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Trophic polymorphism in brook charr revealed by diet, parasites and morphometrics

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Stomach contents, parasite assemblages and morphometrics were compared in brook charr *Salvelinus fontinalis* from the littoral and pelagic zone of two adjacent lakes on the Canadian Shield. In lac Baie des Onze Îles, fish from the littoral zone had greater abundance of benthic prey in their stomach and were more heavily infected by parasites that use intermediate hosts associated with the littoral zone than fish captured in the pelagic zone. Littoral and pelagic brook charr from this lake also differed in regard to body shape and fin length, with each group being anatomically adapted to exploit their respective habitats. The highly significant correlation between morphometric and parasite canonical scores supports the hypothesis of functional diversification of individuals within lac Baie des Onze Îles. While fish from littoral and pelagic zones of lac Caribou did not differ in terms of diet, parasite assemblages or morphometrics, they were different to fish from lac Baie des Onze Îles in that they were less frequently infected with parasites that use gastropods as intermediate hosts, and had shorter pectoral fins. The inter-lake comparisons suggested that parasite assemblages and morphometrics of brook charr reflected the dominance of the limnetic and littoral habitats in lacs Caribou and lac Baie des Onze Îles, respectively.

Key words: biological indicators; competition; habitat; intermediate host; lake morphometry; population discrimination.

INTRODUCTION

Adaptive processes that contribute to a species' fitness over its whole distribution may operate at the intra- or inter-population level. Among them is polymorphism, which allows a species to broaden its niche, in this way providing alternative paths to face unfavourable environmental conditions (Levins, 1963; Futuyma & Moreno, 1988; Griffiths *et al.*, 1997). With trophic (or resource)

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polymorphism, populations evolve in discrete forms, morphologically better adapted to use the different available niches (Smith & Skulason, 1996).

Previous studies show that brook charr *Salvelinus fontinalis* (Mitchill) exhibit subtle trophic polymorphism in some lakes of the Canadian Shield offering two well-defined habitats, the littoral and the open-water zones (Bourke *et al.*, 1997; Dynes *et al.*, 1999; Proulx & Magnan, 2002, 2004). Pelagic individuals have shorter pectoral fins and are more fusiform (Dynes *et al.*, 1999; Proulx & Magnan, 2004) than littoral specimens. Furthermore, field experiments showed that this diversification is adaptive in terms of proximate tissue composition and physiological performance. When restricted to feeding in the pelagic zones, the mean muscle protein content increased in pelagic individuals but not in littoral ones. Furthermore, during the experiment the lipid contents decreased in littoral individuals but not in pelagic ones. These results suggest that specialists of the littoral zone exhibit lower physiological performance than pelagic ones (Proulx & Magnan, 2002). Even when a population is composed of specialists of different habitats, however, specialists of a given habitat may venture into other habitats (Wilson *et al.*, 1996; Bourke *et al.*, 1997). Moreover, habitat segregation breakdown may occur when food is abundant as reported at the intra-species (Hindar & Jonsson, 1982) as well as at the inter-species level (Harnois *et al.*, 1992). Thus, it is possible that fishes caught in a given habitat may be specialists from another habitat. Consequently, the use of a reliable indicator of habitat use can compensate for the blurring effect of fish movements between habitats. Parasites provide accurate information on their host's environment and have been used for decades as indicators of various aspects of their host's biology, including its habitat and resource use (Williams *et al.*, 1992). The parasitic signature of an individual is therefore an indicator of its habitat selection at some point in time for a period at least as long as the parasites' life span in the fish. Parasites have previously proven to be indicators of niche shift for brook charr cohabitating Canadian Shield lakes with competing fish species (Dubois *et al.*, 1996; Bergeron *et al.*, 1997). Food preferences of brook charr competing with white sucker *Catostomus commersonii* (Lacépède) or creek chub S*emotilus atromaculatus* (Mitchill) shift from benthic to pelagic prey (Magnan, 1988). This shift is reflected in changes in parasite assemblages: brook charr living in sympatry with white sucker (Dubois *et al.*, 1996) and creek chub (Bergeron *et al.*, 1997) have fewer parasites transmitted by benthic intermediate hosts than brook charr living in allopatry.

The present study was conducted in two interconnected lakes of the Canadian Shield. The initial objective was to investigate brook charr resource polymorphism at the intra-lake level using stomach contents, fish parasites and morphometrics as indicators of habitat use. The hypothesis was that littoral and pelagic brook charr would differ in their diet, infection rates and morphology, fish from the littoral zone having more benthic organisms in their stomach contents, being infected more heavily by parasites transmitted in the littoral zone and having a morphology better adapted to feeding on the benthic resource than fish from the pelagic zone. As contrasting results were obtained between the two lakes, inter-lake comparisons were performed afterwards in order to better understand mechanisms that promote resource polymorphism in these populations.

