



Individual variations in habitat use and morphology in brook charr

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(Received 6 February 1997, Accepted 6 May 1997)

The specific objectives of this study were to determine if there is individual specialization in habitat use by lacustrine brook charr *Salvelinus fontinalis* and if so, if specialization is related to fish morphology. Localizations of 28 brook charr equipped with thermosensitive radio-transmitters were recorded during three summers (1991, 1992, and 1993) in two lakes of the Mastigouche Reserve (Québec, Canada). Fifty per cent of the fish were found mainly in the benthic zone (hereafter benthic individuals), 18% in the pelagic zone (pelagic individuals), and 32% travelled regularly between the two zones (generalist individuals). The observed interindividual differences in habitat preference were related to differences in body morphology and coloration: (i) the pectoral fins of benthic and generalist individuals were significantly longer than those of pelagic ones; and (ii) the coloration of the lower flank of benthic and generalist individuals was silver-grey while that of pelagic individuals was red. The results of this study suggest that brook charr inhabiting oligotrophic lakes of the Canadian Shield exhibit trophic polymorphisms, where some individuals are specialists better adapted to feeding in the littoral zone whereas others are specialists better adapted to feeding in the pelagic zone. The potential for reproductive isolation between the two morphs is discussed.

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Key words: trophic polymorphisms; intraspecific competition; trophic morphology; coloration pattern; reproductive isolation.

INTRODUCTION

Individual variability in foraging and habitat use by animals of the same cohort has long been ignored because it was considered as ecological noise around a mean or an optimal response (Ringler, 1983; Lomnicki, 1988). Although individual variability in feeding habits was well described by Ivlev (1961) and Bryan & Larkin (1972), its ecological significance in terms of resource partitioning, optimal foraging, population dynamics and community structure is just recently being recognized (Curio, 1976; Chesson, 1978; Morse, 1980; Dill, 1983; Ringler, 1983, 1985; Ehlinger, 1990). For example, resource partitioning among individuals may allow habitats to support more dense populations than they would otherwise and facilitate survival under marginal conditions (Morse, 1980). Such individual variability often leads to trophic polymorphisms, where morphs of the same species differ in habitat, diet, and morphology, and coexist in sympatry (Robinson & Wilson, 1994; Wimberger 1994; Skulason & Smith, 1995). There is also increasing theoretical evidence that individual variability

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may have significant consequences for population dynamics and community structure (e.g. Lomnicki, 1988; DeAngelis & Gross, 1992; Winkle & Rose, 1993; Tyler & Rose, 1994). On a long-term basis, hereditary factors could maintain different strategies within populations, so that not only the mean value of a trait but also its variation may be adaptive (Maynard Smith, 1982; Lomnicki, 1988).

There are essentially two short-term components of individual variability: the within-individual component, which represents the average resource diversity used by a single individual, and the between-individual component, which represents the resource diversity used by different individuals in a population (Roughgarden, 1972, 1979). In a review of variation in foraging tactics of fishes, Ringler (1983) pointed out that between-individual variability may derive from physiological, behavioural, and morphological sources such as visual acuity, hunger state, experience, learning, social interactions, and critical morphological dimensions, while within-individual variability may be caused by specific physiological states (hunger, acclimation) and behavioural contexts (experience, prey type or distribution, motivation).

In fish, most of the available information on between-individual variability comes from laboratory and mark-recapture experiments (e.g. Bryan & Larkin, 1972; Ehlinger, 1990) and from dead individuals obtained by fishing (e.g. Ivlev, 1961; Venne & Magnan, 1995), while information concerning within-individual variability has been obtained only from laboratory experiments (e.g. Ringler, 1985; Ehlinger, 1989, 1990; McCarthy *et al.*, 1992). It is important to assess the two components of individual variability on free-living fish to estimate their real occurrence in the field, support hypotheses concerning underlying mechanisms and adaptive significance, and document assumptions of individual-based models.

