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Physiological performance of two forms of lacustrine brook charr, *Salvelinus fontinalis,* in the open-water habitat

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Synopsis

Although morphological differences among ecotypes have often been observed, little is known about the adaptive value of these differences in terms of the relative performance of individuals. The first objective of this study was to compare specific growth rates, muscle proteins, lipids, and water content in the muscles and digestive tracts of littoral and pelagic brook charr (1+) when individuals of both forms were restricted to feeding on zooplankton for 76 days, in pelagic enclosures of a Canadian Shield lake. The second objective was to determine if differences in the physiological performance of experimental fish were related to differences in their morphology. The specific growth rate was low and did not differ significantly between littoral and pelagic individuals at the end of the experiment. However, littoral individuals lost more lipids and had lower muscle protein content than pelagic fish at the end of the experiment. The pectoral fin was longer in littoral individuals than in pelagic ones. Furthermore, the biochemical discriminant scores of individuals were marginally correlated to those of morphology. Based on a comparison of their proximate tissue composition, our results suggest that trophic diversification is adaptive in brook charr because littoral individuals exhibited lower physiological performance than pelagic ones when restricted to feeding in the pelagic zones. In addition, our results support that morphological descriptors are related to physiological performance. This study is one of the first field attempts to relate differences in trophic morphology of a fish species to physiological performance.

Introduction

Trophic specialization among individuals of the same species is common in vertebrates and may have primarily evolved in response to competition for food (Wimberger 1994, Skúlason & Smith 1995). Fish populations often include both open-water types (limnetic or pelagic forms) and shallow-water types (benthic or littoral forms) in lakes of the northern hemisphere (Robinson & Wilson 1994, Skúlason & Smith 1995, Schluter 1996). Individuals generally exhibit differences in morphology and behaviour that seem to be adaptive because each form appears to be better adapted than the other to forage in its respective habitat (i.e. benthic form in the littoral zone and pelagic form in the open-water habitat) (Elingher 1990, Malmquist et al. 1992, Skúlason et al. 1993, Robinson & Wilson 1994, 1996, Schluter 1995, 1996).

Although morphological differences among forms have often been observed, little is known about the adaptive value of these differences in terms of the relative performance of individuals (Meyer 1989, Schluter 1995, Robinson et al. 1996). In fact, it is difficult to assess the adaptive value of a polymorphism in terms of better performance on the basis of morphological variations only. Individual variations in proximate tissue composition has been studied little in wild populations although they are useful and routinely used to assess the efficiency of nutrient transfer from food to fish in aquaculture (Miglavs & Jobling 1989, Cho & Kaushik 1990, Thorpe & Cho 1995).

Brook charr, *Salvelinus fontinalis* (Mitchill), exhibit individual differences in habitat use in lakes of the Canadian Shield (Québec, Canada). In a study investigating the spatial distribution of young-of-the-year brook charr in Lake Bondi, Venne & Magnan (1995) found that individuals could be divided into two groups. A littoral group was found between 0 and 2 m depth and a profundal group between 3 and 6 m depth. Bourke et al. (1997) also found that adult brook charr exhibit individual differences in habitat use in two other lakes in the same area: 50% of radio-tracked individuals were found mainly in the littoral zone, 18% in the pelagic zone, and 32% travelled regularly between the two zones. Furthermore, individual differences in habitat preference were related to functional differences in body morphology: the pectoral fins of littoral individuals were significantly longer than those of pelagic ones. More recently, the analyses of stomach content data from 3776 brook charr captured in 69 lakes of the Canadian Shield showed that in comparable situations (single-species lakes), the proportion of benthic and pelagic forms fits remarkably well with those based on individual preferences in spatial distribution, as identified through radio-telemetry in a lake of the same area (Bourke et al. 1999), suggesting that the presence of the two forms is typical of these lakes. Bourke et al. (1999) also found that the proportion of littoral brook charr in a given lake is inversely related to the intensity of interspecific competition with creek chub, *Semotilus atromaculatus*, and white sucker, *Catostomus commersoni*. Bourke et al. (1997) reported that two groups belonging to the same population may select different spawning grounds, which represents a potential for the evolution of reproductive isolation. Finally, based on microsatellite DNA analyses of brook charr in two lakes of the same area, Dynes et al. (1999) found that littoral and pelagic individuals were partially reproductively isolated in one lake. All these studies suggest that brook charr inhabiting oligotrophic lakes of the Canadian Shield often exhibit trophic polymorphism, where some individuals are better adapted to feeding in the littoral zone and others are specialists at feeding in the pelagic zone.

