Early microhabitat use by age 0 year brook charr Salvelinus fontinalis in lakes

P. A. BIRO*[†], C. BECKMANN[‡] AND M. S. RIDGWAY§

†Department of Environmental Science, University of Technology, Sydney Box 123
 Broadway, NSW 2007, Australia, ‡School of Biological Sciences, University of Sydney,
 Sydney NSW 2007, Australia and §Harkness Laboratory of Fisheries Research, Aquatic
 Research and Development Section, Ontario Ministry of Natural Resources, Trent
 University, 2140 East Bank Drive Peterborough, Ontario, K9J 7B8 Canada

(Received 15 July 2007, Accepted 12 April 2008)

The early habitat use of age 0 year brook charr *Salvelinus fontinalis* in three north temperate lakes which differ in terms of shoreline physical habitat is described. In the two lakes, which contained abundant shoreline woody debris and inundated vegetation, brook charr were observed in extremely close proximity with these habitat features, near shore and near the surface. Fish were absent from open areas away from shore unless in close proximity with fallen floating logs near the surface, extending offshore. In a third lake that had no woody debris or inundated shoreline vegetation, brook charr were observed exclusively in close proximity with the shoreline itself, and near the surface. In all three lakes, fish were most closely associated with the shoreline and with woody debris and inundated vegetation (when present) shortly after emergence, and significantly farther from shore and deeper in the water column threafter.

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Key words: habitat; habitat selection; nearshore; riparian; woody debris.

INTRODUCTION

Movements of brook charr *Salvelinus fontinalis* (Mitchell) (often termed brook trout) in lakes and streams generally fall into one of two categories: individual fish may remain stationary and forage from a relatively fixed location, or in contrast, fish may move and actively forage for items near or at the surface (Grant & Noakes, 1987; Biro & Ridgway, 1995; McLaughlin, 2001). In streams, density-dependent processes associated with territorial behaviour can contribute to this movement dichotomy (Grant & Noakes, 1987) and in other cases the movement dichotomy is adaptive (McLaughlin, 2001). In lakes, dichotomous movements are not generated by a territorial process but instead reflect outward expansion and redistribution of a cohort away from their site

^{*}Author to whom correspondence should be addressed. Tel.: +61 95148310; fax: +61 95148332; email: peter.biro@uts.edu.au

of origin, the spawning area in the shallow littoral zone (Biro et al., 1997; Ridgway & Blanchfield, 1998; Coombs & Rodriguez, 2007).

Dispersal away from spawning areas ultimately leads to groundwater sites where cool water temperatures extend the habitat suitability of the shallow littoral zone for age 0 year brook charr well into the warm water phase of the annual temperature cycle (Borwick *et al.*, 2006). Seepage habitat for age 0 year brook charr is relatively rare and often located well away from spawning areas. Furthermore, the frequency of this habitat in the shallow littoral zone declines with lake size (Borwick et al., 2006). Movement to seepage habitat is therefore important for sustaining brook charr populations in lakes, and this movement occurs along shoreline areas (Snucins et al., 1992; Biro et al., 1997). Habitat structure provided by coarse woody debris along the shore of brook charr lakes may be centuries old (Guyette & Cole, 1999) and, along with finer woody debris, important in defining shoreline structure because of its high density (Mallory et al., 2000). Conservation of this habitat for young brook charr may be a key element for sustaining lake-based populations of brook charr since entire cohorts use this habitat while dispersing and it may provide additional microhabitats for high densities of fish emerging over short time periods (Coombs & Rodriguez, 2007).

Previous work identified riparian habitat features, such as inundated shoreline vegetation and woody debris, as important elements of the early habitat of brook charr as they relate to individual foraging movements (Biro & Ridgway, 1995) and foraging success (Biro *et al.*, 1996). Habitat use in relation to availability, however, has not been investigated in this species, nor have changes in habitat use over time, in an effort to identify habitats that may be important for early growth, survival and dispersal to summertime thermal refuges. The present field study, quantified the early habitat use of age 0 year brook charr in three small, temperate lakes, two with abundant nearshore habitat features and another with very little. Habitat use was sampled over 2–3 day intervals several times through the month of May 1995 in an attempt to detect changes in microhabitat selection within and among lakes. In addition, the availability of nearshore habitat was quantified in each lake. The aims of this field study are two-fold. First, to provide a detailed quantitative description of early habitat use by age 0 year brook charr that does not yet exist in the literature. Second, to test the null hypothesis that the magnitude of variables used to describe the spatial location of individual fish do not change significantly over time.

