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The impact of intra- and interspecific interactions on young-of-the-year brook charr, in temperate lakes

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The abundance, growth, spatial distribution, and feeding habits of five allopatric brook charr, *Salvelinus fontinalis*, populations (young-of-the-year, 0+ juveniles; YOY) were compared with five other populations living sympatrically with white sucker, *Catostomus commersoni*. The study was made in oligotrophic lakes of the Laurentian Shield (Québec, Canada) during three sampling periods in 1989 (July, August and September). The abundance of YOY charr was significantly higher in allopatric than in sympatric populations (45·3 ± 3·8 *vs* 3·1 ± 3·8 fish/lake caught in 1773 m^2 of gillnets; $P<0·005$). The mean length of YOY charr did not differ among allopatric and sympatric populations at each sampling period; July: 60·2 ± 3·0 *vs* 60·0 ± 4·5 mm; August: 61·9 ± 4·5 *vs* 63·2 ± 4·1 mm; September: 77·9 ± 8·7 *vs* 77·3 ± 7·8 mm respectively. Horizontal distribution of allopatric YOY charr did not differ from that of sympatric charr, 65% of the fish being captured within the first 2 m depth and the rest between 2 and 7 m depth. In contrast, the vertical distribution of allopatric YOY charr from both communities was significantly different; 81% of allopatric charr were captured within 0·5 m from the substrate compared to 64% for sympatric charr ($P<0·001$). Differences in vertical distribution of the fish were related to differences in diet; allopatric charr fed mainly on benthic and large planktonic organisms whereas sympatric charr fed less on these organisms and more on terrestrial organisms. In the lake where YOY charr were most abundant, individuals were spatially segregated into two groups; one ‘ littoral ’, found in 0–2 m depth, and one ‘ profundal ’, found in 3–6 m depth. Growth, condition, and feeding habits of charr from the two groups were different, especially during the last sampling period.

Key words: *Salvelinus fontinalis*; young-of-the-year; intra- and interspecific competition; oligotrophic lakes; abundance; growth; spatial distribution; feeding habits.

INTRODUCTION

Lakes are similar to islands in many ways, suggesting strong interactions between species (Werner, 1986). In this context, the importance of broad competition as a selective force on a community is more related to the frequency of lean periods than to the ensemble of environmental conditions at equilibrium (see Schoener, 1982). In young stages, where metabolism is high, a short period of starvation can have a pronounced influence on survival (Gardiner & Geddes, 1980; Power, 1980; Grant & Noakes, 1987). Considering that periods of low resource abundance could affect even more the young stages, the impact of a competitor could lead to an important bottleneck in the recruitment of a population (Werner, 1986).

A survey of 33 lakes located on the Canadian Shield indicated that juvenile and adult brook charr *Salvelinus fontinalis* (Mitchill) shift their food habits from zoobenthos to zooplankton and their spatial distribution from littoral to pelagic

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TABLE I. General characteristics of the study lakes containing allopatric and sympatric brook charr populations (0+ juveniles)

Lake	Surface area (ha)	Mean depth (m)	Conductivity (µs cm^{-1})	Secchi disk transparency (m)	Other fish species*			
					Pe	*Cco*	*Sm*	*Sa*
Brook charr lakes								
Bondi	23·3	8·0	10·5	3·5	×			
Charme	18·1	3·2	9·2	3·7	×			
Diablos	7·8	2·9	10·5	3·7	×			
Osborn	7·8	4·8	12·0	3·4	×			
Vautour	7·3	4·8	12·5	3·6	×			
Brook charr and white sucker lakes								
Grignon	25·9	7·8	9·0	5·5	×	×	×	
Joe	23·3	N.D.†	N.D.	N.D.	×	×		
Sauterelle	7·5	5·3	11·2	4·5	×	×	×	
Sans-Nom	13·2	0·8	12·7	1·5	×	×		
Vert	15·5	7·6	11·2	6·7	×	×		×

* ×, Presence of other fish species with brook charr; *Pe*, Northern redbelly dace, *Phoxinus eos*; *Cco*, white sucker, *Catostomus commersoni*; *Sm*, pearl dace, *Semotilus margarita*; *Sa*, creek chub, *Semotilus atromaculatus*.

†Not determined.

zone, when living sympatrically with white sucker, *Catostomus commersoni* (Lacépède) (Magnan, 1988; Tremblay & Magnan, 1991; Lacasse & Magnan, 1992). This niche shift of brook charr was correlated with a significant reduction in their relative biomass and abundance (Magnan, 1988; Lachance & Magnan, 1990*a*,*b*). Unlike brook charr, in which prey selection occurs from the first weeks of feeding (Fahy, 1980; McNicol *et al*., 1985; Tremblay & Magnan, 1991), white sucker feed on benthic resources indiscriminately, using prey according to a size pattern similar to that found in the resource (Tremblay & Magnan, 1991). Thus the size range of benthic prey used by brook charr at all stages of its life cycle was included in the feeding niche of white sucker. These considerations and the results obtained by Tremblay & Magnan (1991) suggest the existence of a competitive bottleneck in young-of-the-year (YOY) brook charr when living sympatrically with white sucker.

The first objective of this study was to evaluate the impact of white sucker on abundance, growth, spatial distribution, and feeding habits of YOY brook charr in their first season of growth (juvenile stage *sensu* Balon, 1979). We compared five allopatric brook charr populations with five others living in sympatry with white sucker. The second objective was to evaluate the intraspecific interactions between YOY brook charr when living in allopatry. The present study documents a part of the biology of brook charr that is still unknown in lenthic environments (i.e. juvenile YOY).

STUDY LAKES

The 10 study lakes are located in the Mastigouche Reserve, north of Trois-Rivières (Québec) Canada (46°40′ N, 73°20′ W) (Table I). These are characteristic small oligotrophic temperate lakes with respect to area, mean depth, conductivity, transparency and thermal stratification (Table I; see also Magnan, 1988; Lacasse & Magnan, 1992; Rodríguez *et al*., 1993). As the lakes are located within a 325 km^2 area, they are exposed to similar climatic conditions. The 10 lakes were divided into two groups that will be referred to hereafter as ' brook charr lakes ', containing brook charr, and ' brook charr and white sucker lakes ', containing brook charr and white sucker (Table I). Northern redbelly dace *Phoxinus eos* (Cope) was present in all lakes but their presence did not affect significantly the mean yield of brook charr in the exploited lakes of the Mastigouche Reserve (P. Magnan, unpublished data). Also, pearl dace *Semotilus margarita* (Cope) and creek chub *S. atromaculatus* (Mitchill) were present in three brook charr and white sucker lakes (Table I). However, gillnetting indicated that their relative biomass represented less than 1% of the total fish biomass (P. Magnan, unpublished data).