The first objective of our study was to compare the physiological performance of littoral and pelagic brook charr when individuals of both forms were restricted to feeding on zooplankton in the pelagic zone. We used specific growth rate and proximal tissue composition (proteins in muscle, lipids, and water content in muscles and digestive tracts) as indices of physiological performance. The second objective was to determine if any differences in the physiological performance of the experimental fish could be related to differences in their morphology. If morphological differences between littoral and pelagic individuals are adaptive, one would expect that pelagic individuals would show improved physiological performance compared to littoral fish in the open-water habitat.

Materials and methods

Study sites

The experiments were conducted in the Mastigouche Reserve (46°40′N, 73°20′W), Québec (Canada). Experimental fish were sampled in Lake Ledoux, where littoral and pelagic brook charr have been identified by Bourke et al. (1997) through telemetry. This lake is typical of small oligotrophic temperate lakes with respect to surface area (11.9 ha), mean depth (5.5 m), conductivity (15.3 $\mu S\ cm^{-1}$), dissolved oxygen, thermal stratification, and Secchi disk transparency (4.2 m) (Bourke et al. 1997, Dynes et al. 1999). The only other fish species in the lake is the northern redbelly dace, *Phoxinus eos*. Enclosure experiments were conducted at Lake Des Grives, located about 10 km south of Lake Ledoux. This lake is comparable to Lake Ledoux with respect to the above characteristics and was used for the enclosure experiments because of logistic constraints related with accessibility to Lake Ledoux.

Fish and experimental design

Juvenile brook charr (1+) from Lake Ledoux were captured with monofilament gillnets (7.5 or 15.0 m long × 1.8 m high, stretched mesh of 15.9 mm). One-year-old (1+) brook charr from these lakes can be easily identified from size frequency distributions (Magnan & Fitzgerald 1983). The nets were checked every 15–30 min to prevent fish injury. ‘Littoral’ individuals were captured near the shore, at less than 2 m of depth, while ‘pelagic’ individuals were captured at more than 4 m of depth. All fish were captured on 10 and 11 July 1997, measured (±1 mm), and weighed (±1.0 g) before being placed in enclosures in Lake Des Grives. Ten fish of each form were sacrificed (overdose of tricane methasulfonate, MS 222) at the beginning of the experiment for biochemical analyses (see below).

The experimental system consisted of eight pelagic enclosures (4 m × 3 m × 6 m depth) anchored in the pelagic zone of Lake Des Grives. The enclosures' mesh size (9.5 mm stretched mesh) allowed water and zooplankton to flow through freely (Héroux 1998). Ten fish were placed in each of the eight enclosures, with four enclosures for each form (pelagic and littoral). Each fish was individually marked by fin clipping. Juvenile brook charr (1+) are known to feed exclusively on zooplankton in these enclosures (Héroux 1998). We assumed that any cage effect was the same for littoral and pelagic individuals since our aim was to investigate differences in physiological performance between the two forms; our comparison was based on relative rather than absolute differences. The experiments extended over a 76-day period, between 16 July and 30 September 1997. At the end of this period, every fish was measured and weighed before being frozen.

Biochemical analyses

Biochemical analyses were performed on lateral muscle and on the digestive tract (section between the esophagus and the pyloric valve). We first evaluated the water content (%) in the lateral muscle and digestive tract by drying tissues at 60°C for 48 h. The percent water content was estimated as:

$$\%\ \text{water content} = (\text{WW} - \text{DW})\text{WW}^{-1}100, \quad (1)$$

where WW represents the wet weight (g) and DW the dry weight (g) of tissues.

