of the mean K_1 for 'other species' (see text).
[b] K_1 was the mean calculated for Roach and Gudgeon (see text).

illustrate the total consumption of all fish populations at several sites in small lowland rivers.

Coefficient K_1, which was used for the evaluation of Cons. for the other species, was twice calculated in other ways than was stated in section 'Materials and methods'. At site L_1 the mean value of this coefficient was calculated using only data for gudgeon and roach because among 'other species' were species which lived for several years. Direct data at this site (L_1) were available only for three-spined stickleback which has K_1 value about 5–8 percent higher than K_1 value for longer-lived species. The second case concerns only K_1 value for three-spined stickleback. At sites U_{3-6} the populations of the three-spined stickleback were represented only by the first age-group which is characterized by the highest value of this coefficient. This value was not included in calculating the mean value (used for estimating Cons.) for 'other species'.

In order to transpose the evaluated consumption expressed in energy units (Table 4) to fresh weight of prey the average annual diets for the dominant fish species were first calculated (Fig. 1). In the case of roach, food spectrum for the youngest age-group (0+) and older fish (1+ to 5+) were worked separately because of very significant qualitative and quantitative differences in their diets.

The evaluated caloric content and dry weight of the separated elements of fish diet allowed the energy content to be estimated as fresh weight (Table 5).

On the basis of the food spectra Fig. 1 and data from Tables 4 and 5 the food components in the diet of dominant fish species (and of all fish popula-

