



Diel locomotor activity of brook charr, as determined by radiotelemetry

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Locations by radiotelemetry during eight 24-h sampling periods in 1991, 1992, and 1993 were used to evaluate the diel activity patterns of adult brook charr *Salvelinus fontinalis* in two lakes of the Laurentian Shield (Québec, Canada). Based on the minimum distance travelled between two consecutive locations, adult brook charr were more active at dusk and at night than during the day. During daylight periods, individual fish displayed strong site selection, remaining in the same area along the shore from day to day. The fish left their inshore position at dusk, were highly mobile during the night, and returned to their focal point at sunrise, exhibiting diel homing behaviour. These results are supported by an increase in gillnet captures of adult brook charr in Lac Melchior at night. Data obtained by gillnet fishing in lakes Bondi and Simpson showed that juvenile (1+) brook charr were active throughout the diel cycle and that young-of-the-year were active mainly during the day, suggesting that there is an ontogenetic change in the diel activity of brook charr. Despite its limitations (restrictions on the number and size of tracked individuals, post-manipulation mortality, lifetime of transmitter battery), radiotelemetry allows for collection of multiple behavioural observations (distances travelled, instantaneous activity, site selection and homing) during the activity cycle of individual fish, and thus provides a finer degree of spatial resolution than alternative methods such as gillnetting.

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Key words: *Salvelinus fontinalis*; diel activity pattern; spatial distribution; ontogenetic change; selected temperature.

INTRODUCTION

Salmonids are often characterized as diurnally active fish (Linner *et al.*, 1990). However, preliminary observations by the authors suggested a nocturnal activity pattern in lacustrine adult brook charr *Salvelinus fontinalis* (Mitchill). Although activity patterns have been studied often in anadromous (Smith & Saunders, 1958; Castonguay *et al.*, 1982; Doyon *et al.*, 1991) and stream-dwelling brook charr (Griffith, 1974; McNicol *et al.*, 1985; Grant & Noakes, 1987; Walsh *et al.*, 1988; McLaughlin *et al.*, 1994), little is known about lacustrine populations. The purpose of this study was (1) to evaluate the diel locomotor activity pattern of adult brook charr in two lakes by means of radiotelemetry; (2) to compare these results with those obtained by gillnet fishing in the same system; and (3) to compare diel activity patterns of adult brook charr with those of young-of-the-year (YOY) and juveniles.

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TABLE I. General characteristics of the study lakes

Lake	Year	Area (ha)	Mean depth (m)	Conductivity ($\mu\text{S cm}^{-1}$)	Secchi depth (m)
Melchior	1979	5.2	4.6	—	6.1
Simpson	1992	28.5	3.3	12.5	2.5
Bondi	1993	23.3	8.0	10.5	3.5
Épervier	1991	8.4	5.6	14.1	3.5
Ledoux	1992–1993	11.9	5.5	15.3	4.2

TABLE II. General characteristics of brook charr tracked by telemetry and periods of fish locations

Lake	Year	<i>n</i>	Mean total length (mm)	s.d.	Length range (mm)	Sampling period
Épervier	1991	4	341	18	325–360	29 June–29 August
Ledoux	1992	11	343	45	250–400	21 July–30 October
Ledoux	1993	14	387	30	320–419	22 July–28 October

n=number of fish tracked.

MATERIALS AND METHODS

STUDY LAKES

Brook charr were tracked by radiotelemetry in lakes de l'Épervier (1991) and Ledoux (1992, 1993) located in the Mastigouche Reserve (46°38' N, 73°15' W), Québec, Canada. Gillnet samples were collected in lakes Bondi (1993) and Simpson (1992) in the same Reserve, and in Lac Melchior (1979), located in the St-Maurice Reserve (47°05' N, 73°20' W). These small oligotrophic lakes are typical temperate zone lakes with respect to depth, conductivity, dissolved oxygen concentration, thermal stratification, and Secchi disk transparency (Magnan & FitzGerald, 1982; Magnan, 1988; Lacasse & Magnan, 1992; Table I). Lac Melchior contains only brook charr while lakes Bondi, de l'Épervier, Ledoux, and Simpson contain brook charr and northern redbelly dace *Phoxinus eos* (Cope). The five lakes are subject to sport fishing, and exploitation is carefully controlled by the Québec Government (Magnan, 1988). The lakes were closed to sport fishing during the study.

