

# Shifting gears: enzymatic evidence for the energetic advantage of switching diet in wild-living fish

Graham D. Sherwood, Ivano Pazzia, Andrew Moeser, Alice Hontela, and Joseph B. Rasmussen

**Abstract:** Large variations in the activity and scaling patterns of enzymes involved in anaerobic metabolism exist and appear to be related to species differences in the locomotory habits of fish. Here, we show how the scaling of muscle lactate dehydrogenase (LDH) activity is highly variable in fish, not only among species, but also among populations of yellow perch (*Perca flavescens*) and lake trout (*Salvelinus namaycush*) exhibiting large differences in the scaling of fish activity costs. These differences in LDH scaling properties were significantly related to differences in diet ontogeny. Scaling coefficients and adjusted  $R^2$  values of LDH versus body size relationships were both threefold higher in fish that do not make important diet shifts among planktivory, benthivory, and piscivory than in those that do. We argue that fish activity and related glycolytic potential are reset to lower values whenever fish are able to switch diet to larger prey while growing; we implicate the burst component of foraging (mostly attacks) as being responsible for changes in activity costs. Our results suggest that anaerobic power requirements in fish are highly plastic and adapted to local and recent food web conditions. We discuss these findings in relation to optimal foraging theory and the energetic basis of prey-size selection.

**Résumé :** Il existe de grandes variations dans les patterns d'activité et d'échelonnage des enzymes impliquées dans le métabolisme anaérobie qui semblent être reliées à des différences spécifiques d'habitudes locomotrices chez les poissons. Nous démontrons ici que l'échelonnage de l'activité de la lactate déshydrogénase (LDH) du muscle est très variable chez les poissons, non seulement d'une espèce à l'autre, mais aussi d'une population à l'autre chez la perchaude (*Perca flavescens*) et le touladi (*Salvelinus namaycush*), lorsque les populations possèdent d'importantes différences dans l'échelonnage des coûts de leurs activités. Ces variations dans l'échelonnage de la LDH sont reliées de façon significative à des différences dans l'ontogénie de l'alimentation. Les coefficients d'échelonnage ainsi que les valeurs ajustées de  $R^2$  des relations de la LDH à la taille du corps sont trois fois plus élevés chez des poissons qui ne font pas de changements majeurs dans leur alimentation que chez ceux qui se nourrissent successivement au cours de leur développement de plancton, de benthos et de poissons. Nous pensons que l'activité du poisson et le potentiel glycolytique correspondant s'ajustent à des valeurs plus basses à chaque fois que le poisson peut, au cours de sa croissance, changer son alimentation pour des proies plus grandes; la composante « emballement » de la quête de nourriture (surtout des attaques) est sans doute responsable des changements dans le coût des activités. Nos résultats laissent croire que les besoins de puissance anaérobie sont très variables chez les poissons et que ces besoins s'adaptent aux conditions locales et récentes du réseau alimentaire. Ces résultats sont examinés en relation avec la théorie de la quête optimale de nourriture et de la base énergétique de la sélection des proies en fonction de leur taille.

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## Introduction

Big fish tend to eat big prey. This is a general phenomenon as well known to those who fish as it is to those who study fish. Indeed, the positive trend for larger mean- and maximum-

sized prey with increasing body size across numerous predatory fish species, both freshwater (Mittelbach and Persson 1998) and marine (Scharf et al. 2000), is consistent with one of the most basic relationships in animal ecology (e.g., Peters 1983, for the positive correlation between predator and prey

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**G.D. Sherwood,<sup>1,2</sup> I. Pazzia, A. Moeser, and J.B. Rasmussen.** Department of Biology, McGill University, 1205 Ave. Dr. Penfield, Montreal, QC H3A 1B1, Canada.

**A. Hontela.** Département Sciences Biologiques, TOXEN Research Centre, Université du Québec à Montréal, C.P. 8888, Succ. Centre-ville, Montréal, QC H3C 3P8, Canada.

<sup>1</sup>Corresponding author (e-mail: [grahamsherwood@hotmail.com](mailto:grahamsherwood@hotmail.com)).

<sup>2</sup>Present address: Fisheries Conservation, Fisheries and Marine Institute of Memorial University of Newfoundland, P.O. Box 4920, St. John's, NF A1C 5R3, Canada.

size in animals). How this occurs is logical; only larger fish are able to overcome constraints, such as gape-size limitation, and effectively handle large prey (Townsend and Winfield 1985). Why big fish select bigger prey and what this means for fish energetics, on the other hand, may only be partially understood. The switch to larger prey as fish grow most likely serves to maintain profitability (e.g., continued growth), which, in turn, should entail maximization of gains and minimization of costs (Townsend and Winfield 1985). The cost function may be further broken down into pre- and post-capture investments. A great deal of information exists with regards to prey size related changes in handling costs, a postcapture variable (Mittelbach and Persson 1998). What is perhaps most lacking from our current understanding of the energetic basis of prey-size selection in actively foraging fish is a clear grasp of the costs incurred before capture (Mittelbach and Persson 1998).

A theoretical basis, as well as empirical support, for how fish energy budgets may be affected by prey-size choice is available. Foraging costs, in terms of the time spent actively searching and the number of feeding attempts (attacks) that would lead to satiation, should go up as prey become small in relation to the size of the predator (Kerr 1971; Kerr and Ryder 1977). Pazzia (2001) showed that fish activity costs increase much faster with body size in lake trout (*Salvelinus namaycush*) that do not make the normal ontogenetic diet shift from small benthic invertebrates to larger prey fish, and thus become stunted, than in those that make diet shifts and grow large. This agrees with earlier findings that diet shifts to piscivory are usually associated with increases in growth rate (e.g., Jones et al. 1994), as well as with the knowledge that to achieve maximum growth in artificially fed fish, food pellet size must increase proportionally with increasing fish size (Wankowski and Thorpe 1979). Taken as a whole, existing theory and observation are convincing with respect to the importance of prey size and diet shifts on fish activity and growth. Methods that would allow for the evaluation of fish activity before and after natural diet shifts would certainly contribute to these findings.

Metabolic enzymes represent a potentially useful approach for quantifying fish activity levels on a short-term and individual basis and, thus, for evaluating the energetic basis of prey-size selection in predatory fish. The maximal activity ( $V_{\max}$ ) of certain glycolytic (anaerobic) enzymes, including that of lactate dehydrogenase (LDH), in the axial musculature of fish has been suggested to be related to foraging behaviour and associated fish activity costs (Sullivan and Somero 1980; Childress and Somero 1990). Glycolytic potential, which LDH and a series of other glycolytic enzymes reflect, may facilitate burst swimming performance, which may be important in sustaining long bouts of spontaneous activity while feeding. Furthermore, the activity of enzymes such as LDH may provide a snapshot of recent (days-weeks) energetic requirements; its activity in fish has been shown to respond to altered energetic demands within at least, but not earlier than, 7 days (Nathanailides 1996; Schulte et al. 2000). Sherwood et al. (2002) applied this information to inferring elevated fish activity costs in stunted yellow perch (*Perca flavescens*) from metal-contaminated lakes where prey choice was low and diet shifts were limited. Interestingly, in the case where diet shifts were possible

(for reference populations), LDH activities were observed to decrease sharply at well-defined diet shifts from planktivory to benthivory and from benthivory to piscivory. The results of this study fit well with theory regarding the importance of prey size on fish energetics (Kerr 1971; Kerr and Ryder 1977; i.e., shifting "K-lines") in yellow perch and suggested that LDH would provide a promising biomarker of fish activity applicable to further testing for the influence of diet and habitat shifts on fish energetics in a wide range of species and situations.

In this paper, we explore the relationship between diet shifts and LDH activity and how these both relate to body size and fish energetics (growth and fish activity) in numerous species of fish with different patterns of diet ontogeny. We present a synthesis of three separate field studies examining five different freshwater fish species and complement these findings with an analysis of previously published LDH size-scaling data for numerous marine fish species (Childress and Somero 1990). The overall expectation is that ontogenetic diet shifts towards larger prey types should lead to lower LDH activity corresponding to lower fish activity costs.