MATERIALS AND METHODS

FISH SAMPLING

We studied the abundance, growth, spatial distribution, and feeding habits of YOY brook charr from captures during three sampling periods of 10 days (1 day per lake): 27 June–6 July, 1–12 August, and 29 August–9 September, 1989, hereafter called ' July ', ' August ' and ' September ' sampling periods. At each sampling period, fish were captured with four multifilament and 15 monofilament gillnets (filament diameter: 0·10 mm), both types with stretched meshes of 12·5 mm. Thirteen of these nets were set parallel to the shore; four monofilaments of 15 m long × 0·5 m deep in 0·5 m depth, three monofilaments of 15 m long × 1 m deep in 1 m depth, two monofilaments and one multifilament of 15 m long × 2 m deep in 2 m depth, and two monofilaments and one multifilament of 15 m long × 4 m deep in 4 m depth, giving an effective sampling area of 345 m^2. Six other gillnets were set perpendicular to the shore; two multifilaments of 30 m long × 2 m deep, three monofilaments of 15 m long × 2 m deep, and one monofilament of 10 m long × 2 m deep, for a total of 230 m^2. The area sampled by the perpendicular gillnets was located over the substrate, from the shore to the extremity of the net (up to a maximum depth of 7 m). In September, we also used a 32 m long × 1·5 m deep monofilament gillnet (48 m^2), with stretched meshes of 15·9 mm (filament diameter: 0·10 mm), which was used perpendicularly to the shore. Gillnets were set before dusk and removed after dawn, covering the presumed periods of activity of the species studied (Power, 1980; Tremblay & Magnan, 1991). Furthermore, observation based on our preliminary sampling in 1988 confirmed that YOY brook charr were more active during this period. Some of our results refer to this 1988 sampling; the 12·5 mm stretched mesh multifilament gillnets described above were set parallel to the shore, in 2 and 4 m depths in lakes Diablos, Charme, Osborn and Bondi between 25 June and 16 July.

RELATIVE ABUNDANCE AND SPATIAL DISTRIBUTION

The fishing effort was the same in all lakes for each sampling period. Thus, it was possible to compare the mean relative abundance of YOY charr among allopatric and sympatric populations on the pooled captures of the three sampling periods. As each lake is seen as one replicate in this study, we computed the mean YOY charr abundance for each community type (allopatric and sympatric) from the value of each lake. The mean fish abundances were compared using a Student-*t* test on log $(x+1)$ transformed data to homogenize the variances.

The spatial distribution of fish was estimated from captures in gillnets set perpendicular to the shore, because sample size was too small in those set parallel to the shore. The vertical distribution of YOY charr was determined by noting the position of fish in the water column (± 5 cm). Some specimens were excluded from this analysis because they

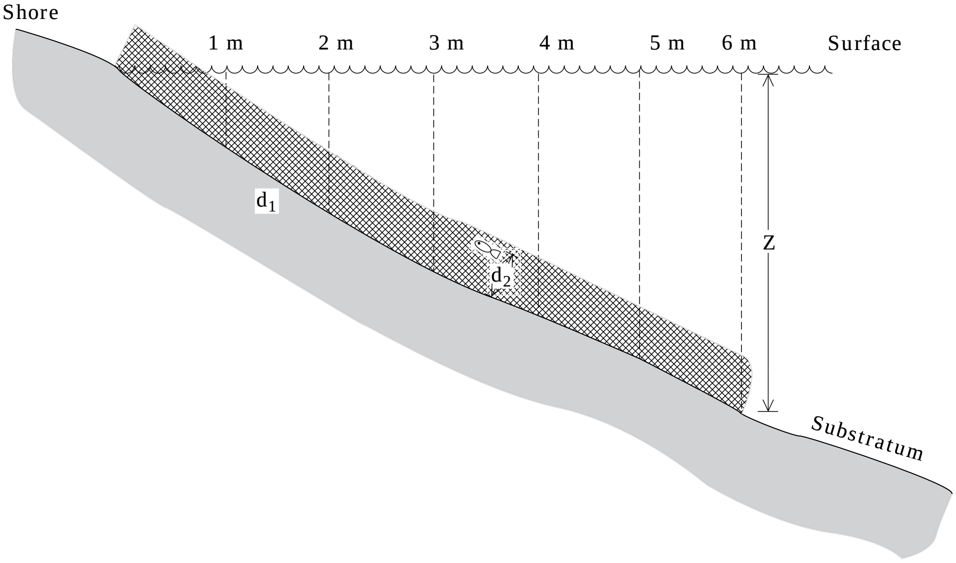

FIG. 1. Representation of measurements used to estimate horizontal and vertical distribution of brook charr (0+ juveniles) in the gillnets set perpendicular to the shore, summer 1989. d_1, distance of the fish from the shore, along the bottom of the lake; d_2, vertical position of the fish in the first 2 m from the substrate (nearest 5 cm); *z*, depth at the end of the gillnet.

fell from the net before we noted their position. Homogeneity of vertical distribution in allopatric and sympatric populations was assessed by χ^2-test on pooled data per community, for each sampling period. Although the vertical distribution of allopatric brook charr among the three sampling periods was not homogeneous ($\chi^2 = 23{\cdot}58$ $P < 0{\cdot}001$), apparently due to the small sample size of August, we combined the data of these three sampling periods before comparing the vertical distribution of the fish between the two communities with a contingency table analysis. This was necessary because the sample sizes of sympatric populations in each of the sampling periods were too small. The horizontal position of fish was determined by triangulation, using the distance from the shore and the depth at the end of the net (Fig. 1). Because all the depths were not fished with the same effort, owing to differences in slope of the lake at each station, we standardized these data in term of catch per unit of effort (cpue), in each depth stratum (i.e. 0 to 1, 1 to 2, 2 to 3 m, etc.; Fig. 1). Only a descriptive presentation of the horizontal distribution is presented here, because tests for goodness of fit cannot be performed with transformed data such as cpue.

