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The distribution of lake trout, *Salvelinus namaycush*, and opossum shrimp, *Mysis relicta*, in small Boreal lakes with respect to temperature, dissolved oxygen, and light

by

Todd Jamieson Sellers ©

A thesis submitted to the Faculty of Graduate Studies and Research
in partial fulfillment of the requirements of the degree of Master of Science

Department of Biological Sciences

Edmonton, Alberta

Fall 1995

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The undersigned certify that they have read, and recommend to the Faculty of Graduate Studies and Research for acceptance, a thesis entitled **The distribution of lake trout, *Salvelinus namaycush*, and opossum shrimp, *Mysis relicta*, in small boreal lakes with respect to temperature, dissolved oxygen, and light** submitted by Todd Jamieson Sellers in partial fulfillment of the requirements for the degree of Master of Science.

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Abstract

The distributions of lake trout, *Salvelinus namaycush*, and opossum shrimp, *Mysis relicta*, were surveyed in small boreal lakes in the Experimental Lakes Area, northwestern Ontario that had differences in thermocline depths, hypolimnetic dissolved oxygen (DO) depletion and light transmission. *M. relicta* were benthic during the day and pelagic at night. In contrast to previous research in larger lakes, parts of the *M. relicta* populations occupied water as warm as 17°C in most lakes during the day and were restricted to <13°C in only two lakes, possibly as a response to predation risk from cisco, *Coregonus artedii*. At night, *M. relicta* were present in the epilimnion of two lakes at 19.7°C. Although use of warm water was common to most lakes, most *M. relicta* were found at <8°C both day and night. *M. relicta* avoided lake regions with <2.2 mg L^{-1} DO. During the spring, *M. relicta* were resident as shallow as 0.5 m. They moved to deeper water as epilimnia warmed above their maximum temperature limits in each lake. *M. relicta* inhabited depths where light intensity (PAR) was as high as 168 $\mu Em^{-2}s^{-1}$ during summer and >500 $\mu Em^{-2}s^{-1}$ during littoral residence in spring. Depths of 1% UV-B penetration were shallower than minimum depths inhabited by *M. relicta*.

Lake trout were not restricted to the 10°±2°C thermal niche indicated by previous studies of temperature preference and distribution in large lakes. Hydroacoustic and net surveys indicated considerable variation among lakes in temperatures occupied during the summer. Lake trout were concentrated at <8°C in Lake 375, broadly distributed from 6–15°C in Lake 442 and concentrated in the epilimnion at 19°C in Lake 468. Warm temperatures (19–21°C) dominated distribution in all three lakes at night, in contrast to previous information indicating avoidance of >15°C. Lake trout inhabited only highly oxygenated water, with 75-90% of fish at >6 mg L^{-1} DO throughout the spring and summer.

Acknowledgements

I thank P. Campbell, K. Mills, E.U. Schindler, and D.W. Schindler for use of their unpublished data. B. Fudge, J. Jorgenson, G. McCullough, K. Mills, and D. Cruikshank provided equipment, technical advice, and assistance at the ELA. B. Townsend provided training, equipment, and logistical support for SCUBA diving. I also thank S. Cauvin, B. Pasula, D. Dunstone, S. Lamontagne, and numerous staff and students at the ELA for help in the field. Special thanks to my supervisory committee, D.W. Schindler, W.M. Tonn, and W.C. Mackay for their support during all stages of this work. B. Miskimmin, S. McNaught, and B. Parker also provided challenging criticism that improved this manuscript. This work was supported by a Boreal Alberta Grant from the Canadian Circumpolar Institute, a Student Education and Experience Development Grant from Employment and Immigration Canada, a Natural Sciences and Engineering Research Council of Canada postgraduate scholarship to T.J.S, and NSERC operating grants to D.W. Schindler and W.M. Tonn.

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General Introduction

In Canada, lake trout, *Salvelinus namaycush*, sustains significant cold water fisheries that have important economic, social and cultural values, particularly in northern communities. Increasingly, these fisheries are threatened by a variety of influences, including loss of habitat, over-exploitation, and genetic dilution from stocking (reviewed in Evans et al. 1991b). Loss of habitat is widely believed to be a major cause of decline and senescence in many lake trout populations, although over-exploitation and stocking of exotic fish (e.g., rainbow smelt, *Osmerus mordax*) and indigenous fish (e.g., walleye, *Stizostedion vitreum*) are also implicated in many cases (Evans et al. 1991b). Loss of lake trout habitat is usually associated with human development in a lake's watershed, leading to eutrophication and depletion of dissolved oxygen (DO) from the hypolimnion (Evans et al. 1991a; 1991b). However, habitat loss can also occur in a less obvious way, and in lakes far from the direct influence of human development in the watershed.

Recent evidence of climate-coupled lake warming and thermocline deepening in small lakes in northwestern Ontario indicates possible loss of cold-water habitat for cold stenotherms, such as lake trout and a key prey species *Mysis relicta* (Schindler et al. 1990; 1995). During the decades of the 1970s and 1980s, the climate of northwestern Ontario warmed almost 2°C and became dramatically drier, leading to a 50% decline in runoff (Schindler et al., 1995). Consequently, dramatic changes occurred in lakes at the Experimental Lakes Area (ELA). These changes included deepening of thermoclines by 1 to 1.5 m, dramatic increases in transparency, and slight expansion of hypoxic regions of the hypolimnion (Schindler et al. 1990; 1995). Based on these observations and generally accepted temperature and oxygen criteria for lake trout habitat, Schindler et al. (1990; 1995) hypothesized that the volume of habitat with suitable temperature and oxygen conditions could be reduced enough to extirpate cold stenotherms from some small lakes. My study was undertaken to test this hypothesis with respect to lake trout and *M. relicta* and describe the temperature, DO, and light conditions of summer habitat for these species in small lakes at the ELA.

Lake trout typifies the cold-water communities of many small lakes on the Canadian Shield. In Ontario, for example, at least 2318 lakes outside of the Great Lakes are known to support (or have once supported) lake trout and 2196 have extant lake trout populations (Lewis et al. 1990). Lake trout is the terminal predator in these lakes and typically accounts for approximately 28% of the fish biomass (Marshall and Ryan 1987). It usually co-occurs with at least one other cold-water species, such as lake whitefish, *Coregonus clupeaformis*, cisco, *Coregonus artedii*, or burbot, *Lota lota* (Marshall and Ryan 1987). However, lake trout is widely believed to be among the freshwater species most restricted by temperature to cold-water habitat and most likely to be at risk from lake warming (Magnuson et al. 1990). The natural distribution of lake trout is restricted to lakes where substantial summer warming does not occur or where thermal stratification isolates substantial hypolimnetic volumes of cold-water refugial habitat from summer warming. Its thermal niche is thought to be restricted to 10°±2°C, based on laboratory-determined temperature preference, optimum temperatures for physiological functions and observations of mid-summer distribution in large lakes (O'Connor et al. 1981; Magnuson et al. 1990). In very large lakes, lake trout yield correlates highly with the volume of 10°±2°C habitat (Christie and Regier 1988). Simulations of changes in thermal habitat volumes in the Great Lakes under climatic warming scenarios indicates potential expansion of 10°±2°C habitat in some lakes and concomitant increased lake trout production (Magnuson et al. 1990). However, these forecasts are based on predictions for shallower, stronger thermoclines in large lakes and do not include habitat restriction from DO depletion. The opposite may be true in small lakes subject to climatic warming where thermocline deepening occurs due to loss of dissolved organic carbon (DOC) and increased wind exposure from deforestation (Schindler et al. 1990; 1995). Also, it is neither known whether the empirical relationship of Christie and Regier (1988) holds for lake trout production in small lakes nor whether 10°±2°C describes adequately thermal habitat of lake trout in these lakes.

In small lakes, constriction of suitable summer habitat (by warm temperature from above and low DO from below) may restrict lake trout to lake areas outside physiological norms, possibly affecting growth, reproduction and survival. However, response of lake trout to changes in habitat quality could occur also indirectly through changes in the food chain. *M. relicta* is a glacial relict crustacean that typically co-occurs with lake trout in lakes on the Canadian Shield (Ryan and Marshall 1991). Although lake trout of all ages prey upon *M. relicta*, juvenile lake trout depend nearly exclusively on them for forage (Martin and Olver 1980; Trippel and Beamish 1989). Also, *M. relicta* constitutes up to 35% of the diet of adult lake trout in lakes that lack substantial stocks of cold-water forage species, such as cisco (Trippel and Beamish 1993).

M. relicta is an omnivore that feeds both while on the lake sediments during the day and pelagically at night. While epibenthic, *M. relicta* ingests detritus, algae, chironomids and benthic macroinvertebrates, such as *Diporeia hoyi* (reviewed in Lasenby et al. 1986). In the pelagic zone, *M. relicta* grazes on diatoms and rotifers and is a major predator of cladocerans, particularly *Daphnia* (reviewed in Lasenby et al. 1986). As a prey species, *M. relicta* is at risk from zooplanktivorous fish in the water column and epibenthic feeders such as sculpin (reviewed in Lasenby et al. 1986). As such, *M. relicta* is an integral component of both benthic and pelagic food-webs with connections to several trophic levels (Trippel and Beamish 1993). Its vertical migration into pelagic waters at night provides a direct connection between benthic and pelagic food-webs, reintroducing energy (and incidentally contaminants) lost to the sediments (Lasenby and Langford 1973; Klump et al. 1991). Although introduction of *M. relicta* is known to have large effects on zooplankton and fish communities (Morgan et al. 1981; Rieman and Falter 1981; Nero and Sprules 1986; Varnhagen et al. 1988), little is known about the potential effects of its removal. Loss of *M. relicta* due to habitat constriction could affect lake trout directly through reduced forage for juveniles, but also, indirectly through complex food-web effects operating at several trophic levels.

As with lake trout, *M. relicta* is widely considered to have a cold stenothermic physiology (Smith 1970; Wetzel 1983). Also, *M. relicta* requires high concentrations of DO because it lacks gills and gas exchange occurs by diffusion through its carapace (Wetzel 1983). Its current distribution is thought to reflect persistence only in lakes where substantial summer warming does not occur or where thermal stratification isolates substantial volumes of cold-water refugial habitat during the summer (Dadswell 1974). Characteristics of this refugial habitat include cold temperature (<10–11°C), high dissolved oxygen, and low light levels, inferred largely from studies of the distribution and diel vertical migration of *M. relicta* in the Great Lakes (Beeton 1960; Carpenter et al. 1974; Morgan and Beeton 1978; Grossnickle and Morgan 1979). *M. relicta* also occurs in many small lakes on the Canadian Shield, where the amount of this cold-water habitat is already limited and expected to constrict further if climatic warming occurs (Schindler et al. 1990; 1995). Absence of *M. relicta* from some small lakes, despite potential for inoculation from upstream lakes (T. Sellers, pers. obs.), suggests that the amount of refugial habitat is critical. However, little is known about what constitutes limits to *M. relicta* summer habitat in these small lakes.

In Chapter 1, I describe the distribution of *M. relicta* in several lakes at the ELA. I identify maximum temperature and minimum dissolved oxygen boundaries to its habitat in these small lakes and describe the role of temperature, DO and light in delimiting the breadth of summer habitat for *M. relicta*. In Chapter 2, I describe the distribution of lake trout in Lake 375, 442, and 468 at the ELA. I consider the roles of temperature, dissolved oxygen, and light in delimiting the breadth of summer habitat for this fish.

The ELA is located in northwestern Ontario, approximately 60 km east of Kenora, between 49°37' N and 49°47' N latitude and 93°35' W and 93°50' W longitude (Fig. I.1). These lakes are located on the southwestern margin of the Canadian Shield, and are typical of the many small lakes that support lake trout and *M. relicta*. The ELA was originally established in 1968 as a site for whole–ecosystem level studies of lake eutrophication problems. It was established under joint agreement between the federal Department of Fisheries and Oceans and the Ontario Ministry of Natural Resources, setting aside a group of lakes and their watersheds for experimental manipulation (Johnson and Vallentyne 1971). ELA is located in a relatively undeveloped area of the Canadian Shield. There is no agricultural, urban, or cottage development, although logging has occurred in some of the area outside of catchments of the Experimental Lakes. Because of restricted public access and protected status of the lakes and their watersheds, ELA lakes are as close to pristine as is possible today in temperate areas of North America.

The ELA has an extensive database of physical, chemical and biological information extending up to 26 years for many of the lakes in the area. Since its inception, a near-continuous record has been collected of the meteorology, hydrology, lake biogeochemistry and some aquatic communities in several calibrated reference lakes. These long-term records have provided the basis for recent analyses linking climatic warming to changes in lake chemistry, lake thermal structure, and possibly loss of habitat for cold stenotherms such as lake trout and *M. relicta* (Schindler et al. 1990; 1995).

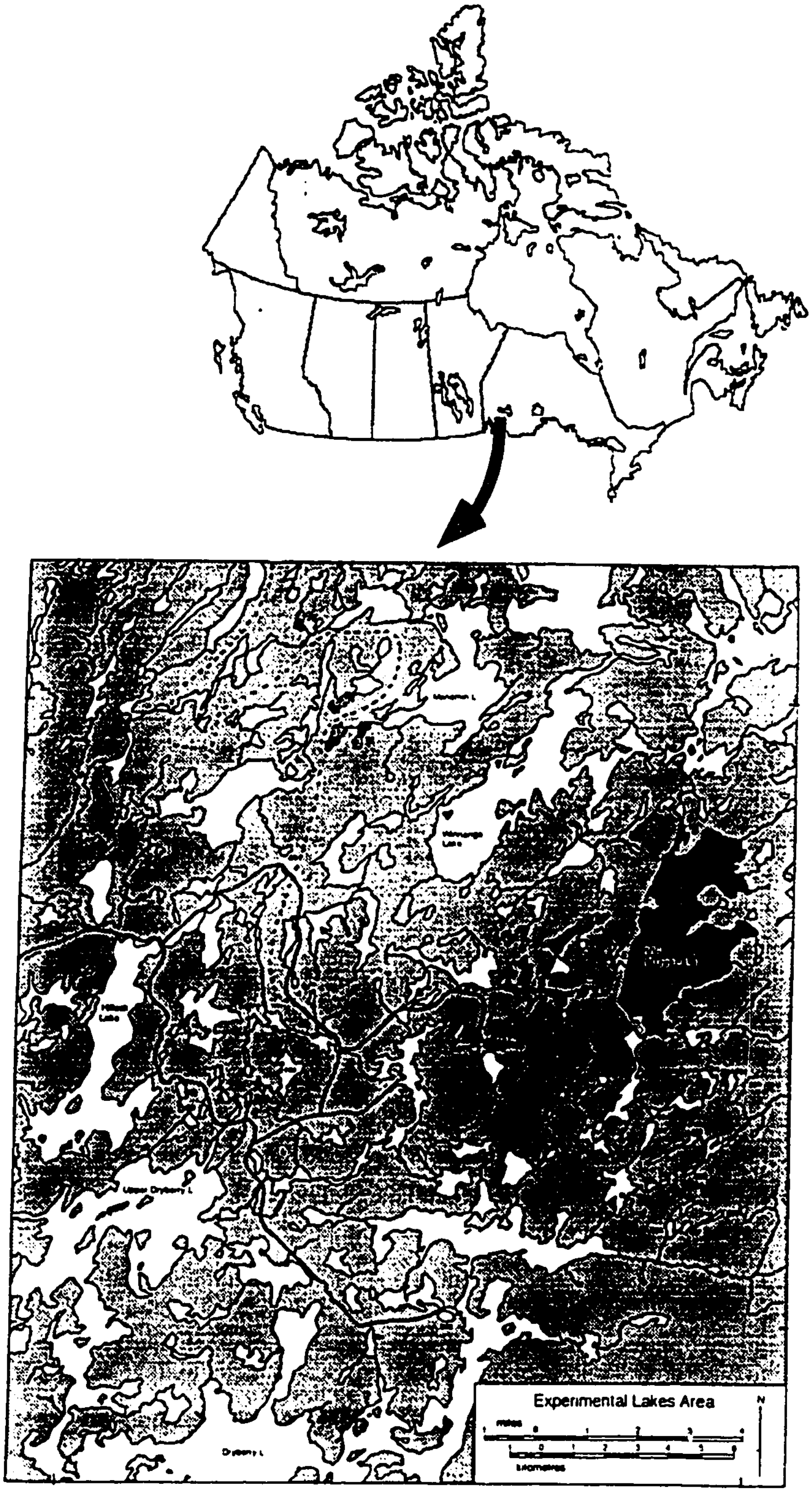

Figure I.1 Map of Canada with inset showing location of the Experimental Lakes Area. Lakes used in study of *Mysis relicta* (Chapter 1) and lake trout (Chapter 2) are indicated by black shading (modified from Beamish et al. 1976).

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Chapter 1: The Distribution of *Mysis relicta* in Small Boreal Lakes with Respect to Temperature, Dissolved Oxygen and Light

1.1 Introduction

Mysis relicta, the opossum shrimp, is an ubiquitous member of the cold, deep lake trout lakes of the Canadian Shield. The natural distribution of this glaciomarine relict crustacean is restricted to drainage basins that were inundated by proglacial lakes during the retreat of the Wisconsin ice sheet at the end of Pleistocene era (Dadswell 1974; Väinölä et al. 1994). Its present day distribution, however, has been extended by extensive introductions by fishery managers in attempts to increase fish growth and improve sport fisheries (reviewed in Lasenby et al. 1986). *M. relicta* is generally considered to have a cold stenothermic physiology (Smith 1970; Wetzel 1983). It also requires high concentrations of dissolved oxygen (DO) because it lacks gills and gas exchange occurs by diffusion through its carapace (Sandeman and Lasenby 1980; Wetzel 1983). As such, its persists only in lakes where substantial summer warming does not occur or where thermal stratification isolates highly oxygenated, cold-water refugia from the effects of summer warming (Dadswell 1974).

In the Great Lakes, *M. relicta* distribution is generally consistent with that of a cold stenotherm, being restricted to deep water with temperatures less than 10–11°C (Smith 1970; Grossnickle and Morgan 1979; Janssen and Brandt 1980; Lehman et al. 1990). At night, they are pelagic at the top of the hypolimnion or in the metalimnion up to the 10–11°C isotherm. During the day, they are located at 4–5°C in the hypolimnion. *M. relicta* is benthic during the day at moderate depths, presumably to avoid high illumination and high predation risk from visually oriented pelagic predators in shallower water (Beeton 1960; Teraguchi et al. 1975; Janssen and Brandt 1980; Bowers 1988). They may remain pelagic at extreme depths (i.e. >100 m), where light intensity and risk of predation are very low (Beeton 1960; Robertson et al. 1968; Carpenter et al. 1974; Bowers 1988; Lehman et al. 1990; Levy 1991).

Stenothermal restriction to water of less than 10–11°C may not be general to all *M. relicta* populations. Results of temperature tolerance tests are contradictory, indicating maximum survival temperatures of 10°C (Smith 1970), 13°C (DeGraeve and Reynolds 1975), and 17°C (Dadswell 1974). Indeed, in several lakes, *M. relicta* inhabits water much warmer (up to 17°C) than in the Great Lakes (Larkin 1948; Nero 1981; Nero and Schindler 1983; Nero and Sprules 1986), although the extent of warm water use is not known.

In small lakes, the amount of summer habitat with cold temperatures, high dissolved oxygen, and low light is limited. Further, evidence from small Canadian Shield lakes of a twenty-year trend of lake warming, deepening of thermoclines, increased light transparency, and accelerated depletion of dissolved oxygen suggests potential constriction of summer habitat for cold stenotherms, such as *M. relicta*, and possible extirpation from small lakes (Schindler et al. 1990; 1995). However, little is known about the distribution of *M. relicta* in lakes with limited summer habitat, or what boundaries constitute that habitat.

In this study, I describe the distribution of *M. relicta* in several small Canadian Shield lakes with respect to temperature, dissolved oxygen, and light. I examine the hypothesis that summer habitat is restricted to a region of the lakes that provides cold temperatures, low light intensity, and high concentrations of dissolved oxygen. I identify maximum temperature and minimum dissolved oxygen boundaries to *M. relicta* habitat, as well as examine lake-to-lake differences. I also describe the roles of temperature, dissolved oxygen, and light in delimiting the breadth of summer habitat for *M. relicta*.

1.2 Methods

Study Sites

The study lakes are located at the Experimental Lakes Area (ELA) in northwestern Ontario, approximately 60 km east of Kenora, between 49°37' N and 49°47' N latitude and 93°35' W and 93°50' W longitude.

These lakes are located on the southwestern margin of the Canadian Shield and are typical of small oligotrophic lakes that support *M. relicta* and lake trout, *Salvelinus namaycush*. Characteristics of the geology, forests, and surrounding land-use are described in Brunskill and Schindler (1971), Salki (1992), and McCullough and Campbell (1993). Records of the climate and hydrology at the ELA are provided in Beaty and Lyng (1989). The effects of recent climate on the physical and chemical characteristics of ELA lakes are summarized in Schindler et al. (1990).

The nine lakes included in this study were L 224, L 228 (Teggau L.), L 239 (Rawson L.), L 305, L 373, L 375, L 442, L 468 (Roddy L.), and L 626. Lake 375, L 442, and L 468 were the focus of detailed study of *M. relicta* distribution (hereafter referred to as focal lakes). Selected morphometric data for the study lakes are summarized in Table 1.1.

Table 1.1 Limnological data for nine study lakes at the ELA, northwestern Ontario. Data were compiled from Brunskill and Schindler (1971), Hesslein et al. (1980), McCullough and Campbell (1993), ELA staff unpubl. data, and T. Sellers unpubl. data.

Lake	Z_{max} (m)	Z_{mean} (m)	Area (ha)	Volume ($10^5 m^3$)
224	27.4	11.6	25.9	30.1
228	167	55.4	1676.5	9284.2
239	30	10.5	56.1	59.1
305	32.7	15.1	52.0	78.6
373	20.8	11.0	27.3	30.1
375	26	11.6	18.7	21.7
442	17.8	9.0	16.0	14.4
468 (east basin)[a]	29	≅11	≅114	≅128
626	12	10.0	27.9	27.9

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[a] Estimates for east basin of L 468 exclude northeast basin with portage to L 305 (~32 ha). Area of west basin of L 468 is approximately 151 ha.

Temperature, Dissolved Oxygen, and Light Profiles

Using a Flett Mark II thermistor (Flett Research, Winnipeg, Manitoba) I determined daytime lake temperature profiles at the deepest point in three focal lakes (L 375, L 442, and L 468) throughout the summer of 1993. The thermistor was calibrated to icewater prior to use. Temperatures were measured to the nearest 0.1°C at 1 m depth intervals, except through the metalimnion where 0.25 m resolution was used. Temperature profiles were measured as often as possible on each lake (every 3–22 days, Appendix 1), usually coincident with surveys of *M. relicta* distribution. Profiles for days when temperatures were not measured were estimated by linear interpolation from nearest sampling dates. Temperature profiles were measured once in other study lakes (L 224, L 228, L 239, L 305, L 373, and L 626) concurrent with daytime surveys of *M. relicta* distribution.

Using the azide modification of the Winkler technique (Carpenter 1965), I measured vertical profiles of dissolved oxygen (DO) concentration during the day in the three focal lakes every 1–3 weeks throughout the summer of 1993 (Appendix 1). DO was measured at the deepest point in each lake at 1–2 m depth intervals, except in regions of very low or rapidly decreasing DO, where 0.25 m resolution was used. Profiles for days on which DO was not measured were estimated by linear interpolation between nearest sampling dates. I also measured DO in Lake 442 during the summer of 1994, concurrent with surveys of maximum depth of *M. relicta*.

Using a Licor submersible light meter, I measured light transmission profiles in the focal lakes as often as possible (every 3–29 days; Appendix 1) during the summer of 1993. Light transmission was measured at midday as photosynthetically active radiation (PAR; ≅390–710 nm) in µE m^{-2} s^{-1} at 1 m depth intervals from the surface to below the 1% light level. I estimated profiles for days when light transmission was not measured by linear interpolation between nearest sampling dates. Light transmission was also measured concurrent with daytime *M. relicta* surveys in Lakes 224, 239, 305, and 373 during 1993 and in Lakes 239, 442, and 468 during 1994. Due to malfunction of the light meter, light transmission was not measured in Lake 228 concurrent with *M. relicta* surveys on August 24, 1993. Instead, I used the August 23 profile for Lake 224 as a surrogate to estimate conservatively light transmission on August 24 in Lake 228. Transparency in Lake 228 was likely greater than in Lake 224. During periods when comparable photometric data were collected for both lakes, extinction coefficients were less in Lake 228 than in Lake 224 (e.g., 0.2 vs. 0.3; ELA unpubl. data). Further, similarly low dissolved organic carbon (DOC) concentrations (ELA unpubl. data) and direct observations of visibility during SCUBA surveys (T. Sellers, pers. obs.) suggest that light transmission in Lake 224 provides a reasonable, although perhaps conservative, approximation of the light transmission in Lake 228.

Light intensity incident on each lake during *M. relicta* surveys was estimated from the continuous record of PAR at the ELA meteorological site (E. Schindler, DFO, Winnipeg, unpubl. data). Where necessary for comparison with previous studies, irradiance was converted to illuminance units based on 1 $\mu E\ m^{-2}s^{-1} \cong 51.2$ lux (Wetzel and Likens 1991).

Maximum potential penetration of ultraviolet-B light (UV-B, 300–320 nm) was estimated for Lakes 224, 228, 239, 305, 373, 375, 442, and 468 using available DOC measurements and the equation for the UV-B extinction coefficient:

$K_{dI}B = 0.415[DOC]^{1.86}$; where DOC is in mg L^{-1} (Scully and Lean 1994).

Values used to estimate UV-B penetration were:

- Lakes 224 and Lake 239 — lowest annual average DOC during the period 1971–1990 (ELA, unpubl. data).
- Lake 228 — single DOC value from August 28, 1986 (ELA, unpubl. data).
- Lake 305 — lowest DOC measurement during period 1984–1991 (ELA, unpubl. data).
- Lake 373 and Lake 442 — lowest DOC during summer of 1993 (P. Campbell, DFO, Winnipeg, unpubl. data).
- Lake 375 and Lake 468 — lowest DOC measurement during period 1987–1991 (ELA, unpubl. data).

Distribution of *Mysis relicta*

I obtained data on the distribution of *M. relicta* within its daytime benthic habitat using SCUBA and in its nighttime pelagic habitat using vertical net hauls.

Using SCUBA, I measured the minimum depth and maximum temperature inhabited by *M. relicta* on the sediments during the day in the three focal lakes (L 375, L 442, and L 468) repeatedly during the summer of 1993 (Table 1.2). During August 1993, I measured minimum depth and maximum temperature inhabited in six additional lakes (L 224, L 228, L 239, L 305, L 373, and L 626; Table 1.2). In the spring of 1994, these measurements were repeated in Lakes 239, 442, and 468 from ice-out (April 24) to the onset of full summer stratification by the end of May (Table 1.3). Surveys were restricted to areas of comparable substrate in each lake (flocculent profundal sediment–littoral sand) to minimize possible effects of substrate type on *M. relicta* distribution (Nero 1981).