The objective of the present study was to investigate the individual variation in habitat use by brook charr *Salvelinus fontinalis* (Mitchill) in two lakes, using radio-telemetry. As many population-level properties (i.e. age structure, birth and death rate) can be influenced directly by the spatial location of individuals, e.g. through differential resource availability, their habitat use is a key component of population dynamics (Roese *et al.*, 1991). The brook charr is a generalist carnivore (Scott & Crossman, 1974; Power, 1980; Magnan, 1988; Lacasse & Magnan, 1992), which has colonized lakes of the Canadian Shield after the last glaciation. Its morphology allows individuals to feed on the two main functional prey types found in these lakes (i.e. zoobenthos in the littoral zone and zooplankton in the pelagic zone; Tremblay & Magnan, 1991). Thus the brook charr is a good model species for studying individual specialization. The specific objectives of the study were to determine if there is individual specialization in habitat use by brook charr in these lakes and if so, if it is related to fish morphology and spawning site selection.

STUDY LAKES

The study was carried out in Lac de l'Épervier (1991) and in Lac Ledoux (1992, 1993), located in the Mastigouche Reserve (46°38'N, 73°15'W), Québec (Canada). These are typical of small oligotrophic temperate zone lakes with respect to surface area (8.4 and 11.9 ha), mean depth (5.6 and 5.5 m),

TABLE I. Mean fork length of brook charr used in the study and sampling periods for fish localizations

Lake	Year	<i>n</i>	Mean fork length (mm)	S.D. (mm)	Range (mm)	Sampling period	Track duration (days)
Épervier	1991	4	341	18	325–360	29 June to 29 August	59*
Ledoux	1992	11	343	45	250–400	21 July to 30 October	87†
Ledoux	1993	13	389	30	320–419	22 July to 28 October	93

*With the exception of one fish, for which the signal was lost on 8 August.

†With the exception of two fish, for which the signals were lost on 4 and 18 August respectively.

conductivity (18.1 and 21.3 mS cm⁻¹), dissolved oxygen, thermal stratification, and Secchi disk transparency (Magnan, 1988; Lacasse & Magnan, 1992). Brook charr and northern redbelly dace *Phoxinus eos* (Cope) are the only fish species in the lakes. The two lakes are 10 km apart, are subject to sportfishing, and exploitation is carefully controlled by the Québec Government (Magnan, 1988). The lakes were closed to sportfishing during the study.

MATERIALS AND METHODS

MARKING

In June or July of each summer (Table I), 20 adult brook charr (250–419 mm fork length) were tagged with 4-g thermosensitive radio-transmitters (model 357; Advanced Telemetry Systems, ATS, Minnesota, U.S.A.). Fish were captured with experimental multifilament gillnets (1.8 m deep by 38.1 m long, with stretched mesh-sizes of 2.5, 3.8, 6.4, and 7.6 cm) arbitrarily set perpendicularly to the shore, mainly in the littoral zone. Gillnets were removed every 15 min and only fish in good condition, usually those caught by the teeth, were retained for marking.

Transmitters were attached externally under the dorsal fin after the fish were lightly anaesthetized with tricaine methanesulphonate (MS-222). Fixation was made with nylon monofilament threaded through muscular tissues at two points. The transmitter was placed on one side of the fish while on the other side the filament and fixation knot were kept apart from the fish by a small rubber plate (Winter, 1983). A neoprene cushion was placed between the fish and the rubber plate to avoid lesions due to rubbing on teguments. In 1992 and 1993 (Lac Ledoux), the fish were measured and photographed over a ruler before release. In 1991 (Lac de l'Épervier), the fish were kept for 2 h in a holding enclosure (littoral zone) before releasing them into the lake. A total of four fish survived these manipulations in 1991 (Lac de l'Épervier) compared to 11 in 1992 and 13 in 1993 (Lac Ledoux). In 1991, longer manipulations and holding periods in the enclosure were probably more stressful for the fish and thus were responsible for the higher observed mortality. In 1992 and 1993, manipulation time was much reduced by using a cone-shaped needle rendering thread insertion easier, and by eliminating the post-operative holding period. Also, colder water than in 1991 was used in the manipulation basin. The tagging process usually lasted <1 min fish⁻¹. It was assumed that a fish died if it was localized at the same position and temperature for more than 10 days. Based on this criterion, 91% of the mortality occurred within the first day of marking while the rest occurred within the next few days. All of the fish that were alive

after this period were tracked until the transmitter batteries were exhausted. These fish were moving from the day of marking to the end of the tracking periods, suggesting that they were in good condition. Mean fork length of fish and periods of tracking are shown in Table I. The length (mm) of the mouth (anterior end to posterior end of maxilla) and the pectoral fin, height of the caudal peduncle, and eye diameter were obtained from photographs of the left side of the fish taken in 1992 and 1993.