## Materials and methods

### Study sites and study species

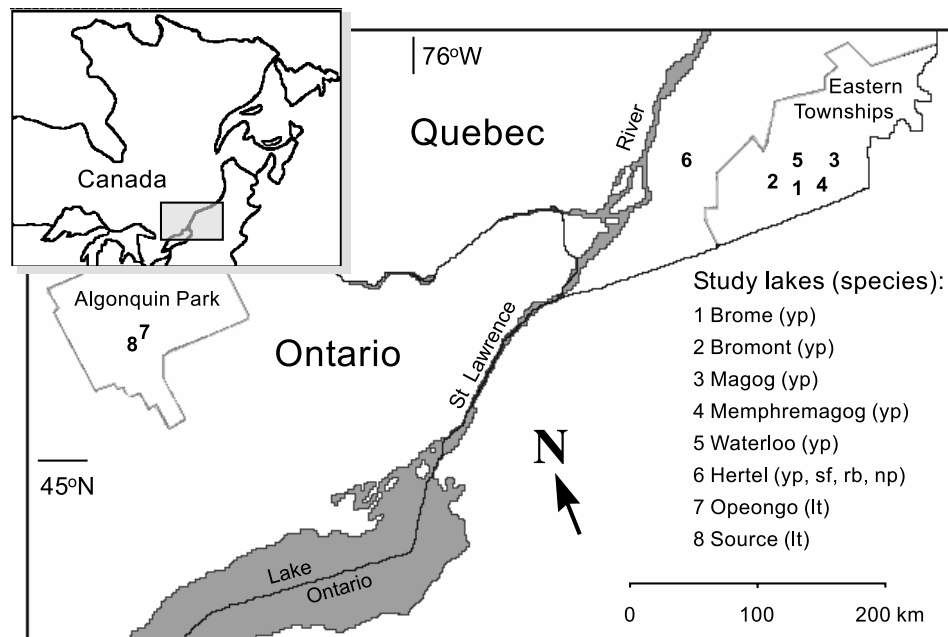
Data was collected from three separate regions including a total of five different fish species from eight populations in eastern Canada (Fig. 1). Data for yellow perch came mostly from five lakes in the Eastern Townships of Quebec (sampled in June 1998) and from Lake Hertel, a Quebec lake in close proximity to the first five lakes (sampled in August 2000). Northern pike (*Esox lucius*), pumpkinseed sunfish (*Lepomis gibbosus*), and rock bass (*Ambloplites rupestris*) were also sampled from Lake Hertel in August 2000. Lake trout were sampled from two Algonquin Park, Ontario, lakes in May 2000. Limnological data for Eastern Townships lakes and Lake Hertel is found in Boisclair and Rasmussen (1996).

Fish from the various lakes were collected using a range of capture techniques (seine, gillnet, and rod-and-reel). Fish were sampled from the entire body size range representative of each species and population. All fish were sacrificed in the field within a few hours subsequent to capture, weighed to the nearest gram, and measured to the nearest millimetre (total length). A small sample (1–2 g) of white muscle tissue anterior to the caudal peduncle was excised for enzyme analysis (see Somero and Childress 1980) and placed in liquid nitrogen before freezing ( $-20^{\circ}\text{C}$ ) of whole carcasses.

### Diet and stable carbon isotope analysis

For Lake Hertel fish, diet was determined from stomach contents immediately after fish capture. Individual prey items were identified to order and measured to the nearest millimetre (total length). For Algonquin Park lake trout and Eastern Townships yellow perch, diet items were identified from thawed stomachs in the laboratory. Carbon isotope ( $^{13}\text{C}$ ) analysis was performed on dried lake trout muscle tissue (dorsal, directly posterior to the head) and representative prey items from lake trout stomachs packed in 4 mm  $\times$  6 mm tin capsules.  $^{13}\text{C}$ , which is a naturally occurring heavy isotope of carbon, is useful for inferring feeding habits of

**Fig. 1.** Map showing the location of study sites in eastern Ontario and southern Quebec (shaded area in inset map of eastern Canada). Abbreviations in parentheses refer to species sampled for that lake: yellow perch (yp), sunfish (sf), rock bass (rb), northern pike (np), and lake trout (lt).



fish because prey from different habitats of lakes (i.e., benthic vs. pelagic) typically have distinct  $^{13}\text{C}$  signatures ( $^{13}\text{C}/^{12}\text{C}$ ) and consumers acquire  $^{13}\text{C}$  signatures similar to that of their prey (Vander Zanden and Rasmussen 1999). Stable nitrogen isotope ratios ( $^{15}\text{N}/^{14}\text{N}$ ), which are also useful in inferring diet shifts (Vander Zanden and Rasmussen 1999), were measured in lake trout but did not provide any additional information beyond that obtained from  $^{13}\text{C}$  analysis and are therefore not presented here. Stable carbon signatures were expressed in delta ( $\delta$ ) notation, defined as the parts per thousand (‰) deviation from a standard material (Pee Dee belemnite limestone):  $\delta^{13}\text{C} = ([R_{\text{sample}}/R_{\text{standard}}] - 1) \times 1000$ ;  $R = ^{13}\text{C}/^{12}\text{C}$ .

### Lactate dehydrogenase assay

LDH assays were performed on frozen white muscle tissue according to kit specifications (LDH-Optimized, Sigma Diagnostics®, St. Louis, Mo.) following a modification of a sample preparation protocol described in Somero and Childress (1980). Before homogenization (using a rough glass and Teflon apparatus) in buffer solution (50 volumes; 0.07 M, pH 7.0  $\text{KPO}_4$  buffer + 1 mM EDTA + 0.2% v/v Triton X-100), muscle samples were crushed to a fine powder in liquid nitrogen to allow for a more complete homogenization. Fifteen microlitres of sample preparation, versus the 100  $\mu\text{L}$  prescribed by Sigma Diagnostics®, were sufficient to initiate and sustain the LDH reaction for a duration of 1 min for the entire range of LDH activities encountered. LDH activities, measured at 20°C and expressed as arbitrary absorbance units (at 340 nm), were normalized to protein concentration to account for variations in homogenized tissue content from one sample preparation to another as well as variations among individuals. Protein analysis was carried out on sample preparations according to BioRad® (Bio-Rad

Laboratories, Hercules, Calif.) specifications. The average coefficient of variation for all LDH assays run in duplicate was less than 5%. We found less than a 1% difference between LDH activities measured on tissue samples stored in liquid nitrogen immediately following field sampling and those resampled from the same fish carcasses stored in the freezer (−20°C).

### Data handling and statistical analysis

Four different line-fitting techniques were used to describe the relationship between  $\log(\text{LDH activity})$  and  $\log(\text{body size})$ . The four line fitting techniques were (i) linear regression, (ii) locally weighted regression smoothing (lowess), (iii) analysis of covariance (ANCOVA), and (iv) polynomial regression. Linear regression was performed in all cases and was sufficient where no diet shifts were evident from the diet data, or in cases where incomplete LDH activity versus body size data meant that important shifts might have been missed. When diet shifts were suspected, lowess curve-fitting, which results in superior fits to linear regression by producing locally weighted regression smoothing through an iterative weighted least-squares method (SPSS for Windows 1994) was used. When diet shifts were well characterized by gut content analysis, it was possible to use ANCOVA with  $\log(\text{LDH activity})$  as the dependent variable,  $\log(\text{body size})$  as the covariate, and diet stage as a class variable with three categories (planktivory, benthivory, piscivory) coded in two dummy variables ( $c$  and  $d$ , see Table 1 caption). In cases where ANCOVA was used (where diet data was sufficient), sample size was restricted to those fish that had stomach contents. We assessed the statistical significance of the increase in “fit” from linear to ANCOVA models by comparing with an  $F$  test. To facilitate visualization of diet shift patterns, our graphical representation of ANCOVA results

