

Differential time budgets of two forms of juvenile brook charr in the open-water zone

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No significant differences were found in the time budget (time spent in feeding, moving and stationary), attack rate (number of feeding bouts min^{-1}), and microhabitat use of juvenile (1+ years) littoral and pelagic brook charr *Salvelinus fontinalis* at 2 and 4 m depth, when restricted to feeding in pelagic enclosures. In contrast, fish of the littoral form allocated significantly more time than pelagic ones to feeding, moving and in total activity at 3 m depth. No significant differences were found in attack rate between the two forms at any given depth. Based on the mean for the water column (all depths pooled), however, fish of the littoral form executed a significantly higher attack rate than fish of the pelagic one. In multiple regressions analyses, the best predictors of time allocated to feeding and attack rate were the dummy variable 'form' (littoral individuals spend significantly more time in feeding than pelagic ones), light intensity at the surface (negative) and water temperature (positive), and explained 48 and 55% of these variations, respectively. Time allocated to moving was only explained by water temperature (negative) and explained 43% of the variation. Time in a stationary position was best explained by water temperature (negative) and light intensity at the surface (positive), explaining 52% of the variation. The results of this study support the hypothesis that littoral brook charr spend more energy in foraging than pelagic ones when restricted to feeding in the pelagic habitat, and thus that trophic diversification is adaptive in this species.

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Key words: activity; attack rate; behaviour; foraging; time budget; trophic polymorphism.

INTRODUCTION

Trophic polymorphism appears to be common in fishes inhabiting lakes of the northern latitudes (Skúlason & Smith, 1995; Robinson & Parsons, 2002). These lakes offer two primary functional habitats, the littoral and the pelagic zones, and studies reporting on trophic polymorphisms almost always include coexisting benthic and pelagic forms (Robinson & Wilson, 1994). These forms have been observed to partition available resources by developing specific local adaptations to different habitats such as variation in spatial distribution, morphology and feeding habits (Skúlason & Smith, 1995; Jonsson & Jonsson, 2001; Adams & Huntingford, 2002a; McKinnon & Rundle, 2002; Robinson &

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Parsons, 2002). There are essentially two kinds of trophic polymorphism in fishes; one involves sharp differences between forms (or morphs), while the other is much more subtle and can only be detected with accurate measurements and statistical analyses. Landlocked Arctic charr *Salvelinus alpinus* (L.) is a good example of sharp polymorphism, which some times exhibit four coexisting morphs (Jonsson & Jonsson, 2001) while pumpkinseed *Lepomis gibbosus* (L.) can be trophically polymorphic, with a planktivorous and a benthic form, exhibiting more subtle differences (Ehlinger & Wilson, 1988; Robinson *et al.*, 1993). Whether they are subtle or sharp, intraspecific differences in morphology and behaviour of individuals seems to be adaptive because there is evidence that each form of a given population is better adapted than the other to forage in its own niche (*e.g.* benthic form in the littoral habitat and pelagic form in the open water habitat; Snorrason *et al.*, 1989; Ehlinger, 1990; Skúlason *et al.*, 1993; Robinson *et al.*, 1993; Robinson & Wilson, 1994; Schluter, 1994, 1995; Skúlason & Smith, 1995; Adams & Huntingford, 2002*b*; McKinnon & Rundle, 2002; Proulx & Magnan, 2002; Robinson & Parsons, 2002).