I confirmed the minimum depth and maximum temperature inhabited by *M. relicta* during each survey with at least 10 cycles of descent and ascent through the shallow-water boundary between *M. relicta* absence and presence. Also, during these surveys I estimated visually an upper limit to daytime aggregations of *M. relicta* on the lake sediments, which I defined as >5 m^{-2}. Maximum depth inhabited was confirmed with at least 5 descent-ascent cycles through the deepwater margin of *M. relicta* presence–absence.

Maximum inhabited temperature was measured to the nearest 0.5°C with a hand-held alcohol thermometer placed alongside *M. relicta* at its shallowest occurrence. Maximum temperature at the shallowest aggregation of *M. relicta* was measured similarly. Thermometers were calibrated against the thermistor (Flett Mark II) used to measure lake temperature profiles.

Minimum and maximum depths were measured with an underwater depth gauge (US Divers ScubaPro in 1993; US Divers DataPro DS3 in 1994) placed on the sediments at the shallowest and deepest occurrence, respectively, of *M. relicta*. In very shallow water (approximately < 1.5 m, spring 1994) minimum inhabited depths were determined by direct measurement from the lake surface to the sediments. Depth gauges were calibrated both before and during use. They were accurate to within ±0.3 m (1993) and ±0.15 m (1994) (Appendix 2). Depths were measured in feet of seawater and corrected to feet of freshwater using mean density of seawater at 4°C relative to freshwater (Wetzel 1983). Depths measured in 1993 were corrected for altitude at ELA. In 1994, no altitude correction was necessary because the gauge was calibrated to atmospheric pressure at the lake surface prior to each dive.

I estimated maximum light where *M. relicta* occur from minimum depths, light transmission profiles, and average irradiance incident during the period of the survey. I inferred the minimum dissolved oxygen where *M. relicta* occur from maximum inhabited depths and dissolved oxygen profiles measured at the deepest point in each lakes.

Table 1.2 Schedule of SCUBA surveys during summer 1993, on which measurements were made of maximum temperature and depth inhabited by *M. relicta*. Multiple surveys were conducted on some dates. Solid circle indicates data collected, blank indicates data not collected.

Lake	**Date**	**Maximum Temperature**	**Maximum Depth**
375	May 18	●	
375	June 11	●	●
375	June 15		●
375	June 17	●	●
375	June 21	●	
375	June 24	●	●
375	July 14	●	
375	August 10	●	●
442	May 19	●	●
442	May 20		●
442	June 1	●	
442	June 8	●	●
442	June 29	●	●
442	July 14	●	
442	August 10	●	●
468	July 14	●	●
468	July 15	●	●
468	August 10	●	
468	August 21		●
468	August 24	●	
224	August 23	●	
228	August 24	●	
239	August 18	●	
239	August 20	●	
239	August 25	●	
239	August 26	●	
239	August 27	●	
305	August 23	●	
373	August 25	●	
626	August 25	●	

Table 1.3 Schedule of SCUBA surveys during 1994, on which measurements were made of maximum temperatures and depth inhabited by *M. relicta*. Solid circle indicates data collected, blank indicates data not collected.

Lake	**Date**	**Maximum Temperature**	**Maximum Depth**
239	April 26	•	
239	May 2	•	
239	May 3	•	
239	May 9	•	
239	May 19	•	
239	May 22	•	
239	May 30	•	
442	April 27	•	•
442	May 5	•	
442	May 10		•
442	May 11	•	
442	May 20	•	
442	May 30		•
442	August 7	•	•
442	August 20	•	•
468	April 26	•	
468	May 2	•	
468	May 3	•	
468	May 9	•	
468	May 19	•	
468	May 31	•	

In a series of additional SCUBA dives, I determined the density of *M. relicta* on the sediments during the day in Lake 442 and Lake 375. Density was calculated from direct counts of *M. relicta* within a 0.25 cm x 0.25 x 10 cm clear acrylic box quadrat placed on the lake bottom (Nero 1981). Counts were conducted over similar flocculent sediment substrates along 1.5 m depth contours from transect A in Lake 442 (Fig. 1.1) and Lake 375 (Fig. 1.2). Quadrats were placed gently on the sediments at approximately 6–7 m intervals (measured as 5 swim-kick cycles) along each 1.5 m depth contour. Occasionally, disturbance and re-suspension of the lake sediments occurred inadvertently during quadrat placement; *M. relicta* were not enumerated at these locations. Quadrats were illuminated with 2 submersible lights during counting. Because some *M. relicta* burrowed in the sediments during counting, each quadrat was tapped gently which dislodged *M. relicta* from the sediments. A total of 60 quadrat counts were made in Lake 442 during the first week of June in 1993, with 7 to 12 counts along each 1.5 m depth contour. Eighty quadrat counts were made in Lake 375 during the third week of June, with 12 to 18 counts at each 1.5 m depth contour.

At night, vertical distribution of *M. relicta* in the water columns of Lakes 375, 442, and 468 was determined from successively deeper (1–2 m) net hauls. A square net (area = 1 m^2; body mesh ≅ 1 mm, cod end = 250 µm) was towed vertically at approximately 0.3 m s^{-1} (Nero and Davies 1982). Duplicate hauls were taken for each depth. Net hauls commenced at least one hour after sunset (usually 23:00) by which time vertical migration into pelagic waters is completed (Nero 1981). Net hauls were taken at the deepest site in each lake, except in Lake 442. In Lake 442, net hauls were taken over the 11 m contour because preliminary sampling indicated that *M. relicta* were virtually absent from pelagic water above the 12–18 m contours.

Net hauls were also conducted in L 224, L 239, L 305, L 373, and L 626 during August 1993 to identify the minimum depth of *M. relicta* as well as the upper limit of aggregations of the *M. relicta* in these lakes at night (vertical resolution, 0.25–1 m). I considered that *M. relicta* density in the water column ≥10 m^{-3} constituted an aggregation.

Catches were preserved in 95% ethanol on site for later enumeration of *M. relicta*. Density within a depth stratum was calculated as the number caught from that depth to the surface, less the number caught in shallower strata, divided by the swept volume of the net (Nero and Davies 1982). I estimated temperatures inhabited at night from vertical distribution and daytime temperature profiles.

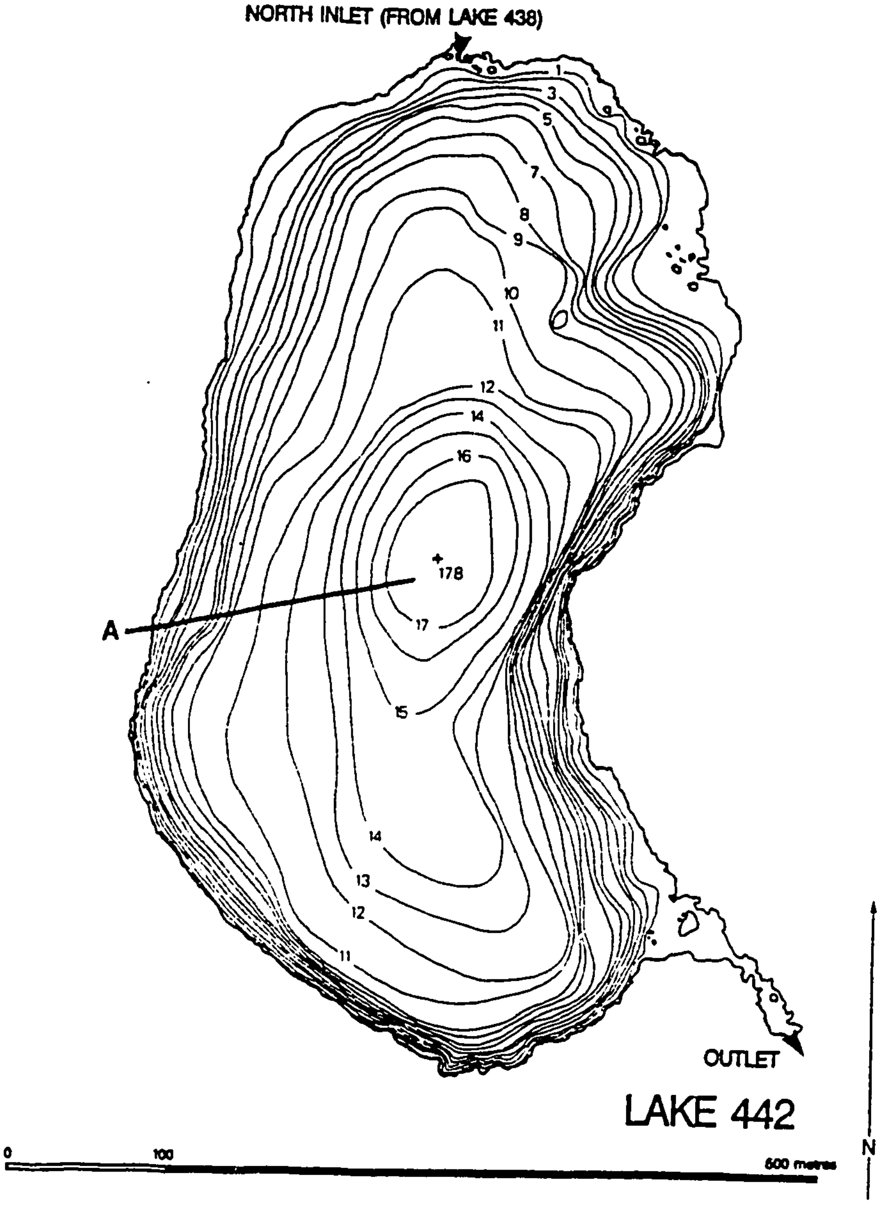

Figure 1.1 Bathymetric map of Lake 442. Solid line A denotes transect for quadrats counts of *M. relicta* benthic density (after McCullough and Campbell 1993).

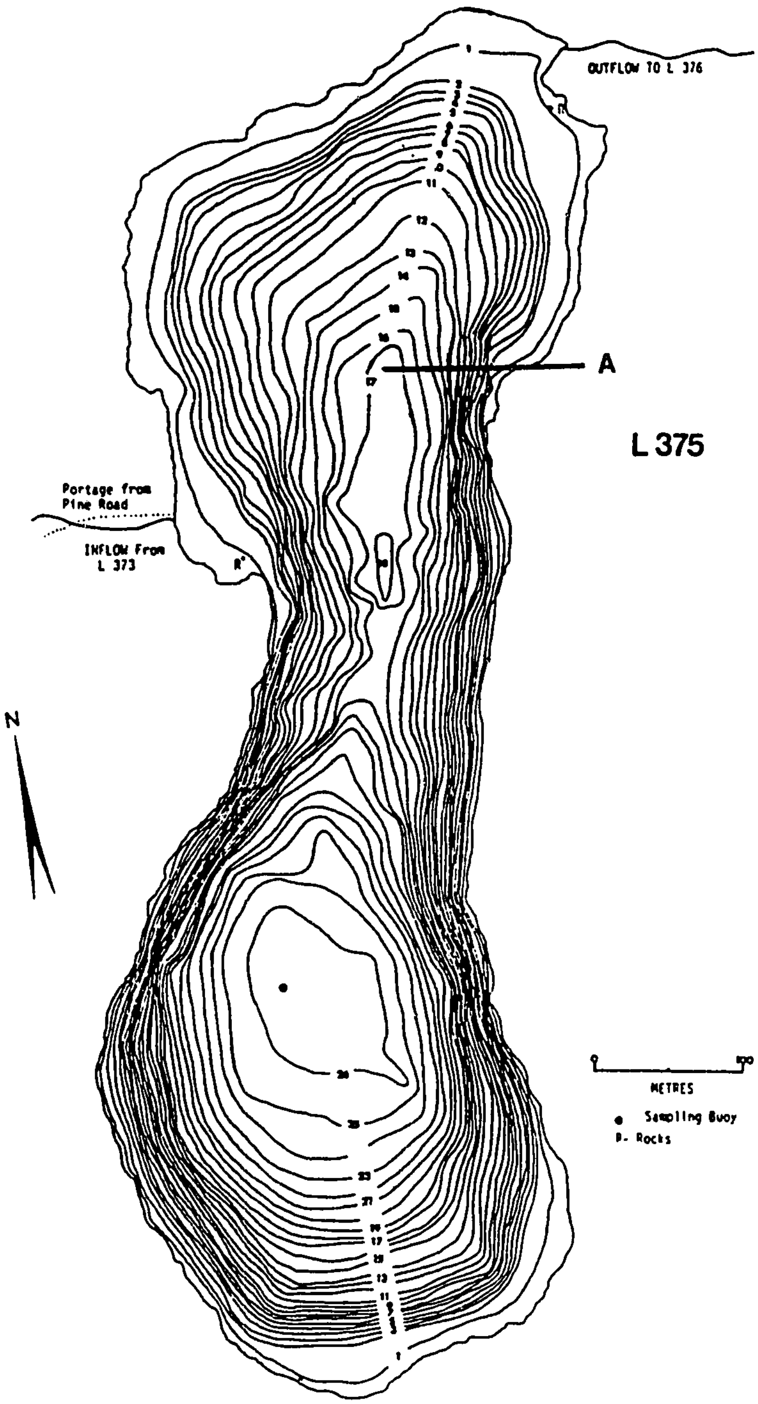

Figure 1.2 Bathymetric map of Lake 375. Solid line A denotes transect for quadrat counts of *M. relicta* benthic density (after ELA unpubl. data).

1.3 Results

General Features of *Mysis relicta* Distribution

M. relicta were present in L 224, L 228, L 239, L 305, L 373, L 375, L 442, and L 468. I did not detect any *M. relicta* in Lake 626. During the day, they were completely benthic except in Lake 224 and Lake 228. In these latter lakes, most were benthic but some were in the water column up to 1 m above the lake sediments.

At night, *M. relicta* were pelagic in each of the lakes that were surveyed (surveys were not conducted in Lake 228). They were distributed throughout nearshore and offshore regions of the lakes, except in Lake 442. In this lake, they were virtually absent from pelagic regions above the central anoxic basin of the lake. Rather, they inhabited a ring of nearshore water that circumscribed the lake above the sediments inhabited during the daytime.

The daytime benthic habitat characteristically featured soft sand or flocculent sediment substrates. *M. relicta* were scarce to absent over regions of the lake where the bottom consisted of bedrock, boulders, hard iron deposits, or hard substrate overlain with a thin layer of sediments. In boulder-strewn areas of the lake bottom, *M. relicta* were present on the sediments between boulders. They were absent over organic-strewn substrates, in particular, the finely shredded wood and bark tailings produced by beavers.

In general, *M. relicta* did not inhabit all depths during the summer. Rather, they were confined vertically to a range of depths in the metalimnion and hypolimnion. I identified distinct boundaries to this inhabited zone associated with warm temperatures at shallow depths and low dissolved oxygen in deep water.

Maximum Temperature Limits

During the day, *M. relicta* were absent from the epilimnion of each lake where temperatures were greater than 19°C. They were present in the middle to upper regions of the metalimnion up to a maximum temperature of 17°C (Fig. 1.3). *M. relicta* did not migrate into, or out of, these warm regions during the period of SCUBA observations (up to 1 hr). Maximum temperature limits, however, differed from lake to lake by as much as 4°C (Fig. 1.3). In three lakes (L 224, L 373, L 375) *M. relicta* were present consistently at 17°C. In contrast, I never observed them at greater than 13°C in Lake 228 and Lake 239 despite repeated surveys (seven in L 239, three in L 228). In Lakes 305, 442, and 468 there was an intermediate temperature limit of 15°–16°C (Fig. 1.3). These maximum temperatures were consistent in lakes that were surveyed repeatedly throughout the summer (L 375, L 442, L 468).

During the night, maximum temperature inhabited also varied by lake. It corresponded to the respective daytime temperature maximum in Lakes 224, 305, 373, and 442 (Fig. 1.3). In contrast, *M. relicta* occupied shallower, warmer water at night in Lakes 239, 375 and 468 (Fig. 1.3). Indeed, they were present in the epilimnion of Lakes 375 and 468 at temperatures of 19.3°–19.7°C.

Minimum Dissolved Oxygen Limits

Lower limits to the daytime distribution of *M. relicta* on the benthic sediments could not be determined directly in Lakes 375 and 468 because they were abundant to depths greater than that which could be surveyed safely using SCUBA (>20 m). At 20 m there was at least 3.6 mg L^{-1} and 5.0 mg L^{-1} of DO in Lakes 375 and 468 respectively throughout the summer stratified season (Figs. 1.4a and b). In these lakes, nighttime vertical net hauls revealed that maximum depth of *M. relicta* occurred where DO was between 3.5 mg L^{-1} and 1.4 mg L^{-1} in Lake 375 and in excess of 3.0 mg L^{-1} in Lake 468 (22.4–24.4 m in L 375, 24.6–26.6 m in L 468).

In contrast, Lake 442 did not undergo spring mixis in 1993, and consequently began the open-water season with a large region of very low DO that expanded progressively upward throughout the summer (Fig. 1.4c). Shortly after ice-out, DO was less than 2 mg L^{-1} in the deepest 4.7 m of the lake. By the third week of June, this hypoxic region encompassed the deepest 8.1 m of this 18 m deep lake and the deepest 3 m were anoxic.

M. relicta displayed an abrupt deepwater cut-off on the sediments during the day in Lake 442. The width of the cut-off zone was 0.3 m of lake depth or less. Beginning in May, they were absent from the deepest 5.5 m of the lake. This lower limit moved shallower by 2.3 m as the summer progressed, following the 2.2 mg L^{-1} DO isopleth (Fig. 1.5). Thus, by August, *M. relicta* were absent below 10.3 m ±0.3 m.

Lake 442 overturned following ice-out in 1994. As a result, DO was greater than 7.8 mg L^{-1} throughout the lake. At this time, *M. relicta* were present on the benthic sediments to a maximum depth of 16.60 m ±0.15 m. Depletion of DO from bottom water strata occurred rapidly, such that by the end of May DO was less than 3.1 mg L^{-1} below 15 m. Maximum depth of *M. relicta* persisted at 16.60 m ±0.15 m at an ambient DO concentration of 2.8 mg L^{-1} (Fig. 1.5). By August, the lower limit for *M. relicta* had moved up along the lake sediments to 11.30 m ±0.15 m, which again corresponded to the 2.2 mg L^{-1} DO isopleth (Fig. 1.5).

Distribution Within The Inhabited Zone

Upper Limit to Aggregations of *Mysis relicta*

During the day, *M. relicta* were not distributed evenly between their shallow and deepwater distribution boundaries. Although some were present in relatively warm water in many of the lakes, they were much more abundant in colder water. At depths near the maximum temperature limits, density of *M. relicta* was too low to be effectively measured using the 25 cm x 25 cm quadrat. At these depths, density on the sediments was visually estimated to be less than 5 m^{-2} in all lakes. In lakes with warm or intermediate daytime temperature limits (15°–17°C), density did not increase until temperatures of approximately 15°C or less were attained. At temperatures centered around 13°C (range 12°–15°C) density increased rapidly and large aggregations were readily apparent (Fig. 1.6). In contrast, in lakes with cold (<13°C) maximum temperature limits (Lakes 228, 239), *M. relicta* did not aggregate on the lake bottom until 8–9°C (Fig. 1.6).

Similarly at night, densities were very low at maximum temperature limits with less than 5 m^{-3} in each of the seven lakes surveyed at night (L 224, L 239, L 305, L 373, L 375, L 442, and L 468). Density increased by an order of magnitude over a narrow depth range in the metalimnion. The width of this boundary between trace occurrence and large aggregations was 0.5 m or less; it corresponded to where temperatures decreased rapidly below approximately 14°–15°C (mean of sampling interval mid-point temperatures = 14.3°C, SD=1.0°C; maximum possible range 11.1 – 16.9°C) (Fig. 1.6). Compared with the daytime, aggregations of *M. relicta* occurred in warmer water at night in Lakes 224, 239, 305, and 468, but at similar temperatures in Lakes 373, 375, and 442 (Fig. 1.6).

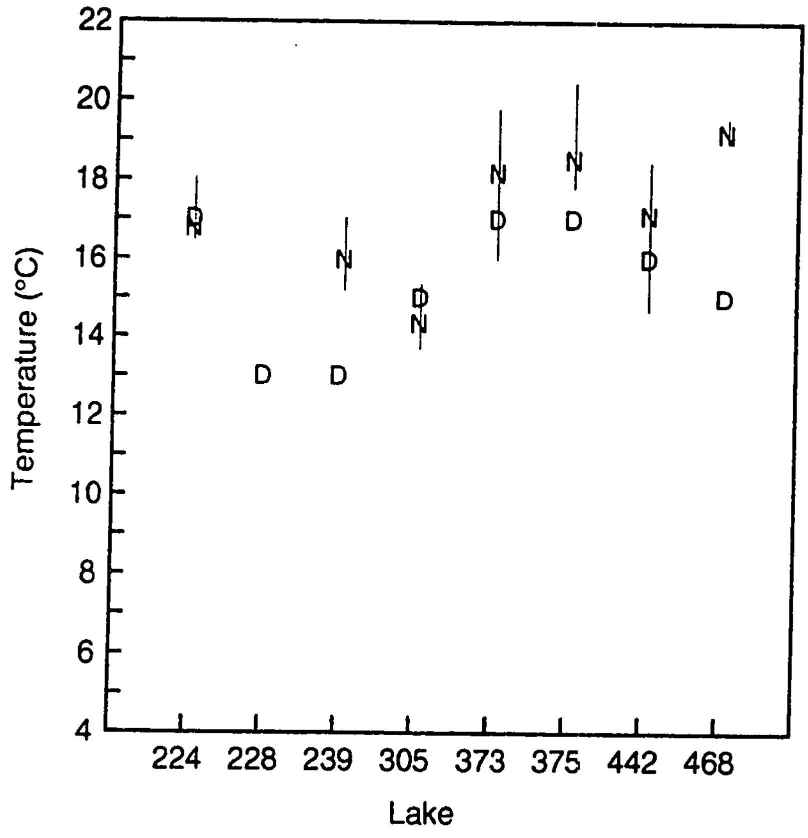

Figure 1.3 Maximum temperature inhabited by *M. relicta* in eight lakes at the ELA during the day (D) and night (N) during August, 1993. Because day values were obtained by direct measurement of temperature at shallowest occurrence of *M. relicta* (D), no confidence limits are shown. Because night values were obtained from vertical net hauls through a depth interval with a range of temperatures, night values were plotted as temperature at the depth midpoint (N) of the sampling interval ± temperature range of that depth interval (vertical bars).

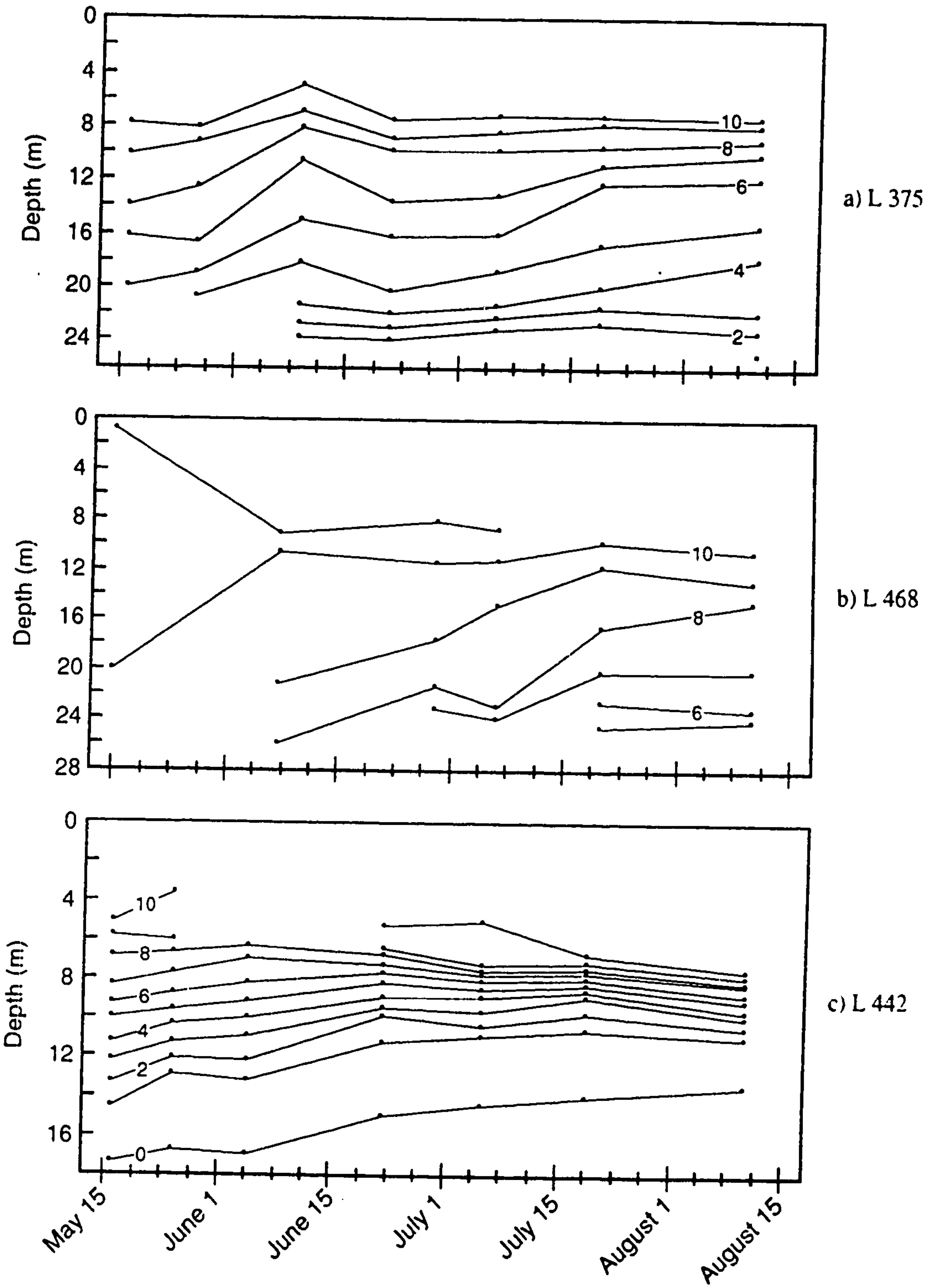

Figure 1.4 Seasonal isopleths for dissolved oxygen (mg L^{-1}) for a) Lake 375, b) Lake 468, and c) Lake 442 during the summer of 1993.