**Table 1.** Summary of results for lactate dehydrogenase allometry.

Lake	Species	Diet shift	Regression type	Equation parameter*							
				<i>a</i>	<i>b</i>	<i>c</i>	<i>d</i>	$R^2_{adj}$	<i>F</i>	<i>p</i>	<i>n</i>
Brome	Perch	Yes†	Linear	2.54	0.07	NA	NA	0.38	11.9	<0.01	19
			Lowess	NA	NA	NA	NA	0.44	15.0	0.001	19
			ANCOVA	Insufficient diet data							
Bromont	Perch	Yes†	Linear	2.57	-0.04	NA	NA	0.01	1.1	0.30	31
			Lowess	NA	NA	NA	NA	0.09	3.8	0.06	31
			ANCOVA	Insufficient diet data							
Magog	Perch	Yes†	Linear	2.48	0.06	NA	NA	0.29	5.9	<0.05	13
			Lowess	NA	NA	NA	NA	NA	NA	NA	NA
			ANCOVA	Insufficient diet data							
Memph	Perch	Yes	Linear	2.51	0.08	NA	NA	0.21	10.9	<0.01	38
			Lowess	NA	NA	NA	NA	0.49	36.5	<0.0001	38
			ANCOVA	2.37	0.29	0.18	0.30	0.34	4.6	<0.05	22
Waterloo	Perch	Yes	Linear	2.68	-0.15	NA	NA	0.14	5.9	<0.05	31
			Lowess	NA	NA	NA	NA	0.32	15.2	<0.001	31
			ANCOVA	2.33	0.23 <sup>ns</sup>	0.29	NA	0.41	6.6	<0.01	17
Hertel	Perch	Yes	Linear	2.37	0.05	NA	NA	0.05	3.2	0.08	47
			Lowess	NA	NA	NA	NA	0.33	23.7	<0.0001	47
			ANCOVA	2.33	0.21	0.12	0.29	0.27	5.0	<0.01	33
Hertel	Sunfish	Yes	Linear	2.00	0.27	NA	NA	0.61	70.0	<0.0001	36
			Lowess	NA	NA	NA	NA	0.51	37.4	<0.0001	36
			ANCOVA	2.05	0.40	0.26	NA	0.75	38.6	<0.0001	26
Hertel	Pike	No	Linear	1.67	0.30	NA	NA	0.77	60.4	<0.0001	19
			Lowess	NA	NA	NA	NA	NA	NA	NA	NA
			ANCOVA	NA	NA	NA	NA	NA	NA	NA	NA
Hertel	Rock bass	No	Linear	1.76	0.27	NA	NA	0.69	32.6	<0.0001	16
			Lowess	NA	NA	NA	NA	NA	NA	NA	NA
			ANCOVA	NA	NA	NA	NA	NA	NA	NA	NA
Opeongo	Lake trout	Yes	Linear	2.81	-0.04	NA	NA	0.00	0.5	0.51	27
			Lowess	NA	NA	NA	NA	0.25	9.9	<0.01	27
			Polynomial	See Note				0.08	3.1	0.09	27
Source	Lake trout	No	Linear	2.27	0.21	NA	NA	0.46	23.1	<0.0001	28
			Lowess	NA	NA	NA	NA	0.55	34.5	<0.0001	28
			Polynomial	See Note				0.61	41.8	<0.0001	28

**Note:** Memph, Memphremagog; NA, not applicable. Polynomial equations are  $\log(\text{LDH}) = -0.13\log W^2 + 0.66\log W + 1.92$  for Lake Opeongo lake trout and  $\log(\text{LDH}) = -0.44\log W^2 + 2.08\log W + 0.34$  for Source Lake lake trout.

\* $\log(\text{LDH}) = a + b\log W$  (or  $\text{LDH} = a \cdot W^b$ ) for linear regression, and  $\log(\text{LDH}) = a + b\log W - c - d$  for ANCOVA, where *c* and *d* are dummy variables for diet shifts from planktivory to benthivory and from benthivory to piscivory, respectively; all model terms were significant (to at least  $p < 0.05$ ) unless otherwise specified (ns).

†Insufficient diet data for curve fitting purposes does not preclude the knowledge that diet shifts do indeed occur in these populations (G. Sherwood, personal observation).

includes connecting lines between the top and bottom of regression segments for successive and sometimes overlapping diet stages. Finally, when diet shifts were known to occur (by a combination of gut content and stable isotope analyses) but had a high degree of overlap (i.e., diet shifts were not discrete), second-order polynomial regressions were used. Whenever possible and appropriate, multiple line fitting techniques were performed for comparison.

### Supplementary data

Published fish activity data for the five Eastern Townships perch populations, as well as for Lake Hertel perch, were available on an age-class basis from Boisclair and Rasmussen (1996). This data was in the form of activity multipliers (*A*), which is simply a multiplication factor of standard metabolic rate (SMR) in bioenergetics models of the form

$$(1) \quad G = C - \text{SMR} \cdot A - \text{SDA} - F - U$$

where *G* is growth rate (both somatic and gonadal), *C* is consumption rate, SDA is specific dynamic action, *F* is egestion, and *U* is excretion (Kitchell et al. 1977). Fish activity data was also available for the two lake trout populations (Pazzia 2001). These independent estimates of fish activity, from both sources, were regressed against body size to obtain allometric scaling coefficients (*b* from  $A = aW^b$ ; where *a* is the intercept, and *W* is body size in grams), which were then compared to scaling coefficients for the LDH activity versus body size relationships over the same body size range for the appropriate species and (or) population.

We supplemented our LDH scaling data with data for 23 marine species from Childress and Somero (1990). The data were divided here into two groups based on diet shift potential (Table 2). Non-diet shifters were those species that are generally considered to be planktivorous (pelagic) for the duration of their lives, whereas diet shifters were species of fish that are generally recognized to shift feeding mode at

**Table 2.** Published lactate dehydrogenase (LDH) scaling coefficients ( $b_{LDH}$ ), maximum size ( $W_{max}$ ), and diet shift behaviour of 23 marine species.

Non-diet-shifting species	$b_{LDH}$	$W_{max}$ (g)	Diet-shifting species	$b_{LDH}$	$W_{max}$ (g)
<i>Ceratoscopelus warmingii</i>	0.47	6.6	<i>Microstomus pacificus</i>	-0.43	4837
<i>Vinciguerrina nimbaria</i>	0.68	1.4	<i>Gillichthys mirabilis</i>	0.08	21.6
<i>Vinciguerrina lucetia</i>	0.66	1.3	<i>Halichoeres bivittatus</i>	-0.01	39
<i>Poromitra crassiceps</i>	0.3	47	<i>Nezumia bairdii</i>	0.36	58
<i>Engraulis mordax</i>	0.21	24.5	<i>Paralabrax clathratus</i>	0.42	381
<i>Lampanyctus regalis</i>	0.57	54.2	<i>Paralabrax nebulifer</i>	0.3	791
<i>Lampanyctus ritteri</i>	0.61	9.1	<i>Atherinops affinis</i>	0.22	44.3
<i>Bajacalifornia burragei</i>	0.29	57	<i>Sebastes altivelis</i>	0.19	250
<i>Parvilux ingens</i>	0.61	85	<i>Sebastes alascanus</i>	0.25	200
<i>Bathylagus antarcticus</i>	0.23	45	<i>Coryphaenoides armatus</i>	0.66	800
<i>Electrona antarctica</i>	0.95	12			
<i>Gymnoscopelus braueri</i>	0.76	20			
<i>Gymnoscopelus opisthopterus</i>	1.02	40			
Mean	0.57	31.0	Mean	0.20*	742.2
Standard error	0.07	7.2	Standard error	0.09	464.4

**Note:** LDH scaling data from Childress and Somero (1990); diet and size data from Froese and Pauly (2001).

\*Means significantly different among groups ( $t$  test,  $p < 0.01$ ).

some point in their development from planktivory to benthivory (demersal), piscivory, or both. It is acknowledged that this grouping scheme may not be entirely accurate; we had no way of controlling for possible site-specific variations in this classification. However, the groupings were used in any case for general exploratory purposes. The means of the reported LDH scaling coefficients ( $b$  from  $LDH = aW^b$ , where  $a$  is the intercept and  $W$  is body size in grams) were compared among these groups by Student's  $t$  test.

