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[Article]

Thermal Habitat Use by Lake Trout in Two Contrasting Yukon Territory Lakes

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Abstract.—Thermal habitat use by lake trout *Salvelinus namaycush* in two northern lakes in the southern portion of the Yukon Territory that differ in morphometry and thermal regime was monitored using temperature-sensitive acoustics and radiotelemetry. We then contrasted in situ temperature selection by lake trout in these lakes with previously published estimates of the species' optimal thermal range of 8–12°C. We found that thermal habitat use by lake trout in the two northern lakes is not consistent with these literature-derived expectations. In Dezadeash Lake, which is isothermal in summer, temperatures typically exceeded the literature-derived upper limit of 12°C. Throughout the summer lake trout sought the coldest water in the lake, which was in the form of shallow coldwater plumes derived from alpine ice-pack meltwater streams. Once lake temperatures declined in the fall, lake trout were distributed throughout the lake. In Kathleen Lake, where water temperatures ranged from approximately 2°C to 12°C in the summer, the majority of lake trout selected habitats throughout the summer and fall that were colder than the 8°C lower limit of their literature-derived optimal thermal range. Our results highlight the importance of summer thermal refugia for lake trout inhabiting marginal systems and the variation in thermal habitat use among populations inhabiting different thermal environments. Given the established importance of thermal habitat availability to lake trout production, our results suggest the need to better understand optimal thermal habitat characteristics in nature, particularly in light of factors such as climate warming.

Fish movement and distribution patterns are governed by biotic and abiotic factors, as well as behavioral and life history characteristics. With few exceptions, fish are obligate ectotherms, such that environmental temperature determines body temperature. Fish, however, can control thermal experience through behavioral thermoregulation. Temperate fish typically occupy systems with considerable thermal complexity, yet most inhabit a relatively narrow, species-specific thermal range that defines the optimal conditions for activity and metabolism (Magnuson et al. 1979), and fish will thermoregulate behaviorally in an effort to remain within this thermal range.

Lake trout *Salvelinus namaycush* are a coldwater stenotherm. They normally occupy waters within a temperature range of 6–13°C (Martin and Olver 1980), and it is generally assumed that temperatures greater than 15.5°C are unsuitable for lake trout (MacLean et al. 1990), at least for extended periods. Assuming food availability and niche interactions are not limiting, temperatures between 8°C and 12°C define the physiologically optimal thermal range for activity, metabolism, and therefore, growth for this species (Christie and Regier 1988); the optimum temperature is 10°C (Stewart et al. 1983; Magnuson et al. 1990). Availability of thermal habitat (thermal habitat volume) for lake trout within this temperature range has also been empirically related to production of this species (Christie and Regier 1988; Payne et al. 1990). Although limited testing of this optimum thermal range has been performed for lake trout in the field, most researchers generally apply the above thermal range to define optimal thermal habitat in the natural environment. This optimum thermal range usually has been determined through laboratory testing of juvenile lake trout, which are often hatchery reared and originate from lake trout stocks in the southern part of their range (Mac 1985; McCauley and Tait 1970; O'Connor et al. 1981). To date, rigorous field verification of juvenile and adult physiological thermal optima for more northerly stocks has not occurred.

Although brief exposure of fish to temperatures that are slightly outside the boundaries of the optimal thermal range probably has little influence on overall growth, survival, or reproduction, prolonged exposure to unfavorable temperatures probably has a dramatic effect on these characteristics. When temperatures become unfavorably warm for prolonged periods, decreases in growth, survival, and reproduction are likely and local extirpation of affected populations occurs (MacLean et al. 1990). Given the importance of lake trout to commercial, sport, and subsistence fisheries, improving our understanding of how lake trout use available thermal habitat may not only shed

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light on important aspects of thermoregulatory behavior, but may improve management actions to promote population persistence, particularly in the light of predicted climate warming (Mackenzie-Grieve and Post 2006).

We examine the general hypothesis that lake trout will be found within their previously defined physiological optimal thermal range of 8–12°C, or as close to it as possible, given thermal conditions in individual lakes. Our primary objectives were to (1) examine thermal habitat use by wild lake trout in two northern study lakes differing substantially in morphology and thermal characteristics, (2) determine if lake trout were using available thermal habitat in proportion to the volume of optimal thermal habitat available, and (3) compare observed thermal habitat use patterns with previously published data for more southerly lake trout stocks.

Methods

Study lakes.—Dezadeash Lake (60°33′N, 137°58′W) is a large (8,250-ha surface area), shallow (4.1-m mean depth, 7.4-m maximum depth) lake that warms considerably in summer months. This lake is more or less isothermal because of its shallow depth and almost constant mixing by wind. Summer surface temperatures can exceed 17°C (Mackenzie-Grieve 2005). In summer months, lake trout are found within cold-water plumes associated with stream discharge into the lake (Mackenzie-Grieve 2005). Temperatures in the creeks range from 2–9°C and discharge is the result of seasonal snow and ice-pack melt. The resulting coldwater plumes provide the coldest habitat in the lake for much of the summer and the only habitat within the 8–12°C optimal range. Kathleen Lake (60°28′N, 136°58′W) is another large (3,376-ha surface area) but deep (55.2-m mean depth, 111-m maximum depth), cold lake where surface temperatures rarely approach 12°C (Mackenzie-Grieve 2005), providing substantial thermal habitat in the 8–12°C optimal range. These two study lakes were chosen because they (1) have contrasting thermal structure, (2) are within the same drainage basin (Alsek River), and (3) have similar postglacial colonization histories (Lindsey et al. 1981; Wilson and Hebert 1998). The lakes are also in close proximity to one another, which facilitated sampling efforts.

