

Empirical analysis of the influence of environmental variables associated with lake eutrophication on perch growth, consumption, and activity rates

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We developed a series of relationships between components of fish bioenergetic model and environmental variables using data for twenty-six combinations of three age classes and eleven perch populations. Perch growth decreased as total fish numerical abundance increased. Growth, consumption, and activity rates decreased with the increase of the percent contribution of small prey to the invertebrate community. Furthermore, consumption and activity rates were negatively related to the biomass of the total invertebrate community but positively related to water transparency. Our analyses offer a more quantitative framework to the suggestion that perch growth and consumption rates may be negatively affected by eutrophication.

1. Introduction

The influence of environmental conditions on perch populations have been the subject of many studies (Persson 1987ab, Karås 1990, Wu & Culver 1992, Parrish & Margraf 1993, Diehl 1993, Paszkowski & Tonn 1994). One of the most common process that affects perch populations is eutrophication (Hartmann & Nüman 1977, Hayward & Margraf 1987).

Leach *et al.* (1977) presented a conceptual framework to describe the influence of eutrophication on perch populations. They suggested that, as the trophic status of a lake progresses from oligotrophy to eutrophy, the "well-being" of perch should increase,

mostly through an increase of prey abundance. However, they also hypothesized that beyond a given level of eutrophy, perch should be negatively affected partly because of a decrease of the biomass of suitable prey. Kitchell *et al.* (1977) proposed a mass balanced bioenergetic equation to model fish growth—one of the indicators of perch "well-being" used by Leach *et al.* (1977). Few studies have made a significant contribution to our understanding of the relationship between variables included in the bioenergetic model and environmental conditions (Hayward & Margraf 1985, Persson 1986, 1987ab, Post & McQueen 1994). However, integration of the conceptual framework developed by Leach *et*

al. (1977) and of the quantitative model proposed by Kitchell *et al.* (1977) has been impeded by the difficulty to develop relationships between key components of fish bioenergetic model and environmental variables for lakes covering a wide range of trophic status.

Boisclair and Leggett (1989a–d) examined the interactions between perch growth and consumption rates and a suite of descriptors of perch diet and fish community structure. Their sampling was executed simultaneously with the study of the limnological characteristics and of the invertebrate community of the same lakes (Rasmussen 1988, 1993). Limnological analyses indicated that these lakes ranged from oligotrophy to eutrophy (Rasmussen 1988, 1993). This allows us to assess the influence of differences of limnological variable and fish and invertebrate community structure on perch. More specifically, the objectives of our analyses were: 1) to use the empirical approach to model the effects of fish and invertebrate communities, and of limnological characteristics on perch growth, consumption, and activity rates, 2) to assess the relative influence of these environmental variables on specific components of perch energy budget, and 3) to evaluate the correspondence between the models developed and the conceptual framework provided by Leach *et al.* (1977).

2. Material and methods

The data used to perform our analyses were extracted from the works of Boisclair and Leggett (1989a–d) and Rasmussen (1988, 1993). The methodology used to collect the samples are described in detail in these papers. We only present a summary of the methods pertaining to our work with an emphasis on the procedures used to combine our data.

2.1. Lakes studied

We modeled the effects of fish and invertebrate communities on the growth, consumption and activity rates for twenty-six combinations of three age classes (I+ to III+) and eleven of the twelve perch populations sampled by Boisclair and Leggett (1989a–d) in the Eastern Township region of Quebec. Lake Massawippi was excluded from the present work because we have no detailed information on its limnology and on its invertebrate community. Each lake was sampled at 3–4 week intervals between May and October 1985. Perch size, daily consumption rate, and diet was estimated for the three age classes.