TAGGING

In June or July of each summer (Table II), 20 adult brook charr (250–419 mm total length) in lakes de l'Épervier and Ledoux were tagged with thermo-sensitive radio-transmitters weighing 4 g (Advanced Telemetry Systems, ATS, model 357). Based on the study of Magnan & FitzGerald (1982) in the same system, these fish were 3 years of age or older. Fish were captured with multifilament gillnets (1.8 m deep \times 38.1 m long, with stretched meshes of 2.5, 3.8, 6.4, and 7.6 cm) set arbitrarily, perpendicularly to the shore, mainly in the littoral zone. Gillnets were removed every 15 min and only fish in good condition, usually those caught by the teeth, were retained for tagging.

Transmitters were attached externally under the dorsal fin after the fish had been lightly anaesthetized with tricaine methanesulphonate (MS-222). Fixation was made with nylon monofilament threaded through muscular tissues at two points. The transmitter was placed on one side of the fish while, on the other side, the filament and fixation knot were kept apart from the fish by a small rubber plate (Winter, 1983). A neoprene cushion was placed between the fish and the rubber plate to avoid lesions due to rubbing. In 1991 (Lac de l'Épervier), the fish were kept for 2 h in a holding enclosure (littoral zone) before release into the lake. A total of four fish survived these manipulations in 1991 (Lac de l'Épervier) compared to 11 in 1992 and 14 in 1993 (Lac Ledoux). In 1991, longer manipulations and holding periods in the enclosure were probably more stressful for the fish and thus were responsible for the higher observed mortality. In 1992 and 1993, manipulation time was much reduced by using a cone-shaped needle rendering thread insertion easier, and by eliminating the post-operative holding period. In these 2 years, colder water than in 1991 was used in the manipulation basin. The tagging process generally lasted <1 min per fish. In each of the 3 years, most of the mortality occurred within the 10 days following tagging. All of the fish that were alive after 10 days were tracked until the transmitter batteries were exhausted. Fish characteristics and periods of tracking are shown in Table II.

FISH LOCATIONS

Individual brook charr were located on average every 2 days during each sampling period (Table II) with an ATS-R2000 radio receiver equipped with a loop antenna. At every visit, each fish was located during the day (0800–1800 hours) by triangulation, using a compass and landmarks spaced regularly around the lakes. The water temperature measured by the thermo-sensitive tag (hereafter ambient temperature) was recorded on four different occasions: when each fish was located (to determine vertical position according to the thermal profile of the lake on a given sampling date); and at the beginning, middle, and end of the period in which all individuals were located, which lasted around 2 h in 1991 and 4–6 h in 1992 and 1993. On each sampling date, the ambient temperature of a given fish was calculated as the mean of the four measurements. Following location of each fish, the lake depth was determined with a graduated cord to position the individuals more accurately on the bathymetric map.

On three occasions in 1991 and 1992 and two occasions in 1993, fish were located every 4 h during complete 24-h cycles. Thus, for a given cycle, four to seven fish were located at 1000, 1400, 1800, 2200, 0200 and 0600 hours to evaluate diel variation in locomotor activity.

GILLNET FISHING

The diel activity pattern of adult brook charr (2+, 3+) was examined by gillnet fishing at two stations in Lac Melchior. At one station, situated in the littoral zone (2 m), a multifilament gillnet (1.8 m deep \times 38.1 m long with stretched meshes of 2.5, 3.8, 5.1, 6.4 and 7.6 cm) was placed parallel to the shore. At the second station, situated in the offshore zone (6–8 m of water), five multifilament gillnets were suspended vertically in the water column. These nets (1.8 m wide \times 8 m long, each with one mesh-size as above) were aligned along a common horizontal axis with 1-m intervals separating adjacent nets. On three sampling periods in 1979 (June, July, and August), the number of charr (217 ± 26 mm fork length) and their position in the water column was recorded every 4 h during a complete 24-h cycle.