Brook charr *Salvelinus fontinalis* (Mitchill) exhibit a subtle trophic polymorphism in lakes of the Canadian Shield, where some individuals are specialists better adapted to feeding in the littoral habitat whereas others are specialists better adapted to feeding in the pelagic habitat (Venne & Magnan, 1995; Bourke *et al.*, 1997, 1999; Dynes *et al.*, 1999; Proulx & Magnan, 2002). Individual differences in habitat preference of fish were related to functional differences in body morphology (Bourke *et al.*, 1997; Dynes *et al.*, 1999; Proulx & Magnan, 2002); pelagic individuals are more fusiform and have shorter pectoral fins than littoral ones. These characteristics minimize drag and allow for efficient cruising (Gatz, 1979; Webb, 1984) which may improve searching and feeding on dispersed and mobile prey, like zooplankton in open water. Longer pectoral fins are associated with slow and precise manoeuvring required to feed in structurally more complex habitats and feeding on benthic organisms (Gatz, 1979; Webb, 1984). The analysis of stomach contents data of 3776 brook charr captured in 69 lakes showed that the proportion of each form in a given lake is related to the intensity of intraspecific competition (Bourke *et al.*, 1999). Bourke *et al.* (1997) showed that two groups belonging to the same population may select different spawning grounds. In another lake, genetic data (microsatellites) also suggested that the pelagic and littoral forms are two populations with partial reproductive isolation and non-random mating (Dynes *et al.*, 1999). Proulx & Magnan (2002) showed that trophic diversification is adaptive in brook charr because littoral individuals exhibited lower physiological performance (proximal tissue composition) than pelagic ones when restricted to feeding in the pelagic zone.

The objective of the present study was to compare time budgets and microhabitat use of littoral and pelagic brook charr when restricted to feeding in pelagic enclosures. Based on the assumption that observed differences in morphology and behaviour of the two forms are adaptive, it was hypothesized that littoral individuals will behave differently and spend more time in foraging than pelagic ones, in the pelagic habitat. A portable underwater camera system used in a series of pelagic enclosures allowed the behaviour and time budget of littoral and pelagic brook charr at different depths and on a gradient of semi-natural conditions to be quantified.

MATERIALS AND METHODS

STUDY SITE AND EXPERIMENTAL SET-UP

The experiments were carried out in Lac Des Grives, Mastigouche Reserve, 120 km north of Trois-Rivières, Québec, Canada (46°38' N; 73°15' W). This lake is a small oligotrophic temperate lake with respect to area (4 ha), maximum depth (6.0 m), Secchi disk transparency (1.7 m), dissolved oxygen (8.75 mg l⁻¹) and thermal stratification. The lake contains populations of brook charr and northern redbelly dace *Phoxinus eos* (Cope). The field experiments were conducted in eight experimental enclosures (3 × 4 × 5 m deep; 9.5 mm mesh size) anchored in the pelagic habitat of the lake in summer 1998. These enclosures allowed water and zooplankton to flow through freely. Zooplankton was the only available prey for fish inside the enclosures. Each enclosure had a net cover to prevent predation by birds.

EXPERIMENTAL FISH

Fifty fish of the pelagic form and fifty fish of the littoral form were captured in Lac Ledoux Mastigouche Reserve, Québec, Canada (46°38' N; 73°15' W). Fish from Lac Ledoux were used because recent studies showed the existence of the two forms (Bourke *et al.*, 1997, 1999; Dynes *et al.*, 1999; Proulx & Magnan, 2002). Individuals were captured with six multifilament gillnets (1.5 × 10 m; 2.5 cm stretched mesh) set in the pelagic and littoral habitats. Nets in the littoral habitat were set within 5 m from shore and in <2 m depth. Nets in the pelagic habitat were set at the surface and bottom of the water column, in the deepest section of the lake. This procedure has been used in other studies and allowed accurate separation of the forms (Venne & Magnan, 1995; Bourke *et al.*, 1997; Dynes *et al.*, 1999; Proulx & Magnan, 2002). Nets were checked every 10 min and brook charr (1+ years of age) were kept in holding enclosures. Fish were transferred to Lac Des Grives and kept in separate enclosures for a 2 week acclimation period. In order to confirm that fish used in the experiments were representative of each form (Bourke *et al.*, 1997, 1999; Dynes *et al.*, 1999; Proulx & Magnan, 2002), a sub-samples of eight littoral and seven pelagic fish were used for morphological measurements. The other individuals were used for laboratory experiments. Fish mass (M , ± 0.01 g), total length (L_T), body height, pectoral length, head height and head length (± 0.01 mm) were measured using a digital calliper. A condition index (K) was calculated from $K = 100 ML_T^{-3}$.