MATERIALS AND METHODS

STUDY LAKES

The study was conducted in Baie des Onze Îles and Caribou lakes (Table I), located in the Parc national du Canada de la Mauricie (PNCLM), Québec, Canada (46°44′ N; 73°07′ W). These adjacent oligotrophic lakes are connected by a navigable shallow channel. Lac Baie des Onze Îles is characterized by many vegetation beds in shallow water along the shoreline and around the numerous islands. Lac Caribou is deeper, with a more limited littoral zone and fewer macrophytes. Brook charr is subject to sportfishing and its exploitation is controlled by the PNCLM. There are no fish species other than brook trout present in both lakes.

FISH SAMPLING

Brook charr were sampled in the littoral (depth <2 m) and pelagic (depth >5 m) zones during summer thermal stratification, in July and August 2001. Fish were captured with multifilament gillnets (38 m long by 1·8 m deep, with stretched mesh-sizes varying between 38 and 100 mm). The gillnets were set perpendicular to the shore in the littoral zone. In the pelagic zone, they were set in order to catch fish within 2 m of the surface. Fish were kept on ice until frozen at −4° C (usually within 6 h). Twenty to 30 brook charr were caught in both zones in the two lakes (hereafter referred to as 'littoral' or 'pelagic' brook charr). The age of fish captured in both lakes ranged from 2 to 4 years. The mean ± S.D. age of littoral and pelagic fish was 2·3 ± 0·5 and 2·5 ± 0·7 years in lac Baie des Onze Îles, and 2·7 ± 0·6 and 2·7 ± 0·6 years in lac Caribou.

MORPHOLOGICAL MEASUREMENTS

After thawing, fish mass (M_T, ±0·1 g), and total length (L_T, ±1 mm) were recorded and 10 morphometric characteristics related to feeding behaviour and swimming habits were measured on the left side of the fish using a digital caliper (Fig. 1; body and lower jaw width not shown). Width of the lower jaw was measured at point of articulation, and body thickness, just anterior to the dorsal fin.

PARASITE ANALYSES

With the exception of blood and nervous systems, all organs and tissues were examined for parasites using a dissecting microscope. Metacercariae encysted in the skin were counted and referred to as 'black spot'. All other parasites found were counted, fixed in 75% ethanol and identified to species or genus. The abundance of parasites was used in statistical analyses while the mean abundance of parasites was used to present the data of each group in tables. Abundance, mean abundance and prevalence are defined according to Bush *et al.* (1997).

STOMACH CONTENTS ANALYSES

The digestive tract contents between the oesophagus and pyloric valve were examined. Prey were identified to family and grouped into functional categories. Furthermore, referring to previous parasitological studies involving brook charr of the same geographical region (Dubois *et al.*, 1996; Bergeron *et al.*, 1997), prey that could serve as intermediate hosts (ephemeropterans, amphipods and copepods) of food-transmitted parasites were grouped into distinct categories. No copepods, however, were found in stomach contents of all fish sampled. Thus, the resulting categories were: prey usually associated with the littoral zone (Ephemeroptera larvae, Ephemeroptera nymphs, Amphipoda and benthos which included Trichoptera and Odonata larvae, Hydrachnidae and

TABLE I. Characteristics of lac Baie des Onze Îles and lac Caribou. Secchi depth, temperature and dissolved oxygen was sampled on 21 August 1997 in lac Baie des Onze Îles and 8 September 1997 in lac Caribou

Lake	Maximum depth (m)	Mean depth (m)	Surface area (ha)	Depth <5 m (% volume of lake)*	Secchi depth (m)	Thermic stratum	Depth (m)	Dissolved O_2 (ppm)
Baie des Onze Îles	23	7·3	140	15	6	Epilimnion	0–6	7·4
						Hypolimnion	11–18	4·3
Caribou	37	13·3	396	4	8	Epilimnion	0–9	9·0
						Hypolimnion	14–30	10·2

*Information was not available for depth <2 m which was considered as the littoral zone.

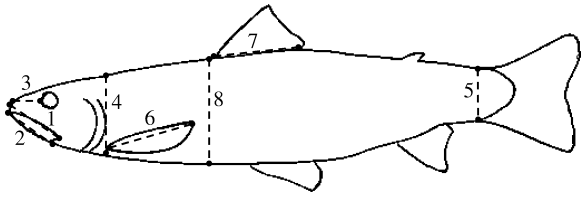

FIG. 1. Characteristic measured on brook charr: 1, upper jaw length; 2, lower jaw length; 3, snout length; 4, head depth; 5, peduncle depth; 6, pectoral fin length; 7, dorsal fin length; 8, anterior body depth.

Mollusca), open water prey (Cladocera, Chaoboridae larvae and Diptera pupae) and prey common to both zones (adult Ephemeroptera and other adult insects which included Hemiptera, Odonata and Coleoptera). Brook charr diet was analysed using the mean per cent dry mass of these categories (Hyslop, 1980).