Pelagic water temperature.—Synoptic sampling at fixed locations across each lake to determine vertical temperature distribution was completed in 2001 and 2002 using a Datasonde 3 Hydrolab with Scout 2 (accuracy, ±0.15°C; Hydrolab Corporation, Austin, Texas). Since Dezadeash Lake is shallow, the entire lake thermal profile was sampled. In Kathleen Lake, sampling of vertical temperature distribution was limited to 80 m by the length of the Hydrolab cable. In addition, in 2002, a series of thermistors (accuracy, ±0.2°C; Optic Stowaway Temp logger WTA08–05 + 37, Onset Computer Corporation, Pocasset, Massachusetts) were positioned at depths of 1, 3, 5, and 7 m in each lake to characterize the spatial and temporal thermal profile throughout the smmer, ice-free period.

Coldwater plumes in Dezadeash Lake.—In Dezadeash Lake, biologists and anglers have long known of lake trout use of the coldwater creek plumes discharging into the west side of the lake. One of these plumes was located in a sheltered bay that had been previously identified as one of the primary thermal refugia used by lake trout in summer. In 2001, a single thermistor was placed in this bay near the mouth of the coldwater creek, where lake trout had been observed in previous years. It recorded water temperature every half-hour from May 29 to September 30. In 2002 we estimated the volume of the six most commonly used coldwater plumes associated with stream inflow. This was done by wading and taking temperature and depth measurements at approximately 1–3 m intervals in a grid pattern to determine the spatial extent of the 8–12°C water within each plume. Volume of water in creek plumes within the lake trout optimal thermal range was approximated using common volumetric formulae associated with simple geometric forms. In most cases, the shape of the plume resembled a rectangle with a triangular component near the mouth of the creek where the gradual deepening of the littoral zone becomes the hypotenuse of the triangle.

Stream temperatures and discharges were recorded in 2001 and 2002. In 2001, temperatures were recorded intermittently over the summer months (once per week on average) approximately 500 m upstream from where streams discharge into the lake. In 2002, thermistors were placed in five of the creeks discharging along the west side of the lake, approximately 20 m upstream from their mouths. Stream temperature was recorded at half-hour intervals from mid-June to mid-September. Two thermistors were also placed in two creeks discharging into the east side of the lake. These two creeks were identified as the highest discharge creeks along the east side of the lake.

Discharge measurements of creeks along the west side of Dezadeash Lake were estimated weekly in 2001 and 2002 using a Price current meter and following the midsection method outlined in Mosley and McKerchar (1993). In 2001 discharge measurements of 10 creeks were recorded initially, but by mid-July, four creeks were too shallow to measure. In 2002 discharges were much lower and discharge measurements of only five creeks could be completed.

Temperature-sensitive transmitters and lake trout relocation.—Because Dezadeash Lake is shallow (i.e., <10-m maximum depth) and specific conductivity is low (<150 μS/cm) (Mackenzie-Grieve 2005), lake trout were equipped with temperature-sensitive radio transmitters that perform well in this type of environment. In 2001, 20 radio transmitters (FRT-2 and FRT-5; Lotek Wireless, Inc., Newmarket, Ontario) were externally attached to lake trout (480–720-mm fork length [FL], mean = 580 mm; 1.05–5.40-kg wet weight, mean = 2.59 kg). In 2002, Lotek transmitters (FRT-2 and FRT-5) were externally attached to 17 lake trout (490–755-mm FL, mean = 580 mm; 1.45–7.76-kg wet weight mean = 3.15 kg). The Lotek (SRX_400A) receiver with firmware version (W4A 4.15) and H-antennas (model AN-ADH) were also used. In 2001, transmitter attachments were completed between June 11 and 21, and in 2002, attachments were completed between June 5 and July 19. Each transmitter was on a unique frequency between 148.010 and 149.390 MHz to allow identification of individual lake trout. Lake trout were also fitted with individually numbered FLOY t-bar anchor tags to allow individuals to be identified if transmitter losses occurred. Lake trout were captured using a combination of short-set gill nets and angling throughout the lake. Fish were anesthetized with a few drops of clove oil mixed into holding-tank water. Transmitters were externally attached to lake trout via a hollow-tipped 18-gauge hypodermic needle tip to guide a nylon-coated stainless steel wire through the flesh at the base of the dorsal fin such that the transmitter was lateral to the dorsal fin. Neoprene backing was placed against the fishes' skin to reduce abrasion, and plastic backing was placed between the neoprene and a short (5 mm) segment of hollow brass piping (approximately 1 mm dimension) that was crimped onto the coated wire in an effort to firmly affix transmitters to trout and reduce any abrasion or tag loss. The coated wire was then tied off next to the piping, and the excess was removed. Fish recovered in plastic tubs filled with freshwater and were returned to the lake when recovery was complete.

Because Kathleen Lake is deep and has a specific conductivity of approximately 225 μS/cm (Mackenzie-Grieve 2005), radio transmitters could not be used. Rather, temperature-sensitive acoustic transmitters (CTT-83, Sonotronics Inc., Tucson, Arizona) were used. Transmitter temperature was calibrated in the laboratory before the beginning of the field seasons. In 2001, 19 transmitters were externally attached to lake trout in Kathleen Lake (412–815-mm FL, mean = 500 mm; 0.75–10.00-kg wet weight, mean = 1.91 kg). In 2002, transmitters were externally attached to 19 lake trout (435–760-mm FL, mean = 530 mm; 1.39–5.70-kg wet weight, mean = 2.18 kg). Transmitters were set on a frequency of 70–78 KHz, each fish receiving a unique frequency that allowed individual identification. The Sonotronics Inc. receiver (Model USR-96) and directional hydrophone (model DH-4) were used in trout relocation. Lake trout were captured using a combination of short-set gill nets and angling throughout the lake. Transmitters and FLOY t-bar anchor tags were attached as described for trout in Dezadeash Lake.