The experiments were carried out in Lac Des Grives, located 10 km south to Lake Ledoux, because it was more accessible and closed to sport fishing for the experiments. Lake Des Grives is comparable to Lake Ledoux with respect to the above characteristics.

EXPERIMENTAL PROCEDURES

Time budgets of littoral and pelagic brook charr were estimated by filming simultaneously individuals of each form, inside two different pelagic enclosures, with two portable underwater camera systems (Boisclair, 1992; Marchand & Boisclair, 1998). Seventeen filming sessions were completed over the summer ($n = 6, 6$ and 5 at $2, 3$ and 4 m depth, respectively, between June and August). Ten experimental brook charr (1+ years) from each form were used for each experiment (mean $L_T \pm$ s.d. littoral: 20.6 ± 2.3 cm; pelagic: 20.8 ± 1.3 cm). One year-old (1+) brook charr from these lakes can be easily identified from size frequency distributions (Magnan & FitzGerald, 1983). Individuals were randomly sampled from the first holding enclosure, transferred to the experimental one and then returned to a second holding enclosure at the end of the experiment. After the 50 experimental fish of a given form were used from the first holding enclosure, fish from the second holding enclosure were sampled for the next experiment. Given this procedure, the same fish was used a mean of 3.4 times during this study. Both forms were acclimated for 3 days before each experiment in separate experimental enclosures. Each experiment consisted of: (1) filming simultaneously in two enclosures, brook charr of each form at a specific depth (*i.e.* 2, 3 or 4 m) for three 1 h periods, to

evaluate their time budget; (2) sampling zooplankton biomass beside the two enclosures at the depth of filming; (3) recording water temperature and oxygen concentration at the three depths and light intensity at the surface; (4) estimating water transparency, cloud cover and precipitation.

FISH TIME BUDGET

On each experimental day, a total of three 1 h periods of filming was taken (at 0600, 0900 and 1200 hours or at 1200, 1500 and 1800 hours). For each filming session, the depth of filming was set at 2, 3 or 4 m. Each hour of filming was then analysed by recording the number of seconds when fish were moving (*i.e.* when fish were observed swimming), feeding (*i.e.* when fish were observed initiating a feeding bout, each attempt being fixed to a duration of 1 s), and in a stationary position (*i.e.* when fish were observed in a stationary position in the water column without travelling). All behaviours were expressed in 'fish-seconds'. A total time budget was estimated by the summation of all observed behaviours. As the fish were feeding only when moving and as the time moving differed between the two forms, an attack rate (AR) was also computed estimated as the number of attacks (*i.e.* feeding bouts) divided by the total number of seconds when fish were seen swimming, times 60, which corresponds to a number of attacks min^{-1} of swimming.

ZOOPLANKTON BIOMASS

Zooplankton was collected beside the two enclosures on each hour of filming using a 2.21 Van Dorn plankton sampler at the depth corresponding to the video cameras. Mean zooplankton biomass was estimated from three replicates. Zooplankton biomass was not estimated inside the enclosure in order not to disturb or modify the behaviour of fish. Previous experiments carried out with the same enclosures showed that zooplankton biomass did not differ inside and outside the enclosures (Héroux, 1998; Marchand *et al.*, 2002). Samples were preserved in a 25% ethanol solution, filtered on pre-weighed (± 0.05 mg dry mass) 1 μm pore fibreglass filters and dried at 60°C for a 6 h period. Filters were then weighed (± 0.05 mg dry mass) for the estimation of the zooplankton biomass ($\text{mg dry mass l}^{-1}$).

ENVIRONMENTAL CONDITIONS

Water temperature ($\pm 0.5^\circ\text{C}$) and oxygen concentration ($\pm 0.1 \text{ mg l}^{-1}$) were estimated using an oxymeter (YSI Model 54) on each hour of filming. Light intensity (expressed in lx) was estimated using a photometer (Pose meter, Sekonic Model L-28 C2) at the water surface, under the net cover of the enclosure. Water transparency was estimated using a Secchi disk. Cloud cover was expressed on a per cent scale (*i.e.* 0, 25, 50, 75 or 100%) and occurrence of rain was noted as a binary variable (*i.e.* 0 or 1).

