Influence of Light Intensity on Activity and Habitat Utilization of Walleye (*Sander vitreus*) in Two Northwestern Ontario Lakes

by

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the Requirements for a Master of Science Degree

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Abstract

Ecologists have paid considerable attention to how and why organisms select particular habitats. Of fundamental importance is discerning which physical factors of the environment restrict the occurrence of organisms to particular habitats. A recent habitat suitability model (HSM) for walleye (*Sander vitreus*) hypothesized that light is the primary controlling variable influencing the spatial and temporal dimensions of feeding habitat. To test the HSM and evaluate the optical and thermal characteristics of walleye habitat I used telemetry to estimate the foraging activity of 24 walleye in two lakes with different water clarity, during periods of changing light intensity. The water clarity in the lakes differed (mean Secchi depths = 2.4 m and 4.8 m); however, the thermal environment, although variable, did not differ consistently between the lakes. Walleye in the stained lake occurred in warmer (mean temperature = 17.0 to 19.0 $^{\circ}$C), shallower (median depth = 3.3 to 7.4 m) water, close to the depth range predicted by the HSM. In contrast, walleye in the clear lake were generally located at depths (median depth = 5.5 to 8.2 m) approximately 8.0 m shallower than predicted by light levels alone (approximately 14.0 to 19.0 m), likely because predicted optimal light levels occurred at depths where the temperature was too cold (approximately 7.0 to 9.0 $^{\circ}$C). The individual activity was highly variable, but the general pattern of behaviour was similar between the two lakes. Walleye activity tended to be low in the afternoon and increased as light levels declined at dusk (i.e., mean change in displacement rate = 35 % between 3 and 5 pm, and 550% between 7 and 9 pm). My results support the hypothesis that subsurface light conditions are a key element of walleye feeding habitat; however, other factors, such as water temperature, submerged structure, and prey-fish behaviours also appear to strongly influence walleye behaviour and distribution. Lake-specific changes to walleye habitat may be the result of predicted changes to water clarity due to exotic species, land-use practises, and global warming.

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Introduction

A fundamental principle in ecology is that relationships between species abundance and quantitative environmental variables are generally nonlinear (Whittaker 1967; Whittaker et al. 1973; ter Braak 1996). Shelford (1919: in Odum 1971) promoted the idea that species not only have a minimum tolerance to some environmental variable, but also a maximum tolerance to that variable, and survival depends on the individual remaining somewhere between those extremes. Hesse (1924: in ter Braak 1996) extended this concept: he stated that species thrive best at some optimum value of an environmental variable and cannot survive when the value is too low or too high. Early works like these helped to identify the unimodal relationship that species generally have with environmental variables (Whittaker 1967; Whittaker et al. 1973). This discovery was integral in formulating the concept of the niche and in the development of habitat selection theory.

Habitat selection occurs almost universally among species (Orians and Wittenberger 1991), and can be thought of as an organism-specific filtering process that uses the organism's morphology and physiology to transduce various environmental variables down to some optimal microhabitat in space and time (Huey 1991). These complex interactions between the physical environment and an organism's physiology and morphology can shape the behaviour, life history, demography, and competitive interactions of organisms, and can sometimes have a dramatic impact on population and community interactions (Huey 1991).

Since habitat selection affects nearly all of an individual's subsequent choices, physiological capacities, and ultimately its ecological performance (Huey 1991; Orians and Wittenberger 1991), considerable attention has been paid to how and why organisms select particular habitats (i.e., Cody 1985; Huey 1991; Jaenike and Holt 1991; Orians and Wittenberger 1991; Pulliam and Danielson 1991; Rosenzweig 1991; Abramsky et al. 2002; Morris 2003). One particular area of interest that has received much attention is the interaction between physiology and the environment. Ecologists have attempted to discern which physical factors of the environment restrict the occurrence of organisms to particular habitats (Huey 1991). Ryder and Kerr (1989), concerned with aquatic habitats of fish, identified a subset of survival determinants that are of high priority: oxygen, heat, light, and nutrients. These four essential environmental determinants influence habitat selection by exerting either a *controlling* or a *limiting* effect on an individual (Fry 1947: in Ryder and Kerr 1989). For example, oxygen and heat can limit the occurrence of a fish: if respiration and metabolism requirements are not fulfilled, it can result in severe physiological stress, and ultimately, death. Light and nutrients are more likely to control or shape the behaviour and distribution of a fish. However, suboptimal levels of light and nutrients rarely, if ever, induce mortality (Ryder and Kerr 1989).

For fish, it is reasonable to believe that survival depends on satisfying the most critical needs first (i.e., the limiting factors: dissolved oxygen, preferred temperature), and the less critical ones second (i.e., the controlling factors: light and nutrients) (Ryder and Kerr 1989). Scherer (1971) documented this hierarchical response to limiting factors, when he observed walleye, a negatively phototactic species, temporarily discontinue its light avoidance behaviours in order to satisfy a more immediate need for dissolved oxygen. Priority was to those factors that most imminently threatened life.