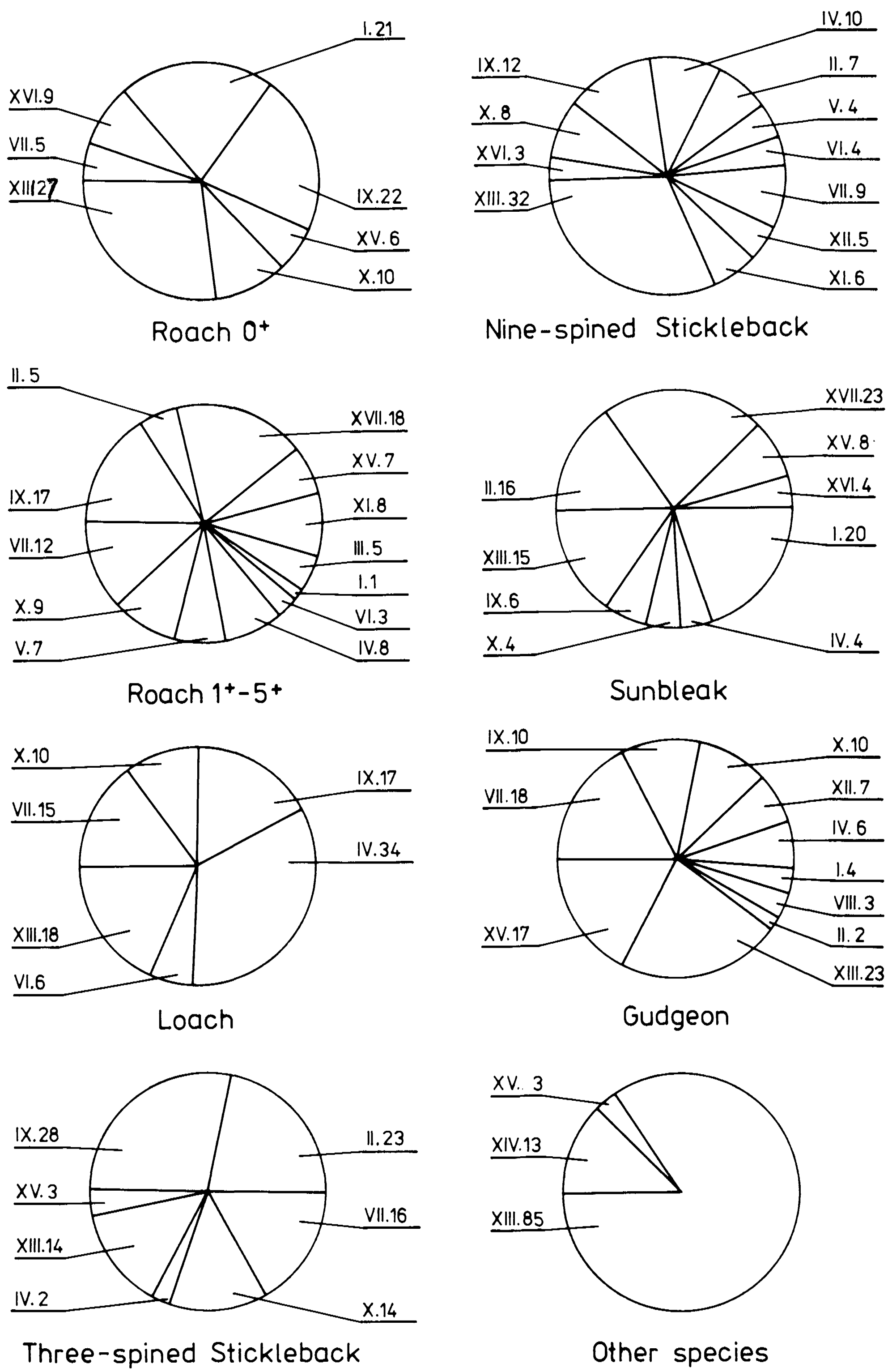

Fig. 1. Diet of the dominant species (I – Cladocera, II – Coleoptera, III – Mollusca, IV – Ephemeroptera, V – Odonata, VI – Plecoptera, VII – Trichoptera, VIII – Lepidoptera, IX – Chironomidae, X – Other Diptera, XI – Gammaridae, XII – Oligochaeta, XIII – Unidentified invertebrates, XIV – Fish, XV – Detritus, XVI – Algae, XVII – Water plants); Arabic numbers – percentages of food types.

Table 5. Dry weight of different food types and their energy content calculated for dry and wet weight.

Food type		Dry weight (%)	Energy content		Reference
			$J\ g^{-1}$ dry wt	$J\ g^{-1}$ wet wt	
I	Cladocera	23.90	15491.1	3702.4	Prus, 1970
II	Coleoptera	30.80	7139.7	2199.0	Prus, 1970
III	Mollusca[a]	12.00	23199.9	2784.0	Prus, 1970
IV	Ephemeroptera	16.96	21553.6	3655.5	Authors' results
V	Odonata	27.32	18855.7	5151.4	Authors' results
VI	Plecoptera	22.60	14059.4	3177.4	Authors' results
VII	Trichoptera	18.63	20179.1	3759.4	Authors' results
VIII	Lepidoptera	23.40	11547.3	2702.1	Authors' results
IX	Chironomidae	25.98	20660.2	5367.5	Authors' results
X	Other Diptera	15.00	21199.4	3179.9	Authors' results
XI	Gammaridae	23.58	14951.9	3525.7	Authors' results
XII	Oligochaeta	17.94	21022.8	3771.5	Authors' results
XIII	Unidentified invertebrates[b]	20.48	17488.3	3581.3	Authors' results
XIV	Fish	24.03	20131.6	5341.7	Authors' results
XV	Detritus	7.50	14977.4	1123.3	Authors' results
XVI	Algae	17.15	20054.8	3439.4	Authors' results
XVII	Water plants[c]	10.20	16838.9	1717.6	Fisher, 1968

[a] Without shell.
[b] Mean calculated from the above data.
[c] Mean calculated for 9 species of aquatic plants.

tions) at the examined sites were evaluated and expressed in units of mass (kg $ha^{-1}\ a^{-1}$ wet wt) and energy (MJ $ha^{-1}\ a^{-1}$). The results of these detailed calculations are not - among other things because of a very big size of the table - included in the text, as the objective of the paper is to investigate the shares of invertebrates, fish, plants and detritus in a fish's diet, and to examine the influence of the changing proportion of the components of the diet upon fish production. Taking into consideration the effect of a diet composed of invertebrates, fish and plant origin, it is not difficult to see that the smallest amount of energy taken, and fresh food mass consumed, for the production of 1 kg of fish tissues (= Prod.), occurs at the sites where invertebrates dominate the fish diet (Table 6). This observation is confirmed by the statistical tests of linear regressions for the following relationships: 1) the quantity of food consumed (kg wet wt) for 1 kg of fish Prod. (x) - amount of consumed plant food (kg wet wt) for 1 kg of fish Prod. (y) - $y = 0.35x - 2.88$ ($r = 0.95$, d.f. $= 7$, $p < 0.001$), 2) amount of energy consumed (MJ) for 1 kg of fish Prod. (x) - weight of food consumed of plant origin (kg wet wt) for 1 kg of fish Prod. (y) - $y = 0.13x - 3.97$ ($r = 0.84$ D.F.$= 7$, $p < 0.01$), and 3) amount of food energy consumed (MJ) for 1 kg of fish Prod. (x) - percentage participation of invertebrates to total consumption (kg wet wt) at 1 kg of fish Prod. (y) - $y = 113.29 - 0.63x$ ($r = -0.77$, d.f. $= 7$, $p < 0.05$).

Discussion

While discussing and verifying the results obtained, data were taken mainly from ichthyological literature concerning river ecosystems. Moreover, the authors must point out a certain deficiency in their paper: namely mean annual diets of dominant species were established on the basis of only two samples. Unfortunately, further sampling was put to an end by the regulation of the river, which made it impossible to continue the researches under the same conditions. It has to be emphasized, however, that in this work main stress was laid on the estimation of food consumption in energy units. In parts of the paper where the efficiency of the utilization of a given food type for fish production was analysed in mass units, on the other hand, the main food types were accepted as the basis of calculations bearing in mind that the assessment of the diet is an approximation (the main food types being: inverte-

Table 6. Consumption (MJ), fish production (kg) in relation to amounts of consumed food type (invertebrates, fish and vegetation) and the energy required to produce 1 kg fish (wet weight) in Utrata River and Zalewka Brook (all sites).