GROWTH

Total length was measured to the nearest mm on preserved specimens (formaldehyde 10%). The mean lengths of sympatric and allopatric YOY brook charr were compared for each sampling period. Data from the five lakes of each community were pooled and compared with *t*-tests. The growth between allopatric populations (except for Lake Osborn; $n = 3$) was compared to evaluate the inter-lake variations. An ANOVA, followed by a Student–Newman–Keuls multiple-range comparison test, was used to compare the mean length of fish in the four lakes, at each sampling period.

FEEDING HABITS

A mean of 20 stomach contents per lake (range 2–39), per sampling period were analysed, excluding empty stomachs. In September, when we fished with 12·5 and 15·9 mm stretched mesh gillnets, only the charr caught in the 15·9 mm mesh were used for the stomach content analysis in order to compare diets from fish of the same size. In the field, each specimen was preserved individually in 10% formaldehyde (fish were dead before preservation). The content of the digestive tract between the oesophagus and the pyloric valve was examined (Magnan & FitzGerald, 1982). The prey were identified to order or family when possible, and measured to the nearest mm (total length, without antennae and appendages, and width of the cephalic capsule) using an ocular micrometer mounted on a dissecting scope (40 ×). The lengths of broken and/or incomplete organisms were estimated using linear regression (prey length : width of cephalic capsule). Regressions were obtained by family, by order (insects of similar stages) or by grouping together different orders of insects of the same functional groups (e.g. terrestrial organisms), from measurements of complete prey. This procedure was done to obtain large enough samples and/or significant linear regressions. If neither the length nor the width of the cephalic capsule were available, the missing values were replaced by mean lengths of the given taxa, computed from data of stomach content analysis. In the specific case of Culicidae pupae and Cladocera, we used the mean prey length. For Cladocera, the mean length was computed from *Daphnia* which corresponded to 67% of the Cladocera in the diet of YOY charr.

The weight of each ingested organism was estimated using length : dry weight regressions, following the same procedure as Tremblay & Magnan (1991); regressions for benthic organisms and terrestrial insects were obtained from data of Tremblay & Magnan (1991), while the one for Cladocera was obtained from Culver *et al*. (1985). These prey weight estimations allowed us to compare the diet of each population using the mean percent weight of prey method (Hyslop, 1980), which overcomes the criticisms of percent occurrence and percent number methods (Wallace, 1981). For the purpose of this study, the different components of the diet were grouped into the following broad functional categories: Cladocera, large planktonic organisms (Diptera pupae, Chaoboridae larvae and Gammaridae), zoobenthos, and terrestrial organisms (i.e. allochthonous). Diet analysis was not performed in Lake Osborn (allopatric population), Joe, Sauterelle, Sans-Nom and Vert (sympatric populations) owing to the small sample sizes.

INTRASPECIFIC INTERACTIONS

A posteriori considerations (see Discussion) led us to compare the growth, condition factor, spatial distribution and feeding habits of YOY charr coming from two groups in Lake Bondi. The first included fish captured between 0–2 m depth while the second included those captured between 3–6 m depth, hereafter called ‘ littoral group ’ and ‘ profundal group ’. The diet analysis was made in the same way as for inter-community comparisons except that it was based on percent numerical composition. The condition factor of charr from the two groups was computed for July and September sampling periods (no capture in profundal zone in August) as:

$$K = \frac{100\,w}{l^b}$$

where w and l are the observed weight (g) and total length (mm) of the fish respectively, and b is the slope of the regression of log (w) on log (l) (Bagenal & Tesch, 1978). A slope was computed for each group, at each sampling period. Also, to decrease the bias due to comparison of fish of different sizes (Bagenal & Tesch, 1978) the computations were made only from specimens caught in the 12·7 mm stretched mesh gillnets in July samples and only from the 15·9 mm stretched mesh gillnets in September samples. The values of length and weight used in the computation of the condition factors were not significantly different ($P>0{\cdot}05$) between the two groups, for each sampling period.

RESULTS

RELATIVE ABUNDANCE AND SPATIAL DISTRIBUTION

YOY brook charr were significantly more abundant in the allopatric than in the sympatric community (45·3 ± 3·8 *vs* 3·1 ± 3·8 fish/lake caught in 1773 m^2 of gillnets; $t=2{\cdot}511$, $P<0{\cdot}005$; Table II).

TABLE II. Mean length (mm), standard deviation (S.D.), and number (n) of brook charr (0+ juveniles) captured in the study lakes at each sampling period, summer 1989

Brook charr lakes					Brook charr and white sucker lakes				
Lake	SP*	$\bar{X}$ (mm)	S.D.	n†	Lake	SP	$\bar{X}$ (mm)	S.D.	n
Bondi	1	60·2	2·9	115	Grignon	1	57·0	—	1
	2	60·8	3·8	36		2	63·2	4·1	22
	3	75·4	8·2	79		3	76·7	7·8	24
Charme	1	59·1	2·6	39	Joe	1	61·0	—	1
	2	65·5	2·9	8		2	—	—	0
	3	80·2	7·1	62		3	—	—	0
Diablos	1	61·5	2·7	28	Sans-Nom	1	57·0	—	1
	2	68·5	0·7	2		2	—	—	0
	3	82·1	10·8	28		3	84·5	3·5	2
Osborn	1	—	—	0	Sauterelle	1	64·0	5·7	2
	2	—	—	0		2	—	—	0
	3	71·3	4·7	3		3	—	—	0
Vautour	1	60·5	3·6	15	Vert	1	—	—	0
	2	61·8	1·0	4		2	—	—	0
	3	72·4	7·1	10		3	—	—	0
Total	1	60·8	3·0	197	Total	1	60·6	4·5	5
	2	61·9	4·1	50		2	63·2	4·1	22
	3	77·9	8·7	182		3	77·3	7·8	26

*SP, sampling period: 1, 27 June–6 July; 2, 1–12 August; 3, 29 August–9 September.

†In some cases mean and standard deviations were computed on one to two fish less than indicated in the table (except Bondi, SP-1, seven fish less; Charme, SP-3, six fish less), owing to the deterioration of these specimens in the gillnets.