MATERIALS AND METHODS

HABITAT USE

Habitat use by age 0 year brook charr was determined from snorkelling observations in three small lakes located in Algonquin Provincial Park, Ontario, Canada. Although information on the habitat of age 0 year brook charr in lakes is sparse relative to information available on stream habitats, particularly for their early habitat (Wurtsbaugh *et al.*, 1975), prior observations have confirmed that brook charr remain in the near-shore littoral zone of lakes during May and early June each year (Snucins *et al.*, 1992; Biro & Ridgway, 1995; Biro *et al.*, 1997; Biro, 1998). In mid to late summer, age 0 year brook charr have been observed in nearshore littoral areas but also occur

in deeper habitats near the substrata many metres from shore (Venne & Magnan, 1995).

Observations began within 2 weeks of when contiguous ice was no longer present. Young brook charr were not observed beyond early June as the fish were quite large and extremely wary by this time preventing observations of undisturbed fish. Dispersal patterns observed early in the spring after ice melting accurately portray movement and distribution of age 0 year brook charr for nearly 2 months following the first week of movement (Coombs & Rodriguez, 2007).

STUDY LAKES

Habitat use was observed in Mykiss, Scott and Charles Lakes all of which contain naturally reproducing populations of brook charr. Mykiss and Scott Lakes contain abundant woody debris, inundated shoreline vegetation, dense riparian vegetation and are forested to the water's edge. Charles Lake was chosen to provide a marked contrast to the other lakes in that it has a homogeneous shoreline and littoral zone composed of sand, pebble and cobble. Virtually no woody debris or inundated shoreline vegetation exists since the riparian vegetation and forest are situated back somewhat from the water's edge relative to Mykiss and Scott Lakes. Mykiss Lake (45°40' N; $78^{\circ}10'$ W) is a small lake (surface area = 23.5 ha; maximum depth = 11 m) with good visibility (Secchi disc = 4.8 m). The study site was an 800 m section of shoreline adjacent to the spawning area of the lake where many recently emerged age 0 year brook charr could be observed. Habitat use in this lake was quantified from 2 to 28 May 1995. For summary of the data and statistical analyses, the data were grouped into four intervals and defined according to a date which approximated the sampling period as follows: 2–4 May = 3 May; 7–8 May = 7 May; 18–19 May = 18 May and 27–28 May = 27 May. Thus, c. 4 days separate the first and second intervals and c. 10 days separate subsequent intervals.

Scott Lake ($48^{\circ}29'$ N; $78^{\circ}43'$ W) is small (surface area = 27.6 ha; maximum depth = 25 m) with excellent visibility (Secchi disc = 7.5 m). The study site was also an 800 m section of shoreline which was adjacent to the primary spawning area. Habitat use was quantified from 3 to 30 May and the sampling days for data summary were grouped as follows: 3-5 May = 4 May; 9-10 May = 9 May; 20-21 May = 20 May and 29-30 May = 29 May. The period between the first and second intervals is therefore *c*. 5 days with 10 days between successive intervals.

Charles Lake $(45^{\circ}54' \text{ N}; 78^{\circ}43' \text{ W})$ is the smallest of the three lakes (surface area = 12·3 ha; maximum depth = 8·2 m) with excellent visibility (Secchi disc = 6·4 m). The study site was a 200 m section of shoreline adjacent to the small, concentrated spawning area. Charles Lake was sampled only on 1 day for each interval, 6, 16 and 26 May because sufficient sample size could be achieved easily in 1 day owing to the concentrated and easily seen young.

BROOK CHARR HABITAT OBSERVATIONS

Snorkelling observations of brook charr habitat use were conducted by a single observer floating at the surface between 1000 and 1500 hours each day. The use of a single observer eliminated the possibility of between-observer bias. Individual fish were haphazardly selected to observe for habitat use as follows: fish were located from a distance of several metres and then, if it appeared undisturbed, were approached to within 2 m. The observer then lay motionless observing fish movements with respect to riparian habitat features present. In Charles Lake, however, fish were considerably more wary of the observer which did not allow observation of fish at close range but did allow their position to be noted at a distance (2–3 m away) before it would begin to avoid the observer. In Scott and Mykiss Lakes, sedentary fish were observed for 1–2 mins and active fish for up to 5 mins; in Charles Lake fish were observed for 1 min due to their high activity and wariness preventing from being individuals followed.

At the end of this observation period the position for sedentary fish, or the most frequently occupied position for active fish, was noted in relation to background features to assist in recording habitat measurements. Fish were then captured with a dip-net whenever possible, measured to the nearest mm (total length, $L_{\rm T}$) and released. In Charles Lake, it was not possible to capture the observed individuals owing to their wariness. Therefore, a beach seine was used to capture fish from several areas within the study site following observations.