STATISTICAL ANALYSES

A Wilcoxon two sample test was used to test for differences in time allocated to each behaviour and AR between the two forms, at each depth strata. Stepwise multiple linear regressions were made with each behaviour as the dependent variable: time allocated to feeding, moving, remaining stationary and AR. The multiple regression analysis was more powerful than the single Wilcoxon two sample test because it used all observations of each behaviour studied and several independent variables (not only depth strata). Collinearity between independent variables (*i.e.* form, light intensity, water temperature, oxygen concentration, depth, cloud cover, Secchi disk and occurrence of rain) was estimated by examination of the pairwise correlation coefficients. When collinearity occurred, each variable was used to build a separate model that was then compared with the other models. Residual scatterplots, normal probability plots (Tabachnick & Fidell, 1983) and partial residual plots (Larsen & McCleary, 1972) were used to

determine if assumptions of the multiple linear regression were satisfied (*i.e.* normality, linearity and homoscedasticity of residuals). When these conditions were not fulfilled, transformations were applied to the data (Montgomery & Peck, 1982). All behaviour estimates were \log_{10} -transformed (*i.e.* time allocated to feeding, moving and in a stationary position) and AR was arcsine transformed to normalize the residuals and reduce their heteroscedasticity. The form was entered as a dummy variable (0 was attributed to the littoral fish and 1 to the pelagic fish) as well as the occurrence of rain (0 was attributed to experiments with no rain and 1 to experiments with rain). The dummy variable form was selected together with light intensity and water temperature in the multiple regression model explaining AR. The effect of light intensity and water temperature on the behaviour of the two forms was thus examined with simple linear regressions and covariance analysis. All analyses were done with the Statistical Analysis System (SAS, 1990) software.

RESULTS

BIOTIC AND ABIOTIC FACTORS

Mean water temperature ranged between 8.2 and 15.4°C and decreased significantly from 2 to 4 m depth (Table I). Oxygen concentration ranged from 8.2 to 9.4 mg l⁻¹ and was significantly higher at 2 m depth than at 3 m, the concentration at 4 m being intermediate (Table I). Mean zooplankton biomass ranged from 0.017 to 0.025 mg dry mass l⁻¹ and decreased significantly from 2 to 4 m depth, with the biomass at 3 m depth being intermediate (Table I). Light intensity at the water surface ranged from 9.7 to 61.4 lx with a mean at 38.8 ± 15.1 lx for the duration of the study. Water transparency ranged between 1.4 and 1.8 m with a mean at 1.6 ± 0.12 m while cloud cover varied between 0 and 100% with a mean at $60 \pm 37\%$ for the duration of the experiments.

FISH MORPHOLOGY

Mean fish mass and L_T were not significantly different between both forms (Table II). Littoral individuals, however, had significant higher K , ratio of head height: head length and longer pectoral fins than pelagic ones (Table II).

FISH TIME BUDGET

No systematic variations with time were observed in fish behaviour. Furthermore, no significant differences were observed between the two forms in any of

TABLE I. Mean \pm S.D. water temperature, oxygen concentration and zooplankton biomass in pelagic enclosures. Means with different letters are significantly different as determined by an ANOVA followed by a Tukey multiple sample comparison test ($P < 0.05$)

Water depth (m)	<i>n</i>	Water temperature (°C)	Oxygen Concentration (mg l ⁻¹)	Zooplankton biomass (mg dry mass l ⁻¹)
2	6	15.4 \pm 0.4 ^a	9.4 \pm 1.6 ^a	0.025 \pm 0.010 ^a
3	6	11.9 \pm 0.4 ^b	8.2 \pm 1.7 ^b	0.020 \pm 0.007 ^{ab}
4	5	8.2 \pm 0.4 ^c	8.8 \pm 1.6 ^{ab}	0.017 \pm 0.004 ^b

TABLE II. Mean \pm S.D., mass, total length, condition index, adjusted pectoral fin length, ratio of head height : head length of littoral and pelagic brook charr