Accuracy and consistency of the relocation equipment and operator interpretation of transmitter location were tested by blindfolding the equipment operator, who then attempted to locate a test transmitter as accurately as possible. The procedure was repeated three times in each lake at two depths (shallow and deeper). In both study lakes the shallow test transmitter was placed about 0.1 m below the surface of the water; the deeper test transmitter was placed at about 4 m below the surface of the water in Dezadeash Lake and at about 6 m below the surface in Kathleen Lake. In Kathleen Lake, relocation of the test transmitter signal was most accurate when the transmitter was near the surface of the water, consistent with results of Flavelle et al. (2002), who found that error in acoustic transmitter location increased with depth. Mean error in fix position was greater than 10 m horizontally at depths of approximately 6 m, and less than 10 m horizontally when the transmitter was about 0.1 m below the water's surface. In Dezadeash Lake, relocation accuracy improved with depth of the transmitter, mean error in fix position being approximately 0.5 m horizontally when the transmitter was at 4 m depth. When the transmitter was about 0.1 m below the surface, mean error was approximately 10 m horizontally. Mean error in fix position in each of the study lakes increased with wave action on the boat and was influenced by lake morphometry and thermal characteristics at the location of testing (as described by Winter 1983).

In Dezadeash Lake, monitoring of radio-tagged lake trout movements was completed in daylight hours (0700–2300 hours) by boat between June 22 and August 21, 2001, and by fixed-wing aircraft between August 22 and September 27, at which time pilots became increasingly available and lake trout began to move out of thermal refugia. In 2002, monitoring was completed between May 16 and September 16 using a combination of boat and fixed-wing aircraft monitoring. High winds, common in this part of the Yukon, limited the monitoring in both years. Rough conditions made travel on the lake difficult and drastically decreased accuracy of transmitter relocations. When monitoring was completed by boat only partial coverage of the lake was normally possible (N = 23 d in 2001, $N = 11$ d in 2002). Entire coverage of the lake was possible by aircraft on four occasions in each of 2001 and 2002. On calm days when monitoring by boat was completed, common congregation locations (refugia) were checked initially, and transect methods (north–south transects approximately 500 m apart marked on a map of the lake) were subsequently followed in the main lake. When a signal was identified, the trout was relocated as accurately as possible, the pulse interval (for temperature calculation) was recorded, approximate location was marked on a map, and a Global Positioning System (GPS) fix was recorded. To obtain increased coverage of the lake during boat tracking, the H antenna was attached to a telescopic pole and raised to a maximum height of 15 ft on calm days.

Aerial tracking was typically from an altitude of 800–1,000 m above the lake surface, which provided adequate coverage of the lake and usually allowed pulse intervals (for temperature calculation) to be obtained. With the receiver set on a 2–3-s delay (depending on conditions), the perimeter of the lake was checked initially. Transect methods (following a GPS heading using the aircraft GPS, usually in a north–south arrangement) were then followed to cover the remaining lake area. Transects were separated by less than 1 km, providing adequate coverage of the lake. When a transmitter signal was identified, the tagged trout was located as accurately as possible and the location was marked on a map. Relocation of a test transmitter deployed at a known location and at a depth of about 3 m suggested that error associated with fix position under these conditions was about 300 m. To obtain a pulse interval, it was often necessary for the aircraft to reduce altitude and perform a series of passes and circles. The pulse interval was often difficult to obtain, particularly when the lake was subjected to any wave action. For aircraft relocations, an H antenna was mounted to each of the wing struts on the aircraft.

Monitoring of lake trout movements in Kathleen Lake was completed between June 28 and September 28, 2001, and between June 4 and September 23, 2002. In 2001 a total of 13 monitoring trips on Kathleen Lake were attempted; 2 of these were cut short due to high winds and wave action that interfered with transmitter signal detection. In 2002, a total of 10 trips were attempted, but 7 of the trips were cut short due to high winds. All monitoring on Kathleen Lake was by boat and was restricted to calm days (to avoid interference from wave action on signal transmission and reception). Detection of acoustic tags is influenced by boat motor noise, turbulence (waves, running water, raindrops), thermoclines (or other temperature gradients) and aquatic plants (Winter 1983). In Kathleen Lake, the perimeter of the lake was checked initially for transmitter signals, and transect methods were followed to locate remaining transmitters. When a signal was detected, direction was ascertained, and the boat was moved short distances checking for increased signal strength until, ideally, equal transmitter signal strength was heard in all directions; this providing the best estimate of lake trout location. Transmitter pulse interval of the relocated trout was then recorded (for temperature calculation), its location was marked on a map of the lake, and a GPS fix was taken.

A linear regression was used to test the hypothesis that the number of lake trout using individual refugia was linearly related to the volume of the refugia in Dezadeash Lake.

Results

Thermal Habitat

Dezadeash Lake was approximately isothermal, having less than a 2°C difference between surface and bottom temperatures throughout the majority of each field season (early June to late September; Mackenzie-Grieve 2005). Surface temperatures exceeded 12°C from mid-June to mid-August, which coincided with the period that lake trout used creek plumes as thermal refuges (Figure 1). We define this "thermoregulatory period" as the period when the pelagic surface temperature exceeded the upper optimal temperature for lake trout (i.e., 12°C). This period extended from June 10 to August 18, as determined from the detailed temperature profiles collected in 2002. Although some yearly variation in lake thermal properties and in duration of the thermoregulatory period is likely, we assumed equivalence across years in our analysis. The temperature record from the thermistor placed in the primary lake trout thermoregulatory plume in 2001 demonstrates that the plume provides intermediate thermal habitat (Figure 1), presumably due to mixing of cold stream and warm pelagic water.

Kathleen Lake was substantially colder than Dezadeash Lake, surface temperatures rarely exceeding 12°C (Figure 2). Temperature gradually decreased with depth, and a weak thermocline existed between 40 and 45 m (where temperature change is >1°C; Figure 3b). Kathleen Lake is also often subject to strong winds, although during the longer calm periods, weak thermoclines sometimes also develop between about 10 and 15 m depth.