Because of the nature of limiting factors, their influence on habitat selection is somewhat obvious: if suitable conditions are not located, death ensues. Less obvious, however, is the influence of controlling factors on habitat selection. Generally, controlling factors, to some degree, shape the behaviour and distribution of fish. Distribution and behaviour ultimately contribute to species survival, although neither appear to have a direct physiological effect that is life threatening (Ryder and Kerr 1989). The same is true for subsurface illumination. Inappropriate light levels have never been linked to massive fish mortalities, whereas low levels of dissolved oxygen or high water temperatures have been linked to fish deaths. However, it is plausible that light may operate at the synecological level by allowing one species adapted for particular light conditions to have competitive advantage over another (Ryder and Kerr 1989; Vogel and Beauchamp 1999). In this way, it has been suggested that light may act as "an ecological cleaver" that determines the relative dominance of species (Ryder and Kerr 1989). If this is true, then a greater understanding of the influence of subsurface illumination on habitat selection of fish would be beneficial to both ecologists and managers alike. A fish species of particular interest is the walleye because of its known sensitivity to light (Scherer 1976; Ryder 1977; Ali and Anctil 1977; Ali et al. 1977; Burkhardt et al. 1980; Vandenbyllaardt et al. 1991). It has been hypothesized that light is the principal abiotic controlling variable that determines the temporal and spatial dimensions of feeding in walleye (Ryder 1977). Therefore, further examination of the influence of subsurface illumination on walleye habitat selection has the potential to provide insight into walleye behaviour, growth, and ultimately, survival.

Walleye are adapted for living in a dimly-lit environment. They are a negatively phototactic (Scherer 1976), benthic species (Scott and Crossman 1973; Christie and Regier 1988; Ryder 1977; Scherer 1976), that have adapted well to crepuscular or nocturnal feeding and spawning (Ali et al. 1977; Ryder 1977). Morphological and physiological adaptations within the eye that enhance scotopic vision have allowed walleye to reach their optimum visual performance under light intensities that cause other competing species to become inactive (Ali et al. 1977; Ryder 1977; Vandenbyllaardt et al. 1991). These adaptations have allowed walleye to colonize almost half of the entire continent of North America, in lakes and rivers displaying a wide range of light regimes. A study of nearly 10 000 lakes in Ontario, Canada (Lester et al. 2002), revealed that the proportion of lakes that contain walleye was greatest for lakes with a mean Secchi depth of approximately 2 m (Figure 1); and walleye yield was also greatest at this Secchi depth (Figure 2). These data further support the large amount of anecdotal knowledge that suggest walleye abundance and persistence are linked to subsurface illumination. For this reason, ecologists would like to improve their understanding of how subsurface light regimes influence walleye behaviour and distribution, as well as the productive capabilities of lakes containing walleye (in terms of sustainable yield).

In freshwater lakes, the subsurface light regime is the end product of two physical processes acting upon submerged light: scattering and absorption. The logarithmic diminution of light with depth by these processes is referred to as light *extinction* (Williams 1970). Each water body has optical characteristics specific unto itself; therefore, transmission of light in water is a function of surface illumination and the specific extinction capability of each water body. In most boreal lakes light extinction

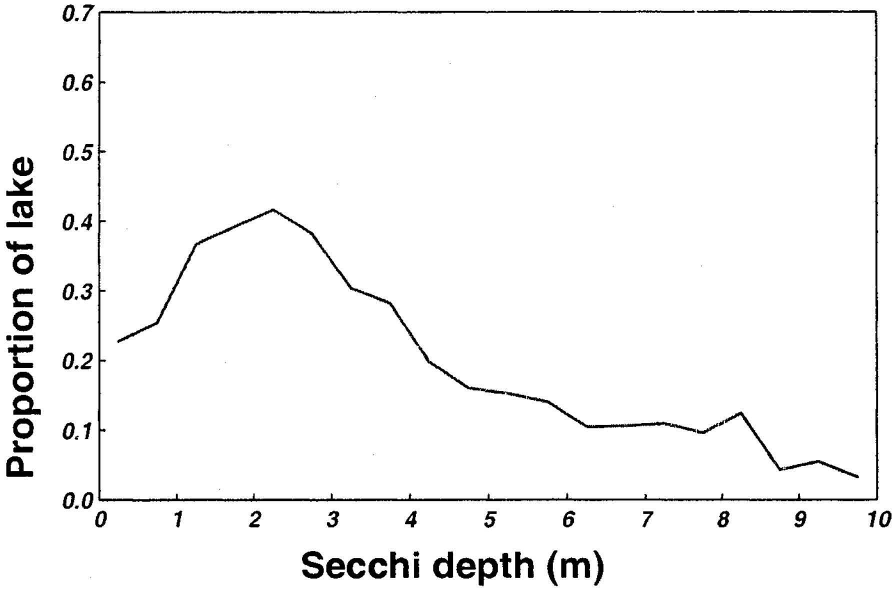

Figure 1. From a study of 9 872 lakes in Ontario, Canada, the proportion of lakes containing walleye varies with mean Secchi depth (from Lester et al. 2002).

