

Pelagic distribution of lake trout (*Salvelinus namaycush*) in small Canadian Shield lakes with respect to temperature, dissolved oxygen, and light

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Abstract: The distribution of lake trout (*Salvelinus namaycush*) with respect to water temperature, dissolved oxygen, and light intensity was surveyed in three small Canadian Shield lakes at the Experimental Lakes Area, northwestern Ontario. Based on hydroacoustic and gillnet surveys, there was considerable variation among lakes in temperatures occupied by lake trout during the summer. During the day, lake trout were concentrated at 4–8°C in Lake 375, broadly distributed from 6 to 15°C in Lake 442, and concentrated in the epilimnion at 19°C in Lake 468. At night, lake trout in all lakes occupied epilimnetic waters at 19–20°C. Lake trout inhabited highly oxygenated water, with 75–90% of fish at >6 mg dissolved oxygen·L⁻¹ throughout the spring and summer in all three lakes. Light intensity did not affect lake trout distribution in Lake 468 but may have contributed to lake trout daytime descent into cool waters in Lakes 375 and 442. We suggest that previously assumed niche boundaries of lake trout do not adequately describe critical habitat for the species in small lakes, the same lakes that are likely most sensitive to erosion of such habitat.

Résumé : Nous avons étudié la distribution du touladi (*Salvelinus namaycush*) en fonction de la température et de la teneur en oxygène dissous de l'eau et de l'intensité de la lumière dans trois petits lacs du Bouclier canadien situés dans la Région des Lacs Expérimentaux, dans le nord-ouest de l'Ontario. D'après les relevés hydroacoustiques et les captures au filet maillants, il y avait une variation considérable d'un lac à l'autre entre les zones de température occupées par le touladi au cours de l'été. Le jour, les touladis se concentraient dans la zone de 4–8°C dans le lac 375, ils étaient dispersés dans les zones de 6 à 15°C dans le lac 442 et ils se concentraient dans l'épilimnion, à 19°C, dans le lac 468. La nuit, les touladis occupaient les eaux de l'épilimnion, à 19–20°C, dans tous les lacs. Par ailleurs, nous avons constaté que le touladi fréquentait les eaux très oxygénées dans tous les lacs, car de 75 à 90% des poissons sont demeurés dans des eaux où la teneur en oxygène dissous était supérieure à 6 mg·L⁻¹ tout le printemps et tout l'été. L'intensité de la lumière n'a pas influé sur la distribution du touladi dans le lac 468, mais pourrait avoir contribué à la descente des touladis vers les couches d'eau plus froides, le jour, dans les lacs 375 et 442. Nous pensons que les limites de la niche qu'on a supposée au touladi jusqu'ici ne représentent pas véritablement l'habitat indispensable à cette espèce dans les petits lacs, ceux-là même où cet habitat est probablement le plus sensible.

[Traduit par la Rédaction]

Introduction

In Canada, lake trout (*Salvelinus namaycush*) fisheries have important economic, social, and cultural values. Increasingly, these fisheries are threatened by a variety of influences including loss of habitat, overexploitation, and genetic dilution from stocking (reviewed in Evans et al. 1991). Recent evidence of climate-coupled lake warming indicates possible loss of habitat for cold stenotherms, such as lake trout, in small Canadian Shield lakes (Schindler et al. 1990, 1996). The lake trout is among the freshwater species thought to be most restricted to cold-water habitat and most likely to be at risk from lake warming (Magnuson et al. 1990). Lake trout zoogeographic distribution is traditionally considered to be limited to lakes

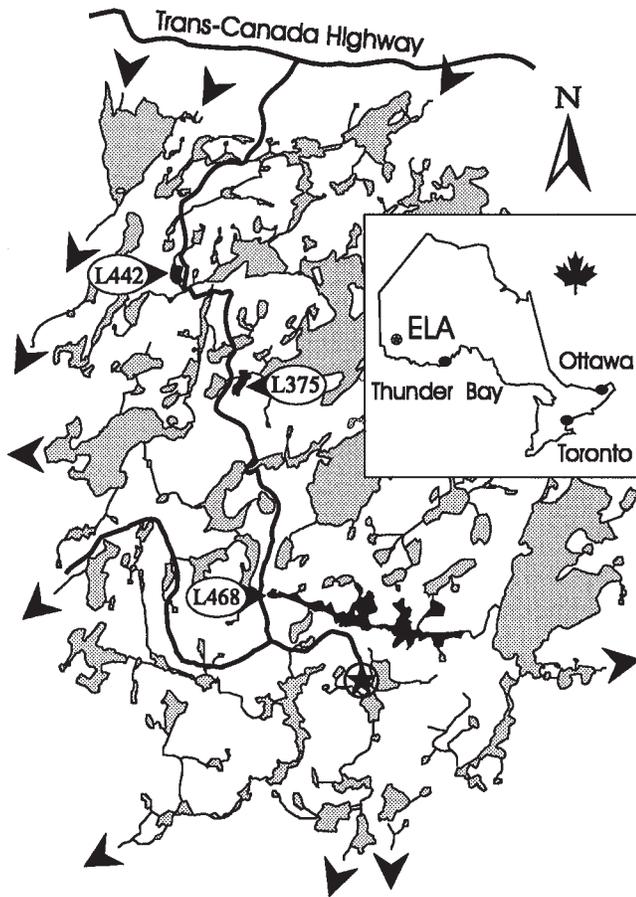
where substantial summer warming does not occur or where thermal stratification isolates large hypolimnetic volumes of cold-water habitat from summer warming. However, recent studies of lake trout in a midlatitude isothermal lake (Snucins and Gunn 1995) challenge this traditional view.

Lake trout prefer and physiologically optimum temperatures indicate a fundamental thermal niche of approximately 10 ± 2°C (O'Connor et al. 1981; Magnuson et al. 1990). Furthermore, lake trout yield has been positively correlated with the amount of 10 ± 2°C habitat in very large lakes (Christie and Regier 1988). Habitat might increase in some of the Laurentian Great Lakes if climate warming occurs (Magnuson et al. 1990). However, this forecast was based on a prediction of shallower, stronger thermoclines in the Great Lakes and does not include habitat restriction from dissolved oxygen (DO) depletion. In small lakes, climatic warming could decrease the amount of 10 ± 2°C habitat if thermocline deepening occurs due to increased solar penetration from loss of dissolved organic carbon (DOC) and increased wind exposure from deforestation (Schindler et al. 1990, 1996). In these lakes, suitable habitat may be restricted by a combination of shallow-water warming and deepwater DO depletion, possibly leading

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Fig. 1. Map of the ELA with study lakes in black.

to extirpation of lake trout from some lakes (Schindler et al. 1990, 1996). Thermal autecology of lake trout in lakes with constricted optimal habitat is not well described. Although generally thought to be strongly restricted to cold water, reports of lake trout in warm water (Kennedy 1941; Martin 1952; Galligan 1962; Dahlberg 1981; Olson et al. 1988; Snucins and Gunn 1995) suggest broader temperature tolerance and a wider range of habitat use.