Spatial and Thermal Location

The majority of lake trout relocations in Dezadeash Lake, however, were obtained in the two coldwater plumes that provided the greatest thermal habitat

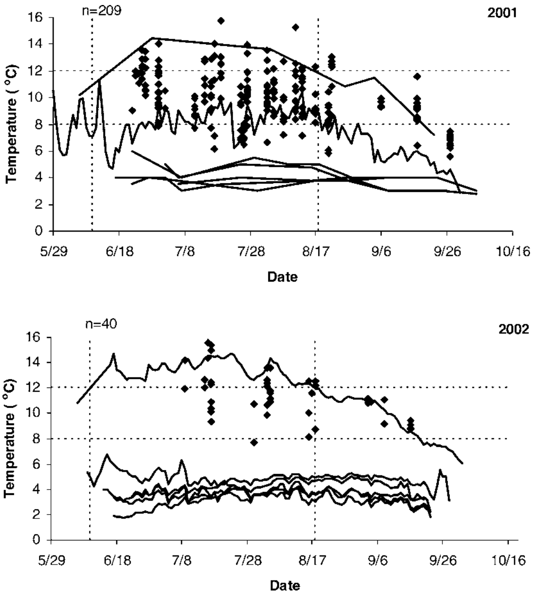


FIGURE 1.—Pelagic temperatures in Dezadeash Lake, Yukon Territory, at the 1-m depth contour (upper solid line), temperature of the main plume used by lake trout (Creek B) within the thermoregulatory period in 2001 (line second from the top in upper panel only), stream temperatures (five lower lines), and temperatures at points of relocation for relocated (radio-tracking) lake trout (diamonds) taken throughout the field season in 2001 versus 2002. Because lake temperatures were approximately isothermal, only pelagic data for the 1-m depth contour are shown. The thermoregulatory period, defined as the duration of the summer when lake temperatures exceeded 12°C is indicated by the pair of dashed vertical lines. The upper (12°C) and lower (8°C) temperatures of the optimal thermal range for lake trout are indicated by the pair of dashed horizontal lines.

volume, as a result of the highest stream discharges in Creeks A and B (Table 1). For example, 75% of relocations within refugia in 2002 were in Creek B, the creek plume with the greatest thermal habitat volume and highest creek discharge; 14% of relocations were within Creek A, the plume with the next-greatest thermal habitat volume (Table 1) and next-highest creek discharge. Distribution of lake trout among creek plumes in 2002 was positively correlated with the volume of the coldwater plume (number of lake trout relocations $= 0.0118 \cdot$refugia volume $+ 0.4807$, $N = 6$, $r^2 = 0.99$, $P < 0.001$). Statistics were performed on 2002 data only because plume volumes were not estimated in 2001. The total number of relocations in 2002 was lower than in 2001 because of high winds throughout most of the summer, which limited monitoring. The temperature profiles of thermal refugia used to calculated optimal thermal habitat volumes varied by less than 1°C from top to bottom.

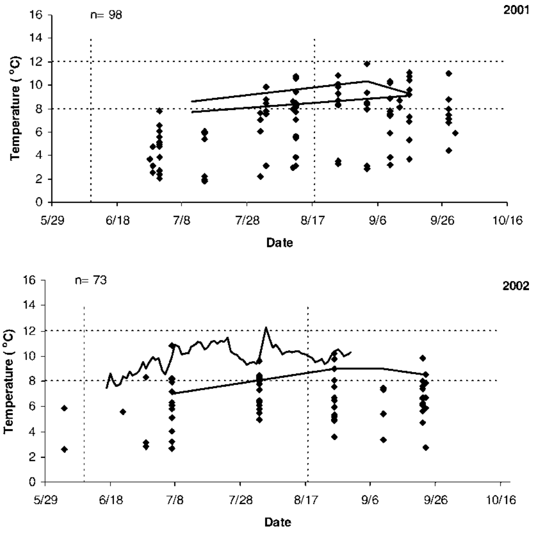
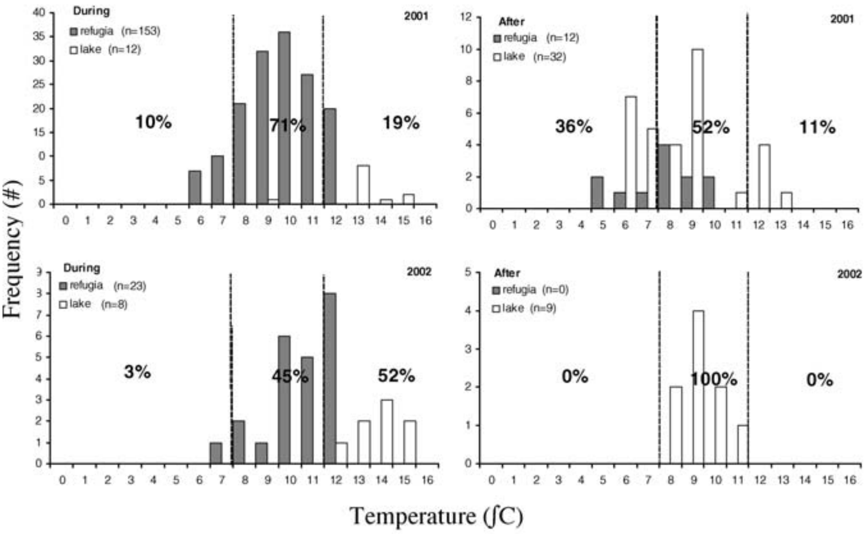


FIGURE 2.—Pelagic temperatures in Kathleen Lake, Yukon Territory, at the 1-m depth contour (upper line) and at a depth of 30 m (lower line) in 2001 versus 2002. Temperature and day of lake trout sonic relocations are indicated by the solid diamonds. The thermoregulatory period, as defined for Dezadeash Lake, is indicated by the pair of dashed vertical lines. The upper (12°C) and lower (8°C) temperatures of the optimal thermal range for lake trout are indicated by the pair of dashed horizontal lines.

