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A PRELIMINARY ECOSYSTEM MODEL OF A EUTROPHIC LAKE (LAKE AYDAT, FRANCE)

by

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ABSTRACT

An attempt was made to model the eutrophic ecosystem of Lake Aydat in the Massif Central, France, with emphasis on the two dominant fish species, perch (*Perca fluviatilis*) and roach (*Rutilus rutilus*). The ECOPATH II model shows among others that assuming a top-predator biomass (i.e., pike and sander) of 1.0 g/m^2 leads to estimates of 3.3 g/m^2 for the perch biomass and of 0.62 g/m^2 for the roach biomass.

INTRODUCTION

In response to the challenge posed by the recently developed ECOPATH II model of Christensen and Pauly (this vol.), an attempt is presented here to model the Lake Aydat, Massif Central, France.

Lake Aydat is classified as a eutrophic dimictic lake (Millerioux 1976) and is situated at the Parc Régional des Volcans d'Auvergne in the Puy de Dôme region in the Massif Central in France (Jamet et al. 1990). Fig. 1 provides various statistics on Lake Aydat.

This lake has been the object of various studies especially by the Freshwater Hydrobiology team of the Zoology-Protistology Laboratory, Université Blaise Pascal, Clermont-Ferrand. The bulk of these studies focused on the estimations of planktonic and bacterioplanktonic biomass. On the other hand, ichthyological studies are scarce. However, a recent study conducted by Jamet et al. (1990) on the diel feeding cycle of roach in Lake Aydat helped to identify this population's feeding habits.

There is practically no fishery in Lake Aydat except for some occasional sports fishermen, whose catches remain largely undocumented, but which can be assumed to be insignificant. No information is available on the benthic populations.

MATERIALS AND METHODS

As the ECOPATH II approach is discussed in more detail in Christensen and Pauly (this vol.), only the balanced equation used in ECOPATH II for each "box" is recalled here, i.e., $B_i * P_i/B_i * EE_i = (B_j * Q_j/B_j * DC_{ij})$ where B_i is the biomass of species i; P_i/B_i, its production/biomass ratio; EE_i, its ecotrophic efficiency; and where B_j is the biomass of predator j, Q_j/B_j its relative food consumption and DC_{ij} is the fraction of species i in the diet of predator j.

In order to work with this model, an estimate of at least three of the four parameters should be available for each box, along with the diet composition. The following paragraphs describe how these parameters were assembled for Lake Aydat.

Biomass estimates

Phytoplankton

The phytoplanktonic populations of Lake Aydat are by far the best-studied part of its ecosystem. This eutrophic lake experiences, throughout the year, three maxima of phytoplanktonic biomass, three of zooplanktonic biomass and three periods of increased water transparency, which follow the increases in zooplanktonic biomass (Aleya and Devaux 1989; Lair and Ayadi 1989). This suggests that grazing by zooplankton controls algal succession in the lake.

Aleya et al. (1988) investigated the 0-4 m zone of the lake and estimated an annual mean phytoplankton production of 78 $mgC/m^2/hour$. They also gave a mean annual top layer biomass estimate of 6.95 mg/l (=47.8 mg/m^2). In a related study, Aleya and Devaux (1989) reported biovolumes for sizes of $< 12\,\mu m$ at 0.12 mg/l at the surface (1 m) and cholorophyll *a* concentrations of 22.5 $\mu g/l$ at the bottom.

Bacterioplankton

Lair and Ali (1990) suggested that, in Lake Aydat, the considerable bacterioplankton biomass (free bacteria plus bacteria attached to detritus) in the 4-7 m zone is an important source of rotifer food. Marvalin et al. (1989), moreover showed that bacterioplankton is not only found in the 4-7 m depth zone, and reported (i) 0.08 mgC/l at 2 m, (ii) 0.1 mgC/l at 7 m and (iii) 0.09 mgC/l at 14 m. These leads to a mean biomass of 0.09 mgC/l. If a conversion factor from carbon to wet weight of 12 is assumed, then the mean wet bacterioplanktonic biomass is 1.08 mg/l or 7.42 g/m^2.

Zooplankton

Lair (in press) estimated zooplankton biomasses in 1984-1985. Her data led to annual mean biomasses of (i) rotifer = 2,905 mg/m^3 (20 g/m^2), (ii) copepod = 3,250 mg/m^3 (22 g/m^2) and (iii) cladoceran = 2,130 mg/m^3 (15 g/m^2). If rotifers and cladocerans are considered to be herbivorous/detritivorous feeders and copepods carnivorous feeders, then the total biomass of herbivorous zooplankton in Lake Aydat is 35 g/m^2 and that of carnivorous zooplankton is 22 g/m^2.