In this paper, we describe the distribution of lake trout in three small Canadian Shield lakes with different amounts of oxygen-rich optimal thermal habitat. We examine the hypothesis that summer habitat is restricted to areas with cold temperatures, high DO, and low light intensity. We identify maximum temperature and minimum DO boundaries to lake trout habitat and describe their role in delimiting the breadth of summer habitat for lake trout.

Materials and methods

Study site

The study lakes are part of the Experimental Lakes Area (ELA) of the Canadian Department of Fisheries and Oceans (DFO). The ELA is located in northwestern Ontario, 60 km east of Kenora, between 49°37'N and 49°47'N latitude and 93°35'W and 93°50'W longitude (Fig. 1). The lakes are on the southwestern margin of the Canadian Shield and are typical of numerous small Shield lakes that support lake trout.

The study lakes, lakes 375, 442, and 468 (L375, L442, and L468,

Table 1. Limnological data and fish species composition, with approximate population sizes where known (a dash indicates that the population size is unknown), for the three study lakes (K. Mills, unpublished data).

	L375	L442	L468
Z_{\max} (m)	26	17.8	29
Z_{mean} (m)	11.6	9	11 ^a
Area (ha)	18.7	16	114 ^a
Volume (10^5 m^3)	21.7	14.4	128 ^a
Lake trout (<i>Salvelinus namaycush</i>)	387 ^b	364 ^c	>4000 ^d
White sucker (<i>Catostomus commersoni</i>)	<45 ^e	500 ^f	—
Lake whitefish (<i>Coregonus clupeaformis</i>)	—	—	— ^g
Yellow perch (<i>Perca flavescens</i>)	—	—	—
Slimy sculpin (<i>Cottus cognatus</i>)	—	—	—
Fathead minnow (<i>Pimephales promelas</i>)	—	—	—
Pearl dace (<i>Margariscus margarita</i>)	—	—	—
Finescale dace (<i>Phoxinus neogaeus</i>)	—	—	—
Northern redbelly dace (<i>Phoxinus eos</i>)	—	—	—
Blacknose shiner (<i>Notropis heterolepis</i>)	—	—	—
Longnose dace (<i>Rhinichthys cataractae</i>)	—	—	—
Bluntnose minnow (<i>Pimephales notatus</i>)	—	—	—

^aEstimates are for portion of east basin surveyed.

^bMean of Jolly–Seber multiple mark–recapture estimates from 1988 to 1994.

^cMean of multiple mark–recapture estimates from 1990 to 1994.

^dBased on an extrapolation of Petersen mark–recapture estimates for one of four known spawning sites. Additional unidentified spawning sites are suspected.

^eThere were 45 white sucker >220 mm (similar to size of lake trout) in L375 at the time of this study. This estimate is based on evidence of near complete capture in the initial 1988 fish survey. In the seven succeeding years, about seven adult white sucker per year were caught that were not marked in 1988. White suckers between 150 and 220 mm (ages 1–3 years) were rare from 1988 from 1993. At the time of this study, juveniles (<50 mm) were numerous.

^fMean of Peterson estimates of 468 and 550 for 1991 and 1992.

^gEssentially a single size-class (mean fork length = 227 mm, SD = 16 mm), which is approximately half the length of the smallest lake trout typically caught in L468 (T.J. Sellers, unpublished data).

east basin only) (Cleugh and Hauser 1971), were selected based on the following criteria: (i) all three lakes have simple assemblages of fish species with lake trout as the only large-bodied fish thought to be pelagic during the summer (Table 1), (ii) lake basins are steep sided, littoral zones are small, and the lakes can be nearly completely sampled with echosounding equipment, and (iii) the lakes have large differences in temperature, DO, and light regimes. Limnological data for these lakes are summarized in Table 1.

Hydroacoustic surveys of vertical distribution of fish

Using hydroacoustic echosounding, we surveyed the depth distribution of pelagic fish in L375, L442, and L468 (east basin only; seasonal migration of lake trout between the east and west basins of L468 does not occur) during the open-water seasons of 1992 and 1993. Surveys were conducted at approximately midday along equally spaced parallel transects oriented perpendicular to the long axis of each lake. Transects were spaced 60 m apart in L375, 55 m apart L442, and 90 m apart in L468. This spacing yielded nonoverlapping transects at all depths, with transect separation at maximum lake depth of 37 m in L375, 40 m in L442, and 66 m in L468. Similar surveys were conducted at approximately midnight on one midsummer date in L375 and L442 and on several nights in L468.

The overall percentage of each lake surveyed was (by volume) 11% in L375, 12% in L442, and between 1 and 2% in L468. The

estimated proportion of the lake trout populations sampled during midday surveys, assuming that all observed echoes were lake trout, was 5–36% in L375, 10–29% in L442, and 1–3% in L468.

In 1992, we used a narrow-beam echosounder (BioSonics, Inc., 105, 420 kHz, 6° beam-width transducer) to survey fish distribution. Data were recorded on digital audiotape for later signal processing. In 1993, we used a wide-beam echosounder (Lowrance, Inc., 50 kHz, 45° beam-width transducer) to increase survey coverage at shallower depths where most echoes were observed. Fish depths were recorded as traces on a paper chart recorder. We operated the two systems simultaneously during two surveys in 1992 to compare echo returns; both systems yielded similar vertical profiles. In 1992, acoustic sampling theoretically covered from 1.5 m below the lake surface to ~1 m above the lake bottom and in 1993 from 2 m below the lake surface to ~0.3 m above the lake bottom. We acknowledge that, in practice, the effective coverage could have been less than the theoretical because of the potential influences of boat avoidance by lake trout near the surface and acoustic shadowing from adjacent bottom contours at near-bottom depths.