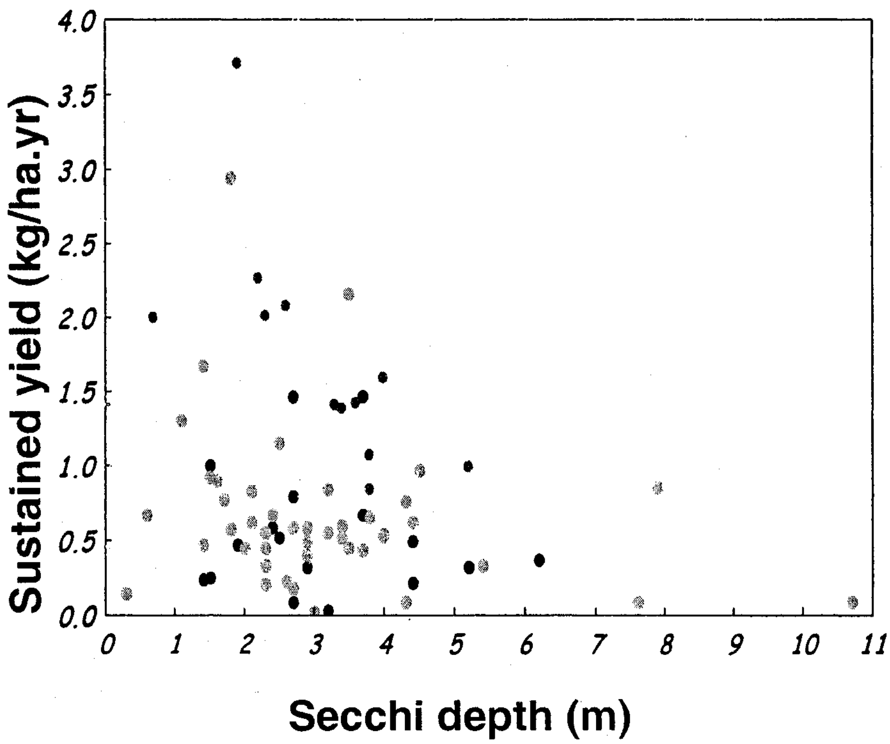

Figure 2. Commercial and angler walleye yield from lakes with different mean Secchi depths (from Lester et al. 2002).

capabilities are a function of water colour (Koenings and Edmundson 1991; Fee et al. 1996) and, to a lesser extent, turbidity (Koenings and Edmundson 1991). Water colour in these lakes is mostly due to the presence of dissolved organic compounds (Dillon et al. 1988; Koenings and Edmundson 1991; Fee et al. 1996; Perez-Fuentetaja et al. 1999; Bukaveckas and Robbins-Forbes 2000; Patrick 2003), and their ability to absorb selectively in the shorter wavelengths. Because inputs of dissolved organic matter can vary dramatically within and amongst watersheds, water clarity can vary dramatically from one lake to the next.

To gain a better understanding of how subsurface illumination influences walleye behaviour and distribution, as well as the productive capabilities of lakes containing walleye, Lester et al. (2004) developed a habitat supply/potential yield model for walleye that integrated the important, but often overlooked, role of water clarity with climate, nutrients, and lake morphometry. The model is based on the idea that walleye have a preferred light intensity that they will occupy, when all other variables are equal or nonrestricting. As walleye are known to be a negatively phototactic (Scherer 1976; Ryder 1977; Ali and Anctil 1977; Ali et al. 1977; Burkhardt et al. 1980; Vandenbyllaardt et al. 1991), crepuscular species it was reasonable to apply the idea of an optimum light intensity.

Using empirical data from two different experiments, Lester et al. (2004) estimated an optimum light intensity range for walleye. In the first experiment, Scherer (1976) applied three surface-light treatments (high, medium, low) to walleye in a tank and observed their vertical positioning. For the bright light tests (275 lux at the top of the tank to 245 lux at the bottom), walleye were observed to stay at the bottom of the tank. For the medium light tests (32 to 25 lux) walleye tended to stay near the middle of the tank. For the low light tests (3.3 to 2.6 lux) walleye stayed near the surface of the tank. These observations suggested that walleye prefer light intensities near 28 lux. The second experiment, conducted by Ryder (1977), used angling catch per unit effort to describe the effect of light on walleye foraging behaviour. During the summer months, walleye were angled while surface illumination was measured. Angling catch rate increased as the light levels decreased (with the setting of the sun) until surface illumination reached approximately 300 lux. Once levels dropped below that point, angling success dramatically decreased. Since the fish were angled in depths of 2 to 6 m, subsurface illumination at fish depth had to be estimated using the Lambert-Beer law:

$$l_z = l_o e^{-\varepsilon * z} \qquad (1)$$

where l_z is light at-depth, l_o is surface illumination, ε is the vertical extinction coefficient, and z is depth. The calculations resulted in an optimum light intensity of 28 lux; a range of 8 to 68 lux described light conditions within 50 % of the maximum response (Figure 3). Together, the results from these two experiments suggested that walleye have a final preferendum of approximately 28 lux, and prefer to forage when subsurface illumination is in the range of 8 to 68 lux.