MICROHABITAT MEASUREMENTS

The following microhabitat measurements were made from the noted position of each fish: (1) depth of the fish in the water column measured from the surface, or simply fish depth, because brook charr feed from the surface and water column exclusively (Biro & Ridgway, 1995), (2) distance from the nearest object (*e.g.* rock and log), (3) distance from shore, (4) water column depth, (5) overhead riparian canopy and (6) water temperature. Overhead riparian cover was quantified using a clear plexiglas sheet overlain with a 60×60 mm grid following the observation; the observer positioned his head over the observed position of each fish, looked up from the water surface and through the grid system and recorded the number of squares containing branches or vegetation. In cases where fish were found within inundated vegetation, the grid was placed over the noted position to estimate the amount of overhead canopy.

Substratum was not recorded since age 0 year brook charr do not forage from or near the substratum and occupy positions near the surface in these lakes (Biro & Ridgway, 1995; Biro *et al.*, 1997; pers. obs.). Water temperature was recorded with an electronic thermistor at, or as close as possible to the position of the observed fish within 1 h of the observation. To estimate the ability of different habitat features to attract young brook charr, the number of conspecifics within a square metre with the observed individual at its centre were counted, producing an estimate of local population density (Grant, 1990).

HABITAT FEATURES

The submerged and floating objects associated with individual fish positions were classified into seven categories which encompassed the breadth of habitat features used by the fish and that available in the environment: (1) inundated leatherleaf *Chamae-daphne calyculata* (L.) Moench, which consisted of dense stems overhanging into the water or growing out of the shore providing a very complex habitat (fish were often well within the stems), (2) coarse woody debris (CWD; woody debris >100 mm diameter) which was then further categorized with respect to its orientation relative to the shore-line as parallel (<45°) or (3) perpendicular (pointing offshore; >45°), (4) boulder, which was taken to include any rock >0.5 m in diameter located within 1–2 m of shore, (5) the shoreline itself, (6) sticks, that included any accumulation of fine woody debris <20 mm in diameter and (7) inundated grass. The CWD comprised logs floating adjacent to the shoreline (*i.e.* parallel and within 3 m of shore) or fallen trees floating at or near the surface and extending many metres offshore

HABITAT AVAILABILITY

Habitat availability was surveyed on a series of linear transects, perpendicular to the shoreline and extending 12 m from the shore. Each transect line was surveyed at 2 m intervals for water column depth and overhead riparian cover. In addition, at each point on the transect each habitat feature was recorded which was located both within a 1 m radius of the sampling point and within 0.5 m of the water surface. This second criterion was chosen since previous observations indicated that age 0 year brook charr occupied only shallow positions within 0.3 m of the surface (Biro & Ridgway, 1995).

At the shoreline (0.10 m from shore), overhead canopy and the habitat feature present at that point were measured. A total of 80 transect lines were surveyed in each lake, extending 100 m to either side of the centre of the spawning area (*i.e.* transects were spaced 2.5 m apart).

STATISTICAL ANALYSES

Raw data are presented in all tables and figures. To determine if the relative use of each habitat type differed significantly with sampling date a row by column ($R \times C$) independence test (Sokal & Rohlf, 1981) was used. All other statistical analyses were performed on log₁₀ transformed data. ANOVA was used to test for significant differences in the distance from shore, distance from object and fish depth between sampling intervals. These variables were chosen because they are significantly related to age 0 year brook charr foraging movements and foraging success (Biro & Ridgway, 1995; Biro et al., 1996). The variables riparian canopy and water depth were not used in this analvses as they are correlates of distance from shore (P < 0.05). To meet the assumptions of the ANOVA, homogeneity of variances among sampling intervals was tested using Bartlett's χ^2 test and, when homogeneous (P > 0.05), Tukey's honestly significant difference (HSD) all pair-wise post hoc test was used to detect where significant differences occurred (Wilkinson, 1990). Instances when variances among treatments were unequal (P < 0.01), a Games–Howell (GH) unplanned *post hoc* test for comparisons of means with unequal variances or sample sizes was used (Games & Howell, 1976; Sokal & Rohlf, 1981; Day & Quinn, 1989). Games-Howell and independence test statistics were calculated using a calculator (Sokal & Rohlf, 1981) and all other analyses using the SYSTAT statistical package (Wilkinson, 1990).

RESULTS

PHYSICAL HABITAT FEATURES PRESENT

Shoreline vegetation and woody debris was abundant in Mykiss and Scott Lakes but almost entirely absent in Charles Lake (Table I). The only habitat features present in Charles Lake was inundated leatherleaf and grass along the shoreline. Woody debris, in the form of logs floating at the surface, was common at distances up to 6 m from shore in Mykiss and Scott Lakes with a few large fallen trees extending out to 12 m from shore (Table I). The greatest variety and total number of habitat features were present 2 m from shore in Mykiss and Scott Lakes and at the shoreline in Scott Lake. Floating logs were the only habitat feature present at transects points which were >6 m from shore (Table I) which is not surprising given the relatively deep depths in those locations.