Echo signals from 1992 surveys were digitized from the audiotapes using a BioSonics 181™ signal processor and Biosonics PCAcquire™ software. Individual echo depths were measured using Biosonics TS™ software for those identified as single echoes by the software (based on minimum and maximum pulse width of echo = 300 and 550 μ s, respectively, measured at -6 dB level). Depth of the transducer below the lake surface was added to each recorded echo depth.

For 1993 surveys, we measured depths of individual fish directly from the paper chart records. Depths were measured using a digitizing tablet, from the recorded lake surface (=transducer depth) to the apex of the arch shape that is characteristic of individual fish echoes passing completely through the sonar beam. Depths of echoes without this arch shape were not measured. These latter echoes represented fish detected at the periphery of the sonar cone for which we could not confidently assign a vertical depth. Although the wide-angle transducer produced relatively broad tracings, the arch shape was clearly distinguishable at the maximum depths encountered during these surveys. Transducer depth was added to the depth assigned to each echo.

Because hydroacoustic transmissions spread approximately as a cone with distance from the transducer, the volume surveyed increased with depth. Deeper echoes, therefore, were represented disproportionately in echo returns. We applied a correction to the depth distribution of echoes, based on the volume surveyed along each transect at 0.5-m depth increments. We estimated these volumes from the product of the cross-sectional area of the hydroacoustic cone and the transect length at each depth interval, measured from bathymetric maps for each lake. The depth distribution was also weighted for lake morphometry by the relative volume of water at each 0.5-m depth interval to produce a lake-wide representation of vertical distribution. We used the corrected fish distributions for all subsequent analyses and interpretation.

Fish collection

To corroborate the assumption that echoes were lake trout, we set gill nets in the littoral and pelagic zones of L442 and L468 during mid-summer 1993. Fish collection was not permitted in L375 because it is a long-term reference lake for ELA experiments. In L442, five vertical gill nets (3 m wide \times lake depth; mesh sizes = 25-, 38-, 51-, 76-, and 102-mm stretched mesh) were set in midbasin for a total of 42.5 h (19.5 h during the day, 23 h at night) between July 28 and 30. In L468, the nets were set over the 18-m depth contour in midbasin on July 8 (4.5 h during the day) and semicontinuously for a total of 56.5 h (29.5 h during the day, 27 h at night) between July 14 and 19. The nets were checked periodically and fish depths determined to the nearest metre from the locations of fish in the nets. Fish were removed from the nets, weighed, measured, and released if alive.

Two horizontal gill nets were set along the shoreline in the epilimnion of L442 and L468 (25 m long \times 2 m deep; mesh sizes = 38-, 51-, 89-, and 121-mm stretched mesh). In L442, nets were set diagonally to shore to the 6-m contour for 33.5 h (11.5 h during the day, 9.5 h during the evening, 12.5 h at night) and in L468 to the 7-m contour (17 h during the day, 14 h at night). Fish depths were estimated from location in the nets.

Temperature, DO, and light measurements

We measured profiles of lake temperature, DO, and light with depth at the deepest point in each lake at approximately biweekly intervals throughout the open-water season of 1993. In 1992, temperature was measured concurrent with hydroacoustic surveys, and DO profiles were obtained once during August. Temperatures were measured at 1-m depth intervals, except in the metalimnion where 0.25-m intervals were used. DO was measured by Winkler titration at 1- to 2-m depth intervals, except in regions of very low or rapidly decreasing DO where 0.5-m intervals were used. Light was measured using a Licor submersible light meter at 1-m intervals from the surface to below the 1% level. Usually, these profiles were measured concurrent with the hydroacoustic survey of fish vertical distribution. For dates when these parameters were not measured, profiles were linearly interpolated between the nearest sampling dates.

Results

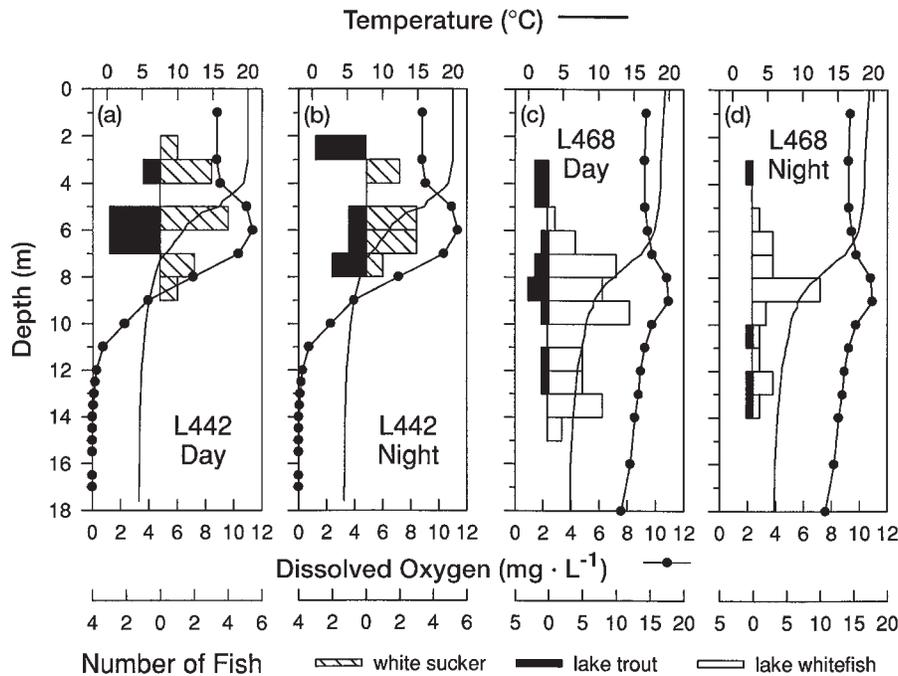
Species composition

In L442, 14 lake trout and 20 white sucker (*Catostomus commersoni*) were caught in vertical gill nets (Figs. 2a and 2b). Seventeen lake trout and 80 lake whitefish (*Coregonus clupeaformis*) were caught in L468 (Figs. 2c and 2d). These catches represent a lake trout catch rate of approximately 0.3-h^{-1} (240-m² net area) in both lakes. The catches in vertical gill nets confirmed the presence of lake trout in the hydroacoustic surveys of L442 and L468. They also demonstrated that lake trout occur in epilimnetic waters as warm as 19–20°C during both day and night in these lakes (Fig. 2).