Lipids were extracted from the lateral muscle and digestive tract by successive washes of dehydrated samples with diethyl ether anhydrate (99%) (Reznick & Braun 1987). Samples were immersed in ether for periods of 24 h between washes until all residual ether was completely free of lipids (no weight variations). The percent lipid was estimated as:

$$\%\ \text{lipids} = (\text{DW} - \text{DWE})\text{DW}^{-1}100, \quad (2)$$

where DW represents the dry weight of tissues (g) before and DWE the dry weight of tissues (g) after lipid extraction.

Only muscle samples were used to determine total protein content (g kg^{-1} dry weight). We used the Biuret–Lowry method described by Sigma Diagnostic Co. (Phenol reagent method for biologic fluids, procedure no. 690) to estimate the total protein quantity in lateral muscle as:

$$\text{Protein content} = (\text{MC} - \text{PC})\text{MC}^{-1}1000, \quad (3)$$

where MC represents the muscle concentration (g l^{-1}) and PC the protein content in the sample (g l^{-1}). Tissues were previously crushed and proteins were digested in a solution of NaOH (1N). Specific growth rate (SGR) was estimated as:

$$\text{SGR} = (\ln x_2 - \ln x_1)\text{T}^{-1}100, \quad (4)$$

where x_1 represents the initial length (mm), x_2 the final length (mm), and T the duration of the experiment (76 days). We used the total fish length to compute SGR rather than wet weight because of the low accuracy associated with our fish weight measurements in the field.

Morphological measurements

After thawing, morphological measurements were made on the left side of all individuals using a digital caliper (±0.01 mm). Eleven body descriptors associated with swimming and trophic characteristics were measured (Figure 1). We also measured the length of the longest gill raker and the space between two adjacent gill rakers at the bend of the gill arch with an ocular micrometer mounted on a compound microscope (±0.025 mm).

Statistical analyses

Difference in mean length and weight of littoral and pelagic individuals between the beginning and the end

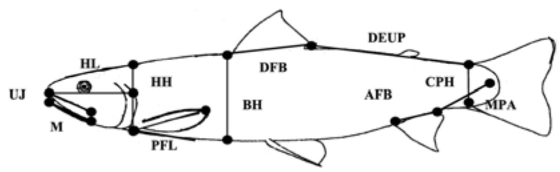

Figure 1. Location of the 11 body descriptors associated with swimming and trophic characteristics used in the discriminant function analysis. Points and lines refer to: UJ = upper jaw length, M = mandible, HL = head length, HH = head height, PFL = pectoral fin length, BH = body height, DFB = dorsal fin base, DEUP = dorsal fin end to the upper and most posterior peduncle point, CPH = caudal peduncle height, MPA = middle peduncle to the end of anal fin, and AFB = anal fin base.

of the experiment were compared using t-tests. Biochemical descriptors did not vary with fish length or weight and were only transformed when necessary (log or arcsin for percentages) and standardized to stabilize their variance prior to statistical analyses (see below). All morphological characters were significantly related to fish length ($p < 0.05$). We removed the effect of fish size on body and fin measurements with a regression technique (Flemming et al. 1994). The data of each morphological descriptor were first log transformed and standardized (mean of 0 and standard deviation of 1). Each descriptor was then expressed as the deviation of individuals (regression residuals) from the pooled within-group regression line describing the relationship between that descriptor and standard length. These residuals are considered to be approximately independent of fish size and should reflect variation resulting from measurement error and the biological deviation of individuals from the predicted character–length relationship (Kuhry & Marcus 1977).