Data on the diel locomotor activity of YOY (0+) and juvenile (1+) brook charr were obtained in two other studies (YOY: Magnan; juveniles: Héroux & Magnan, unpublished data). In Lac Simpson, juvenile brook charr (106–188 mm total length, TL) were captured in the littoral zone with five multifilament gillnets (1.5 m in height \times 30 m long with stretched mesh of 2.5 cm) at 3-h intervals starting at 1500 hours on 10 June 1992 and continuing for 48 h. The nets were never left more than 60 min in the water (mean \pm S.D.: 37 ± 8 min). In Lac Bondi, YOY brook charr (60.0 ± 4.5 mm TL) were captured in the littoral zone also at 0800, 1200, 1600 and 2000 hours. Gillnets (1.8 m in height \times 14.5

TABLE III. Minimum distance travelled between two consecutive locations during different periods of the day, for all fish tracked in the present study

Period	<i>n</i>	Distance (m)	s.d.
1000–1400 hours	29	42·8	78·2
1400–1800 hours	29	45·0	68·5
1800–2200 hours	29	108·9	71·5
2200–0200 hours	29	104·4	91·4
0200–0600 hours	29	109·8	91·4

n = number of locations.

or 29·0 m long with stretched mesh of 1·25 cm) were set perpendicularly to the shore at eight sampling stations around the lake for periods of 4 h. Although no information is available on daytime activity for the sampling periods of 24 h and 4 h, these data are used here to support information found in the literature.

QUANTITATIVE ANALYSES

To evaluate the diel locomotor activity pattern of adult brook charr followed by radiotelemetry, two different measures of displacement were used for all fish tracked during the eight 24-h sampling periods. The first measure, the minimum distance travelled, represents the linear distance (m) between two consecutive locations, irrespective of the length of the actual trajectory of the fish between these two points. Five measures of minimum distance travelled were obtained for each fish, one for each interval of the diel cycle (i.e. 1000–1400, 1400–1800, 1800–2200, 2200–0200 and 0200–0600 hours). The locations indicated that on a day-to-day basis, individual fish tended to be very faithful to a given site during the daylight period (see Results). Thus, for each fish a focal point corresponding to the centroid of its daily locations (1000–1800 hours) during the summer was calculated. To investigate the diel locomotor activity of brook charr in relation to the focal point, the mean distance of all tracked individuals from their focal point was compared among the different periods of the day. The mean ambient temperature of all tracked individuals was also compared among the different times of the day, for each diel sampling period.

The diel locomotor activity pattern of adult brook charr captured by gillnet fishing was evaluated by comparing the frequency distribution of the number of fish captured in different periods of the day, for each of the 24-h sampling periods in lakes Melchior, Simpson, and Bondi.

RESULTS

DIEL LOCOMOTOR ACTIVITY

Radiotelemetry

Based on the minimum distance travelled between two consecutive locations, adult brook charr were more active at dusk and at night than during the day (Table III). During daylight periods, individual fish displayed strong site selection, remaining in the same restricted area along the shore from day to day (Table IV). The sites selected by the fish were located in the same part of the lake for almost all individuals (Fig. 1). Fish displacement from the focal point was restricted in daytime relative to the distances travelled at dusk and night (Fig. 2).

TABLE IV. Mean distance of each fish from their focal point during daylight locations (1000–1800 hours)

<i>n</i>	Mean distance (m)	S.D.
21	24.9	20.1
16	30.5	26.1
21	31.5	22.9
21	29.4	29.2
16	29.0	26.9
21	31.8	41.2
21	13.6	10.4
15	20.7	14.9
16	20.3	21.1
21	16.1	10.9
16	20.3	19.1
21	21.6	17.2
16	17.2	13.7
20	18.5	16.5
16	17.9	19.5
20	15.5	13.7
16	25.4	20.9
14	21.7	23.4
20	21.0	9.5
12	21.3	23.3
20	15.0	11.8
20	24.9	24.4
20	14.3	14.0
16	21.2	23.0
16	20.9	13.3
15	19.8	16.5
13	27.3	18.8
15	22.1	18.6
15	33.8	18.6
Mean	22.3	19.3

n = number of locations.

For example, typically fish leave their inshore position at dusk, are highly mobile during the night, and then return to their focal point at sunrise (Fig. 3).

For each of the eight 24-h sampling periods, no significant difference was found between the mean temperatures selected by the fish during day and night ($P > 0.05$). The overall mean selected temperature (eight cycles) was $12.3 \pm 1.8^\circ \text{C}$ during the day and $11.9 \pm 1.2^\circ \text{C}$ during the night.