In L442, lake trout and white sucker were present at similar depths above the anoxic central basin of the lake (Figs. 2a and 2b). Both species were absent below 9 m during the day (Fig. 2a) and night (Fig. 2b). Because lake trout and white sucker were caught at a similar range of depths, we assumed that hydroacoustic echoes represented the distribution of both species. Although we interpreted echoes from hydroacoustic surveys in L442 as lake trout, we recognized that white sucker contributed to the echo distributions. Nevertheless, the presence of white sucker in these signals should not have biased our interpretation with respect to lake trout.

In L468, only lake trout and lake whitefish were pelagic (Figs. 2c and 2d). Although white sucker were numerous in the littoral zone of L468, they were never caught in pelagic net sets. Lake trout were caught at a wide variety of depths, from 3 to 14 m, during day and night, and importantly, it was the only species caught pelagically in the epilimnion. Lake whitefish were caught primarily in the metalimnion and hypolimnion (Figs. 2c and 2d). For this reason, we assumed that hydroacoustic echoes, which were most numerous in the epilimnion, were representative of lake trout.

During 33.5 h of shoreline gillnet sets on L442, 22 lake trout and 39 white sucker were caught. Lake trout were caught between 3 and 6 m; most individuals were caught between 4 and 5 m. White sucker were caught between 2 and 6 m but

Fig. 2. Vertical profiles of temperature and DO and fish catch in vertical gill nets in L442 and L468.

primarily occurred between 3 and 5 m. Although lake trout were caught in shallow waters during the day, most (19 of 22) were caught in the littoral zone during the evening and night. In L468, although white sucker were the most abundant species caught in the littoral net sets, three lake trout were captured (two during the day, one at night) between 2 and 3 m depth. These net catches demonstrate that lake trout use warm littoral waters during the day and night in both lakes.

Although L375 contained both lake trout and white sucker, the adult white sucker population was small (Table 1) and unlikely to have contributed substantially to pelagic echoes. Because white sucker were rare, we assumed that pelagic echoes in L375 were representative of lake trout.

Depth distribution

During the summers of 1992 and 1993, lake trout in L375 and L442 were predominantly at or just below the thermocline, concentrated in the lower half of the metalimnion and the top of the hypolimnion (Figs. 3 and 4). In L442, fish distribution was consistent with gillnet catches (Fig. 2). Lake trout in L468 occurred predominantly in the epilimnion throughout the summer (Fig. 5) in contrast with the broader depth distribution of fish in vertical gill nets. In all lakes, fish were either absent or at very low density below the top of the hypolimnion (Figs. 3–5).

In early spring 1993, lake trout in L375 inhabited shallow depths (mean depth = 4.5 m) but moved to deeper water by the middle of June (Fig. 3). This movement was not observed in 1992, probably because the initial survey was conducted after the epilimnion had warmed. For the remainder of both summers, the mean depth did not change significantly (Scheffé test, $p > 0.05$) but remained between 8.3 and 9.6 m in 1992 and between 8.8 and 10.9 m in 1993 (Fig. 3).

Lake trout in L442 inhabited shallower depths than those in L375 both in 1992 and 1993. They occupied a wide range

of depths (2–17 m) in early June but were concentrated between approximately 4 and 8 m for most of the summer (Fig. 4). Mean depths of fish in L442 ranged from 5.1 to 6.8 m in 1992 and from 5.3 to 7.3 m in 1993 and did not change significantly ($p > 0.05$) over the course of the summer.

In contrast, lake trout in L468 did not move out of the epilimnion as it warmed during spring and summer but remained at mean depths of 2.6–3.2 m throughout July (Fig. 5). Predominant use of shallow water was evident during hydro-acoustic surveys both day and night.

Nighttime use of shallow-water habitat by lake trout was common to all three lakes. In L375 and L442 the majority of lake trout ascended into the epilimnion at night even during midsummer (Fig. 6). High echo returns in L375 and L468 at night were partly attributed to offshore movement of forage fish into the epilimnion (Price et al. 1991).

Temperature distribution

Lake trout in L375 were concentrated at a narrow range of cold temperatures in 1992 and 1993. In 1992, most lake trout (72–92%) occurred at $<9^{\circ}\text{C}$. In the spring of 1993, they were distributed over a wide range of temperatures (4– 15°C), although most individuals occurred in surface waters at 14 – 15°C (Fig. 3). They moved to colder waters after the epilimnion warmed above 15°C . Few ($<15\%$) individuals were in water $>8^{\circ}\text{C}$ and most (44–77%) occurred at $<6^{\circ}\text{C}$ throughout the summer. The depth distribution was unimodal, with 33–50% of fish at 5 – 6°C on any date during the summer.

Lake trout in L442 were distributed over a wider range of warmer temperatures than those in L375, in 1992 and 1993 (Fig. 4). There was considerable variation in their temperature distribution from survey to survey. Temperature modes in the 7 – 10°C range existed on several survey dates but were not evident on others. Most fish were located at 6 – 15°C during midsummer in both 1992 (79–88%) and 1993 (77–92%), in

Fig. 3. Midday lake trout depth distribution from hydroacoustic profiles with temperature and DO profiles for L375. Echo frequency <0.4% indicated by ♦.