Relative production and food consumption

Phytoplankton

Aleya and Devaux (1989) estimated P/B ratios using three methods for three different size ranges (< 12 μm, 12-45 m and 45-160 μm). Estimated P/B ratios are (i) using biovolumes, 5 mg/l (34.4 g/m^2); (ii) using chlorophyll *a* estimates, 18 μ/l; and (iii) using counting of chlorophyll *a* cells, 0.044/hour.

Bacterioplankton

The P/B ratio for bacterioplankton was obtained from Jørgensen (1979, Table A174) where a mean value of 0.45/day (about 160/year) was reported for the "southern seas of the USSR". Assuming a gross efficiency of 50%, Q/B was set at 320/year.

Zooplankton

Herbivorous zooplankton P/B values listed in Jørgensen (1979, Table A469) were averaged to obtain an annual ratio of 16/year. Only one estimate was given for predatory zooplankton (P/B = 5/year). Since rotifers appear to be the most important non-predatory zooplankton in Lake Aydat, their Q/B = 20/year (Lair, in press) was used. There is no available estimate for herbivorous zooplankton; therefore, a gross efficiency of 30% was used which set Q/B at 53/year.

Insects and molluscs

There is no available information in the literature on the benthic populations in Lake Aydat. However, Jørgensen (1979, Table A269) lists P/B ratios for several species of invertebrates including some that occur in Lake Aydat. Thus, P/B values for *Asellus, Chaoborus, Chironomus, Gammarus* and miscellaneous annelids, coelenterates, and molluscs were averaged to give a mean value of 3/year. Assuming a gross efficiency of close to 30%, Q/B can be set at 11/year.

Fish populations

There is no regular fishery in Lake Aydat and thus, P/B was here set equal to natural mortality (M), as obtained from the empirical formula of Pauly (1980) and the growth parameter estimates listed in Table 1. (Note that the M estimates were adjusted downward in cases where the gross efficiency estimates reached 30% or more.)

The Q/B estimates were obtained from the empirical formula of Palomares and Pauly (1989), except for roach. Several estimates of daily ration were obtained from independent sources (see Table 2) and turned, using the model of Pauly (1986), into estimates of Q/B. An annual Q/B value of 29.3 was estimated for roach fry by integrating between W_r = 0.001 g and W_{max} = 1.4 g, based on the assumption that 0+ roach reach a maximum length of 5 cm (about 1.5 g). A value of Q/B = 9.21/year was estimated for adult fishes by integrating between W_r = 1 g and W_{max} = 90% of W. The final estimates used in the ECOPATH II model were the means of the estimates obtained as described above and those listed in Table 1 (i.e., based on the empirical formula of Palomares and Pauly (1989)).

Ecotrophic efficiencies and diet compositions

Ecotrophic efficiencies were assumed at 0.95 for perch, roach and benthos while a value of 0.50 was assumed for benthic producers. This latter value was adopted because the bulk of benthic production (e.g., plant material such as grasses) is not consumed alive, but in the form of detritus. Consumption of "live" matter was limited to diatoms and blue-green algae which form a relatively small proportion of the biomass of the benthic producers (although not of their production).

Table 3 presents the diet composition of the different species/groups. This information was mostly obtained from the literature. Note that the diet composition of the top predator box is based on the diet of pike while the perch/pope box is based on the diet of perch.

RESULTS AND DISCUSSION

Fig. 2 illustrates the ECOPATH II box model obtained for Lake Aydat in the mid-1980s. Assuming a pike/sander biomass of 1 g/m^2, the perch/pope biomass could reach 3.3 g/m^2 and the total roach biomass a level of 0.62 g/m^2. Note that the detritus biomass was here set at 5 g/m^2.

Benthic producers attain 190 g/m^2 which is not unreasonable considering that plant material, consumed as detritus, make up the bulk of this biomass. However, the biomass also includes small organisms such as diatoms and cyanophytic algae which are important in the diet of fishes (Jamet et al. 1990). Note that the P/B (= 10) ratio assumed for benthic producers is a mean value which takes into account the fast turnover rates of small organisms and the relatively lower turnover rates of leafy plants and grasses.