Gillnet fishing

With the exception of the 2400 and 0400 hours sampling periods, for which no data are available, YOY brook charr (0+) were active mainly between 1000 and 1800 hours [Fig. 4(a)]. The juveniles (1+) were active in all sampling periods [Fig. 4(b)], and adults (2+, 3+) were mainly active between 1800 and 0200 hours

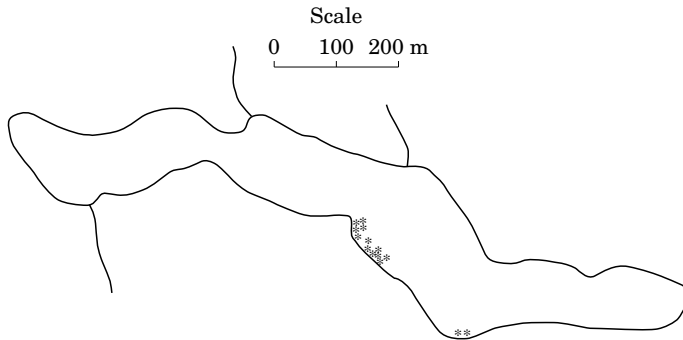


FIG. 1. Focal points of 14 fish, as determined from all daylight locations in summer 1993: Lac Ledoux.

[Fig. 4(c)]. As observed with telemetry, captures by gillnet fishing in Lac Melchior also suggested higher locomotor activity for adult brook charr during dusk and around midnight [Fig. 4(c)]. The distances from the focal point were highest in the 2400 and 0400 hours periods (Fig. 5).

DISCUSSION

DIEL LOCOMOTOR ACTIVITY IN ADULT BROOK CHARR

The results suggest that over a 24-h period both the distribution and the locomotor activity of adult brook charr in the lakes have distinct diurnal and nocturnal phases. During daylight periods, brook charr were less active compared to dusk and night periods, as shown by the minimum distance travelled between two consecutive locations. During night and dusk, the fish were also found further from their focal point than during the day. This displacement from the focal point was initiated around 1800 hours, and was characterized by dispersion of individuals in the lake associated with active swimming during the night. Soon after sunrise, the fish returned to their focal point near shore, exhibiting diel homing behaviour. The night-time increase in gillnet captures in Lac Melchior supported this diel pattern of locomotor activity. Numerous studies have identified similar patterns of locomotor activity in lakes for golden shiner *Notemigonus crysoleucas* (Mitchill) (Hall *et al.*, 1979), roach *Rutilus rutilus* (L.), rudd *Scardinius erythrophthalmus* (L.), bream *Abramis brama* (L.), and bleak *Alburnus alburnus* (L.) (Bohl, 1980), goby *Pomatoschistus pictus* (Malm) (Hesthagen, 1980), creek chub *Semotilus atromaculatus* (Mitchill) (Magnan & FitzGerald, 1984) and walleye *Stizostedion vitreum* (Mitchill) (Prophet *et al.*, 1989).

A question that arises is whether the diel locomotor activity of adult brook charr closely reflects their feeding pattern. Although some authors have demonstrated clearly a strong relationship between feeding and activity in fish (Elliott, 1976; Magnan & FitzGerald, 1984; Boisclair, 1992), there is some ambiguity regarding this relationship. In *Alosa pseudoharengus* (Wilson) for instance, swimming activity is diurnal and feeding is nocturnal (Hesthagen, 1980). However, Boisclair (1992) identified a positive correlation between feeding (digestive tract contents; cal 30 min^{-1}) and activity (estimated by an underwater video camera system; cal 30 min^{-1}) for 0+ brook charr, a result that should

