

Within-population heterogeneity of habitat use by lake trout *Salvelinus namaycush*

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To learn more about the degree of individual variation in resource use by lake trout *Salvelinus namaycush*, ultrasonic telemetry was used to study their habitat use in a lake without pelagic schooling fish prey. Individuals spent most of their time within the metalimnion in favourable water temperatures. They also made frequent excursions, however, into lake temperatures exceeding their optimum for physiological performance at all temporal scales considered. Their frequent use of nearshore habitats suggested that feeding in littoral areas may be common. Habitat use was highly variable among individuals, but spatial habitat use by individuals showed remarkable consistency between years. In particular, some lake trout exhibited high site fidelity to shallow, nearshore areas, whereas others used deep areas extensively. This level of between-individual variation indicated niche partitioning by depth and the possibility of alternative foraging strategies.

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INTRODUCTION

Many freshwater fish species inhabiting postglacial lakes show interindividual variation in their resource use ('individual niche variation'), particularly in relation to their use of littoral and pelagic habitats (Schluter & McPhail, 1992; Skúlason *et al.*, 1993; Snorrason *et al.*, 1994). Such variation may be categorized into two or more distinct niches (*e.g.* ontogenetic niche shifts and resource polymorphisms) or may reflect continuous niche variation (individual specialization; Bolnick *et al.*, 2003). Individual niche variation influences how individuals interact with one another and with other species and influences their vulnerability to habitat-specific stressors. As a result, quantifying individual niche

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variation can be useful for building more precise individual-based population dynamic models, testing theories about the evolution of trophic polymorphisms and assessing resilience to environmental change (Bolnick *et al.*, 2003). Despite these potential applications, individual niche variation is still poorly described for most species. The objective of this study was to increase this base of knowledge for lake trout *Salvelinus namaycush* (Walbaum), a species of management and conservation concern.

Native populations of lake trout currently inhabit trophically diverse, cold-water lakes distributed widely across north temperate regions (Power, 2002). They are top predators of aquatic communities, but their diet can be highly variable depending on the food web structure (Trippel & Beamish, 1993; Vander Zanden & Rasmussen, 1996; Vander Zanden *et al.*, 2000). Whereas the preferred diet of adults is pelagic schooling fish prey with a similar preference for cold, well-oxygenated water (*e.g.* cisco *Coregonus artedii* Lesueur), lake trout in lakes lacking pelagic schooling fish prey consume variable amounts of zooplankton, benthic invertebrates and littoral fishes (Martin, 1970; Vander Zanden & Rasmussen, 1996; Pazzia *et al.*, 2002). In lakes of the latter type, lake trout may make extensive use of littoral or epilimnetic habitats warmer than their physiological optimum (Snucins & Gunn, 1995; Sellers *et al.*, 1998). In addition to this among-population variation, there is also evidence of individual niche variation within populations. Using stable isotope analyses, Vander Zanden *et al.* (2000) found that 22% of the total variation in trophic position was accounted for by individual variation within populations. Questions remain, however, about the degree of niche partitioning within lakes and the underlying causes of individual niche variation.

In the current study, individual variation in lake trout movement and habitat use were assessed in Lake Louisa, Ontario, a north temperate lake without pelagic fish prey where use of warm-water habitats might be expected. The three specific objectives were to 1) quantify individual variation in habitat use in relation to lake morphometry, 2) quantify diurnal, within-season and annual variation in warm-water habitat use and 3) quantify individual and diurnal variation in the frequency of warm-water forays. These objectives required an individual approach that could most easily be met using acoustic telemetry.

MATERIALS AND METHODS

STUDY SITE

Lake trout habitat use was studied in Lake Louisa (45°28' N; 78°29' W; area = 531 ha, mean depth = 16 m, maximum depth = 61 m, total phosphorus = 3.4 µg l⁻¹, Secchi disc depth = 6.5 m, dissolved organic carbon = 2.9 mg C l⁻¹; Dillon *et al.*, 2003) during the summers of 2002 and 2003. Lake Louisa is a mesotrophic, dimictic lake in eastern Ontario with several inflow streams, bays and islets [Fig. 1(a)]. Located within Algonquin Park, this relatively pristine lake has an undeveloped foreshore with only minor human impact from campers, canoeists and anglers. In 2000, the spawning population of lake trout was estimated at 6005 with upper and lower CL of 4477 and 7740 [Algonquin Fisheries Assessment Unit (AFAU), Ontario Ministry of Natural Resources, unpubl. data]. Longnose sucker *Catostomus catostomus* (Forster) and brook trout *Salvelinus fontinalis* (Mitchill) occur in small numbers, and there is a diverse community of littoral

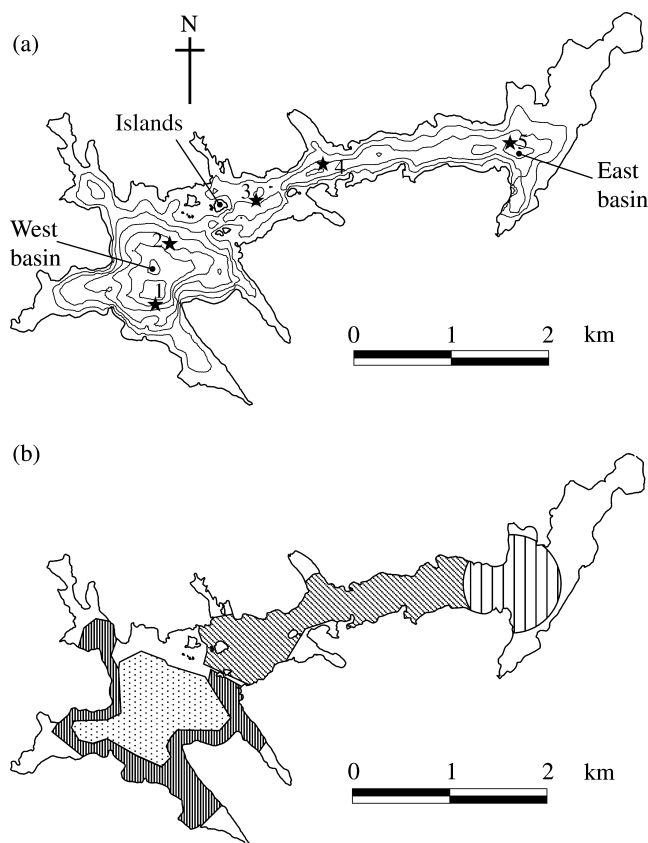


FIG. 1. A map of Lake Louisa (a) showing bathymetry in 10 m contours (from 10 to 60 m) and the positions of the five automated receivers (★) and (b) the locations of the four regions (region 1, ▨; region 2, ▤; region 3, ▥; region 4, ▦). Boundaries of regions 1–3 are based on the observed locations of manually tracked lake trout, whereas region 4 includes the 500 m detection radius of automated receiver number 5. Empty areas correspond to regions of the lake with few or no detections of lake trout.

fishes. The current study focused on lake trout movement and use of warm-water habitats during the period of thermal stratification (*i.e.* summer). Oxygen levels were high throughout the water column in July ($>6 \text{ mg l}^{-1}$; AFAU, unpubl. data) and were not expected to limit lake trout habitat use (MacLean *et al.*, 1990).

