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The central-place territorial model does not apply to space-use by juvenile brook charr *Salvelinus fontinalis* in lakes

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Summary

1. Territoriality is widely accepted as the mechanism responsible for density-dependent mortality, emigration, and 'self-thinning' of populations of juvenile salmonine fishes in streams. Numerous studies have focused on territoriality exclusively in stream (lotic) environments and thus have fostered a stereotyped view of juvenile salmonines as sedentary and territorial. We term this behavioural paradigm the central-place territorial model (CPTM).

2. We tested predictions characterizing the CPTM for young-of-the-year (YOY) brook charr (*Salvelinus fontinalis*) in two Canadian lakes to determine if territoriality may also potentially limit space and population size of brook charr in lakes.

3. Our findings were not consistent with the CPTM. Fish in both lakes were not central-place foragers. Maximum displacement distance did not increase with body length as predicted by the general salmonine model of Grant & Kramer (1990). Net displacement distance increased with the proportion of time spent moving. Aggressive frequency was greatest for fish which spent large proportions of time moving and did not defend from a central-place.

4. Fish in both lakes were rarely aggressive, highly active, and often moved back over the same areas. However, lake fish which migrated to a tributary stream had no net displacement (central-place foraging) illustrating the immediate effects of current on foraging tactics and space-use.

5. The effect of hydrodynamic environment (flowing vs. still water) on fish behaviour needs to be explicitly considered in future models of salmonine behaviour.

Key-words: behaviour, lentic, population regulation, Salmonidae.

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Introduction

Territorial behaviour has long been thought to limit the population density of juvenile (age 0) salmonines (Pisces, Salmonidae) in streams (Newman 1956; Gerking 1959; Chapman 1962, 1966; Gibson 1993). Young salmonines are typically territorial in their first year of life (see Elliott 1994) and evidence suggests that the population dynamics of young stream salmonines is related to density-dependent growth, mortality or emigration (Elliott 1989, 1990a,b; see also Grant & Kramer 1990, Table 2), and populations 'self-thin' as individuals within a cohort increase in size and crowd one another (Elliott 1993; Grant 1993a). Territoriality provides a mechanism for space-limitation and 'self-thinning', given that territory size increases with body size for a number of salmonine species (Grant, Noakes & Jonas 1989; Elliott 1990b; Grant & Kramer 1990). Since young salmonines in running water typically forage and defend food from a central-place (McNicol, Scherer & Murkin 1985; Grant *et al.* 1989; Grant 1990; Keeley & Grant 1995), we refer to this conceptual model as the central-place territorial model (CPTM).

The CPTM has developed from numerous field and laboratory studies and has become the dominant behavioural paradigm put forth as a mechanism

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responsible for population regulation of salmonines. This stereotyped view of salmonines as territorial central-place foragers is probably a consequence of: (i) the focus on territorial behaviour, which can create a bias (see Gowan *et al.* 1994); and (ii) the observation that quantitative behavioural studies are almost invariably carried out solely in streams despite the large number of salmonine populations residing in lake environments (but see Biro & Ridgway 1995; Biro, Ridgway & McLaughlin 1996). This field study tests the CPTM for young-of-the-year (YOY) brook charr (*Salvelinus fontinalis* Mitchill) in lakes, to determine whether central-place territoriality exists as a potential mechanism of population regulation as proposed for stream salmonines.

Based on stream observations, territoriality is not predicted to occur in stillwater environments given that invertebrate food resources are abundant and predictable in flowing water but not in stillwater (Elliott 1970; Allen & Russek 1985; Grant & Noakes 1987); for example, YOY brook charr in stillwater side-pools in streams are active and rarely aggressive (McLaughlin, Grant & Kramer 1992, 1994) but, when in running water, are sedentary and territorial (Grant & Noakes 1987, 1988). However, if food resources in stillwater environments occur as spatially clumped or spatially predictable food patches, fish may become territorial (Grant 1993b); for instance, spatial clumping (Grant & Guha 1993) and spatial predictability (Grand & Grant 1994) of food promoted convict cichlids (*Cichlasoma nigrofasciatum* Gunther) to be sedentary, aggressive, and monopolize food resources in stillwater aquaria. Thus, salmonines in lakes may be territorial even in the absence of current, which has traditionally been thought to determine the presence or absence of territoriality (Noakes & Grant 1986; Noakes 1989).