Shoreline morphology probably played a role in the creeks used by lake trout. For example, the plume most commonly used by lake trout, Creek B, was in a relatively protected bay where wind-driven mixing of the coldwater plume with lake water was probably minimized, leading to greater stability and consistency in plume habitat. The other coldwater plumes were more exposed to wind-driven mixing and were therefore probably smaller and less stable. In some cases, spatial extent of these plumes did appear to shift somewhat with prevailing wind direction.

The thermal refuges provided the coldest thermal habitat available in Dezadeash Lake, which was close to the optimal thermal range for lake trout. The importance of coldwater plumes to lake trout in Dezadeash Lake within the thermoregulatory period is clear because the majority of relocations were within the thermal refugia (Figure 3a). For example, in 2001, 85% of relocations were in refugia, and in 2002, 59% of relocations were within refugia during this warm-water period. During the thermoregulatory period when the majority of relocations were within thermal refugia, (Figure 4a, b), lake trout were often relocated at temperatures within the physiologically optimal range; in 2001, 71% of the relocations were within the optimal thermal range, and only 19% of relocations were at

a) Dezadeash Lake



b) Kathleen Lake

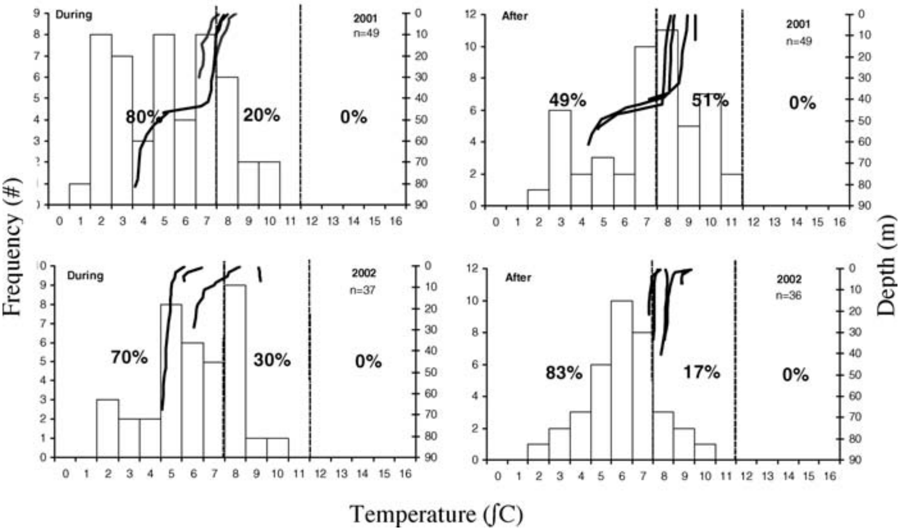


FIGURE 3.—Frequency of lake trout relocations (left *y*-axis) with respect to 1°C increments in temperature during and after the thermoregulatory period in 2001 and 2002 for **(a)** Dezadeash Lake and **(b)** Kathleen Lake, both in the Yukon Territory. Both lake and refugia relocations were obtained in Dezadeash Lake but only lake relocations in Kathleen Lake. Dashed vertical lines indicate the lower (8°C) and upper (12°C) boundaries of the optimal thermal range. The percentages of relocations below, within, and above the optimal range are shown. Temperature profiles (dark, irregular lines; right *y*-axis) are also indicated for Kathleen Lake. The deepwater profiles are the result of the synoptic sampling effort; the shallow-water profiles (upper 7 m) were obtained from the 2002 thermistors. Only the warmest and coldest profiles are indicated for the thermistor data; water temperatures throughout the remainder of the season fell between these two extremes. The number of deepwater profiles varies by sampling period. Sample sizes differ from those in Table 1 because only relocations for which temperatures were obtained are included in this figure.

TABLE 1.—Number of radio-tagged lake trout relocations within each of the coldwater plumes in Dezadeash Lake, Yukon Territory, in 2001 and 2002 during the thermoregulatory period. The volumes of coldwater plumes associated with six creek mouths (A–F) at which lake trout commonly congregated were estimated in 2002. Within the thermoregulatory period, 11 relocations were obtained in the main lake in 2001, and 16 relocations were obtained in the main lake in 2002.

		Creek discharge (m^3/s)		Lake trout in refugia[a]	
Creek	Refuge volume (m^3)	2001	2002	2001	2002
A	415	0.63	0.22	37	6
B	2,258	0.76	0.36	95	27
C	180			10	1
D	107	0.14	0.08	8	3
E	20	0.16	0.07	3	0
F	5	0.17	0.09	2	1
Total	2,985			155	38

[a] Number of relocations in 2002.

temperatures greater than 12°C (Figure 3a). Within the thermoregulatory period in 2002, however, only 45% of relocations were within the preferred range, and 52% of relocations were at temperatures greater than 12°C (Figure 3a). As with 2001 data, the greatest numbers of relocations in 2002 were also within thermal refugia (Figure 4b), but at temperatures between 12°C and 13°C (Figure 3a), only slightly above the optimal range. Lower creek discharges in 2002 compared with 2001 (Table 1) probably provided less coldwater thermal habitat in 2002, thus reducing the size of the thermal plumes and forcing lake trout into slightly warmer waters in 2002. For example, mean temperature used by lake trout was 11.9°C ($N = 35$) in 2002 but was 10.3°C ($N = 166$) in 2001. Lake trout were not, however, exclusively restricted to thermal refugia within the thermoregulatory period, and there was some movement between refugia and between refugia and the main lake (refer to Mackenzie-Grieve 2005).