To examine the differentiation between littoral and pelagic individuals at the end of the experiment, we used discriminant function analysis, which allowed us to determine the most useful descriptors for separating population groups (Legendre & Legendre 1998). Biochemical and morphological descriptors were analyzed separately in two discriminant functions. We built discriminant functions with all biochemical and morphological descriptors (in lieu of a step-wise selection procedure) because we considered that these descriptors better represent the proximate tissue composition and overall shape of the fish in our experiment. The morphological scores were plotted against biochemical ones to show the variation and the magnitude of separation between and within groups. Pearson product-moment correlation coefficients were determined between biochemical and morphological discriminant scores. This allowed us to determine whether the physiological performance of an individual was related to its morphology. Discriminant function analysis was not used to compare littoral and pelagic individuals at the beginning of the experiment due to the low sample size in each group ($n = 10$). We tested differences in muscle protein as well as lipids and water content in the muscles and digestive tracts of littoral and pelagic individuals at the beginning of the experiment with t-tests. Finally, we compared the results of the meaningful descriptors (i.e., those selected by the discriminant function analyses or that varied significantly during the experiment) at the beginning and the end of the experiment for reference only. All statistical analyses were performed using SYSTAT, version 8 (Wilkinson 1998).

Results

Biochemical variation

The mean percent water in muscle and digestive tract, lipids in the digestive tract, and protein in muscle of littoral and pelagic individuals were not significantly different at the beginning of the experiment (Table 1). In contrast, the mean percent muscle lipid content was significantly higher in littoral than in pelagic individuals at the beginning of the experiment while it showed no differences between forms at the end (Figure 2). The specific growth rate (SGR) was low, exhibited high variation, and did not differ significantly between littoral and pelagic individuals at the end of the experiment (pelagic: 0.083 ± 0.047 mm d^{-1}, littoral: 0.079 ± 0.049 mm d^{-1}; $t = 0.336$, $p > 0.05$).

The discriminant function analysis on biochemical descriptors yielded a highly significant difference between littoral and pelagic individuals at the end of the experiment ($F = 5.111$, $p \leqslant 0.001$; Table 2). Examination of the standardized canonical coefficients indicated that the total muscle protein content was the

Table 1. Proximate tissue composition of littoral and pelagic juvenile brook charr (1+) from Lake Ledoux at the beginning of the experiment with values for the t-tests comparing the two forms. Data are means ± SD. NS = not significant, $p > 0.05$. Actual data are presented here but analyses were performed on transformed data (see text).

Descriptor	Littoral (n = 10)	Pelagic (n = 10)	t	p
Water in muscle (%)	68.10 ± 1.17	69.66 ± 1.91	0.694	NS
Water in digestive tract (%)	65.56 ± 7.29	65.55 ± 8.04	0.411	NS
Lipids in muscle (%)	9.75 ± 2.39	6.92 ± 1.62	3.188	<0.05
Lipids in digestive tract (%)	56.50 ± 17.15	51.21 ± 19.34	1.016	NS
Proteins in muscle (g kg^{-1})	530.20 ± 53.51	588.52 ± 94.59	1.011	NS