STATISTICAL ANALYSES

Intra-lake comparisons between littoral and pelagic brook charr, and inter-lake comparisons between brook charr from lac Baie des Onze Îles and lac Caribou were performed for all response variables. *t*-tests or Mann–Whitney *U*-tests revealed that diet, parasite abundances, and host morphometrics did not vary with host sex. Further statistical analyses were therefore performed on pooled fish of both sexes. The mean per cent of littoral prey, open water prey and prey common to both zones (dry mass) was compared between littoral and pelagic fish within each lake and among fish from both lakes using *t*-tests following exclusion of specimens with empty stomachs and arcsin conversion of dry mass percentages. Ephemeropteran dry mass percentages were also compared between the two lakes.

Variation in parasite abundances and fish morphometrics were examined with discriminant function analysis (DFA), after distributions of morphometric characteristics and parasite counts (with the exception of counts for *Echinorhynchus lateralis* and *Salmincola edwardsii*) were brought closer to normality by $\log_{10}$ transformation. *Echinorhynchus lateralis* and *S. edwardsii* were excluded from the DFA and analysed with a non-parametric Mann–Whitney *U*-test. Morphometrics of fish from both lakes, the abundance of *Tylodelphys* sp. in lac Baie des Onze Îles, and the abundance of *Sterliadochona ephemeridarum*, *Eubothrium salvelini*, *Tylodelphys* sp. and black spot in lac Caribou varied significantly with host L_T ($P < 0{\cdot}05$). The effect of fish size on these variables was removed with a regression technique (Fleming *et al.*, 1994). The $\log_{10}$ transformed data were first standardized (mean of 0 and S.D. of 1). Each variable was then expressed as the deviation of individuals (regression residuals) from the pooled within-group regression line describing the relationship between the variable and L_T. These residuals were considered to be approximately independent of fish size and should reflect variation resulting from measurements error and the biological deviation of individuals from the predicted variable and L_T relationship (Kuhry & Marcus, 1977). All statistical analyses were performed using SYSAT, version 8 (Wilkinson, 1998).

RESULTS

INTRA-LAKE COMPARISONS

In lac Baie des Onze Îles, the mean per cent mass of benthic prey found in stomachs of brook charr was significantly higher in littoral than in pelagic individuals (*t*-test, $P < 0{\cdot}05$) (Table II). Benthic prey accounted for 75% of mean per cent mass of stomach contents of littoral individuals and for 46% of mean per

TABLE II. Mean ± S.D. per cent mass of littoral prey, open water prey and prey common to both zones found in stomachs of littoral and pelagic brook charr of lac Baie des Onze Îles and lac Caribou. Fish with empty stomach were excluded from the analysis

		Mean ± S.D. per cent mass of prey			
		Baie des Onze Îles		Caribou	
		Littoral ($n = 23$)	Pelagic ($n = 19$)	Littoral ($n = 22$)	Pelagic ($n = 23$)
Littoral prey	Ephemeroptera larvae	30 ± 32	15 ± 20	34 ± 29	22 ± 27
	Ephemeroptera nymphs	19 ± 25	5 ± 20	5 ± 12	16 ± 24
	Amphipoda	<1 ± 1	<1 ± 1	<1 ± 1	0
	Benthos	27 ± 36	26 ± 33	24 ± 30	10 ± 21
	Total	75 ± 36	46 ± 39	64 ± 32	49 ± 37
Open water prey	Cladocera	11 ± 30	4 ± 10	15 ± 28	10 ± 22
	Chaoboridea pupae	<1 ± 1	18 ± 31	2 ± 4	5 ± 10
	Diptera pupae	1 ± 3	24 ± 32	1 ± 3	11 ± 21
	Total	12 ± 30	46 ± 39	18 ± 28	26 ± 32
Prey common to both zones	Adult Ephemeroptera	5 ± 14	<1 ± 1	5 ± 13	9 ± 18
	Other adult insects	7 ± 20	7 ± 13	13 ± 18	16 ± 24
	Fish	0	0	1 ± 3	<1 ± 1
	Total	13 ± 23	7 ± 13	19 ± 21	25 ± 29

cent mass of stomach contents of pelagic individuals (Table II). The mean per cent mass of zooplankton was significantly higher in stomach contents of pelagic individuals than in littoral ones (*t*-test, $P < 0{\cdot}01$). Pelagic prey accounted for 46% of mean per cent mass of stomach contents of pelagic individuals and for 12% of stomach contents of littoral fish (Table II). No significant difference in prey common to both the littoral and pelagic zones was observed between the two groups ($P > 0{\cdot}05$). In lac Caribou, no significant difference of diet was detected between littoral and pelagic individuals (*t*-test, $P < 0{\cdot}05$).