YOY brook charr were closely associated with the substrate at all depths sampled with gillnets set parallel to the shore (i.e. in the entire water column from the 0·5 to 4·0 m depth stations); 26 of the 27 fish captured in 1988 and all of the 47 captured in 1989 in these nets were found within 1·5 m from the bottom. Gillnets set perpendicularly to the shore did not show if fish were present higher than 1·5–2 m above the substrate (Fig. 1). However, the vertical distribution estimated from gillnets set perpendicular to the shore was representative, as most of YOY charr were found within the first 1·5 m from the bottom in gillnets set parallel to the shore. With the exception of the sympatric community in July, the vertical distribution of YOY brook charr was not homogeneous, the fish being more associated to the first 0·5 m from the substrate (perpendicular gillnets) (Table III). Furthermore, in the presence of white sucker a significant lower proportion of YOY charr were found near the substrate; 64% of sympatric charr were found within 0·5 m from the substrate compared with 81% for allopatric charr ($\chi^2=19{\cdot}9$, $P<0{\cdot}001$; Table III). In the gillnets set parallel to the shore this proportion rose to 92% in the allopatric community.

In July and September, the horizontal distribution of YOY charr in Lake Bondi was bimodal, with a first mode between 0–2 m depth, and a second between 3–6 m depth (Fig. 2). In August, fish from this population were the only ones among allopatric populations to go deeper than 3 m depth (Fig. 2). In

TABLE III. Number of allopatric and sympatric brook charr (0+ juveniles) caught at different depths in gillnets set perpendicular to the shore

Community	Depth classes (m)				Total catch	χ^2	*P*
	0–0·5	0·5–1	1–1·5	1·5–2			
			July				
Allopatric	105	16	8	4	132	203	<0·001
Sympatric	2	0	0	0	2	6	>0·05
			August				
Allopatric	20	2	4	8	34	21	<0·001
Sympatric	16	5	4	0	25	23	<0·001
			September				
Allopatric	146	19	3	0	159	383	<0·001
Sympatric	14	4	5	0	23	16	<0·005

contrast, the horizontal distribution of all other populations was conspicuously unimodal at every sampling period, with the exception of Lake Diablos in July (Fig. 2). In these cases, YOY brook charr tended to be near the shore in July and August (0–2 m depth) and moved deeper in September (1–3 m depth; Fig. 2). In September, the smaller specimens, captured with the 12·7 mm stretched mesh gillnets, were essentially found in the littoral zone (less than 2 m depth). In the sympatric communities, the general tendencies were similar to those found in the allopatric ones (Fig. 2).

GROWTH

There was no significant difference between the mean length of allopatric and sympatric YOY brook charr (July: $t=20$, $P=0{\cdot}852$; August: $t=1{\cdot}28$, $P=0{\cdot}208$; September: $t=0{\cdot}36$, $P=0{\cdot}722$; Table II). However, the analysis of growth in the four allopatric populations showed inter-lake variations; in July, the mean length of charr from Lake Charme was lower, from 1·1 to 2·4 mm, than those from the three other allopatric populations ($F=3{\cdot}83$, $P<0{\cdot}01$). In September, the mean lengths of YOY brook charr from Lakes Charme and Diablos were significantly higher than those found in Lakes Bondi and Vautour ($F=7{\cdot}87$, $P<0{\cdot}001$; Table II). No comparison was performed in August owing to the small sample size in three of the five lakes.

FEEDING HABITS

Through the three sampling periods, allopatric YOY brook charr fed in various degrees on Cladocera, large planktonic organisms and benthic organisms, and more rarely on terrestrial organisms (Fig. 3). Cladocera were represented mainly by *Daphnia* spp., large planktonic organisms by Chaoboridae larvae and Culicidae pupae, benthic organisms by Ephemeroptera larvae, while Hymenoptera and adult Diptera were the two predominant terrestrial organisms.

In July and August, benthic organisms represented the most important part of the diet of charr in all lakes, followed by large planktonic organisms (except in