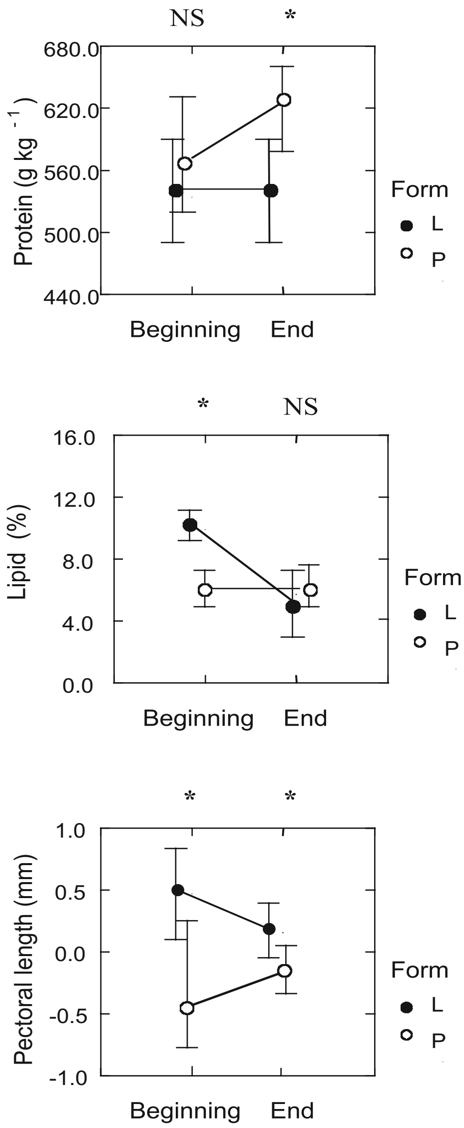

Figure 2. Comparisons of muscle lipid and protein contents and adjusted pectoral fin lengths (mm) of pelagic and littoral brook charr (1+) at the beginning and the end of the experiment. Data are means ± SD (*means: $p < 0.05$ as determined by a t-test; NS = differences not significant.)

most powerful descriptor separating the two groups. Littoral fish had significantly lower muscle protein content than pelagic ones at the end of the experiment while we found no difference between forms at the beginning ($t = 1.011$, $p > 0.05$; Figure 2). The classification accuracy of the discriminant function based on biochemical descriptors indicated that 78% of pelagic individuals and 61% of littoral ones were correctly reclassified into their appropriate group, for an overall classification accuracy of 70%. We found a significant negative relationship between the percent water and the amount of other energetic constituents (proteins + lipids) in muscles of pelagic fish ($t = 2.346$, $p = 0.024$; Figure 3); this relationship was not significant for littoral individuals ($t = 0.021$, $p > 0.05$).

Morphological variation

Littoral and pelagic individuals did not show any significant differences in total length and weight at the beginning or the end of the experiment (Table 3). The discriminant function analysis based on morphological descriptors yielded a significant difference between littoral and pelagic individuals ($F = 2.413$, $p < 0.05$; Table 4). The standardized canonical coefficients revealed that the pectoral fin length best accounted for the between-group variation. Littoral individuals had longer pectoral fins than pelagic ones (Figure 2). The classification accuracy of the discriminant function indicated that 59% of pelagic individuals and 64% of littoral ones were correctly reclassified into their appropriate group, for an overall classification accuracy of 62%.

Relationship between physiological performance and morphology

In spite of some overlap, the distribution of the canonical scores illustrates that morphological and biochemical descriptors were more variable between than within the two forms (Figure 4). The biochemical discriminant scores were also marginally correlated with those of morphology ($r = 0.23$, $p = 0.052$).

Discussion

Biochemical variation

The proximate tissue composition of a fish is a good indicator of its performance in food acquisition (Shearer 1994). Muscle protein contents of littoral and pelagic individuals were significantly different after a 76-day period of feeding exclusively in the pelagic zone. The mean muscle protein content was significantly lower in littoral than in pelagic individuals while it was the same at the beginning of the experiment.

Table 2. Results of the discriminant function analysis used to compare biochemical descriptors of littoral and pelagic juvenile brook charr (1+) from Lake Ledoux at the end of the experiment. Data are means ± SE.

Descriptor	Littoral (n = 39)	Pelagic (n = 38)	St. canonical coefficient	Wilks' lambda	F	p
Water in muscle (%)	77.33 ± 0.458	75.61 ± 0.463	0.175	0.730	5.111	0.0005
Water in digestive tract (%)	76.63 ± 0.478	75.95 ± 0.484	−0.145			
Lipids in muscle (%)	5.53 ± 0.468	5.50 ± 0.473	0.005			
Lipids in digestive tract (%)	29.23 ± 2.04	25.26 ± 2.06	0.035			
Proteins in muscle ($g\,kg^{-1}$)	549.28 ± 12.95	643.37 ± 13.09	1.033			