The ecotrophic efficiencies estimated by ECOPATH II for pike, zooplankton, bacterioplankton and phytoplankton appear reasonable. The low EE value of 0.037 for the top predator box implies that most of this group's production ends up as detritus as these fishes die of old age.

The phytoplankton EE of 0.747 is, as expected, relatively low. Blooms were observed to occur prior to zooplankton biomass maxima (Lair and Ayadi 1989). During these periods, supply exceeds demand. With a fast turnover rate, much of this excess production dies off to become detritus. However, the remaining phytoplankton is consumed (perhaps totally) by the subsequently increasing zooplankton population. As pointed out by Lair and Ayadi (1989), the phytoplankton biomass of Lake Aydat is largely controlled by zooplankton grazing and thus periods of clear waters (i.e., low abundance of phytoplankton) occurred after zooplankton blooms.

When the food source is depleted, it is possible that zooplankton die off (to become detritus) before they can be exploited by the roach population which builds up around the same time. However, the total roach biomass as estimated by ECOPATH II does not seem large enough to be able to deplete its zooplankton food source. Thus the relatively low EE values of 0.466 and 0.393 for predatory and herbivorous zooplankton, respectively.

Table 4 presents some of the outputs obtained from ECOPATH II for the Lake Aydat system. Further discussion of these statistics is deferred until more information is available on the different species considered here (specially the fishes). However, it is important to appreciate the usefulness of such preliminary models in further documenting a previously unknown system. It is recommended, therefore, that studies be conducted which aim at testing these results.

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Table 1. Growth parameters, mortality, condition factors, aspect ratios and food types for five fish species considered in the Lake Aydat model. These parameters were averaged for each species and used in the food consumption model of Palomares and Pauly (1989) to obtain estimates of Q/B. Note that mean environmental temperature used was 12.2°C.

Common name	Scientific name	Area	L_∞ cm. TL	K year	Ø'	Sources/ Remarks
Pike	*Esox lucius*	Windermere (M)	75.00	0.238	3.127	Johnson (1966)
		Windermere (F)	100.00	0.264	3.422	
		Wisconsin	93.30	0.310	3.431	Pauly (1978), based on Nikolsky (1957)
		Aral Lake	80.60	0.204	3.122	
		Peipus Lake (M)	64.40	0.332	3.139	
		Peipus Lake (F)	97.50	0.208	3.296	
		Chany Lake (M)	106.00	0.123	3.141	
		Chany Lake (F)	141.00	0.097	3.285	
		Schlei-Fjord	106.00	0.248	3.445	Nauen (1984)
		MEANS:	96.00	0.201	3.268	t_0 = -0.61; M = 0.312; AR = 3.392; F = piscivore; Q/B(year) = 1.179; condition factor (a = 0.009276) computed from data in Muus and Dahlström (1967), i.e., 455 g/32.5 cm, 6,500 g/95 cm, b = 3.
Sander	*Lucioperca lucioperca*	Kuban River	85.60	0.238	3.242	Pauly (1978), based on Nikolsky (1957)
		Don River	86.00	0.168	3.094	
		Aral Lake	79.50	0.204	3.110	
		Ilmen Lake	104.00	0.129	3.145	
		So, Caspian	.00	0.333	2.727	
		Schlei-Fjord	79.20	0.216	3.132	Nauen (1984)
		MEANS:	79.00	0.190	3.075	t_0 = -0.683; M = 0.317; AR = 1.690; F = piscivore; Q/B(year) = 0.933; condition factor (a = 0.008957) computed from data in Muus and Dahlström (1967), i.e., 1,000 g/45.5 cm, 12,000 g/120 cm, b = 3.
Perch	*Perca fluviatilis*	Aral Lake	23.30	0.405	2.342	Pauly (1978), based on Nikolsky (1957)
		Petschora	38.00	0.124	2.253	
		Sweden	30.00	0.200	2.255	Alm (1952)
			34.00	0.130	2.177	Alm (1952)
		Orava Reservoir	41.90	0.123	2.334	Pauly (1978), based on Nikolsky (1957)
			36.90	0.119	2.210	
			29.30	0.354	2.480	
		Schlei-Fjord	50.00	0.172	2.633	Nauen (1984)
			50.90	0.120	2.493	
		Lake Aydat	31.80	0.161	2.212	
		MEANS:	36.60	0.163	2.339	t_0 = -0.989; M = 0.356; AR = 1.690; F = piscivore; Q/B(year) = 0.933; length-weight relation $W = 0.008618 L^{3.171}$ was based on data provided by Jamet (pers. comm.).