To evaluate quantitatively the apparent link between spatial preferences of individuals and their coloration pattern, five persons were asked to classify individuals from Lac Ledoux (1992–1993) into two distinct groups based on the coloration of their lower flank on photographs; a red group and a non-red group. Then a percentage of correct classification was computed based on the evaluation of the five persons. This classification was compared to the one obtained from the spatial preferences of individual fish.

FISH LOCALIZATION

Individual brook charr were localized on average every 2 days during each sampling period (Table I) using a radio-receiver (model R2000; ATS) equipped with a loop antenna. On each sampling date, the horizontal (x and y) coordinates of each fish were determined during the daylight period (0800 to 1800 hours) by triangulation, using a compass and landmarks spaced regularly around the lakes. Fish depth (z coordinate) was determined by comparing the temperature of the fish surroundings, measured by the thermosensitive transmitter (hereafter ambient temperature), and the thermal profile of the lake measured on the same sampling date. This procedure was sensitive enough to determine if a fish was in the epi-, meta- or hypolimnion. For each fish localization, the lake depth was measured also with a graduated cord to position the individuals more accurately on the bathymetric map. On eight occasions between 1991 and 1993, a total of five to seven individuals were localized every 4 h during complete 24 h cycles.

PRESPAWNING MOVEMENT

At the beginning of the 1992 spawning season, the batteries of nine transmitters were still working. The fish were tracked until they migrated to their spawning sites in three different inlets. The relationship between the spatial preferences of individuals during summer and the selection of a spawning site was evaluated. In 1993, the fish were not yet on the spawning grounds on 28 October. After this period the lake could not be reached due to snow accumulation.

STATISTICAL ANALYSES

The zone where each fish was located was coded using the following method: first, the lake volume was divided according to thermal stratification (epilimnion, metalimnion, and hypolimnion) and then, each stratum was divided into zones associated with the bottom (up to 1 m from the bottom; zones 1 and 2; Fig. 1) and zones associated with the open water (zones 4, 5 and 6; Fig. 1). Zones 1 and 2 will be referred to hereafter as the benthic zone and zones 4, 5 and 6 as the pelagic zone (Fig. 1). Localizations in zones 3 and 7 (Fig. 1) were not considered in the analyses because no fish were localized in zone 7 and only 1% of the 486 localizations were done in zone 3. For each sampling date, fish depth, lake depth, ambient temperature, and thermal profile of the lake were used to ascribe fish to one of these zones.

Only the fish localized during the thermal stratification of the lakes were considered in the analysis of spatial distribution.

Spearman correlation coefficients were computed between each morphological trait (adjusted for fish size; Packard & Broadman, 1988) and the frequency of occurrence (%) of fish in the benthic zone (zone 1 and 2; Fig. 1), to evaluate the relationship between morphological characteristics and habitat use.

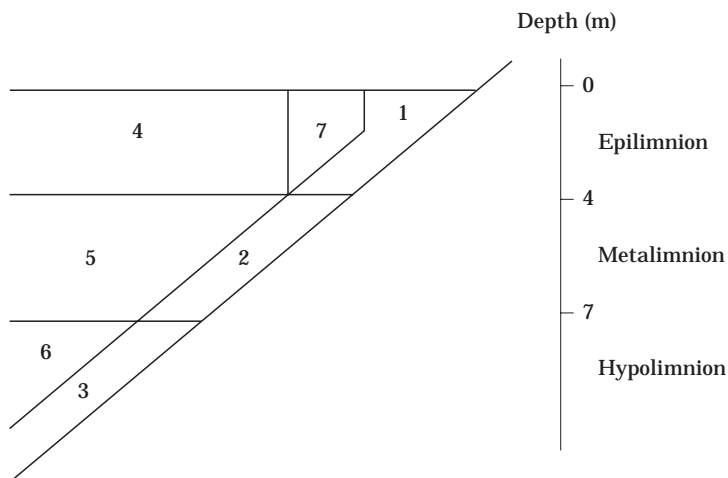


FIG. 1. Classification of the different zones for statistical analyses; 1 and 2: benthic zones; 4, 5 and 6: pelagic zones; 3 and 7: intermediate zones; not included in statistical analyses.