ENVIRONMENTAL MONITORING

Water temperature profiles were measured with a vertical string of stationary thermographs (StowAway TidbiT Temperature Logger; Onset Computer Corporation, Bourne, MA, U.S.A.) buoyed and anchored at a depth of *c.* 60 m in the deepest part of the lake. Temperatures were recorded every 8 min from 5 July to 29 October 2002 and from 21 May to 6 October 2003. Littoral temperatures were monitored by placing thermographs (2002: $n = 4$; 2003: $n = 3$) on the lake bottom at *c.* 1–2 m depth. Temperatures were recorded every 8 min from 5 July to 27 August 2002 and from 27 June to 24 October 2003. Seasonal variation in the temperature profile and littoral temperature (averaged for the three to four loggers) was described by using the daily information

collected at 1200 hours. The depth of the 10° C isotherm on each day was interpolated from the daily temperature profile at 1200 hours. The diurnal temperature cycle in the epilimnion during July to August was described by averaging all measurements of littoral temperatures at each 8 min interval.

TELEMETRY

The movements and habitat use of individual lake trout were tracked during July and August using manual telemetry (2002 and 2003) and automated telemetry (2003). For the manual telemetry component, lake trout were caught between 23 and 29 May 2002 using gillnets set as part of standard surveys or set in places of probable lake trout activity. In order to minimize the probability that the transmitter exceeded the recommended 1.25% of the fish's mass out of water (Winter, 1996), fish needed to be >720 g. This corresponded to fork lengths (L_F) >400 mm (AFAU, unpubl. data). Seventeen fish meeting the L_F requirement (based upon measurements done on unanaesthetized fish) were tagged with acoustic transmitters (Tables I and II), applying anaesthetization and surgical procedures similar to those used by Flavelle *et al.* (2002). Briefly, fish were anaesthetized in a bath containing clove oil, a transmitter was implanted in the peritoneal cavity through a small incision on the abdomen, the incision was closed with two surgical staples and the fish was allowed to recover in a freshwater bath prior to release. After surgery, an external t-bar anchor tag (Hallprint Pty, Ltd, Victor Harbor, South Australia) was inserted into the base of the dorsal fin, and the L_F and mass of each fish were measured.

Individuals were tracked on a daily basis during July and August in each year and sporadically during May to June 2002, June 2003 and September to October 2003. Each transmitter emitted a unique pulse, detectable with a directional hydrophone (Sonotronics Model DH-4; Sonotronics Inc., Tucson, AZ, U.S.A.) and ultrasonic receiver (Sonotronics Model VSR-90). The direction and strength of the acoustic signal were used to orient a small boat directly above the fish (*i.e.* the pass-over technique; Winter, 1996). Once its position was 'fixed,' the transmitter code, date, time and co-ordinates based on the Universal Transverse Mercator (UTM) projection system [using the North American Datum 1983 (NAD83) co-ordinate system, Zone 17] and position accuracy from a hand-held Garmin E-trex portable GPS unit [wide area augmentation system (WAAS)-enabled to improve position accuracy] were recorded. In the nine lake trout with temperature coded transmitters, the interval between pulses was temperature sensitive and was converted to body temperature using linear calibration relationships previously established in the laboratory. Body temperatures were expected to lag

TABLE I. Information about the transmitters used for manual and automated telemetry of lake trout in Lake Louisa

Telemetry method	Transmitter description	Model	Transmitter mass (in water) (g)	Battery life (months)	Number tagged	Number monitored in 2002	Number monitored in 2003
Manual	Standard coded	CT-82-2 ^a	9	14	6	5	5
	Temperature coded	CTT-83-2 ^a	9	14	11	9	5
Automated	Pressure coded	V16P-1L ^b	9	5	6	—	5
	Pressure coded	V16P-4H ^b	12	13	14	—	10

^aSonotronics, Inc., Tucson, AZ, U.S.A.

^bVemco, Shad Bay, Nova Scotia, Canada.

TABLE II. Biological information and habitat use of the manually tracked lake trout in Lake Louisa. Region of concentrated use (1, main basin; 2, main basin perimeter; 3, east of islands), core area and lake depth of daily fixes for individuals in 2002 and 2003 [mean \pm s.d. (n)]. Per cent of core area in 2002 that was re-used in 2003 is also shown for each surviving individual

Transmitter code	Transmitter model	L_F (mm)	Mass (g)	Region		Core area (ha)		Per cent re-used	Lake depth (m)	
				2002	2003	2002	2003		2002	2003
2223	CTT-83-2	393	570	1	—	16.1	—	—	29.4 \pm 15.1 (40)	—
2226 ^a	CTT-83-2	398	605	—	—	—	—	—	—	—
2334	CTT-83-2	449	1040	1	—	49.1	—	—	26.7 \pm 15.7 (38)	—
3225	CTT-83-2	438	965	1	1,2	69.7	7.7	0	34.0 \pm 16.5 (37)	25.4 \pm 15.3 (38)
5426	CT-82-2	421	925	1	1	79.2	47.5	4.1	37.6 \pm 15.9 (37)	42.1 \pm 13.9 (39)
2225	CTT-83-2	428	755	2	2	36.5	2.5	6.4	15.1 \pm 10.8 (37)	16.3 \pm 10.7 (39)
4224	CT-82-2	438	880	2	2	4.3	1.6	17.2	13.8 \pm 7.4 (39)	17.9 \pm 7.1 (15)
5225 ^{b,c}	CT-82-2	456	1275	—	—	—	—	—	—	—
2442 ^b	CTT-83-2	464	1095	—	—	—	—	—	—	—
4332	CT-82-2	518	1320	2	2	1.2	7.3	100	13.0 \pm 5.4 (40)	17.8 \pm 6.0 (39)
4446	CTT-83-2	458	960	2	2	8.1	14.9	34.5	13.3 \pm 8.3 (40)	28.3 \pm 15.1 (37)
5434	CT-82-2	540	1990	2	2	6.8	5.3	2.3	18.7 \pm 4.7 (38)	16.7 \pm 5.1 (16)
6633	CT-82-2	522	1790	2	2	2.8	2.3	66.9	14.1 \pm 3.9 (39)	14.4 \pm 3.9 (39)
345	CTT-83-2	422	685	3	—	42.3	—	—	14.7 \pm 7.6 (39)	—
2333	CTT-83-2	405	665	3	3	15.1	10.2	67.4	10.4 \pm 3.9 (40)	10.9 \pm 2.0 (31)
3335	CTT-83-2	387	605	3	—	38.3	—	—	13.0 \pm 6.4 (37)	—
5556	CTT-83-2	405	750	3	3	49.0	33.1	63.9	11.5 \pm 6.9 (42)	14.5 \pm 5.7 (37)

L_F , fork length.

^aTransmitter found in stomach of 82 cm lake trout.

^bTransmitter was stationary after 19 June 2002.

^cWhite cysts were visible in the abdominal cavity at the time of tagging.

behind a 1° C change in water temperature by *c.* 30 min \geq (Snucins & Gunn, 1995). The occasional recording of unusually low body temperatures suggested some inaccuracy in the technology when applied in the field. Consequently, analyses only included measurements within the range of observed water temperatures.