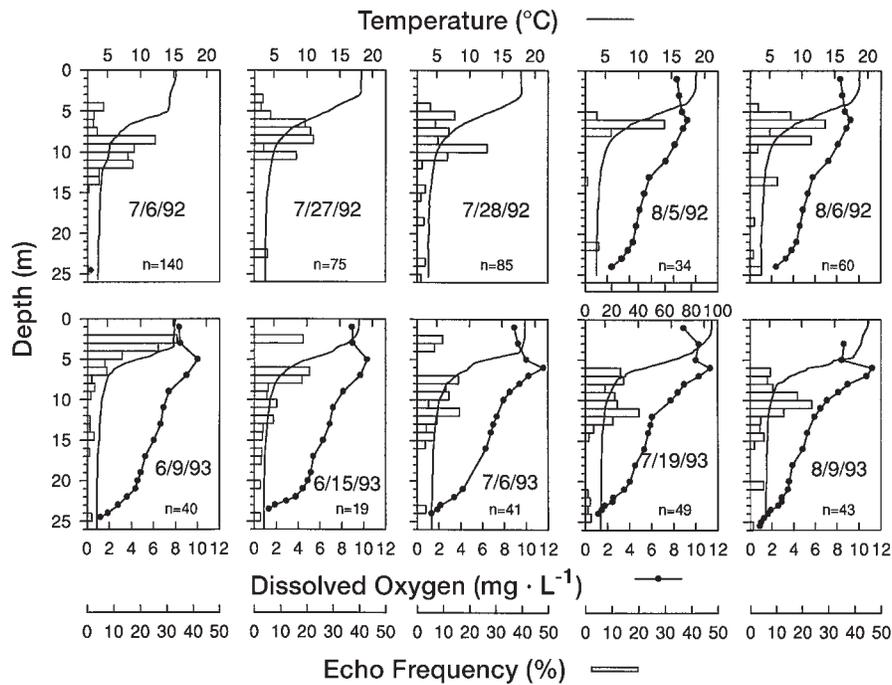
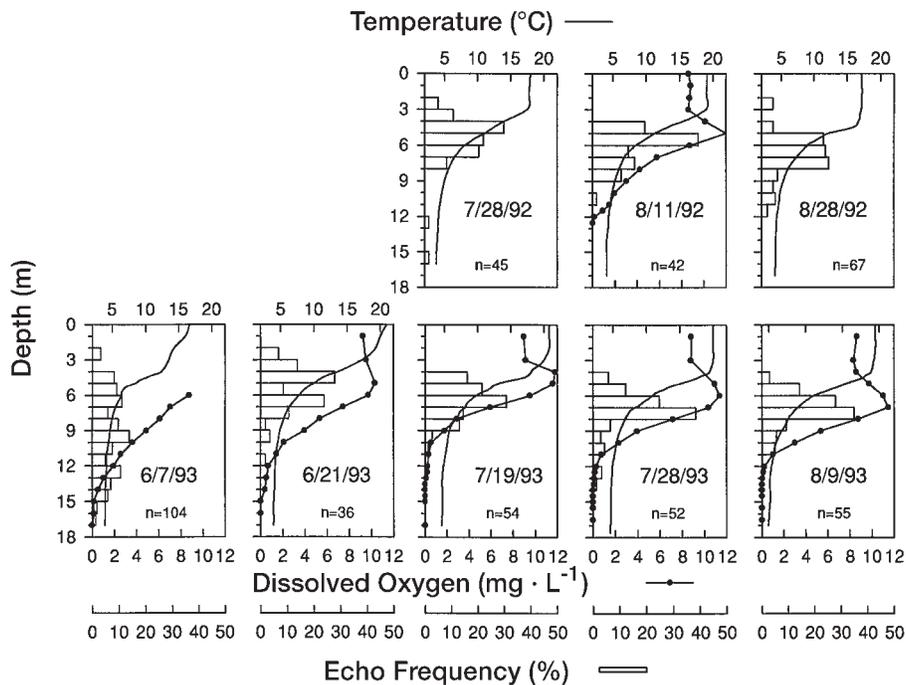


Fig. 4. Midday lake trout depth distribution from hydroacoustic profiles with temperature and DO profiles for L442.



marked contrast with fish in L375. Few fish (0–12%) occupied water warmer than 15°C during the day in both 1992 and 1993.

In contrast with L375 and L442, our interpretation of L468 hydroacoustic records suggests that most lake trout occupied the epilimnion in water that was warmer than 17°C throughout the summer and reached 19.5°C by the third week of July. A few fish did inhabit colder regions of L468, but over 90% of fish in the hydroacoustic records were in the epilimnion. Use

of 19°C habitat persisted throughout the day and night, although lake trout were caught at a wide range of depths (and colder temperatures) in vertical gillnet sets that integrated many hours of fishing during the day and night (Fig. 2).

At night, the majority of fish inhabited warm water up to 19–21°C in all three lakes (Fig. 6). Compared with the daytime, fish inhabited much warmer water at night in L375 and L442 and remained at warm temperatures in L468.

Fig. 5. Midday lake trout depth distribution from hydroacoustic profiles with temperature and DO profiles for L468. Echo frequency <0.8% indicated by ◆.

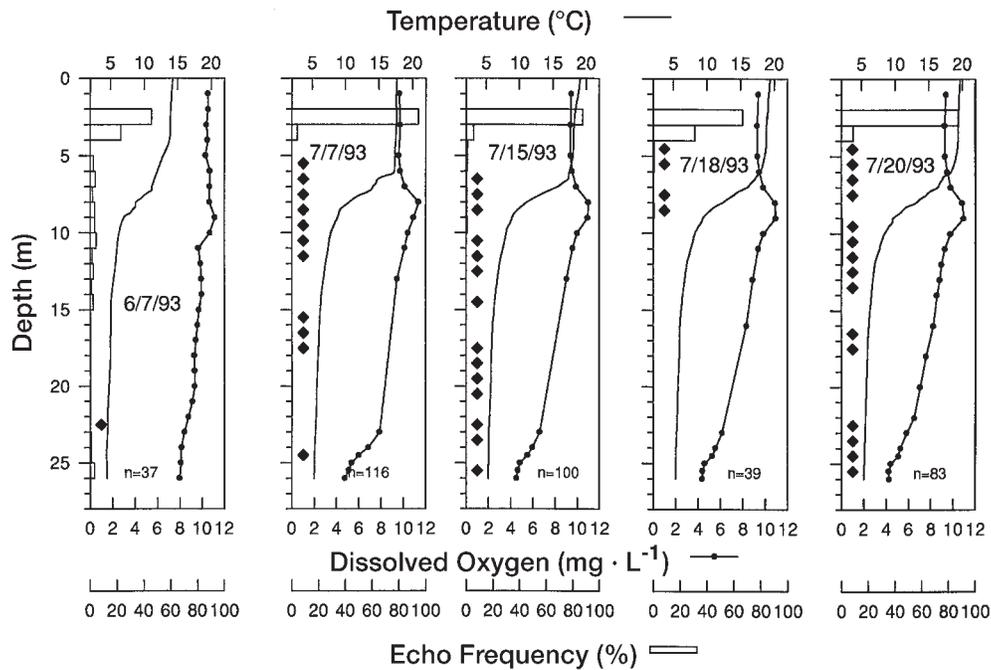
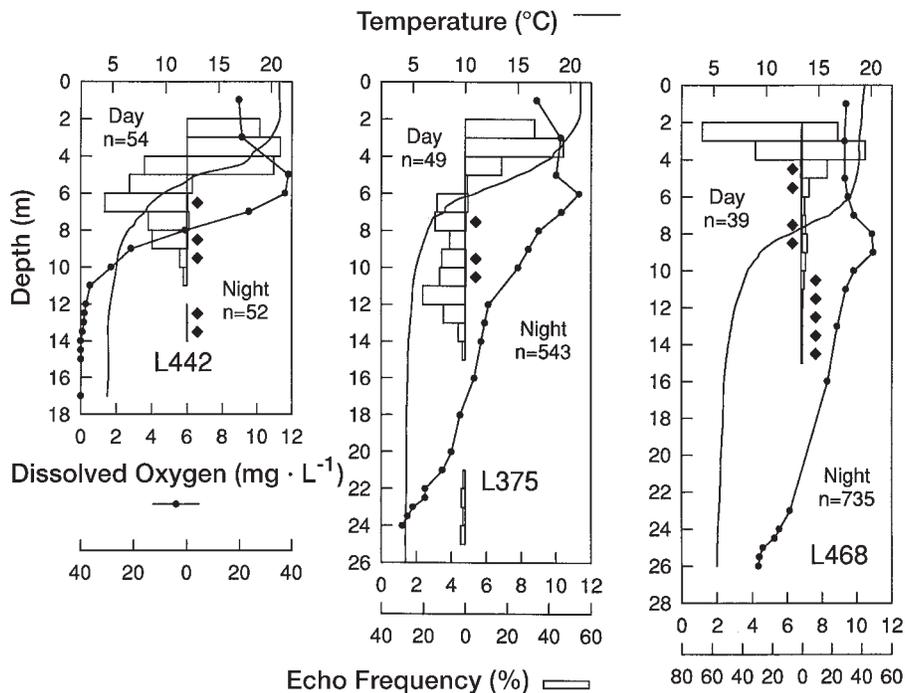