With this estimated optimal light intensity range, one can predict the location within the water-column of the optimal optical habitat. Figure 4 illustrates how the location of the preferred light intensity is dependent on surface illumination (i.e., the height and location of the sun), and water clarity (represented by a change in mean Secchi depth). It is calculated for a stained lake with a mean Secchi depth of 2 m, and a moderately clear lake with a mean Secchi depth of 4 m. In the clear lake, the preferred optical habitat has

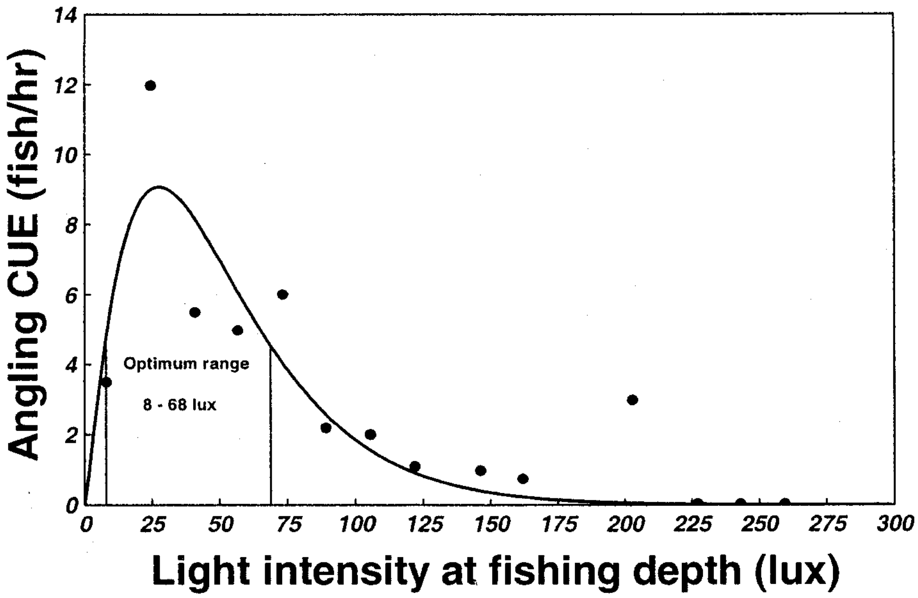

Figure 3. Walleye angling catch per unit effort during changing light intensities at fishing depth. Vertical broken lines indicate subsurface light intensities that correspond with a CUE +/- 50% of the maximum CUE. These light intensities represent the upper and lower bounds of a hypothesized optimal range of subsurface illumination for walleye foraging behaviour (figure from Lester et al. [2004]).

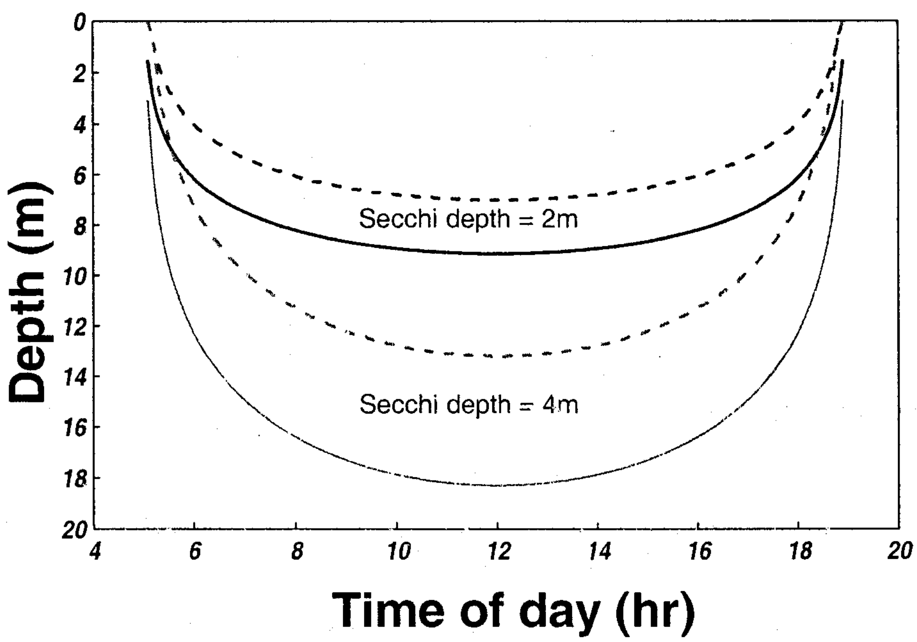

Figure 4. Optimal walleye depth, predicted from the location of the optimal light intensity range in both a stained lake with a mean Secchi depth of 2 m (the upper pair of solid and broken lines), and a clear lake with a mean Secchi depth of 4 m (the lower pair of solid and broken lines). In each pair of solid and broken lines, the broken line represents 68 lux and the solid line represents 8 lux (figure from Lester et al. [2004]).

moved deeper and increased in size. Ryder and Kerr (1989) noted that subsurface illumination likely has more of a behaviour-controlling effect, rather than a behaviour-limiting effect like that of dissolved oxygen or temperature, and suggested that a walleye's desire to satisfy light preferences may be of less priority than that of its thermal preferences. Because walleye growth and metabolism are strongly influenced by temperature (Shuter and Meisner 1992; Kershner et al. 1999; Quist et al. 2002), it is reasonable to assume then, that unfavourable temperatures will interfere with, or modify, this light-avoidance behaviour. When the preferred temperature range of walleye (defined by Christie and Regier [1988] as 18 to 22 $^{\circ}$ C, and then expanded by Lester et al. [2004] to 11 to 25 $^{\circ}$ C) is taken into consideration it becomes apparent that the amount of preferential habitat could potentially be restricted by sub-optimal water temperatures (represented in Figure 6 by a deep water exclusion zone). For example, in clear lakes, the optically preferential habitat within the cold hypolimnetic waters may become undesirable walleye habitat. For this reason, Lester et al. (2004) concluded that preferred walleye habitat is best described as *thermal-optical* habitat: the area of the lake where both optimal temperatures (11 – 25 $^{\circ}$ C) and optimal light levels (8 – 68 lux) coexist. Using this definition of preferred walleye habitat, it is reasonable to expect walleye inhabiting lakes of differing water clarity to utilize different habitat and perhaps display different foraging patterns. Walleye in clear lakes may be forced to move to colder, deeper depths to find areas of suitable light intensity. Or, if suitable thermal-optical habitat only exists during dawn and dusk, walleye may limit foraging activities to these periods of the day. In stained lakes where optimal thermal-optical habitat exists throughout the entire day, walleye may forage continually and diurnal peaks in activity