In order to compare behaviour among individuals and between years, analyses of the manual telemetry data were restricted to the common period of intensive daily tracking between 2 July and 27 August. During this period in 2002, *c.* 50 fixes were obtained for each surviving fish with zero to four daily fixes per fish, all collected during 0545–1850 hours. During this period in 2003, *c.* 70 fixes were obtained per surviving fish with zero to two daily fixes per fish, all collected during 0837–1727 hours. Telemetry error was estimated using daily fixes obtained from four transmitters at stationary, but unknown, locations (*i.e.* from lake trout that had died or lost their transmitters), and is expressed as the average displacement of fixes from the average UTM co-ordinates. The low amount of telemetry error measured for one transmitter in 2002 (11.6 m, *n* = 29 fixes) was consistent with previous studies (Flavelle *et al.*, 2002). The greater error measured for three transmitters in 2003 (24.0–37.4 m, *n* = 5–52 fixes) may have been due to observer differences but should not bias the interpretation of the results. Field error in measuring temperatures could not be assessed from the stationary transmitters because they were too shallow to be in stable water temperatures.

In addition to the daily fixes, lake trout were intensively tracked for 2 h periods beginning mean \pm s.d. 29.2 \pm 10.2 min after sunrise (*n* = 10 individuals) and for 2 h periods beginning 30.9 \pm 4.8 min after midday (*n* = 14 individuals) in 2002. Once a fish's position was fixed and the GPS location and interval were recorded, the next search was initiated after 5 min of waiting to minimize disturbance to the fish. Preliminary analyses of these data indicated that lake trout made frequent forays into very shallow water. Intensive tracking in shallow water, however, occasionally influenced lake trout movement in unexpected ways (*e.g.* lake trout remained below the boat as it floated downwind, along the shore) and so these data are not considered further.

In 2003, an automated telemetry system (Vemco, Shad Bay, Nova Scotia, Canada) was set up to remotely record the movements of lake trout, thereby avoiding the disturbance caused by intensive boat tracking in shallow water. With this system, the actual depths of lake trout within the water column (*i.e.* fish depth) were tracked, allowing the duration of trips into warm water to be quantified. During May, lake trout were angled in areas of probable lake trout activity for subsequent tagging with small (9 g) or large (12 g) pressure-sensitive acoustic transmitters (Table I). Twenty lake trout meeting the size target (720 g or 400 mm for the 9 g transmitters; 960 g or 437 mm for the 12 g transmitter) were tagged and measured (Table III). These transmitters emitted unique coded pulses on a very frequent basis (<1 min), which could be decoded by one or more of the five receivers (Vemco Model VR2) anchored and buoyed at different positions in the lake [Fig. 1(a)]. The ability of each receiver to correctly decode fish depths (recorded to the nearest 0.4 m) after an almost immediate equilibration time was confirmed prior to tagging. The detection radius of each receiver was *c.* 500 m in open water and so spatial coverage of the entire lake was incomplete.

Most of the lake trout with depth-sensitive transmitters were monitored remotely between 8 June and 22 September (Table III), but analyses focus on the 2 July to 27 August period to facilitate comparison with the manual telemetry data. Incomplete coverage for some individuals during 2 July to 27 August was attributable to some technical difficulties during the downloading of data and battery expiration. Over this time period, most of the lake trout had >50 depth detections per day.

ANALYSES

In order to compare the area of concentrated use among individuals and between years, fixed kernel utilization areas were calculated for each individual in each year using the Animal Movement extension (Hooge & Eichenlaub, 1997) in ArcView GIS 3.2 (ESRI, Redlands, CA, U.S.A.). The utilization area defines the area within which

TABLE III. Characteristics of the surviving lake trout tracked with the automated system in 2003, showing fork length (L_F), mass (g), the per cent of detections from each receiver during 2 July to 27 August [from west to east; see Fig. 1(a)], the lake region used most frequently and the period of coverage. Individuals are sorted according to their average location from west to east; individuals that did not survive are shown in the bottom rows

Fish number	Transmitter model	L_F (mm)	Mass (g)	Receiver					Region	Dates of coverage
				1	2	3	4	5		
17	V16P-1L	416	695	68	26.8	5.2	0	0	2	8 June to 25 August
12	V16P-4H	414	805	16.8	55.7	27.3	0.3	0	1	10 June to 22 September
8	V16P-4H	590	2555	22.5	42.4	30.6	4.5	0	1	10 June to 22 September
10	V16P-4H	551	2072	2.8	35.7	61.3	0.2	0	3	14 August to 22 September
14	V16P-4H	433	860	15.6	22.1	42.3	14.9	5.2	3	10 June to 22 September
4	V16P-4H	444	1010	0	0	71.2	28.8	0	3	8 June to 22 September
11	V16P-4H	483	1235	0.4	3.8	55.3	40.5	0.1	3	10 June to 22 September
7	V16P-4H	410	760	4.1	35.4	7.5	6.8	46.3	3	9 June to 22 September
3	V16P-4H	571	2585	3.2	9.5	18	63.7	5.6	3	9 June to 22 September
19 ^a	V16P-1L	404	745	1.3	6.9	36.6	32.4	22.8	3	2–31 July
16	V16P-1L	396	705	0.4	0	1.6	82.4	15.6	3	8 June to 27 August
18	V16P-1L	410	790	0	0	1.3	21.1	77.6	3	8 June to 2 August
1	V16P-4H	436	965	0	0	0	0	100	4	9 June to 22 September
15	V16P-4H	474	1160	0	0	0	0	100	4	10 June to 22 September
20	V16P-1L	417	765	0	0	0	0	100	4	8 June to 7 August
2	V16P-4H	488	1250	—	—	—	—	—	—	—
6	V16P-4H	489	1410	—	—	—	—	—	—	—
9	V16P-4H	442	855	—	—	—	—	—	—	—
13	V16P-4H	409	790	—	—	—	—	—	—	—
21	V16P-1L	442	770	—	—	—	—	—	—	—

^aDepth information could not be retrieved from this individual.

an individual has a fixed probability (*e.g.* 25, 50 and 95%) of being found, and the advantage of the kernel method is that it accommodates irregular distributions. The 'core' utilization area, which defines the area within which a fish has a 50% chance of being observed, is presented.

For these analyses, all data collected during 2 July to 27 August were used in order to meet or closely approach the minimum of 50 observations recommended for kernel

analysis (Seaman *et al.*, 1999). Thus, in some cases up to four observations in a single day were included. The smoothing parameter H was calculated using least squares cross validation (Silverman, 1986). Terrestrial portions were eliminated from the utilization areas by 'clipping' with the polygon outline of the shore in ArcView. Insufficient sample sizes (<50) for individuals 4224 ($n = 29$) and 5434 ($n = 27$) in 2003 may have resulted in underestimates of their core areas.

The interpretation of utilization areas as areas of concentrated use (or home range) requires that successive locations are independent. This assumption was tested in the 2002 data following Swihart & Slade (1985). This method derives critical threshold values for Schoener's (1981) ratio $\bar{r}^2:r^2$, the ratio of the mean squared distance between successive fixes divided by the mean squared distance from the centre of activity (*i.e.* the mean UTM co-ordinates). For each individual, the observed ratio was compared to the critical value, which was derived from Swihart & Slade (1985) using a conservative sample size of 40. Ratios below the threshold indicate positive autocorrelation of subsequent locations or spatial clumping. The usual α -level for significance (0.05) was adjusted for multiple tests using Bonferroni correction. Causes of non-independence of successive locations were assessed by first order autocorrelations in successive move distances and move speeds and by the distribution of turning angles between successive moves (Turchin, 1998). All analyses were done using SAS vers. 8.2 (SAS, 1990).