## Results

### Eastern Townships yellow perch populations

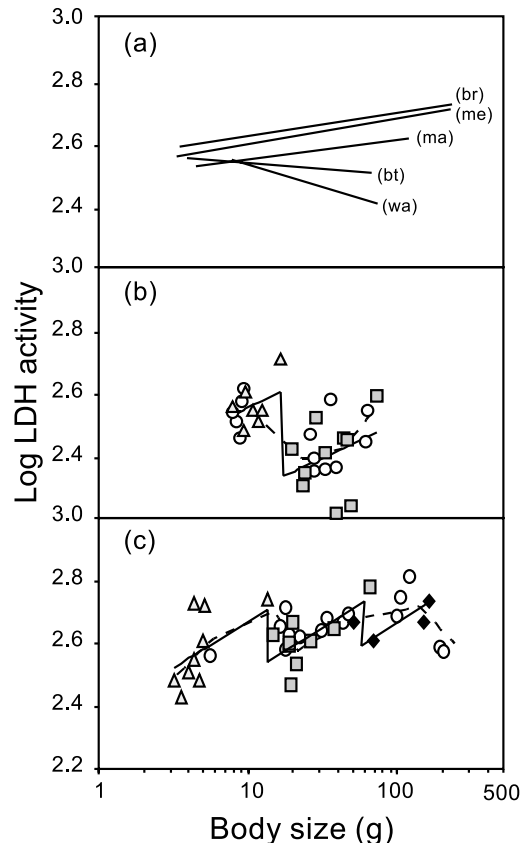
Muscle lactate dehydrogenase activity and diet were determined for individual yellow perch from various Eastern Townships populations and were plotted as a function of body size (Fig. 2). Lines fitted by lowess and (or) ANCOVA described the relationship between log(LDH activity) and log(body size) better than linear regression (i.e., they had higher adjusted  $R^2$  values, Table 1); the most considerable improvements in adjusted  $R^2$  values were for lakes Memphremagog and Waterloo ( $F_{2,18} = 3.6$ ,  $p < 0.05$ , and  $F_{1,14} = 8.3$ ,  $p < 0.01$ , respectively, for the difference between linear and ANCOVA models). For Lake Memphremagog perch (Fig. 2c), both the lowess line fit and ANCOVA showed substantial and significant decreases in LDH activity (ANCOVA,  $p < 0.05$  for both shifts) at about 15 g and another starting around 60 g. The overall pattern could be described as "saw-toothed" allometry with individual "saw-teeth" corresponding to changes in feeding habit from planktivory (mostly cladocerans of 250–500  $\mu$ m) to benthivory (various insect larvae and pupae as well as crustaceans 5–20 mm in length) and from benthivory to piscivory (various unidentified minnows and young-of-the-year yellow perch 20–70 mm in total length). A significant drop in LDH activity was also evident for Lake Waterloo (Fig. 2b) at about 15 g, again, corresponding to a shift from planktivory to benthivory (various insect larvae and pupae

and crustaceans 5–10 mm in length) (ANCOVA,  $p < 0.05$ ). Linear regression results show a large variation in scaling coefficients among populations ( $b_{LDH} = 0.08$  to  $-0.15$ ; Fig. 2a). Although specific diet data is lacking, the negative slope for Lake Bromont is likely to reflect a diet shift from zooplankton to benthic invertebrates similar to that for Lake Waterloo. Both lakes are very similar in limnological and food web characteristics (Boisclair and Rasmussen 1996).

### Lake Hertel yellow perch, sunfish, rock bass, and northern pike

Muscle lactate dehydrogenase activity and diet were determined for four species of fish from Lake Hertel and were plotted as a function of body size (Fig. 3). For yellow perch, a significantly better relationship between log(body size) and log(LDH activity) was obtained by considering two distinct and well-defined diet shifts from planktivory (mostly cladocerans of 250–500  $\mu$ m) to benthivory (aquatic insects and crustaceans 10–25 mm in body length) to piscivory (sunfish, golden shiners, *Notemigonus crysoleucas*, and young-of-the-year yellow perch, 20–60 mm in total length) (i.e., by performing an ANCOVA;  $F_{2,29} = 6.3$ ,  $p < 0.01$ , for the increase in fit from linear to ANCOVA models; see Table 1 for summary of line fit results). For sunfish, a significantly better fit ( $F_{1,23} = 15.1$ ,  $p < 0.001$ , for the difference between linear and ANCOVA models) was obtained by considering a single diet shift from planktivory (cladocerans of 250–500  $\mu$ m) to benthivory (in this case, snails 2–10 mm in shell length). For rock bass and pike, linear regression was sufficient to describe the relationship between log(LDH activity) and log(body size). In these species, no diet shifts were present for the range of body sizes sampled; rock bass fed only on benthic invertebrates (odonates and crayfish 5–30 mm in length) and pike fed only on small fish (sunfish, golden shiners, and young-of-the-year yellow perch, 40–75 mm in total length). Overall, the best linear fit between log(LDH activity) and log(body size) was obtained in the species for which the least amount of diet shifting took place (rock bass and pike).

**Fig. 2.** Log muscle lactate dehydrogenase (LDH) activity (expressed in arbitrary absorbance units per milligram protein) versus body size for Eastern Townships yellow perch. (a) Linear regression results for all five populations. Abbreviations in parentheses are first two letters of lake name, except for Lake Bromont (bt). (b) Lowess (broken) and ANCOVA (solid) line fits for Lake Waterloo. (c) Lowess (broken) and ANCOVA (solid) line fits for Lake Memphremagog. Individual diet, determined from stomach contents, is indicated by symbols: shaded triangles are for zooplankton, shaded squares are for benthic invertebrates, solid diamonds are for fish, and open circles are for empty stomachs (unknown diet). Statistics for all line fits are included in Table 1.



#### Algonquin Park lake trout

Muscle lactate dehydrogenase activities,  $\delta^{13}\text{C}$  values, and diet were determined individually and plotted against body size for two populations of lake trout (Fig. 4). The overall pattern for  $\log(\text{LDH activity})$  versus  $\log(\text{body size})$  in lake trout was qualitatively different than it was for Lake Hertel fish and Eastern Townships perch. As opposed to positive allometry punctuated by discrete downshifts in LDH activity, there was a gradual downward inflection in LDH activity that was best described by fitting a second-order polynomial to the data (Table 1). These curves also agreed very well with lowess curve fits. This was most true for Lake Opeongo where this downward inflection in LDH activity corresponded to a downward shift in  $\delta^{13}\text{C}$  values. Gut contents revealed that this shift in  $\delta^{13}\text{C}$  values was likely the result of a move from feeding on invertebrates and small littoral forage fish (minnows and yellow perch) to feeding on larger pelagic forage fish (cisco, *Coregonus artedii*, and lake whitefish,

*Coregonus clupeaformis*). For Source Lake, no diet shifts were evident from gut content analysis (100% chironomids at the time of sampling). For the most part,  $\delta^{13}\text{C}$  values mirrored this result and suggested that these fish were feeding in the profundal zone on chironomids (which have very negative  $\delta^{13}\text{C}$  signatures) up until the largest body sizes where a shift to inshore invertebrates or prey fish (which would have more positive  $\delta^{13}\text{C}$  values) may have taken place as evidenced by significantly higher  $\delta^{13}\text{C}$  in the four largest individuals (Student's  $t$  test,  $p < 0.0001$ ). In the case of Source Lake, LDH activity followed positive allometry for most of the body size range; a slight downward shift in LDH activity in the largest individuals driving the superior polynomial fit corresponded to higher (shifted)  $\delta^{13}\text{C}$  values. Overall, LDH activity was much less variable, as a function of body size, in Source Lake where limited diet shifting was likely to have occurred compared with Lake Opeongo where more complete diet and habitat shifts took place. This is consistent with the overall finding that adjusted  $R^2$  values for the linear relationship between  $\log(\text{LDH activity})$  and  $\log(\text{body size})$  for all species and (or) populations examined were significantly higher ( $\sim$ threefold; Student's  $t$  test,  $p < 0.05$ ,  $n = 11$ ) when no diet shifts took place (mean =  $0.64 \pm 0.16$ ) than when they did (mean =  $0.21 \pm 0.21$ ). There was no effect of sex or stage of maturity on LDH scaling for lake trout.