Lake-dwelling YOY brook charr are active foragers and show little aggression overall, but a substantial portion ($\approx 30\%$) of one population was quite sedentary and spent less than 20% of search time moving (Biro & Ridgway 1995). Unfortunately, that study did not relate aggression to the spatial distribution of foraging and aggressive behaviour so it is not known whether the sedentary portion of the population was defending territories. In streams, only a portion (40%) of the population may be territorial (Grant 1990) and account for the density-dependent population regulation proposed for salmonines (Grant & Kramer 1990). Those fish that are not territorial are relatively active due to displacement from preferred foraging sites (McNicol *et al.* 1985; Grant & Noakes 1988) and presumably emigrate downstream (Chapman 1962; Mason & Chapman 1965; Nakano 1995) or die (Elliott 1986). Similarly, it is possible that the sedentary brook charr in the lake are territorial, displace subordinate individuals and account for the many active individuals.

The CPTM may be evaluated for YOY brook charr in lakes by testing several predictions derived from numerous field studies.

1. There is no net displacement (distance between fish's position at start and end of observation should be approximately equal to zero). Since territorial fish hold stable positions to which they return following aggressive and foraging excursions (see above), there should be no net displacement as a result of their movements (Fig. 1). To validate this prediction, and to evaluate the effect of hydrodynamic environment on space-use, we measured net displacement distances for brook charr residing in a stream following an initial period of lake residence where they were spawned.

2. Maximum displacement distance (distance between two furthest points visited by the fish; Fig. 1) increases with body size within the bounds of the general salmonine model adopted from Grant & Kramer (1990; see Methods).

3. Net displacement distance does not vary with the proportion of search time spent moving, with an upper bound of 20% of search time spent moving. Fish in running water typically spend less than 20% of search time moving relative to the substrate while away from the central-place (Grant & Noakes 1988; McLaughlin & Grant 1994). Thus, with little or no variation in net displacement and such low and invariable mobility (relative to the substrate), net displacement is not expected to vary with the proportion of search time

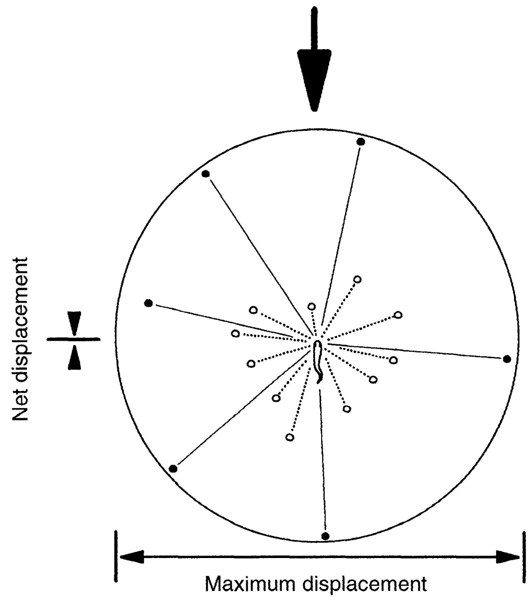

Fig. 1. Overhead view of a typical juvenile salmonine in its territory. The snout of the fish represents the location of the central-place and the circle represents the boundary of the territory. Solid lines and circles represent the direction and location of aggressive interactions, respectively. Dotted lines and open circles represent the direction and location of attempts to capture prey, respectively. Length of lines represent relative distances of each behaviour from the central-place. The arrow indicates direction of the water current. Adopted and redrawn from figures in Grant *et al.* (1989) and Keeley & Grant (1995).

spent moving and data are expected to fall within these bounds.

4. The frequency of aggression is (i) inversely related to the proportion of search time spent moving, and (ii) inversely related to net displacement. Aggressive fish are more sedentary than occasionally aggressive or nonaggressive fish and so an inverse relationship between aggression and the proportion of search time spent moving is predicted (Grant *et al.* 1989). Given that territorial fish in running water have no net displacement, aggressiveness should be greatest for those fish and decline for those fish with slightly greater net displacement distances.

If the CPTM is supported, it would suggest that territoriality exists and may potentially limit space and population size as proposed for stream salmonines. If rejected, then the space-limitation hypothesis may be discarded and other potential mechanisms of population regulation may be investigated.