Overhead cover, in the form of overhanging trees and shoreline brush was extremely abundant along the shoreline in Mykiss and Scott Lakes (80 and 80 and 78 and 80 transects, respectively, had some cover). There was almost complete overhead cover present at those shoreline locations in both lakes (mean = 97%). Charles Lake, however, had considerably less shoreline cover with only 57 and 80 transects possessing some cover and, where present, had moderate coverage of 75%. Except for these shoreline transects, there was no cover further from shore. Mykiss and Scott Lakes had small to moderate amounts of cover at 2 and 4 m from shore and sporadic amounts of cover farther from shore.

		Distance from shore (m)							
Lake	Habitat feature	0	2	4	6	8	10	12	
Charles	п	77	0	0	0	0	0	0	
	L-L	66							
	Log-P								
	Log-OS								
	Boulder								
	Grass	34							
	Sticks								
Mykiss	n	76	113	44	23	9	12	7	
-	L-L	82	17						
	Log-P		38	57	26	11			
	Log-OS		29	43	61	89	100	100	
	Boulder	12	15		13				
	Grass	6	1						
	Sticks								
Scott	n	38	106	70	22	16	11	6	
	L-L	47	1	3					
	Log-P		40	22	14	6			
	Log-OS		45	67	86	96	100	100	
	Boulder	5	1						
	Grass	24	6	4					
	Sticks	24	7	4					

 TABLE I. Number of habitat features enumerated (n) and the per cent relative frequency of the habitat types as a function of distance from shore in the three study lakes. A total of 80 transect points were sampled at each distance from shore

L-L, leatherleaf (inundated shoreline plant); Log-OS, floating log pointing offshore; Log-P, floating log with parallel orientation.

HABITAT USE BY INDIVIDUAL BROOK CHARR

Mykiss and Scott Lakes

Charr in Mykiss and Scott Lakes were observed near the shoreline and in relatively shallow water (Table II). Some individuals were as close as 10 mm from shore in 30 mm depths ranging up to 26.5 m from shore in >5 m depths. Fish were consistently near the surface (mean fish depth = 0.40 m) and were close to habitat features (mean distance <0.14 m; Table II). Numerous fish were as little as 0.005 to 0.01 m below the surface and 0 to 0.02 m from habitat features, although a very few fish occurred as much as 0.29 m below the surface and 2.7 m from habitat features. Fish occurred in areas of moderate riparian canopy (57–86% cover) ranging from 100% cover for those close to shore and none for those further from shore (Table II).

There were significant changes in the distance from shore, distance from submerged objects and fish depth of individual fish positions among the sampling intervals in Mykiss and Scott Lakes (ANOVA, all P < 0.01). Fish were significantly further from shore in the second, third and fourth intervals than in the first interval in Mykiss Lake [HSD test, P < 0.05; Fig. 1(a)] and Scott Lake

			r.	loc	al popula	tion den	sity			,		
Variable		Mean			S.D.			Range			и	
Lake	C	Μ	S	С	Μ	S	U	Μ	S	C	Μ	S
Distance to shore (m)	0.51	2.25	1.33	0.39	$4 \cdot 18$	$1 \cdot 80$	0.05 - 2.70	0.01 - 20.50	0.01 - 14.00	159	196	179
Distance to object (m)	Na	0.06	0.14	Na	0.06	0.27	Na	0.01 - 0.37	0.00-2.40	Na	196	180
Fish depth (m)	0.06	0.04	0.04	0.07	0.04	0.02	0.01 - 0.66	0.01 - 0.29	0.01 - 0.17	159	188	180
Depth (m)	0.11	0.74	0.41	0.84	$1 \cdot 11$	0-44	0.01 - 0.70	0.03 - 5.53	0.03 - 3.50	159	192	180
Overhead cover (%)	7·0	57.0	86.0	25.0	46.0	32.0	0 - 100	0 - 100	0 - 100	109	196	180
Temperature (° Č)	12·8	11.3	12.5	$6 \cdot 0$	2.6	3.0	$12 \cdot 0 - 14 \cdot 8$	$8 \cdot 1 - 16 \cdot 5$	8.2 - 18	Na	188	182
$L_{\rm T}$ (mm)	33·0	29.0	28.0	5.1	4.6	5.0	25-50	23-42	21-43	107	188	186
Local fish	5.1	$2 \cdot 1$	2.7	3.6	l·l	1.5	1 - 16	1 - 6	1^{-7}	134	169	171
density (number m^{-2})												
Na, not applicable.												