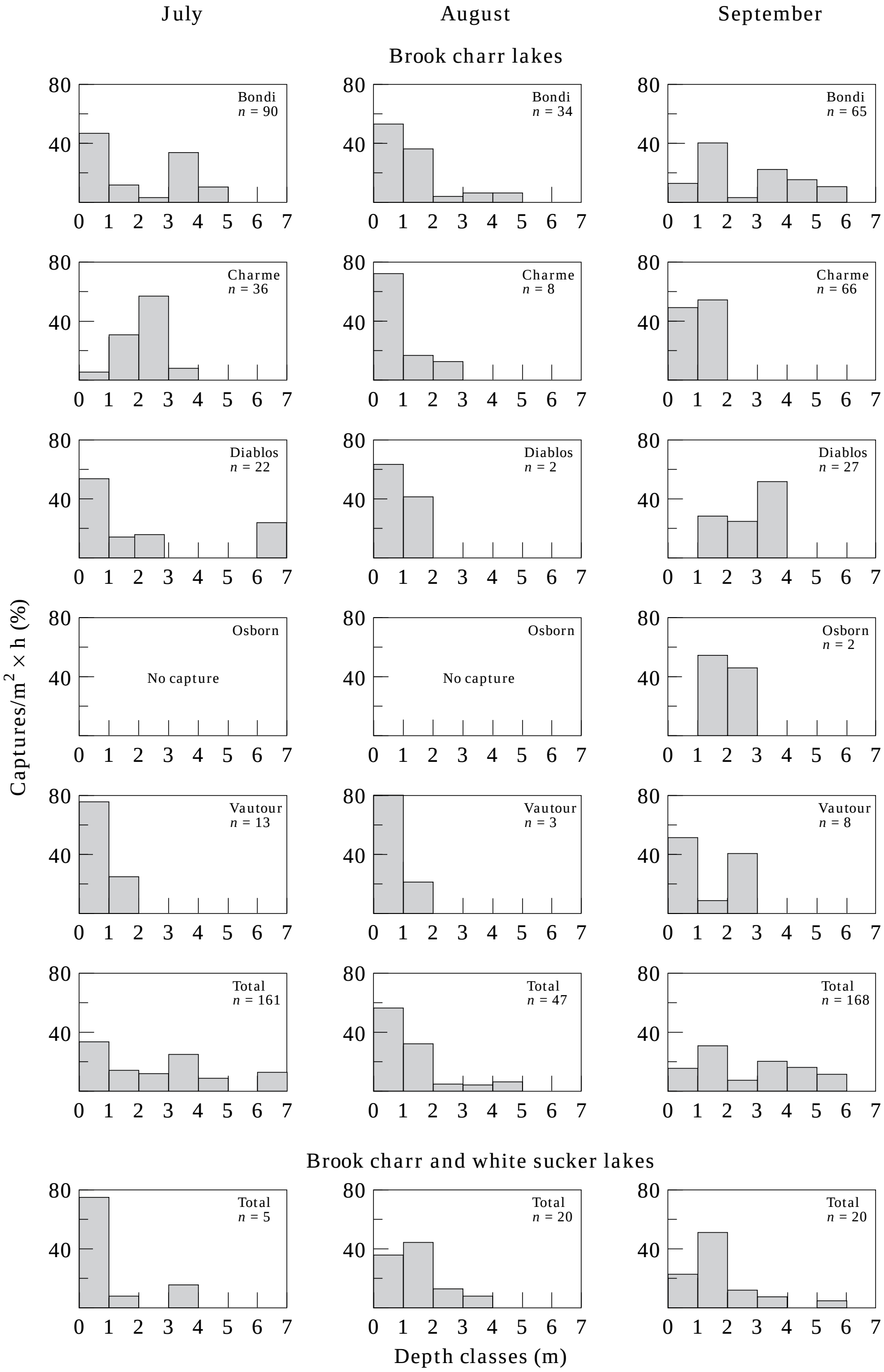

FIG. 2. Horizontal distribution of brook charr (0+ juveniles) from gillnets set perpendicular to the shore, summer 1989. Data are percent catch per unit of effort, by depth classes (see text).

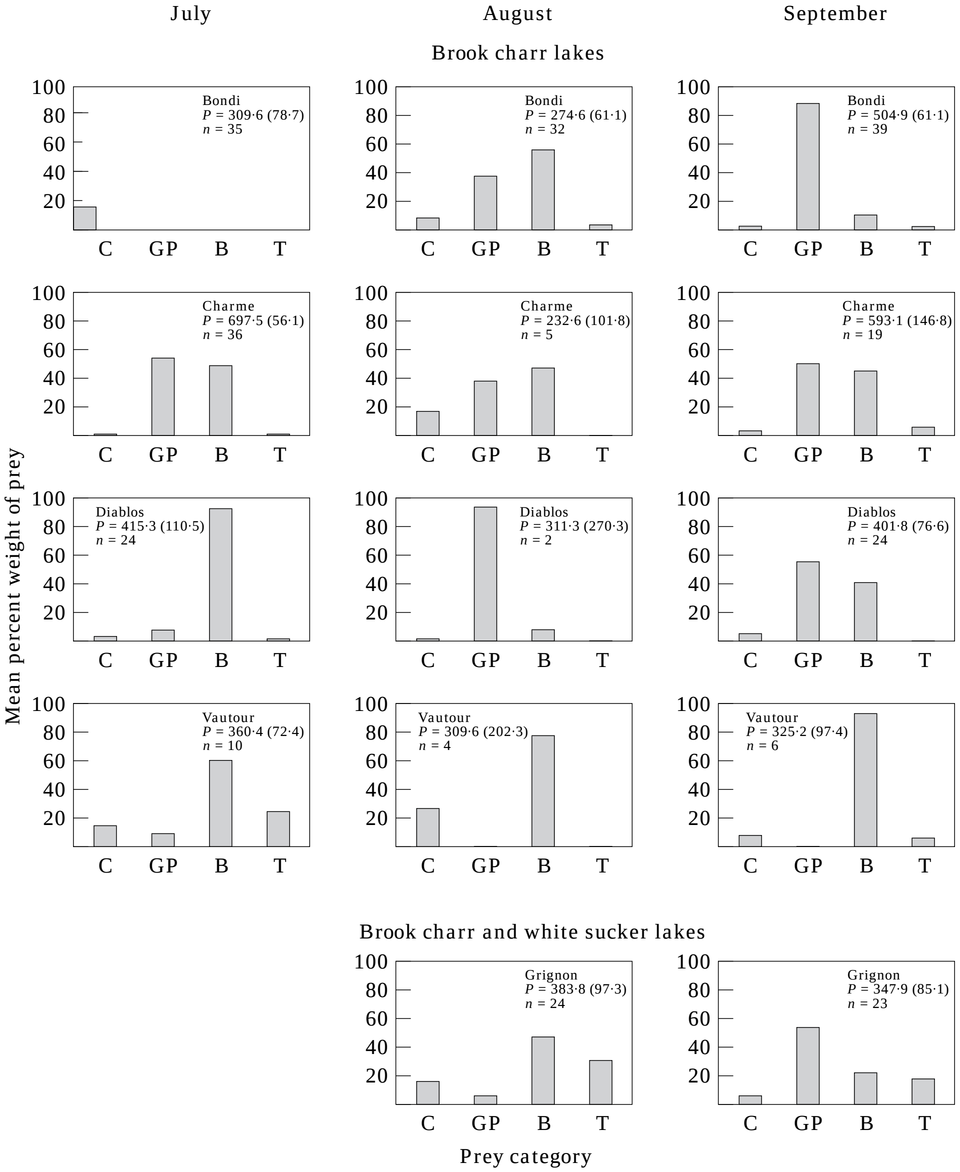

FIG. 3. Mean percent weight of prey in the stomach contents of brook charr (0+ juveniles) from the study lakes, summer 1989. C, Cladocera; GP, large planktonic organisms (Diptera pupae, Chaoboridae larvae and Gammaridae); B, benthic organisms; T, terrestrial organisms; P, mean stomach content weight (mg dry weight) and standard deviation in parentheses; n, number of stomach contents analysed.

Lake Diablos in August where the sample size was only of two; Fig. 3). The proportion of Cladocera consumed by the fish during these sampling periods varied from 2 to 25% in weight. In September, large planktonic organisms became dominant in the diet of charr in Lakes Bondi, Charme and Diablos (Fig. 3). Charr from Lake Vautour fed almost exclusively on benthic organisms.

TABLE IV. Mean length (mm), standard deviation (S.D.) and number of captures (*n*) of brook charr (0+ juveniles) from littoral (0–2 m depth) and profundal (3–6 m) zones of Lake Bondi in 1989

Sampling period	Zone					
	Littoral			Profundal		
	$\bar{X}$	S.D.	*n*	$\bar{X}$	S.D.	*n*
July	60·0	3·3	59	60·5	2·5	53
August	60·9	3·4	29	*	*	*
September	73·4	9·2	41	77·8	5·4	34

*No captures in the profundal zone.