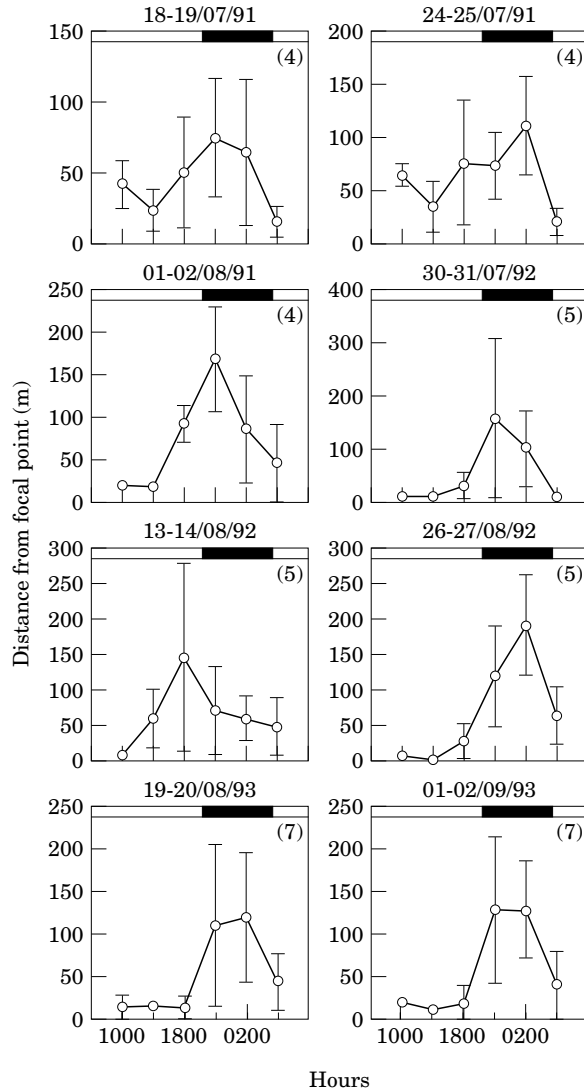


FIG. 2. Mean distance of tracked individuals from their focal point for different periods of the day, for each of the eight 24-h cycles in lakes Ledoux and de l'Épervier. The date (top of figure) and number of individuals (inset in parentheses) are given for each figure.

apply also for adults: (1) adult brook charr should feed more actively at night to profit from a greater availability of benthic prey (e.g. Grossman *et al.*, 1980). Some invertebrates [e.g. amphipods and chironomid pupae (Mundie, 1959); gammarids (Grossman *et al.*, 1980)] seem to be more active at night and presumably are more available to fish at that time (Magnan & FitzGerald, 1984); (2) Naud & Magnan (1987) found that northern redbelly dace, a species also present in Lac Ledoux and Lac de l'Épervier, displays a diel onshore–offshore migration. These fish swim in shoals in the littoral zone during the day, migrate at sunset to the pelagic zone, where the shoals break up, and then return to the littoral zone at sunrise (Fig. 5). This movement pattern agrees clearly with that

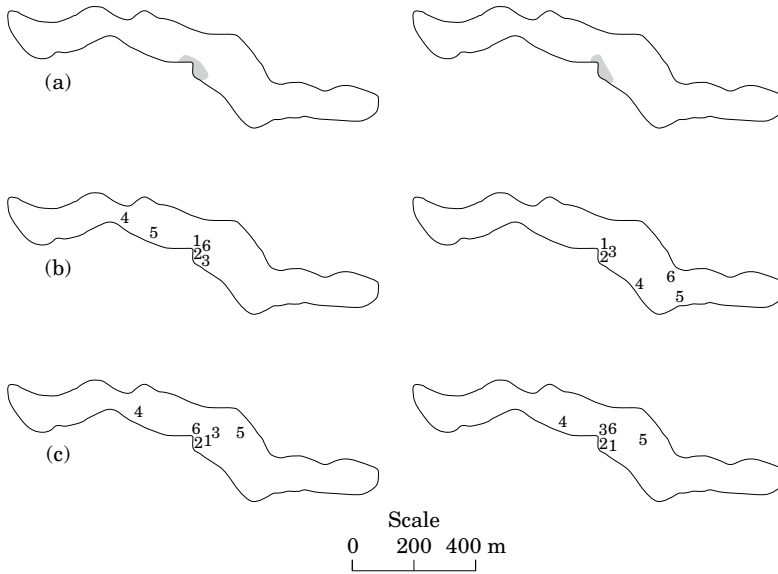


FIG. 3. Diel movement pattern and daylight site selection for two fish tracked in 1992, Lac Ledoux; (a) area containing 90% of the daylight locations (10–18 h); (b) and (c) movement of first (b) and second (c) fish during two 24-h cycles in 1992. Numbers 1–6 represent the position of the fish for the 1000, 1400, 1800, 2200, 0200 and 0600 hours locations respectively.

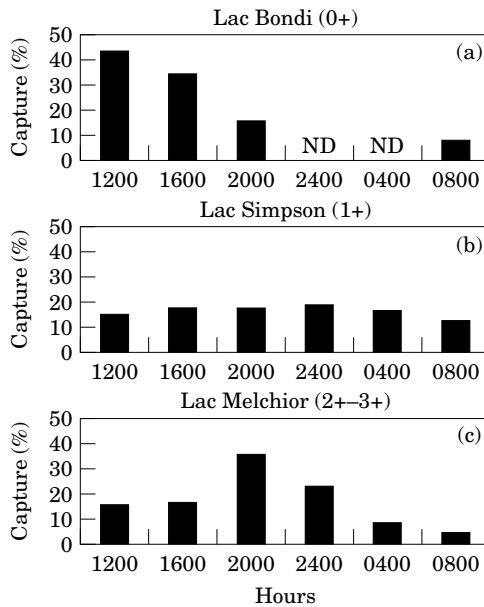


FIG. 4. Frequency distribution of captures (gillnet fishing) in relation to the period of the day; (a) young-of-the-year; (b) juveniles; and (c) adult brook charr. ND, no data.