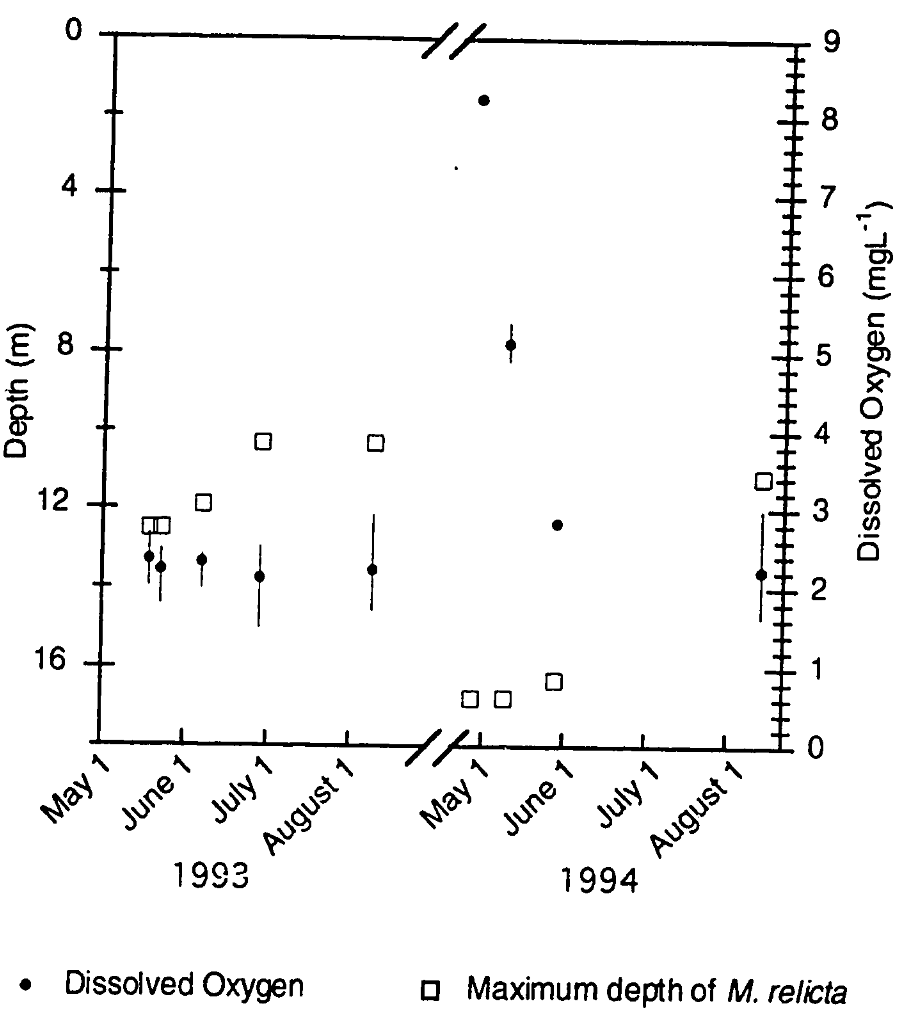

Figure 1.5 Minimum dissolved oxygen concentration and maximum depth inhabited by *M. relicta* during the day in Lake 442 during spring and summer of 1993 and 1994. Minimum DO inhabited was plotted as DO inferred from measured depth ± the potential error of the gauges used (±0.3 m in 1993 and ±0.15 m in 1994).

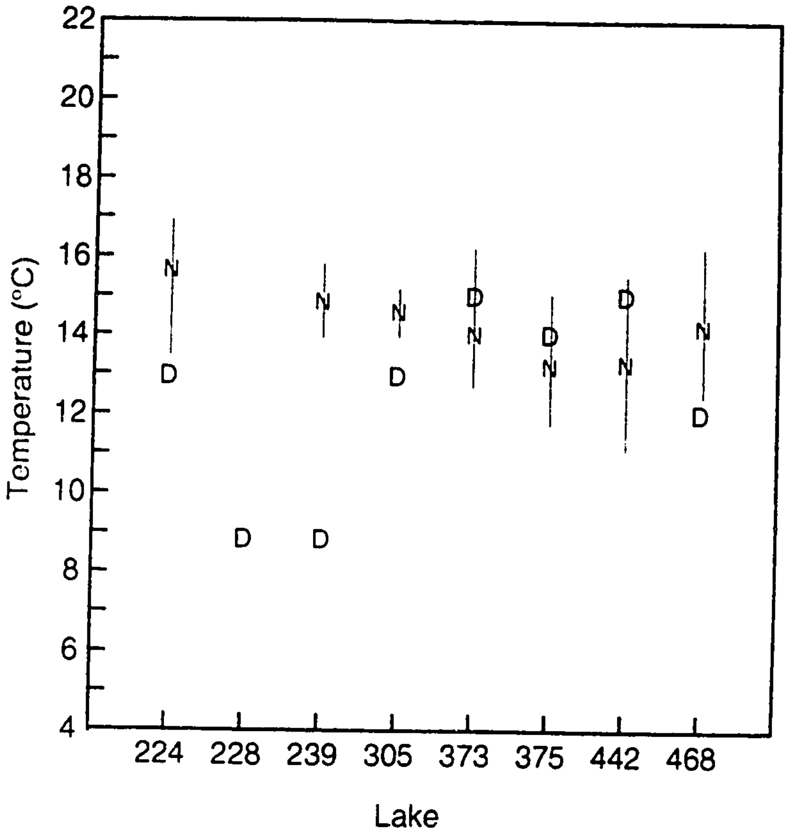

Figure 1.6 Maximum temperature at which aggregations of *M. relicta* occurred in eight lakes at the ELA during the day (D) and night (N). Because day values were obtained by direct measurement of temperature at shallowest occurrence of *M. relicta* (D), no confidence limits are shown. Because night values were obtained from vertical net hauls through a depth interval with a range of temperatures, night values were plotted as temperature at the depth midpoint (N) of the sampling interval ± temperature range of that depth interval (vertical bars).

Vertical Distribution During the Day

During the early period of stratification in Lake 442 (week of June 1) epilimnetic temperatures ranged from 12.5°C to 16.9°C. *M. relicta* were present on the lake bottom as shallow as 3–5 m in numbers too sparse to assess quantitatively using the 25 cm x 25 cm quadrat. Density was less than 5 m^{-2} (estimated visually). Most *M. relicta* were confined to a narrow depth band of sediments (5.25–12 m) below the epilimnion where temperatures were less than 7°C and dissolved oxygen was greater than 2.2. mg L^{-1} (Fig. 1.7a). Mean density of *M. relicta* on the lake bottom ranged from 28 m^{-2} to 108 m^{-2}. There were, however, no consistent trends in density with depth, temperature, or dissolved oxygen between their shallow and deepwater distribution limits (Fig. 1.7a).

M. relicta in Lake 375 were present in both the hypolimnion and metalimnion during the day where temperatures were 17°C or less (Fig. 1.7b). They occurred in sparse numbers in the upper half of the metalimnion between 17°C and 11°C (3.7–5.2 m). Density could not be assessed quantitatively at these depths because *M. relicta* avoided SCUBA divers and the clear acrylic quadrat at these shallow, well-illuminated depths. Below these depths, maximum mean density of 104 m^{-2} was similar to that in Lake 442. Unlike Lake 442, however, there was a trend of decreasing mean density with depth between 6.2 m and 13.8 m, corresponding to a temperature range of 11°C to 4°C (Fig. 1.7b). Quantitative estimates of density could not be obtained at depths below 13.8 m, because benthic sediments were too flocculent to use the quadrat successfully. Qualitative observations suggested that densities changed little between 13.8 m and 16 m but peaked at depths greater than 16 m. Density in this near-bottom region was judged to be as great as the maximum densities measured between 6.2 m and 7.7 m. This deep group of *M. relicta* were, almost exclusively, large-bodied adults.

Vertical Distribution During the Night

At night, *M. relicta* were present at up to 19°–20°C in the epilimnia of Lakes 375 and 468 (Figs. 1.8a-c). However, they occurred at very low density (<4 m^{-3}) at these temperatures. Indeed, the majority in each lake were at 15°C or less. *M. relicta* at greater than 15°C constituted less than 10% of the catch in each lake.

In each of the three focal lakes, densities increased rapidly below 15°C and reached a maximum of approximately 57 m^{-3}, 75 m^{-3}, and 20 m^{-3} in Lakes 375, 442, and 468 respectively (Figs. 1.8a-c). Maximum density occurred between 10.8°C and 7.7°C in Lake 375, 8.5°C and 6.4°C in Lake 442, and 12.4°C and 6.0°C in Lake 468.

In Lake 375, *M. relicta* occurred over a wide range of depths (2–4 m to 22–24 m; Fig. 1.8a). Approximately 80% were at less than 10.8°C (5–24 m). Peak density (57 m^{-3}) occurred between 10.8°C and 7.7°C (5–6 m) where 30% were located (Fig. 1.8a). Density decreased by about 50% at colder depths, and remained below 15 m^{-3} to the lake bottom. Nevertheless, one half of the *M. relicta* were in the hypolimnion at temperatures of less than 7.7°C.

In Lake 442, *M. relicta* were concentrated into a 5 m wide band below 5.1 m (Fig. 1.8b). Less than 15% occupied water warmer than 11°C (0–6.1 m), and two-thirds occurred at temperatures below 8.5°C (≥7.2 m). The majority of these were concentrated into a 2 m thick layer above 9.2 m where dissolved oxygen was greater than 4.9 mg L^{-1} (Fig. 1.8b).

In Lake 468, *M. relicta* occurred over a wide range of depths in the hypolimnion and lower metalimnion (Fig. 1.8c). Maximum density (20 m^{-3}) was between 12.4°C and 6.0°C (8.2–18.4 m), accounting for three-quarters of the *M. relicta* in the water column. Furthermore, approximately two-thirds were at temperatures of 8°C or less (>10.2 m).

Early Spring Distribution and Temperature

Under isothermal conditions (≅4°C) following ice-out in 1994 (April 24), *M. relicta* were widely distributed on the lake sediments from profundal to shallow littoral regions in Lakes 239, 442, and 468. They were consistently present in less than 2 m of water in each lake, and on one occasion in Lake 239 in less than 0.5 m of water. They persisted at shallow depths, until the third week of May in Lake 239 and the last week of May in Lake 442 and 468 when they moved to deeper water following the 12.5°C littoral isotherm in Lake 239, 14°C in Lake 442, and 15°C in Lake 468.

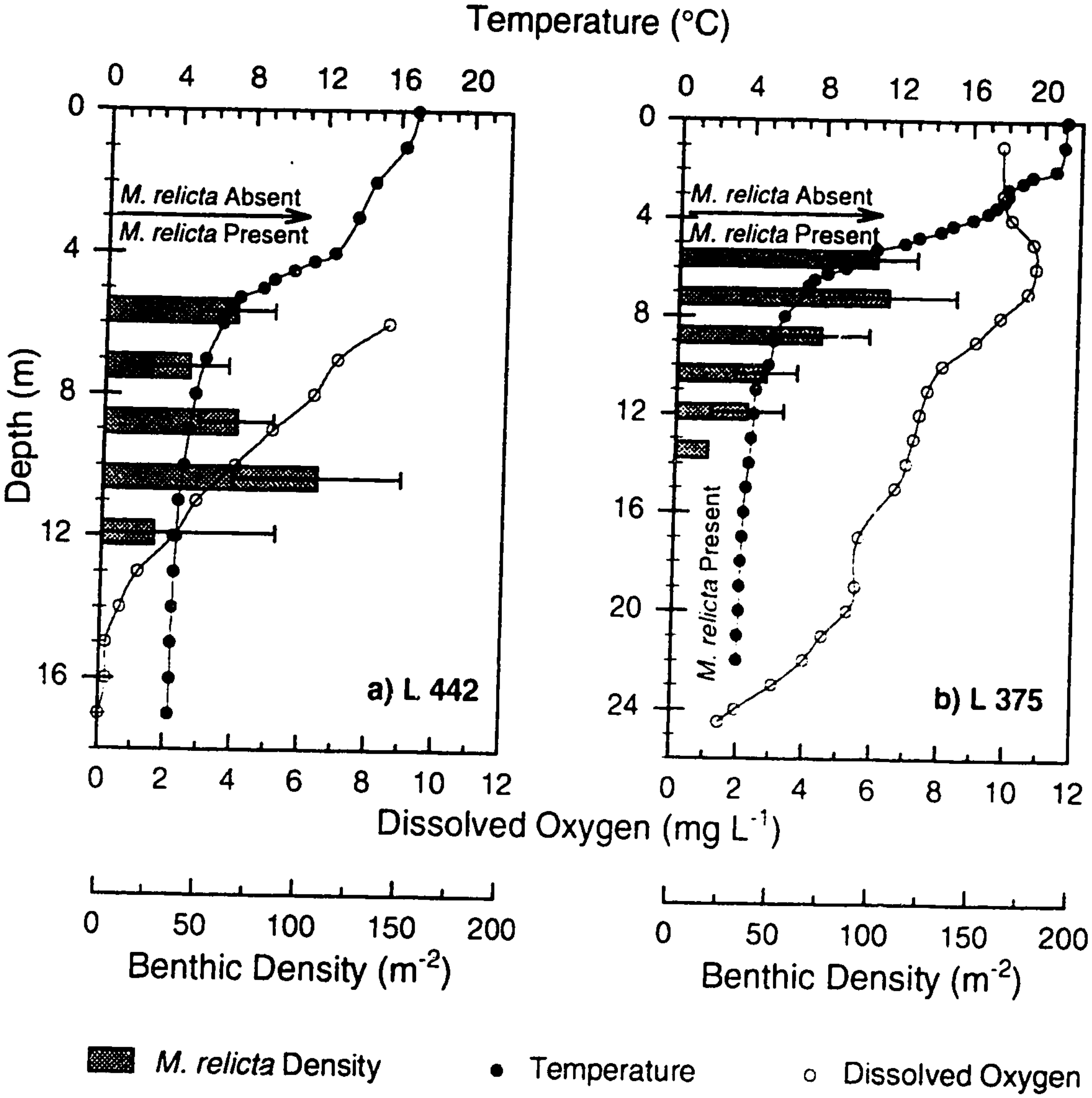

Figure 1.7 Mean density of *M. relicta* on lake sediments during the day in a) Lake 442 during the period June 1-8, 1993 and b) Lake 375 during the period June 11-21, 1993, along with corresponding profiles of temperature and dissolved oxygen. Error bars represent 95% confidence intervals about the means.

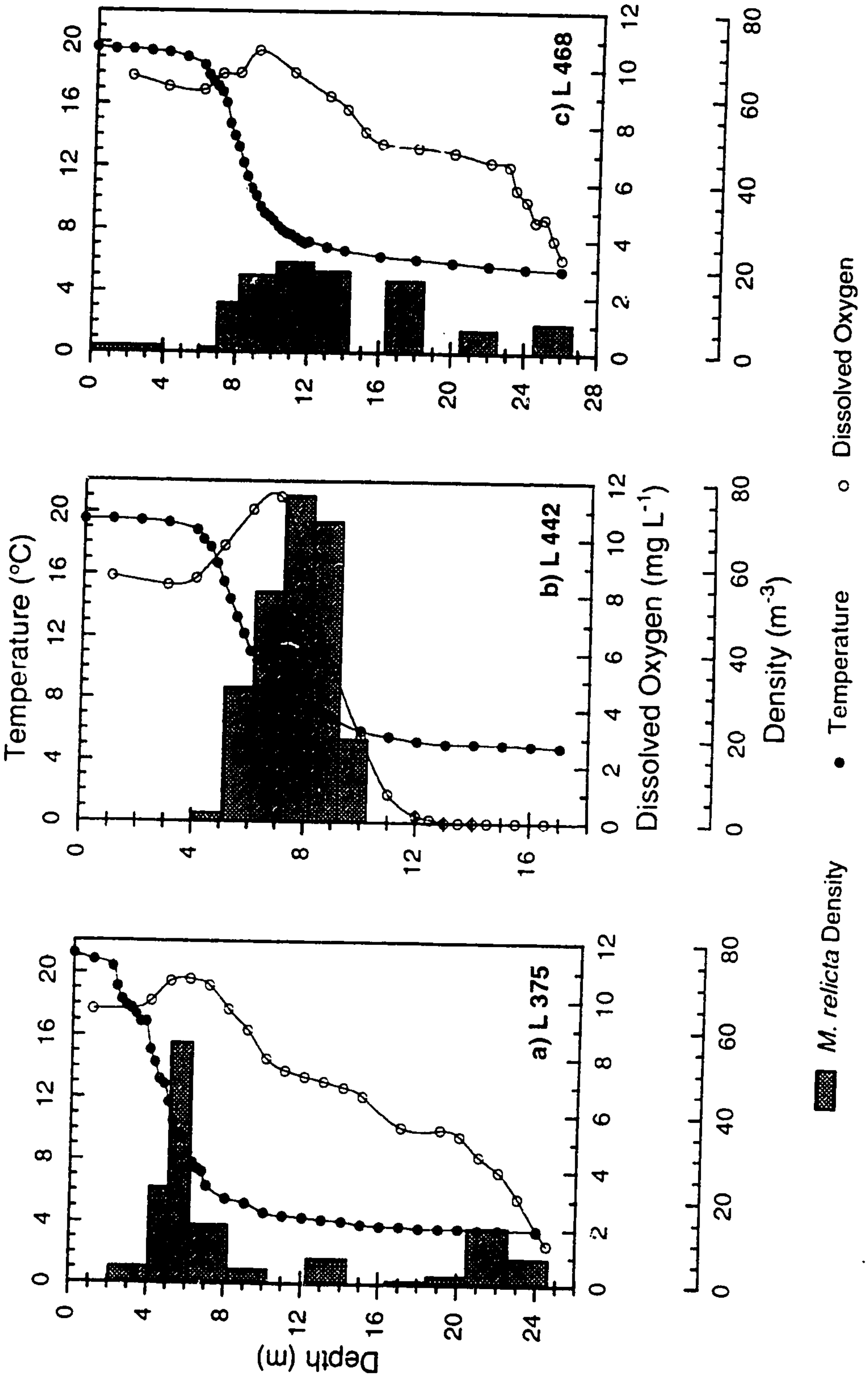

Figure 1.8 Vertical distribution of *M. relicta*, temperature and dissolved oxygen in a) Lake 375 on night of June 22, 1993 at a 26 m deep station, b) Lake 442 on night of August 10, 1993 at a 11.5 m deep station, and c) Lake 468 on night of July 28, 1993 at a 26.7 m deep station.

Mysis relicta Distribution and Light

M. relicta inhabited well-illuminated depths during the daytime in most lakes (Table 1.4). Maximum illumination inhabited ranged from approximately 8 μE m^{-2} s^{-1} in Lake 239 to over 168 μE m^{-2} s^{-1} in Lake 375. Within each lake, maximum illumination inhabited varied between survey times, likely as a result of differences in incident intensity at the time of survey (Appendix 3). They inhabited similarly shallow depths on cloudy and sunny days regardless of incident light intensity at the time of the survey. In lakes that were surveyed repeatedly throughout the summer (L 375, L 442, L 468) *M. relicta* were consistently present at high illumination throughout the summer.

M. relicta inhabited even more brightly illuminated depths in the early spring. In littoral areas, they were exposed to a wide range of illumination that reached over 500 μE m^{-2} s^{-1} on occasions (Table 1.4). Raw data for each survey is included in Appendix 3.

Estimates of UV-B extinction depths (1% level) ranged from 37–185 cm in the study lakes (Table 1.5). The shallowest occurrence of *M. relicta* was deeper than the 1% UV-B depth in all cases except on May 3, 1994 in L 239. On this survey, *M. relicta* were present as shallow as the 1% UV-B depth.

Volume of Habitat for *Mysis relicta*

The relative volume of each lake with preferred temperature and DO conditions (≤11 °C to 2.2 mg L^{-1} DO) ranged from less than 25% in Lake 442 to nearly 60% in Lake 375 (Fig. 1.9). Although there was substantial DO depletion in Lake 442, the relative volume of hypoxic water did not change appreciably through July and August. Oxygenated habitat for *M. relicta* in Lake 442 was probably maintained by metalimnetic photosynthesis during the daytime (e.g., Fig. 1.8b). In each lake, volume of suitable habitat declined during the summer largely as a result of progressive deepening of thermoclines (Fig. 1.9).

Table 1.4 Estimates of maximum light irradiance and illuminance inhabited by *M. relicta* in eight lakes at the ELA during summer, 1993 and spring, 1994. Data are presented as ranges of lowest to highest estimates from the numerous survey dates in each lake. Maximum light inhabited was estimated as average irradiance per second from ten minute accumulations of irradiance at the ELA meteorological station (E. Schindler, DFO, Winnipeg, unpubl. data) multiplied by percent light transmission at the minimum depth inhabited by *M. relicta*. Values for Lake 228 were estimated using the light transmission profile for Lake 224 because light transmission was not measured on Lake 228. The speculative nature of the derived values for Lake 228 is indicated by question marks. Conversion of irradiance to illuminance units was based on 1 $\mu E\ m^{-2}S^{-1} \equiv 51.2$ lux (Wetzel and Likens 1991).

	Lake	Number of surveys	Ambient light at upper distribution limit of *M. relicta* at time of survey $\mu E\ m^{-2}s^{-1}$	(lux)
Summer 1993	224	2	102–121	(5226–6209)
	228	2	$50^{?}$–$59^{?}$	($2545^{?}$–$3015^{?}$)
	239	4	3–8	(142–414)
	305	2	9–24	(450–1231)
	373	1	70	(3591)
	375	6	64–168	(3256–8588)
	442	6	28–123	(1421–6311)
	468	4	47–90	(2412–4610)
Spring 1994	239	10	13–208	(657–10672)
	442	5	17–576	(878–29483)
	468	7	210–541	(10740–27679)

Table 1.5 Estimates of potential penetration of UV-B light in Lakes 224, 228, 239, 305, 373, 375, 442 and 468. Penetration depths are maximum estimates of location of 1% of surface UV-B irradiance, based on available, historical DOC data. DOC values used were: a) L 224, L 239 — lowest annual average during the period 1971–1991 (ELA, unpubl. data); b) L 228 — single value from August 28, 1986 (ELA, unpubl. data); c) L 305 — lowest DOC measurement during period 1984–1991 (ELA, unpubl. data); d) L 375, L 468 — lowest DOC measurement during period 1987–1991 (ELA, unpubl. data); and e) L 373, L 442 — lowest DOC during summer of 1993 (P. Campbell, DFO, Winnipeg, unpubl. data).

Lake	Estimated 1% UV-B Penetration Depth (m)
224	1.85
228	0.98
239	0.49
305	1.25
373	0.91
375	0.65
442	0.37
468	0.71

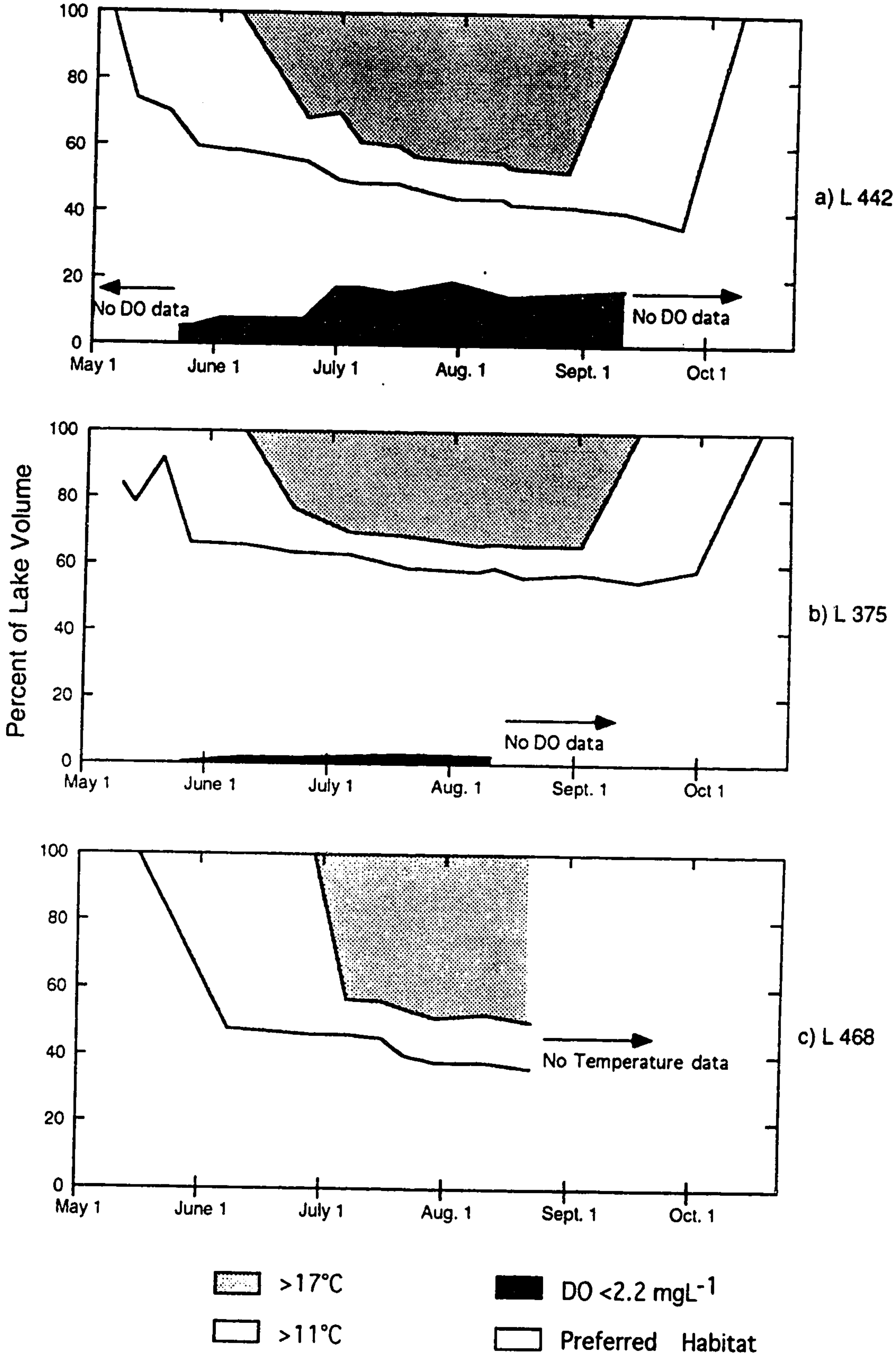

Figure 1.9 Percentage of lake volume providing habitat for *M. relicta* during summer 1993 in a) Lake 442, b) Lake 375, and c) Lake 468.

1.4 Discussion

Mysis relicta Distribution and Temperature

M. relicta were not restricted to the narrow temperature range (<10°–11°C) suggested by earlier studies (Smith 1970; Grossnickle and Morgan 1979; Janssen and Brandt 1980; Sherman et al. 1987; Lehman et al. 1990). Because *M. relicta* were not obligate cold-water inhabitants during the summer stratified period in small Canadian Shield lakes, I conclude that stenothermal restriction is not a general case for *M. relicta* in all lakes. Indeed, at least for small lakes, use of water as warm as 17°C may be a more general case (Larkin 1948; Nero 1981; Nero and Schindler 1983; Nero and Sprules 1986).