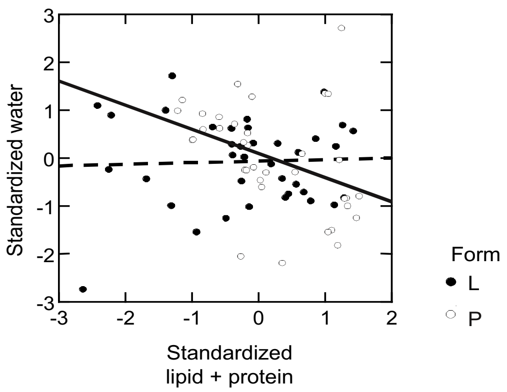

Figure 3. Relationship between standardized muscle water content and energetic constituents (lipids + proteins) of littoral (- - - -) and pelagic (——) juvenile brook charr (1+) from Lake Ledoux at the end of the experiment. Littoral group: $y = -0.004x - 0.057$, $R^2 = 0.0$, $p > 0.05$; pelagic group: $y = -0.369x + 0.215$, $R^2 = 0.136$, $p = 0.025$.

Furthermore, the muscle lipid content was significantly higher in littoral than in pelagic individuals at the beginning of the experiment but was the same at the end of the experiment. This suggests that the muscle lipid content of littoral individuals decreased during the experiment. Variations in protein and lipid contents then suggest that pelagic individuals had a higher fitness in the pelagic habitat than littoral ones.

Although growth in length and weight was low during the experiment, the mean protein contents observed in our study are in the range of those estimated on cultured charr fed ad libitum (Miglavs & Jobling 1989) and thus indicate no major stress due to experimental conditions. Temperature, fish size, life interval, diet composition (energy intake), and growth rate are the five factors known to have an influence on protein concentration in muscles (Fauconneau 1985, Shearer 1994). Our experimental fish were at the same life interval, had the same length (at the beginning of the experiment), and experienced low specific growth rates during the experiment. In this context, two hypotheses could explain the observed differences in protein content of littoral and pelagic individuals at the end of the experiment. The first hypothesis is that protein digestion, which is associated with energy intake and food acquisition, was higher in pelagic individuals. The second hypothesis is that the balance between protein synthesis and protein breakdown in muscle was more efficient in pelagic than in littoral individuals in the open-water environment. The resulting difference between protein synthesis and protein breakdown is reflected either by protein deposition or protein loss (Fauconneau 1985). It has also been reported that protein synthesis is mainly directed towards protein deposition in fish muscle (Fauconneau 1985). The better performance of pelagic individuals with respect to protein digestion and (or) synthesis could be related to differences in thermal preferendum (Alanara 1994), oxygen consumption (Cho & Kaushik 1990), or swimming efficiency (East & Magnan 1987) between pelagic and littoral individuals.

Lipids are cheap sources of respiratory substrate and are easily used in energy metabolism (Jobling 1994a). In general, the percent of fatty acids in charr muscle is a direct function of their respective digestible concentrations in the diet (Guillou et al. 1995). Jobling (1994a) reported that a freshwater zooplankton diet contains approximately 21% (dry weight) lipids compared to about 14% in a benthic diet (mixed insect larvae). The lower lipid content in the muscle of wild pelagic individuals at the beginning of the experiment might be related to the presence of wax ester in their diet, which is the principal lipid storage product in many zooplankters and is less easily digested by charr than acyglycerol and phospholipids (Jobling 1994b). The 5.5% lipid content observed in the muscle of littoral and pelagic individuals at the end of our experiment (corresponding to 1.3% of the dry weight) may

Table 3. Total length and weight of littoral and pelagic juvenile brook charr (1+) from Lake Ledoux at the beginning and the end of the experiment with values for the t-tests comparing the two forms. Data are means ± SD. NS = not significant, p > 0.05. Actual data are presented here but analyses were performed on transformed data (see text).