Sympatric YOY brook charr (from Lake Grignon) fed less on benthic and large planktonic organisms and more on terrestrial organisms (Hymenoptera and adult Diptera) than allopatric ones during both August and September sampling periods (Fig. 3).

INTRASPECIFIC INTERACTIONS

Based on the total number of captures, YOY brook charr from Lake Bondi were two to eight times more abundant than charr in the other allopatric populations (excluding Lake Osborn, where the total number of captures was only three) (Table II). Brook charr from Lake Bondi were the only ones to be segregated spatially into two groups, in July and September, that we called ‘ littoral ’ and ‘ profundal ’ groups (Fig. 2). The profundal group may have been missed in August owing to the absence of 15·9 mm stretched mesh gillnet (see Discussion). The mean lengths of individuals coming from the two groups were not significantly different in July ($t=0{\cdot}89$, $P=0{\cdot}374$) but differed significantly in September ($t=2{\cdot}57$, $P<0{\cdot}01$) (Table IV). In August, the mean length of charr from the littoral group was not significantly different from that of the same group in July (Table IV).

We observed significant differences among the condition factors of the two groups in July and September (Table V). These showed that the length–weight ratio was higher in the littoral group in July and lower in September. Also, condition factors of both groups decreased in September, the decrease being proportionally higher for the littoral than for the profundal group. Finally, coefficients of variation of length, weight and condition factors were also higher for the littoral group, especially in September (Table V).

In July, the diets of both groups were similar, while in September the consumption of Cladocera was higher for the littoral than for the profundal group, for which the diet was based mainly on large planktonic organisms (Fig. 4). As for the mean length, the diet of the littoral group in August did not differ from that of the same group in July (Fig. 4).

TABLE V. Length (mm), weight (g), and condition factor of brook charr (0+ juveniles) from littoral (0–2 m depth) and profundal (3–6 m) zones of Lake Bondi in 1989

	Zone							
	Littoral				Profundal			
	$\bar{X}$	S.D.	CV	*n*	$\bar{X}$	S.D.	CV	*n*
July								
Length (mm)	60·0a	3·4	5·57	59	60·5a	2·5	4·07	53
Weight (g)	2·03a	0·30	14·70	17	2·19a	0·31	14·29	21
Condition	5·68a	0·52	8·90	17	2·00b	0·14	7·19	21
September								
Length (mm)	77·5a	6·8	8·81	30	78·4a	4·8	6·14	32
Weight (g)	4·67a	1·59	34·22	20	4·53a	0·84	18·70	20
Condition	0·65a	0·05	7·67	20	1·34b	0·06	4·54	20

Data are mean ($\bar{X}$), standard deviation (S.D.), coefficient of variation (CV) and sample-size (*n*). Means followed by different letters are significantly different as determined by a Student *t*-test ($P<0·05$).

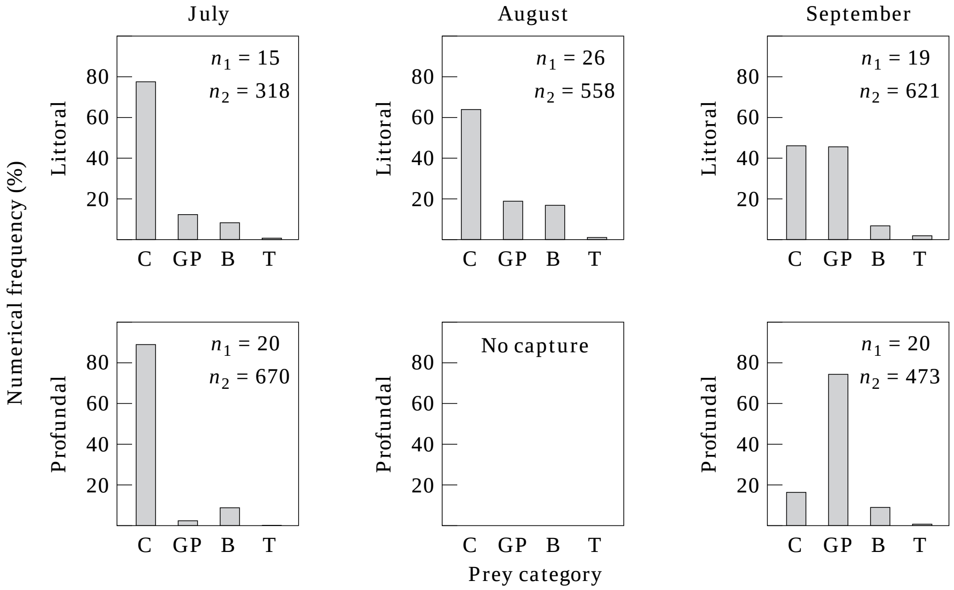

FIG. 4. Percent numerical frequencies of prey in the stomach contents of brook charr (0+ juveniles) from littoral and profundal zones of Lake Bondi, summer 1989. C, Cladocera; GP, large planktonic organisms (Diptera pupae, Chaoboridae larvae and Gammaridae); B, benthic organisms; T, terrestrial organisms; n_1, number of stomach contents analysed; n_2, total number of prey found in stomach contents.

DISCUSSION

ECOLOGY AND BEHAVIOUR OF YOY BROOK CHARR IN FRESHWATER LAKES

Apart from the work of Wurtsbaugh *et al.* (1975), who studied food and distribution of individuals along the shore of one lake in California (U.S.A.), virtually no study has investigated the ecology of YOY brook charr (0+ juveniles) in lake environments. The present study provides original data on abundance, growth, horizontal and vertical distributions, diet, and impact of intra- and interspecific interactions on YOY of this species, in 10 temperate lakes. The general lack of information on young salmonids in these habitats is due mainly to the difficulties related to their capture. Including our preliminary study in 1988, we tested a total of five different fishing gears to catch YOY brook charr; 30 fry traps adapted from Breder (1960) (with two opposite entries rather than one; see also Bagenal & Braum, 1978), six light traps adapted from Floyd *et al.* (1984), 12·5 mm stretched mesh multifilament gillnets, 12·5 mm stretched mesh monofilament gillnets with 0·18 mm filament diameter, 12·5 and 15·9 mm stretched mesh monofilament gillnets with 0·10 mm filament diameter. Of these gears, only the multifilament and the monofilament gillnets with 0·10 mm filament diameter allowed us to capture YOY brook charr. The seine was withdrawn from our study because it gave very poor or no information on horizontal and vertical distribution of the fish and also because it was not convenient in all littoral microhabitats (e.g. zones with macrophytes and emergent vegetation, abrupt slope, log and woody debris).