2.2. Sampling

On each sampling date, 10 perch were collected at 8 h intervals over a period of 24 h using a 50 × 3 m (0.6 cm² mesh size) beach seine. Fish were killed with an overdose of 2-phenoxyethanol (1 ml l⁻¹) immediately following capture. Fish weight (± 0.01 g wet) and total length (± 1 mm) were determined on site. Ten to 20 scales were collected from each fish for aging. The complete digestive tract content of fish was removed and weighed individually (± 0.01 g wet). These data allowed the estimation of daily mean digestive tract content. Fifty to 100 additional perch were collected each date near the peak of feeding to estimate evacuation rate. These fish were stocked in a 1-m diameter pool supplied with a continuous flow of filtered lake water. This maintained the water temperature inside the pool within ± 1°C of the mean epilimnion water temperature. Ten to 20 perch were sacrificed and processed as described previously at the time of stocking and at 4- to 5-h intervals for 20 to 24 h. The slope of the exponential decrease of complete digestive tract content through time provided an estimate of perch evacuation rate. Daily ration was estimated as the product of daily mean digestive tract content and evacuation rate (Boisclair & Leggett 1989a). Another group of 15 to 20 perch having full stomach were retained from each population on each sampling date. Total length of each fish was noted, its stomach content was spread on a 3 × 5 cm plexiglass tray and was photographed in the field within 3 h of capture. In the laboratory, images of the stomach contents of individual fish were projected on a digitizer calibrated with reference to a ruler photographed on each picture series. All prey items were identified and measured to the nearest 0.1 mm. Prey length was transformed to weight using empirical relationships (Boisclair & Leggett 1989b, Rasmussen 1988, see below). Preys were classified in nine size classes (SC1 to SC9) following a geometric scale (Table 1). The fish communities were described in July–September 1985. During that period, 4 seine hauls each covering an area of 460 m² of the littoral zone were executed in each lake. All sampled fish > 50 mm total length were identified, measured, and weighed within 4 h of capture. This sampling allowed the estimation of the total fish numerical density (*TN*; number of fish per square meter) and biomass as well as the numerical density and the biomass of each fish species collected (Boisclair & Leggett 1989c).

Invertebrate and macrophyte communities (taxonomic composition and biomass) and the limnological characteristics of a given lake were always estimated within one week of sampling for fish. A SCUBA diver collected five 40 cm² cores in the littoral zone. Samples were rinsed through a 0.2 mm screen and the sieve residue containing the benthic invertebrates was preserved in 5% formalin. The animals were picked from the samples under a dissecting microscope (6×) and their lengths were measured with an image analysis system (CORECO Inc St-Laurent, Que.) equipped with an Oculus 200 digitizer board. Fresh weights were estimated from total body lengths using a series of length-weight regressions constructed from animals collected during the study of Rasmussen (1988). Biomass of epiphytic invertebrates (g × g plant matter⁻¹) was

estimated using the hand held box sampler described by Rasmussen (1988). A SCUBA diver enclosed a sample of undisturbed vegetation and trimmed off all plant matter protruding from the sampler. As the sampler was removed from the water, the water inside was allowed to drain through the 0.2 mm screen on its side, and the contents of the sampler were placed in a plastic bag. In the laboratory, the vegetation was rinsed free of animals, marl, and most periphyton, spun for 1 min in a salad spin-dryer, and weighed (g wet). The material washed from the plants was preserved in 5% formalin. On each sampling date where vegetation was present, two such samples were taken at mid-canopy, two within 50 cm of the substrate, and two were taken within 50 cm from the surface if the canopy grew that high. The animals were picked from the samples, lengths measured, and weights estimated as described above for the substrate cores. Biomass of zooplankton was estimated on an areal basis ($\text{g wet} \times \text{m}^{-2}$) by integrating vertical plankton net (30 cm diameter opening) tows hauled from the substrate to the surface. Three replicate tows were taken at each sampling time in areas of the littoral where macrophyte density did not interfere with the free movement of the net through the water column. Samples were analysed under a dissecting microscope (12 \times) connected by a video-camera to the CORECO image analysis system. The biomass of zooplankters was estimated from length measurements in the same manner as that described for the benthic and epiphytic invertebrates. All invertebrates (benthic, zooplanktonic and epiphytic) were classified using the size classes described for food items. This allowed the calculation of the contribution of each size classes to the biomass of the total invertebrate community (*TCB*; $\text{g wet} \times \text{m}^{-2}$). Secchi disk transparency (*SED*; m) was measured beyond the macrophyte bed at each site since it was intended to characterize the clarity of the water moving into the littoral through wave action. It was impractical to make this measurement within the macrophyte bed since it was either too shallow or macrophyte density was sufficient to interfere with the measurement. Biomass of submerged macrophyte was estimated by taking

five replicate 0.1 m² quadrat samples that were randomized by tossing the quadrat from a boat within the area of maximum canopy height. A SCUBA diver retained in a diving bag all plants that were rooted within the area of the quadrat, in addition to non-rooted stems of *Ceratophyllum* that were judged to have come from within the quadrat area. After returning to the laboratory, samples were rinsed free of debris, identified to species, spun in a salad spinner to remove excess water, and weighed (kg wet). This allowed the estimation of the total macrophyte biomass (TMB; $\text{kg wet} \times \text{m}^{-2}$) and of the biomass of each species of submerged plants.