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FIG. 1. Tukey box plots showing the distance from shore (a) in Mykiss, (b) Scott and (c) Charles Lakes, distance from submerged habitat features in (d) Mykiss and (e) Scott Lakes and fish depths in (f) Mykiss, (g) Scott and (h) Charles Lakes of individual age 0 year brook charr in May 1995. The extents of the boxes indicate the 25th and 75th percentiles. The thin line inside the box indicates the 50th percentile and the thick line indicates the mean. The capped bars indicate the 10th and 90th percentiles and symbols mark all data outside the 10th and 90th percentiles.

[GH test, P < 0.01; Fig. 1(b)]. Fish were significantly further from habitat features in the third and fourth intervals than in either the first or the second interval in Mykiss Lake [GH test, all P < 0.05; Fig. 1(d)] whereas the distance from these objects increased significantly in the second and third intervals from the first interval in Scott Lake [GH test, P < 0.01; Fig. 1(e)]. Fish were significantly deeper in the third interval than in the first interval in Mykiss Lake [HSD test, P < 0.05; Fig. 1(f)]. In Scott Lake, fish depth was significantly greater in the third and fourth intervals than in the first [GH test, P < 0.05; Fig. 1(g)].

Charles Lake

In contrast to that observed in the other two lakes, brook charr in Charles Lake were associated solely with the shoreline and were confined to a narrow band with fish only 0.5 m from shore on average and all fish within 3 m of shore during May (Table II). Fish were observed in water as shallow as 0.01 m deep and 0.05 m from shore to as much as 0.70 m deep and 2.7 m from shore (Table II). The depth of fish in the water column (fish depth) increased with the distance from shore (r = 0.45, P < 0.01). This reflects the fact that age 0 year brook charr tended to be in the mid-portion of the water column (mean fish depth = 0.06 m, mean water depth = 0.11 m; Table II). Further, when disturbed by the observer, fish moved closer to shore and away from the observer rather than orienting to, or hiding among the substratum (*e.g.* cobble) or other habitat features (none present) when frightened. For these reasons the nearest object is reported as shore in all cases. Thus, distance from shore can be thought of as being equivalent to distance from cover.

There were significant changes in the distance from shore and fish depth of individual fish among the sampling intervals in May (ANOVA, both P < 0.01). The distance from shore and fish depth in the water column did not differ between 6 May and 16 May [P > 0.05; Fig. 1(c), (h)]. Fish were, however, significantly further from shore on 26 May than on either 6 May or 16 May [HSD test, both P < 0.05; Fig. 1(c)] and were significantly deeper in the water column on 26 May than on 6 May [GH test, P < 0.05; Fig. 1(h)].

CHANGES IN HABITAT FEATURES USED BY BROOK CHARR

In Mykiss and Scott Lakes, age 0 year brook charr were closely associated with a variety of riparian habitat features in the littoral zone while in Charles Lake fish were closely associated only with the shoreline itself. Other habitat features, such as inundated vegetation or woody debris, were not present in Charles Lake, thus, the only habitat feature associated with fish was the shoreline (Table I). Habitat features associated with individual fish positions changed significantly with date over the study period in Mykiss ($R \times C$ independence test, G = 41, P < 0.01; Table III) and Scott lakes (G = 29, P < 0.05; Table III). In Mykiss and Scott Lakes, inundated leatherleaf and floating logs pointing offshore were some of the most frequently used riparian habitat features followed by floating logs (Table III). Other shoreline habitat features made up lesser proportions in both lakes except in Scott Lake where grass made up a large proportion of habitat types used while grass was unused in Mykiss Lake owing to its rarity (Tables I and III).

Habitat types which attracted the highest local fish densities were complex shoreline features such as the shoreline itself, shoreline boulders, sticks and leatherleaf in Mykiss Lake (Fig. 2). Relatively low local densities were associated with CWD on average in both lakes, perhaps due to its simple structure. Some caution should be applied in interpreting these density-habitat results because while many nearshore habitat features occurred in patches, more than one habitat type was often close by, such as a log among a patch of leatherleaf. In the absence of CWD and inundated vegetation, fish in Charles Lake were not only restricted in distribution to within a metre of the shoreline (Fig. 1) but were observed at considerably higher mean and maximum density than brook charr in the other two lakes (Table II). On average, local fish density

Habitat feature	3 May		7 May		18 May		27 May	
Lake	S	Μ	S	М	S	М	S	Μ
Shore	10	7	11	2	11	6	0	8
Boulder	14	16	5	7	9	9	5	2
Grass	22	0	19	0	11	0	15	0
Sticks	10	4	11	0	2	2	2	5
Leatherleaf	19	54	16	29	25	26	25	25
Log-parallel	19	4	14	15	26	19	22	22
Log-offshore	7	13	24	46	25	38	30	38
n	59	68	37	41	44	47	40	40

TABLE III. Percentage of age 0 year brook charr in association with various habitat features at each sampling interval at Scott (S) and Mykiss (M) Lakes. Charles Lake is omitted due to absence of shoreline habitat features

n, number of fishes.