The habitats used by lake trout were described using one random fix per day to minimize autocorrelation and pseudoreplication. First, based on their use of space during July and August, individuals were assigned to one of four regions: 1) the main basin at the western end of the lake, 2) the main basin's perimeter, 3) the area east of the main basin and adjacent islands and into the east to west oriented channel and 4) the smaller basin at the east end of the lake [Fig. 1(b)]. Second, each location was associated with a lake depth using bathymetric data provided by the AFAU. The frequency with which individuals used particular lake depths (<10 , 10–20, 20–30, 30–40, 40–50 and ≥ 50 m) or lake depths associated with different isotherms (≤ 10 , 10–15, 15–20 and $>20^\circ\text{C}$) was quantified. Third, for the sub-set of individuals with temperature coded transmitters, the frequency of having body temperatures within specific ranges (≤ 10 , 10–15, 15–20 and $>20^\circ\text{C}$) was quantified.

Some of the above habitat characteristics were also quantified for the lake trout monitored with the automated system in 2003. Individual use of different lake regions [1–4; Fig. 1(b)] was assigned based on the location of the receivers that picked up their signals. Descriptors of habitat use (*i.e.* the depth above which individuals spent 50% of their time and the per cent time spent in depths shallower than the 10°C isotherm) were derived from the cumulative proportion of time spent at each depth. Rarely, large changes in the recorded fish depth were clearly impossible when considering the flanking depths and times; spurious detections were eliminated.

Additional analyses of the manual telemetry data tested whether the frequency of using nearshore strata (above the 10°C isotherm) differed among years or among individuals using χ^2 analyses. Lake trout are known to prefer cold, well-oxygenated water (Martin & Olver, 1980) and are physiologically adapted to a narrow range of ambient temperatures with performance peaking between 8 and 12°C (Magnuson *et al.*, 1990). The choice of 10°C as a threshold is consistent with the optimal habitat boundary used by Dillon *et al.* (2003), although lake temperatures of up to 15°C are often considered 'usable' by lake trout (MacLean *et al.*, 1990). For the between year comparison, a heterogeneity χ^2 analysis was first performed to determine if individual lake trout could be pooled (Zar, 1999). Logistic regression was used to test whether the manually tracked lake trout differed in their probability of using habitat $>10^\circ\text{C}$ (or having body temperatures $>10^\circ\text{C}$) as the summer progressed in each year. The independent variables in these analyses included individual, date and an individual by date interaction.

FORAYS INTO $>10^\circ\text{C}$ WATER

The number and duration of forays into warm water were quantified from the automated telemetry data. A foray was assumed to begin and end when a fish entered and

departed lake depths above the 10° C isotherm. Only forays >2 min in duration were analysed in an attempt to eliminate random movements made while resting or cruising (*i.e.* not foraging). For each individual, the duration of warm-water forays and the distribution of minimum depths attained during forays were calculated. χ^2 analyses were used to examine diurnal variation in the frequency of warm-water forays; this was facilitated by dividing the day into 10 2-4 h periods. A heterogeneity χ^2 analysis was done to test whether individuals differed in their diurnal pattern of foray activity. Variation in the frequency of warm-water forays among daily or weekly time periods was not assessed because incomplete temporal coverage made it difficult to establish null expectations of foray frequency.

RESULTS

TEMPERATURE PROFILES

In both years, the lake was thermally stratified throughout June (data available for 2003 only), July, August and September. From early July to late August, the thermocline dropped slightly as the end of summer approached [Fig. 2(a), (b)]. During this period, the thermocline was located between 5 and 10 m in both years, but epilimnion temperatures were warmer in 2002. Average littoral temperatures during July and August, although variable, were generally warmer in 2002 than in 2003 [Fig. 2(c)]. Littoral temperatures during July and August cycled diurnally with a minimum at dawn (0600 hours) and a maximum in the late afternoon (1500 hours) in both years (Fig. 3).

MORTALITY

Fourteen of the 17 manually tracked lake trout survived until the end of the 2002 for a mortality rate of 17.6% (Table II). The transmitter from one of the three 'mortalities' (2226) was recovered 11 days after tagging in the stomach of an 82 cm lake trout during standard gillnetting surveys and was presumably the victim of a cannibalistic attack. Transmitters from the two remaining lake trout (2442 and 5225, which had white cysts visible in the abdominal cavity at the time of tagging) were stationary after 19 June 2002. Five of the tagged lake trout were below the 720 g threshold in part because L_F was overestimated prior to anaesthetization and in part because of variation in condition. Mass, however, did not appear to be a factor contributing to short-term mortality. The transmitter exceeded the recommended mass in the cannibalized fish and in four other fish, which survived to have typical movement patterns in 2002. Overwinter mortality between 2002 and 2003 could not be assessed because the batteries of some transmitters may have expired. In 2003, three transmitters were missing (2223, 3335 and 2334), one transmitter was stationary (345) and two transmitters (4224 and 5434) disappeared during the tracking season.

For the lake trout tracked with the automated system in 2003, 15 of the 20 tagged individuals survived until the end of the season for a mortality rate of 25%. Fish depth information was available for 14 of these (the transmitter in individual 19 was incorrectly calibrated; Table III). The five individuals that did not survive had L_F ranging from 409 to 489 mm and masses ranging from

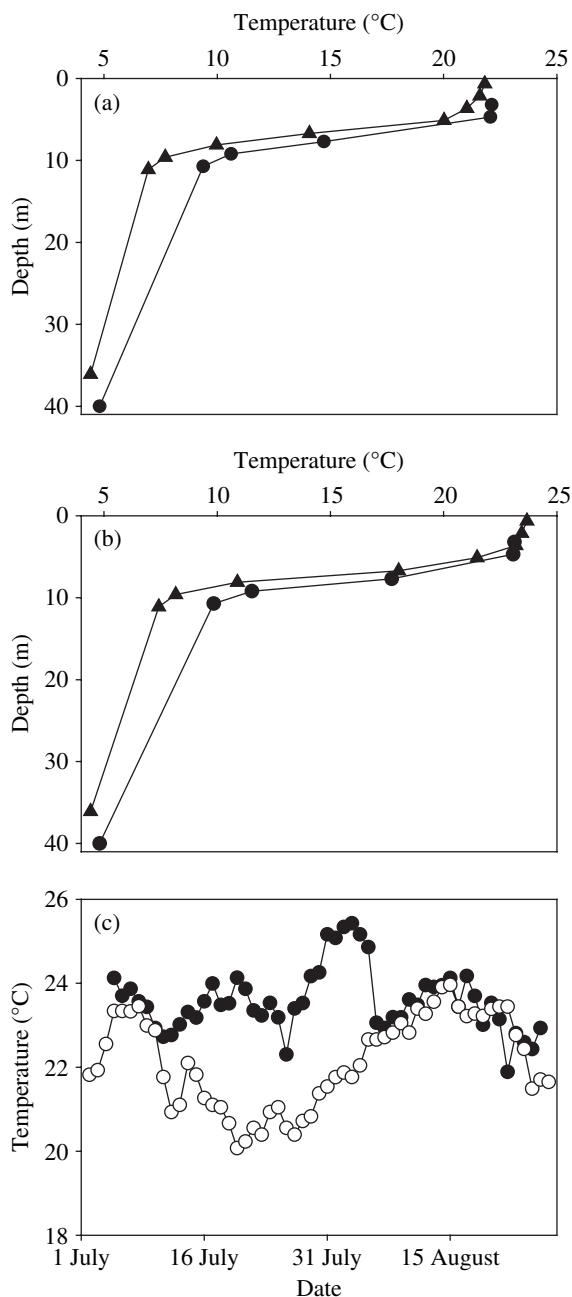


FIG. 2. Lake Louisa temperature profiles on (a) 15 July and (b) 15 August in 2002 (●) and 2003 (▲).
(c) Average littoral temperatures at noon in 2002 (●) and 2003 (○).