2.3. Computation of fish characteristics

The analyses performed by Boisclair and Leggett (1989a–d) have been the subject of an unresolved debate (see Hayward 1990 & Hewett *et al.* 1991 for comments; see Boisclair & Leggett 1990, 1991 for replies). One of the most important criticism directed towards their work concerns the potential confounding effect of body size and the possible problems associated with the analysis of relative ($\text{g} \times \text{g}^{-1} \times \text{d}^{-1}$) instead of absolute growth and consumption rates of fish that varied in size. We tried to minimize the potential effects of this bias by estimating fish growth, consumption, and activity rates in absolute units. Growth rates ($\text{g wet} \times \text{d}^{-1}$) were calculated by dividing weight increment between the first and last sampling session by the time interval between these dates. Daily consumption rates ($\text{g wet} \times \text{d}^{-1}$) were calculated as the product of relative daily ration and perch mean weight that day (g wet). Consumption rates ($\text{g wet} \times \text{d}^{-1}$) were estimated by dividing the area under the curve of daily consumption rate versus Julian days by the number of days between the first and last sampling. Activity rates were estimated by using our data on perch size (and hence growth rates) and daily consumption rates as inputs to the bioenergetic model proposed by Kitchell *et al.* (1977) with the parameters presented by Hewett and

Table 1. Definition of the size classes of invertebrates used during our analyses and values of their contribution to the diet of perch and to the biomass of communities (min. = minimum contribution; max. = maximum contribution; avg. = average contribution).

Size class	Weight interval (mg wet)	% contribution to perch diet			% contribution to invertebrate biomass		
		min.	max.	avg.	min.	max.	avg.
SC1	0–1	0.5	77.6	22.8	7.8	39.0	21.2
SC2	1–2	1.2	37.6	15.6	9.3	25.6	16.6
SC3	2–4	2.0	36.0	10.6	9.6	32.2	19.3
SC4	4–8	0	39.9	13.2	3.9	20.8	12.1
SC5	8–16	0	60.7	12.7	1.3	15.8	5.8
SC6	16–32	0	36.1	7.3	0	8.1	4.0
SC7	32–64	0	25.6	5.4	0	9.9	4.7
SC8	64–128	0	56.4	7.0	0	25.2	8.6
SC9	128–256	0	26.4	3.2	0	19.6	7.7

Johnson (1987). This model was run on a daily basis and, for each day modeled, activity was estimated as the difference between consumption and a suite of expenditures and losses such as standard metabolic rate, excretion, secretion, and heat increment (Boisclair & Leggett 1989d). Activity rates ($\text{g wet} \times \text{d}^{-1}$) were estimated by dividing the sum of all daily activity rates by the time interval between the first and last day modeled. Activity multipliers were defined as the ratio of spontaneous metabolism (activity costs + standard metabolism) to standard metabolism.

The preference of perch for a given prey size class was estimated using a rank preference index proposed by Johnson (1980). The percent contribution of any prey size class to perch diet was estimated as described by Boisclair and Leggett (1989b). The measure of relative preference was defined as the difference between the rank of the percent contribution of a prey to the diet minus the rank of the percent contribution of that prey to the biomass of the invertebrate community. During the calculations, tied ranks were replaced by an average ranking. The difference between the contribution of prey size classes to perch diet and to invertebrate community was computed as the sum, for the nine prey size classes, of the absolute difference between their percent contribution to the diet and to the invertebrate community (hereafter referred to as the discrepancy index; *DI*). All other data on perch diet and of fish communities were extracted from Boisclair and Leggett (1989bc).