	<i>n</i>	Mass (g)	L_T (cm)	K	Adjusted length of pectoral fin (mm)	Ratio head height : head length
Littoral	8	85.3 \pm 38.4	20.6 \pm 2.3	1.2 \pm 0.2	27.1 \pm 0.5	0.73 \pm 0.04
Pelagic	7	69.5 \pm 11.5	20.8 \pm 1.3	1.0 \pm 0.1	26.4 \pm 0.2	0.69 \pm 0.02
<i>P</i>		0.31	0.81	0.03	0.018	0.04

the behaviours studied at 2 and 4 m depth (Table III). In contrast, littoral fish allocated significantly more time than pelagic ones to feeding, moving and in total activity at 3 m depth (Table III). No significant differences in AR between the two forms at any given depth (Table III) were found. Based on the mean for the water column (all depth pooled), however, fish of the littoral form executed a significantly higher attack rate than fish of the pelagic form (littoral: 1.20 ± 1.93 ; pelagic: 0.18 ± 0.31 ; ANOVA, d.f. = 1 and 32, $P < 0.03$). No aggressive behaviours were observed among experimental fish in the enclosures.

Correlations were found between depth, water temperature and zooplankton biomass, between zooplankton biomass, water temperature, oxygen concentration, light intensity at surface and Secchi disk, and between light intensity at surface and oxygen concentration. These independent variables were not considered simultaneously in regression analyses. The best predictors of time allocated to feeding were the dummy variable form (littoral *v.* pelagic), light intensity at water surface (negative) and water temperature (positive), and they explained 48% of the variation (Table IV). The sign of coefficients indicate that littoral individuals spend significantly more time in feeding than pelagic ones (Table IV). Furthermore, light intensity was negatively related and water temperature positively related to this response variable (Table IV).

The best predictor of time allocated to moving was water temperature (negative) which alone explained 43% of the variation (Table IV). The best predictors of time allocated in a stationary position were water temperature (negative) and light intensity at the surface (positive) and they explained a total of 52% of the variation (Table IV). The best predictors of AR were the dummy variable form (littoral individuals executed significantly more time in feeding than pelagic ones), light intensity at the surface (negative) and water temperature (positive), and explained 55% of the variation (Table IV). The slopes of the relationships between AR and water temperature, and between AR and light intensity were significantly higher in littoral than in pelagic individuals (Fig. 1; (a) $P < 0.01$, (b) $P < 0.0001$).

DISCUSSION

FISH MORPHOLOGY

The results of this study support the existence of littoral and pelagic individuals in brook charr inhabiting lakes of the Canadian Shield, identified by

TABLE III. Mean \pm s.d., time allocated to moving, feeding (in a stationary position) and total activity of littoral and pelagic brook charr, and attack rate number, at 2, 3 and 4 m depth in pelagic enclosures

	Water depth (m)	<i>n</i>	Moving (number of fish s ⁻¹)	Feeding (number of fish s ⁻¹)	Stationary position (number of fish s ⁻¹)	Total activity (number of fish s ⁻¹)	Attack rate (number min ⁻¹ of swimming)
Littoral	2	6	241.5 \pm 133.4	10.5 \pm 11.6	22.8 \pm 27.2	274.0 \pm 160.2	2.38 \pm 2.22
Pelagic	2	6	270.2 \pm 135.9	2.8 \pm 4.2	123.3 \pm 236.7	396.3 \pm 279.2	0.46 \pm 0.38
<i>P</i>			0.87	0.23	0.50	0.42	0.12
Littoral	3	6	603.0 \pm 488.6	5.2 \pm 9.3	2218.2 \pm 4494.4	2826.0 \pm 4939.3	1.05 \pm 1.98
Pelagic	3	6	193.3 \pm 92.4	0.2 \pm 0.4	13.2 \pm 21.9	206.6 \pm 96.0	0.05 \pm 0.13
<i>P</i>			0.03	0.05	0.18	0.03	0.10
Littoral	4	5	1034.6 \pm 567.2	0.2 \pm 0.4	5111.2 \pm 6350.7	6146.0 \pm 6553.0	0.01 \pm 0.04
Pelagic	4	5	1010.8 \pm 423.8	0.2 \pm 0.4	12684.8 \pm 17260.2	13695.8 \pm 17591.9	0.01 \pm 0.02
<i>P</i>			0.75	0.99	0.3403	0.34	0.88