(number m⁻², was substantially greater in Charles Lake (mean = $5 \cdot 1$ and range 1–16) than in either Mykiss (mean = 2 and range 1–6) or Scott lakes (mean = $2 \cdot 7$ and range 1–7; Table II).

There is evidence that the increasing distance from shore and increasing distance from habitat features (including the shoreline for fish in Charles Lake) may be linked with increasing temperatures and $L_{\rm T}$. The rapid increase in the distance from shore and the distance from habitat features between the first, second and third intervals follows a pattern similar to the rapid temperature increases over those intervals (Fig. 3). Fish $L_{\rm T}$ also increased over this period in all lakes (P < 0.05; Fig. 3).

DISCUSSION

Underwater observations of age 0 year brook charr over several periods within the year have made it possible to provide for the first time, a detailed quantitative description of the early habitat use by this species. This study has revealed that edge habitat, including inundated riparian vegetation, CWD and the shoreline itself are important elements of the early habitat of age 0 year brook charr in lakes. Comparison of habitats used in relation to those available indicated that young brook charr used habitat structure based on availability, using complex woody debris when present and shoreline areas when it was absent. Through several weeks after ice-out there were changes in the habitat features associated with individual fish positions and the microhabitat variables describing individual fish positions. The largest changes occurred over very short periods in early May, in as few as 4 or 5 days in Mykiss and Scott Lakes.

The earliest habitats of young brook charr were those within 1 m of the shoreline, and included inundated shoreline vegetation and CWD adjacent to shore. Many of these areas become dry by late summer illustrating that the forest riparian zone actually contributes to age 0 year brook charr production in



FIG. 2. Local population density of age 0 year brook charr at individual fish positions associated with the different habitat features (SH, shore; B, boulder; GR, grass; ST, sticks; LL, leatherleaf; LP, log; parallel to shore and LOS, = log; pointing offshore) during May in (a) Mykiss and (b) Scott Lakes. Charles Lake is omitted as fish were associated solely with the shoreline.

spring and early summer. Over periods as short as 4-5 days at the start of May, and over 10 day periods later in May, fish were found significantly further from both the shoreline and riparian habitat features. The relative use of different habitat features paralleled the changes in these microhabitat variables; those which were further from shore, namely fallen floating logs, became more important. By late May, the use of habitats >3 m from the shore declined as did the relative use of CWD. Early in May when fish were quite small and temperatures were low (Fig. 3), brook charr foraging activity was relatively low at this time when fish were very near habitat features; later in May, fish were larger, the water much warmer and fish foraged more actively further from habitat features (Biro & Ridgway, 1995).



FIG. 3. Plots showing mean ± s.D. (a) temperatures associated with fish positions in Mykiss (●) and Scott (●) and Charles (▲) Lakes and (b), total length (L_T) of age 0 year brook charr captured in Mykiss, Scott and Charles lakes as functions of date.

In Mykiss Lake, cohort-scale dispersal of age 0 year brook charr in spring is described by an exponential decay model incorporating two groups (mobile and sedentary) (Coombs & Rodriguez, 2007). The model predicted the spatial distribution of the cohort in the shallow littoral zone several weeks later based on variables describing cohort distribution in the first week or so after emergence. Therefore, subtle habitat changes described in the first weeks after emergence, indeed within the first week, do not appear to mark fundamental changes in the spatial spread of a cohort since early movement variables are sufficient to predict cohort distribution 7 weeks after emergence. Rather, the trend for fish to be farther from shoreline edge habitats over time probably reflects greater rates of activity associated with increasing food requirements and improved abilities to evade predators (Biro & Ridgway, 1995). In any case, the presence of complex shoreline habitat may serve to increase the area of edge

habitat and therefore reduce local population density (this study) and potentially reduce competition.

These results are consistent with the only other published works on recently emerged brook charr habitat in lakes which reported only that they were most abundant near springs used for spawning, in areas within 0.10 to 0.20 m from shore (Wurtsbaugh et al., 1975; Snucins et al., 1992). The multiple functions of CWD in streams have been well documented, but its importance in lakes remains largely unstudied. In streams, CWD has been shown to reduce emigration and increase production of juvenile salmonids (Dolloff, 1986; Bilby & Bisson, 1987) and areas lacking CWD tend to contain fewer salmonids (Dolloff, 1986; Murphy et al., 1986; Fausch & Northcote, 1992). It has also been suggested that CWD may provide cover and reduce predation (Bustard & Narver, 1975a, b; Reiser & Bjornn, 1979; Tschaplinski & Hartman, 1983). The significance of CWD to brook charr in lake environments may play a similar role in spring (this study) and perhaps, to a lesser extent, throughout the summer as well. In one lake without CWD, however, brook charr were observed in tight association with the shoreline and the shallowest habitats present, and there was no indication that there were fewer brook charr or that their growth rates were lower. Therefore, the role of CWD in affecting growth or survival of brook charr in lakes is not clear.