of adult brook charr in the present study (Fig. 5). Predation on northern redbelly dace by large brook charr (TL>250 mm) can represent up to 30% by weight of the charr’s diet in the same study area (East & Magnan, 1991). The

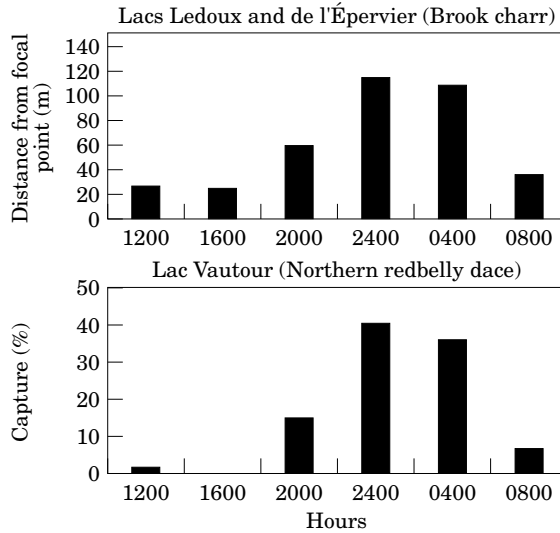


FIG. 5. Locomotor activity pattern of brook charr (mean distance of all the fish from their focal point) and of northern redbelly dace (frequency distribution of captures) in relation to the period of the day.

total length of the 29 brook charr in the study lakes was >250 mm (Table II), which renders them large enough to consume dace and lends support to the hypothesis explaining the increased nocturnal movements of brook charr in terms of predatory activity.

Behavioural thermoregulation may explain why the focal points of almost all individuals were concentrated in one area in lakes de l'Épervier and Ledoux during daylight periods. In both lakes the bottom slope is steepest in those areas ($\sim 45^\circ$). Because the lakes are thermally stratified, individuals could minimize horizontal movements between a feeding area (littoral zone and upper part of the water column; see Tremblay & Magnan, 1991) and a thermal refuge area deeper in the water column. If feeding is nocturnal, as suggested above, this diurnal thermoregulation could enhance growth by allowing the fish to completely digest the nighttime meal during the day, providing a significant bioenergetic advantage (Neverman & Wurtsbaugh, 1994). As observed by Brett (1971) and suggested by Neverman & Wurtsbaugh (1994), it would be easy for fish residing near a thermocline to adjust their temperature after feeding.

ONTOGENETIC CHANGE IN DIEL LOCOMOTOR ACTIVITY

Some studies have shown that YOY brook charr in lakes (Boisclair, 1992) and both YOY and juveniles (1+) in streams (Hoar, 1942; Allan, 1981; Walsh *et al.*, 1988; Forrester *et al.*, 1994) are diurnally active. Although no data were available for the nocturnal periods, YOY from Lac Bondi appeared to be active during the day. Furthermore, the diel locomotor activity of juveniles (1+) from Lac Simpson [Fig. 4(b)] shows that they were active both diurnally and nocturnally. This activity pattern contrasts with that of adult (2+, 3+) fish and suggests an ontogenetic change in the diel activity of brook charr. This change may be related to age-related differences in feeding efficiency. For anatomical

and physiological reasons, small fish could be less efficient when foraging at lower light intensities because their eyes capture less light than those of larger fish (Helfman, 1979). Developmental change in visual anatomy could allow large fish to function more effectively at lower light levels (Helfman *et al.*, 1982), thus profiting from the greater availability of benthic prey at night (Grossman *et al.*, 1980). Furthermore, as fish grow, their mouth gape increases, allowing large individuals to consume the larger prey which are often more active during the night (Helfman, 1986).

The results illustrate some of the advantages of radiotelemetry over gillnetting for studying the diel locomotor activity of fish. Despite its limitations (restrictions in the number and size of tracked individuals, post-manipulation mortality, lifetime of transmitter battery), radiotelemetry allows for collection of multiple behavioural observations (travelled distances, instantaneous activity, site selection and homing) during the diel activity cycle of individual fish, and thus provides a finer degree of spatial and temporal resolution than does gillnetting.

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