RESULTS

SPATIAL DISTRIBUTION

Individual brook charr were classified arbitrarily as benthic or pelagic, when they were localized over 60% of the time in one of the two zones, and as generalist when they travelled regularly between the two zones. Of the 28 individuals tracked during this study, 14 were benthic, five pelagic, and nine generalist. Benthic individuals were localized in the benthic zone $81.7 \pm 9.7\%$ of the time (mean \pm s.d.), while pelagic individuals were localized in the pelagic zone $68.6 \pm 4.7\%$ of the time. Generalist individuals were found in the benthic zone $48.7 \pm 6.4\%$ of the time (approximately the same time as in the pelagic zone; Fig. 2).

Individuals were much more active during the night (2200–0600 hours) than during the day (1000–1800 hours) according to the distance travelled between two consecutive localizations (night: 26.2 ± 18.7 m h⁻¹; day: 12.4 ± 15.8 m h⁻¹; $n=64$). However, no significant difference was found in the mean distance travelled between two consecutive localizations among benthic, pelagic, and generalist individuals (night: $F=0.02$, $P>0.05$; day: $F=0.96$, $P>0.05$).

Based on the frequency of occurrence of fish in each zone, benthic individuals were more faithful to the benthic zone than were pelagic ones to the pelagic zone ($81.7 \pm 9.7\%$ v. $68.6 \pm 4.7\%$; $F=81.9$, $P<0.0001$).

MORPHOLOGICAL CHARACTERISTICS AND COLORATION PATTERN

The length of the pectoral fin was positively correlated with the occurrence of individuals in the benthic zone (Table II). The adjusted mean length of the pectoral fin of benthic (5.2 ± 0.5 mm) and generalist (4.9 ± 0.4 mm) individuals was significantly higher than that of pelagic ones (4.1 ± 0.5 mm; ANCOVA, $F=6.63$, $P<0.007$). No other morphological characteristics were correlated significantly with the occurrence of brook charr in the benthic zone, including the length of the mouth, which, however, tended to be related to the occurrence of fish in the benthic zone (Table II).

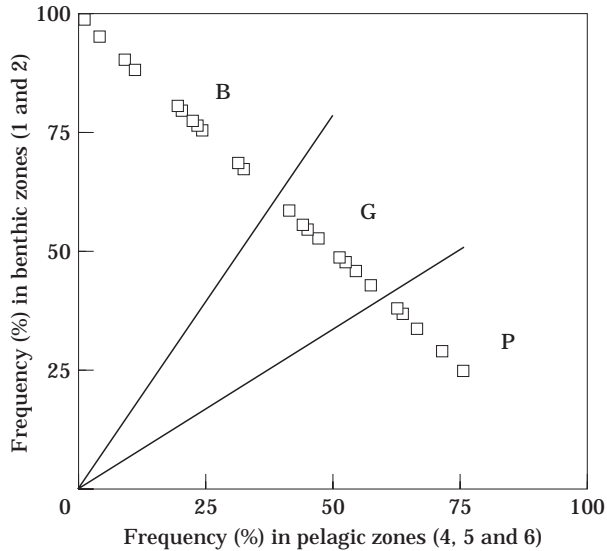


FIG. 2. Frequency of occurrence of the 28 brook charr in benthic (1 and 2) and pelagic zones (4, 5 and 6). B, G, and P represent benthic, generalist, and pelagic individuals, respectively.

TABLE II. Spearman correlations between morphological characteristics and the occurrence of individuals in the benthic zone

Variable	n^*	r	P
Fish length	28	-0.08	0.718
Length of pectoral fin	21	0.64	0.002
Length of mouth	24	0.42	0.056
Height of caudal peduncle	18	0.25	0.390
Eye diameter	22	0.20	0.340

*It was not possible to measure all the characteristics on each fish due to the presence of artifacts on some of the pictures, such as reflection of light on the water surface.

Based on the classification of individuals according to their colour pattern, all of the four pelagic fish were red while all of the 13 benthic fish and six of the seven generalist fish were non-red, for an overall 96% of good reclassification.