Seven taxa of parasites transmitted either by feeding or by contact were present in brook charr from both lakes (Table III). All fish sampled were infected with *S. ephemeridarum* (Nematoda) and black spot (Trematoda) (Table III). In addition, all fish collected in the littoral zone of lac Baie des Onze Îles and in the pelagic zone of lac Caribou were infected with *E. salvelini* (Cestoda), which also occurred in ≥90% of the fish from pelagic and littoral zones of lakes Baie des Onze Îles and Caribou, respectively (Table III). *Tylodelphys* sp. (Trematoda) infected >95% of brook charr in both zones of lac Baie des Onze Îles and *Crepidostomum* spp. (Trematoda) infected >95% of fish in the littoral zone of lac Baie des Onze Îles and in the pelagic zone of lac Caribou (Table III). In contrast, prevalences of *E. lateralis* (Acanthocephala) and *S. edwardsii* (Copepoda) varied between 59 and 83% in the two lakes (Table III).

The DFA indicated that differences in parasite abundances in littoral and pelagic fish of lac Baie des Onze Îles were highly significant (Wilk's $\lambda = 0{\cdot}615$, $F_{5,14}$, $P < 0{\cdot}001$; Table IV). The *a posteriori* classification accuracy was high for both groups: 22 of the 27 (81%) littoral individuals and 15 of the 20 (75%) pelagic individuals were correctly reclassified, and overall classification accuracy was 79%. Examination of the standardized canonical coefficients indicated that *Crepidostomum* spp. was the most powerful descriptor separating the two groups, followed by *Tylodelphys* sp. and *S. ephemeridarum*. *Crepidostomum* spp. was almost four times more abundant, while *S. ephemeridarum* as well as *Tylodelphys* sp. were at least two times more abundant in the littoral individuals than in pelagic ones. The distribution of parasite canonical scores illustrate the overlap between littoral and pelagic fish (Fig. 2). The DFA of parasite abundance was not significant in lac Caribou, ($P > 0{\cdot}05$; Table IV). Littoral and pelagic fish did not differ significantly in abundance of *E. lateralis* or *S. edwardsii* in either lac Baie des Onze Îles (Mann–Whitney, both $P > 0{\cdot}05$) or lac Caribou (Mann–Whitney, both $P > 0{\cdot}5$).

Littoral and pelagic fish did not differ significantly in L_T in either lake (*t*-tests, $P > 0{\cdot}05$). The DFA of brook charr morphometrics revealed significant differences between littoral and pelagic individuals of lac Baie des Onze Îles (Wilk's $\lambda = 0{\cdot}562$, $F_{10,36}$, $P < 0{\cdot}05$; Table V). Cross-validation indicated that 19 of the 27 (70%) littoral individuals and 13 of the 20 (65%) pelagic individuals were classified correctly into their appropriate group, and overall classification accuracy was 68%. Examination of the standardized canonical coefficients revealed that the lower and upper jaw length and anterior body depth were the three most powerful morphological descriptors distinguishing littoral and pelagic fish: littoral fish had longer jaws while pelagic fish had deeper bodies (Table V). The distribution of morphometric canonical scores illustrate the overlap between the two groups (Fig. 2). There were no significant morphometric differences, however, between littoral and pelagic fish from lac Caribou ($P > 0{\cdot}05$; Table V).

A significant correlation was observed between the canonical scores (DFA) of parasite abundances and host morphometrics for brook charr from lac Baie des Onze Îles ($r = 0{\cdot}53$; $P < 0{\cdot}001$; Fig. 2). No such correlation was found for brook charr from lac Caribou ($P > 0{\cdot}05$).

INTER-LAKE COMPARISONS

Ephemeropterans accounted for an important part of stomach contents of brook charr from lac Baie des Onze Îles and lac Caribou (Table II). In lac Baie des Onze Îles, 54% of the diet of littoral brook charr and 20% of that of pelagic brook charr consisted of ephemeropterans, including larvae, nymphs and adults. In lac Caribou, this percentage was of 44 and 47% for littoral and pelagic fish, respectively (Table II). Mean mass of ephemeropterans did not differ between fish from both lakes (*t*-test, $P > 0{\cdot}05$). Amphipods were almost absent in stomach contents of all fish sampled (Table II). Mean mass of littoral prey, pelagic prey and prey common to both zones did not differ between fish from both lakes (*t*-test, $P > 0{\cdot}05$).

TABLE III. Life cycle and prevalence of parasites found in littoral and pelagic brook charr from lac Baie des Onze Îles and lac Caribou

Parasite life cycle				Prevalence (%)			
				Baie des Onze Îles ($n = 47$)		Caribou ($n = 47$)	
Parasite	Transmission mode to fish	Intermediate hosts	Final host	Littoral	Pelagic	Littoral	Pelagic
Sterliadochona ephemeridarum (Nematoda)	By ingestion of infected intermediate host	Ephemeropteran[1]	Fish	100	100	100	100
Crepidostomum spp. (Trematoda)	By ingestion of infected second intermediate host	First: sphaeriid clam; Second: ephemeropteran[2]	Fish	96	75	87	96
Tylodelphys sp. (Trematoda)	By contact with the free living infective larval stages	First: gastropod; Second: fish[3]	Piscivorous bird	96	95	65	67
Black spot (Trematoda)	By contact with the free living infective larval stages	First: gastropod; Second: fish[4]	Piscivorous bird	100	100	100	100
Echinorhynchus lateralis (Acanthocephala)	By ingestion of infected intermediate host	Amphipod[5,6]	Fish	59	80	70	71
Eubothrium salvelini (Cestoda)	By ingestion of infected intermediate host	Copepod[7]	Fish	100	90	91	100
Salmincola edwardsii (Copepoda)	By contact with the free living infective larval stages[8]			67	55	83	71