#### LDH scaling versus fish activity scaling

Independent estimates of fish activity ( $A$ , see eq. 1) were available from other sources for certain species and (or) populations examined here (Table 3). There was a significant positive relationship between the size scaling of these estimates ( $b_A$ ) and scaling of LDH activity ( $b_{\text{LDH}}$ ) over the same body size ranges ( $R^2 = 0.71$ ,  $p < 0.01$ ,  $n = 8$ ;  $b_A = 1.26b_{\text{LDH}} + 0.13$ ). That is, if the overall slope for LDH versus body size was low in a given population, the slope for activity versus body size was also likely to be low.

#### LDH scaling versus diet ontogeny

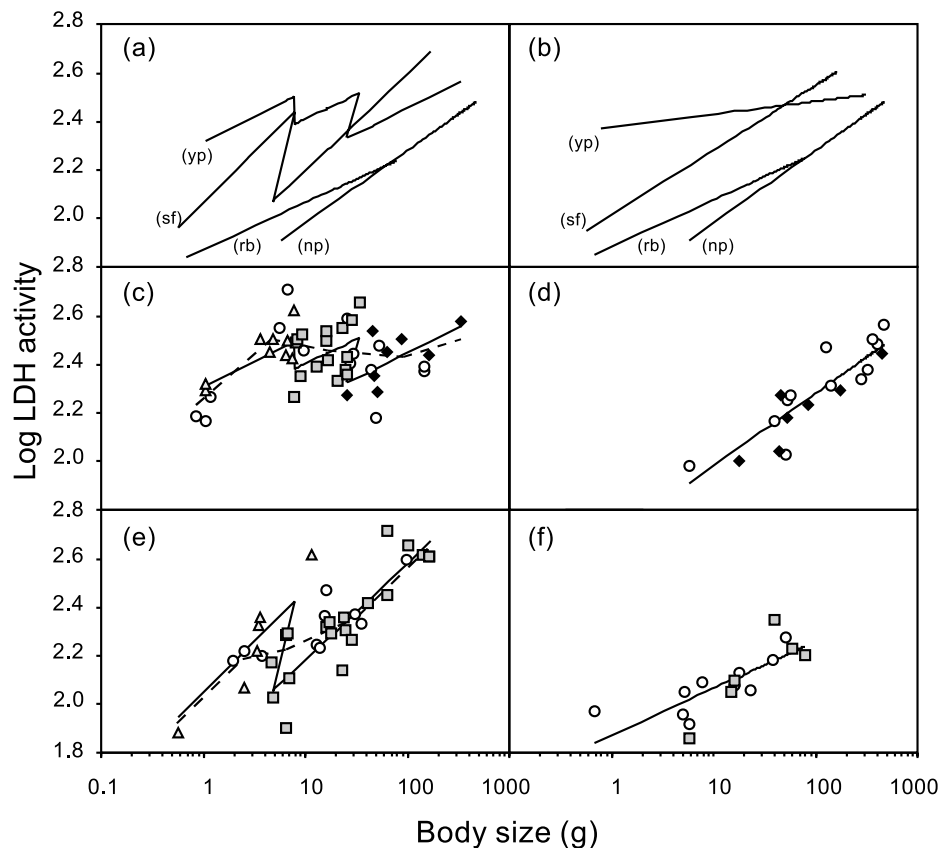
Fish from the present study, as well as those from previous studies (Childress and Somero 1990), were grouped into non-diet shifters, those species that remain planktivorous for their entire lives or in cases where incomplete sampling covered only one diet stage, and into diet shifters, those species that shift diet from planktivory to benthivory, piscivory, or both at some point in their lives (Tables 1 and 2). There was a significant difference in LDH scaling between these two groups ( $t = 3.76$ ,  $p < 0.001$ ,  $df = 37$ ) such that the scaling coefficient for LDH activity ( $b_{\text{LDH}}$ ) was threefold higher in non-shifters ( $b_{\text{LDH}} = 0.47 \pm 0.26$ ) than it was in diet shifters ( $b_{\text{LDH}} = 0.16 \pm 0.25$ ). Once diet shifts were taken into account through the use of ANCOVA, there was no difference in LDH scaling among diet groups ( $t = 0.92$ ,  $df = 22$ ).

## Discussion

#### Glycolytic enzyme scaling and diet ontogeny

It has previously been recognized that the activity of glycolytic (anaerobic) enzymes (including LDH) in fish muscle does not follow the same metabolic size-scaling paradigm that governs activities of aerobic enzymes (Sullivan and Somero 1980; Childress and Somero 1990). As opposed to

**Fig. 3.** Log muscle lactate dehydrogenase (LDH) activity (expressed in arbitrary absorbance units per milligram protein) versus body size for four species of fish from Lake Hertel. (a) Combined best-fit lines for all four species. (b) Combined linear regression for all four species. Abbreviations in parentheses (a, b) refer to species names: yellow perch (yp), pumpkinseed sunfish (sf), rock bass (rb), northern pike (np). (c) Lowess (broken) and ANCOVA (solid) line fits for yellow perch. (d) Linear regression for northern pike. (e) Lowess (broken) and ANCOVA (solid) line fits for sunfish. (f) Linear regression for rock bass. Individual diet, determined from stomach contents, is indicated by symbols (c–f): shaded triangles are for zooplankton, shaded squares are for benthic invertebrates, solid diamonds are for fish, and open circles are for empty stomachs (unknown diet). Statistics for all line fits are included in Table 1.



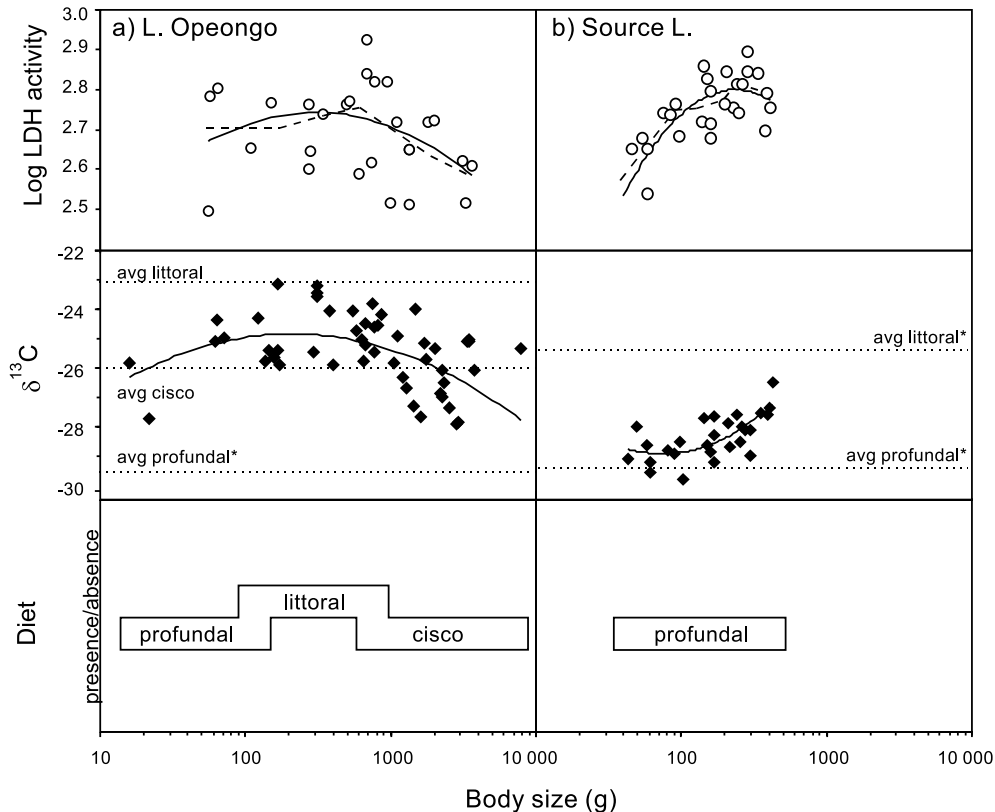
negative allometry confined to a narrow range of scaling coefficients (typical values for aerobic enzymes centre around  $-0.25$ ), glycolytic enzymes possess highly variable and mostly positive size dependence. The fact that glycolytic enzymes usually scale positively to body size has been suggested to be related to increasing anaerobic power requirements in larger fish that may experience higher drag forces when generating short bursts (Sullivan and Somero 1980). The fact that glycolytic scaling coefficients are highly variable has led to the suggestion that there is strong selection for large differences in anaerobic power requirements related to differences in locomotory habits and feeding types among species (Childress and Somero 1990).