PRESPAWNING MOVEMENT

At the end of October 1992, all fish had selected a spawning site (Fig. 3). All the pelagic individuals selected inlet 2, the single benthic individual tracked at this time selected inlet 1, while generalist individuals were found in the three inlets (Fig. 3). Fish number 430, a generalist, did not move to these spawning sites (Fig. 3).

In the weeks preceding the spawning ground selection, four of the nine fish moved among two or the three inlets before selecting one (Fig. 4). For example,

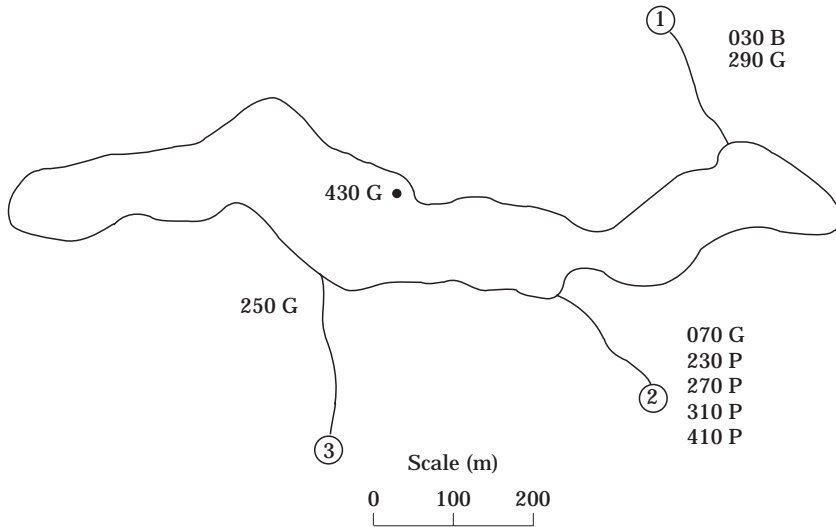


FIG. 3. Localization of individual brook charr in the spawning sites at the end of the sampling period (Lac Ledoux, 1992). Inlets are represented by circled numbers. Each number represents an individual fish. B, G, and P represent benthic, generalist, and pelagic individuals, respectively.

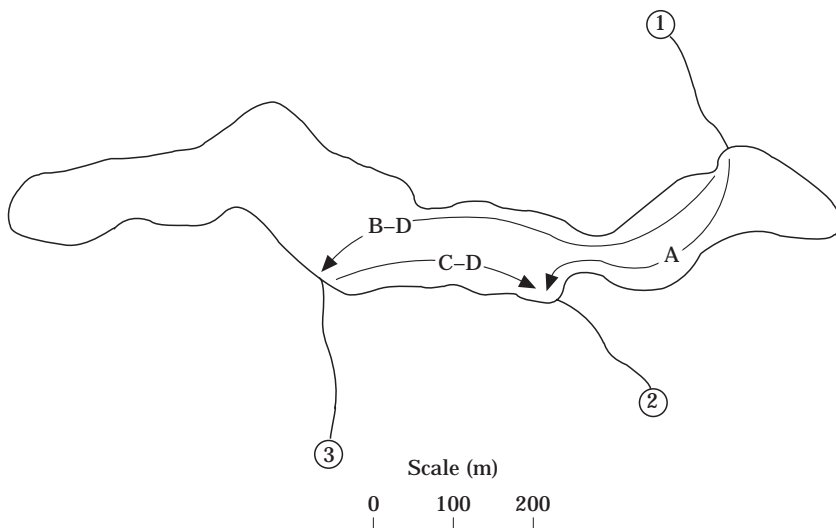


FIG. 4. Selection of spawning sites (Lac Ledoux, 1992). Inlets are represented by circled numbers. Each letter represents an individual fish.

fish number 410 began the prespawning period by visiting inlet 1. Two weeks later, it moved to inlet 3 before selecting inlet 2 at the end of autumn (Fig. 4).

DISCUSSION

The results of this study show interindividual differences in habitat use by brook charr. Fifty per cent of the fish were found mainly in the benthic zone, 18% in the pelagic zone, and 32% travelled regularly between the two zones. The

ecological significance of the three groups identified is reliable because each individual showed a given preference over a minimum of 2 months of tracking. Furthermore, the study was done in two lakes, over three different summers. These interindividual differences in habitat use suggest interindividual differences in resource utilization. Two studies based on gillnet fishing in lakes of the same area support this hypothesis; the diet of 1+, 2+, and 3+ brook charr is related to their spatial distribution between the littoral and pelagic zones (Tremblay & Magnan, 1991), while the diet of 0+ brook charr is related to the distribution of individuals between the littoral and profundal zones (Venne & Magnan, 1995).