Materials and methods

We observed the behaviour of YOY brook charr from 7 to 30 May, 1994 in two lakes, Mykiss Lake and Scott Lake, located in Algonquin Provincial Park, Ontario, Canada. Both lakes are small (surface area <28 ha) with good visibility (Secchi disc depth >5 m). Location, physical and chemical characteristics, and species assemblages of each lake are given in Fraser (1981, 1989) and Quinn *et al.* (1994). Fish were not observed into June as they became too wary to allow undisturbed observations of their behaviour.

YOY brook charr remain in the littoral zone of Mykiss (Biro & Ridgway 1995) and Scott (Biro 1996) lakes during May and early June each year in very close proximity to shoreline vegetation and woody debris. The study sites were sections of shoreline adjacent to the spawning area of Mykiss (M. Ridgway & P. Blanchfield, unpublished data) and Scott (Blanchfield & Ridgway, 1997) lakes where many recently emerged YOY brook charr could be observed. It was not possible to mark individual fish for behavioural observations. However, the chance of re-observing any particular fish was low since fish densities were high in many parts of the study sites (up to 50 fish in some 10 m sections of the study site) and observations of individual fish were spaced over the entire study site. Local population density of conspecifics measured about the focal fish varied from 0 to 7 and averaged 2·4 charr m^{-2} in Scott Lake and 2·2 charr m^{-2} in Mykiss Lake (Biro 1996).

Focal animal observations (Altmann 1974) of brook charr were made by a single observer (PAB) between 09:45 and 15:30 h on days which were bright and relatively calm. Observations were made using mask and snorkel and recorded by a second observer floating nearby. Fish were observed at a distance of ≈ 1 m away. Prior to commencing observations, the observer lay motionless for several minutes to ensure the focal fish was not disturbed and was feeding. Next, the position of the fish in the water column relative to background features was noted. The number of body lengths travelled by each fish and behavioural events were then called out through the snorkel during alternating 5 s intervals according to methods described in Biro & Ridgway (1995) and Biro *et al.* (1996). A few very mobile fish could not be followed for this length of time due to heavy shoreline debris which impeded the observer. Consequently, observation duration varies among individuals (median duration = 5 min, range = 0·5–5·5 min, $n = 226$). The position of the fish at the end of the observation interval was noted, then the fish was captured with a dipnet and measured (total length, ± 1 mm), and released at the point of capture. The mean body size of YOY brook charr was 30 mm in both lakes (range = 23–42 mm in Mykiss Lake and 22–43 mm in Scott Lake, $n = 109$ for each lake).

Agonistic behaviour was recorded when the focal fish either chased (aggressive behaviour), or was chased (submissive) by a conspecific or, in rare instances, by a heterospecific (see Discussion). Charges and nips were also observed but were included with chases when recording data. More subtle aggressive displays, such as lateral displays (see Keenleyside & Yamamoto 1962) may have occurred but we were unable to detect them.

Forages were defined as the capture of a potential prey item (Biro *et al.* 1996). Intervals without forages or agonistic behaviour were considered intervals of search (McLaughlin *et al.* 1992; Biro & Ridgway 1995). The proportion of search time spent moving was calculated as the proportion of observation intervals where the focal fish moved one body length or more, and the average search speed (calculated for reasons explained below) was calculated as the mean of all search intervals for each individual (McLaughlin *et al.* 1992; Biro & Ridgway 1995).

The net and maximum displacement distances of each fish over the observation period were used as estimates of space used by fish. Net displacement was defined as the linear distance between the starting and finishing position of the fish. Maximum displacement was defined as the linear distance between the two farthest positions visited by the fish. Both displacement measures were estimated by summing together the linear segments of the fish's path along and around the shoreline and shoreline debris (Fig. 2). We used these space-use measures as it was not possible to map the locations of aggressive interactions and forages to calculate areas directly; small hand movements associated with writing on slates underwater clearly disturbed fish, and the presence of overhanging and submerged vegetation made shoreline observations impossible. We also calculated the total displacement distance, the total distance moved by fish, as a third space-use measure which should reflect any tortuousity or redundancy (movement back over previous path) of fish movements. The total displacement