Results of the present study provide further evidence for highly variable scaling of anaerobic metabolism in fish and offer some new insights as to the underlying environmental causes of this variation (within and among species), as well as provide an alternative explanation for predominantly positive size-scaling of anaerobic power requirements. A considerable and consistent effect of diet ontogeny on the scaling properties of muscle lactate dehydrogenase activity was found in a wide range of fish species both within and among species. Tightness of fit (adjusted  $R^2$  values) and slopes (scaling coefficients) for LDH activity versus body size rela-

tionships were both greater (threefold) in fish that do not make diet shifts than in those that do. The implication is that the normal tendency for LDH activity, in the absence of appreciable diet shifts and regardless of species, is to increase quite rapidly and invariably with body size. Negative and variable LDH allometries are thus likely to be artefacts of resetting power requirements and glycolytic potential around diet and (or) habitat shifts. Once the effect of diet shifts was taken into account through ANCOVA, the slope for LDH activity versus body size became much less variable (the coefficient of variation decreased from 150% to 36%) and the mean increased threefold to 0.32, which is not significantly different from the average slope obtained for populations in which diet shifting does not occur. These findings suggest that overall glycolytic scaling patterns are not a fixed and selected-for species property. In contrast, they are more likely to be a consequence of variable food web structure and related feeding opportunities, the successful exploitation of which can vary as much within a species (Pazzia 2001) as it can among species.

The observation that LDH activity can be reset to lower values following diet shifts in actively foraging fish calls into question previous interpretations for positive allometry of anaerobic enzymes. In particular, it is difficult to imagine

**Fig. 4.** (Top panels) Log muscle lactate dehydrogenase (LDH) activity (expressed in arbitrary absorbance units per milligram protein) versus body size for two populations of lake trout from Algonquin Park. Statistics for polynomial and lowess curve fits (seen here) and linear regressions are included in Table 1. (Middle panels)  $\delta^{13}\text{C}$  versus body size for (a) Lake (L.) Opeongo (polynomial regression  $R^2 = 0.20$ ,  $p < 0.01$ ,  $n = 51$ ) and (b) Source Lake (polynomial regression  $R^2 = 0.43$ ,  $p < 0.001$ ,  $n = 27$ ). Dotted lines show average  $\delta^{13}\text{C}$  values for representative profundal (mostly chironomids), littoral (various insects and littoral forage fish), and pelagic (cisco) prey items for each lake (asterisks indicate data from Vander Zanden 1999). (Bottom panels) Diet expressed as range of body sizes observed while feeding on profundal (mostly chironomids), littoral (various insects and small prey fish including young-of-the-year yellow perch and minnows), and pelagic (cisco) prey sources.



**Table 3.** Scaling results for fish activity ( $b_A$ ) and lactate dehydrogenase activity ( $b_{\text{LDH}}$ ) over the same body size range.

Lake	Species	Size range (g)	$b_{\text{LDH}}$	$b_A^*$	Source†
Brome	Yellow perch	1–24.4	0.17	0.43 (2)	1
Bromont	Yellow perch	1–26.5	–0.04	0 (3)	1
Hertel	Yellow perch	1–10.1	0.26	0.41 (4)	1
Magog	Yellow perch	1–31.8	0.09	0.32 (3)	1
Memphremagog	Yellow perch	1–26.4	0.08	0.21 (4)	1
Waterloo	Yellow perch	1–23.0	0.01	0 (4)	1
Opeongo	Lake trout	55–3655	–0.04	0.21 (11)	2
Source	Lake trout	40–382	0.22	0.38 (8)	2

\*Regressions for yellow perch include origin; it was assumed that a 1-g fish should have negligible activity costs (i.e.,  $A = 1$ ); slope was set at 0 when less than 0 ( $A$  values of less than 1 are artefacts of the method used to estimate activity); value in parentheses is sample size for each regression.

†Source for fish activity values: 1, Boisclair and Rasmussen (1996); 2, Pazzia (2001).

why burst swimming requirements, in terms of the power required to generate single bursts, should go down suddenly and significantly in fish that make diet shifts, particularly from benthivory to piscivory. If LDH scaling mirrored power scaling, as suggested by Sullivan and Somero (1980), where power increases with burst speed and body size (Webb 1977), then only decreases in burst speed would ac-

count for decreases in power requirements (and hence lower LDH activity) following such a diet shift. It is unlikely that piscivores require lower burst speeds than benthivores. Decreases in burst swimming speed may still be implicated in cases where diet or habitat shifts entail major changes in locomotory habits towards highly sedentary behaviours (e.g., Seibenaller 1984), or if fish suddenly overcome gape limita-



tion of their predators (i.e., enter a size refuge) and need to rely less on escape potential. On the other hand, it is quite reasonable to expect that burst swimming requirements, in terms of number of bursts or duration of burst swimming, should decline quite sharply as prey size suddenly becomes much larger. As an example, to achieve satiation (~5% body weight per day), a 100-g benthivorous perch would need to consume (i.e., actively seek out and attack) about 500 benthic invertebrates (~10 mg each) per day. In addition, time spent actively feeding is time spent interacting with other fish (conspecifics, competitors, as well as predators), which may have important energetic consequences (e.g., Boisclair and Leggett 1989). The same 100-g perch, actively feeding on other fish (~2.5 g each), would only need to make about two attacks per day to satisfy its feeding requirements, thereby spending much less time actively foraging and interacting. Thus, whenever possible (i.e., when prey availability and predator morphology allow), feeding on larger prey should entail considerably less effort in terms of time spent actively foraging and attacking prey. This, in turn, should lead to lower energetic needs, with respect to minimizing time spent bursting, and lower increases in glycolytic potential. Conversely, feeding on constant prey size should lead to rapid increases in activity costs (number of bursts) with body size and highly positive scaling of glycolytic potential. To our knowledge, the influence of prey size and time spent bursting (or number of bursts) on muscle glycolytic potential has never been tested. The predator-prey size ratio dependent and bioenergetic explanation (after Kerr 1971, for the influence of prey size on fish growth) for positive scaling of anaerobic power in fish put forth here, unlike previous explanations based on hydrodynamic theory (Sullivan and Somero 1980), is consistent with the observation that glycolytic potential often scales weakly or negatively to body size (Childress and Somero 1990), even when fish seem to maintain high burst swimming potential (Garenc et al. 1999).