The higher proportion of benthic individuals in the present study may be related to ecological factors such as the profitability of littoral habitat. There is evidence that brook charr feed preferentially on benthic organisms of the littoral zone in this system; in allopatry, individuals feed mainly on zoobenthos, while in sympatry with white sucker *Catostomus commersoni* (Lacépède) they shift to feeding on zooplankton in the pelagic zone (Magnan, 1988; Tremblay & Magnan, 1991; Lacasse & Magnan, 1992). As white sucker is absent from lakes Ledoux and de l'Épervier, it is possible that a high proportion of brook charr selected the benthic habitat. Recent *in situ* experiments also suggested that the littoral zone is more profitable than the pelagic zone for brook charr in terms of the net energy intake (J day^{-1}) in each habitat (Héroux & Magnan, unpublished data). Alternatively, the higher proportion of benthic individuals may be due to sampling bias; as the gillnets were effective mainly in the littoral zone (see Materials and Methods) it is possible that more benthic individuals were sampled and then tracked.

The observed interindividual differences in habitat preference were related to differences in morphology and coloration. The pectoral fin of benthic and generalist individuals was significantly longer than that of pelagic ones. Long pectoral fins are related to the slow and precise manoeuvring (Gatz, 1979; Webb, 1984) required to feed on benthic organisms on the bottom, while shorter pectoral fins are associated with cruising, which is necessary for searching efficiently in the open water habitat (Ehlinger, 1990). A similar relationship between length of pectoral fin and foraging behaviour was found for bluegill sunfish *Lepomis macrochirus* (Rafinesque) (Ehlinger, 1990), suggesting a strong functional relationship between pectoral fin morphology and feeding tactics in fishes. Also, as for bluegill sunfish, other differences in morphology related to habitat selection were observed in young-of-the-year brook charr (Venne & Magnan, 1995), suggesting that such functional relationships can occur early in the life history of fishes (Ehlinger, 1990).

The lower flank coloration of benthic and generalist individuals was silver-grey while that of pelagic individuals was red. In fish, red coloration is due mainly to carotenoid pigments (Brush & Reisman, 1965; Fujii, 1993). Carotenoids cannot be synthesized by the fish and must be acquired through the diet (Fujii, 1993). If the spatial distribution of pelagic individuals is correlated effectively with a rich zooplankton diet, their red coloration suggests that there is a high carotenoid content in these pelagic prey. It is known that copepods are a major source of carotenoids (Folstad *et al.*, 1992) but they were found rarely in stomachs of brook charr (Magnan, 1988; Lacasse & Magnan, 1992), suggesting that the red coloration is due to carotenoid contained in other zooplankton found in their

diet, such as cladocerans. It is noteworthy that generalist individuals are similar to benthic ones as regards the length of the pectoral fin and coloration pattern, two traits apparently related to diet. There is evidence that these differences were not related to sexual dimorphism, which is characterized by differences in the general shape of the body (the male body is more compressed laterally and deeper, and has a small kype or hook on the lower jaw) and in fin, jaw and dorsal coloration (Power, 1980). Also, later follow-up samples to this project revealed that 25% of the 12 silver-grey individuals were male and that 29% of the 17 red ones were female (P. East & P. Magnan, pers. obs.). These results may suggest that differential use of space is associated to male/female differences. However, sex dimorphism in coloration could not explain all the variation in spatial segregation among individuals because sex ratio was 1.07 in this sample (as usually found for brook charr in the study area; P. Magnan, pers. obs.).

The results of the present study support the hypothesis that ecotypes of the same species (here benthic and pelagic individuals) may select different spawning grounds. At the beginning of the 1992 spawning season, four of the nine tracked individuals moved among the three identified spawning grounds before finally selecting one. At the end of this spawning season, the four pelagic individuals were found in one inlet, the only benthic individual in another inlet, while three generalists were distributed in the three inlets. The results of O'Connor & Power (1973) support the hypothesis of homing in brook charr in one lake containing two spawning grounds. Because of the small sample size of reproductive individuals in the present study, further work will be needed to evaluate this hypothesis.