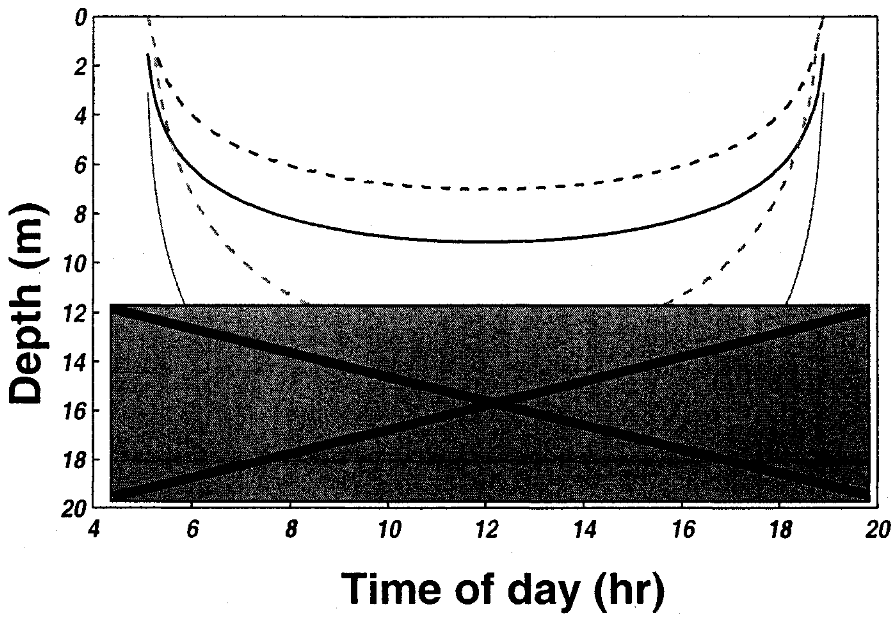

Figure 5. In lakes where optimal optical habitat extends into deep, cold waters, thermal preferences of walleye (11-25°C) may render some optimal depths undesirable. The grey zone with the crossed lines represents cold, hypolimnetic waters (figure from Lester et al. [2004]).

may not occur.

To evaluate the influence of light on the feeding habitat and activity of walleye, I monitored the hourly movements of walleye under changing light conditions, in two lakes with differing water clarity. Specifically, light intensity was measured to see if it was the same at all fish depths within, and between lakes. Next, fish depth was examined to see if fish were at the same depth within, and between lakes. Then, water temperature at the fish's depth was measured to determine if walleye were utilizing the same thermal habitat within and between lakes. Lastly, activity levels were recorded for walleye in each lake, and were examined to determine whether they differed within and between lakes.

Methods

The study was conducted in Upper Marmion Lake and Lower Marmion Lake, in northwestern Ontario (Figure 6). The lakes are approximately 230 km west of Thunder Bay, Ontario, and just north of the town of Atikokan. Upper and Lower Marmion Lakes are part of the Seine River system that flows from Lac des Milles Lacs in the north, through to Rainy Lake and Lake of the Woods in the south (for study site details see Appendix I).

Upper and Lower Marmion Lakes were chosen for three main reasons. First, the two lakes display contrasting water clarities. Upper Marmion Lake is considered a stained lake and has an orangey-brown (or "tea colour") appearance. It has approximately half the mean Secchi depth, 5 times the colour, and twice the concentration of DOC as Lower Marmion Lake (Table 1). Lower Marmion Lake is a moderately clear lake, displaying a yellowish-green appearance. Second, they are located very close together (see Figure 6 or Appendix I). Third, another study conducted by the Ontario Ministry of Natural Resources (Atikokan Area Office), using radio tagged walleye in Lower Marmion Lake, was in its second year of operation when this thesis project began, and the radio tagged fish, telemetry equipment, boat, motor, and trailer could be utilized for this study.

Secchi depth measurements were made to describe the water clarity of the two lakes at each radio-tagged walleye location and temperature sampling location, in the summer of 2003 and 2004 (Figures 7 and 8). The Secchi depth measurements were taken using a standard black and white 25 cm Secchi disk, dropped down into the water on the