#### Other examples of ontogenetic shifts in LDH activity

We know of only two other studies where sawtooth-like allometry of LDH activity was discussed in detail. Seibenaller (1984) found that muscle LDH activity dropped sharply in wild-caught *Sebastes altivelis* juveniles following a shift from active, pelagic to sedentary, demersal feeding, an ontogenetic vertical migration which involved changes in hydrostatic pressures of 130 atmospheres or more. Adaptation in the expression of different isozyme forms of LDH, with possible differences in substrate-conversion efficiencies (Somero and Seibenaller 1979), to differences in pressure were not involved in this downshift in LDH activity. Instead, it was argued that differences in metabolic requirements arising, in part, from changes in locomotory costs were responsible for changes in enzyme activity levels. More recently, Garenc et al. (1999) reported on a pattern of LDH scaling strikingly similar to what we show here. They noted that LDH activity in the muscle of threespine sticklebacks (*Gasterosteus aculeatus*) reared under controlled laboratory conditions followed positive allometry in juveniles and that this relationship broke down in adults which had significantly lower LDH activities than juveniles. They explained that this may have been due to an

increased mobilization of energy reserves in the muscle towards reproductive costs in adults. Although admittedly speculative, our findings suggest that this pattern could also have arisen inadvertently as the result of a facilitated diet shift from fine-ground powdered food (Tetra Marin staple food) to larger *Artemia* and bloodworms. Such a change in diet would be functionally similar to a shift from feeding on zooplankton to benthic invertebrates and may in fact be expected to elicit a decrease in burst swimming requirements in terms of number of feeding bursts. Consideration of burst speed, which continued for the most part to follow positive allometry in adults (Garenc et al. 1999), would not have necessarily captured changes in swim performance in this sense. Future experiments could be designed to specifically test for the possible influence of induced diet shifts towards larger food particles on spontaneous fish activity (measured as rate or number of bursts) and muscle glycolytic potential.

#### Implications for optimal foraging

The results of the present study provide evidence for the importance of a component of foraging in fish which may be underappreciated in optimality models, that is, the cost of pursuit, attack, and capture. That glycolytic enzymes are involved in supplying quick, burst energy to spontaneous movements in fish (Childress and Somero 1990), that fish body mass is typically made up of >50% white (anaerobic) muscle (Somero and Childress 1980), and that the activity of glycolytic enzymes corresponds very well to independent estimates of total fish activity costs (Sherwood et al. 2002) and diet ontogeny all suggest that spontaneous (anaerobic) activity in fish is not a trivial component of foraging costs. Routine swimming involving spontaneous movements, such as would be required for attacking prey, has been found to be the most costly form of activity in free-swimming fish (Krohn and Boisclair 1994). Optimality models already incorporate activity expenditures associated with obtaining prey, focusing mainly on the amount of time spent searching for and handling prey (Townsend and Winfield 1985), both aerobic forms of activity. Here, we simply add to existing models by suggesting that consideration of how energy is expended during a given bout of foraging (e.g., mostly searching, an aerobic process, versus mostly attacking, an anaerobic process) can be just as important. Explicitly assigning high and variable energy costs to the attack component of foraging, perhaps with the aid of LDH measurements, may result in more finely tuned model predictions of optimal prey size for fish in nature. For example, our results suggest that activity costs should be higher when fish spend most of their time attacking small prey than when they spend most of their time searching for large prey. In this case, prey abundance may become less important in compensating for small prey size (e.g., Kerr 1971). The finding that fish growth usually accelerates after diet shifts to larger prey (Jones et al. 1994), which should be less abundant (Rasmussen 1993) and harder to find (Kerr 1971), would be consistent with this expectation.

Thus, in terms of foraging, highly costly spontaneous activity and high glycolytic potential should be most useful in attacking prey and perhaps less involved in searching for and handling prey, which may implicate aerobic processes. How-

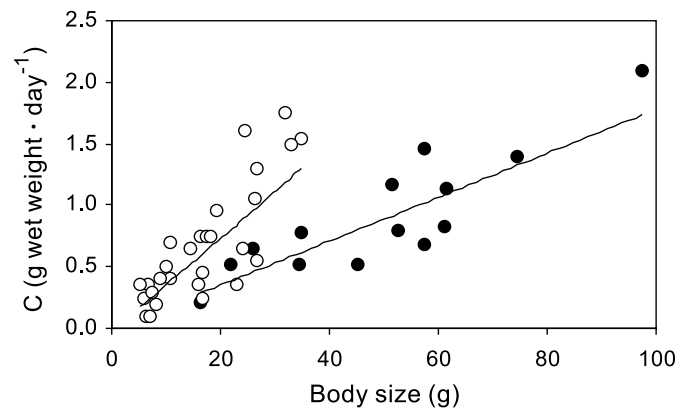
ever, attacking prey may or may not involve burst speeds. For instance, it may be hard to imagine that sunfish "attack" sedentary snails in the same way that pike are likely to attack their fish prey and that attacks are involved in the observed pattern of positive LDH allometry for sunfish. It is possible that fish actually do attack sedentary prey in the same manner that they attack moving prey. The appearance of individual prey items, even sedentary ones, in the presence of potential competitors may be a fleeting phenomenon and require quick reactions and high burst capabilities for successful captures. An alternative explanation is that the time spent searching for and handling prey, which should increase as predator size – prey size ratios increase in the same way that number of attacks should increase, may expose fish to competitive interactions (both exploitative and nonexploitative) and predators that may require high levels of burst swimming performance. All of these possibilities, which are functionally similar, would not be distinguishable from the point of view of enzyme activities. Future studies may be undertaken to explore further the influence of prey type (sedentary versus mobile), competition (both inter- and intra-specific), and predation on fish activity and LDH scaling patterns in fish.

Finally, it should be stated that the saw-toothed model may not always appear as such. For instance, lake trout seem to follow more gradual shifts in diet and associated LDH activity. This probably has more to do with timing than any real modifications on the saw-toothed model itself. In addition to making ontogenetic diet shifts, lake trout are forced to undergo annual habitat shifts from inshore to offshore communities as a result of their intolerance to warm temperatures. Lake trout for the present study were captured in May around the time that they would have been making the characteristic move from inshore, littoral feeding into deeper, colder waters (Pazzia 2001). LDH activities measured at the time of capture should have depended on the length of the time interval that trout were actually feeding offshore (i.e., on large forage fish, such as cisco, which should be less costly) and whether or not they were large enough to make this shift following thermal exclusion from inshore resources. Not moving to colder water may also affect LDH activity directly (e.g., Nathanailides 1996); this would not have affected our results for yellow perch, sunfish, rock bass, and pike as these are all warm-water fish and, at the time of capture, were all foraging in surface waters (1–2 m, 15–20°C) regardless of diet. Those trout not poised to shift to cisco may have continued to make costly forays into warmer waters, either inshore or surface, to exploit smaller forage fish. These considerations should have the effect of increasing the variance in LDH activity around this habitat shift thereby leading to the highly variable and gradual shift patterns that we observe. Regardless of the shape of the relationship, diet and habitat shifts still had the overall effect of lowering LDH activity and fish activity in lake trout.

#### Implication for bioenergetics models

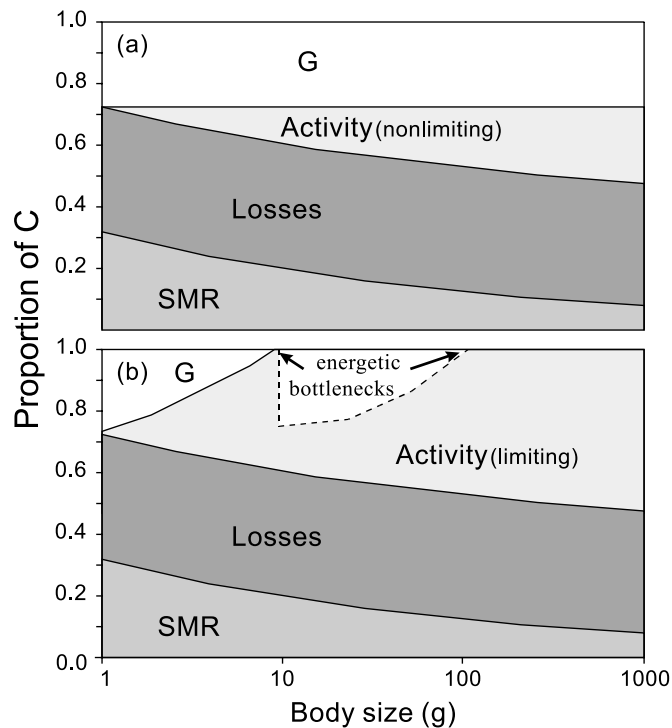
Our study complements previous findings (Childress and Somero 1990) that the activity of anaerobic enzymes scales mostly positively, but extremely variably, with body size.