2.4. Computations of invertebrates and macrophyte characteristics

Biomass of benthic and planktonic invertebrates ($\text{g wet} \times \text{m}^{-2}$; by taxonomic groups and size classes) and that of macrophyte species ($\text{kg wet} \times \text{m}^{-2}$) were estimated as described by Rasmussen (1988, 1993). The biomass of epiphytic invertebrates ($\text{g wet} \times \text{m}^{-2}$) was calculated as the product of values obtained from the box samplers ($\text{g wet invertebrates} \times \text{kg wet}^{-1} \text{ plant}$) and plant biomass estimates obtained by quadrat sampling ($\text{kg wet} \times \text{m}^{-2}$). Special attention was given to *Amphipoda* because Boisclair and Leggett (1989b) suggested that the percent contribution of this group to the diet may play a major role in explaining among-population variability in perch growth rates. The biomass of *Amphipoda* was divided in two values: organisms living on the weeds (*AMP_w*; part of epiphyton) and invertebrates on the bottom of lakes (*AMP_b*; part of the benthos).

2.5. Analyses

We used simple and multiple regression analyses to examine the relationship between seasonal mean perch growth, consumption, and activity rates (all in $\text{g wet} \times \text{d}^{-1}$) and descriptors of the fish, invertebrate, and macrophyte communities. Activity rates plus one ($A + 1$) were used as dependent variables to make all values of activity positive and allow the modeling of the logarithm of activity rates. Multiple regression were not performed with independent variables that had a correlation coefficient larger than 0.3. Furthermore, variables that explained less than 10% of components of perch energy budget

were not considered. As showed by Boisclair and Leggett (1989a), growth and consumption rates in $\text{g wet} \times \text{d}^{-1}$ are directly related to fish weight. Hence, to account for the existence of this relationship and to simplify our work, we pooled the three age classes during our analyses (analysing the three age classes together) and used seasonal mean fish weight as an independent variable. However, fish of different age that inhabit a single lake may not be biologically or statistically independent. Similarly, three age classes of perch from a given lake were often associated with a same set of independent variables (e.g. total invertebrate biomass is the same for the 3 age classes of perch from Lake Bromont). Because our strategy may unduly increase our degrees of freedom, we emphasize that the *F*- and *P*-values we present should be interpreted as qualitative indications of the strength of our models. To further evaluate the potential bias of pooling age classes, we complemented our work with analyses in which each age classes were examined individually. Again, fish weight was included as an independent variable.

3. Results

3.1. Fish characteristics

Mean perch weight, and perch growth and consumption rates varied 6- to 17-fold among age classes and populations (Table 2). The statistical significance of these differences was established by Boisclair and Leggett (1989a). Six of the twenty-six activity values were negative because the precision of our growth and consumption rates, or that of the parameters from the bioenergetic model used, was not sufficient to discriminate calculated values of activity from close to zero expenditures. Perch growth ($P < 0.03$; $r^2 = 0.20$), consumption ($P < 0.0001$; $r^2 = 0.70$), and activity rates ($P < 0.03$; $r^2 = 0.20$) were positively and linearly related to fish weight. The contribution of prey size classes to diet ranged from 3.2% (*SC9*) to 22.8% (*SC1*; Table 1). The most selected prey size classes covered the complete range of prey weight. The discrepancy index ranged from 32% to 182% (Table 2). Total fish numerical density (all species combined) varied significantly among lakes and covered a 7-fold range (Table 3; see Boisclair & Leggett 1989c for other characteristics).

3.2. Invertebrate, macrophyte and limnological characteristics

Zooplanktonic, epiphytic and benthic components of the invertebrate communities varied, respectively,

12-, 31-, and 3-fold among lakes (Table 3). Total invertebrate community biomass (zooplankton + epiphyton + benthos) ranged from 16.4 (Lake Silver) to 83.6 g wet \times m⁻² (Lake Bromont). On average zooplankton represented 2% of the total invertebrate community biomass compared to, respectively, 42% and 56% for the epiphytic and benthic invertebrates. *Amphipoda* were practically absent from Lake d'Argent (0.04 g wet \times m⁻²) and reached 4.2 g wet \times m⁻² in Lake Magog (Table 3). *Amphipoda* on the surface of the sediments averaged 65% of the total *Amphipoda* biomass. The size structure of invertebrate communities and the biomass of the twelve species of aquatic plants found in the lakes studied were presented and analyzed by Rasmussen (1993). For our purposes, it is useful to underline that total macrophyte biomass varied 14.5-fold among lakes and that water transparency measured using a Secchi disk ranged from 0.9 to 5.8 m (Table 3).