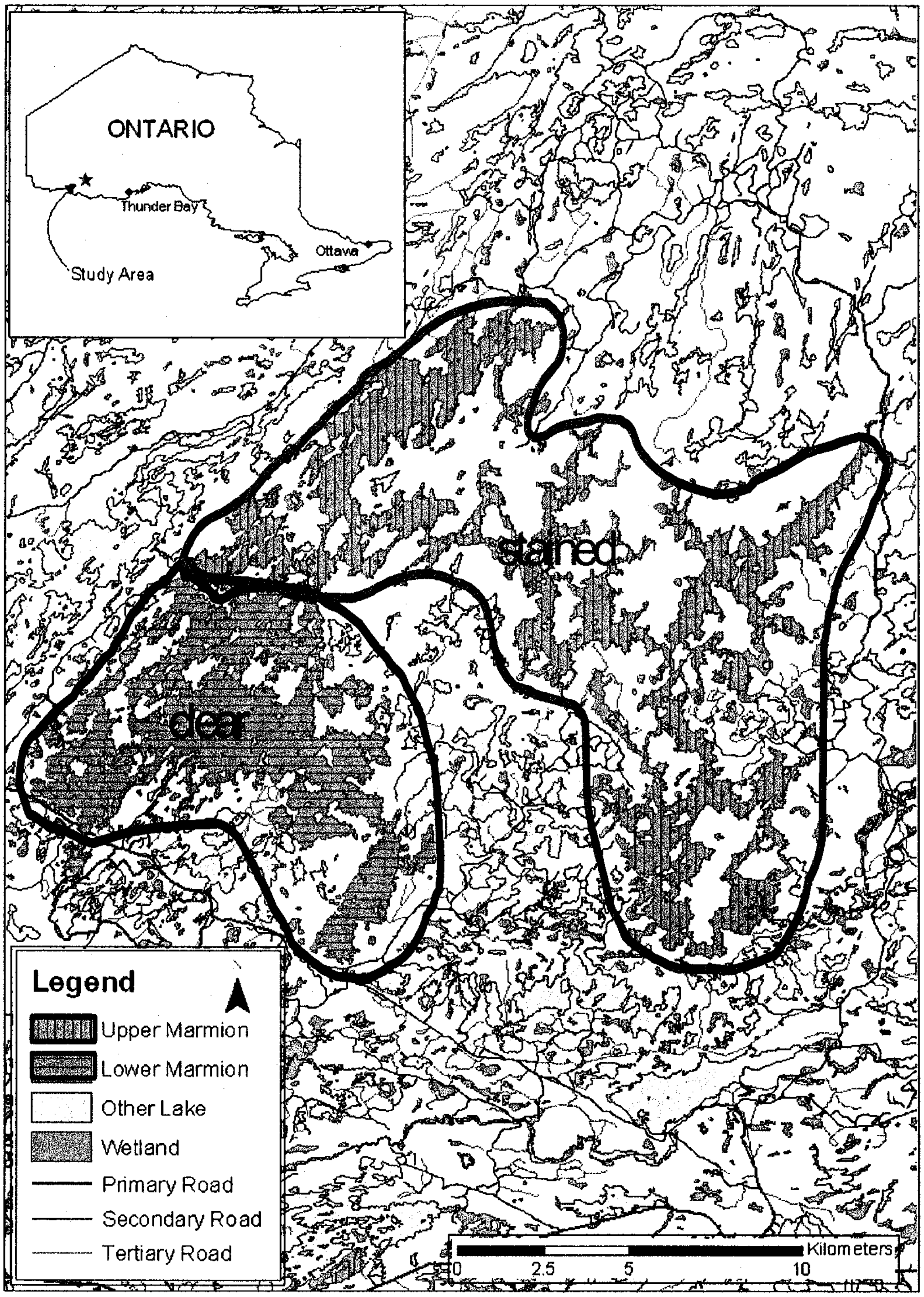

Figure 6. The relative locations of Upper Marmion Lake (stained) and Lower Marmion Lake (clear). Insert shows the location of the lakes in relation to cities within Ontario, Canada.

Table 1. Physical and limnological characteristics for Upper and Lower Marmion Lakes, Atikokan, Ontario (data from June 2003 survey).

	Upper Marmion Lake	Lower Marmion Lake
Surface area (ha)	5599	3982
Max. depth (m)	36	24
Mean depth (m)	7	7
Turbidity (ntu)	9.83	10.68
Mean Secchi depth (m)	2.5	4.6
Colour (tcu)	54.55	9.86
DOC (mg/L)	11	5.40