Although I did not quantify the duration of warm water exposure or identify the physiological tolerance limits of *M. relicta* to high temperature, my findings indicate that they can tolerate extended exposure to a relatively wide range of temperatures (up to 17°C), in contrast to the colder limits of 10°C (Smith 1970) and 13°C (DeGraeve and Reynolds 1975) established in laboratory temperature-tolerance bioassays. Consistent presence and persistence of *M. relicta* at 17°C in several lakes (day and night) and presence at >19°C in two lakes at night also shows that tolerance limits were greater than the 16°C boundary to short term (minutes) survival reported earlier (DeGraeve and Reynolds 1975). Although it is possible that they make excursions of relatively short duration into these warm waters during the day, they did not migrate into or out of these regions during the period of SCUBA observations (up to approximately 1 hour, T. Sellers pers. obs.). This suggests that use of warm water habitat is persistent, rather than a brief excursion into unfavorable environmental conditions.

Despite the persistent use of warmwater habitat, overall distribution of *M. relicta* indicates a preference for cold temperatures. As shallow water warmed during the spring, *M. relicta* moved to deeper regions following temperatures similar to their summer maximum temperature limits in each lake. During the summer, they made limited use of warm water habitat and most occupied much colder temperatures (<11°C) during both day and night. It is possible that use of warm water is dependent on ready access to a cold-water refugium for some part of the day. This could help explain warm water residence in small lakes at the ELA, yet absence from inshore areas of the Great Lakes (Smith 1970; Grossnickle and Morgan 1979; Janssen and Brandt 1980;

Bowers 1988). In the former case, access to cold water would involve a migration of a few metres, whereas in the latter case, cold-water access would require a much more extensive migration.

Differences in thermal habitat preference could possibly reflect real differences in *M. relicta* between ELA and the Great Lakes. Genetic analysis of North American populations, (including *M. relicta* from L 468) indicates descent from at least two differentiated refugial stocks (Väinölä et al. 1994). *M. relicta* from ELA belong to a northwestern group that arose from a Mississippian or Missourian refugium. They are remnant from glacial Lake Agassiz 8–11.7 thousand years ago (Väinölä et al. 1994). In contrast, Great Lakes *M. relicta* are of Atlantic refugial origin, although some intermixing with the northwestern group may have occurred in the upper Great Lakes (Väinölä et al. 1994).

Similar temperature distributions in the three focal lakes, despite different relative availability of cold water, also suggest a strong preference for cold temperatures. This was particularly evident in Lake 442 (Fig. 1.8) where access to cold water was limited by low dissolved oxygen in the hypolimnion. Despite this, *M. relicta* were not generally distributed into warmer water, but rather, they concentrated into a narrow band of cold water that contained dissolved oxygen at low concentrations shown to restrict metabolic rate (Sandeman and Lasenby 1980). This suggests that *M. relicta* have a strong requirement for these temperatures and will endure less than optimal oxygen conditions in order to occupy them.

Temperature preference alone, however, cannot explain adequately the distribution of *M. relicta* in the study lakes. Differences in temperatures inhabited during the day (e.g., cold distribution in Lake 228 and Lake 239, Figs 1.3 and 1.6) and day vs. night differences within each lake, suggest that distribution of *M. relicta* was influenced strongly by other aspects of habitat particular to each lake, such as prey location and relative risk of predation (Janssen and Brandt 1980). Distribution at night was generally consistent with previous studies indicating that *M. relicta* aggregate to feed on phytoplankton and zooplankton concentrated near the thermocline when light levels and risk from pelagic, visual predators are low (Beeton 1960; Lasenby and Langford 1973; Bowers and Grossnickle 1978; Rybock 1978; Janssen and Brandt 1980).

During the day, *M. relicta* occupy a trophic niche distinct from that at night. They feed actively on epibenthic fauna, such as *Diporeia hoyi*, and detritus while resident on the lake sediments during the day (Lasenby and Langford 1973; Bowers and Grossnickle 1978; Grossnickle 1979; Parker 1980; Grossnickle 1982). However, this represents a relatively minor component of their daily ration (Grossnickle 1979). Descent at daylight to benthic habitat is likely a strategy to minimize risk of predation from pelagic, visual predators (Janssen and Brandt 1980), although at the expense of increased risk from bottom-feeding fish, such as slimy sculpin (Wojcik et al. 1986).

Colder distribution of *M. relicta* during the day in Lake 228 and Lake 239 was more similar to that expected from previous studies in the Great Lakes. This could possibly reflect differences in distribution of prey within the daytime habitat, or population specific variation in temperature preference. However, I speculate that it is more likely that these colder distributions are a response to differential risks of predation in the study lakes. Indeed, Lake 228 and Lake 239 are the only two lakes that contain cisco, *Coregonus artedii*, which is a major predator on *M. relicta* (Scott and Crossman 1973; Trippel and Beamish 1989; 1993), and in these lakes, *M. relicta* aggregated only at temperatures colder than the lower preferred temperature of cisco (9.7° C, Aku et al. 1995).

Effects of Low Oxygen

The distribution of *M. relicta* in Lake 442 was strongly restricted by low oxygen concentrations in the hypolimnion. Avoidance of hypoxic water has been documented previously, both in experimental avoidance chambers (Sherman et al. 1987) and in lakes (Lasenby 1971; Nero 1981; Sherman et al. 1987). Reported lower avoidance limits for dissolved oxygen range between 1 and 5.7 mg L^{-1} (Table 1.6). My findings showed persistent fidelity to 2.2 mg L^{-1} as the lower limit to *M. relicta* habitat.

Table 1.6 Minimum Dissolved Oxygen Concentration Inhabited by *M. relicta* in six field studies

[DO] mg L^{-1}	**Location**	**Study**
>1.0	Crystal Lake, Ontario	Sherman et al. (1987)
1–2	Stony Lake, Ontario	Lasenby (1971)
0.3–10.2	L 223, ELA, Ontario	Nero and Davies (1982)
<1.4	Green Lake, Wisconsin	Birge and Juday (1927) in Larkin (1948)
5.7		Thienemann (1926) in Larkin (1948)
2.2	L 442, ELA, Ontario	This study

This limit corresponds closely to the 96 hour LC_{50} of 2 mg L^{-1} reported by Brownell (1970). *M. relicta* may survive exposure to as little as 1.0 mg L^{-1} for short periods in bioassays (Sherman et al. 1987). On this basis, brief forays into water with < 2.2 mg L^{-1} might be possible. Because dissolved oxygen decreases rapidly within the first few millimetres in lake sediments (Wetzel 1983; Sweerts et al. 1989), *M. relicta* may have entered, at least briefly, very low dissolved oxygen during the sediment-burrowing escape response noted previously. Nevertheless, I did not observe any *M. relicta* below the 2.2 mg L^{-1} isopleth during either the day or night.

Although I was unable to directly observe the maximum depths inhabited by *M. relicta* in Lake 375 and Lake 468, based on a minimum dissolved oxygen limit of 2.2 mg L^{-1}, they would be restricted from the bottom 3 m of Lake 375 throughout most of the summer, but distributed right to the bottom in Lake 468.

M. relicta are less resistant to low dissolved oxygen at temperatures warmer than 5°C (Sandeman and Lasenby 1980). In small lakes that are subject to increased seasonal warming and deepening of thermoclines from long term climatic warming (Schindler et al. 1990), such as Lake 442, it is conceivable that the deleterious effects of low oxygen exposure could be intensified if warm water and low oxygen coincided. Also, deepening of thermoclines and increased depletion of dissolved oxygen would reduce the volume of habitat suitable for *M. relicta* in these lakes, possibly leading to their extirpation. This could help to explain the absence of *M. relicta* from other small lakes, such as Lake 240 (T. Sellers, unpubl. data) and Lake 626, despite potential inoculation populations in upstream lakes.

Effects of Light

M. relicta did not avoid bright light, in contrast to previous studies that implicated light as the major proximate factor that determines their daytime distribution (Beeton 1960; Teraguchi et al. 1975). In my study, *M. relicta* inhabited light intensities that were orders of magnitude greater than those considered to restrict them to deep water during the day in the Great Lakes (Beeton 1960; Bowers 1988). Light levels (PAR) were 3–12 times greater than that reported to cause mortality of *M. relicta* in light exposure experiments (Smith 1970). My findings support previous reports of *M. relicta* at greater than 2000 lux (approximately 39 $\mu E\ m^{-2}s^{-1}$) in Lake 224 and Lake 305 (Nero and Schindler 1983) and in surface waters of Great Slave Lake (Larkin 1948) and Lac la Ronge (Mundie 1959). My findings suggest that well illuminated waters are consistently inhabited during the day in most of the study lakes throughout the summer.

Illumination in *M. relicta* habitat during the summer was similar to levels that depress eye sensitivity severely for up to several days in *M. relicta* from humic Lake Päärjärvi, Finland (Linström and Nilsson 1988). Exposure to light in the ELA lakes during early spring was an order of magnitude more extreme. *M. relicta* from more transparent waters, however, are less affected by exposure to bright light and recover visual sensitivity faster (Linström and Nilsson 1988). Indeed, Cooper and Goldman (1982) found that *M. relicta* from Lake Tahoe feed as efficiently in bright light (150 $\mu Em^{-2}s^{-1}$) as they do in the dark, suggesting that light tolerance of some populations is much greater than indicated by Linström and Nilsson (1988). Although the visual tolerance of *M. relicta* in the ELA study lakes is not known, I suggest that it must be relatively high because they would be unlikely to inhabit areas that rendered them blind and they avoided SCUBA divers in these shallow, well illuminated regions.

In contrast to most of the ELA lakes, *M. relicta* in Lake 239 inhabited darker depths during the summer. It is not known whether this represents a different tolerance or adaptation to the photic environment of this lake, such as described in Scandinavian *M. relicta* populations (Linström and Nilsson 1988). Given that L 239 *M. relicta* inhabit well illuminated waters in the spring, it is possible that their deeper, darker residence is an artefact of temperature preference, or a strategy to minimize predation by zooplanktivorous fish (Janssen and Brandt 1980).

Although *M. relicta* can detect and respond to very low levels of visible light (Beeton 1959; Teraguchi et al. 1975; Linström and Nilsson 1988), it is not known whether they have similar abilities within the UV range. Exposure to the most biologically active range of UV light (< 320 nm) was likely limited, despite relatively shallow residence of *M. relicta* in the small lakes at the ELA. Inhabited depths were greater than the historical maximum 1% UV-B depths, even during ultra-shallow daytime residence in the spring. I speculate that UV penetration may not be currently a significant factor affecting *M. relicta*. However, UV-B penetration depth has increased 30–55% in small lakes at the ELA because of decreased DOC resulting from climate warming and drought in the 1970s and 1980s (Schindler et al. unpubl. data). UV-B penetration depths of several metres are expected in very transparent lakes, such as L 224, if DOC declines further (Scully and Lean 1994; Schindler et al. unpubl. data). This suggests the future possibility of UV photodamage impacts in transparent lakes, particularly if *M. relicta* does not have a behavioral avoidance mechanism to UV light.

Tolerance of *M. relicta* to UV-B is not known; however, impacts of UV-B are documented for other crustaceans, particularly for *Daphnia. spp.* Sensitivity of *Daphnia* is variable among the different species and clones, and is most acute at short wavelengths (Hessen 1994). Based on laboratory-determined tolerance, natural exposure of *Daphnia* to UV-B in transparent lakes is currently near tolerance thresholds in shallow water (Hessen 1994). Acutely lethal effects begin just below the surface in very transparent lakes; short-term (i.e., 2 day) exposure to natural levels of UV-B induces mortality down to at least 1.5 m (Zagarese et al. 1994). However, *Daphnia* can detect a broad range of UV including UV-A and respond with downward migration (Hessen 1994). It is not known whether they respond to UV-B wavelengths. Similarly, it is not known whether *M. relicta* can detect and avoid UV. If *M. relicta* lacks this ability, it is conceivable that it could receive harmful exposure to UV-B if lake transparency increases due to climate-driven DOC loss or lake acidification (Schindler et al. unpubl. data). This would be most likely to occur in lakes that are already low in DOC, such as Lake 224 (≅220 μM L^{-1}), because UV-B penetration increases exponentially as DOC declines below approximately 200 μM L^{-1} (Scully and Lean 1994; Schindler et al. unpubl. data). Exposure would be greatest during shallow residence in the spring (Nero 1981; this study).

My results indicate that *M. relicta* was not restricted (as hypothesized) to a region of the lakes that provided cold temperature and low light intensity. In contrast, low dissolved oxygen in the hypolimnion strongly restricts the amount of summer habitat. *M. relicta* commonly inhabited warm water in most of the lakes, although the extent of warm water use was limited. *M. relicta* inhabited deeper, colder water in two lakes, possibly as a response to risk of predation by cisco in these lakes. My results indicate that the breadth of *M. relicta* habitat is bounded by ≤ 17°C and ≥ 2.2 mg L^{-1} DO. Preferred habitat is confined to lake areas ≤ 11°C. At night, temperature and oxygen characteristics of pelagic habitat are generally similar to daytime benthic habitat.

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Chapter 2: The Distribution of Lake Trout in Small Boreal Lakes with Respect to Temperature, Dissolved Oxygen, and Light

2.1 Introduction

Recent evidence of climate-coupled lake warming indicates possible loss of habitat for cold-water fish in small Canadian Shield Lakes (Schindler et al. 1990; 1995). Lake trout, *Salvelinus namaycush*, is among the freshwater species most restricted by temperature to cold-water habitat and most likely to be at risk from lake warming (Magnuson et al. 1990). Preferred and physiologically optimum temperatures indicate a thermal niche of approximately 10°±2°C (O'Connor et al. 1981; Magnuson et al. 1990). Natural distribution is limited to lakes where substantial summer warming does not occur or where thermal stratification isolates substantial hypolimnetic volumes of cold-water habitat from summer warming. Lake trout yield is positively correlated to the amount of 10° ±2°C habitat in very large lakes (Christie and Regier 1988) and might increase in some of the Great Lakes if climate warming occurs (Magnuson et al. 1990). However, this forecast is based on a prediction of shallower, stronger thermoclines in the Great Lakes and does not include habitat restriction from dissolved oxygen (DO) depletion. The opposite may be true in small lakes subject to climatic warming where thermocline deepening occurs due to increased solar penetration from dissolved organic carbon (DOC) loss and increased wind exposure from deforestation (Schindler et al. 1990; 1995). In these lakes, suitable habitat will be restricted by warming (from above) and DO depletion (from below), possibly leading to extirpation of lake trout from some lakes (Schindler et al. 1990; 1995). Thermal autecology of lake trout in lakes with constricted optimal habitat is not well described. Although generally thought to be restricted strongly to cold water, isolated reports of lake trout in warm water (Martin 1952; Galligan 1962; Dahlberg 1981; Olson et al. 1988; Snucins and Gunn 1995) suggest broader tolerance and a wider range of habitat-use.

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

2.2 Methods

Study Sites

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, approximately 60 km east of Kenora, between 49°37' N and 49°47' N latitude and 93°35' W and 93°50' W longitude. These lakes are on the southwestern margin of the Canadian Shield and are typical of small lakes that support lake trout and *M. relicta.*

The three lakes included in this study were L 375, L 442, and L 468 (Roddy L.). They were selected based on the following criteria:

- Simple assemblages of fish species with lake trout as the only large-bodied fish thought to be pelagic during the summer.
- Steep-sided basins and small littoral zones. Because of this they could be surveyed effectively and completely with hydroacoustics.
- Different temperature, oxygen and light regimes

Limnological data for these lakes are summarized in Chapter 1, Table 1.1. Each lake contains lake trout and white sucker, and a variety of smaller fish species (Table 2.1).

Hydroacoustic Surveys of Vertical Distribution of Fish

Using hydroacoustic echosounding, I surveyed the depth distribution of pelagic fish in Lakes 375, 442, and 468 during the open-water seasons of 1992 and 1993 (Table 2.2). Surveys were conducted at approximately midday along regularly spaced transects in each lake (Figs. 2.1–2.3). Similar surveys were conducted at approximately midnight on one mid-summer date in Lake 375 and Lake 442, and on several nights in Lake 468 (Table 2.2).

Table 2.1 Fish species composition and approximate population size where known in Lake 375, Lake 442, and Lake 468 (K. Mills, DFO, Winnipeg, unpubl. data; T. Sellers, pers. obs.). Black circle indicates species is present, but population size is unknown.

	lake trout	white sucker	Lake whitefish	yellow perch	slimy sculpin	fathead minnow	pearl dace	finescale dace	n. redbelly dace	blacknose shiner	longnose dace	bluntnose minnow
L 375	~387[a]	<45[b]			●	●	●	●	●			
L 442	~364[c]	~500[d]			●	●	●	●				
L 468	>4000[e]	●	●	●			●	●		●	●	●

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[a] Mean of annual estimates calculated using Jolly-Seber multiple mark recapture model for annual fall surveys 1988–1994 (K. Mills, DFO, Winnipeg, unpubl. data).

[b] Although annual surveys have been conducted since 1988, there are too few white sucker > age 1 in Lake 375 to calculate Jolly-Seber multiple recapture estimates (K. Mills, DFO, Winnipeg, pers. comm.). Dr. Mills estimates that there are <45 white sucker > 220 mm (similar to sizes of lake trout) in Lake 375. This estimate is based on evidence of near-complete capture in the initial 1988 survey. In the 7 succeeding years, only about 7 fish per year were caught that were not marked in 1988. White sucker between 150 and 220 mm (age 1–3 years) were not caught in significant numbers from 1988–1993, which includes the period of my study. Juveniles were numerous and similar in size to fathead minnows (e.g., 50 mm) which are abundant in this lake (K. Mills, DFO Winnipeg, pers. comm.).

[c] Mean of annual estimates calculated using Jolly-Seber multiple mark recapture model for annual fall surveys 1990–1994 (K. Mills, DFO, Winnipeg, unpubl. data).

[d] Based on Petersen estimates of 468 and 550 for 1991 and 1992 respectively (K. Mills, DFO, Winnipeg, unpubl. data).

[e] Rough estimate based on extrapolation of Petersen mark recapture data for 1 of 4 known spawning sites in L 468, during fall surveys 1981–1983 (K. Mills, DFO, Winnipeg, unpubl. data). This is possibly an underestimate because very large lake trout have never been caught on any of the 4 known spawning beds. There are substantial numbers of large lake trout in L 468 (up to at least 100 cm total-length) suggesting that not all lake trout spawning locations are known (K. Mills pers. comm.; T. Sellers, pers. obs.).

Table 2.2. Dates of hydroacoustic survey of depth distribution of fish in Lakes 375, 442, and 468 during the day (d) and night (n).

1993	Lake 375	June 7 (d), June 15 (d), July 6 (d), July 19 (d/n), August 9 (d)
	Lake 442	June 7 (d), June 21 (d), July 19 (d/n), July 28 (d), August 9 (d)
	Lake 468	June 7 (d), July 7 (d/n), July 15 (d/n), July 18 (d/n), July 20 (d)
1992	Lake 375	July 6 (d), July 27 (d), July 28 (d), August 5 (d), August 6 (d)
	Lake 442	July 28 (d), August 11 (d), August 28 (d)

In 1992, I used a narrow beam echosounder (Biosonics 105, 420 kHz, 6° beam-width transducer) to survey fish distribution. Data were recorded on digital audio tape for later signal processing. In 1993, I used a wide-beam echosounder (Lowrance, 50 kHz, 45° transducer beam-width) to increase survey coverage, particularly at shallower depths. Fish depths were recorded as traces on a paper chart-recorder. In addition, I operated the two systems simultaneously during two surveys in 1992 to compare echo-returns from the systems.

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

For 1993 surveys, I 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 echoes represented fish detected at the periphery of the sonar cone and thus no vertical depth along the main axis of the sonar cone could be assigned unambiguously to them. Transducer depth was added to each echo.

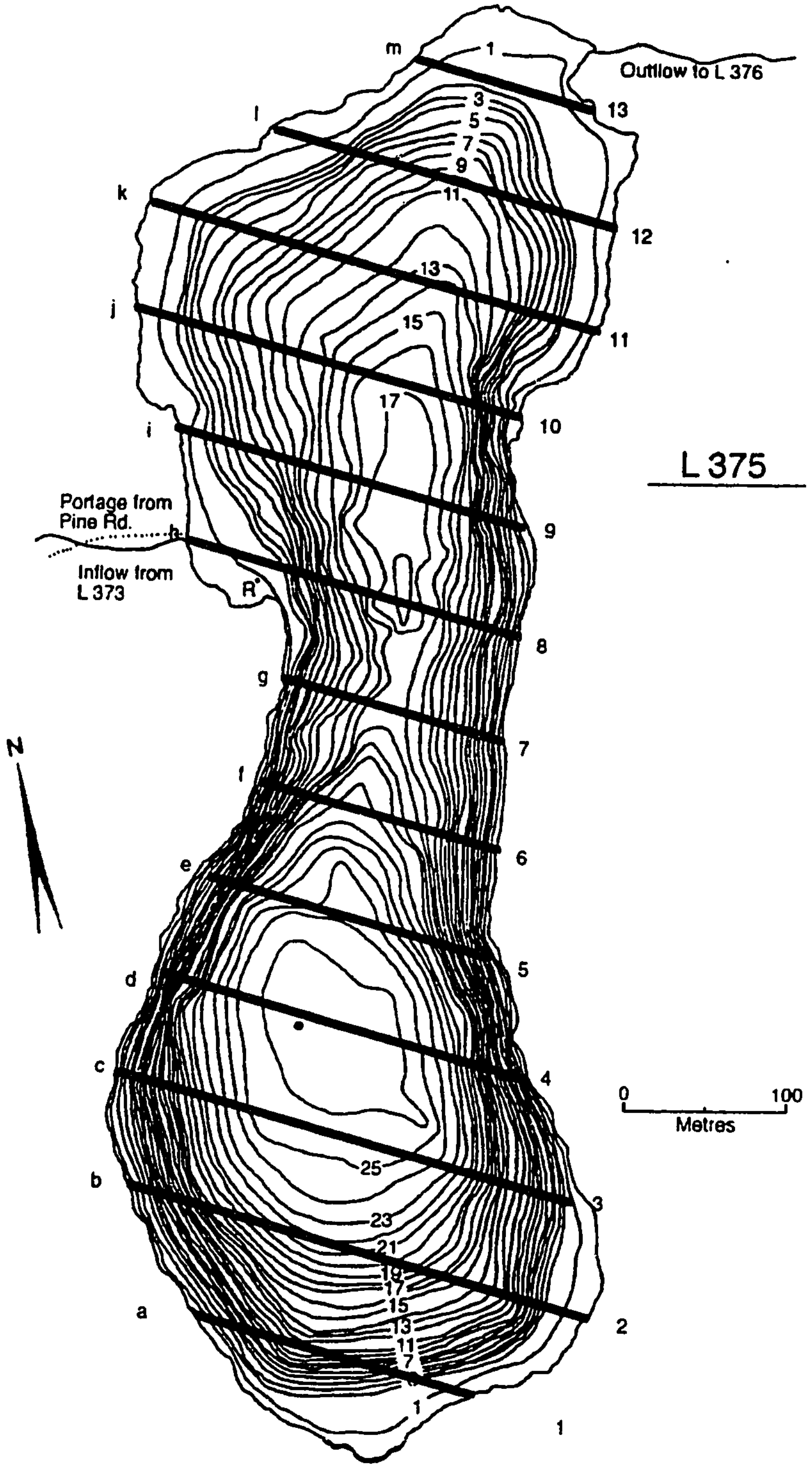

Figure 2.1 Bathymetric map of Lake 375, showing transects for hydroacoustic surveys of depth-distribution of pelagic fish (after ELA unpubl. data).

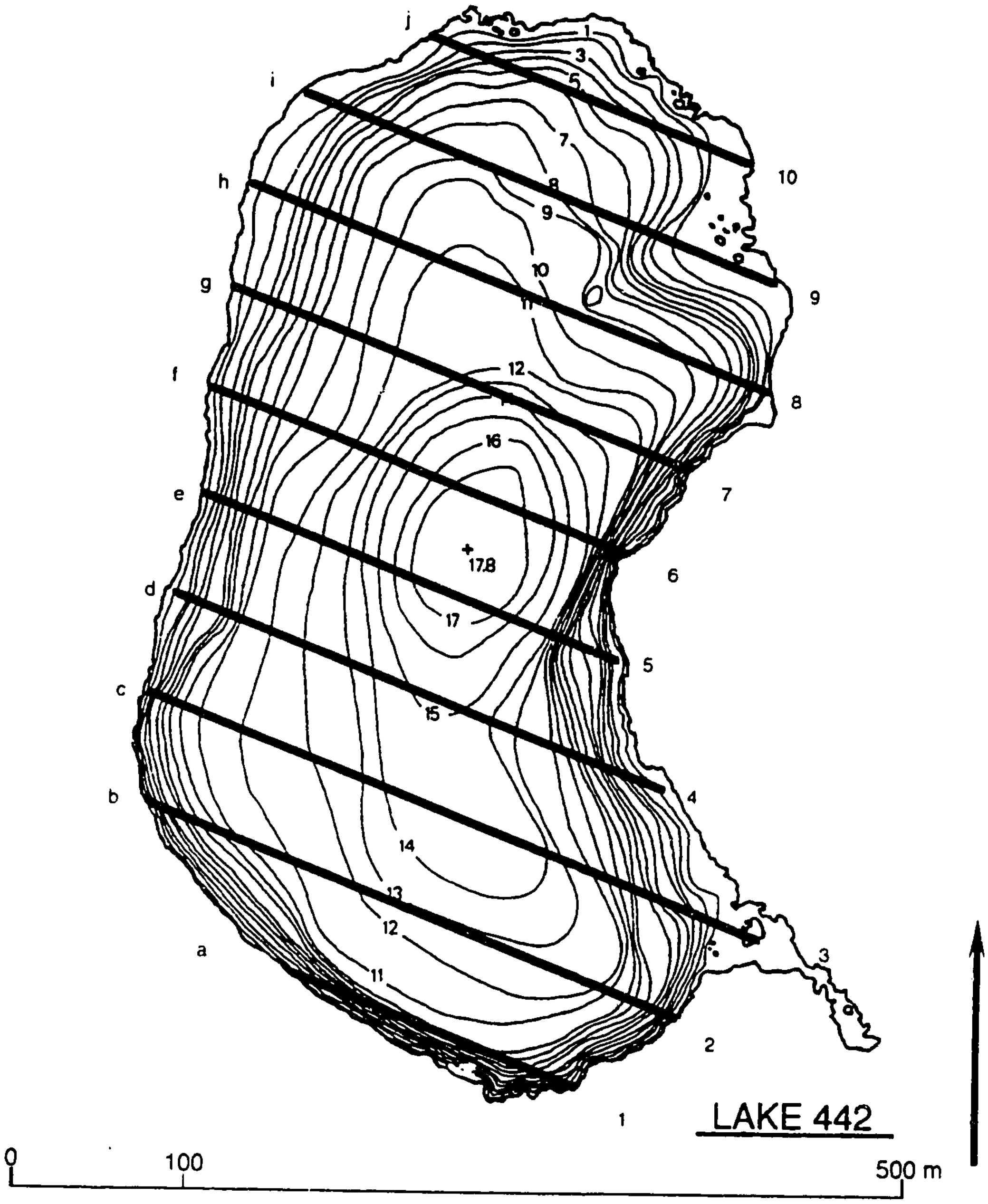

Figure 2.2 Bathymetric map of Lake 442, showing transects for hydroacoustic surveys of depth-distribution of pelagic fish (after McCullough and Campbell 1993).