1, Choquette (1955); 2, Choquette (1954); 3, Kennedy (1987); 4, Miller (1942); 5, Richardson (1937); 6, Marcogliese & Cone (1991); 7, Vik (1963); 8, Conley & Curtis (1994).

TABLE IV. Results of the analysis used to compare parasite abundances in littoral and pelagic brook charr from lac Baie des Onze Îles and lac Caribou. *Echinorhynchus lateralis* and *Salmincola edwardsii* were not considered in the discriminant function analysis (see text) but their mean abundances are presented for reference. Mean ± S.D. parasite abundance are presented for littoral and pelagic fish

	Baie des Onze Îles			Caribou		
		Mean abundance (± S.D.)			Mean ± S.D. abundance	
Parasite	Standardized canonical coefficients	Littoral ($n = 27$)	Pelagic ($n = 20$)	Standardized canonical coefficients	Littoral ($n = 23$)	Pelagic ($n = 24$)
Sterliadochona ephemeridarum	0·485	736·1 ± 681·7	339·4 ± 320·8	−0·198	2500·5 ± 1568·0	2416·7 ± 1459·7
Crepidostomum spp.	0·791	24·7 ± 33·0	6·2 ± 7·1	0·368	16·4 ± 20·6	17·9 ± 19·0
Tylodelphys sp.	0·537	11·7 ± 10·8	5·1 ± 4·3	0·102	4·3 ± 5·6	3·7 ± 6·0
Black spot	−0·345	588·9 ± 399·8	655·3 ± 512·6	−0·275	339·0 ± 440·1	271·0 ± 281·1
Eubothrium salvelini	−0·047	14·2 ± 16·8	16·7 ± 19·2	0·869	19·7 ± 19·7	39·8 ± 54·6
E. lateralis		4·7 ± 12·2	3·0 ± 3·1		4·1 ± 6·1	9·4 ± 30·9
S. edwardsii		9·4 ± 11·3	4·6 ± 10·8		14·7 ± 13·6	6·9 ± 10·1

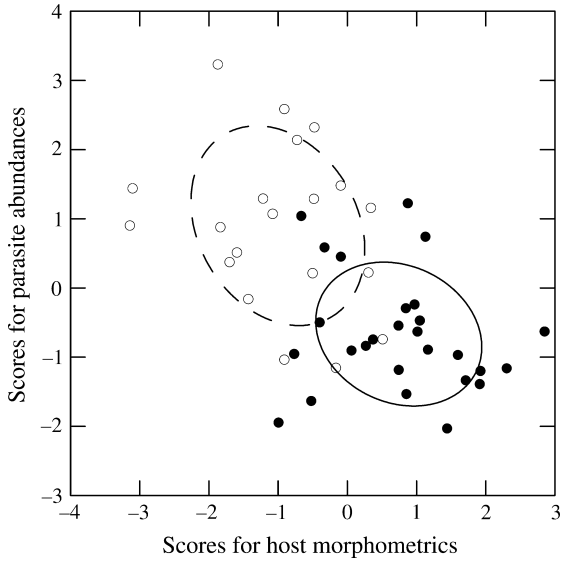

FIG. 2. Distribution of canonical scores obtained from the discriminant function analysis of parasite abundances and morphometrics of littoral (● and ○) and pelagic (—— and - - -) brook charr from lac Baie des Onze Îles (tension of ellipses was set to 0·5).

The DFA of parasite abundance yielded a highly significant difference between fish from lac Baie des Onze Îles and lac Caribou (Wilk's $\lambda = 0{\cdot}416$, $F_{5,88}$, $P < 0{\cdot}001$; Table VI). The *a posteriori* classification correctly identified 42 of the 47 individuals (89%) from lac Baie des Onze Îles and 41 of the 47 individuals (87%) from lac Caribou, and overall classification accuracy was 88%. Examination of the standardized canonical coefficients indicated that *S. ephemeridarum* abundance was the most significant variable in the analysis, followed by *Tylodelphys* sp., black spot and *E. salvelini*. *Tylodelphys* sp. and black spot were almost twice as abundant in fish from lac Baie des Onze Îles than they were in lac Caribou fish. Abundances of *S. ephemeridarum* and *E. salvelini* in lac Caribou fish were approximately four-fold and two-fold greater, respectively than they were in fish from lac Baie des Onze Îles (Table VI). The distribution of parasite canonical scores illustrate the overlap between the two groups (Fig. 3). Fish from the two lakes did not differ significantly, however, with respect to abundances of *E. lateralis* and *S. edwardsii* (both $P > 0{\cdot}05$).