3.3. Relationship between perch growth, consumption, and activity rates and the environment

Growth rates were most directly related to total fish numerical density (*TN*; Table 4). Fish growth tended to decrease with *TN* ($r^2 = 0.67$). Perch growth was negatively related to *SC3* and *SC4* but positively related to *SC8* ($0.30 < r^2 < 0.44$; Table 4). Two series of models were developed to explain variations of consumption and activity (Table 4). First, a combination of fish weight and the percent contribution of *SC2* to the invertebrate community (mostly chironomid larvae) explained 75% and 58% of the variation of consumption and activity rates respectively. Fish weight was always the most important variable (partial $R^2 = 0.67$ for consumption and 0.47 for activity). Both consumption and activity rates tended to increase with fish weight but to decrease with *SC2*. Second, fish weight (partial $R^2 = 0.67$)

Table 2. Mean fish weight (W_m) and specific components of the bioenergetic budget and activity multipliers for the twenty-six combinations of perch population and age class used in the analysis. The prey size class for which perch displayed the highest selectivity (*MSP*) and the discrepancy index (*DI*) are also presented.

Population	Age	W_m (g wet)	Growth	Consumption	Activity	<i>ACTM</i>	<i>MSP</i>	<i>DI</i>
Brome	III+	24.4	5.3	226.9	92.2	3.9	<i>SC6</i>	71.9
Bromont	I+	6.2	4.9	17.6	-6.1	0.5	<i>SC9</i>	109.9
	II+	15.8	4.5	46.0	-1.9	0.9	<i>SC8</i>	182.3
	III+	26.8	4.3	77.5	3.7	1.1	<i>SC7</i>	118.0
Brompton	I+	5.9	6.3	38.5	6.3	1.6	<i>SC1</i>	115.8
	II+	16.4	11.7	106.3	27.8	2.3	<i>SC6</i>	79.9
	III+	26.8	8.9	178.6	60.7	2.8	<i>SC6</i>	115.6
d'Argent	I+	8.0	7.4	28.1	-3.4	0.7	<i>SC1</i>	87.3
	II+	16.7	2.1	59.6	11.0	1.5	<i>SC1</i>	118.8
	III+	24.1	5.1	86.8	16.1	1.5	<i>SC7</i>	71.9
Drolet	I+	14.3	19.2	86.6	14.1	1.8	<i>SC9</i>	78.1
	III+	34.8	14.4	227.3	80.0	3.0	<i>SC5</i>	42.6
Hertel	II+	6.8	2.4	48.4	14.6	2.3	<i>SC5</i>	79.6
	III+	10.1	2.0	72.4	24.4	2.5	<i>SC5</i>	77.0
Magog	II+	19.3	18.3	138.3	36.8	2.4	<i>SC5</i>	50.0
	III+	31.8	11.9	246.5	90.8	3.3	<i>SC5</i>	90.9
Memphremagog	I+	7.4	11.0	42.4	2.3	1.2	<i>SC6</i>	130.2
	II+	17.4	14.0	102.1	21.8	1.9	<i>SC9</i>	82.1
	III+	26.4	12.9	150.1	41.7	2.2	<i>SC6</i>	88.8
Roxton	II+	10.7	6.2	58.4	9.7	1.5	<i>SC3</i>	98.0
	III+	18.1	7.1	101.0	24.0	1.9	<i>SC4</i>	91.9
Silver	I+	8.9	12.9	55.4	6.5	1.5	<i>SC5</i>	88.7
	II+	33.0	34.6	210.4	49.8	2.3	<i>SC7</i>	67.6
Waterloo	I+	7.0	7.1	14.4	-9.8	0.1	<i>SC9</i>	90.2
	II+	16.8	6.4	36.5	-7.7	0.7	<i>SC4</i>	49.7
	III+	23.0	14.9	49.8	-15.1	0.5	<i>SC9</i>	32.0