Although most of the fish were found within the first 2 m depth along the shore, 35% were captured in depths up to 7 m depth. Thus, the horizontal distribution of YOY brook charr was not limited to a depth less than 2 m, as reported by Wurtsbaugh *et al.* (1975), who studied fish of comparable size range to those in our study (30–80 mm). Results of vertical distribution showed that YOY charr were associated with the substrate because over 80% of fish in allopatric populations were caught within 0·5 m from the bottom.

Overall, the diet of YOY charr observed in the present study is comparable to that of charr of the same age in Castle Lake, California, U.S.A. (Wurtsbaugh *et al.*, 1975); the fish fed mainly on benthic organisms (40 to 90% in weight) but also on important proportions of terrestrial and limnetic organisms (which we divided into cladoceran and large planktonic organisms). However, as we analysed our results for each sampling period, we observed that YOY charr shifted their diet from mainly benthic organisms, in July and August, to large planktonic organisms in September. This shift could result from the fact that (1) larger charr can feed on large zooplanktonic prey, which could bring some energetic advantages over benthic organisms (as they are captured in the water column, their capture may require less energy than capturing benthic organisms in relation to the terminal position of the mouth, and their digestion is probably easier owing to absence of cuticle), or (2) the abundance of benthic organisms decreases as the summer progresses in many temperate lakes (Mittelbach, 1981; Rodríguez & Magnan, 1993).

Differences in mean length of brook charr from allopatric populations indicated an interlake variability in growth among two sampling periods. An extrapolation of growth rate from data of July and September sampling periods shows that the smaller size of charr from Lake Charme measured in July could have been the result of a bias due to sampling delays (Fig. 5; data from August were not used in this analysis because of the small sample size). Differences in growth patterns observed in September cannot be attributable to such a

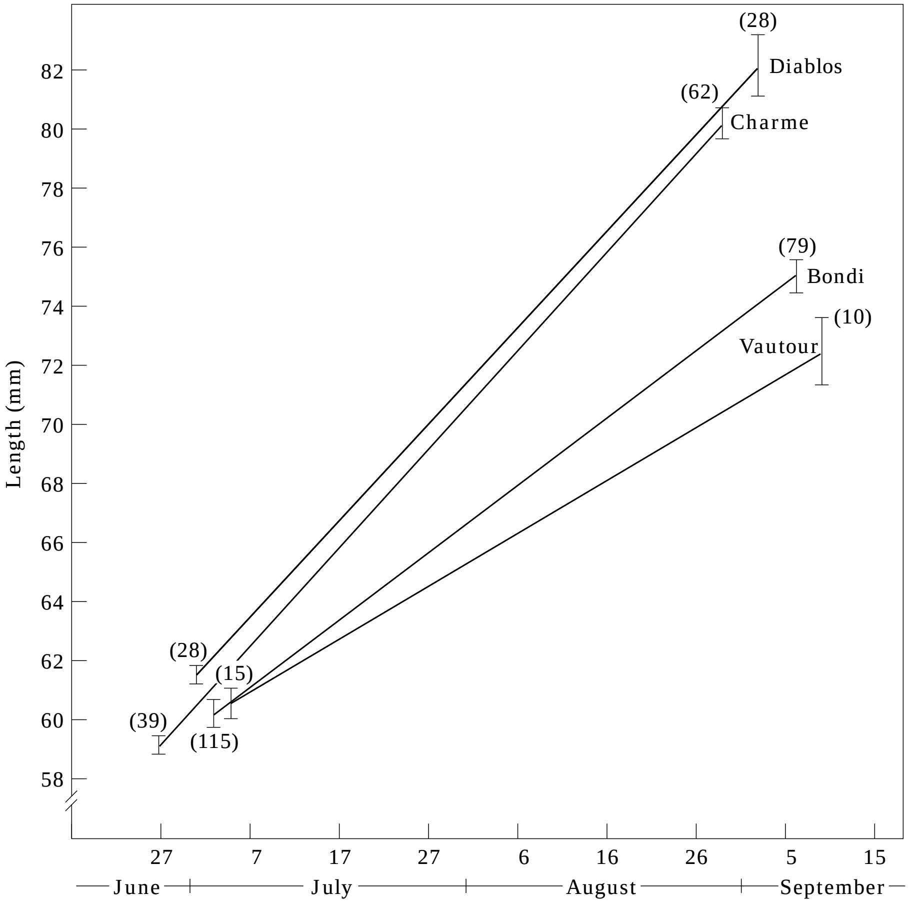

FIG. 5. Growth of brook charr (0+ juveniles) from July to September in four allopatric populations, summer 1989. Each point represents the mean length with standard error (sample size is in parentheses). Data from August were not used owing to the low sample size.

sampling bias (Fig. 5) and thus would have been more the result of ecological differences among lakes.

INTERSPECIFIC INTERACTIONS

Our hypothesis was that a competitive bottleneck occurs in YOY brook charr because their food and spatial distribution overlap with those of small and large white sucker (Tremblay & Magnan, 1991). In this system, charr from all sizes compete with white sucker not only for benthic organisms, but also for zooplankton, which is the main competitive refuge of charr along the food axis (Magnan, 1988; Tremblay & Magnan, 1991). Small white sucker ($\sim$13–23 mm) are planktivorous (Carlander, 1969; Scott & Crossman, 1973) whereas larger ones may feed heavily on cladocerans, especially late in the summer (Tremblay & Magnan, 1991). This competition for food should result in a reduction of growth rate in charr during the first summer and thus, to an increased overwintering mortality (see Rose, 1986; Tremblay & Magnan, 1991). Following this hypothesis, we predicted that (1) relative abundance of YOY brook charr would not differ among allopatric and sympatric populations, and (2) growth of YOY brook charr would be significantly lower in sympatric than in allopatric populations, two predictions that were not supported by our observations. In fact, we observed that the abundance of YOY brook charr was significantly higher in allopatric than in sympatric populations and that growth did not differ among allopatric and sympatric populations. These results suggest that the competitive bottleneck occurs at a previous stage in the life cycle of charr, before June.