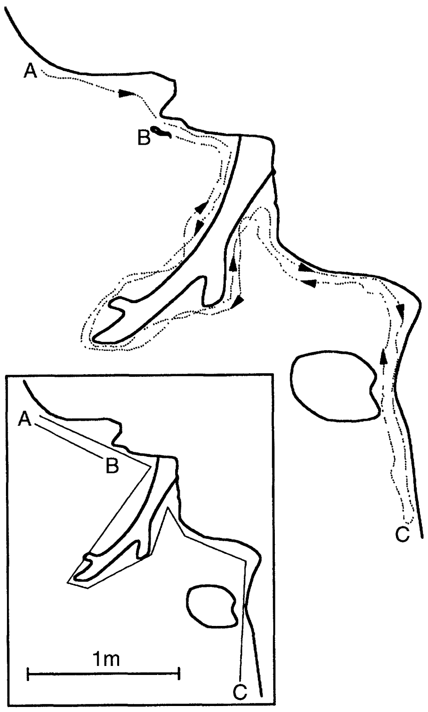

Fig. 2. Overhead view of one particularly active YOY brook charr in relation to the shoreline, and a partially submerged log and boulder. The dotted line and arrowheads indicate the path and direction of the fish, respectively. A and B indicate the positions of the fish at the start and finish of the observation period; C indicates the other extreme position visited by the fish. The distance A–B represents the net displacement (see inset box); A–C represents the maximum displacement distance, measured as the sum of the line segments joining A and C.

(cm) was calculated as the sum of the body length distances moved during search (average search speed [body lengths $5\,s^{-1} \times 12$] × body length [total length in cm] × duration of observation [min]).

For comparative purposes, we also collected net displacement data on 10 and 11 June 1994 for YOY brook charr which had moved from Mykiss Lake into a small inlet stream, hereafter named Mykiss Creek. These stream observations allowed us the opportunity to validate the no-net-displacement prediction for fish in running water (see Results). It also allowed direct comparisons of space-use to be made between individuals originating from a single population but temporarily inhabiting different environments. Observations were made while crouched on the bank after a slow and careful approach to the stream edge and a 5 min wait to ensure fish were not disturbed. The initial and final position of the focal fish over a 5 min observation was plotted on a slate with bottom features sketched on it. Net displacement distance was then measured directly along the bottom using the slate to guide measurements.

Univariate statistics and descriptive graphs are presented using raw data unless indicated otherwise. To meet the required assumptions for parametric statistical tests, aggressive frequencies were square-root transformed while the proportion of time spent moving was arcsine-square-root transformed. Net and maximum displacement distances were $\log_{10}(x + 1)$ transformed since there were several zero values.

Only fish observed for 5 min (165/226) were used to test the predictions of the central-place model. This was to allow comparisons of space-use to be made between individuals since it was not possible to determine whether the measures of space-use vary as a function of observation time; skewness of observation durations was high and could not be corrected with transformation (mean and median duration = 4·5 and 5 min, respectively, skewness = −2·3, kurtosis = 4·4). Consequently, our data are biased toward more sedentary individuals which will make tests of the CPTM conservative. We calculated the maximum displacement vs. body size regression for stream salmonines from the table of raw data used in the interspecific regression of territory size vs. body size by Grant & Kramer (1990) to provide an equivalent regression for comparison to our lake data. Although salmonine territories may be eccentric (Noakes & McNicol 1982), a circle is a reasonable approximation of territory shape (Grant *et al.* 1989; Keeley & Grant 1995) and therefore, the maximum displacement distance of territorial fish should approximate the diameter of the territory (see Fig. 1).

Results

TEST OF THE CPTM

Net displacement distances of brook charr in Mykiss Creek were not significantly different from zero (one-sample $t = 2{\cdot}61$, d.f. = 20, one-tailed $P > 0{\cdot}02$; Bonferroni adjusted critical $P = 0{\cdot}017$). Further, 62% of brook charr (13/21) in Mykiss Creek had net displacement distances equal to zero and 86% (18/21) had net displacement distances $\leqslant 3$ cm, supporting our prediction that the net displacement distance for a central-place forager in running water should approximate zero (Fig. 3). In contrast, brook charr in the lakes had large, variable net displacement distances (Fig. 3). Net displacement distances of brook charr in each lake was significantly greater than zero (Mykiss Lake: $t = 16{\cdot}3$, d.f. = 87, $P \ll 0{\cdot}017$, Scott Lake: $t = 18{\cdot}0$, d.f. = 76, $P \ll 0{\cdot}017$). Only 13% of brook charr (12/88) in Mykiss Lake, and 6% of brook charr (5/77) in Scott Lake, had zero net displacement distances. Brook charr spawned in Mykiss Lake, upon entering Mykiss Creek had significantly lower net displacements than when in the lake (Mann–Whitney $U = 379$, $P < 0{\cdot}00001$; Fig. 3) thus becoming central-place foragers (Fig. 1 vs. Fig. 2).