could be combined with the biomass of the total invertebrate community (*TCB*; partial $R^2 = 0.13$) and with the biomass of *Amphipoda* found on the bottom of lakes (AMP_b ; partial $R^2 = 0.12$) to explain 92% of perch consumption rates. Consumption rates were positively related to fish weight and AMP_b , and negatively related to total invertebrate community biomass (Fig. 1ab). Similarly, a combination of fish weight (partial $R^2 = 0.47$), *TCB* (partial $R^2 = 0.16$), and AMP_b (partial $R^2 = 0.16$) explained a total of 79% of activity rates (Fig. 1ab). A model of activity multipliers followed the same tendencies with the exception that fish weight (partial $R^2 = 0.21$), *TCB* (partial $R^2 = 0.27$), AMP_b (partial $R^2 = 0.30$), and *TN* (partial $R^2 = 0.14$) explained a more comparable proportion of the variance. Activity rates and multipliers tended to increase with fish weight, and AMP_b but to decrease with *TCB*. Finally, our analyses uncovered two models specifically for activity. Activity rates were positively related to fish weight (partial $R^2 = 0.46$) and water transparency (*SED*; partial $R^2 = 0.18$). Similarly, activity multipliers increased with *SED* and fish weight (Fig. 2). These variables explained, respectively, 48 and 21% of the variance of activity multipliers. These results suggested that 64% to 69% of perch activity could be explained using only fish weight and *SED* as independent variables.

Models obtained by analyzing the growth of each age class individually are not presented in detail

because they were similar to those obtained by pooling them. Water transparency explained between 58% and 66% of the consumption rates of age I+ and II+. Furthermore, water transparency was the most important variable to explain activity rates for age I+ and II+ ($r^2 = 0.64$), and activity multipliers for all age classes ($0.65 < r^2 < 0.93$). Consumption and activity always increased with water transparency. One model for consumption and activity rates of age III+ perch was similar to that developed when all age classes were combined. Consumption ($\ln C = 0.24 \ln AMP_b - 0.35 TMB + 0.80$; $R^2 = 0.83$) and activity ($\ln A + 1 = 0.15 \ln AMP_b - 0.22 TMB + 1.79$; $R^2 = 0.76$) rates of III+ perch were positively related to AMP_b (partial $R^2 = 0.48 - 0.52$) and negatively related to the total macrophyte biomass (*TMB*; partial $R^2 = 0.28 - 0.30$).

4. Discussion

Our analyses suggest that the type of variable explaining perch growth, consumption, or activity rates depends on the component modelled. Perch growth was mostly related to a characteristic of the fish community (*TN*) and, to a lesser extent, to the percent contribution of specific size classes to the invertebrate community. In contrast, consumption and activity rates were primarily associated to fish weight, limnological variables and characteristics of the invertebrate community. Whether the similitude be-

Table 3. Selected environmental variables in each lake studied (Zoop = Zooplankton; Epi = Epiphytic invertebrates; Bent = Benthic invertebrates; Amp_w = *Amphipoda* found on the weeds; Amp_b = *Amphipoda* found at the surface of the sediments).

Lake	Total fish numerical density (n/m ²)	Invertebrate community biomass (g wet/m ²)					Total macrophyte biomass (kg wet/m ²)	Water transparency (m)
		Zoop	Epi	Bent	Amp_w	Amp_b		
Brome	0.65	0.29	2.2	21.3	0.91	3.91	0.2	2.8
Bromont	0.43	0.29	68.6	14.6	2.76	0.66	2.9	2.1
Brompton	0.35	0.16	4.2	15.4	0.01	0.23	0.3	4.2
d'Argent	0.35	0.21	2.5	16.9	0	0.04	0.3	2.6
Drolet	0.14	1.18	3.5	17.0	0.15	0.44	0.2	3.8
Hertel	0.75	0.11	24.5	8.4	0.92	0.15	2.1	3.5
Magog	0.24	0.60	20.2	16.0	2.13	2.06	1.2	2.3
Memphremagog	0.24	0.38	10.5	25.6	0.16	1.79	0.8	4.2
Roxton	0.28	1.30	11.9	9.8	0.20	0.69	1.3	2.3
Silver	0.11	0.81	3.1	12.5	0.13	0.51	0.2	5.8
Waterloo	0.31	0.46	29.2	10.4	0.08	0.03	1.3	0.9