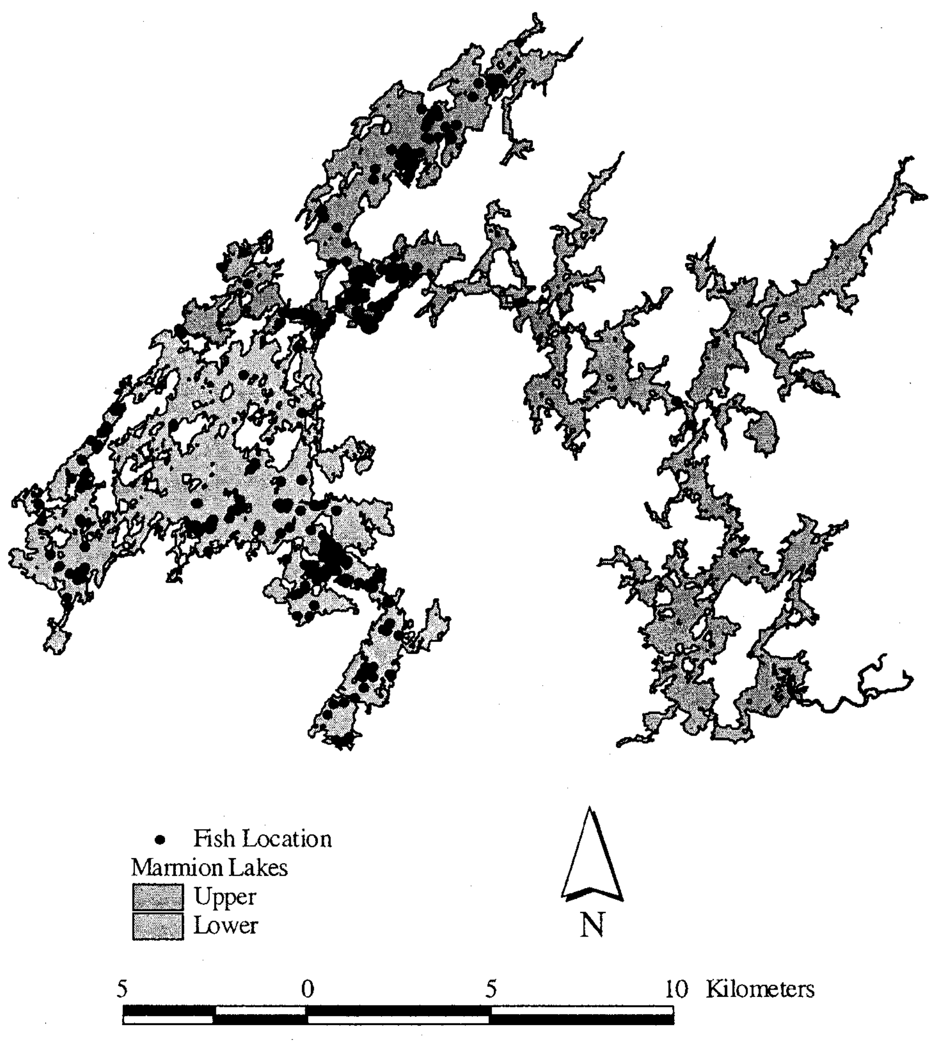

Figure 7. The locations of where radio-tagged walleye were found in Upper and Lower Marmion Lakes, May to August, 2003 and 2004 (represented by dots).

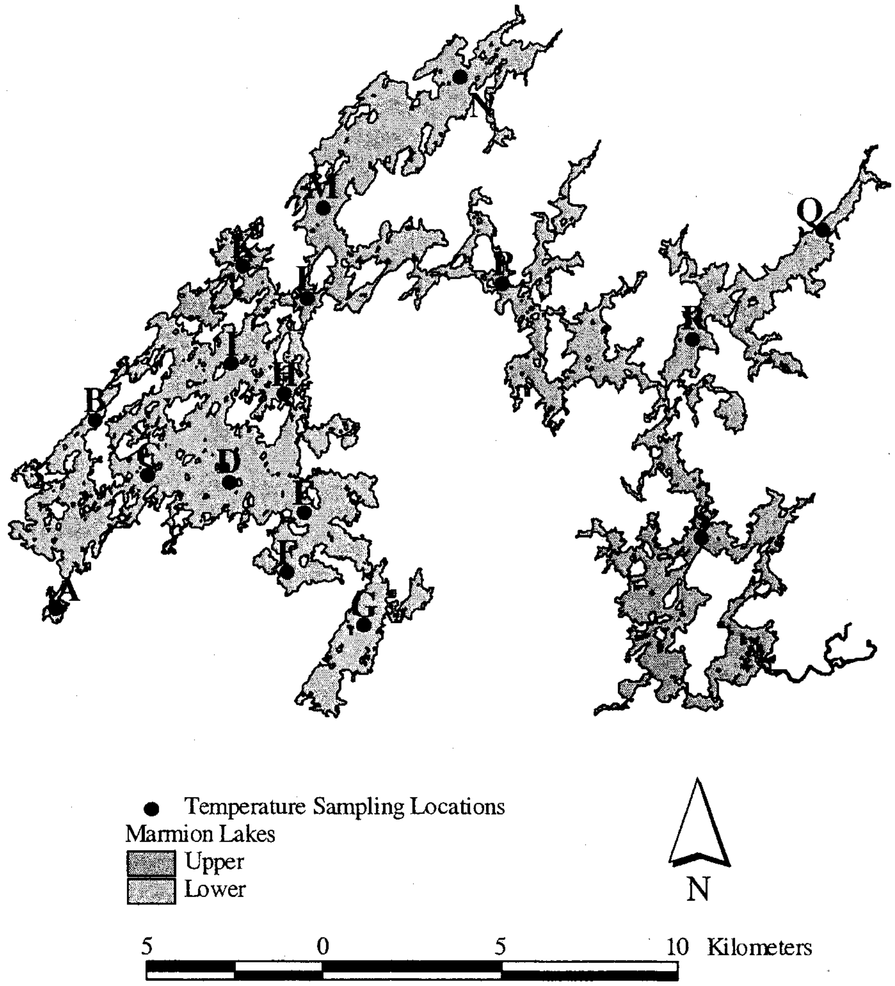

Figure 8. The location of 17 thermal profile sampling sites. Dots and letter labels represent sampling sites.

shaded side of the boat. A reading was taken at the point the disk disappeared and then again when it reappeared, and the two readings were averaged.