Larger brook charr had greater maximum displacements than smaller fish in Mykiss Lake ($r^2 = 0{\cdot}05$, $P < 0{\cdot}05$, $n = 82$) but not in Scott Lake ($r^2 = 0{\cdot}03$, $P > 0{\cdot}05$; Fig. 4). Although statistically significant, the variance in maximum displacement

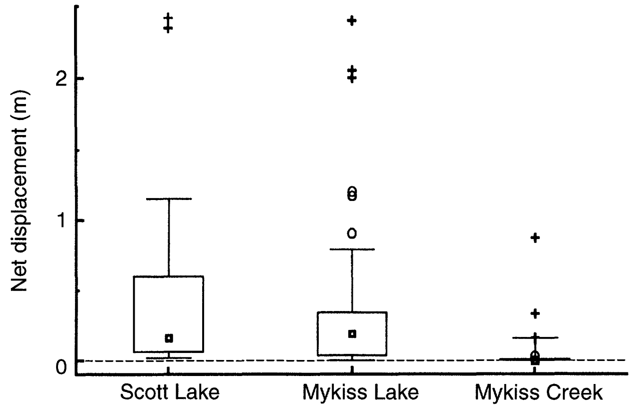

Fig. 3. Box-whisker plot of the net displacement distances of individual brook charr in Mykiss Lake, Scott Lake, and Mykiss Creek. The box indicates the lower 25th and upper 75th percentiles and the whiskers indicate the lower 10th and upper 90th percentiles. The small square within the box indicates the median value. Open circles indicate outliers (values > 1·5 × height of the box) and the addition symbol indicates extreme values (> 3 × height of the box).

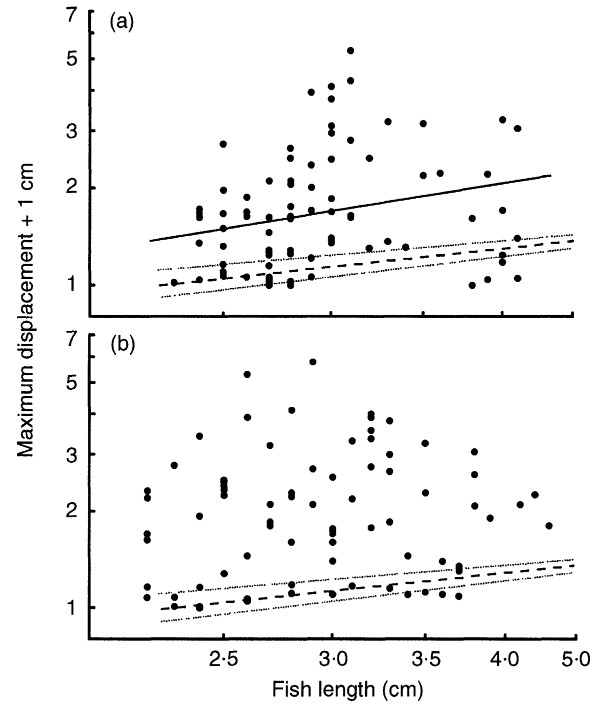

Fig. 4. Maximum displacement distance vs. fish total length in (a) Mykiss Lake and (b) Scott Lake. The solid line in (a) represents the least-squares regression $\log_{10}$ (displacement + 1) = 0·60 $\log_{10}$ length − 0·06, $r^2 = 0{\cdot}05$, $n = 85$, $P < 0{\cdot}05$. The dashed and dotted lines in each plot represent the least-squares regression ($\log_{10}$ (displacement + 1) = 0·45 $\log_{10}$ length − 0·16, $r^2 = 0{\cdot}85$, $n = 23$, $P < 0{\cdot}001$) and 95% confidence limits, respectively, calculated from an interspecific regression of territory size vs. body length for stream salmonines (Grant & Kramer 1990).

explained by body size in Mykiss Lake was low (5%) compared to the equivalent regression for stream salmonines where body size explained 85% of the variation (Fig. 4). Maximum displacement distances of brook charr in both lakes were generally much greater in magnitude and variability at a given body size than for salmonines in stream environments. However, several individuals in each lake were within, or even below, the bounds of the stream regression (Fig. 4).