Correlations between morphology and specific behaviour of individuals (this study; Grant & Noakes, 1987; Ehlinger & Wilson, 1988; Ehlinger, 1990) address the question of within-individual stability of these behaviours in the field. The present results show that habitat use by brook charr did not reflect frequent and random changes in fish distribution but corresponded instead to relatively stable habitat use in most individuals (i.e. benthic and pelagic). The results also indicated that approximately a third of marked individuals were generalists showing no specific preference for a given habitat. In a mark-release experiment, Bryan & Larkin (1972) studied food specialization of brook charr, cutthroat trout *Oncorhynchus clarki* (Richardson) and rainbow trout *O. mykiss* (Walbaum) in a stream and ponds. Their results showed that the degree of individual specialization was high over short periods of time and that some specialization persisted for over half a year. No striking correlations were found between degree of specialization and individual characteristics such as size, growth rate, or weight and number of food items, previous specialization, and area of capture (Bryan & Larkin, 1972). In a study of foraging movements of recently emerged brook charr in still-water pools, McLaughlin *et al.* (1994) found no correlation between foraging behaviour (sedentary *v.* active fish) and body size or shape of individuals. Although most fish tended to specialize in one role, some individuals clearly switched between the two modes while they were foraging, over the duration of the observations. In another study, McLaughlin & Grant (1994) found significant differences in morphology of recently emerged brook charr foraging in slow- *v.* fast-running water, two more contrasting environments. The results reported above and those of the present study suggest

that differences in morphology, as well as stability of within-individual behaviours, will occur only when available habitats require specific abilities (e.g. fast *v.* slow swimming in streams; slow and precise manoeuvring *v.* cruising in littoral and pelagic zones of a lake). The magnitude of these differences should also be related to the degree of difference among habitats.

The results of this study suggest that brook charr inhabiting oligotrophic lakes of the Canadian Shield exhibit trophic polymorphisms, where some individuals are specialists better adapted to feeding in the littoral zone whereas others are specialists better adapted to feeding in the pelagic zone. This polymorphism is more subtle than the more contrasting one reported for arctic charr *Salvelinus alpinus* L. (Hindar & Jonsson, 1982; Walker *et al.* 1988) and may have evolved in response to intraspecific competition and the availability of an unutilized resource axis, the zooplankton, associated with an empty niche (Robinson & Wilson, 1994; Skulason & Smith 1995). In a recent review, Robinson & Wilson (1994) showed that such trophic diversification is common in species-poor lakes and almost always includes benthic and pelagic forms. In this context, the lake environment can be viewed as a set of non-Hutchinsonian or environmental niches that exist independently from the species that may occupy them (Robinson & Wilson, 1994).

Whether such interindividual differences in morphology and behaviour are of phenotypic or genotypic nature is still unknown. Morphological differences appear very early in the life history of brook charr (McLaughlin & Grant, 1994; Venne & Magnan, 1995) and bluegill sunfish (Layser & Clady, 1987), and the potential for reproductive isolation (as suggested in this study) could maintain underlying genetic variation among individuals. On the other hand, interindividual differences may result from phenotypic variation among individuals (e.g. experience, learning; Ringler, 1983) or by environmental characteristics acting on a single plastic genotype (see Ehlinger, 1990). In this context, morphological differences among individuals may result from different foraging tactics *per se* (like a training effect). The investigation of proximate mechanisms underlying individual variability in trophic morphology and behaviour and the testing of models considering such phenotypic differences among individuals will certainly be featured among the next challenging research problems in animal ecology.

We thank P. East for his help at the time of marking operations, N. Dugas, D. Dumont, P. Hamel, D. Héroux, G. Lacroix, M. Lapointe, P. Laurendeau, S. Veilleux, S. Verville for their field and laboratory assistance; and le ministère de l'Environnement et de la Faune du Québec for logistic support. This research was supported by grants from the Natural Sciences and Engineering Research Council (NSERC) of Canada and le Fonds pour la Formation de Chercheurs et l'Aide à la Recherche (FCAR), Québec Government, to PM, and by a grant from le Fonds de Développement Académique Réseau, Université du Québec (FODAR) to MAR and PM. PB was supported by post-graduate fellowships from NSERC and la Fondation Universitaire du centre du Québec.

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