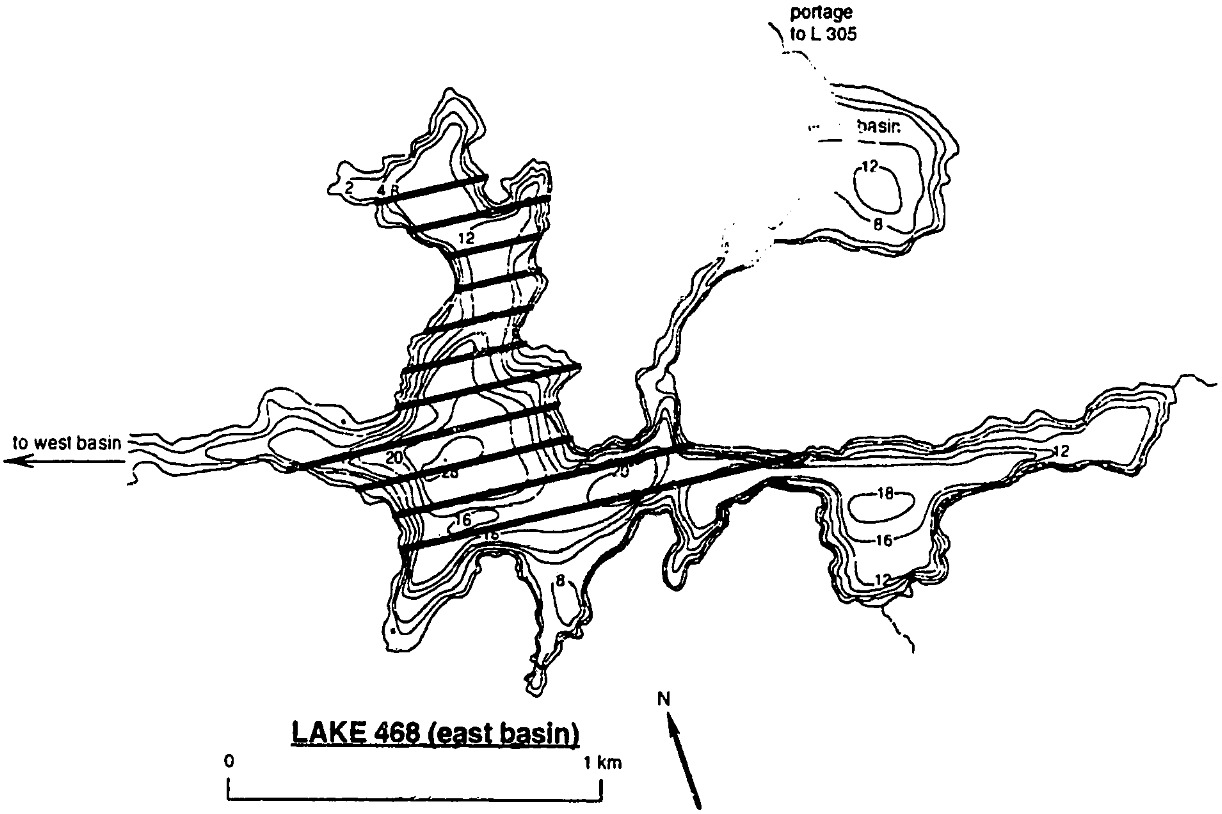

Figure 2.3 Bathymetric map of the east basin of Lake 468, showing transects for hydroacoustic surveys of depth-distribution of pelagic fish (after ELA unpubl. data).

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. I applied a correction to the depth distribution of echoes, based on the volume surveyed along each transect at 0.5 m depth increments. I 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. 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. I used these corrected fish depths for all subsequent analysis and interpretation.

Fish Collection

To corroborate the assumption that echoes were lake trout, I set gill nets in the pelagic zone of Lake 442 and Lake 468 during mid-summer 1993. Fish collection was not permitted by DFO in Lake 375 because it is a long-term reference lake for biomonitoring studies. However, annual fall surveys have been conducted since 1988 in Lake 375 that indicate that lake trout is the only large-bodied fish likely to be pelagic in significant numbers K. Mills, DFO, Winnipeg, unpubl. data). In Lake 442, 5 vertical gill nets (3 m wide x lake depth; mesh sizes = 25 mm, 38 mm, 51 mm, 76 mm, and 102 mm stretched mesh) were set in mid-basin continuously for a total of 42.5 hours (19.5 hours during day, 23 hours at night) between July 28 and 30. In Lake 468, these nets were set over the 18 m contour in mid-basin on July 8 (4.5 hours during day) and semi-continuously for a total of 56.5 hours (29.5 hours during day; 27 hours at night) between July 14 and 19. The nets were checked periodically and fish depths determined to nearest metre from their locations in the nets. Fish were removed from the nets, weighed, measured, and released if possible.

Two horizontal gill nets (multi-mesh 25 m long x 2 m depth, mesh sizes = 38 mm and 51 mm stretched mesh; multi-mesh 25 m long x 3 m depth, mesh sizes = 89 mm and 121 mm stretched mesh) were set along the shoreline in the epilimnion of Lakes 442 and 468 to assess use of shallow, nearshore areas by lake trout. In Lake 442, nets were set from the shore diagonally along the bottom to the 6 m contour for a total of 33.5 hours (11.5 hours day; 9.5 hours evening; 12.5 hours night). In Lake 468, these nets were set from the shore to the 7 m contour for a total of 31 hours (17 hours day; 14 hours night). Fish depths were estimated from location in the nets. All fish were weighed, measured, and released if possible.

Temperature, Dissolved Oxygen, and Light Measurements

I measured profiles of lake temperature, dissolved oxygen, and light with depth at the deepest point in each lake at approximately biweekly intervals throughout the open-water season of 1993 (detailed in Chapter 1 and Appendix 1). In 1992, temperature was measured concurrent with hydroacoustic surveys and DO profiles were obtained only once during August (Appendix 1). Briefly, temperatures were measured at 1 m depth intervals, except through the metalimnion where 0.25 m resolution was used. Dissolved oxygen was measured by Winkler titration at 1–2 m intervals, except in regions of very low or rapidly decreasing DO where 0.25 m resolution was used. Light was measured 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 nearest sampling dates. To each fish echo, I assigned mean temperature, dissolved oxygen and light values from the 0.5 m depth interval corresponding to the fish depth. These values were used to describe the distribution of fish with respect to these environmental variables, and to describe the temperature, DO and light characteristics of their habitat.

2.3 Results

Species Composition in Pelagic Zone

Catch rates were low in all vertical gill net sets. In Lake 442, only 13 lake trout were caught during the 42.5 hours of fishing (Fig 2.4a–b). Similarly, in Lake 468, only 17 lake trout were caught during the 61 hours of fishing (Fig. 2.4c–d). These catches represent a lake trout catch rate of approximately 0.3 $hour^{-1}$ (240 m^2 net area) in both lakes. Nevertheless, catches in vertical gill nets confirmed the presence of lake trout in the hydroacoustic surveys of Lake 442 and Lake 468. They also confirmed that lake trout inhabit epilimnetic waters as warm as 19–20°C during both day and night in these lakes (Fig. 2.4).

In Lake 442, both lake trout and white sucker were present at similar depths above the anoxic central basin of the lake (Fig. 2.4a-b). They were absent below 9 m during the day (Fig. 2.4a) and night (Fig. 2.4b). Because lake trout and white sucker were caught at a similar range of depths, I assumed that hydroacoustic echoes were representative of the distribution of either species. For the purposes of this paper, I interpreted echoes from hydroacoustic surveys in Lake 442 as lake trout, although I recognize that white sucker likely contributed to these echo distributions.

In Lake 468, both lake trout and lake whitefish were caught in the vertical gill nets (Fig. 2.4c-d). White sucker were not pelagic in this lake. Lake trout were caught at a wide variety of depths, from 3 m to 14 m, both day and night. It was the only species caught pelagically in the epilimnion. Broad depth distribution of fish in vertical gill nets differed markedly from hydroacoustic surveys that showed predominantly epilimnetic distributions (detailed below). Lake whitefish, caught in the metalimnion and hypolimnion (Fig. 2.4c–d) at some time during the net-set, were apparently underrepresented or not represented in hydroacoustic surveys. For these reasons, I assumed that hydroacoustic echo distributions were most representative of lake trout.

Fishing was not permitted by the Department of Fisheries and Oceans in Lake 375. Although Lake 375 contains both lake trout and white sucker, the sucker population is very small (approximately 45, Table 2.1) and unlikely to have contributed substantially to pelagic echoes. Because white sucker were very rare, I assumed that pelagic echoes in Lake 375 were representative of the lake trout.

Species Composition in Littoral Zone

During the 33.5 hours of gill-netting along the shoreline of Lake 442, 22 lake trout and 39 white sucker were caught. Lake trout were caught at depths between 3 m and 6 m; most were between 4 m and 5 m. White sucker were caught between 2 and 6 m; most were between 3 and 5 m. Although lake trout were caught in shallow waters during the day, most were caught during the evening and night (Table 2.3).

In Lake 468, white sucker dominated catches in gill nets set in the littoral zone (Table 2.3). The three lake trout caught were at between 2 m and 3 m.

Table 2.3 Composition of catches in gill nets set in littoral zone of Lake 442

Time of day	Catch	Total hours
day	3 lake trout 11 white sucker	11.5
evening	9 lake trout 9 white sucker	9.5
night	10 lake trout 19 white sucker	12.5

Table 2.4 Composition of catches in gill nets set in littoral zone of Lake 468

Time of day	Catch	Total hours
day	2 lake trout 1 lake whitefish 8 white sucker 8 yellow perch	17
night	1 lake trout 1 lake whitefish 11 white sucker 1 yellow perch	14

Depth Distribution

During the summers of 1992 and 1993, the hydroacoustic surveys indicated that fish were predominantly just below the thermocline, concentrated at the top of the hypolimnion and in the lower half of the metalimnion in Lake 375 and Lake 442 (Figs 2.5 – 2.8). In contrast, fish in Lake 468 remained predominantly in the epilimnion throughout the summer (Fig. 2.9). In all lakes, fish were either absent or at very low density throughout most deeper depths of the hypolimnion (Figs 2.5 – 2.9).

In early spring, fish in Lake 375 inhabited shallow depths (mean depth = 4.5 m) but moved to deeper water by the middle of June when the epilimnion warmed past 15°C (Fig. 2.6). For the duration of the summer, mean depth of fish did not change significantly (Scheffé test, $p > .05$) but remained between 8.3–9.6 m in 1992 and 8.8–10.9 m in 1993 (Figs. 2.5 and 2.6).

Fish in Lake 442 inhabited shallower depths than those in Lake 375 both in 1992 and 1993. They occupied a wide range of depths in early spring but were concentrated between approximately 4 m and 8 m for the duration of the summer (Figs 2.7 and 2.8). Mean depths of fish in Lake 442 ranged from 5.1 m to 6.8 m in 1992 and 5.3 to 7.3 m in 1993 but did not change significantly over the course of the summer.

In contrast, fish in Lake 468 did not move out of the epilimnion as the summer progressed but remained at mean depths of 2.6–3.2 m throughout July (Fig. 2.9). Use of shallow water was not transitory, but rather, persisted throughout the day and into the night (Fig 2.10)

Nighttime use of shallow water habitat was common to all three lakes. In Lake 375 and Lake 442 the majority of fish ascended into the epilimnion at night even during mid-summer (Figure 2.11).

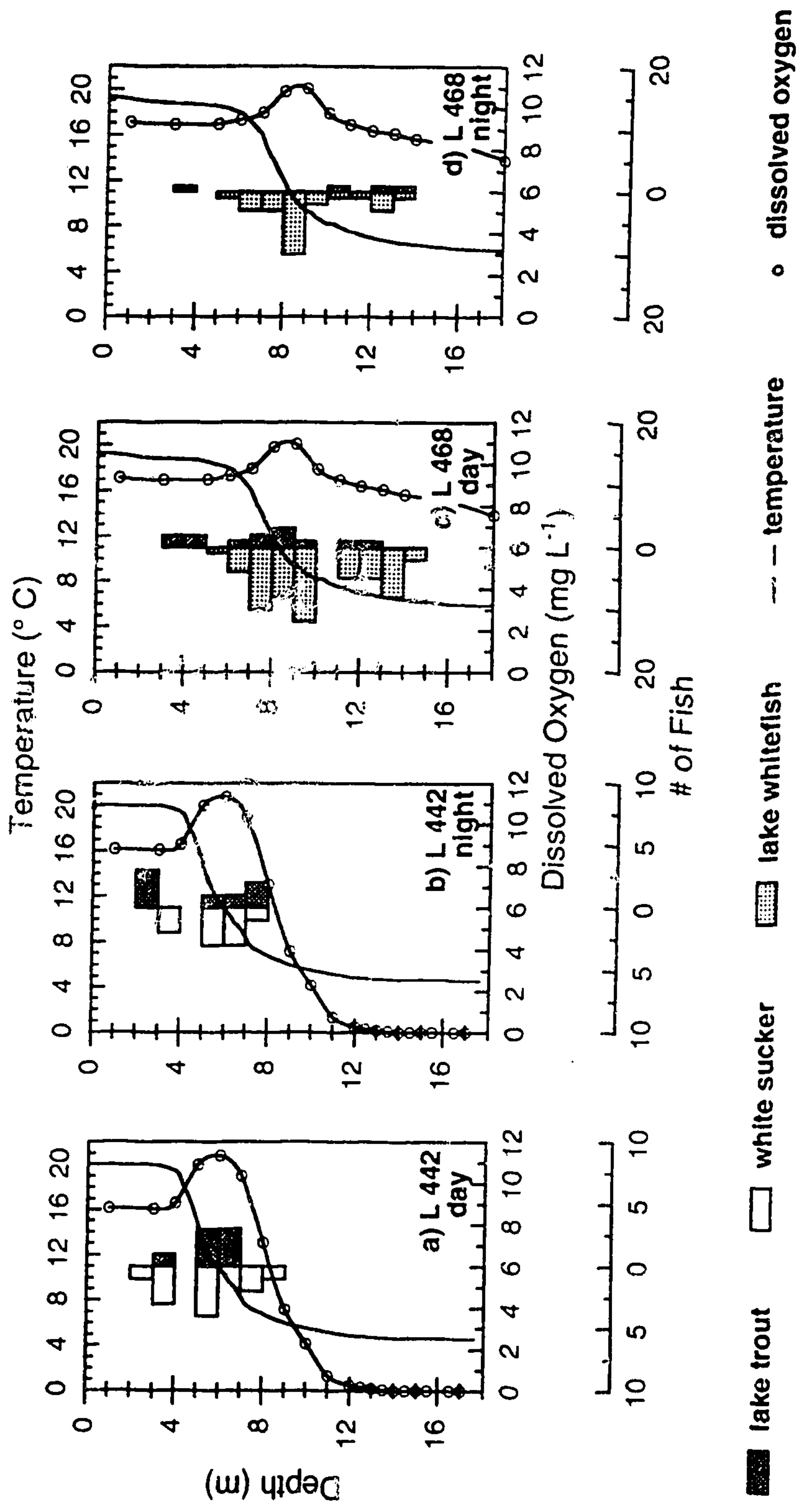

Figure 2.4 Fish catch in vertical gill nets during: a) day in Lake 442, b) night in Lake 442, c) day in Lake 468, and d) night in Lake 468. Fishing was not conducted in Lake 375 due to restrictions by the Department of Fisheries and Oceans.

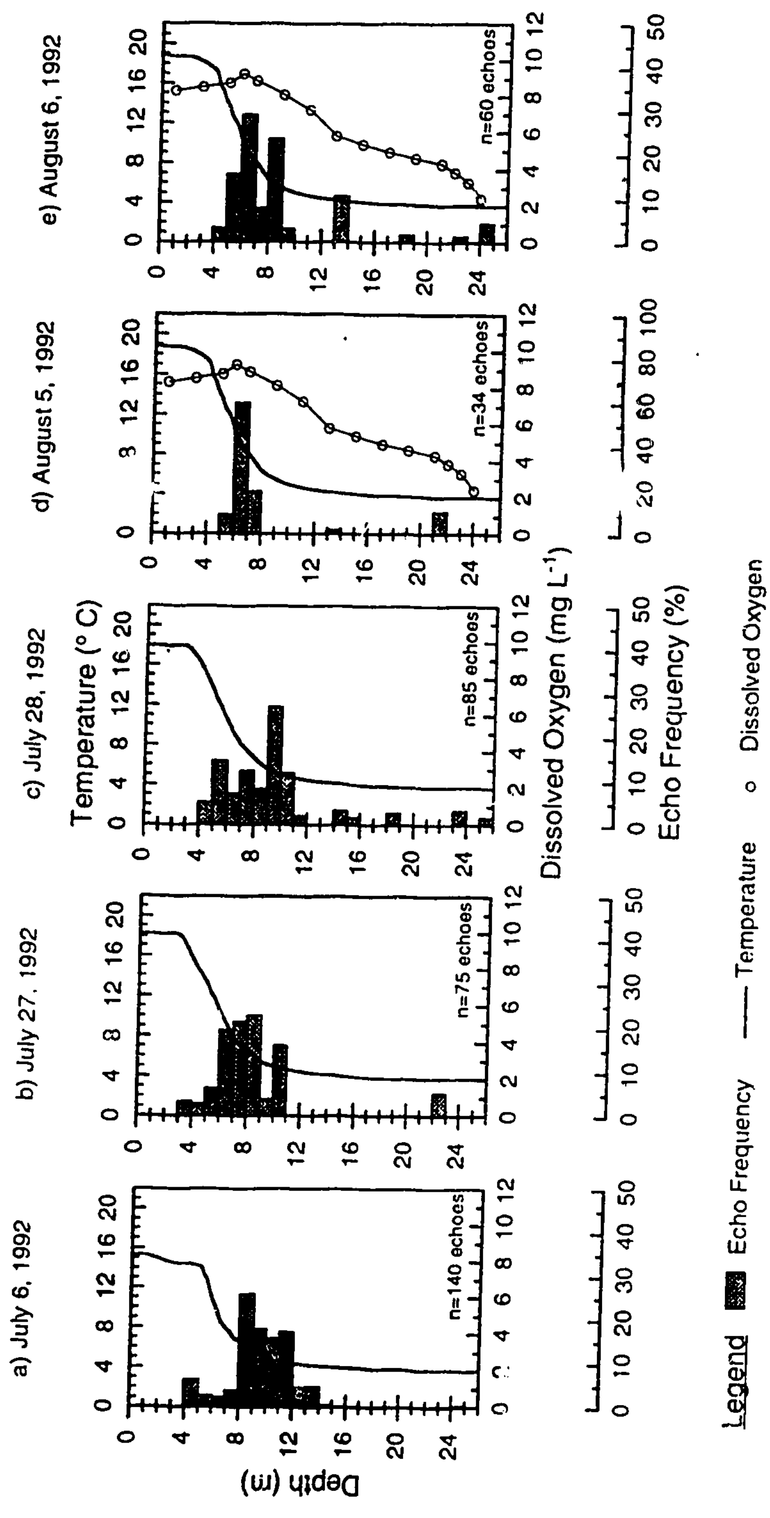

Figure 2.5 Vertical distribution of fish echoes in Lake 375 during July and August, 1992, with corresponding profiles for temperature and dissolved oxygen. Temperatures on July 28 were interpolated from July 27 and July 30; temperatures on August 6 were interpolated from August 5 and August 10. Dissolved oxygen profile was for August 14.

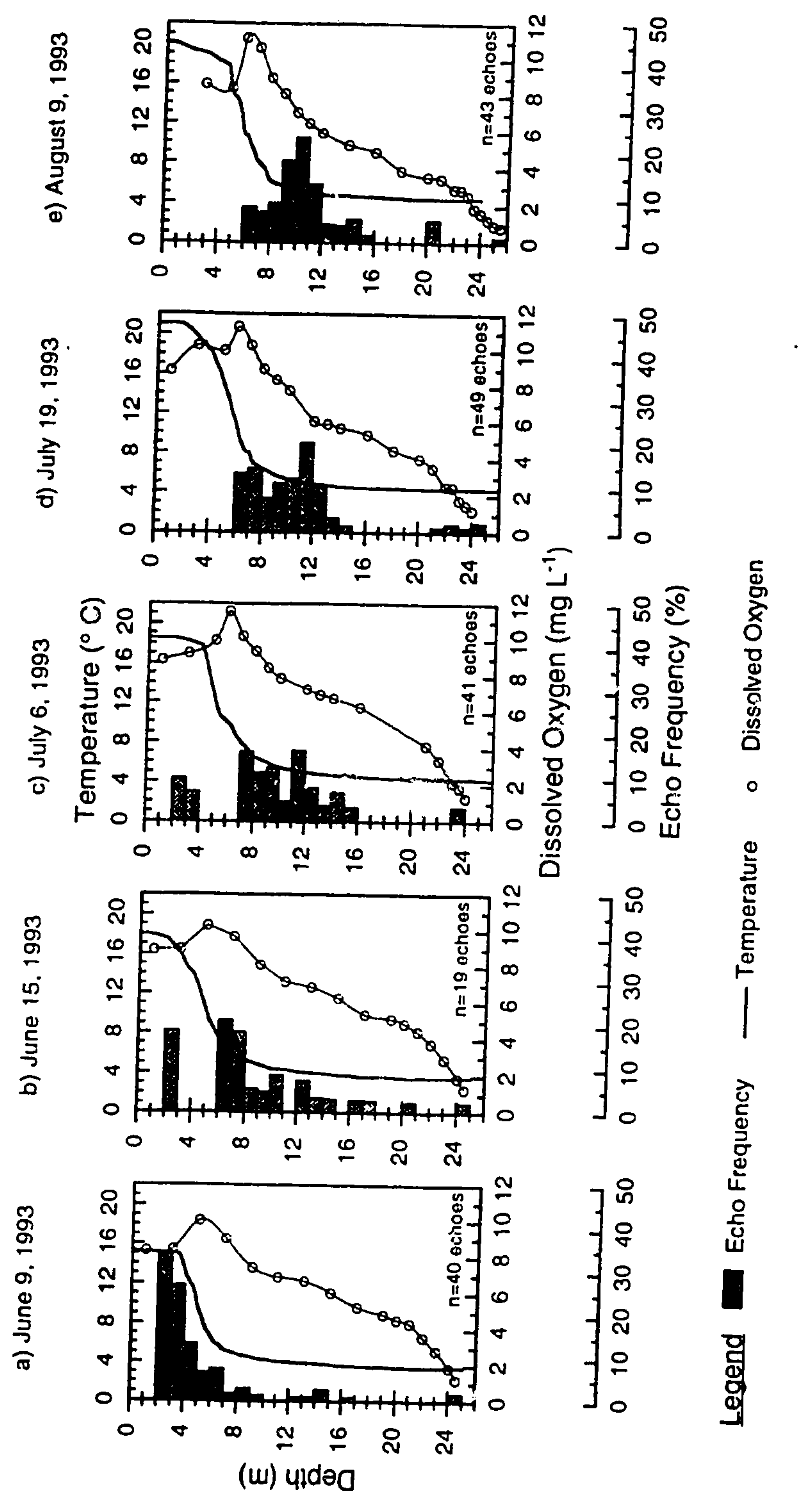

Figure 2.6 Vertical distribution of fish echoes in Lake 375 between June and August, 1993, with corresponding profiles for temperature and dissolved oxygen. Temperature on July 6 was interpolated from July 5 and July 19. Dissolved oxygen on June 15 was interpolated from June 9 and June 22. Dissolved oxygen on July 6 was interpolated from July 5 and July 19.

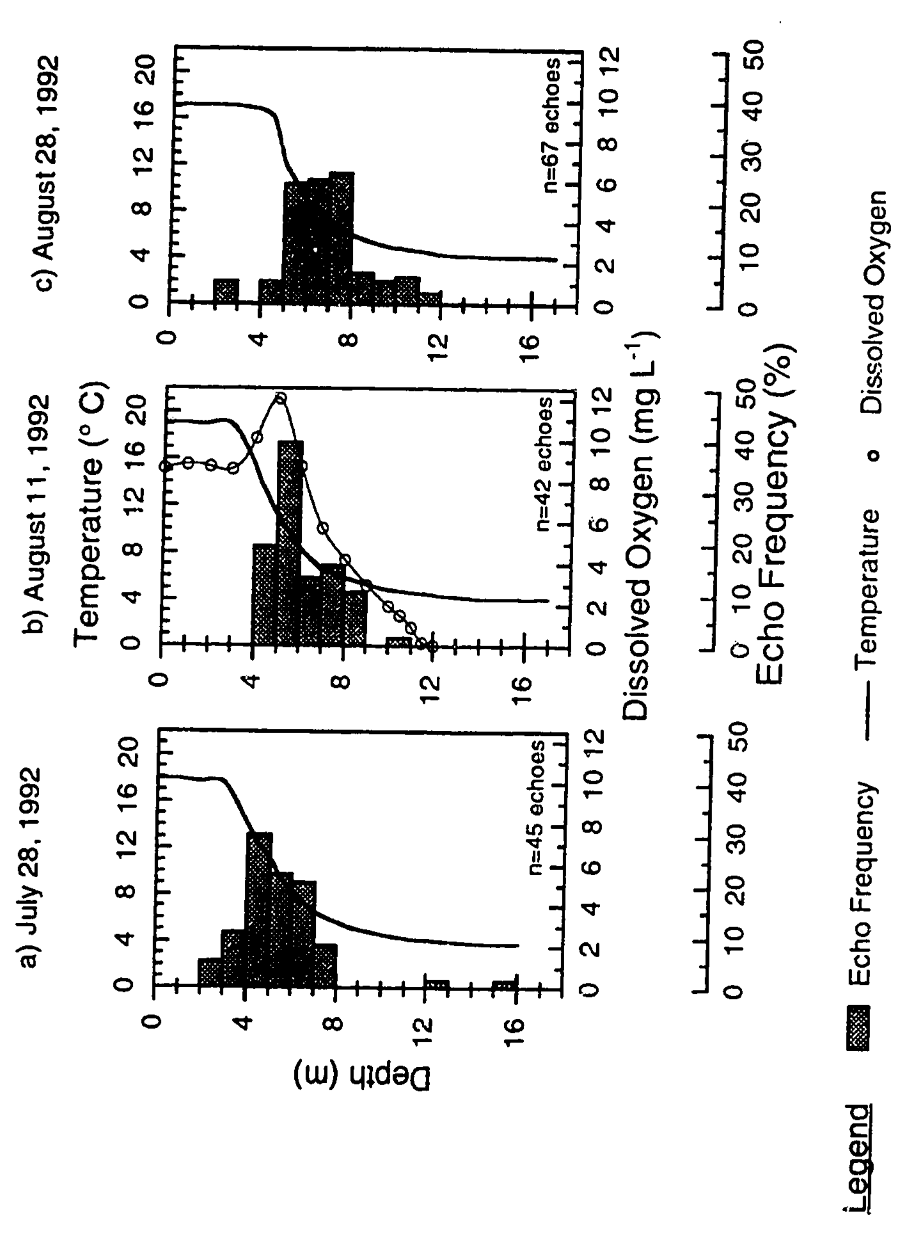

Figure 2.7 Vertical distribution of fish echoes in Lake 442 during July and August, 1992, with corresponding profiles for temperature and dissolved oxygen.