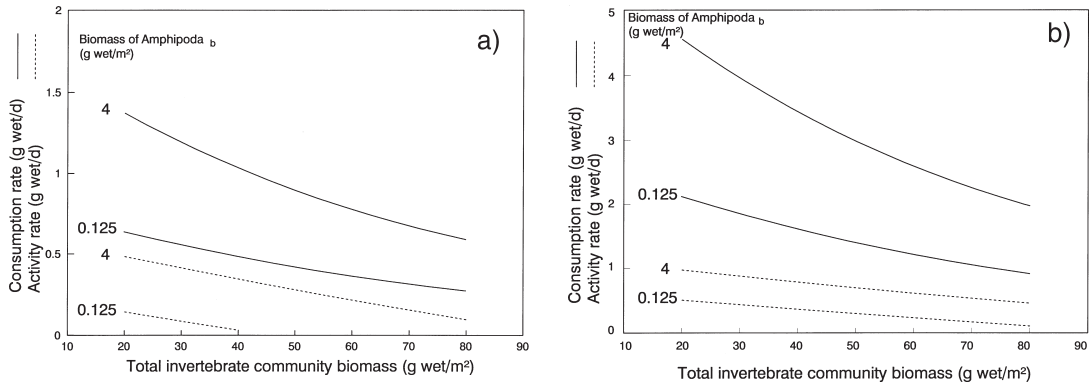


Fig. 1. Expected relationship between consumption (full lines) or activity rates (broken lines) and total invertebrate community biomass for two levels of biomass of *Amphipoda* found on the surface of the sediments of lakes (AMP_b). The simulations were performed for perch weighing 15 g wet (a) and 35 g wet (b).

tween the models developed for consumption and activity rates reflects a biological reality or a bias is difficult to evaluate. Kerr (1982) suggested the existence of a positive relationship between fish consumption and activity rates. Similar variables could therefore be expected to affect both components. However, in the study of Kerr, as well as ours, activity rates were estimated using the difference between consumption and growth rates.

Two hypotheses can be proposed to explain that variables such as the biomass of the total prey com-

munity and that of *Amphipoda* on the bottom of lakes explained a significant proportion of the variance of consumption and activity rates, but did not contribute to explain growth. First, there may be other interactions between activity and growth rates that were hidden by the method used to estimate activity rates. For instance, Boisclair and Leggett (1989c) hypothesized that *TN* may operate via non-exploitative interactions. Following this hypothesis, an increase of fish density may diminish fish feeding efficiency with no notable changes of consumption rates but

Table 4. Models developed to explain the variations of perch growth (G), consumption (C), activity rates (A), and activity multipliers ($ACTM$). Independent variables are the seasonal mean fish weight (W_m), the total fish numerical density (TN), the percent contribution of specific size classes to the invertebrate community ($SC2$, $SC3$, etc), the biomass of the total invertebrate community (TCB), the biomass of *Amphipoda* found on the surface of the sediments of lakes (AMP_b), and the water transparency (SED). 'ln' indicate the use of natural logarithm.

Model	F-value	P-value	R ²
Growth			
$\ln G = -1.14 \ln TN - 3.92$	49.6	0.0001	0.67
$\ln G = -0.06 SC3 - 1.32$	18.8	0.0002	0.44
$\ln G = -0.07 SC4 - 1.64$	10.3	0.004	0.30
$\ln G = 0.06 SC8 - 3.02$	13.7	0.001	0.36
Consumption			
$\ln C = 0.069 W_m - 0.036 SC2 - 0.91$	34.9	0.0001	0.75
$\ln C = 0.059 W_m - 0.014 TCB + 0.216 \ln AMP_b - 0.61$	86.8	0.0001	0.92
Activity			
$\ln(A + 1) = 0.017 W_m - 0.013 SC2 + 0.10$	15.8	0.0001	0.58
$\ln(A + 1) = 0.014 W_m - 0.005 TCB + 0.075 \ln AMP_b + 0.18$	26.8	0.0001	0.79
$\ln(A + 1) = 0.017 W_m + 0.19 \ln SED - 0.30$	20.4	0.0001	0.64
$ACTM = 0.05 W_m - 0.03 TCB + 2.8 TN + 0.37 \ln AMP_b + 1.28$	57.0	0.0001	0.92
$\ln ACTM = 0.58 \ln W_m + 0.97 \ln SED - 2.20$	25.1	0.0001	0.69