Following the thermoregulatory period, when temperatures in Dezadeash Lake had cooled to less than 12°C, lake trout were most often relocated within their preferred thermal range; in 2001, 52% of relocations were within the preferred range, and in 2002 all relocations were within the preferred range (Figure 3a). Mean temperature at which lake trout were relocated within this period was 8.7°C ($N = 46$) in 2001 and 9.9°C ($N = 12$) in 2002, and lake trout were relocated throughout the lake in both years (Figure 4c, d). Postthermoregulatory period relocations of lake trout in 2001 within the refugia (Figure 4c) occurred immediately following the end of this period. Lake trout were never relocated in areas associated with stream inflows on the east side of the lake throughout the thermoregulatory period. Thermistors placed in these eastside creeks revealed that optimal thermal habitat did not exist within these creek plumes, and temperatures as high as 18°C were recorded during the thermoregulatory period (Mackenzie-Grieve 2005).

Water temperature data from Kathleen Lake show that habitat within the optimal range for lake trout does exist in this lake, particularly within the upper epilimnion (Figure 2). In both years, lake trout were not found exclusively within the optimal range of 8–12°C but were often found at lower temperatures, which were available at greater depths (Figures 2, 3b). Data were inadequate to determine whether lake trout were using thermal habitat in proportion to availability.

During the summer of 2001 (i.e., the thermoregulatory period as defined for Dezadeash Lake), 80% of relocations in Kathleen Lake were below the optimal range for lake trout, and only 20% were within the optimal thermal range (Figure 3b). The mean temperature at which lake trout were relocated within this period was 5.7°C ($N = 49$). Within the same period in 2002, 70% of relocations were below the optimal range and only 30% were within the optimal range (Figure 3a). The mean temperature at which lake trout were relocated was about 6.4°C ($N = 37$). In both 2001 (Figure 5a) and 2002 (Figure 5b), lake trout were relocated throughout Kathleen Lake at similar locations in each of the two years. Once the lake began to cool in the autumn (i.e., following the thermoregulatory period as defined for Dezadeash Lake), mean temperature used by lake trout was lower in 2002 (6.6°C, $N = 36$) than in 2001 (7.7°C, $N = 49$). Within this period in 2002, 83% of relocations were at temperatures less than 8°C, and only 17% of relocations were within the optimal thermal range (Figure 3b). In 2001, approximately equal numbers of lake were found in temperatures less than 8°C (49%) and within the optimal range (51%) (Figure 3b). Within this period, locations most commonly used by lake trout were similar in both 2001 and 2002 (Figure 5c, d).

Discussion

Thermal habitat use by lake trout in these two northern lakes was not consistent with expectations