790 to 1410 g. Seven of the 20 lake trout were below the minimum mass threshold (720 g for V16P-1L transmitters and 960 g for V16P-4H transmitters) owing to error in measuring L_F prior to anaesthetization and variation in length-specific mass. Mortality, however, appeared to be independent of size.

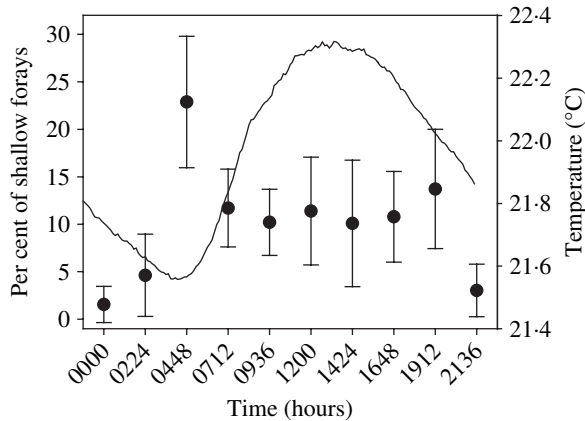


FIG. 3. The per cent of shallow forays that were made at different times of day for lake trout tracked with the automated telemetry system in 2003 (●; mean \pm s.d. of 11 individuals that made at least 50 warm-water forays >2 min in duration). The diurnal pattern of variation in the average littoral temperature (—) is also shown.

Mortality rate was 29% (2/7) among the undermass fish v. 23% (3/13) among the overmass fish (one-tailed Fisher exact test, $P > 0.5$).

HABITAT USE

The manually tracked lake trout differed widely in the location and size of their core areas (Table II). In general, lake trout could be categorized by their use of different regions of the lake (Fig. 4). Four individuals used region 1 extensively in both years, although one of these individuals (3225) also spent considerable time in region 2 in 2003. Without these latter observations, individuals using region 1 had relatively deep (26.7–42.1 m) and often large (16.7–79.2 ha) core areas. Six lake trout used region 2 extensively and had relatively shallow (13.0–28.3 m) and often very small (1.2–36.5 ha) core areas. These six lake trout frequently used lake depths above the 10° C isotherm and rarely ventured far offshore. They also had significantly longer L_F than lake trout from the other two regions (ANOVA, d.f. = 2, 11, $P < 0.05$) and were close to being significantly heavier (ANOVA, d.f. = 2, 11, $P = 0.06$). Finally, four lake trout used region 3 extensively and had shallow (10.4–14.7 m) core areas of variable size (10.2–49.0 ha). Despite the large body sizes of fish using region 2 and their tendency to have small core areas, core area was not related to L_F (linear regression, d.f. = 12, $P > 0.05$) nor mass (linear regression, d.f. = 12, $P > 0.05$) when all lake trout were considered. The regions used by individual lake trout were similar between years, but the degree of spatial overlap was variable (Table II and Fig. 4). The lake trout tracked with the automated system used different regions of the lake than those that were manually tracked (Table III). Two individuals used region 1 most frequently, one individual used region 2 most frequently and eight individuals used region 3 most frequently. Unlike any of the manually tracked lake trout, three individuals used region 4 most frequently.

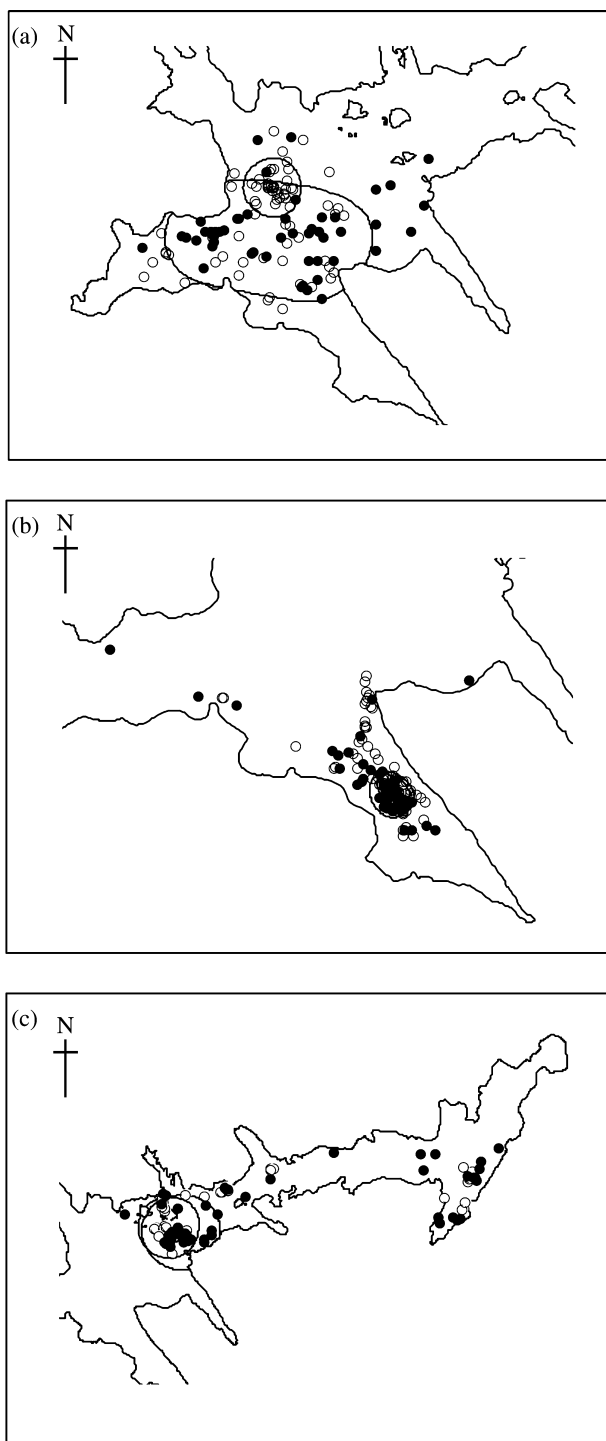


FIG. 4. Locations of representative lake trout from regions (a) 1 (5426), (b) 2 (6633) and (c) 3 (5556) during the summers of 2002 (●) and 2003 (○). Core utilization areas are outlined in each year.