While fish from the two lakes did not differ in regard to L_T (*t*-test, $P > 0{\cdot}05$) DFA indicated a significant difference in the morphometrics of the two populations (Wilk's $\lambda = 0{\cdot}771$, $F_{10,82}$, $P < 0{\cdot}05$; Table VII). Twenty eight of the 47 (60%) fish from lac Baie des Onze Îles and 32 of the 47 (70%) fish from lac Caribou were correctly reclassified, and the overall accuracy of classification was 65%. Canonical coefficients revealed that fish from lac Baie des Onze Îles had longer pectoral fins than fish from lac Caribou (Table VII). The distribution of morphometric canonical scores illustrate the overlap between the two groups (Fig. 3). The correlation between canonical scores (DFA) for parasite abundances and host morphometrics was significant for brook charr from both lakes ($r = 0{\cdot}34$; $P = 0{\cdot}001$; Fig. 3).

TABLE V. Results of the discriminant function analysis used to compare morphometric characteristics of littoral and pelagic brook charr from lac Baie des Onze Îles and lac Caribou. Mean ± S.D. length of morphometric characteristics (± S.D.) were adjusted for fish mean total length (L_T) of 282·2 mm in lac Baie des Onze Îles and 293·5 mm in lac Caribou because morphometric characteristics were related to fish size. Mean ± S.D. length were computed on raw data but statistical analyses were done on transformed data. Fish mean L_T are presented for reference

	Baie des Onze Îles			Caribou		
Morphometric characteristic	Standardized canonical coefficients	Mean ± S.D. length (mm)		Standardized canonical coefficients	Mean ± S.D. length (mm)	
		Littoral (n = 27)	Pelagic (n = 20)		Littoral (n = 23)	Pelagic (n = 24)
Fish mean L_T		278·0 ± 27·4	287·8 ± 33·0		289·8 ± 31·1	297·0 ± 40·0
Upper jaw length	−1·620	32·9 ± 3·1	32·1 ± 2·7	0·417	33·5 ± 3·8	33·2 ± 3·0
Lower jaw length	1·930	38·2 ± 3·4	36·6 ± 2·7	0·011	38·2 ± 3·8	38·1 ± 3·4
Snout length	0·365	14·6 ± 1·5	13·9 ± 1·0	0·464	14·8 ± 1·4	14·8 ± 1·8
Lower jaw width	0·288	20·6 ± 2·8	19·9 ± 3·2	−0·450	21·6 ± 3·4	22·8 ± 4·3
Head depth	0·119	36·6 ± 2·0	36·4 ± 1·8	−1·067	37·3 ± 2·1	38·9 ± 1·7
Peduncle depth	0·804	21·5 ± 1·2	21·2 ± 1·1	0·474	22·6 ± 1·0	22·7 ± 1·1
Pectoral fin length	−0·247	36·1 ± 1·7	36·2 ± 2·1	−0·602	35·9 ± 2·5	36·5 ± 2·7
Dorsal fin length	0·141	27·3 ± 2·3	27·5 ± 2·5	0·199	28·7 ± 1·8	28·7 ± 2·0
Body thickness*	−0·249	32·8 ± 2·9	33·8 ± 2·1	0·131	34·6 ± 2·4	35·1 ± 2·1
Anterior body depth	−1·144	56·5 ± 3·5	58·2 ± 3·8	0·103	59·9 ± 4·8	61·4 ± 3·4

*Body thickness was measured just anterior to the dorsal fin.

TABLE VI. Results of the analysis used to compare parasite abundance of brook charr from lac Baie des Onze Îles and lac Caribou. *Echinorhynchus lateralis* and *Salmincola edwardsii* were not considered in the discriminant function analysis but their mean abundances are presented for reference. Mean ± S.D. abundance were computed on raw data but statistical analyses were done on transformed data

Parasite	Standardized canonical coefficient	Mean ± S.D. abundance	
		Baie des Onze Îles ($n = 47$)	Caribou ($n = 47$)
Sterliadochona ephemeridarum	0·833	567·3 (586·9)	2457·7 (1497·6)
Crepidostomum spp.	0·103	16·8 (26·9)	17·1 (19·6)
Tylodelphys sp.	−0·397	8·9 (9·2)	4·0 (5·7)
Black spot	−0·349	617·1 (447·2)	304·3 (365·1)
Eubothrium salvelini	0·243	15·3 (17·7)	30·0 (42·2)
Echinorhynchus lateralis		4·0 (9·4)	6·9 (22·4)
Salmincola edwardsii		7·3 (11·2)	10·7 (12·4)

DISCUSSION

INTRA-LAKE COMPARISONS

In lac Baie des Onze Îles, the analysis of stomach contents, parasite abundance and morphometrics suggest that some individuals use either the littoral or the pelagic habitat. Fish captured in the littoral zone and the pelagic zone had a higher abundance of littoral prey and open water prey, respectively in