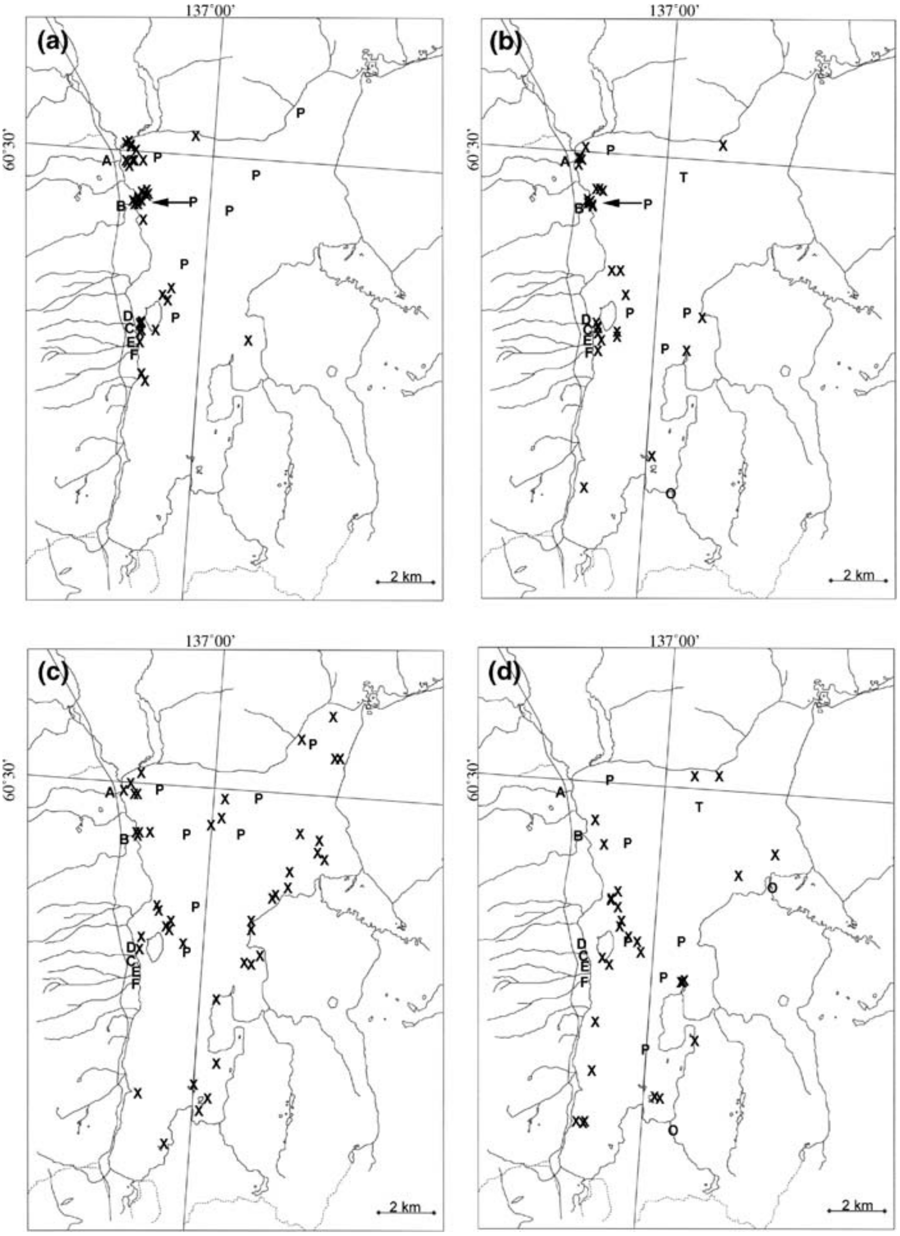


FIGURE 4.—Radiotelemetry relocations (*x*) within Dezadeash Lake, Yukon Territory, of tagged lake trout during the thermoregulatory period in **(a)** 2001 and **(b)** 2002 and after the thermoregulatory period in **(c)** 2001 and **(d)** 2002. Letters A–F identify six tributary creeks where thermistors were placed in 2002. The arrow shows the creek plume most commonly used by lake trout; the 2001 thermistor was positioned within this bay. The location of the 2002 thermistor profile is indicated by T, synoptic sampling sites in 2001 and 2002 are indicated by P, and thermistor placements in eastside creeks are indicated by O. The discharge location of Creek D into the main lake was not represented on the map (developed from 1979 data).

based on previous studies of more southerly populations. For example, in Kathleen Lake, thermal habitat between 8°C and 12°C was available to lake trout throughout summer months but the majority of tagged trout were relocated at temperatures less than 8°C, and often substantially below the optimal thermal range for lake trout (8–12°C; Christie and Regier 1988; Payne et al. 1990; Magnuson et al. 1990). In Dezadeash Lake, a lake with a very different thermal regime, lake trout appear to seek out the coldest habitat in the lake, which

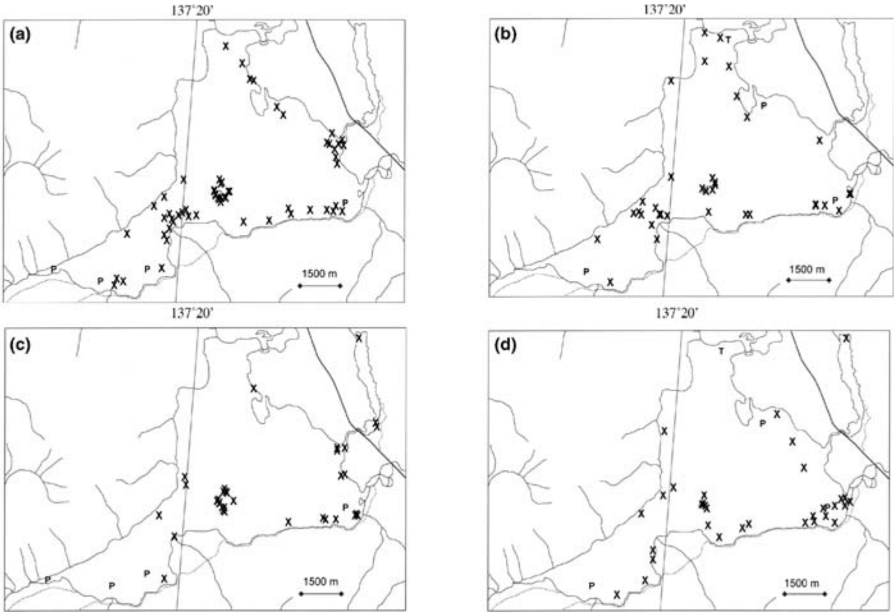


FIGURE 5.—Sonic relocations (*x*) of tagged lake trout in Kathleen Lake, Yukon Territory, during the thermoregulatory period (as defined for Dezadeash Lake) in **(a)** 2001 and **(b)** 2002 and after the thermoregulatory period in **(c)** 2001 and **(d)** 2002. The location of the 2002 thermistor profile is indicated by T, and synoptic sampling sites in 2001 and 2002 are indicated by P.

was in the form of coldwater plumes, resulting from coldwater creek discharges. Temperatures within thermal refuges often approached the upper limit of the optimal range but were colder than pelagic temperatures in the lake. Even though lake trout did either temporarily leave refugia, or move among refugia over the summer, importance of thermal refugia to lake trout in Dezadeash Lake was clear because the majority of summer relocations in each year of the study were within these thermal refugia. It is not possible to ascertain whether Dezadeash lake trout were seeking temperatures within their previously defined optimal thermal range or were simply seeking the coldest habitat available.

Behavioral thermoregulation by salmonids using various forms of thermal refugia is not uncommon. For example, in a stream system, juvenile bull trout *S. confluentus* were located within the coldest water available in the stream, an area below a discharging tributary stream (Bonneau and Scarnecchia 1996). In a river system, Baird and Kruger (2003) reported a similar situation where brook *S. fontinalis* and rainbow trout *Oncorhynchus mykiss* used thermal refugia, also in the form of tributary confluences, in an effort to avoid near-lethal temperatures within the main flow of the river. In lake systems, fish typically move deeper in the water column to seek colder temperatures in the hypolimnion as the epilimnion warms. Occasionally lakes are not deep enough for thermal discontinuity to develop and provide thermal refugia below the thermocline. Snucins and Gunn (1995) reported the use of a cold groundwater discharge by lake trout in a shallow Ontario lake in an effort to avoid elevated lake temperatures. Lake trout behavior in Dezadeash Lake is similar to that documented by these authors, although the source of the coldwater refuge differs.