The manual telemetry data demonstrated that individuals had shifting areas of concentrated use, using the same area for days or weeks before moving on. As a result, subsequent locations of all but individual 4332 were significantly spatially clumped (all $P < 0.01$). Autocorrelations in move distances and turning angles contributed to the spatial clumping of successive locations in some individuals. Successive move distances were significantly and positively correlated in three individuals (2223, 4332 and 5556; all $P < 0.01$), indicating a concentration of short moves interspersed with long moves. The turning angles of four individuals (3335, 4224, 4332 and 4446) were significantly clumped in the 150–180° range (all $P < 0.01$), demonstrating a high frequency of direction reversals. Move speeds were significantly autocorrelated in just one individual (5556; $P < 0.01$).

The manual telemetry data indicated that in both years, lake trout most frequently used lake depths between 10 and 20 m, used lake depths deeper than the 10° C isotherm, and had body temperatures $\leq 10^\circ\text{C}$ (Fig. 5). The automated telemetry data also indicated extensive use of depths in the 10–20 m range. For these data, the depth above which lake trout spent 50% of their time varied from 8.6 to 18.9 m with a median of 11.3 m ($n = 14$ individuals).

Individual lake trout differed in their use of warm-water habitats, with the strength of the effect dependent upon the year and the indicator under consideration. The manual telemetry data demonstrated that individuals differed in their use of lake depths above the 10° C isotherm in 2002 (χ^2 analysis, d.f. = 13, $P < 0.001$); the trend was not significant in 2003 (χ^2 analysis, d.f. = 9, $P > 0.05$), possibly because of the lower sample size. In 2002, use of lake depths above the 10° C isotherm was least frequent for lake trout from region 1 (2.7–10.5%), intermediate for lake trout from region 2 (5.3–25.0%) and most frequent for lake trout from region 3 (18.0–42.9%). Similarly, lake trout with temperature coded transmitters differed in their frequency of exceeding 10° C in 2002 (χ^2 , d.f. = 8, $P < 0.001$) and 2003 (χ^2 , d.f. = 4, $P < 0.001$; Table IV). For example, in 2002, lake trout from region 3 exceeded 10° C more often (5.9–81%) than lake trout from region 1 (9.7–27.0%) and region 2 (17.1–24.0%). The automated telemetry data also indicated extensive individual variation in the use of warm-water habitats. For these data, the per cent of time spent at depths shallower than the 10° C isotherm ranged from 0.05 to 26.2% with a median of 7.5% ($n = 14$ individuals).

In order to compare warm-water habitat use between years, it was first necessary to determine if individuals could be pooled in the analysis rather than doing separate analyses for each individual. When considering the 10 lake trout tracked in both 2002 and 2003, pooling was justified because the annual difference in the frequency of using depths above or below the 10° C isotherm was similar among individuals (heterogeneity χ^2 , d.f. = 9, $P > 0.05$). After pooling data for these 10 lake trout, use of depths above the 10° C isotherm was greater in 2002 than in 2003 [χ^2 , d.f. = 1, $P < 0.001$; Fig. 5(b)]. Similarly, the five lake trout with body temperature information from both years were homogeneous with respect to the annual difference in their frequency of exceeding 10° C (heterogeneity χ^2 , d.f. = 4, $P > 0.05$). After pooling the data for these five individuals, body temperatures more often exceeded 10° C in 2002 than in 2003 [χ^2 , d.f. = 1, $P < 0.05$; Fig. 5(c)].

TABLE IV. Habitat use of the manually tracked lake trout in Lake Louisa, showing the region of concentrated activity in 2002 and 2003 (from Table II), the per cent of fixes in lakes depths above the 10° C isotherm, the per cent of fixes in which body temperature exceeded 10° C and body temperature [mean \pm S.D. (*n*)]

Transmitter code	Region	Per cent >10° C isotherm		Per cent >10° C body temperature		Body temperature (° C)	
		2002	2003	2002	2003	2002	2003
2223	1	5.0	—	23.1	—	7.9 \pm 3.0 (39)	—
2334	1	10.5	—	27.0	—	9.5 \pm 4.2 (37)	—
3225	1,2	8.1	2.6	9.7	16.2	8.7 \pm 1.4 (31)	8.1 \pm 3.5 (37)
5426	1	2.7	2.6	—	—	—	—
2225	2	16.2	12.8	24.0	13.6	11.2 \pm 3.8 (32)	9.4 \pm 3.8 (36)
4224	2	20.5	0	—	—	—	—
4332	2	22.5	2.6	—	—	—	—
4446	2	25.0	0	17.1	13.0	7.8 \pm 2.3 (36)	6.7 \pm 3.4 (33)
5434	2	5.3	12.5	—	—	—	—
6633	2	10.3	0	—	—	—	—
345	3	18.0	—	5.9	—	8.4 \pm 2.1 (34)	—
2333	3	27.5	6.5	81.1	64.3	13.6 \pm 3.6 (37)	11.1 \pm 4.0 (28)
3335	3	21.6	—	62.9	—	11.8 \pm 3.6 (35)	—
5556	3	42.9	8.1	70.3	43.2	11.9 \pm 2.5 (36)	11.2 \pm 3.9 (37)

Obvious seasonal changes in habitat use during July and August were not apparent. The use of lake depths above the 10° C isotherm did not change seasonally in either year (logistic regression, 2002: Wald χ^2 , d.f. = 1, $P > 0.05$; 2003: Wald χ^2 , d.f. = 1, $P > 0.05$) after statistically controlling for differences among individuals. Non-significant individual by date interactions ($P > 0.05$) were eliminated from the statistical models before assessing the main effects. Seasonal variation in the probability of having body temperatures >10° C differed among individuals in 2002 (logistic regression, Wald χ^2 , d.f. = 8, $P < 0.05$), with one individual (2225) showing a significant seasonal decrease. In 2003, there was no individual by date interaction ($P > 0.05$) and no seasonal trend in the probability of exceeding 10° C (logistic regression, Wald χ^2 , d.f. = 1, $P > 0.05$) after controlling for differences among individuals.

WARM-WATER FORAYS

Among the 14 lake trout tracked with the automated telemetry system in 2003, 3879 warm-water forays >2 min in duration were detected. Eleven individuals made at least 50 warm-water forays, and for each individual, the duration of warm-water forays was non-normal with the majority being short. The median duration of warm-water forays ranged from 5.6 to 15.7 min among individuals and the median minimum depth attained ranged from 6.8 to 8.5 m. For each individual, the frequency of warm-water forays differed among the 10 sub-daily time periods (all $P < 0.01$). Individuals, however, differed with respect to their daily pattern of warm-water forays (heterogeneity χ^2 , d.f. = 79, $P < 0.001$). Most lake trout had a peak in warm-water forays during dawn