Studies of age 0 year brook charr and rainbow trout Oncorhynchus mykiss (Walbaum) in lakes suggest that selection of complex cover in nearshore areas, and selection of shallow nearshore areas, represents a trade-off between foraging offshore to exploit abundant zooplankton prey and remaining near cover to minimize risk of predation (Wurtsbaugh et al., 1975; Tabor & Wurtsbaugh, 1991; Biro et al., 2003a, b). Supporting this trade-off hypothesis, adult brook charr and mergansers (Mergus sp.) were often observed feeding in littoral areas and age 0 year brook charr frightened by them would move closer to the shoreline or woody debris and attempt to place distance and visual barriers between themselves and the predator (P. Biro, pers. obs.). Cannibalism may be the largest predation risk to young brook charr in the lakes studied, as one previous study (Griswold, 1967) observed that 20% of adult brook charr captured before mid-July had one to two age 0 year brook charr in the in gut with as many as 10 in one adult fish. Adult brook charr were observed successfully capturing young brook charr in the nearshore littoral zone, in particular those which stray away from floating logs in Mykiss Lake, at rates of up to one capture every 5 or 10 mins (P. Biro, pers. obs.).

It will probably be some time before a better understanding is gained of whether the production of young salmonines in lakes is limited by habitat, competition or predation. Studies such as this one, in addition to those investigating foraging and social behaviours in relation to habitat use, should improve knowledge of these potentially limiting factors. In the meantime, shoreline development practices (*i.e.* cottage development) should consider leaving buffer strips around the shoreline to ensure that inputs of CWD and shoreline vegetation will persist over time until its role is more fully understood. Finally, steps should be taken to minimize the shoreline development of brook charr lakes especially near spawning areas which tend to be few and spatially concentrated (Ridgway & Blanchfield, 1998). This is important since woody debris and shoreline vegetation are often the first features to disappear from the shoreline with recreational and cottage development.

We thank H. Brunstad for field assistance and R. McLaughlin for statistical advice. This study was funded by the Ontario Ministry of Natural Resources. We thank the staff at Harkness Lab for field support. PAB was supported by an NSERC and UTS Chancellors postdoctoral fellowships during completion of this manuscript.

References

- Bilby, R. E. & Bisson, P. A. (1987). Emigration and production of hatchery Coho salmon (*Oncorhynchus kisutch*) stocked in streams draining and old-growth and a clear- cut watershed. *Canadian Journal of Fisheries and Aquatic Sciences* 44, 1397–1401.
- Biro, P. A. (1998). Staying cool: behavioral thermoregulation during summer by young-ofthe-year brook trout in a lake. Transactions of the American Fisheries Society 127, 212–222.
- Biro, P. A. & Ridgway, M. S. (1995). Individual variation in foraging movements in a lake population of young-of the-year brook charr (*Salvelinus fontinalis*). *Behaviour* **120**, 1–12.
- Biro, P. A., Ridgway, M. S. & McLaughlin, R. L. (1996). Does the rate of foraging attempts predict ingestion rate for young-of-the-year brook trout (Salvelinus fontinalis) in the field? Canadian Journal of Fisheries and Aquatic Sciences 53, 1814–1820.
- Biro, P. A., Ridgway, M. S. & Noakes, D. L. G. (1997). The central-place territorial model does not apply to space-use by juvenile brook charr (*Salvelinus fontinalis*) in lakes. *Journal of Animal Ecology* 66, 837–845.
- Biro, P. A., Post, J. R. & Parkinson, E. A. (2003a). From individuals to populations: risktaking by prey fish mediates mortality in whole-system experiments. *Ecology* 84, 2419–2431.
- Biro, P. A., Post, J. R. & Parkinson, E. A. (2003b). Population consequences of a predator-induced habitat shift by trout in whole-lake experiments. *Ecology* 84, 691–700.
- Borwick, J., Buttle, J. & M. S. Ridgway (2006). A topographic index approach for identifying groundwater habitat of young-of-year brook trout (*Salvelinus fontinalis*) in the land-lake ecotone. *Canadian Journal of Fisheries and Aquatic Sciences* 63, 239–253.
- Bustard, D. R. & Narver, D. W. (1975a). Aspects of the winter ecology of juvenile coho (*Oncorhynchus kisutch*) and steelhead trout (*Salmo gairdneri*). Journal of the Fisheries Research Board of Canada **32**, 667–680.
- Bustard, D. R. & Narver, D. W. (1975b). Preferences of juvenile coho salmon (*Oncorhynchus kisutch*) and cutthroat trout (*Salmo clarki*) relative to simulated alteration of winter habitat. *Journal of the Fisheries Research Board of Canada* 32, 681–687.
- Coombs, M. F. & Rodriguez, M. A. (2007). A field test of simple dispersal models as predictors of movement in a cohort of lake-dwelling brook charr. *Journal of Animal Ecology* 76, 45–57.
- Day, R. W. & Quinn, G. P. (1989). Comparisons of treatments after an analysis of variance. *Ecological Monographs* 59, 433–463.
- Dolloff, C. A. (1986). Effects of stream cleaning on juvenile coho salmon and dolly varden in southeast Alaska. *Transactions of the American Fisheries Society* 115, 743–755.
- Fausch, K. D. & Northcote, T. G. (1992). Large woody debris and salmonid habitat in a small coastal British Columbia stream. *Canadian Journal of Fisheries and Aquatic Sciences* 49, 682–693.
- Games, P. A. & Howell, J. F. (1976). Pairwise multiple comparison procedures with unequal n's and/or variances: a Monte Carlo study. *Journal of Educational Statistics* 1, 113–125.