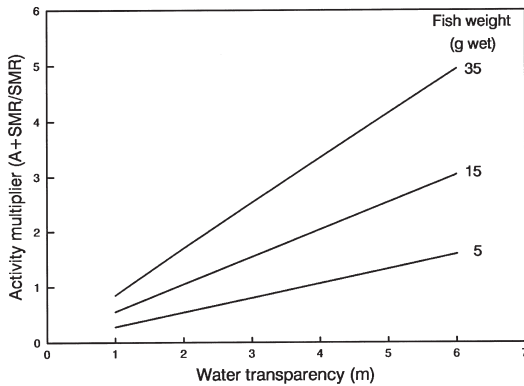


Fig. 2. Predictions of the empirical model we developed to explain the variability of perch activity multipliers (activity + standard metabolism/standard metabolism) using fish weight and water transparency as independent variables.

with an increase of activity rates (see also Diehl 1993). This hypothesis, and the relative importance of non-exploitative and exploitative interactions, remains to be appropriately tested. Second, our consumption, and consequently, our activity rates could be flawed. Indeed, the data we used to perform our analysis have been the subject of criticisms (Hayward 1990, Hewett *et al.* 1991) for which replies have been issued (Boisclair & Leggett 1990, 1991). While we recognize that our data may not be without weaknesses, we nevertheless believe that they are sufficient to explore general tendencies regarding the influence of environmental conditions on components of perch energy budget. One general tendency suggests that fish activity and, for I+ and II+ perch, consumption rates may be associated with fish weight and water transparency. The mechanism by which this tendency occurs is not clear. It can be hypothesized that perch behaviour or performance, such as the motivation or ability to search or capture prey may be altered by an increase of eutrophication through a decrease of visibility, an increase of habitat complexity (such as an increase of macrophyte biomass; Diehl 1988) or a decrease in the biomass of suitable preys. This hypothesis is consistent with the conceptual framework provided by Leach *et al.* (1977) to define the influence of eutrophication on perch. As expected by Leach *et al.* (1977), within the range of eutrophication covered by our data (water transparency = 1–6 m), water transparency always had a positive coefficient in our models for

consumption rates (well-being of perch increases as lakes depart from eutrophy). In contrast, total invertebrate biomass, which can be expected to increase with eutrophication, always had a negative coefficient in those models. Furthermore, growth and consumption rates decreased with the contribution of small prey items to the invertebrate community and growth increased with the contribution of large invertebrate to the community. The biomass of *Amphipoda* found on the bottom of lakes, which may be more profitable than prey associated with eutrophication such as *Diptera*, always had a positive coefficient in our models. The positive relationship between perch growth and the percent contribution of *Amphipoda* and the negative relationship between perch growth and the percent contribution of *Diptera* (and other small preys) was also noted by Leach *et al.* (1977), Boisclair and Leggett (1989b), and Hayward and Margraf (1987). Hayward and Margraf (1987) also proposed that perch feeding rate may be expected to decrease as a result eutrophication because of a decrease of the more profitable larger preys. Our work supports their proposition and further suggests that losses of large preys may not only affect consumption but also activity rates. The coefficients of the biomass of the total invertebrate community and of the percent contribution of small prey size classes were always smaller for our consumption models than for our activity models. One consequence of this situation may be that, as eutrophication progresses, consumption rates decrease faster than activity costs leaving gradually less energy for growth (Figs. 1 and 2). Regardless of the exact mechanisms underlying the empirical relationships revealed by our work, these models may allow a better integration of the conceptual framework provided by Leach *et al.* (1977) and of the quantitative model proposed by Kitchell *et al.* (1977). Furthermore, the prospect of explaining a significant fraction of among-population variability of activity rates, the most misunderstood component of perch energy budget, with two simple variables (fish weight and water transparency) may be appealing to ecologists interested in predicting the influence of changes of environmental conditions on perch using bioenergetic models. Considering the potential weaknesses of our data, validations of the models we developed, using direct methods to estimate fish consumption and activity rates appear necessary.

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