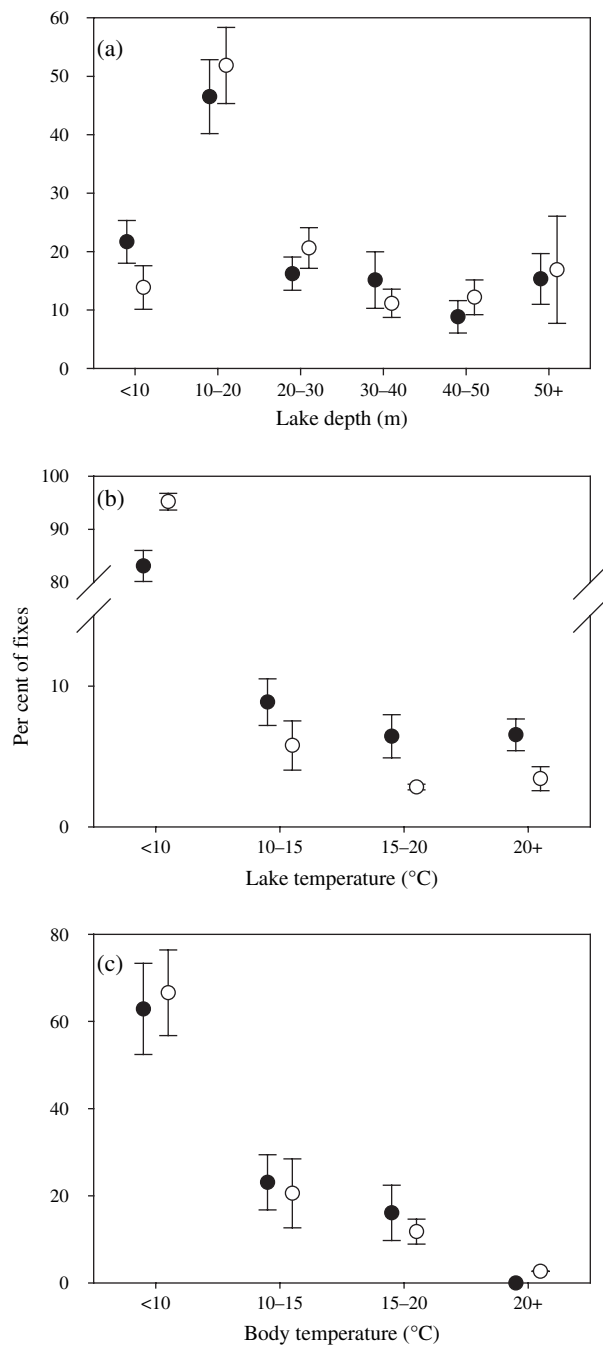


FIG. 5. Aspects of lake trout habitat use in 2002 (●) and 2003 (○). The per cent of fixes (mean \pm S.E. for all individuals) (a) located at different lake depths (<10, 10–20, 20–30, 30–40, 40–50 and \geq 50 m), (b) located in lake depths associated with different isotherms (<10, 10–15, 15–20 and \geq 20° C) (note the break in the y-axis from 15 to 80%) and (c) within different body temperatures (<10, 10–15, 15–20 and \geq 20° C).

(0448–0712 hours, $n = 10$ individuals) and half of these had a second, usually smaller, peak in activity at dusk (1912–2136 hours, $n = 5$ individuals; Fig. 3). One individual (transmitter code 4) stood out by having frequent forays throughout the day from 0448 to 1912 hours without any obvious peak in activity at dawn or dusk. On average, warm-water forays were most frequent at dawn (0448–0712 hours) and least frequent during the three night-time periods (2136–0448 hours; Fig. 3). Thus, most forays occurred when water temperatures during the daily cycle were at their lowest.

DISCUSSION

In Lake Louisa, lake trout most often occupied thermally favourable depths within the metalimnion. Similar to what happens in small lakes without pelagic fish prey (Snucins & Gunn, 1995; Sellers *et al.*, 1998), however, lake trout frequently made excursions into lake temperatures exceeding their thermal optimum of 10° C. Forays above the 10° C isotherm occurred at all times of day and night, throughout the summer, and in all individuals. It is likely that many of these forays were related to foraging because these most often occurred at dawn and dusk periods, when active foraging by lake trout is usually observed. Whether lake trout were seeking littoral fishes, benthic invertebrates or zooplankton (*e.g.* cladocerans) during forays was not determined, but several lines of evidence suggest that lake trout may feed extensively on littoral fishes during the summer. Lake trout were often found in nearshore habitat (littoral) during the day and the percentage of littoral fishes in the summer diet of Lake Louisa lake trout can be high (>75% by mass or volume; Konkle & Sprules, 1986; Vander Zanden & Rasmussen, 1996; Y. E. Morbey, unpubl. data).

Average body temperature differed among the individuals with deviations from 10° C ranging from –21 to +36%. The occupation of habitat warmer or cooler than the assumed preferred temperature of 10° C has implications for estimating maximum consumption rates and growth with bioenergetic models. To demonstrate the sensitivity of key parameters of bioenergetic models to observed deviations in body temperatures from 10° C, the empirically derived equations in Stewart *et al.* (1983) and the observed body temperatures of lake trout were used to calculate the consumption rate, metabolic rate and proportion of assimilated energy excreted for each individual. These calculations took into account the mean and s.d. of body temperature (Table IV) by apportioning time spent at temperatures between 5 and 20° C. The body mass of each individual was also accounted for in the calculations of maximum consumption rate and metabolic rate; this limited the number of comparisons to the eight individuals tagged in 2002 with temperature sensitive transmitters. After these calculations, each value was compared to the expected maximum consumption rate, metabolic rate and proportion of assimilated energy excreted under 10° C and observed body mass (Table V). Predicted consumption rates, metabolic rates and proportions of assimilated energy excreted under observed body temperatures showed large deviations from expected values. Moreover, the responses of the bioenergetic parameters to a positive temperature deviation were larger than the responses to a negative temperature deviation. This

TABLE V. Sensitivity of key bioenergetic parameters (maximum consumption rate, metabolic rate and excretion) to deviations in mean body temperature (T) from 10°C [$(T_{\text{obs}} - 10^\circ\text{C}) 10^\circ\text{C}^{-1}$]. Sensitivity of each output parameter (x) is measured as the per cent deviation from that expected under 10°C [$(x_{\text{obs}} - x_{\text{exp}}) x_{\text{exp}}^{-1}$] using parameters from Stewart *et al.* (1983)

Transmitter code	Temperature deviation from 10°C (%)	Sensitivity (%)		
		Consumption ^a	Metabolism ^b	Excretion ^c
2223	-21	-12	-8	-9
2334	-5	14	8	-1
3225	-13	-14	-9	-8
2225	12	31	18	7
4446	-22	-18	-13	-12
345	-16	-14	-10	-9
2333	36	65	39	18
3335	18	37	22	10
5556	19	33	20	10

^aMaximum consumption ($\text{g g}^{-1} \text{day}^{-1}$) = $aM^b e^{qT}$; $a = 0.059 \text{ g g}^{-1} \text{day}^{-1}$, $b = -0.307$, $q = 0.123$, M = mass (g) and T = body temperature ($^\circ\text{C}$).

^bMetabolism at *in situ* swimming speed ($\text{g O}_2 \text{day}^{-1}$) = $\alpha M^\beta e^{\rho T} e^{vU_{\text{opt}}}$; $\alpha = 0.00463 \text{ g O}_2 \text{day}^{-1}$, $\beta = -0.295$, $\rho = 0.059$, $v = 0.0232$, $U_{\text{opt}} = 11.7 M^{0.05} e^{0.0405T} (\text{cm}\cdot\text{s}^{-1})$, M = mass (g) and T = body temperature ($^\circ\text{C}$).