Brook charr that spent a higher proportion of search time moving had higher net displacement distances than fish that spent a lower proportion of time moving in both Mykiss ($r = 0{\cdot}67$, $P < 0{\cdot}01$, $n = 88$) and Scott lakes ($r = 0{\cdot}57$, $P < 0{\cdot}01$, $n = 77$; Fig. 5). Only four individuals in each lake had no net displacement and spent less than 20% of search time moving (Fig. 5).

The occurrence and frequency of agonistic behaviour was low in both lakes. Agonistic behaviour was observed in ≈25% of observations in both Mykiss (29/115) and Scott (30/111) lakes which lasted an average of 4·5 min (median = 5 min, range = 0·5–5·5 min). In addition, intervals with agonistic behaviour accounted for less than 2% of the total observation time in both Mykiss (53/3223, 5-s intervals) and Scott (52/2935, 5-s intervals) lakes. We had detailed data on

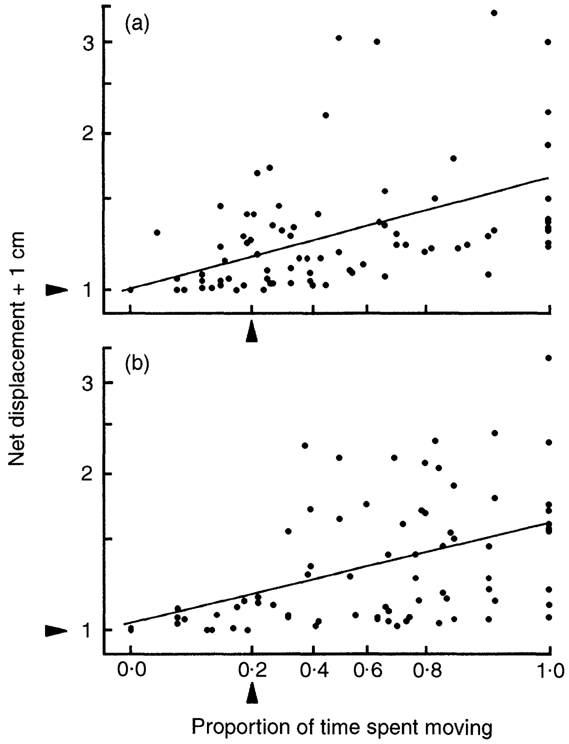

Fig. 5. Net displacement distance vs. the proportion of search time spent moving for brook charr in (a) Mykiss Lake and (b) Scott Lake. Solid lines represent the least-squares regression in each. Arrowheads indicate the net displacement distance and upper time spent moving values predicted by the CPTM.

agonistic behaviour for 45 of the cases in which it was observed. Of these, 63% of fish (28/45) were aggressive and 11 individuals from each lake were observed for 5 min which were used in analyses. Aggressive interactions ($n\,\mathrm{min}^{-1}$) were not correlated with the proportion of time spent moving in either lake ($P > 0{\cdot}05$) contrary to the predicted inverse relationship (Fig. 6a). All but one of the aggressive individuals (from Mykiss Lake) spent more than 20% of search time moving (Fig. 6a). This did not reflect an absence of sedentary individuals in the sample, however, as there were substantial numbers of fish in Mykiss (36/115) and Scott (17/111) lakes that spent less than 20% of search time moving. Aggressive frequency was not correlated with net displacement ($P > 0{\cdot}05$). In contrast to the CPTM which predicts no net displacement for the most aggressive fish, the most aggressive fish observed in the lakes had intermediate ($\approx 0{\cdot}25$ m) net displacement distances (Fig. 6b).