- Grant, J. W. A. (1990). Aggressiveness and the foraging behaviour of age-0 brook charr (Salvelinus fontinalis). Canadian Journal of Fisheries and Aquatic Sciences 47, 915–920.
- Grant, J. W. A. & Noakes, D. L. G. (1987). Movers and stayers: foraging tactics of young-of-the-year brook charr, *Salvelinus fontinalis*. *Journal of Animal Ecology* 58, 773–789.
- Griswold, B. L. (1967). Some aspects of the shore spawning of brook trout (*Salvelinus fontinalis* Mitchell). MSc Thesis, University of Maine, Orono, ME.
- Guyette, R. P. & Cole, W. G. (1999). Age characteristics of coarse woody debris (*Pinus strobus*) in a lake littoral zone. *Canadian Journal of Fisheries and Aquatic Sciences* 56, 496–505.
- Mallory, E. C., Ridgway, M. S., Gordon, A. M. Kaushik & N. K. (2000). Distribution of woody debris in a small headwater lake, central Ontario. *Archiv für Hydrobiologie* 148, 587–606.
- McLaughlin, R. L. (2001). Behavioural diversification in brook charr: adaptive responses to local conditions. *Journal of Animal Ecology* 70, 325–337.
- Murphy, M. L., Heifetz, J. H., Johnson, S. W., Koski, K. V. & Thedinga, J. F. (1986). Effects of clear-cut logging with and without buffer strips on juvenile salmonids in Alaskan streams. *Canadian Journal of Fisheries and Aquatic Sciences* 43, 1521–1533.
- Reiser, D. W. & Bjornn, T. C. (1979). Habitat requirements of anadromous salmonids. USDA Forest Service General Technical Report PNW-96.
- Ridgway, M. S. & Blanchfield, P. J. (1998). Brook trout spawning areas in lakes. *Ecology* of Freshwater Fish 7, 140–145.
- Snucins, E. J., Curry, R. A. & Gunn, J. M. (1992). Brook trout (Salvelinus fontinalis) embryo habitat and timing of alevin emergence in a lake and a stream. Canadian Journal of Zoology 70, 423–427.
- Sokal, R. R. & Rohlf, F. J. (1981). Biometry, 1st edn. San Francisco, CA: W. H. Freeman.
- Tabor, R. A. & Wurtsbaugh, W. A. (1991). Predation risk and the importance of cover for juvenile rainbow trout in lentic systems. *Transactions of the American Fisheries Society* 120, 728–738.
- Tschaplinski, P. J. & Hartman, G. F. (1983). Winter distribution of juvenile coho salmon (*Oncorhynchus kisutch*) before and after logging in Carnation Creek, British Columbia, and some implications for overwinter survival. *Canadian Journal of Fisheries and Aquatic Sciences* **40**, 452–461.
- Venne, H. & Magnan, P. (1995). The impact of intra- and interspecific interactions on young-of-the-year brook charr, in temperate lakes. *Journal of Fish Biology* 46, 669–686.
- Wilkinson, J. D. (1990). SYSTAT: the System for Statistics. Evanston, IL: SYSTAT Inc.
- Wurtsbaugh, W. A., Brocksen, R. W. & Goldman, C. R. (1975). Food and distribution of underyearling brook and rainbow trout in Castle Lake, California. *Transactions of* the American Fisheries Society 104, 88–95.