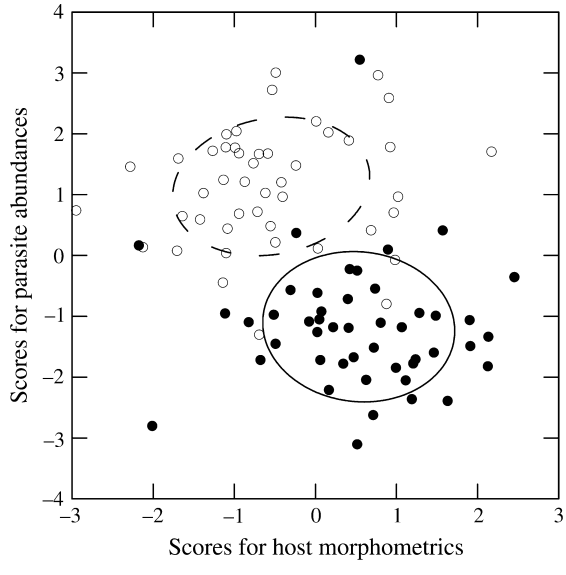

FIG. 3. Distribution of discriminant scores obtained from the discriminant function analysis of parasite abundances and morphometrics of brook charr from lac Baie des Onze Îles (● and ○) and lac Caribou (—— and - - -) (tension of ellipses was set to 0·5).

TABLE VII. Results from the analysis used to compare mean length of morphometric characteristics of brook charr from lac Baie des Onze Îles and lac Caribou (Wilk's $\lambda = 0{\cdot}771$, $F_{10,82}$, $P < 0{\cdot}05$). Mean lengths of morphometric characteristics ($\pm$ S.D.) were adjusted for fish mean length of 287·8 mm because morphometric characteristics were related to fish size. Mean length and S.D. were computed on raw data but statistical analyses were done on transformed data

Morphometric characteristics	Standardized canonical coefficients	Mean $\pm$ S.D. length (mm)	
		Baie des Onze Îles ($n = 47$)	Caribou ($n = 47$)
Upper jaw length	−0·613	33·3 ± 3·0	32·6 ± 3·4
Lower jaw length	0·495	38·4 ± 3·2	37·2 ± 3·6
Snout length	0·052	14·6 ± 1·3	14·4 ± 1·6
Lower jaw width	−0·142	20·8 ± 3·0	21·6 ± 3·9
Head depth	0·034	37·3 ± 1·9	37·3 ± 2·0
Peduncle depth	−0·366	21·8 ± 1·2	22·2 ± 1·0
Pectoral fin length	1·051	36·9 ± 1·9	35·4 ± 2·6
Dorsal fin length	−0·285	28·0 ± 2·4	28·2 ± 1·9
Body width	−0·190	33·9 ± 2·6	34·2 ± 2·2
Anterior body depth	−0·163	58·5 ± 3·7	59·3 ± 4·2

their stomachs. Differences in parasite abundance were also observed. *Sterliadochona ephemeridarum*, *Crepidostomum* spp. and *Tylodelphys* sp. were significantly more abundant in fish captured in the littoral zone than in those from the pelagic zone. The two former parasites use ephemeropterans as intermediate hosts. Ephemeropteran larvae are highly sensitive to low levels of oxygen (Winter *et al.*, 1996; Lowell & Culp, 1999) and will avoid anoxic hypolimnetic waters such as those observed in lac Baie des Onze Îles. *Tylodelphys* sp. uses gastropods, which live in shallow waters (Smith, 2001), as its first intermediate host. Consequently, the two- to four-fold difference between littoral and pelagic brook charr in the abundance of parasites that use mayflies or gastropods as intermediate hosts indicates that littorally caught fish spend more time in the littoral zone than do pelagically caught individuals. Parasites also have been used as indicators of individuals' habitat selection in other fish species such as Arctic charr *Salvelinus alpinus* (L.) (Frandsen *et al.*, 1989; Curtis *et al.*, 1995; Knudsen *et al.*, 1997), bluegill *Lepomis macrochirus* Rafinesque (Wilson *et al.*, 1996) and pumpkinseed *Lepomis gibbosus* (L.) (Robinson *et al.*, 2000; McCairns & Fox, 2004). In every case, fishes were more heavily infected by parasites that use littoral or open-water invertebrates as intermediate hosts, according to their zone of capture.

Littoral and pelagic brook charr from lac Baie des Onze Îles were morphologically different. Littoral individuals had a longer upper and lower jaw, a higher peduncle and a lower anterior body depth than pelagic ones. These differences appear adaptive given the positive relationship established between prey size and mouth size at both the interspecific and intraspecific level (Gatz, 1979; Malmquist, 1992; Huskey & Turingan, 2001). Having a larger mouth, littoral brook charr seem better adapted to exploitation of large littoral

invertebrates. Furthermore, with body depth being greater anteriorly but not as deep at the peduncle, pelagic brook charr have a more fusiform shape than littoral ones. These characteristics might reduce the energetic cost of swimming by minimizing drag (Gatz, 1979; Webb, 1984; Langerhans *et al.*, 2003) which would improve searching and feeding performance on dispersed and mobile prey such as zooplankton in open water.