Considerable variation exists with respect to lake trout thermal habitat use (see reviews in Coutant 1977 and MacLean et al. 1990), and laboratory-determined values for lake trout thermal preference are generally higher than field-determined values (Reynolds 1977). Following Christie and Regier (1988) and Magnuson et al. (1990), we assumed that the optimal temperature range for lake trout is 8–12°C, which is an average of laboratory-determined final preferenda (Peterson et al. 1979; Goddard et al. 1974; McCauley and Tait 1970; Mac 1985) and laboratory-determined values of optimal temperature for growth (O'Connor et al. 1981; Gibson and Fry 1954). The fundamental thermal niche for lake trout has been defined as 10 ± 2°C by Magnuson et al. (1990), and Evans et al. (1991) determined that 10°C is the optimal temperature for growth for juveniles and adults alike. Recent evidence however, suggests that lake trout may be able to cope with warmer conditions than previously thought. For example, Gunn (2002) reported that lake trout were able to feed and survive at core body temperatures near or greater than 20°C for several weeks, but he also reported a loss, by some unknown mechanism, of all hatchery-reared juveniles in this lake over the warm summer of the study. Sellers et al. (1998) also reported lake trout in epilimnetic waters between 19°C and 20°C in small Ontario lakes, but they were not able to measure temporal exposure to these elevated water temperatures.

Although it is well known that temperature influences fish growth (Martin and Olver 1980), growth rates, particularly in a natural environment, are normally attributed to food supply, which may be lower in northern lakes because of lower overall productivity resulting from a shorter growing season. Mac (1985) showed that reduced preferred temperatures, as observed in Kathleen Lake lake trout, could result from lower food availability, which would limit energy gain, leading to a lower of metabolic rate. Biette and Geen (1980) found that under conditions of severe food limitation, growth of sockeye salmon *O. nerka* was best under constant and cold thermal conditions. Although primary production in Kathleen Lake is probably lower than many other lake trout lakes (Secchi disk depth of 20–23 m), prey production in the lake is actually higher than in several other cold, oligotrophic lakes within the same drainage (Wickstrom 1978). In Dezadeash Lake, lake trout food supply is probably less limiting than in Kathleen Lake, although spatial access to the food supply may be partially restricted because of the elevated temperatures within the main lake. Limited evidence associated with feeding behavior suggests that feeding by lake trout in Dezadeash Lake is restricted, but not eliminated, throughout the warmest part of the summer when trout congregate within coldwater plumes. Of the seven stomach samples obtained from lake trout caught by anglers within thermal refugia, five were empty (J. Mackenzie-Grieve, unpublished data). Fish prey species are rarely observed in the vicinity of lake trout thermoregulatory areas, and fish within a coldwater plume are generally all large lake trout (J. Mackenzie-Grieve, personal observation). It is more likely that lake trout leave refugia for brief feeding forays into the warmer parts of the lake and then return to thermal refugia. Similar behavior was observed by Baird and Kruger (2003) in river-dwelling brook trout. These results support observations by local recreational anglers on Dezadeash Lake that lake trout within thermal refugia do little feeding.

Brett (1971) examined behavioral thermoregulation by juvenile sockeye salmon and found that they fed in the warm epilimnion at consumption rates that could be maximized before needed retreat to cooler waters, where food could be digested more efficiently and less energy would be expended on maintenance metabolism. Jobling (1996) also discussed the possible growth advantages associated with movement between warmer and colder waters, as per lake trout in Dezadeash Lake that move in and out of thermal refugia; this strategy minimizes metabolic costs and maximizes feeding opportunities. He suggested that if food resources were restricted to areas of warmer temperature (e.g., the pelagic zone of Dezadeash Lake), it would be a growth advantage for fish to move into colder areas following feeding because metabolic costs would be lower than in warmer habitats.

Ecological data (e.g., life history, growth rates, and spawning preferences) suggest that inland lake trout populations are well adapted to their environment (Martin and Olver 1980; Wilson and Mandrak 2004), and native populations may have become uniquely adapted over many generations to localized conditions within individual lakes (Wilson and Mandrak 2004). As a result, there is probably some genetic basis for selection of thermal habitat by lake trout, leading to geographic variation in optimal thermal range. Perhaps the more southerly lake trout populations, which have been the focus of temperature preference studies to date, have been subjected to directional selection for increased optimal temperature (i.e., individual phenotypes of greater fitness and producing the most progeny are to one side of the population average, leading to a shift in the distribution of phenotypes in succeeding generations). Perhaps lake trout in Kathleen Lake have not been subjected to this type of directional selection and currently exist in their postglacial colonization form or have been subjected to directional selection, but for colder optimum temperatures. Although the lake trout populations in each of the two study lakes probably resulted from the same stock historically (Wilson and Hebert 1998), genetic divergence in temperature preference of lake trout in these two systems could have occurred since lake trout colonization of this area approximately 10,000 years ago (Wilson and Hebert 1998). Crawshaw and O'Connor (1996) suggest that when fish are faced with a sustained increase in the thermal environment there could be genetic selection acting on the intraspecific variability in preferred temperature. Should this be the case, some adaptation to local temperature regime should be possible provided changes occurred at a slow enough rate to allow for selection to operate. It is equally possible that thermal optima of lake trout do not differ in the two study lakes; lake trout in Dezadeash Lake are simply unable to access colder habitat and are therefore limited to habitat provided by coldwater plumes throughout the warmest part of the summer. Selection experiments addressing this possibility are lacking in fish (Crawshaw and O'Connor 1996), and further field and laboratory assessments of thermal preferences in northern lake trout stocks would be timely. This study asserts the importance of thermal refuge habitats in Dezadeash Lake and results could apply to other lakes of similar morphology and thermal regime (Mackenzie-Grieve and Post, in press). Should the strong relationship between thermal habitat volume and production shown by Christie and Regier (1988) and Payne et al. (1990) apply to this population (and other populations inhabiting similar habitats), we can expect significant reductions in population production should availability of refugia habitats be reduced through climate change.

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