Fig. 6. Day and night depth distributions of lake trout with temperature and DO profiles. Data collected on July 19–20, 1993. Echo frequency <0.8% (L442 and L375) and <2% (L468) indicated by ◆.



DO in the inhabited zone

In all three lakes, fish occupied highly oxygenated waters throughout most of the summer (Figs. 3–5). However, during the June 7, 1993, survey in L442, numerous fish were in low DO as well (<2 mg·L⁻¹, Fig. 4). These echoes were clustered tightly near the central basin of the lake and appeared, subjectively, to consist mostly of small fish. With this exception,

nearly all fish (86–100%) in each lake concentrated in areas where DO was >5 mg·L⁻¹ and most (75–90%) were at >6 mg·L⁻¹ throughout the spring and summer.

There was no single DO value around which fish consistently congregated; rather, they inhabited waters with a variety of DO concentrations in excess of 5 mg·L⁻¹. In L375, modal DO inhabited ranged from 6.5 to 9.5 mg·L⁻¹ (Fig. 3). In L442

and L468 the modal DO inhabited was $>9 \text{ mg}\cdot\text{L}^{-1}$ throughout the summer (Figs. 4 and 5).

Light in the inhabited zone

During midsummer, the maximum light intensity at depths inhabited by fish at the time of hydroacoustic surveys ranged from 44 to 164 $\mu\text{E}\cdot\text{m}^{-2}\cdot\text{s}^{-1}$ in L375, from 54 to 400 $\mu\text{E}\cdot\text{m}^{-2}\cdot\text{s}^{-1}$ in L442, and from 215 to 482 $\mu\text{E}\cdot\text{m}^{-2}\cdot\text{s}^{-1}$ in L468. Ambient light at mean fish depth ranged from 6 to 34 $\mu\text{E}\cdot\text{m}^{-2}\cdot\text{s}^{-1}$ in L375, from 17 to 99 $\mu\text{E}\cdot\text{m}^{-2}\cdot\text{s}^{-1}$ in L442, and from 215 to 482 $\mu\text{E}\cdot\text{m}^{-2}\cdot\text{s}^{-1}$ in L468. Light in the zone inhabited by lake trout changed with day-to-day variations in surface light intensity. Light did not appear to affect fish distribution in any of the lakes, although it may have contributed to the daytime descent of lake trout in L375 and L442.

Discussion

Thermal habitat of lake trout

In small lakes, lake trout utilized habitat with a wide range of temperatures up to 21°C, the maximum water temperatures observed in the summers of 1992 and 1993. Lake-to-lake variation in water temperatures where lake trout occurred was considerable. Fidelity to the hypothesized thermal habitat of $10 \pm 2^\circ\text{C}$ (O'Connor et al. 1981; Magnuson et al. 1990) was not characteristic of lake trout distribution in any of the lakes studied. Thermal habitat was different than expected from temperature preferences of juveniles held under laboratory conditions (mean from seven studies = $10.2 \pm 1.1^\circ\text{C}$) and previous field studies where the median temperature occupied by adults averaged $9.5 \pm 1.1^\circ\text{C}$ (Evans et al. 1991). During the day, lake trout in L375 were in water 3–4°C colder than the generally accepted lower bounds of their fundamental thermal niche ($10 \pm 2^\circ\text{C}$) (Magnuson et al. 1979, 1990). Although lake trout prefer colder temperatures when food rations are restricted, this effect is small (approximately -1.5°C at 50% of maintenance ration, Mac 1985) and unlikely to have been responsible for the observed preference for cold temperatures. Conversely, most lake trout occupied water as warm as 19–20°C in L468, although they occurred over a wide range of temperatures. Although white sucker contributed to the hydroacoustic signal from L442, they should not have biased the apparent broad temperature distributions of lake trout because the two species were caught at the same range of depths in vertical gill nets. In all lakes at night, lake trout occupied waters 7–8°C warmer than their previously hypothesized thermal niche.