Table 1 Cont'd...

Common name	Scientific name	Area	L∞ cm. TL	K year	Ø'	Sources/ Remarks
Pope	*Acerina cernua*	Lake Aydat	15.00	0.306	1.838	Analyzed with ETAL II by last author using Lmax of length-at-age data obtained by scale reading.
			25.00	0.055	1.535	Analyzed with ETAL II by last author using L_{max} from Terofal (1984) and length-at-age data from scale readings by Jamet (pers. comm.)
		MEANS:	20.00	0.121	1.687	t_o = -1.592; M = 0.348; AR = 0.846; F = omnivore; Q/B(year) = 2.578; length-weight relation W = 0.003372 $L^{2.705}$ was based on data provided by Jamet (pers. comm.)
Roach	*Rutilus rutilus*	Tjeukemeer	20.65	0.231	1.993	Analyzed with ETAL II (rss = 1.098 using data in Goldspink (1979).
		Rostherne Mere	21.80	0.707	2.526	Analyzed with ETAL II (rss = 0.1501) using data in Goldspink (1979).
		Mälaren	31.44	0.146	2.159	Analyzed with ETAL II (rss = 11.05) using data in Kempe (1962).
		Sövdeborgssjon	30.75	0.0569	1.811	Analyzed with ETAL II (rss = 0.2139) using data in Lessmark (n.d.).
		Volvi	32.75	0.076	1.913	Analyzed with ETAL II (rss = 2.767) using data in Papageorgiou (1979).
		Hainslon	18.90	0.158	1.752	Analyzed with ETAL II (rss = 0.277) using data in Kempe (1962).
		Petschora	42.50	0.080	2.166	Pauly (1978), based on Nikolsky (1957)
		Ilmen Lake	26.20	0.180	2.092	Pauly (1978), based on Nikolsky (1957)
		Aral Lake	51.30	0.101	2.425	Pauly (1978), based on Nikolsky (1957)
		Don River	35.50	0.173	2.338	Pauly (1978), based on Nikolsky (1957)
		Lake Aydat	25.00	0.900	2.750	Analyzed with ELEFAN, data provided by Jamet (pers. comm.).
			53.30	0.128	2.561	Analyzed with Bhatttacharya's method, data provided by Jamet (pers. comm.).
			30.00	0.147	2.122	Analyzed with ETAL II (rss = 2.52) using scalimetry data provided by Jamet (pers. comm.).
		MEANS:	32.30	0.152	2.200	t_o = -1.592; M = 0.353; AR = 1.479; F = omnivore; Q/B(year) = 2.408; mean weights were obtained from three length-weight relationships: A) W = 0.03954$L^{2.863}$ (Pivnicka 1975) B) W = 0.0356$L^{3.405}$, males (Papageorgiou 1979) C) W = 0.0215$L^{3.606}$, females (Papageorgiou 1979)

Table 2. Daily ration estimates for adult roach (natural populations) used in the estimation of Q/B with the integration method of Pauly (1986).

W (g)	Rd % BWD	T°C	Source
20	4.00	14	Persson (1982)
46	1.09	-	Persson (1983)
66	1.02	-	Persson (1983)

Table 3. Diet composition of the species groups considered in the ECOPATH II model of Lake Aydat. Note that rows denote predators and column preys.

No.	Common Names	1	2	3	4	5	6	7	8	9	10	11	Sources
1	Pike/sander	1.0	35.9	35.0	20.0	8.1	-	-	-	-	-	-	Bregazzi and Kennedy (1980), Diana (1979)
2	Perch/pope	-	13.0	3.6	7.1	64.3	4.0	3.6	-	-	-	4.4	Persson (1986), Eie and Borgstrom (1981), Thorpe (1972-73)
3	Roach adults	-	-	-	0.1	39.3	13.5	3.6	0.4	24.2	7.0	11.9	Weatherly (1987)
4	Roach fry	-	-	-	-	17.0	61.9	10.0	2.0	0.1	9.0	-	Eie and Borgstrom (1981)
5	Insects/molluscs	-	-	-	-	-	10.0	20.0	40.0	10.0	10.0	10.0	
6	Predatory zooplankton	-	-	-	-	-	10.0	10.0	20.0	-	50.0	1.0	
7	Herbivorous zooplankton	-	-	-	-	-	-	-	20.0	-	75.0	5.0	
8	Bacterioplankton	-	-	-	-	-	-	-	-	-	40.0	60.0	
9	Benthic producers	-	-	-	-	-	-	-	-	-	-	-	
10	Phytoplankton	-	-	-	-	-	-	-	-	-	-	-	
11	Detritus	-	-	-	-	-	-	-	-	-	-	-	

Table 4. Summary statistics obtained from ECOPATH II for Lake Aydat in the mid 1980s.