TABLE IV. Best predictive models of feeding, moving, in a stationary position, total activity and attack rate from biotic and abiotic factors measured. The estimates, the probability associated with each independent factor, the s.e. of the coefficients, the r^2 associated with the model, the adjusted r^2 , and the s.e. of the estimate (S_{xy}) are given

Dependent variable	Independent variable	Estimates	$P > t$	s.e.	r^2	Adjusted r^2	S_{xy}
Feeding	Intercept	+0.14			0.48	0.44	0.32
	Form	-0.28	0.02	0.12			
	Light intensity at surface	-0.12	0.007	0.04			
	Water temperature	+0.06	0.005	0.02			
Moving	Intercept	+3.56			0.43	0.41	0.21
	Water temperature	-0.084	0.0001	0.01			
Stationary position	Intercept	+4.95			0.52	0.49	1.02
	Light intensity at surface	+0.22	0.11	0.13			
	Water temperature	-0.33	0.0001	0.06			
Attack rate	Intercept	+0.02			0.55	0.50	0.05
	Form	-0.047	0.01	0.017			
	Light intensity at surface	-0.027	0.002	0.006			
	Water temperature	+0.010	0.002	0.002			

Bourke *et al.* (1997), Dynes *et al.* (1999) and Proulx & Magnan (2002) in Lake Ledoux and other lakes of the same area. The results on fish morphology also show that fish used in the present experiments were representative of each form. Pelagic individuals are more fusiform (lower condition index and ratio of head height: head length) and have shorter pectoral fins than littoral ones. A similar relationship between length of pectoral fin and foraging behaviour was found in other freshwater fishes, such as pumpkinseed (Ehlinger, 1990) and Arctic charr (Malmquist *et al.*, 1992), suggesting a strong functional relationship between pectoral fin length and feeding behaviour in fishes. If a given morphotype can feed more efficiently on a specific resource and thus, it has a higher fitness, morphological differences between littoral and pelagic brook charr could indicate adaptation to different feeding resources.

INFLUENCE OF BIOTIC AND ABIOTIC FACTORS ON FISH TIME BUDGET

Littoral individuals allocated more time to feeding and moving, and in total activity than pelagic ones at 3 m depth in the pelagic enclosures. They also executed a significantly higher AR than fish of the pelagic one, regardless of the depth (*i.e.* mean for the water column). In both forms, the time allocated to feeding and AR were positively related to water temperature and negatively related to light intensity at the surface. Based on differences in slope of the regression analyses (Fig. 1), however, the effect of these two factors were not the same on littoral and pelagic brook charr: littoral individuals allocated more time to feeding and executed more attacks as the water temperature increased