Temperature preference and lake thermal structure do not adequately explain the observed distribution of lake trout in these lakes. Extended epilimnetic residence of lake trout in L468, despite temperatures approaching published lethal limits (23.5°C, Gibson and Fry 1954), suggests that the benefits of foraging in warm water outweighed the metabolic costs of maintaining body temperature $>16^\circ\text{C}$ (Gibson and Fry 1954; Mac 1985). Although lake trout – prey relationships were not studied explicitly in these lakes, we speculate that prey distribution may be important in structuring lake trout distribution, irrespective of water temperatures. Despite the preponderance of echoes in warm water in L468, lake trout were caught in vertical gill nets over a wide range of temperatures, at depths

coincident with catches of lake whitefish. It is possible that lake trout were attempting to feed on lake whitefish captured by the nets. Rawson (1961) and B.R. Parker (personal observation) have noted similar situations involving lake trout and prey fish. Our observations of lake trout feeding at the surface at midday (at 19–20°C) on lake whitefish lost during removal from the vertical gill nets (T.J. Sellers, personal observation) also suggest this orientation to prey. Further, the observed pattern of nocturnal ascent into the base of the epilimnion in L375 and L442 suggests that distribution in these lakes may have been oriented to vertically migrating prey species or by nightly offshore movements of littoral forage-fish species, such as fat-head minnow (*Pimephales promelas*) (Price et al. 1991), which is abundant in L375 and L442 (K. Mills, DFO, Winnipeg, Man., personal communication; T.J. Sellers, personal observation). We suggest that the observed patterns of lake trout distribution in the study lakes were not responses primarily to temperature preference, but rather were more consistent with orientation to prey location.

Seasonal stratification provides a gradient in thermal resources along which discrete thermal guilds of fish may segregate (Magnuson et al. 1979; Brandt et al. 1980; Crowder and Magnuson 1982; Coutant 1987; Olson et al. 1988). In this view, fishes can partition the available thermal habitat in the lake, reducing interactions between species. If true, the epilimnion represents both a spatial and thermal refuge for warmwater assemblages of fishes and invertebrate prey from predation by lake trout. Further, the hypolimnion may represent a refuge for lake trout from competition and predation by other large predators, such as northern pike (*Esox lucius*). However, based on our findings, we suggest that lake trout thermal habitat was not so discretely partitioned in these small lakes. As a result, the epilimnia of our study lakes were neither spatial nor thermal refugia for prey species nor refugia for white sucker (and other predominantly shallow-water species) from competition with lake trout for food. Perhaps low representation of other thermal guilds, both as competitors of and predators on lake trout, in these small lakes permits more generous distribution of lake trout with respect to available resources. We speculate that the presence of warm- and cool-water predators, such as northern pike, may limit the thermal distribution of lake trout in many lakes with more diverse species assemblages by confining lake trout to cold hypolimnetic regions. Indeed, both in our and other small Ontario lakes in which lake trout occupied warmwater habitats (Snucins and Gunn 1995), no other large predatory fishes were present. In the absence of large, cold refugia, we further suspect that northern pike may eliminate lake trout populations from small lakes with simple fish assemblages. For example, lake trout do not coexist with northern pike in lakes under 50 ha in area and 10 m in depth in the ELA (K. Mills, unpublished data).

Use of warmwater habitat by lake trout was common in each of the three study lakes, especially during the night. Although presence of lake trout in warm waters of stratified lakes has been noted previously, it was usually interpreted as brief foraging forays into unfavorable environmental conditions (Martin 1952; Galligan 1962; Dahlberg 1981; Olson et al. 1988). We found that lake trout commonly inhabit waters warmer than the laboratory-determined avoidance temperature (15°C, McCauley and Tate 1970) at night.

Our findings do not preclude the possibility that use of

warmwater habitat depends on refuge in cold water for some part of the day. Diel thermal history included residence in cold water in L375 and L442. Indeed, lake trout are absent from several small ELA lakes with restricted cold-water habitat, even when connected to lakes with extant lake trout populations (however, these lakes also contain northern pike populations and might simply lack a refuge from competition or predation). Body core temperature of small lake trout (1100 g) requires nearly an hour to equilibrate to a 5°C rise in ambient temperature, and this temperature lag increases with fish size (Snucins and Gunn 1995). Given these time lags, epilimnetic residence could occur for significant periods of the day without incurring substantial costs. In a warm isothermal lake, some lake trout offset their warmwater exposure through refuge in the plume of a cold (10°C) groundwater seep (Snucins and Gunn 1995). Although this likely reduced metabolic costs by about 6%, survival did not depend on this refuge (Snucins and Gunn 1995). Indeed, most of this self-sustaining population did not behaviorally thermoregulate in this manner, at least on a daily basis, and maintained body core temperatures between 16 and 18°C (Snucins and Gunn 1995). The epilimnetic and littoral gillnet catches of lake trout and the persistence of shallow hydroacoustic echoes in L468 confirm that such residence can occur in thermally stratified lakes.

Lake trout may be more tolerant of warm temperature than previously documented. Clearly, the thermal niche of lake trout in small lakes is broader than the $10 \pm 2^\circ\text{C}$ definition of thermal habitat that has been used in empirical models relating habitat volume to sustained yield in very large lakes (Christie and Regier 1988) and in simulation modeling of the potential effects of lake warming induced by climate change on lake trout production in the Laurentian Great Lakes (Magnuson et al. 1990).

DO in lake trout habitat

Lake trout inhabited only highly oxygenated regions of the three ELA lakes, with oxygen concentrations usually in excess of $6 \text{ mg}\cdot\text{L}^{-1}$, and apparently avoided regions having $<5 \text{ mg}\cdot\text{L}^{-1}$, even when large volumes of appropriate thermal habitat were available. Further, hydroacoustic and vertical gillnet surveys in L442 confirmed that lake trout avoided less oxygenated regions even when the amount of highly oxygenated cool-water habitat was limited. Rather, they inhabited warmer waters with high oxygen concentrations.

The majority of hydroacoustic fish echoes occurred in highly oxygenated water; however, some fish were present at very low DO concentrations. Although the species causing these echoes is not known, brief feeding forays into hypoxic waters have been documented for rainbow trout (*Oncorhynchus mykiss*, Leucke and Teuscher 1994), yellow perch (*Perca flavescens*, Hasler 1945), and central mudminnow (*Umbra limi*, Rahel and Nutzman 1994). It is possible that these echoes were juvenile lake trout because they may inhabit waters with DO as low as $2\text{--}4 \text{ mg}\cdot\text{L}^{-1}$, presumably to avoid predation by cannibalistic adults (Evans et al. 1991).

Our findings support the available information about oxygen requirements for lake trout habitat, although detailed information is lacking about the tolerance of adults to low oxygen. The lower threshold level of no excess activity was $2.8 \text{ mg}\cdot\text{L}^{-1}$ at 10°C and $3.5 \text{ mg}\cdot\text{L}^{-1}$ at 22°C for yearlings and slightly higher for age 2 individuals (Gibson and Fry 1954).