BROOK CHARR MOVEMENTS AND SPACE-USE

Movements of brook charr were not unidirectional, but rather there was a tendency for brook charr to turn around and move back over the same areas (see Fig. 2) resulting in maximum displacement distances of brook charr that were approximately twice their net displacement distances (Fig. 7; Table 1). Within individual brook charr, the maximum displacement distance was, on average, 0·45 m greater than its net displacement distance in Mykiss Lake (paired *t*-test, $t_{114} = 8{\cdot}0$, SD $= 0{\cdot}60$, one-tailed $P < 0{\cdot}0001$), and 0·64 m greater in Scott Lake ($t_{109} = 8{\cdot}85$, SD $= 0{\cdot}75$, $P < 0{\cdot}0001$). The total distance moved by fish (total displacement) was, on average, more than six times greater than net displacement distances moved over the same observation period (Table 1) indicating tortuosity and significant redundancy in fish movements. On average, the total displacement distance moved by individual brook charr was 2·56 m farther than their net displacement distance in Mykiss Lake (paired $t_{108} = 7{\cdot}46$, SD $= 3{\cdot}57$, $P < 0{\cdot}0001$), and 3·36 m farther in Scott Lake ($t_{107} = 10{\cdot}44$, SD $= 3{\cdot}34$, $P < 0{\cdot}0001$).

Discussion

Space-use of YOY brook charr in both lakes was not consistent with the central-place territorial model (CPTM) developed from observations of young salmonines, including brook charr, in streams. Brook charr in both lakes had net displacement distances that were dramatically greater and more variable than the predicted no net displacement. However, Mykiss Lake brook charr, when in a stream environment, had

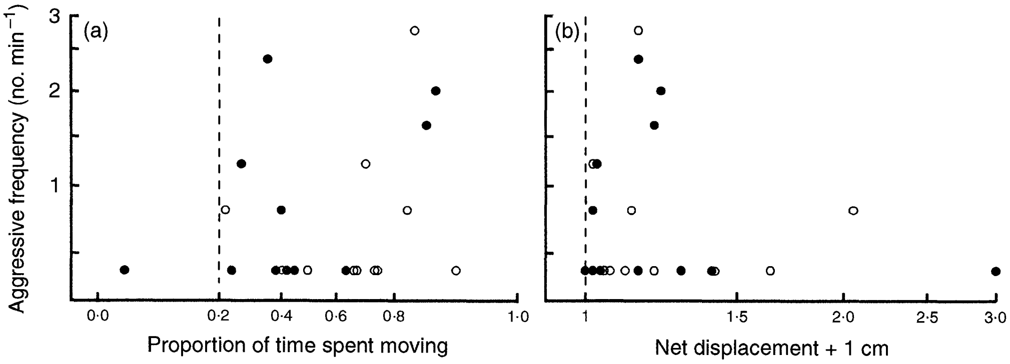

Fig. 6. (a) Aggressive frequency vs. the proportion of search time spent moving and, (b) aggression vs. net displacement distance for brook charr in Mykiss Lake (l) and Scott Lake (m). Each point represents one individual. Dashed lines in (a) indicate the upper time spent moving and in (b) indicate the net displacement values predicted by the CPTM.

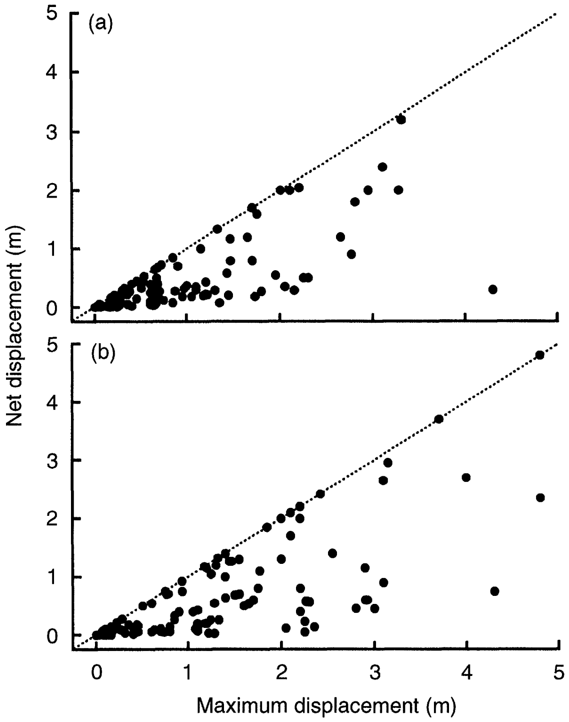

Fig. 7. Net displacement distance vs. maximum displacement distance for brook charr in (a) Mykiss Lake and (b) Scott Lake. The dotted line (1 : 1) is for reference. Observation duration varies among individuals.