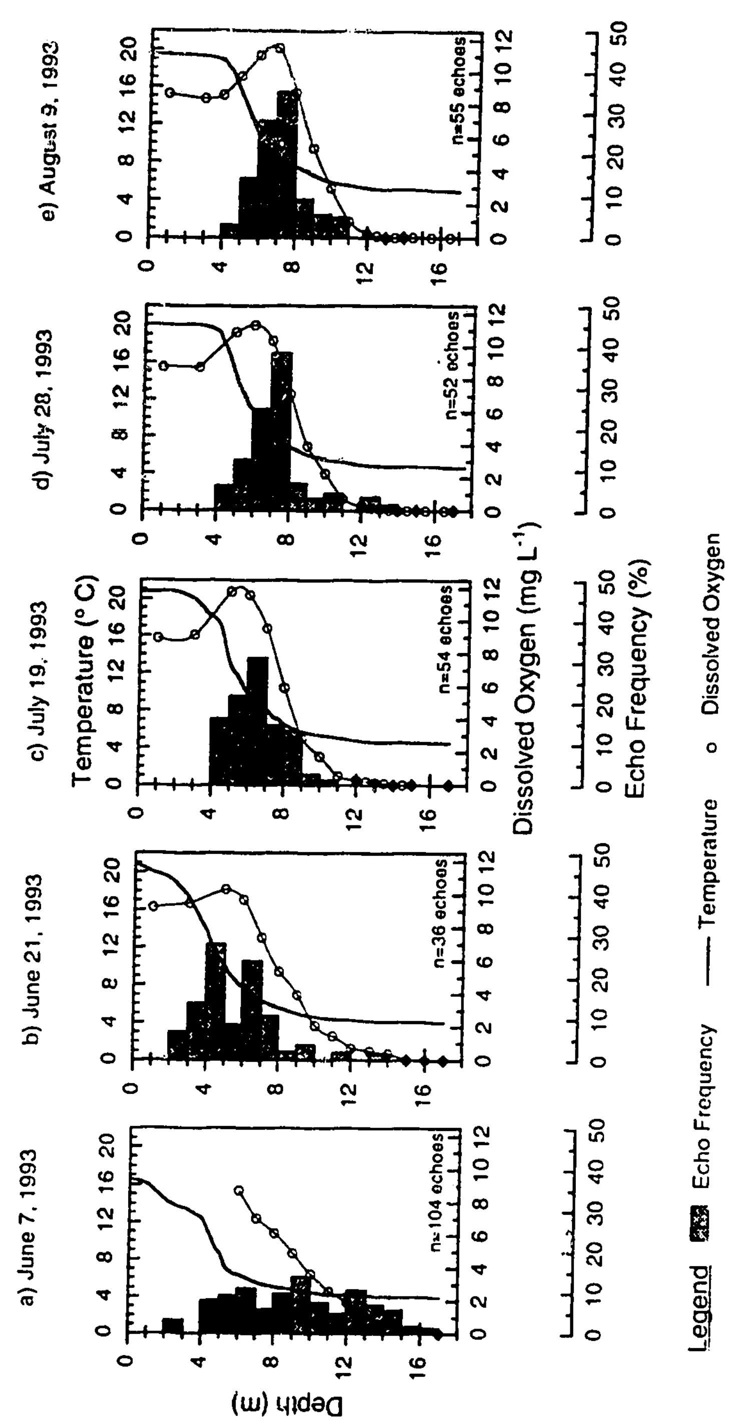

Figure 2.8 Vertical distribution of fish echoes in Lake 442 between June and August, 1993, with corresponding profiles for temperature and dissolved oxygen. Temperature on June 7 was interpolated from June 6 and June 15. Temperature on June 21 was interpolated from June 15 and June 22. Dissolved oxygen on June 7 and June 21 was interpolated from June 4 and June 22. Dissolved oxygen on July 28 was interpolated from July 19 and August 9.

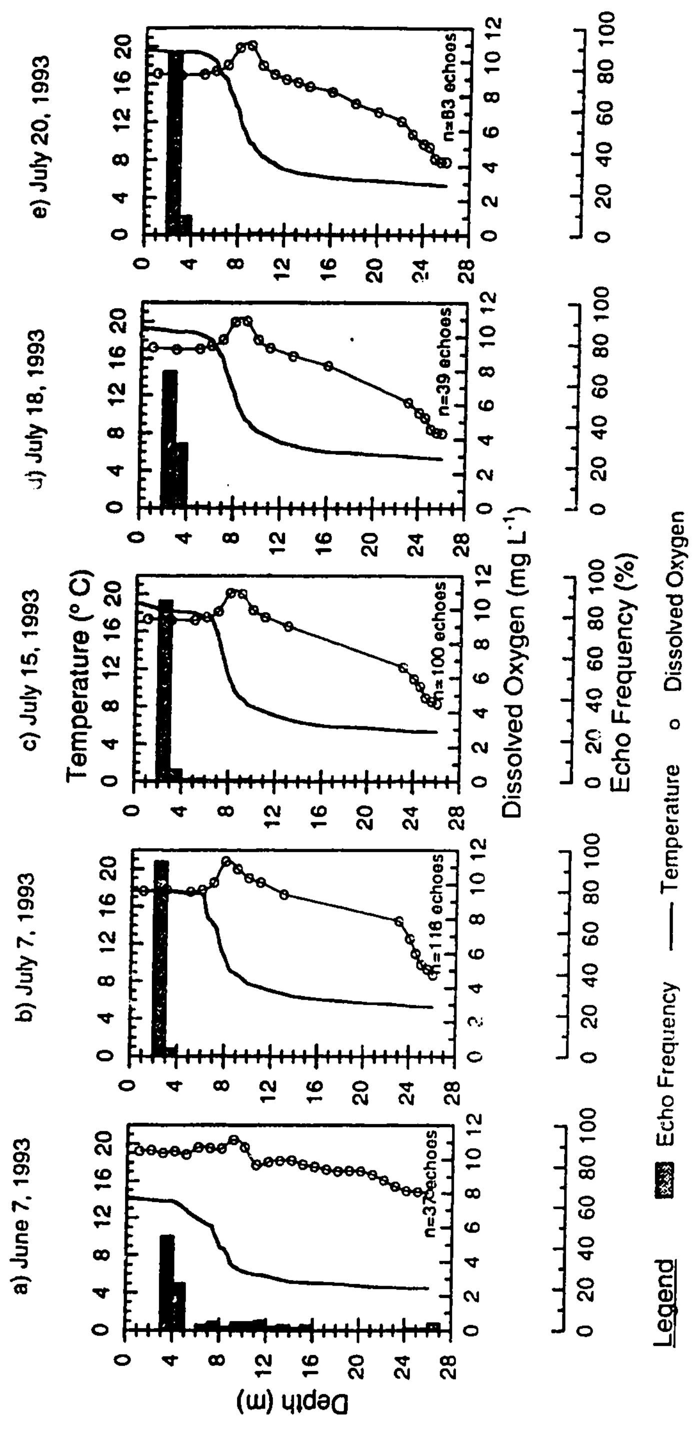

Figure 2.9 Vertical distribution of fish echoes in Lake 468 during June and July, 1993, with corresponding profiles for temperature and dissolved oxygen. Temperature on July 7 was interpolated from July 6 and July 15. Temperature on July 18 was interpolated from July 15 and July 20. Dissolved oxygen on July 7, July 15, and July 18 was interpolated from July 6 and July 20.

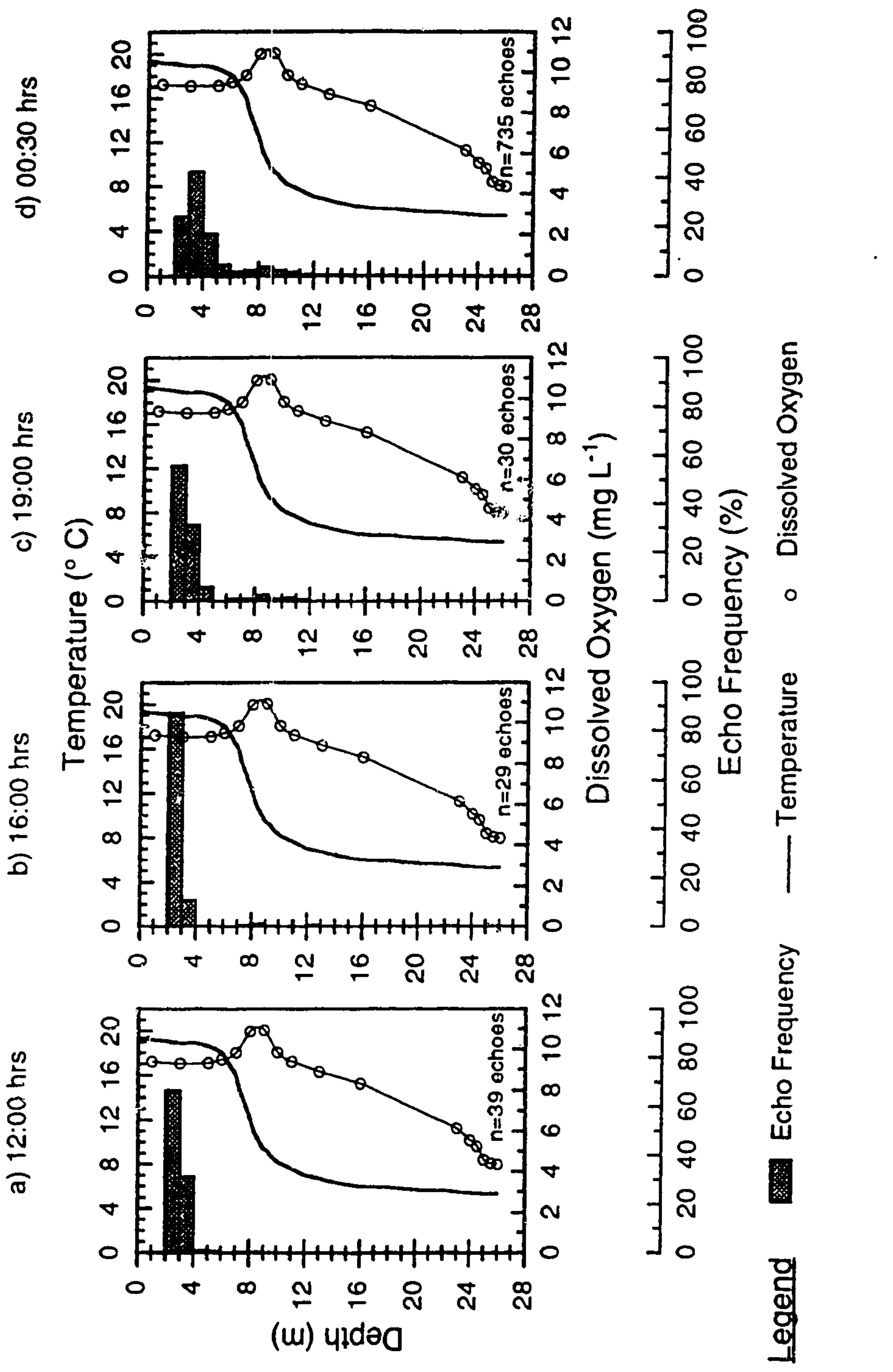

Figure 2.10 Vertical distribution of fish echoes in Lake 468 during surveys starting at 12:00 hours, 16:00 hours, 19:00 hours on July 18, and 00:30 hours July 19, 1993. Temperature was interpolated from July 15 and July 20. Dissolved oxygen was interpolated from July 6 and July 20.

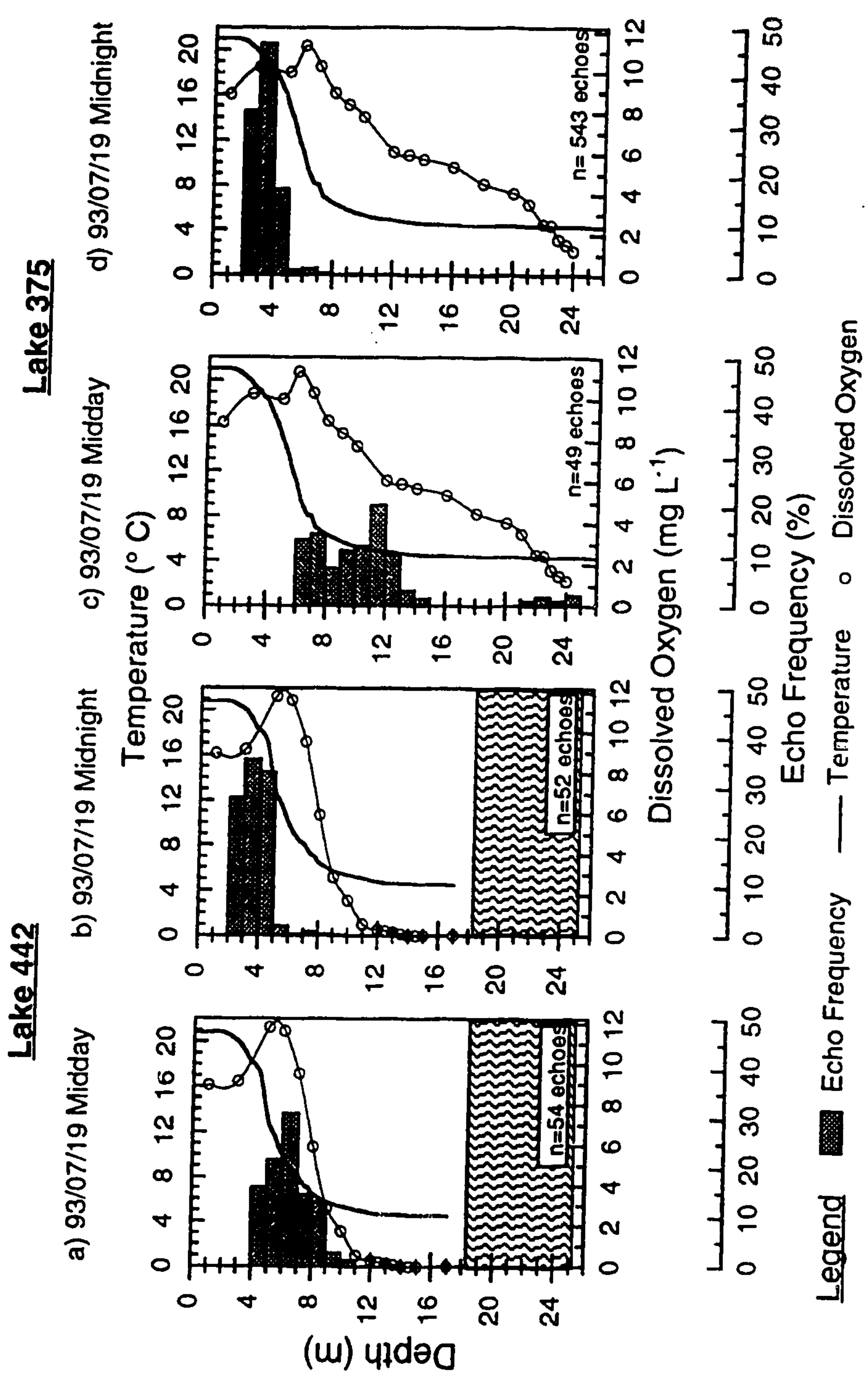

Figure 2.11 Vertical distribution of fish echoes at approximately midday and midnight in Lake 375 and Lake 442 on July 19, 1993 with corresponding profiles for temperature and dissolved oxygen.

Temperatures Inhabited During the Day

Lake 375

Despite low densities throughout most of the hypolimnion, the fish in Lake 375 occupied a narrow range of cold temperatures both in 1992 and 1993 (Fig. 2.12). In 1992, less than 15% of pelagic fish were at greater than 12°C and most (72–92%) occupied temperatures of ≤ 9°C. Nevertheless, there was considerable variability in the distribution of occupied temperatures, with modal temperatures evident on some surveys but not others (Fig. 2.12).

In the spring of 1993, fish were distributed over a wide range of temperatures (4–15°C) with most fish found in surface waters at 14–15°C (Fig 2.12f). They moved to colder waters after the epilimnion warmed above 15°C (Fig 2.12f–g). For the duration of the summer, they remained concentrated in cold water. Few (<15%) were at greater than 8°C and most (44–77%) were at ≤ 6°C throughout the summer (Fig 2.12g–j). Distribution was modal, with 33–50% of fish at 5–6°C on any date during the summer (Fig 2.12g–j).

Lake 442

Fish in Lake 442 were distributed over a wider range of warmer temperatures than those in Lake 375, both in 1992 and 1993 (Fig. 2.13). 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 at 6–15°C during midsummer in both 1992 (79-88%) and 1993 (77-92%) (Fig 2.13) in marked contrast to fish in Lake 375 (Fig. 2.12). Few fish occupied water warmer than 15°C during the day in both 1992 and 1993 (range 0–12%).

Lake 468

In contrast to Lakes 375 and 442, most fish in Lake 468 occupied warm water in the epilimnion throughout the summer (Fig. 2.14). They inhabited water that was warmer than 17°C throughout the summer and reached as high as 19.5°C by the third week of July. Use of habitat as warm as 19 °C persisted throughout the day and night (Fig. 2.15). A few fish did inhabit colder regions of this lake, but over 90% of fish were in water with very warm temperatures.

Temperatures Inhabited During the Night

At night, the majority of fish inhabited similarly warm temperatures in all three lakes (Fig. 2.16). Compared with the daytime, fish inhabited much warmer water at night in Lake 375 and Lake 442, and remained at warm temperatures in Lake 468. In all three lakes fish were concentrated in the epilimnion at temperatures as warm as 19–21°C. Fewer than 4% of fish were located below 14°C throughout the metalimnia and hypolimnia of all three lakes (Fig. 2.16).

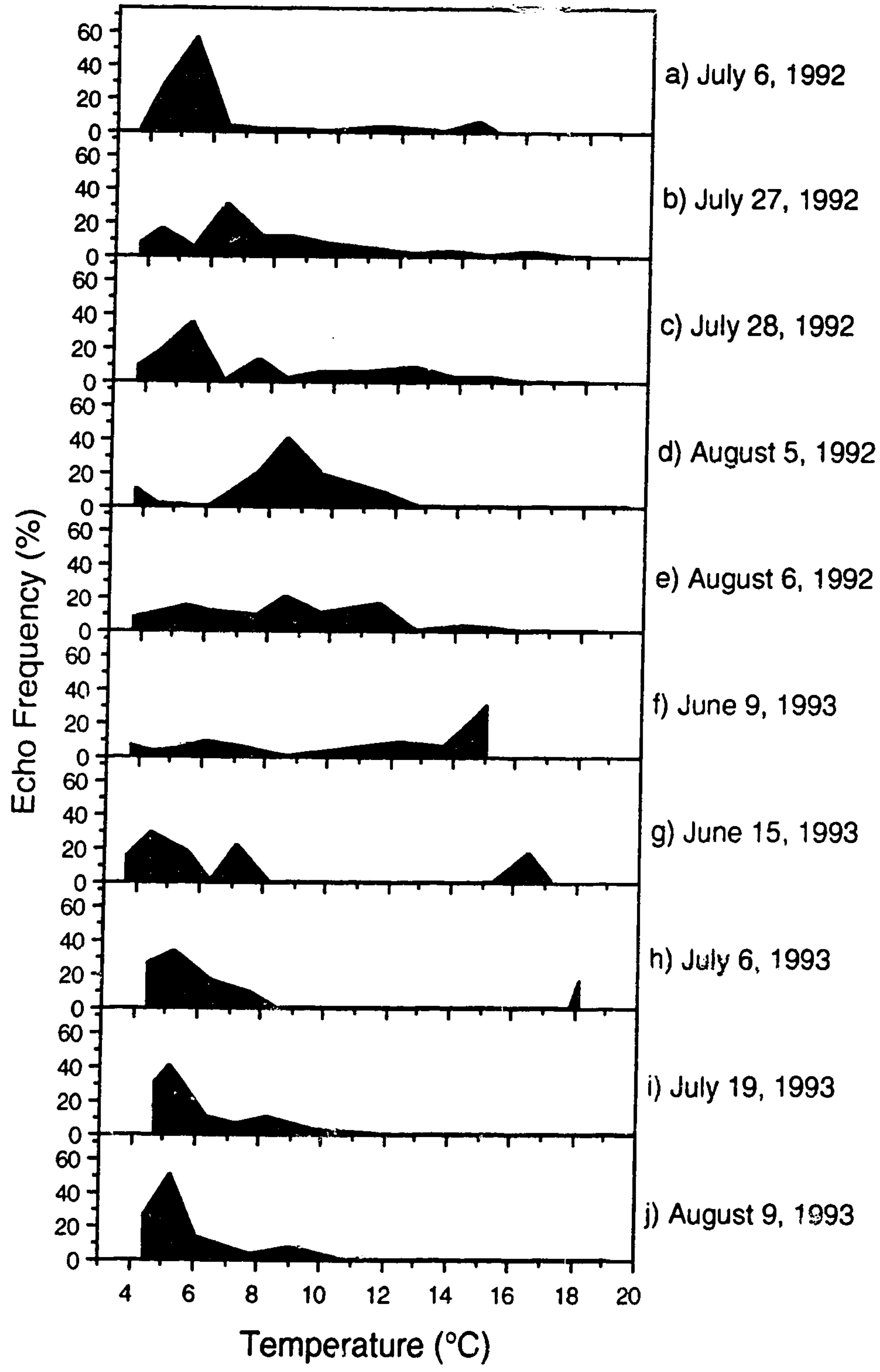

Figure 2.12 Distribution of temperatures inhabited by pelagic fish in Lake 375, at midday during the periods: a–e) July 6 to August 6, 1992; and f–j) June 9 to August 9, 1993.

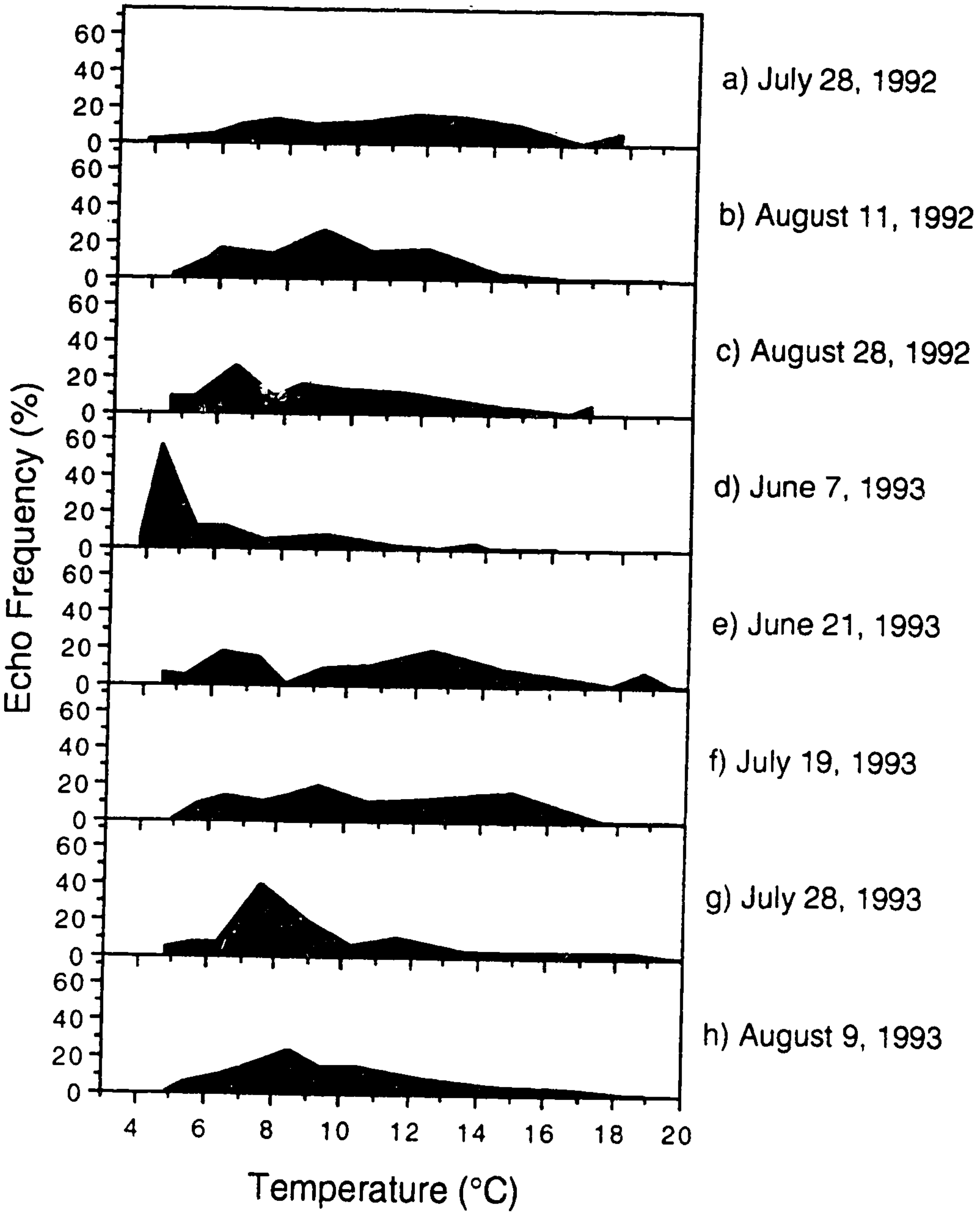

Figure 2.13 Distribution of temperatures inhabited by pelagic fish in Lake 442, at midday during the periods: a–c) July 28 to August 28, 1992; and d–h) June 7 to August 9, 1993.