The highly significant correlation between morphometric and parasite canonical scores supported the hypothesis of functional diversification of individuals within the lake. Extreme phenotypes had a parasitic and morphometric signature characteristic of either the littoral or the pelagic zone. The overlap in the distribution of both parasites and morphological scores, however, suggested that some individuals use both zones. These results were consistent with those obtained by Bourke *et al.* (1997) who used telemetry to show that some brook charr were either littoral or pelagic specialists, while others were generalists using both zones.

The intra-population divergence in two phenotypes observed in lac Baie des Onze Îles contrasts with the absence of divergence in the brook charr population of lac Caribou, where no difference was observed between fish captured in the littoral and the pelagic zones for all response variables. Environmental variation for resources is an essential pre-condition for adaptive divergence (Robinson & Wilson, 1994; Skulason & Smith, 1995; Schluter, 1996, 2000). In many postglacial lakes, this condition is fulfilled by the presence of discrete littoral and pelagic environments. The relatively important surface area and lake volume where depth <5 m in lac Baie des Onze Îles suggested that in that lake two well-developed discrete niches were available unlike lac Caribou which was essentially dominated by the open-water zone. Similarly, Robinson *et al.* (2000) observed that while some pumpkinseed populations exhibit subtle morphological differentiation between littoral and pelagic individuals, divergence was reduced in lakes dominated by large open-water environments favouring one open-water form rather than two specialized forms.

INTER-LAKE COMPARISONS

No difference in fish stomach contents was observed between lakes. In contrast, brook charr from lac Caribou and lac Baie des Onze Îles differed significantly in their parasitic and morphometric characteristics. *Eubothrium salvelini* and *S. ephemeridarum* were more abundant in lac Caribou while *Tylodelphys* sp. and black spot were more abundant in lac Baie des Onze Îles. The high abundance of *S. ephemeridarum* in lac Caribou suggested that this lake supported an important ephemeropteran population. When waters are well-oxygenated, as in lac Caribou (Table I), mayflies are found in the hypolimnion (Lyman, 1943). In such a case, infection by *E. ephemeridarum* will not indicate littoral habitat use as parasite transmission can occur throughout the lake. The elevated abundance of *E. salvelini* in lac Caribou, which used a copepod as its first intermediate host, however, reflected a limnetic-oriented diet. Furthermore, the relatively light infections by *Tylodelphys* sp. and black spot, trematodes that include a gastropod in their life cycles, reflected the limited importance of the littoral habitat in lac Caribou compared to lac Baie des Onze Îles.

The contrasting results obtained between analyses of stomach contents and parasites demonstrated the power of parasites to reflect resource and habitat characteristics. In addition to the information provided by *S. ephemeridarum* about the ephemeropteran population of lac Caribou, the presence of *E. salvelini* and *E. lateralis* in that lake indicated that copepods and amphipods were part of the fish diet while being almost absent in fish stomach contents. Furthermore, the weak overlap of parasite canonical scores of fish from both lakes suggested that there were no fish movement between the two basins and that brook charr belonged to two well-defined populations. Parasites have been successfully used in identification of fish stocks and have corroborated data on stock discrimination based on tagging, genetic, morphometric and meristic measurements (Khan & Tuck, 1995; Melendy *et al.*, 2005; Marques *et al.*, 2006).

Brook charr from lac Baie des Onze Îles had longer pectoral fins than charr from lac Caribou. Long pectoral fins are related to slow and precise manoeuvring required for exploitation of benthic organisms in complex littoral environments (Gatz, 1979; Webb, 1984). Long pectoral fins have been observed on littoral specialists in earlier intra-population studies of brook charr (Bourke *et al.*, 1997; Proulx & Magnan, 2002, 2004; Sacotte & Magnan, 2006). Hence, from an anatomical standpoint, brook charr from lac Baie des Onze Îles were better adapted to a littoral environment than those from lac Caribou.

In conclusion, brook charr exhibited resource polymorphism both at the intra- and inter-population levels. At the intra-population level, stomach contents, parasites and morphometrics revealed differences in habitat selection between littoral and pelagic individuals. Parasites also reflected the role, otherwise undetected, that some aquatic invertebrates played as a fish resource. At the inter-population level, only parasites and morphometrics allowed the differentiation of the two groups. In contrast with parasites, however, the important overlap in the distribution of morphometric scores of fish of both lakes did not suggest the presence of two distinct populations. These results suggest that parasites are very sensitive and more powerful descriptors of individuals' habitat than stomach contents analysis and morphometric characteristics.

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