Table 1. Univariate statistics summarizing the net and maximum displacement distances, and the total distance moved by individual brook charr. Duration of observation varies among individuals (see Results)

Space-use measure	Mean	Range	SD	Individuals (*n*)
Mykiss Lake				
Net displacement (m)	0·45	0–3·2	0·62	115
Maximum displacement (m)	0·90	0–4·3	0·88	115
Total distance moved (m)	3·00	0–23·0	3·71	109
Scott Lake				
Net displacement (m)	0·66	0–4·8	0·85	110
Maximum displacement (m)	1·30	0–4·8	1·10	110
Total distance moved (m)	4·00	0–12·0	3·42	109

no net displacement supporting this prediction. Body size explained little or no significant variation (≤5%) in maximum displacement distances of brook charr in our lakes, leaving most or all of the variation unexplained, in contrast to the equivalent relationship for stream salmonines (85%; Grant & Kramer 1990). Maximum displacement distances were also greater in magnitude for fish of a given length in lakes as compared to salmonines in streams. Individuals that spent a larger proportion of search time moving also had larger net displacements in contrast to the CPTM. Agonistic behaviour (includes aggressive and submissive behaviour) was rare in occurrence and low in frequency; the few aggressive individuals we observed were not sedentary and did not defend from a central-place. We therefore reject the CPTM and conclude that territoriality does not exist as a potential mechanism to limit the population density of YOY brook charr in lakes, as has been proposed for salmonines in streams.

Our results suggest that environmental effects (flowing vs. stillwater) are important in determining foraging tactics and social behaviour of young salmonines. Previous studies have suggested that genetic effects are a more important determinant of aggression and mobility than environmental (still vs. flowing) effects in charrs and their hybrids (Ferguson & Noakes 1982, 1983). However, the dramatic differences in space-use of Mykiss Lake brook charr when in the lake, as compared to when in the stream, provide compelling evidence of the immediate effects of hydrodynamic environment on foraging tactics and space-use; Mykiss brook charr in the lake were rarely aggressive, moved large distances and often back over the same areas but, when in the stream, became central-place foragers. Primarily qualitative evidence indicates that the presence or absence of territoriality and central-place foraging by salmonines in streams is related to whether they inhabit lotic (flowing) or lentic (stillwater) environments, respectively, (see Table 3 in Grant & Noakes 1988; Noakes 1989). The present study appears to be the first to support this general trend for a salmonine species in a true lentic, lake environment.

Water movements in the nearshore littoral zone of lakes where we observed YOY brook charr appeared unpredictable and turbulent, if present at all (P. Biro, personal observation), in contrast to streams which have relatively predictable and stable current regimes and thus have predictably abundant renewal of food resources drifting past fish (see Introduction). It is this fundamental difference between lake and stream environments (unpredictable vs. predictable water movements) which we feel accounts for the lack of territoriality and active foraging mode of brook charr in lakes. The high mobility and great use of space by brook charr in the lakes, compared to salmonines in streams, is consistent with the prediction that fish in lakes are attempting to increase their encounter rate with relatively sedentary and dispersed prey (Gerritsen & Strickler 1977). Supporting this prediction, active YOY brook charr in both lakes capture more potential prey items per unit time but have lower foraging success than sedentary fish (Biro & Ridgway 1995; Biro 1996; Biro *et al.* 1996).

Two major findings have emerged from our field study. First, rejection of the CPTM strongly suggests that availability of space is not limiting populations of young brook charr in lakes and indicates that mechanisms of population regulation other than the traditional territoriality hypothesis need to be sought out. Second, the effect of lentic vs. lotic environments on the space-use and social behaviour of salmonines clearly needs to be explicitly accounted for in future discussion of salmonine behaviour and behavioural models. In the absence of the territorial hypothesis, perhaps alternative forms of competition, such as interspecific or exploitative competition, or risk of predation may be important in the population dynamics of these fish. For example, we have observed YOY brook charr chasing solitary cyprinids in Mykiss Lake and brook sticklebacks (*Culaea inconstans* Kirtland) in Scott Lake, and we have also observed brook charr actively avoiding schools of passing cyprinids. Also, cannibalism by brook charr has been observed in our lakes and others (Griswold 1967; P. Biro, personal observation), and selection of nearshore areas close to cover by young salmonines in lakes has been shown to reduce predation by adult salmonines (Tabor & Wurtsbaugh 1991). Disentangling factors which might influence the abundance and distribution of young salmonines in lakes will be a challenging venture for future research.

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