	Descriptors	Littoral	Pelagic	t	p
Beginning	Total length (mm)	172.2 ± 14.0	170.5 ± 23.1	0.199	NS
	Body weight (g)	57.0 ± 13.5	53.8 ± 20.6	0.408	NS
		(n = 10)	(n = 10)		
End	Total length (mm)	180.3 ± 15.5	176.1 ± 17.0	1.201	NS
	Body weight (g)	55.5 ± 12.4	50.6 ± 13.8		
		(n = 38)	(n = 39)	1.625	NS

Table 4. Results of the discriminant function analysis used to compare morphological descriptors of littoral and pelagic juvenile brook charr (1+) from Lake Ledoux at the end of the experiment. Data are means ± SE.

Descriptors (mm)	Littoral (n = 38)	Pelagic (n = 39)	St. canonical coefficient	Wilks' lambda	F	p
Caudal peduncle height	14.78 ± 0.11	14.58 ± 0.10	−0.199	0.660	2.413	0.011
Pectoral fin length	24.22 ± 0.17	23.33 ± 0.16	0.975			
Gill raker space	1.31 ± 0.03	1.34 ± 0.03	−0.431			
Gill raker length	2.31 ± 0.04	2.30 ± 0.04	−0.257			
Head height	28.81 ± 0.28	28.35 ± 0.27	−0.064			
Head length	35.61 ± 0.25	35.81 ± 0.24	−0.708			
Body height	32.77 ± 0.38	31.78 ± 0.36	0.302			
Anal fin base	14.45 ± 0.12	14.32 ± 0.12	0.146			
Dorsal fin base	17.91 ± 0.18	17.70 ± 0.17	0.157			
Dorsal fin end – top peduncle	53.32 ± 0.36	53.38 ± 0.34	0.513			
Anal fin end – middle peduncle	27.33 ± 0.25	27.50 ± 0.24	−0.192			
Mandible	23.25 ± 0.19	22.89 ± 0.18	0.145			

reflect lipid use from muscle in food-deprived charr. Miglavs & Jobling (1989) observed that the mean lipid content in the muscle of juvenile Arctic charr held in a food-deprived regime was 1.6% (of dry weight) after a 112-day period. At such levels, the fish would resort to protein metabolism for energy (Shearer 1994).

A loss in energetic constituents (lipids and proteins) is generally compensated by an increase in water content in fish muscle (Shearer 1994). We expected to find such a negative relationship between muscle water content and energetic substrate in both groups, but it was significant only in pelagic individuals. This result indicates that the loss in muscle lipid content, which appeared to be higher in littoral than in pelagic individuals, was not compensated by water in littoral fish. The distribution of mean scores among enclosure shows that the biochemical composition of littoral individuals was generally more variable than that of pelagic ones (Figure 4). This more variable response of littoral individuals may reflect their lower ability to forage and (or) assimilate food in the open-water habitat.

Morphological variation

The discriminant function analysis revealed that juveniles captured in littoral and pelagic zones of Lake Ledoux differed significantly in their morphology, specifically in the length of their pectoral fin: littoral individuals had longer pectoral fins than pelagic fish. Discriminant analysis using all morphological variables also allowed for an effective reclassification of individuals into their appropriate group. These results support the existence of distinct littoral and pelagic individuals in Lake Ledoux. Bourke et al. (1999) and Dynes et al. (1999) also found that adults of the littoral form had longer pectoral fins than pelagic ones in this lake. Long pectoral fins are related to