^cProportion of consumption excreted = $\varepsilon_1 T^{\varepsilon_2} e^{\varepsilon_3 P}$; $\varepsilon_1 = 0.0314$, $\varepsilon_2 = 0.58$, $\varepsilon_3 = -0.299$; T = body temperature ($^\circ\text{C}$), $P = 0.5$.

suggests that sensitivity is non-linear and that even if average body temperature among individuals was 10°C , ignoring individual deviations from 10°C would cause consumption, metabolism and excretion to be underestimated.

Variation in thermal habitat use by lake trout appears to be due, in part, to optimal habitat selection behaviour, in which lake trout evaluate the thermal costs and foraging benefits of different habitats (MacArthur & Pianka, 1966). This may help explain why lake trout appear to use warmer water habitat to a greater extent in small lakes without pelagic schooling fish prey (Sellers *et al.*, 1998; Snucins & Gunn, 1995; this study) than in larger lakes with pelagic schooling fish prey. For example, individuals in Lake Louisa had body temperatures during July and August ranging from 6.7 to 13.6°C . In contrast, lake trout stocked into Lake Huron had body temperatures during July and August of *c.* 7 and 8.5°C , depending on their hatchery origin (Bergstedt *et al.*, 2003). Lake trout in Lake Louisa may feed in warm-water habitat to access larger, more profitable prey (*e.g.* littoral fishes), even though thermal costs may be incurred as body temperatures rise in response to higher lake temperatures (Gibson & Fry, 1954; Mac, 1985). Thermal costs, however, probably limit the extent of littoral feeding. Visits to warm-water habitat were usually short, possibly as a mechanism to reduce thermal costs. Moreover, the lake trout that were manually tracked were never found in broad littoral areas at the head of bays, far from any thermal refuge. The high frequency of forays at dawn, when epilimnion temperatures were at their coolest, may also function to minimize the thermal costs of foraging during a time with adequate light (Beauchamp *et al.*, 1999).

All indicators of warm-water use were higher in 2002 than in 2003. In particular, lake trout using the perimeter of the main basin (region 2) made more excursions into nearshore habitats and their core areas were shifted nearer to shore in 2002 than in 2003. The greater use of shallow water in the warmer year is surprising given the importance of temperature in defining usable habitat boundaries for lake trout and the role of temperature in influencing optimal habitat selection. Under these paradigms, lake trout should be found in shallower depths when cooler temperatures cause the thermocline to form at a shallower depth. The results of the current study suggest that habitat use depends on other factors, in addition to temperature, that may vary between years (Sellers *et al.*, 1998).

Individuals showed significant heterogeneity in their core areas and use of warm-water habitat. Lake trout using region 1 probably foraged primarily on zooplankton because they rarely used nearshore habitats. In contrast, lake trout with nearshore core areas (regions 2 and 3) probably fed extensively on littoral fishes and benthic invertebrates. They frequently entered shallow water and often had elevated body temperatures. Of these nearshore fish, some had particularly small core areas near the islands and around the perimeter of the basin. It is likely that these areas offered opportunities for concentrated foraging on littoral fishes, especially given the extensive foraging by large ($n = 40\text{--}60$) aggregations of piscivorous mergansers (*Mergus* spp.) in the same areas throughout July and August (Y. E. Morbey, pers. obs.). Other individuals from regions 2 and 3 had large, shifting home ranges. Why some lake trout appeared to show greater site fidelity than others is not known, but it appears that lake trout size may play an important role because the six lake trout from region 2 were significantly larger than those from regions 1 and 3. Moreover, standardized gillnetting surveys also tend to capture larger lake trout closer to shore in Lake Louisa (AFAU, unpubl. data).

Individual differences in habitat use indicate resource partitioning between littoral and pelagic habitats, possibly caused by three processes. First, larger individuals could preferentially feed on larger prey (*i.e.* littoral fishes and benthic invertebrates; Keast, 1977; Polis, 1984). This is a possibility, especially given the observation of ontogenetic diet shifts towards larger prey in lake trout (Trippel & Beamish, 1993; Madenjian *et al.*, 1998; Vander Zanden *et al.*, 2000). Second, some individuals may be better competitors, possibly because of their larger size, and may exclude poorer competitors from preferred, littoral foraging areas ('resource polymorphism': Wimberger, 1994; Skulason & Smith, 1995; Smith & Skulason, 1996). Although lake trout are not known to be territorial, it is not known whether agonistic interactions between individuals could cause such partitioning. An intriguing possibility is that such niche partitioning between littoral and pelagic habitats may result in morphological differentiation, to a lesser extent but similar to other freshwater fishes (Schluter & McPhail, 1992; Skulason *et al.*, 1993; Snorrason *et al.*, 1994). Sympatric differentiation of lake trout based on depth preferences and morphology occurs in Lake Superior (Moore & Bronte, 2001) and a trophic dimorphism (insectivorous *v.* piscivorous) has been reported for lake trout inhabiting Great Bear Lake, North West Territories, Canada (Blackie *et al.*, 2003). The existence of resource polymorphisms has not been reported in other lakes, but it may be possible in Lake

Louisa. Third, among-individual variation may be unrelated to any size-based difference (individual specialisation: Bolnick *et al.*, 2003). This seems unlikely, however, given the evidence of ontogenetic diet shifts by lake trout.

To assess the causes of niche partitioning by lake trout in Lake Louisa or in other lakes, a more exhaustive study is needed. Given what is now known about individual heterogeneity in habitat use, this poses a challenging sampling problem. For example, lake trout were initially captured in the spring when isothermal conditions were expected to favour extensive movements throughout the lake, thus enabling a more or less random sample. Lake trout, however, often used the same region of the lake as where they were captured (unpubl. obs.), suggesting that lake trout do not necessarily travel more extensively during isothermal periods. As a consequence of non-random sampling, individuals were distributed unevenly among the different regions of the lake. Another potential problem is the shifting nature of habitat use, which poses statistical difficulties when interpreting home ranges and quantifying habitat use. Future telemetry studies should consider these issues, and attempt to stratify their samples by lake region, depth and body size.

Individual niche variation can have important consequences for a variety of ecological and evolutionary processes, such as population dynamics, bioaccumulation of contaminants and life-history evolution (Partridge & Green, 1985; Lomnicki, 1988; Madenjian *et al.*, 1993; Bolnick *et al.*, 2003). For example, it is thought that populations with high individual niche variation (*i.e.* trophic flexibility) may have greater capacity to persist under changing environmental conditions (Dieckmann & Doebeli, 1999). Whether lake trout are more resistant to fluctuations in prey availability and possibly climate change in Lake Louisa than in lakes with less trophic flexibility will depend on how much of the among-population variation in habitat use and diet is driven by phenotypic plasticity and how much is driven by genotypic differentiation. From a human health perspective, individual variation in habitat use and diet may also cause individual variation in the concentration of contaminants, which has implications for stocking policies and for the setting of safe consumption levels (Madenjian *et al.*, 1993). This may be an important consideration for inland lakes in Ontario, where mercury contamination can be high (Anon., 2005). Finally, individual variation in habitat use may influence how fishing mortality selects at different life stages. Given that low levels of competitive interference and a high degree of social or habitat-mediated aggregation can contribute to increased vulnerability (Gillis *et al.*, 1993; Gillis & Peterman, 1998), larger lake trout in Lake Louisa may be more vulnerable to anglers than smaller lake trout because of their tendency to concentrate their activities inshore, coincidentally near camping sites.

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