Parameters	U_1	U_2	U_3	U_4	U_5	U_6	L_1	L_2	L_3
Consumption (MJ)	22390.69	7958.11	13023.74	6859.12	2274.70	5754.10	1818.56	3915.71	1450.20
Production (kg)	806.30	230.28	330.98	168.20	57.61	148.89	54.50	75.92	29.82
Energy consumed (MJ) for 1 kg fish production	27.77	34.56	39.35	40.78	39.48	38.65	33.37	51.58	48.63
Invertebrates consumed (kg)	5759.02	1999.27	3327.88	1735.29	515.67	1474.34	421.62	978.84	396.51
Invertebrates consumed (kg) per 1 kg of fish production	7.14 (99.17)*	8.68 (92.34)	10.05 (85.46)	10.32 (91.98)	8.95 (84.83)	9.90 (91.75)	7.74 (86.58)	12.89 (83.81)	13.30 (79.03)
Fish consumed in kg	31.16	40.57	23.15	21.30	76.04	0.04	52.54	16.60	2.57
Fish consumed (kg) per 1 kg of fish production	0.04 (0.56)*	0.18 (1.91)	0.07 (0.59)	0.13 (1.16)	1.32 (12.51)	0.00	0.96 (10.74)	0.22 (1.43)	0.09 (0.53)
Detritus, Algae and plants consumed (kg)	14.24	124.92	541.54	129.83	16.20	131.84	13.00	171.98	102.51
Vegetation consumed (kg) per 1 kg of fish production	0.02 (0.27)*	0.54 (5.74)	1.64 (13.94)	0.77 (6.86)	0.28 (2.65)	0.88 (8.16)	0.24 (2.68)	2.26 (14.70)	3.43 (20.39)
Consumption (kg wet wt) per 1 kg of fish production	7.20	9.40	11.76	11.22	10.55	10.78	8.94	15.37	16.82

* In percentage to consumption (kg wet wt) per 1 kg of fish production.

brates, fish-prey, plants, detritus).

The results of these researches and data of Penczak *et al.* (1982b) confirm a direct relationship between increasing consumption and increasing density of fish populations in rivers (LeCren, 1972). That is why, when estimating Cons. of fish populations with different densities, it is better to compare coefficients of ecological efficiency and the weight of food consumed for 1 kg of fish Prod., and to examine these values separately for different species and in relation to different diets.

Cons. expressed in kg or MJ (ha^{-1} a^{-1}) informs us only about the wealth of the environment because fish can use a big part of invertebrates' production. Sometimes it is difficult to state real proportion between fish and their prey because production of benthos may not be large enough to support the total fish consumption in rivers (Mann, 1972; Mann *et al.*, 1972). Iwaszkiewicz's (1964) research showed how significant the pressure of fish populations on food organisms can be. After removing fish from several fragments of the River Stobnica quantitative increase of bottom fauna was observed many times.

At the examined sites of both rivers invertebrates contribute 88% (79.03–99.17) to the production of fish tissue (Table 6) and they occur exclusively in the diet of some fish species. In the Utrata River and the Zalewka Brook ($\bar{x} \pm$ S.D.) 9.88 $\pm$ 2.10 (range 7.14–13.30) kg of invertebrates was used as an average for the production of 1 kg fish, and at the site at the Wolborka River 13.8 kg (minimum value 11.9 kg) (Penczak *et al.*, 1982b). In two small woodland lakes in Sweden, perch fed only on invertebrates, and increased in body weight by 1 kg using 13.9 and 19.3 kg of invertebrates (Nynberg, 1979). The energetic cost of 1 kg production of fish tissue for the examined fish populations at any one site was, on an average, 39.35 $\pm$ 7.34 MJ ($\bar{x} \pm$ S.D.). The large variability of the amount of energy for production values observed 27.77-51.58 MJ kg^{-1} was conditioned by fish diet (Table 6). A statistically significant correlation ($p < 0.05$) was observed between decreasing amount of energy consumed and an increase in the contribution of invertebrates to the diet.

The coefficients of growth efficiency (K_1, K_2) vary in different species, with high values occurring in predatory fish (Elliott, 1975; Staples & Nomura, 1976; Mortensen, 1981; Penczak *et al.*, 1982a). Diet has greater influence on K_1 and K_2; especially low values were noticed for some Cyprinid species in which detritus of low caloric content and poor assimilation was very important as a diet component (Mann, 1965; Mann *et al.*, 1972). But probably K_1 and K_2 are most clearly correlated with fish age (Tables 2 and 3; Mann, 1965; Adams, 1976; Mortensen, 1981; Penczak *et al.*, 1982a).

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