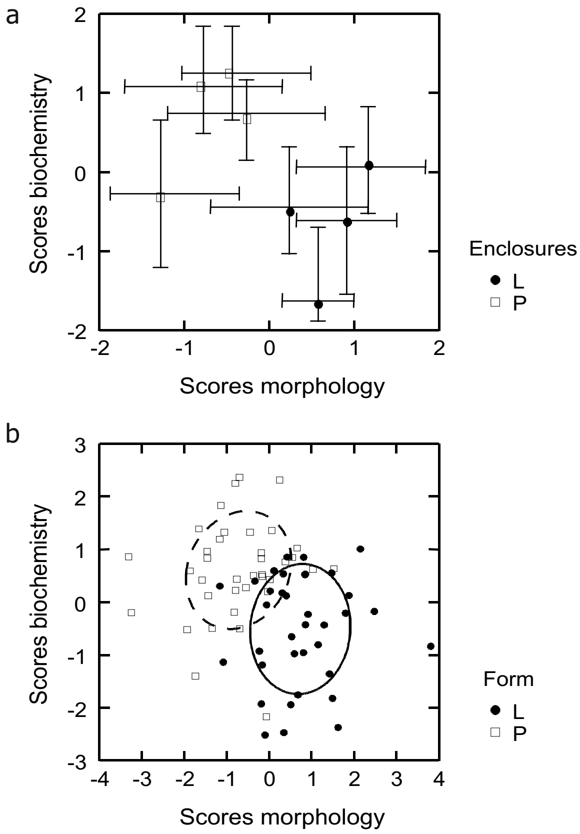

Figure 4. Distribution of biochemical and morphological discriminant scores: a – between enclosures (mean ± SD) and b – for littoral (- - - -) and pelagic (—–) juvenile brook charr (1+) from Lake Ledoux (tension of ellipses was set to 0.5).

slow and precise manoeuvring in a complex habitat and to feeding on benthic organisms (Gatz 1979, Webb 1984). A similar relationship between the length of the pectoral fin and the foraging behaviour was found in other freshwater fishes, such as pumpkinseed sunfish (Ehlinger 1990) and Arctic charr (Malmquist et al. 1992), suggesting a strong functional relationship between pectoral fin size and feeding style. Apart from the differences in pectoral fin length, the other morphological descriptors had little significance for group discrimination. However, taken together, the pattern of canonical scores indicated the presence of two forms with a high degree of overlap (Figure 4). This high overlap could indicate that the diversification between littoral and pelagic brook charr is recent in this system and more subtle than observed in other sympatric pairs of northern freshwater fish (e.g., Schluter & McPhail 1993, Taylor & Bentzen 1993a,b, Snorrason et al. 1994, Pigeon et al. 1997). Dynes et al. (1999) studied the microsatellite DNA of littoral and pelagic brook charr in two lakes of the same system (Bondi and Ledoux). While they found evidence of microsatellite differentiation between forms in Lake Bondi, the genetic structure parameters revealed that the degree of divergence was low.

Relationship between physiological performance and morphology

The morphological differences between littoral and pelagic brook charr from Lake Ledoux seem to be stable since they have been observed in four different studies to date (Bourke et al. 1999, Dynes et al. 1999, Marchand 2001, this study). To state that morphological differences between littoral and pelagic individuals represent an adaptation to different resources implies that particular morphotypes have higher foraging ability and thus higher fitness in their respective niche. One should also be able to find partial correlation between morphological descriptors and surrogates of fitness, like growth and proximate tissue composition, to assess the relationship between form and function (Winemiller 1991, Wainwright 1996, Robinson et al. 1996). The marginally significant correlation between biochemical and morphological discriminant scores support the idea that morphological descriptors are related to physiological performance in 1+ brook charr. The weak correlation between biochemical and morphological discriminant scores may also be related to the fact that diversification between littoral and pelagic brook charr is recent in this system.

Conclusion

Our study investigated the performance of littoral and pelagic individuals in only one habitat, the open-water zone. In this context, our results only provide indirect evidence that trophic diversification is adaptive in brook charr from Lake Ledoux. We found that individuals of both forms differ in morphology, especially in a character related to benthic foraging (pectoral fin length), and that when restricted to feeding in the pelagic zones, littoral individuals exhibited lower physiological performance than pelagic ones based on a comparison of their proximate tissue composition. Furthermore, the physiological performance of individuals was marginally correlated to their morphology.

This study is one of the first field attempts to relate differences in trophic morphology to physiological performance. The proximate composition of a fish is probably the first indicator of change in environmental conditions and thus represents a good index for investigating variations in foraging success. Further studies will have to investigate these relationships with a complete reciprocal transplant experimental design, looking at the performance of littoral and pelagic individuals in both habitats.

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