Statistic	Units	Value
Sum of all production	$g/m^2/year$	4,270
Sum of all respiratory flows	$g/m^2/year$	3,552
Sum of all flows into detritus	$g/m^2/year$	3,345
Total system throughput	$g/m^2/year$	11,167
Full development capacity	flowbits	27,478
Full ascendency		9,308
Overhead on respiration		6,319
System redundancy		11,852

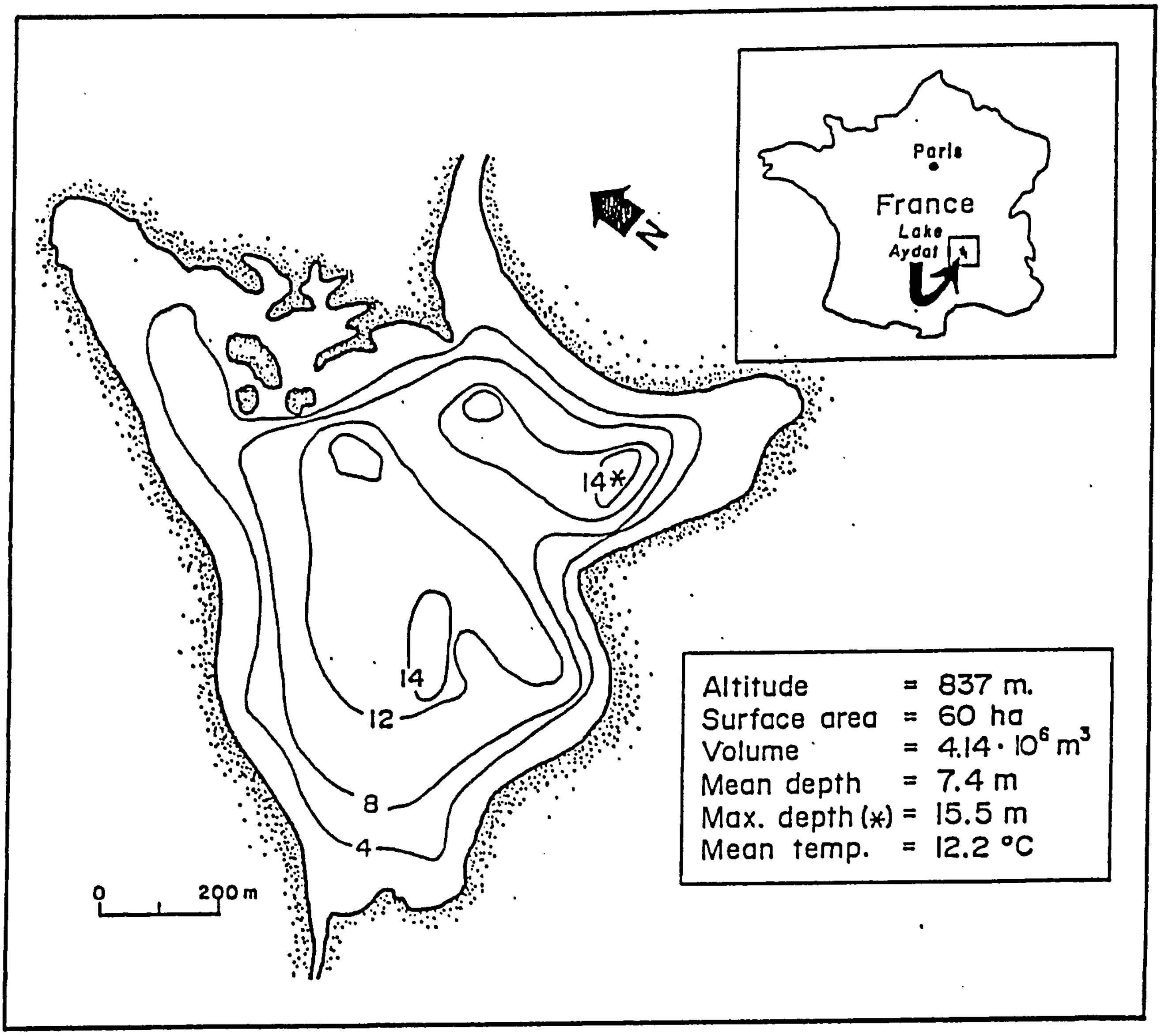

Fig.1. Lake Aydat, Puy-de-Dôme, Massif Cetral, France, showing depth isolines (adapted from Aleya et al. 1988).