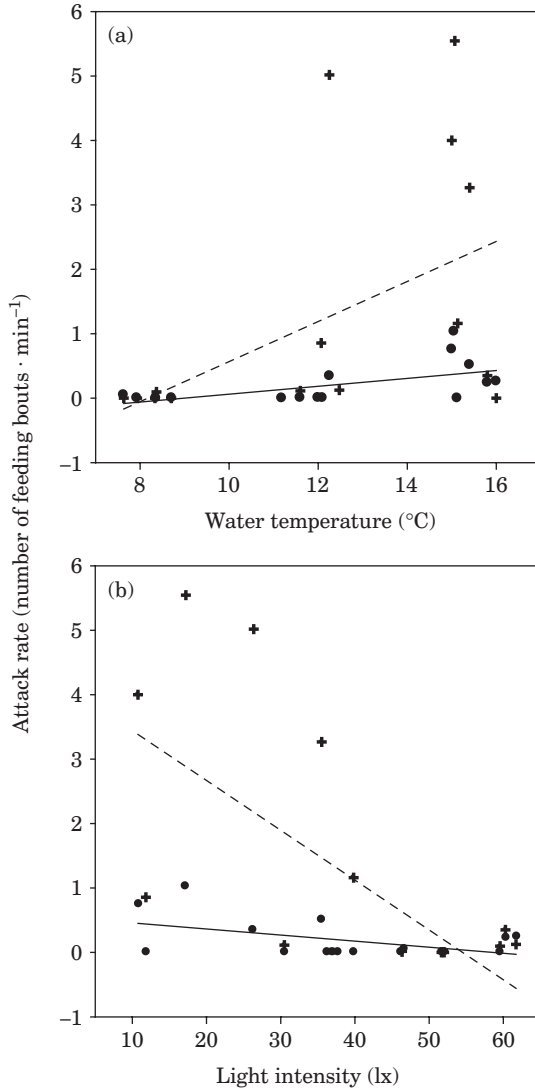


FIG. 1. (a) Simple linear regressions between attack rate and (a) water temperature and (b) light intensity for littoral (+) and pelagic (●) brook charr. The curves were plotted by (a) littoral (---) $y = -2.53 + 0.31x$ ($r^2 = 0.23$, $P < 0.05$) and pelagic (—) $y = -0.54 + 0.06x$ ($r^2 = 0.35$, $P < 0.01$); (b) littoral (---) $y = -4.21 - 0.07x$ ($r^2 = 0.42$, $P < 0.005$) and pelagic (—) $y = 0.55 - 0.01x$ ($r^2 = 0.24$, $P < 0.04$).

and as light intensity decreased, compared to pelagic individuals. The higher feeding activity of littoral compared with pelagic individuals at higher temperatures could be related to their higher acclimation to the warmer littoral habitat. In the same way, the lower feeding activity of pelagic than littoral individuals at lower light intensity could be related to a difference in light intensity between these littoral and pelagic habitats; the structural complexity and shadow areas of the littoral zone offers cover and zones of lower light intensities than pelagic ones. The observed difference in the feeding behaviour of the two forms in the

pelagic zone could thus reflect long-term past experience (e.g. temperature and light intensity) and different adaptation to feed on zooplankton (e.g. morphology).

In contrast to feeding activity, the non-feeding activities (moving and in a stationary position) were inversely related to water temperature, based on the multiple regression analysis. Most of these activities occurred at 3 and 4 m depth, where the mean water temperature ranged between 11.9 and 8.2°C. This result suggests that the experimental fish took refuge in colder temperatures during non-feeding activities. It is known that some fish species select particular temperatures after feeding periods, presumably to optimize their digestion (Brett, 1971; Neverman & Wurtsbaugh, 1994). Such short-term movements from one temperature to another were termed 'behavioural thermoregulation' and should allow a fish to conserve energy, run some metabolic functions (e.g. enzymatic activities) most efficiently, or narrow the range of temperatures to which it must compensate by other means (Hazel, 1993; Moyle & Cech, 2000). Owen & Wiggs (1971) found that extracts of gastric mucosa from brook charr acclimated at 5°C were 30% more active than extracts from those acclimated at 12°C. They found no qualitative differences in proteolytic action but the increased activity would enhance digestion rates in cold acclimated fish (Power, 1980). The range of temperature at which non-feeding activities were observed might thus be related to the optimization of digestive processes in the experimental fish. It would be expected that brook charr would allocate greater time to the moving or stationary states around its final preferendum, near 16°C (Coutant, 1977; Wismer & Christie, 1987). The present results, however, rather suggest that brook charr exhibited behavioural thermoregulation because they spent more time moving or stationary at 8°C than at 12 and 16°C. Biro (1998) observed that brook charr competed for thermal habitat and avoided water temperature near their upper thermal tolerance (c. 20°C). The present experimental fish chose also to spend more time in colder water and made up-and-down movement to the warmer water generally to feed.

The results of this study support the hypothesis that littoral individuals spend more time, and thus probably more energy in foraging than pelagic ones, when restricted to feed in the pelagic habitat. Pelagic individuals would have a higher fitness in the pelagic habitat than littoral individuals because they seem more efficient to feed in this open water habitat due to genetic and environmental factors (e.g. long-term experience to temperature and light intensity).

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