Adult lake trout would be expected to avoid lake regions with DO less than these concentrations. Indeed, the median avoidance threshold was $4.2 \text{ mg}\cdot\text{L}^{-1}$ in five studies that reported lake trout distribution or response to DO (Evans et al. 1991). Similarly, the median threshold at which swimming activity increased in response to declining oxygen was $5.8 \text{ mg}\cdot\text{L}^{-1}$ (Evans et al. 1991).

Light in lake trout habitat

Light appears to have had little influence on the distribution of lake trout in these small lakes. Our findings indicate that lake trout inhabited waters with a variety of illuminations and did not congregate at a preferred light level. Lake trout did not appear to avoid bright light at levels typically encountered in the shallowest regions in L468, in contrast with avoidance suggested for other species (Rudstam and Magnuson 1985). However, it is possible that the daytime descent of lake trout in L375 and L442 was caused in part by avoidance of light.

Assessment of temperature and oxygen requirements

Christie and Regier (1988) showed that the commercial yield of lake trout was correlated with the volume of "optimum" thermal habitat ($10 \pm 2^\circ\text{C}$) in very large lakes. Using similar relationships, Magnuson et al. (1990) simulated potential changes in lake trout production under scenarios of future climatic warming and suggested that thermal habitat and lake trout production would expand in many of the Laurentian Great Lakes. However, it is not known how these relationships apply to lake trout production in smaller lakes. Because of the great depth of most lakes included in the Christie and Regier (1988) and Magnuson et al. (1990) studies, the potential effects of low DO in restricting cold-water habitat were not included in their analyses. Indeed, given evidence of lake trout persisting in warm water (Snucins and Gunn 1995; this study), temperature alone may not be as important as high DO in determining the persistence of lake trout in smaller lakes (Evans et al. 1991). In smaller lakes, hypolimnetic oxygen depletion restricts not only adult thermal habitat but also deep-water nursery habitat for juveniles. In small lakes in central and eastern Ontario subject to cultural eutrophication, loss of juvenile refuge habitat due to DO depletion is thought to cause low recruitment and senescence in many lake trout populations (Evans et al. 1991). Of particular concern in the future is that climatic warming may cause the low-oxygen regions of small lakes to increase (Schindler et al. 1996).

Measures of lake trout habitat volume that explicitly include both temperature and DO have been developed by the Ontario Ministry of Natural Resources to predict both presence of native lake trout and the extent that a lake can sustain a population by natural reproduction (Evans et al. 1991). These measures were volume of preferred habitat (10°C , $6 \text{ mg DO}\cdot\text{L}^{-1}$; upper temperature and lower DO limits), volume of vital habitat (15.5°C , $4 \text{ mg DO}\cdot\text{L}^{-1}$), and habitable volume (15.5°C , $2 \text{ mg DO}\cdot\text{L}^{-1}$) (Evans et al. 1991). However, only a single small lake trout lake ($<1000 \text{ ha}$) in northwestern Ontario was used for this synthesis, reflecting the paucity of data available for these lakes. Application of empirical measures of critical habitat (Evans et al. 1991) to lakes beyond the scope of the original data set may lead to spurious conclusions about the existence and significance of lake trout populations in small northwestern Ontario lakes. Indeed, based on minimum habitat

Table 2. Comparison of L375, L442, and L468 with empirical measures of critical habitat developed for lake trout lakes in Ontario (Evans et al. 1991).

Habitat criteria	Threshold for lake trout presence-absence				
	Nonnative population introduced by stocking	Native population sustained by natural reproduction	L375	L442	L468
Preferred habitat volume (10°C, 6 mg DO·L ⁻¹)	18	48	5	2	65
Vital habitat volume (15.5°C, 4 mg DO·L ⁻¹)	57	96	11.8	3.8	79
Habitable volume (15.5°C, 2 mg DO·L ⁻¹)	76	115	13	5.5	79
Volume with 2–4 mg DO·L ⁻¹ (%)		<8	9	5	<1
Volume with <2 mg DO·L ⁻¹ (%)		<19	4	19	0

Note: Thresholds provided are minimum lake volumes ($\times 10^5$ m³) with temperatures less than or equal to stated limit and DO greater than or equal to stated limit.

thresholds set forth in Evans et al. (1991), L468 barely meets minimum habitat requirements (Table 2). In the absence of population-specific data, these guidelines indicate that native lake trout could not be present nor could introduced populations be self-sustaining in the many small lakes similar to L375 and L442 (Table 2). These characterizations are particularly unfortunate because lake trout populations in the many small northwestern Ontario lakes will be among the most sensitive to erosion of temperature- and DO-suitable habitat whether caused by long-term climatic warming or human development in the watershed.

Ryan and Marshall (1994) showed empirically that thickness of the oxygenated hypolimnion was important to lake trout presence or absence in 88 near-pristine northwestern Ontario lakes. Lake trout were absent in lakes where summer DO depletion in the hypolimnion exceeded 40% of the total entrained at spring overturn (Ryan and Marshall 1994). However, separation of lake trout and non-lake-trout lakes in the Patricia Lakes data set cannot be attributed unequivocally to summer DO depletion alone. Mean depth of 6.3 m separates these lakes equally well into lake trout and non-lake-trout lakes (Ryan and Marshall 1994, their fig. 3). This depth corresponds to the division between lakes that stratify and those that do not (Marshall and Ryan 1987), suggesting that lack of cold-water refugia could contribute to the absence of lake trout as integrated in the Ryan and Marshall (1994) model.

In summary, current empirical models do not describe adequately critical habitat for lake trout, particularly in small lakes. We suggest that previously assumed niche boundaries based on temperature are too low and too narrow for lake trout in small lakes with simple fish assemblages. Although our findings do not directly address physiological tolerance of lake trout to high temperature or low DO, we suggest that the standard limits (12°C, 4 mg DO·L⁻¹) of lake trout habitat do not adequately describe usable habitat. The thermal niche of lake trout is much broader in small lakes than previously believed. In these small lakes, the lake trout niche includes epilimnetic resources and lake trout may be an integral component of the epilimnetic and littoral (France and Steedman 1996) food web. Conversely, a 4 mg DO·L⁻¹ lower limit to lake trout habitat may be too liberal. Based on our findings, we suggest that 5 or even 6 mg DO·L⁻¹ more realistically describes the lower bounds of adult lake trout habitat.

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