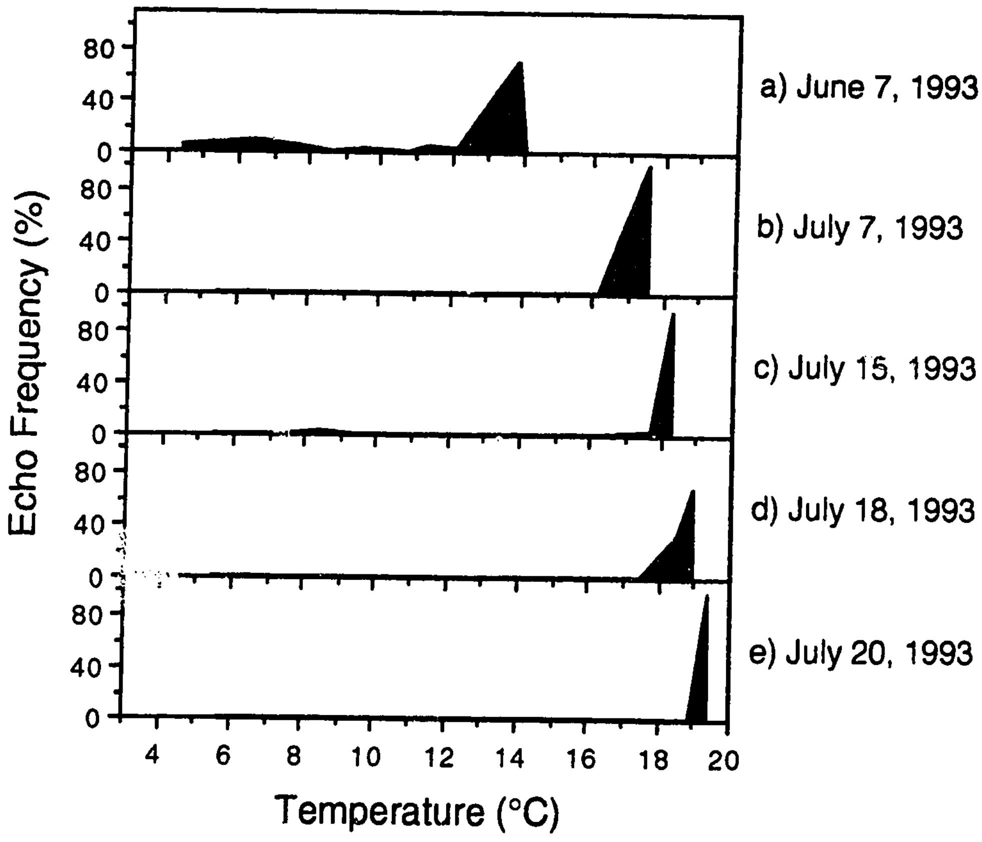

Figure 2.14 Distribution of temperatures inhabited by pelagic fish in Lake 468, at midday during the period June 7 to July 20, 1993.

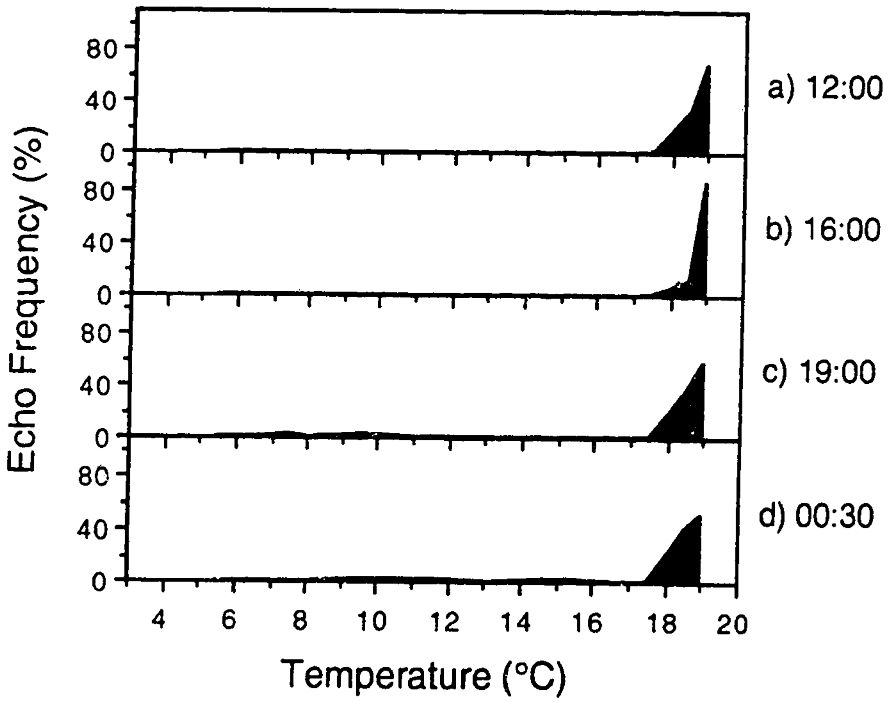

Figure 2.15 Distribution of temperatures inhabited by pelagic fish in Lake 468 on July 18, 1993 at 12:00 hours, 16:00 hours, 19:00 hours, and 03:00 hours.

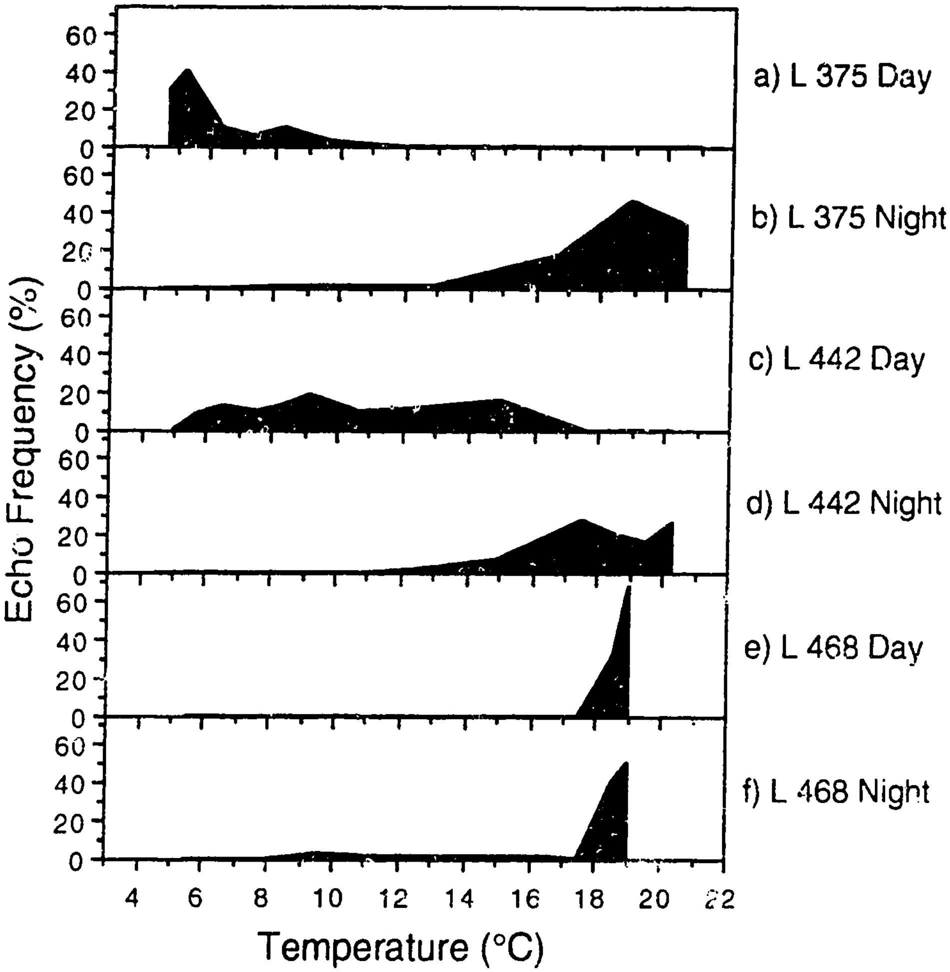

Figure 2.16 Comparison of temperatures inhabited by pelagic fish during the day and night in Lake 375, Lake 442, and Lake 468. Lake 375 and Lake 442 were surveyed on July 19, 1993. Lake 468 was surveyed on July 18, 1993.

Dissolved Oxygen in the Inhabited Zone

In each of the three lakes, fish occupied only highly oxygenated waters throughout most of the summer (Fig 2.17). This was the case even in Lake 442, despite severe hypoxia in the bottom half of this lake. However, during one survey of Lake 442 in the spring (June 7) numerous fish were in very low DO as well (Fig 2.17b). These echoes were clustered tightly near the central basin of the lake and appeared, albeit subjectively, to consist mostly of small fish (Fig 2.18). 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 (Fig 2.17).

There was no single DO value around with fish congregated consistently, rather, they inhabited waters with a variety of DO concentrations in excess of 5 mg L^{-1}. In Lake 375, modal DO inhabited ranged from [illegible].5 mg L^{-1} to 9.5 mg L^{-1} (Fig. 2.17). In Lake 442 and 468 the modal DO inhabited were consistently greater than 9 mg L^{-1} over the course of the summer (Fig 2.17).

Light in the Inhabited Zone

During mid-summer, maximum light at depths inhabited by fish at the time of hydroacoustic surveys ranged from 44–164 µE m^{-2}s^{-1} in Lake 375, 54–400 µE m^{-2}s^{-1} in Lake 442, and 215–482 µE m^{-2}s^{-1} in Lake 468. Ambient light at mean fish depth ranged from 6 to 34 µE m^{-2}s^{-1} in Lake 375, 17 to 99 µE m^{-2}s^{-1} in Lake 442, and 215 to 482 µE m^{-2}s^{-1} in Lake 468. Light in the inhabited zone changed with day to day variations in surface light intensity. There were no trends in fish frequency with decreases in light with depth in these lakes.

Comparison with Conventional Limits to Habitat

Lake volumes within previously assumed upper temperature and lower DO bounds of summer refuge habitat for lake trout (12°C, Magnuson et al. (1990) to 4 mg L^{-1} DO, Evans et al. (1991)) decreased over the course of the summer to approximately 17%, 56%, and 42% of total volumes in Lakes, 442, 375, and 468 respectively. As noted previously, however, lake trout distribution varied among lakes and was not necessarily confined to lake regions within the previously assumed 12°C upper temperature boundary of lake trout habitat (Fig. 2.20). As for *M. relicta* (Chapter 1), oxygenated habitat for lake trout in Lake 442 was likely maintained by metalimnetic photosynthesis during the daytime (e.g., Figs. 2.7b and 2.8c–e).

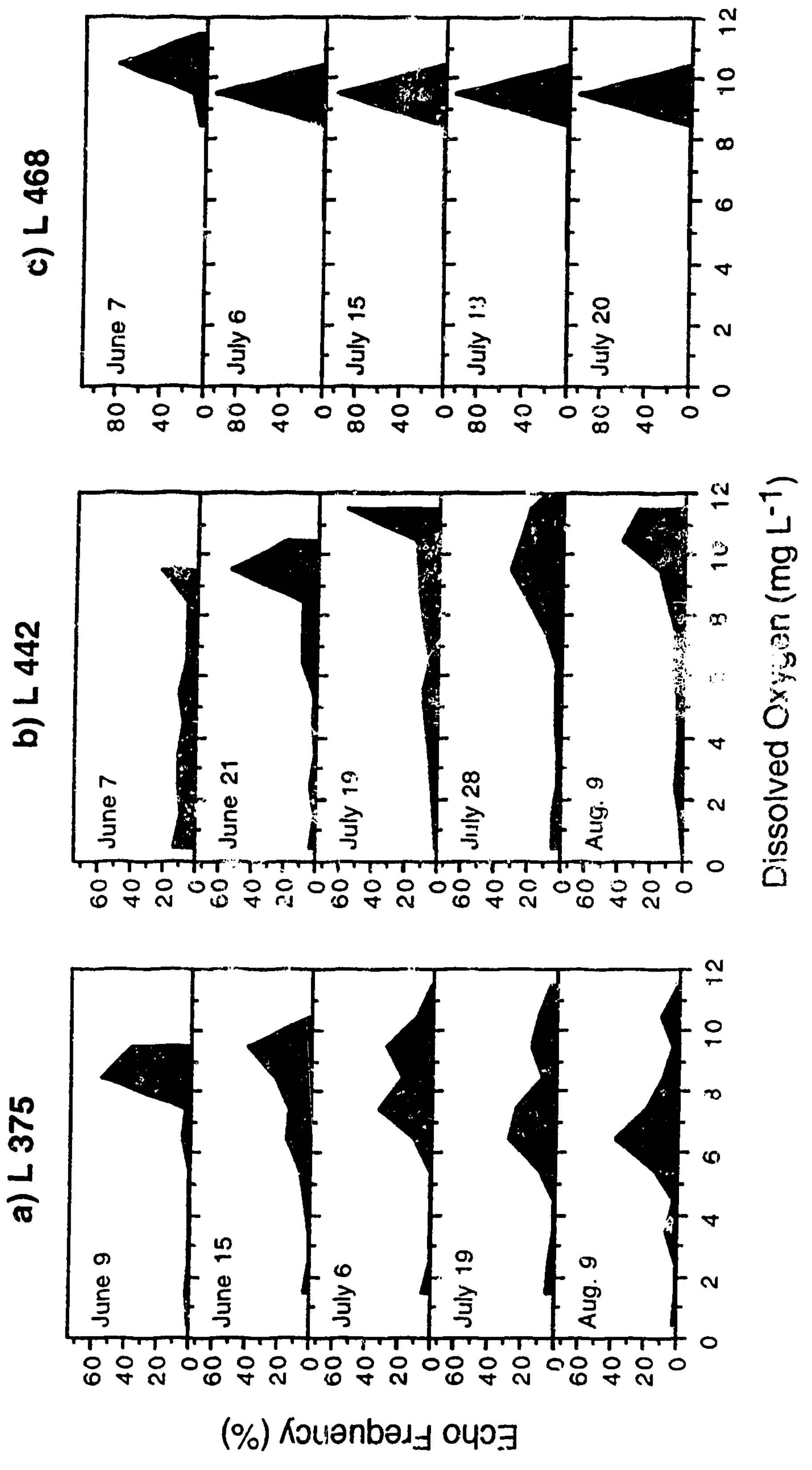

Figure 2.17 Dissolved oxygen concentrations inhabited by pelagic fish in Lake 375 over the period June 9 – August 9, 1993

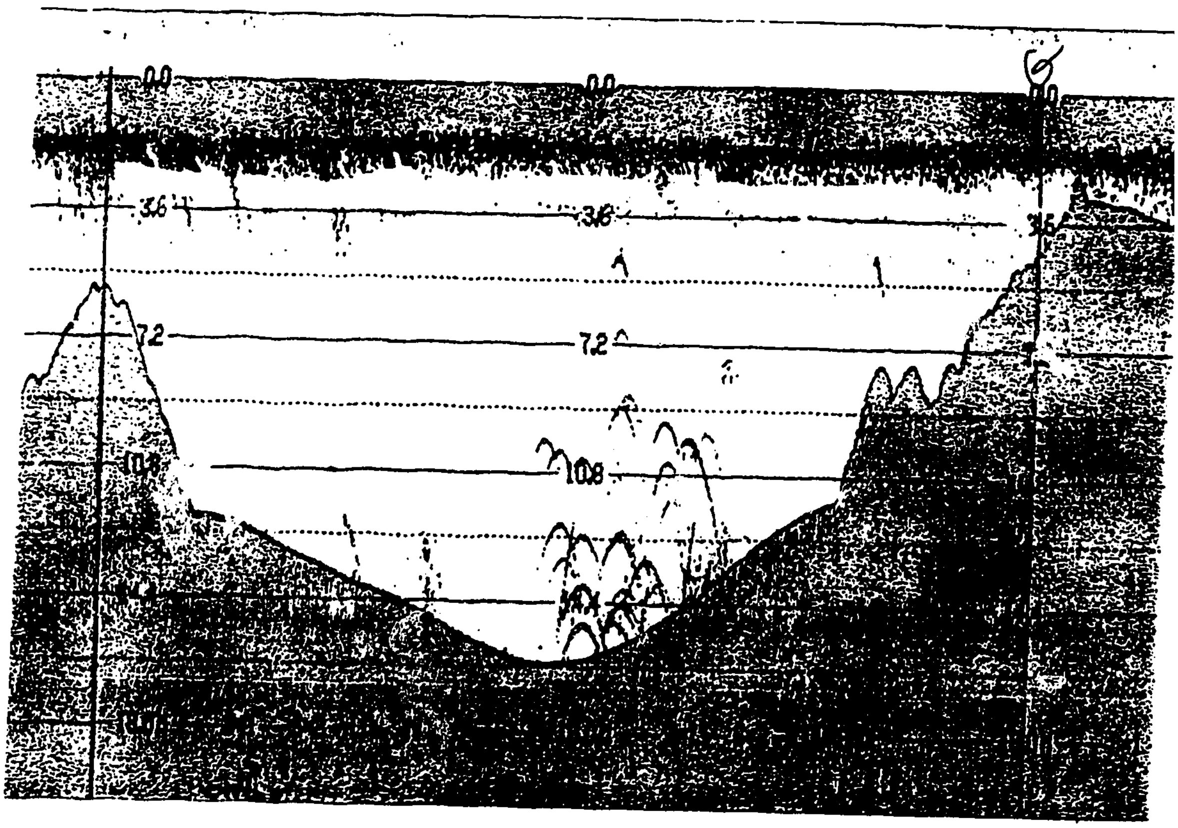

Figure 2.18 Hydroacoustic chart record of transect 7–G in Lake 442 on June 6, 1993 showing cluster of echoes at depths where dissolved oxygen was between 0 and 4 mg L^{-1}.

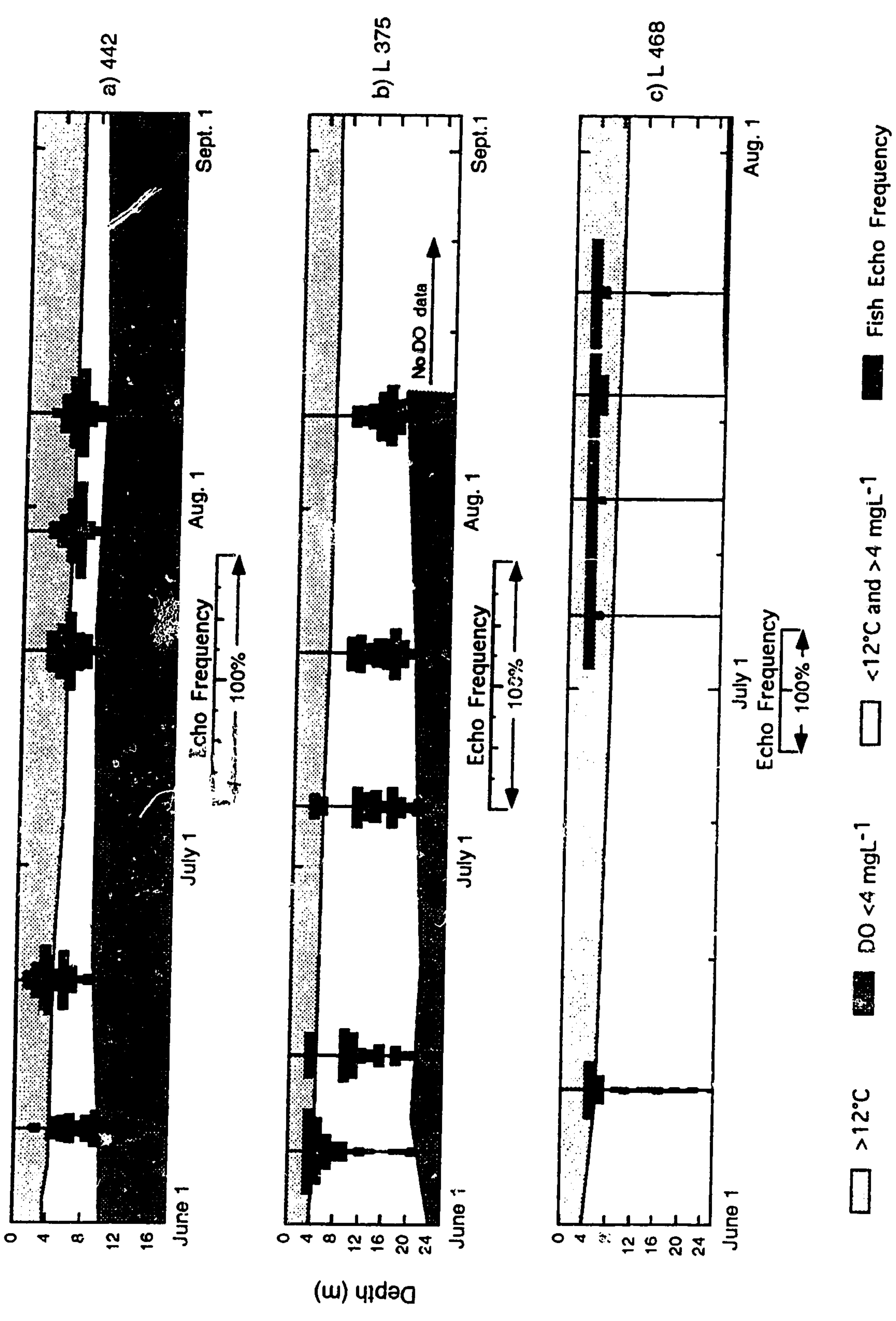

Figure 2.19 Location of previously assumed limits to summer habitat bounded by 12°C and 4 mg L^{-1} DO in a) Lake 442, b) Lake 375, and c) Lake 468 and respective fish distributions during the summer of 1993.

2.4 Discussion

Thermal Habitat Of Lake Trout

My findings show that lake trout inhabit a wide range of temperatures up to 20°C during mid-summer in small lakes. Fidelity to a thermal habitat of 8–12°C was not characteristic of lake trout distribution in any of the three lakes studied, in contrast to expectations based on temperature preference of juveniles under laboratory conditions (mean from 7 studies = 10.2° ±1.1°C) and previous field studies where the median temperature occupied by adults averaged 9.5 ±1.1°C (Evans et al. 1991). During the day, lake trout in Lake 375 were 3–4°C colder than the generally accepted bounds of the lake trout's thermal niche (10°±2°C). 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 cold distribution. Conversely, lake trout occupied water as warm as 19–20°C in Lake 468, although they occurred over a wide range of temperatures. The occurrence of white sucker in the hydroacoustic signal from Lake 442 may have contributed to the broad temperature distributions of fish into warm water. However, I consider that these distributions accurately reflect those of lake trout because the two species were caught at the same range of depths in vertical gill nets. Also, in all lakes at night, lake trout occupied waters 7–8°C warmer than the standard definition of the lake trout thermal niche. I suggest that my findings indicate that lake trout are more plastic in their response to available temperatures in the lake environment than is commonly believed.

Temperature preference acting with lake thermal structure alone does not explain adequately the observed distribution of lake trout in these lakes. Extended epilimnetic residence of lake trout (L 468), despite temperatures approaching lethal limits (23.5°, Gibson and Fry 1954), suggests that benefits of foraging in warm water outweighed metabolic costs of maintaining body temperature greater than 16°C (Gibson and Fry 1954; Mac 1985). Although lake trout – prey relationships were not studied explicitly in these lakes, evidence suggests that prey distribution was important in structuring lake trout distribution irrespective of water temperature. Despite the preponderance of echoes in warm water in Lake 468, lake trout were caught over a wide range of temperatures, at depths coincident with catches of lake whitefish in the vertical gill nets. Rawson (1961) noted a similar situation where lake trout were frequently caught in small-mesh nets while feeding on cisco already gilled in the nets. Observations of lake trout feeding at the surface (at 19–20°C) on lake whitefish lost during removal from the vertical gill nets (T. Sellers, pers. obs.) also suggests this orientation to prey. Further, the observed pattern of nocturnal ascent into the base of the epilimnion in Lakes 375 and 442 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 fathead minnow, *Pimephalus promelas* (Price et al. 1991), which is abundant in Lake 375 and Lake 442 (K. Mills, DFO, Winnipeg, pers. comm.; T. Sellers, pers. obs.). I suggest that the observed patterns of lake trout distribution in my 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 segregate (Magnuson et al. 1979; Brandt et al. 1980; Crowder and Magnuson 1982; Coutant 1987; Olson et al. 1988). In this view, fish partition the available thermal habitat in the lake, reducing interactions between species. As a consequence, the epilimnion would represent both a spatial and thermal refuge from predation by lake trout on both fish and invertebrate prey species. My findings indicate that lake trout d [illegible] on thermal habitat so discretely in these small lakes As a result, the epili [illegible] udy lakes were neither spatial nor thermal refugia for prey species, nor refu [illegible] nite sucker (and other predominantly shallow water species) from competition with lake trout for food. Perhaps, low representation of other thermal guilds of predators in these small lakes permits more generous distribution with respect to available resources.

Use of warm water habitat 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 interpreted as an uncommon occurrence that represented brief foraging forays into unfavorable environmental conditions (Martin 1952; Galligan 1962; Dahlberg 1981; Olson et al. 1988). My findings suggest that lake trout commonly inhabited waters warmer than the laboratory-determined avoidance temperature (15°C, McCauley and Tate 1970) at night and in some lakes persisted both day and night at temperatures hitherto considered as uninhabitable.

My findings do not preclude that use of warm water habitat depended on refuge in cold water for some part of the day. Daytime distributions in Lake 375 and Lake 442 and gill net catches in Lake 468 show that diel thermal history included residence in cold water. Indeed in a warm isothermal lake, some lake trout offset their warm-water 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 it (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). This indicates that extended residence at high temperatures is possible, such as that suggested by the persistence of shallow hydroacoustic echoes in Lake 468 (Figs 2.9 and 2.10).

I speculate that presence of lake trout in the epilimnion in my study could represent more than brief foraging forays. Body-core temperature of small lake trout (1,100 g) requires nearly a 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. Also, detailed tracking of lake trout implanted with temperature-sensing tags has shown considerable individual variation with some maintaining consistently elevated (>15°C) body-core temperatures even in lakes with readily available cold-water habitat (Snucins and Gunn 1995).

It is thus possible that lake trout may be more tolerant of warm temperature than previously thought. Clearly, lake trout habitat in small lakes is broader than the 10° ±2°C definition of thermal habitat used in very large lakes in an empirical relation of habitat volume to sustained yield (Christie and Regier 1988) and in simulation modeling of the potential effects of climate change-induced lake warming on lake trout production (Magnuson et al. 1990).

Dissolved Oxygen In Lake Trout Habitat

In contrast to their broad thermal niche, my findings indicate that lake trout inhabited only highly oxygenated regions of lakes. The preferred habitat had oxygen concentrations in excess of 6 mg L^{-1}. Further, lake trout apparently avoided regions with less than 5 mg L^{-1} even when large volumes of suitable thermal habitat were available. Hydroacoustic and vertical gill net surveys in Lake 442 confirmed that lake trout did not occupy less oxygenated regions when the amount of highly oxygenated cool-water habitat was limited. Rather, they inhabited slightly warmer but highly oxygenated waters.

The majority of hydroacoustic fish echoes were in highly oxygenated water; however, some fish were present at very low concentrations of dissolved oxygen (e.g., Fig. 2.17b). Although the species causing these echoes is not known, brief feeding forays into hypoxic waters has been documented previously in rainbow trout, *Oncorhynchus mykiss* (Leucke and Teuscher 1994), yellow perch, *Perca flavescens* (Hasler 1945), and central mudminnow, *Umbra limi* (Rahel and Nutzman 1994). In Lakes 442 and 375 in particular, possible species include white sucker, pearl dace, finescale dace, fathead minnow, and slimy sculpin. It is also possible that these echoes may have been juvenile lake trout, because they do inhabit waters with dissolved oxygen as low as 2 to 4 mg L^{-1}, presumably to avoid predation by cannibalistic adults (Evans et al. 1991).