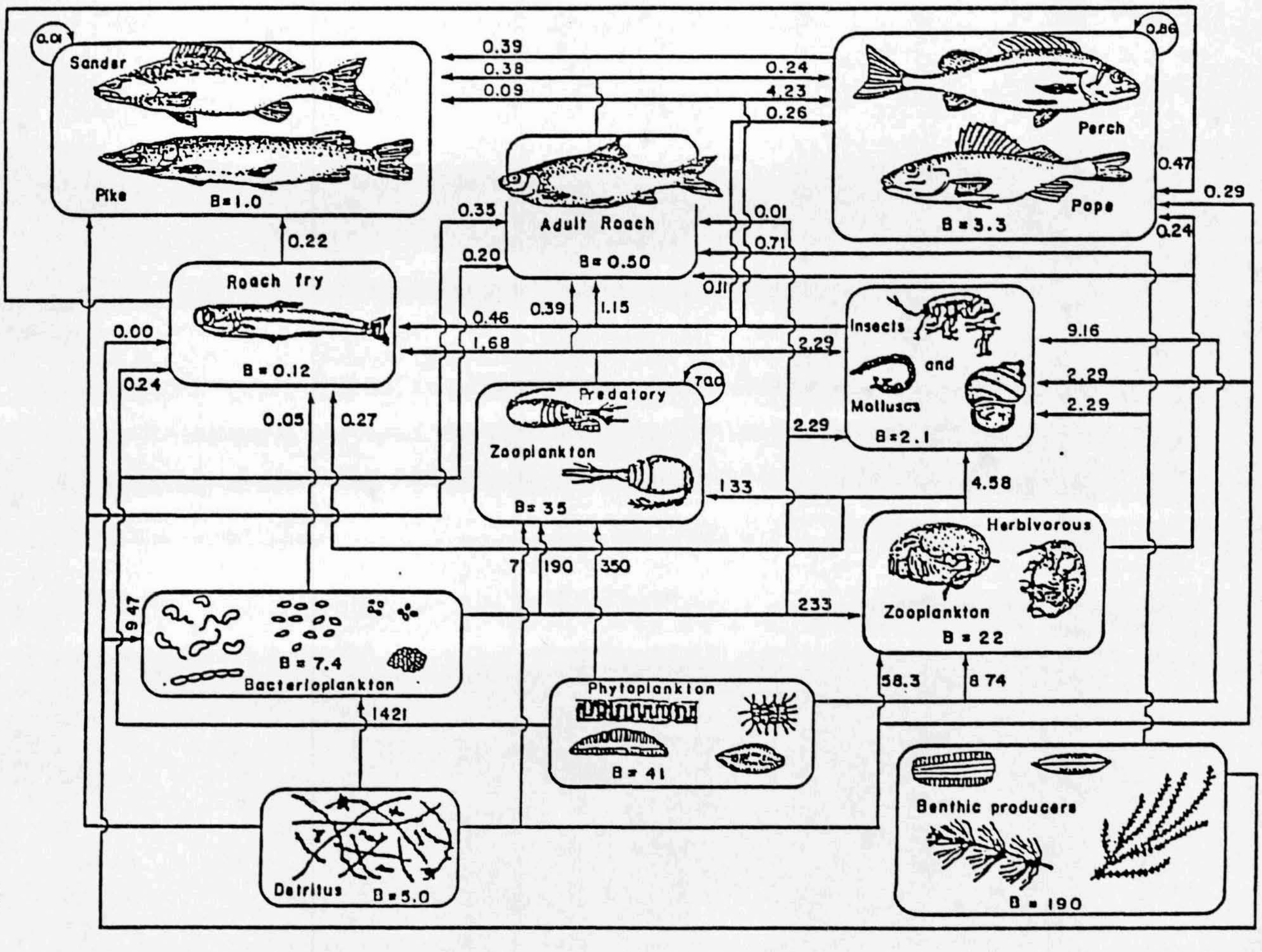

Fig. 2. A quantitative representation of the trophic interaction in Lake Aydat, France. All flows are expressed in $g/m^2/year$, while biomasses (B) are in g/m^2.