**Fig. 5.** Relationship between body size and consumption rate ( $C$ ) for yellow perch. Open circles are data from Boisclair and Rasmussen (1996);  $C = 0.03 \cdot W^{1.04}$  ( $R^2 = 0.63$ ,  $p < 0.0001$ ). Solid circles are data from Sherwood et al. (2000);  $C = 0.02 \cdot W^{1.00}$  ( $R^2 = 0.75$ ,  $p < 0.0001$ ). In both cases,  $C$  scales isometrically to body size (slopes are not significantly different than 1). Data were not combined because they represent different sampling time intervals and different methodologies; open circles are estimates during summer based on gut clearance models; solid circles are annual estimates made with a radiocesium mass-balance method.



This, as well as the finding that LDH scaling has been found to be strongly related to the scaling of fish activity costs, has important implications for bioenergetic modelling in fish. For example, when consumption rates scale isometrically with body size (Fig. 5), the energy available for growth and activity would increase with body size (Fig. 6). This is because standard metabolic costs tend to decrease with body size, and remaining costs (SDA,  $F$ , and  $U$ , see eq. 1) are considered to be fixed proportions of consumption rate (Kitchell et al. 1977). The implication of highly variable LDH activity scaling is that when LDH activity, and hence fish activity, increase sharply with body size, the scope for growth should become severely limited and fish should stunt (Fig. 6). Or, when activity costs, plus all other bioenergetic costs (not including growth), equal 100% of the energy budget set by feeding rate, growth efficiency should become zero and growth should cease, thus constituting an energetic bottleneck. In this instance, energy available for reproduction should also be quite limited. In cases where LDH and fish activity do not scale sharply with body size (argued here to occur when fish frequently shift diet), other factors may become more important in limiting growth. This may involve decreasing consumption rates; in an extensive meta-analysis of feeding rates covering numerous fish species with a large range in body sizes, consumption rates were found to scale with an exponent of about  $-0.2$  (Trudel et al. 2000). The important point to note is that generic fish activity multipliers derived from forced swimming trials performed in the laboratory, which are known to greatly underestimate the cost of spontaneous (free) swimming (Krohn and Boisclair 1994), when applied to bioenergetics models (Kitchell et al. 1977), would not allow one to distinguish when fish activity costs are limiting to growth in field

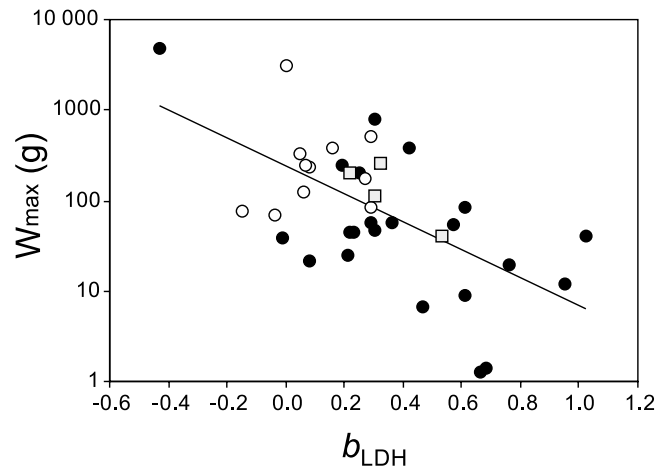
**Fig. 6.** Typical size scaling of various metabolic costs for two different populations of yellow perch as a proportion of the total energy budget ( $C$ , see also eq. 1). SMR is standard metabolic rate; Losses are the sum of all losses resulting from excretion, egestion, and specific dynamic action; and  $G$  is growth (both somatic and gonadal). All else being equal, the two panels illustrate fish activity scaling for (a) Lake Memphremagog perch ( $b_{LDH} = 0.08$ ) and (b) Lake Hertel perch ( $b_{LDH} = 0.27$ ; for first diet stage), which were known to stunt at quite small sizes as planktivores (Heath and Roff 1987). The dotted line represents a hypothetical diet shift that would allow stunted perch to grow out of a bottleneck. These two lakes were chosen here for comparison because they have similar specific consumption rates (about 4% body weight per day, Boisclair and Rasmussen 1996) but vastly different LDH activity scaling coefficients. The scaling coefficient for  $C$  was set at zero (i.e.,  $C$  was assumed to be isometric, based on data presented in Fig. 5). The  $P$  value (Kitchell et al. 1977) was set so as to result in consumption rates approximating those observed for lakes Hertel and Memphremagog perch. Fish activity ( $A$ ) was given by  $A = W^{b_A}$  (values for  $b_A$  are from Table 3). All other model parameters were set as default values given by Kitchell et al. (1977).



settings. Finally, the idea that fish activity, as inferred from LDH scaling, can be limiting to growth has some empirical support. We found a significant negative relationship between maximum fish size and field-derived LDH scaling across numerous populations and species of fish (Fig. 7;  $R^2 = 0.37$ ,  $p < 0.0001$ ; relationship without largest extreme value, *Microstomus pacificus*, was significant,  $R^2 = 0.28$ ,  $p < 0.001$ ).

The above modelling and empirical results for the relationship between LDH activity and fish growth in nature may provide some ecological context for some recent laboratory findings. Positive correlations have been found be-

**Fig. 7.** Relationship between LDH scaling coefficient ( $b_{LDH}$ ) and maximum size ( $W_{max}$ ) for 23 species of marine fishes (solid circles; Table 2). Open circles are data for freshwater fish presented here (Table 1). Open squares are data for yellow perch from Sherwood et al. (2002).



tween various muscle enzyme activities (including LDH) and growth and condition in captive-held Atlantic cod (*Gadus morhua*) (Pelletier et al. 1994; Couture et al. 1998). In these cases, growth was controlled by varying levels of feeding. It was suggested that this information could be useful in estimating growth rates of wild cod (Couture et al. 1998). We caution against this approach, which is likely to lead to overestimation of cod growth rates in nature. Under controlled laboratory conditions, higher growth rates can be achieved by higher feeding rates, which would entail higher fish activity (and therefore higher enzyme activities). However, it would appear that feeding rates in nature are not the only important factor in determining fish growth (Tucker and Rasmussen 1999; Sherwood et al. 2000; Trudel et al. 2001). Perhaps more important, maximum fish growth in nature should coincide with minimal activity costs (Fig. 6). Therefore, as opposed to the above laboratory findings where activity costs would have been artificially manipulated (i.e., kept relatively low) by varying feeding levels on a constant, preferred prey source, we conclude that the highest growth and size in wild-living fish should be accompanied by minimal increases in LDH activities.

On a final note, our results suggest that any changes in food web structure, either natural or human induced, that limit feeding opportunities may lead to what we call energetic bottlenecks resulting from an inability to shift diet and reset activity costs and, ultimately, stunting in fish. Energetic bottlenecks have been implicated in the stunting of yellow perch living in pollutant-impacted food webs (Sherwood et al. 2002), should be involved in stunting the growth of lake trout living in invasion-impacted food webs (Vander Zanden et al. 1999; Pazzia 2001), and may play an important role in producing variable growth in North Atlantic cod (Krohn et al. 1997) living in fluctuating ocean food webs (Rose et al. 2000). The application of LDH measurements, and perhaps other enzymes involved in anaerobic fish activity, should provide a powerful tool in future ecological studies for as-

sessing the consequence of variable food webs on the bioenergetic performance of wild-living fish.

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