My findings generally support the available information about oxygen requirements for lake trout habitat, although detailed information is lacking about the tolerance of adults to low oxygen. For yearlings, the level of no excess activity (i.e., swimming not possible) is 2.8 mg L^{-1} at 10°C and 3.5 mg L^{-1} at 22°C and slightly higher for two year-olds (Gibson and Fry 1954). Adult lake trout would be expected to avoid lake regions with less than these concentrations. Indeed, the median avoidance threshold is 4.2 mg L^{-1} in five studies that report lake trout distribution or response to dissolved oxygen (Evans et al. 1991). Similarly, the median threshold at which swimming activity increases in response to declining oxygen is 5.8 mg L^{-1} (Evans et al. 1991).

High dissolved oxygen in deep waters is important for juvenile nursery habitat (Evans et al. 1991). In deep lakes, juveniles segregate from adults and occupy depths deeper than 27 m, likely as a strategy to minimize cannibalism (Evans et al. 1991). In many smaller lakes, such as those at the ELA, this physical segregation is not possible because of shallow depth or depletion of dissolved oxygen in the hypolimnion. Lack of segregation may contribute to low recruitment in small lakes. Indeed, by minimum criteria set forth by Evans et al. (1991) for both the amount of juvenile nursery habitat and the dissolved oxygen therein, Lake 442, Lake 375 and possibly Lake 468 should not sustain lake trout populations at all. In contrast, Lake 468 maintains high lake trout recruitment and production (K. Mills, DFO, Winnipeg, pers. comm.).

Light In Lake Trout Habitat

Light appears to have had little influence on the distribution of lake trout in these small lakes. My 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 avoid bright light at levels typically encountered in the shallowest regions of these lakes, in contrast to avoidance suggested for other species (Rudstam and Magnuson 1985).

Amount of Temperature and Oxygen-Sufficient Habitat

For very large lakes, Christie and Regier (1988) showed that commercial yield of lake trout was correlated with the volume of optimum thermal habitat (10°±2°C). 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 dissolved oxygen in restricting cold-water habitat was 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 dissolved oxygen deep in the hypolimnion 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 deepwater nursery habitat for juveniles. Deepwater nursery habitat is thought to provide juveniles with a critical refugium from cannibalism by adults (Evans et al. 1991). In small lakes in central and eastern Ontario subject to cultural eutrophication, loss of juvenile refuge habitat due to DO depletion is suspected as the cause of low recruitment and senescence in many lake trout populations (Evans et al. 1991).

Measures of lake trout habitat volume that include explicitly 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 to 6 mg L^{-1} DO), vital habitat (15.5°C to 4 mg L^{-1} DO), and habitable volume (15.5°C to 2 mg L^{-1} DO) (Evans et al. 1991). However there are few data for the many small lake trout lakes in northwestern Ontario. Indeed, although 22% of known lake trout lakes in Ontario occur in the northwestern region (Lewis et al. 1990), only 6 (2.8% of the data-set; 0.25% of provincial total) were included in the analysis of Evans et al. (1991). Of these, 5 were large (>1000 ha) and thus atypical of lake trout lakes in both the region and the province where approximately 80% are less than 1000 ha (Martin and Olver 1976). 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 thresholds set forth in Evans et al. (1991), Lake 468 barely meets minimum habitat requirements (Table 2.5). In the absence of population-specific data, these guidelines indicate that native lake trout could not be present in the many small lakes similar to Lake 375 and Lake 442 (Table 2.5). Further, even if lake trout were introduced, the population could not be self-sustaining (Table 2.5). These characterizations are particularly unfortunate because lake trout in the many small northwestern Ontario lakes will be among the most sensitive to further erosions of temperature and DO-suitable habitat whether caused by long-term climatic warming or human development in the watershed.

Table 2.5. Comparison of Lake 375, Lake 442, and Lake 468 to empirical measures of critical habitat developed for lake trout lakes in Ontario (Evans et al. 1991).

Habitat Criteria	**Threshold for lake trout**		**L 375**	**L 442**	**L 468**
	Adults present	**sustained by natural reproduction**			
Preferred Habitat Volume ($\times 10^5 m^3$) (10°C – 6 mg L^{-1}DO)	18	48	5	2	65
Vital Habitat Volume ($\times 10^5 m^3$) (15.5°C – 4 mg L^{-1}DO)	57	96	11.8	3.8	79
Habitable Volume ($\times 10^5 m^3$) (15.5°C – 2 mg L^{-1}DO)	76	115	13	5.5	79
Volume with DO 2 – 4 mg L^{-1}		<8%	9%	5%	<1%
Volume with DO < 2 mg L^{-1}		<19%	4%	19%	0%

In addition to the apparent inapplicability to small lakes, these measures of critical habitat (Table 2.5) should be viewed with caution for another reason. Although these measures of habitat volume appear to be highly related to indices of lake trout population success (i.e., relative extent of natural reproduction), they are based on regressions of 7 points, each representing "average" conditions in a category of lakes, without any associated measure of variation (Evans et al. 1991). Analysis of the 212 lakes in the original data-set shows that measures of lake trout habitat that incorporate both temperature and DO (Table 2.5) explain extremely small amounts of the variation in the relative extent of natural reproduction in these lakes ($r^2 \cong 0.04$; their Table 26, page 87, regressions #8, 15, and 72, Evans et al. 1991). Similarly, habitat measures based on lake volumes with very low DO explain very little of the variation in relative extent of natural reproduction ($r^2 \cong 0.08$ and 0.13; their Table 26, page 88, regressions 75 and 80 respectively, Evans et al. 1991). In contrast, 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 (Patricia 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. Mean depth of approximately 6.3 m separates these lakes equally well into lake trout and non-lake trout lakes (their Fig. 3, Ryan and Marshall 1994). 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 also explain absence of lake trout.

Current empirical models do not describe adequately critical habitat for lake trout, particularly in small lakes. Evidence from my study shows that previously assumed niche boundaries based on temperature are not necessarily applicable to lake trout in small lakes. Although my findings do not address directly tolerance of lake trout to high temperature or low DO, they suggest that the standard limits (12°C – 4 mg L^{-1} DO) of lake trout habitat may not describe adequately required habitat. Also, my finding that use of warm water in the epilimnion dominated at night in all three lakes challenges the notion of thermal habitat restriction. A rigid 12°C bound may be conservative, given both the warm temperatures inhabited and considerable variation in my study lakes. Clearly, the breadth of the thermal niche of lake trout is much broader in small lakes than commonly believed. In these small lakes, the lake trout niche includes epilimnetic resources and lake trout may be an integral component of the epilimnetic food web. Conversely, a 4 mg L^{-1} DO lower limit to lake trout habitat may be too liberal. Based on my findings, I suggest that 5 or even 6 mg L^{-1} DO describes more realistically the lower bounds of adult lake trout habitat.

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General Discussion

Summary of Habitat Constraints for Lake Trout *M. relicta*

My findings indicate that lake trout are not as restricted to cold-water habitat as commonly believed. In these small lakes there is considerable variation among lakes in thermal exposure of lake trout populations and all use warm regions of the epilimnion, particularly at night. Lake trout summer habitat in these small lakes includes highly oxygenated regions of the hypolimnion and the epilimnion.

Although warm temperatures dominated nighttime distributions, there was no clear pattern in temperatures occupied among the three lakes during the day. Occupied temperatures did not correspond to the 10°±2°C breadth of thermal habitat suggested by previous studies in larger lakes (Kennedy 1941; Rawson 1961; Galligan 1962; Johnson 1975; Dahlberg 1981), laboratory-determined temperature preference of juveniles (McCauley and Tate 1970), and optimal temperatures for physiological processes (O'Connor et al. 1981). Clearly, 10°±2°C does not describe adequately thermal niche or thermal history of lake trout in small lakes. Use of this measure of habitat in models of lake trout production (Christie and Regier 1988; Magnuson et al. 1990) may not be applicable to small lakes. A rigid definition of thermally-suitable habitat is not possible, given current information. Habitat may include regions with temperatures as warm as 19–20°. Depletion of dissolved oxygen in the hypolimnion can impinge on suitable thermal habitat, restricting lake trout distribution to regions with greater than 5–6 mg L^{-1} DO.

My findings do not preclude that some amount of cold-water refuge habitat may be necessary for adult survival and use of warm water. Perhaps, use of warm water resources in these small lakes is possible because of (or depends on) offsetting exposure to cold temperatures during some period of the day or night. Vertical and horizontal scales are compressed in small lakes relative to large lakes, providing close proximity of warm-water and cold-water habitats. Possibly, the physical accessibility of resources in warm water permits their exploitation without substantial costs or risks from temperatures greater than physiologically optimum. However, evidence that lake trout persist in warm water in Lake 468 suggests that offsetting cold-water residence may not be necessary, similar to the findings of (Snucins and Gunn 1995). Although my findings suggest that lake trout may make extensive use of water as warm as 19–

20°, detailed tracking of the thermal history of individual fish would be needed to assess both the duration and extent of warm water vs. cold water use. Given time lags for body-core temperature to equilibrate (Snucins and Gunn 1995), this might be best accomplished by tracking temperature exposure of lake trout using externally attached telemetry thermistors.

In the long-term, survival of a population depends on more than broad tolerances of adults and the breadth of habitat for them in the lake. It depends also on successful reproduction and replacement at least at periods more frequent than the generation span of the reproductive cohort. Although my findings suggest that summer habitat may not be as restricted as commonly believed, they do not address the suitability of habitat for earlier life stages. Senescence or extirpation of populations in lakes subject to eutrophication and hypolimnetic DO depletion suggests that highly oxygenated, deepwater habitat is essential for adequate recruitment of juveniles in some lakes (Evans et al. 1991b). In lakes with constricted habitat, juvenile and adult habitat could coincide, possibly leading to high rates of cannibalism by adults on the young (Evans et al. 1991b). This would be expected to be an important mechanism in small lakes with high adult density (e.g., Trippel and Beamish 1993) and in lakes lacking forage-fish species. Perhaps, future changes in lake thermal structure and DO storage will manifest first in reproductive failure and senescence of lake trout populations, rather than loss of adults. These effects would be expected to occur first in very small lakes where habitat is already limited and in lakes subject to nutrient loading from human development in the watershed.

However, accurate assessment of the effects of further erosions of cold-water habitat on lake trout populations requires a thorough understanding of tolerances of all life stages to high temperature and low DO. Data on physiological tolerances of lake trout to high temperatures and low DO are restricted to tests of a limited number of hatchery-reared yearling and two year-old lake trout (Gibson and Fry 1954). Mechanistic information is also required on how competition, cannibalism, and prey distribution and composition affect life history of lake trout in small lakes and how these would change as habitat constricts. These data are currently lacking.

Because lake trout are relatively long-lived and their reproductive period spans many years, populations may be somewhat resistant to periodic recruitment failures cause by inhospitable conditions. *M. relicta* however, would be much more sensitive to periodic environmental unsuitability, because their generation period is long (2 years in most

ELA lakes) relative to their life span of 3 years (Nero 1981). Extirpation could occur rapidly as a result of only a year or two of inhospitable conditions, as was seen during experimental acidification of Lake 223 (Nero and Schindler 1983). Perhaps, this could help explain absence of *M. relicta* from some lakes with limited cold-water habitat (such as L 626) yet persistence of lake trout (T. Sellers, unpubl. data).

Despite indications that adult lake trout may persist in warm water (Snucins and Gunn 1995; this study) native lake trout are usually absent at temperate latitudes from lakes too shallow to thermally stratify during the summer (Marshall and Ryan 1987). Usually, they are absent also in small stratified lakes where the amount of highly oxygenated cold-water habitat is very small (Evans et al. 1991b; Ryan and Marshall 1994). Absence of lake trout from some small lakes with limited cold-water habitat (e.g., L 240 and L 626), despite connection to extant populations, suggests that some threshold amount of cold-water habitat is required. Perhaps, this question might be approached most efficiently by extending empirical analyses of measures of temperature and oxygen-sufficient habitat to small lakes where habitat is limited and where population numbers and structure are known. Lakes at the ELA would be good candidates because at least basic fish surveys have been conducted on many lakes (at least 34 with lake trout; population estimates are known to varying degrees of accuracy on at least 19, K. Mills, Department of Fisheries and Oceans, unpubl. data). This could help address limitations in current information used by resource managers in Ontario which lacks resolution for small lakes (Evans et al. 1991b). A similar approach could be taken with *M. relicta.*

Overlap between *M. relicta* and Lake Trout Habitat

In all lakes at night, there was little overlap in the distribution of *M. relicta* and lake trout in pelagic waters. Because *M. relicta* were predominantly distributed at less than 11°C, they were several metres deeper than the fish. Based on standard definitions of lake trout temperature preference (10°±2°C; Magnuson et al. 1990), nighttime distribution of these species would have been expected to coincide.

This suggests that lake trout were not primarily oriented to *M. relicta* at night, in contrast to tightly coupled distributions observed for other fish that prey on *M. relicta* (Janssen and Brandt 1980). At about 200 mm, lake trout switch from an invertebrate diet to small forage fish (Martin and Olver 1980; Trippel and Beamish 1989). Lake trout under 200 mm (< 2 years old) are rare in Lake 375 and Lake 442 (K. Mills, DFO, Winnipeg, unpubl. data). It is thus, not altogether surprising that nighttime distribution of lake trout in these lakes was not coupled to *M. relicta* distribution, as has been shown for aiewife in Lake Michigan (Janssen and Brandt 1980). Cold stenothermal habits of lake trout in previous studies, particularly in large lakes, could possibly reflect orientation of lake trout to cold-water forage-fish species in these lakes, such as cisco. In lakes where cold-water forage is absent, I speculate that lake trout could forage on epilimnetic species. Studies of lake trout diet in very small lakes are needed to confirm this.

Similarly, during the day, the dominant distribution of lake trout in L 468 overlaps little with the depth distribution of *M. relicta*. Although lake trout range widely in this lake, depth distribution was predominantly shallower than that of *M. relicta*. In contrast, both *M. relicta* and lake trout were concentrated into a narrow range of similar depths in Lake 442 during the day. This degree of overlap might be expected to result in a high predation rate of *M. relicta* by lake trout during the day, despite their somewhat cryptic habits on the sediments. As the terminal predator in many of these small lakes, the effects of lake trout predation cascades through several trophic levels of hypolimnetic species (Trippel and Beamish 1993). My findings suggest that this trophic structuring effect might not be confined to species that inhabit the hypolimnion but could extend to epilimnetic communities as well. This variation in the trophic position of lake trout is supported by (Kidd et al. 1995).

Cumulative Stresses on Lake Trout

Deepening of thermoclines and expansion of hypoxic zones in small lakes subject to climatic warming (Schindler et al. 1990; Schindler et al. 1995) are not the only potential stresses on lake trout and *M. relicta* populations. Increased UV exposure, lake acidification, cultural eutrophication, chemical pollution, and fishing mortality could also contribute cumulatively to stress.

Increased UV exposure is expected in these lakes because of DOC loss induced by climatic warming ▯(Schindler et al. unpubl. data). This could possibly affect both *M. relicta* and lake trout. Increased exposure could occur both from elevated UV incident on the lake and from increased penetration of UV from DOC loss caused by warming and drying of climate (Schindler et al. 1995). For fish, effects of elevated UV exposure involve immune depression, sunburn-lesions and sunburn-induced cellular changes in dermal tissue, increased susceptibility to dermal infections, and possibly development of cataracts (Dunbar 1959; Bullock 1993). Experimental exposure to UV-B, at levels typical of high elevation streams at mid-latitudes, produced sunburn and subsequent fungal infections in rainbow trout, *Oncorhynchus mykiss*, and Lahontan cutthroat trout, *Oncorhynchus clarki henshawi* (Little and Fabacher 1994). For Lahontan cutthroat trout, mortality resulted within six days of exposure (Little and Fabacher 1994). For crustaceans, elevated UV-exposure results in more acute effects including lethality (Zagarese et al. 1994). It is not known whether lake trout or *M. relicta* can detect and avoid UV light. At the least, increased UV penetrations could constrict the amount of habitat suitable for these species.

I speculate that increased UV penetration would be most likely to affect early life stages of both lake trout and *M. relicta*. UV-B penetration depths of several metres are expected in very transparent lakes if DOC declines further due to climatic warming and drying (Scully and Lean 1994; Schindler et al unpubl. data). Lake trout spawning sites are typically shallow (<3 m) in these small lakes. Elevated exposure to UV during early incubation (before fall freeze-up) and at the swim-up stage (in the spring) could be substantial; however, the effects are not known. Similarly, *M. relicta* release their broods in shallow water in the spring (Nero 1981) and they remain at shallow depths (< 2 m) for approximately 1 month (this study).

The effects of lake acidification are well documented for *M. relicta* (Nero and Schindler 1983) and for lake trout (Schindler et al. 1985; Mills et al. 1987). Usually, *M. relicta* are absent from lakes with pH <5.7 (Dadswell 1974). During experimental acidification of L 223 at the ELA, mortality occurred between pH 5.6 and 5.9, probably as the result of direct hydrogen ion toxicity rather than reproductive failure (Nero and Schindler 1983). For lake trout, lake acidification causes recruitment failure beginning at pH 5.6 (Beggs and Gunn 1986; Mills et al. 1987; Gunn et al. 1990). However, collapse of the lake trout food-chain begins at higher pH, resulting in dramatic loss of condition and starvation beginning as early as pH 5.9 (Schindler et al. 1985). Aluminum ion toxicity is also implicated in declines of some populations, particularly in areas subject to high acid deposition and export of aluminum from the watershed (Beggs et al. 1985; Beggs and Gunn 1986). Because aluminum binds with DOC reducing its toxicity, DOC loss from climatic warming could act synergistically with acidification to increase direct ion toxicity (Evans et al. 1991a).

As well as reducing oxygenated summer habitat for juveniles, nutrient loading from human development can impair lake trout spawning habitat, resulting in decreased egg survival (Sly 1988). This effect is particularly pronounced in lakes where agricultural fertilization in the watershed results in high ammonia levels and low DO in interstitial water between spawning substrate (Sly 1988).

In addition to these physical and chemical stresses, most lake trout populations have been subject to some degree of mortality from fishing. Historically, the many small lakes in northwestern Ontario have been relatively unaffected by fishing pressure, in contrast to lakes in central and southeastern Ontario where many populations are in decline or have been lost, partly as a result of exploitation by anglers (MacLean et al. 1990; Evans et al. 1991b). However, the small lakes in northwestern Ontario are becoming increasingly subject to fishing pressure. Access to small northwestern Ontario lakes has increased tremendously during the past 15 to 20 years, as a result of construction of logging and fire roads and popularization of snowmobiles and all-terrain-vehicles. My findings suggest that lake trout in these small lakes could be highly vulnerable to exploitation even during mid-summer, given that they are concentrated into a narrow range of relatively shallow depths, particularly during the night (e.g., Figs 2.5 - 2.11).

Habitat for lake trout may not be as restricted by temperature as previously believed. However, lake trout in small lakes may be most susceptible to changes in lake environment induced by climatic warming. Climatic warming likely will have greatest effects on thermal structure of small lakes (<100 ha) where loss of wind protection from deforestation and increased depth of heating due to DOC loss will both contribute to thermocline deepening (Schindler et al. 1990; Fee et al. 1995). Initially, *M. relicta* may be more sensitive than lake trout to changes in lake thermal structure in these small lakes. Changes in food-web structure for lake trout could occur rapidly if habitat was lost for *M. relicta*, although the specific effects of this are not known. Given cumulative effects of climatic warming and other stresses (e.g., fishing mortality, eutrophication, acidification) strong protection of both habitat and harvest may be particularly important for long-term survival of lake trout in small lakes.

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Appendix 1 Dates on which temperature, dissolved oxygen (DO) and light profiles were obtained in Lakes 375, 442, and 468 during the summers of 1992, 1993 and 1994.

L 375			L 442			L 468		
Temp.	**DO**	**Light**	**Temp.**	**DO**	**Light**	**Temp.**	**DO**	**Light**
5/11/92	8/14/92	5/10/93	5/20/92	8/11/92	5/5/93	5/16/93	5/16/93	5/16/93
5/25/92	5/17/93	5/13/93	6/3/92	5/17/93	5/11/93	6/7/93	6/7/93	6/7/93
6/8/92	5/26/93	5/18/93	7/28/92	5/25/93	5/19/93	6/28/93	6/28/93	7/6/93
6/22/92	6/9/93	5/20/93	8/11/92	6/4/93	5/26/93	7/6/93	7/6/93	7/15/93
6/22/92	6/22/93	5/27/93	8/28/92	6/22/93	6/2/93	7/15/93	7/20/93	7/22/93
7/6/92	7/5/93	6/7/93	5/5/93	7/5/93	6/4/93	7/20/93	7/28/93	8/9/93
7/20/92	7/19/93	6/9/93	5/11/93	7/19/93	6/16/93	7/28/93	8/9/93	
7/27/92	8/9/93	6/21/93	5/19/93	7/28/93	6/22/93	8/9/93		
7/30/92		7/5/93	5/20/93	8/9/93	6/30/93			
8/5/92		7/19/93	5/26/93	4/27/94	7/5/93			
8/10/92		7/22/93	6/2/93	5/4/94	7/14/93			
8/14/92		8/5/93	6/6/93	5/11/94	7/19/93			
8/17/92		8/9/93	6/15/93	5/30/94	7/28/93			
8/31/92		8/30/93	6/22/93	8/20/94	8/9/93			
9/14/92			6/30/93		8/11/93			
5/10/93			7/5/93		8/25/93			
5/13/93			7/14/93		5/4/94			
5/20/93			7/19/93		5/11/94			
5/27/93			7/28/93		5/30/94			
6/7/93			8/10/93		8/20/94			
6/9/93			8/11/93		8/31/94			
6/21/93			8/25/93					
6/24/93			9/8/93					
7/5/93			9/22/93					
7/19/93			10/6/93					
8/5/93			10/20/93					
8/9/93			4/27/94					
8/16/93			5/4/94					
8/30/93			5/11/94					
9/13/93			5/30/94					

Appendix 2 Accuracy of underwater depth gauges used during SCUBA surveys of *M. relicta* distribution in 1993 and 1994.

Two gauges were used during surveys in 1993. Prior to use, the accuracy of each gauge was checked in a hyperbaric chamber at Divers Den (Manitoba) Ltd. Results of these tests are presented in the following table.

Tested Depth (Feet of Sea Water)	Gauge Reading (Feet of Sea Water) US DIVERS #D32A 1941	Gauge Reading (Feet of Sea Water) US DIVERS #D32A 1961
10	11	11
20	21	20
30	31	31
50	51	51
100	102	100

Accuracy of the gauge used during 1994 was checked *in situ* against measured depths on a decent line anchored in Roddy L. Readings on this gauge were within 0.5 feet of the actual depth, after correction for relative density of freshwater vs. sea water. Results of this in situ test are detailed below.

Actual Depth on Measured Decent Line (Feet)	Expected Gauge Reading in Feet of Sea water (Actual depth÷ 1.02822)	Gauge Reading (Feet of Sea water)
5.5	5.4	5
8.7	8.5	8
12.3	12.0	12
15.7	15.3	15
18.9	18.4	18
22.4	21.8	22
25.8	25.1	25
29.1	28.3	28
32.5	31.6	32
35.9	34.9	35
39.3	38.2	38
42.6	41.4	41
46.0	44.7	45

Appendix 3 Data used in calculation of ambient light (PAR) at shallowest depths inhabited by *M. relicta* during surveys in a) summer 1993 and b) early spring 1994.

a) summer 1993

Lake	Date	Time	Upper Depth Limit of *M. relicta* (m)	Light at ELA Meteorological Site ($\mu Em^{-2}s^{-1}$)	% Light Trans-mission	Calculated Light at *M. relicta* Upper Limit
224	8/23/93	14:40	6.90	1213	0.10	121
224	8/23/93	15:40	6.90	1021	0.10	102
228	8/24/93	9:40	10.90	1243	0.04	50
228	8/24/93	10:40	10.90	1472	0.04	59
239	8/18/93	11:20	7.30	1616	0.01	8
239	8/20/93	13:50	7.90	1570	0.01	8
239	8/25/93	14:10	9.90	972	0.01	5
239	8/26/93	13:20	6.90	463	0.01	3
239	8/27/93	21:20	6.96	0	0.01	0
305	8/23/93	9:50	7.30	147	0.06	9
305	8/23/93	11:10	7.80	481	0.05	24
373	8/25/93	10:50	6.90	1477	0.05	70
375	5/18/93	10:50	1.80	nd		nd
375	6/11/93	11:20	4.80	1813	0.07	118
375	6/17/93	11:40	4.00	2097	0.08	168
375	6/21/93	11:30	3.20	1772	0.08	142
375	6/24/93	15:10	4.10	1558	0.06	86
375	7/14/93	12:20	4.4	1650	0.06	99
375	8/10/93	11:40	4.8	1673	0.04	63
442	5/19/93	15:40	1.25	273	0.23	61
442	6/1/93	13:40	5.35	945	0.04	34
442	6/8/93	15:10	5.5	617	0.05	28
442	6/29/93	11:40	4.7	826	0.10	83
442	7/14/93	10:40	4.9	630	0.06	38
442	8/10/93	10:40	4.9	1541	0.08	123
468	7/14/93	16:10	8.4	1267	0.06	70
468	7/15/93	14:30	8.4	857	0.06	47
468	8/10/93	14:20	9.1	1543	0.05	77
468	8/24/93	14:00	7.6	1501	0.06	90
626	8/25/92	9:55				

b) early spring 1994

Lake	Date	Time	Upper Depth Limit of *M. relicta* (m)	Light at ELA Meteorological Site ($\mu Em^{-2}s^{-1}$)	% Light Trans-mission	Calculated Light at *M. relicta* Upper Limit
239	4/26/94	10:40	1.52	710.33	0.27	192
239	4/26/94	11:30	1.52	772.00	0.27	208
239	5/2/94	13:40	0.99	nd	0.11	nd
239	5/3/94	15:20	0.46	nd	0.33	nd
239	5/9/94	14:20	0.91	983.83	0.15	143
239	5/19/94	11:30	3.66	1796.67	0.08	144
239	5/19/94	15:40	4.88	471.50	0.04	17
239	5/19/94	14:20	3.66	1082.67	0.08	87
239	5/22/94	13:20	2.74	1240.17	0.14	174
239	5/30/94	14:30	3.96	171.17	0.08	13
442	4/28/94	11:40	1.07	1495.67	0.41	606
442	5/4/94	14:30	1.37	nd	0.34	nd
442	5/11/94	11:10	1.52	1472.50	0.26	375
442	5/20/94	10:40	1.83	1696.67	0.22	373
442	5/30/94	12:50	3.66	201.67	0.17	35
468	4/26/94	15:00	1.37	594.33	0.37	220
468	4/26/94	14:10	1.07	615.17	0.44	271
468	5/2/94	14:30	1.37	nd	0.37	nd
468	5/3/94	14:30	1.37	nd	0.37	nd
468	5/9/94	13:10	1.62	635.67	0.33	210
468	5/19/94	10:20	1.52	1501.67	0.36	541
468	5/31/94	11:10	4.88	nd		nd