Three hypotheses can be identified to explain this earlier mortality of brook charr. (1) The rate of mortality during the exogeneous feeding phase of the larval stage is higher in sympatric than in allopatric populations, owing to deprivation following competition for food with white sucker. The larval stage is characterized by a high rate of mortality in brook charr (Shetter, 1961; Latta, 1962; Power, 1980; Grant & Noakes, 1987). Nutritional deficiency, even for a short period of time, would be the main cause of mortality (Gardiner & Geddes, 1980). In a river, brook charr and brown trout *Salmo trutta* L., larvae aged only a few weeks appeared to select benthic and terrestrial invertebrates (Fahy, 1980; Williams, 1981) and in lakes, Wurtsbaugh *et al.* (1975) observed that brook charr less than 30 mm long fed on benthic organisms in May (52·8% by weight). If we assume that energetic requirements at larval stages are *per se* a bottleneck for recruitment, the effect of a competitor at this time of the life cycle could lead to a rise in rate of mortality. As white sucker feed on benthic resources without any discrimination, using prey according to a size pattern similar to that found in the benthos (Tremblay & Magnan, 1991), we can presume that the size range of benthic prey used by brook charr of all sizes is included in the feeding niche of white sucker. (2) The lower abundance of juvenile YOY brook charr in sympatric populations is the result of predation by white sucker and/or brook charr. Predation on larvae and juvenile (0+) by white sucker and brook charr was never observed, despite the fact that the contents of 3516 charr and 487 sucker stomachs have been examined since 1985 in this system (Magnan, 1988; Lachance & Magnan, 1990*b*; Tremblay & Magnan, 1991; East & Magnan, 1991; Lacasse & Magnan, 1992; M. Lapointe & P. Magnan, unpubl. data). These results confirm that white sucker is not a piscivore (Scott & Crossman, 1973), and that even if cannibalism has been observed in some salmonids (Riget *et al.*, 1986), it results from specific, unusual conditions. Predation on the eggs of brook charr would be more plausible considering the morphology and feeding behaviour of the white sucker (inferior mouth sieving the sediment without any prey selection). However, although it has been reported that different species of sucker eat eggs of salmonids, there is no evidence that such predation has an effect on prey populations (Holy *et al.*, 1979). (3) Because adult brook charr are less abundant in lakes containing white sucker (Magnan, 1988) and fecundity compensation was not observed (P. Magnan, unpubl. data), the total egg production is lower in sympatric populations thus affecting recruitment. This hypothesis is valid as far as the spawning sites are not already a limiting factor to recruitment in allopatric and sympatric populations.

The white sucker has an impact on the vertical distribution and diet of YOY brook charr; a significantly higher proportion of sympatric charr were found in the water column (i.e. above 0·5 m from the substrate) and individuals fed less on benthic and large planktonic organisms and more on terrestrial organisms. A similar niche shift in vertical distribution and feeding habits of charr of one year and more has been observed in the study system (Magnan & FitzGerald, 1982; M. Lapointe & P. Magnan, unpubl. data). Here, the change in vertical distribution of charr is probably related to higher consumption of terrestrial organisms. Generally, coexisting species partition the food resources according to their functional morphology and their ability to exploit a given type of prey (see Tremblay & Magnan, 1991). White sucker, which has an inferior mouth, is better adapted than charr to feed on zoobenthos whereas brook charr, which has a terminal mouth, is better adapted to feed in open water and on surface prey.

Alternatively, observed differences in vertical distribution and feeding habits between allopatric and sympatric YOY brook charr might result from a sampling bias in sympatric populations; all the data came from only one population (Lake Grignon) which may be atypical. However, this bias cannot explain differences in fish abundance among sympatric and allopatric populations, because the same fishing effort was used in all the 10 study lakes.

INTRASPECIFIC INTERACTIONS

Juvenile YOY charr from Lake Bondi were the only ones to be spatially segregated into littoral and profundal groups, although it is not clear if these two groups corresponded to real ecological entities. However, four kinds of evidence support their existence. First, this bimodal pattern in horizontal distribution was observed only in Lake Bondi, which contains two to eight times more YOY charr than other allopatric populations, suggesting a spatial segregation in response to intraspecific interactions. Second, this pattern was observed only during July and September, when we fished, respectively, with 12·5 and 15·9 mm stretched mesh gillnets. As the mean lengths of individuals from the two groups differed significantly in September, the profundal group may have been missed in August through the absence of 15·9 mm stretched mesh gillnet (i.e. charr from the profundal group may have been large enough in August to avoid capture by the 12·5 stretched mesh gillnets). Third, a discriminant function analysis, based on 21 meristic and morphometric characters, retained mouth height, basal length of the dorsal fin, eye–snout distance, and operculum–snout distance as the most discriminant characters and, although not statistically significant, allowed 90% of individuals to be correctly reclassified into the appropriate group (M. A. Rodríguez, J.-F. Duchesne and P. Magnan, unpubl. data). Such a result suggests a real morphometric difference between the two groups but a sample size too small to attain significance (the above analysis was performed from measurements on 20 specimens of each group captured in September). Fourth, differences in the size of ingested prey appeared to be related to differences in growth in September, fish of the profundal group eating larger prey and experiencing significantly higher growth than those of the littoral group.

In July, YOY brook charr from the littoral group were in better condition than those of the profundal group. However, as the season progressed, the condition of littoral charr decreased almost tenfold while that of profundal charr remained stable. Also, length, weight, condition factor, and diet were more variable in the littoral group, suggesting more variable conditions and/or more intense intra- and interspecific competition in the littoral zone.

Salmonid fish of the genus *Salvelinus* are known to be flexible in their behaviour and morphology. Examples of ecological and morphological shifts in sympatric and/or allopatric communities have been reported respectively for brook charr (Magnan, 1988; Magnan & Stevens, 1992) and Arctic charr, *Salvelinus alpinus* L. (Hindar & Jonsson, 1982; Jonsson *et al*., 1988; Gardner *et al*., 1988; Malmquist, 1992). Whether morphologic differences reported in these studies are of phenotypic or genotypic nature still remain unclear (see Magnan, 1988; Svedäng, 1990; Hartley *et al*., 1992). Further research will be needed to understand better proximal mechanisms underlying these shifts in behaviour and morphology.

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