A second method was used to describe the light environment. A Li-Cor light meter, fitted with a surface mounted LI-200SZ Pyranometer sensor, and a submersible LI-190SZ Quantum sensor was used to determine a mid-summer vertical light extinction coefficient that could be used with the Lambert-Beer Law to describe light at-depth (more explanation of how the vertical light extinction coefficient was calculated and used to determine light at-depth follows below). Ground level solar radiation, used in the determination of light-at-depth, was measured using a Li-Cor LI-200SZ Pyranometer Sensor, part of a meteorological station located approximately 50 km northwest of Upper and Lower Marmion Lakes, in one of the Cold Water Lakes experimental cut sites (unpublished data provided by Blake LaPorte, Centre for Northern Forest Ecosystem Research, Ontario Ministry of Natural Resources).

To describe the thermal regimes of each lake, a MK. II Digital Telethermometer was used to measure water temperature. Vertical thermal profiles were constructed by measuring the water temperature at 1.0 m intervals, with a surface reading taken at approximately 0.1 m deep. Thermal profiles were measured sporadically over the summer month of 2003 and 2004, at locations D and L (Figure 8), for the purpose of monitoring stratification and thermocline depth. Thermal variation within each lake was measured on two occasions (mid-July and mid-August, 2004) at various locations (Figure 8).

A number of walleye were selected from Upper and Lower Marmion Lakes and were fitted with Advance Telemetry Systems (ATS) radio transmitters. By May, 2003, when this study began, 14 tagged walleye from the previous study were still available for use in Lower Marmion Lake. In the first week of June, 2003, I implanted 10 additional transmitters into walleye in Upper Marmion Lake. For walleye collection and transmitter implantation methods, see Appendix II. For body size information on the tagged walleye, please see Table 2, Figures 9 and 10.

I tracked the radio tagged fish during June, July, and August of 2003 and 2004. The majority of June, 2003, was spent learning the layout of both lakes, locating navigational hazards, perfecting the tracking technique, and calibrating the depth sounder with an underwater camera. Much of June, 2004, was lost from tracking because of outboard motor breakdowns.

Radio tagged walleye were tracked on an hourly basis during daylight hours (09:00 to 22:00). However, the majority of tracking occurred between 14:00 and nightfall so that walleye behaviour could be observed during changing light conditions. For safety reasons, night tracking on both lakes was not possible. An ATS receiver unit was used with a bow-mounted bi-directional antenna. Tracking by boat was done at speeds of approximately 30 to 40 km/h with the receiver continuously scanning (at 2 or 4 second intervals) all frequencies. Once a transmitter signal was picked up, locating the tagged fish occurred at low speeds (i.e., less than 5 km/h). Transmitters could generally be detected at distances of approximately 800 m (with distance decreasing with fish depth).

To determine the location of a tagged fish, the receiver sensitivity (gain) was decreased as the distance to the fish decreased until the strongest signal was obtained from the lowest gain. This generally would indicate that the fish was within a 30 m radius of the boat. At this time, the cable connecting the antenna to the receiver was

Table 2. Transmitter and biological data for tagged walleye (TLEN = total length, FLEN = fork-length, and RWT = round-weight).

Sample	Transmitter Freq. (MHz)	Antenna Length (mm)	Date Implanted	Lake	TLEN (mm)	FLEN (mm)	RWT (g)	Age (years)	Tag ID
1	48.031	35.56	20-Jun-03	Upper Marmion	558	519	1450		115965
2	48.052	35.56	09-May-01	Lower Marmion	666		3200	12	115931
3	48.091	30.48	30-May-01	Lower Marmion	529		1600	5	115917
4	48.132	35.56	22-May-02	Lower Marmion	594		2100	7	115812
5	48.152	30.48	31-May-01	Lower Marmion	555		1380	5	115941
6	48.191	35.56	10-May-01	Lower Marmion	587		2100	6	115936
7	48.211	35.56	20-Jun-03	Upper Marmion	642	609	2080		115954
8	48.251	35.56	29-May-02	Lower Marmion	686		3200	11	113465
9	48.272	35.56	23-May-02	Lower Marmion	609		2100	7	113491
10	48.312	35.56	05-Jun-03	Upper Marmion	605	571	1950		115928
11	48.331	30.48	08-Jun-01	Lower Marmion	512		1290	6	115877
12	48.351	35.56	08-Jun-01	Lower Marmion	635		2950	14	115855
13	48.431	35.56	28-May-02	Lower Marmion	522		1200	6	115958
14	48.471	30.48	16-May-02	Lower Marmion	520		1300	6	115878
15	48.491	35.56	07-Jun-01	Lower Marmion	583		1700	11	113681
16	48.562	35.56	06-Jun-03	Upper Marmion	558	520	1625		115892
17	48.674	35.56	06-Jun-03	Upper Marmion	578	540			115845
18	48.695	35.56	06-Jun-03	Upper Marmion	510	478	1200		115899
19	48.715	35.56	06-Jun-03	Upper Marmion	610	579	1980		113498
20	48.734	35.56	06-Jun-03	Upper Marmion	569	533	2575		113461
21	48.754	35.56	06-Jun-03	Upper Marmion	564	538	2525		115828
22	48.774	35.56	20-Jun-03	Upper Marmion			1520		
23	48.794	35.56	20-Jun-03	Upper Marmion	628	593	2100		
24	48.811	35.56	20-Jun-03	Upper Marmion	595	559	1850		

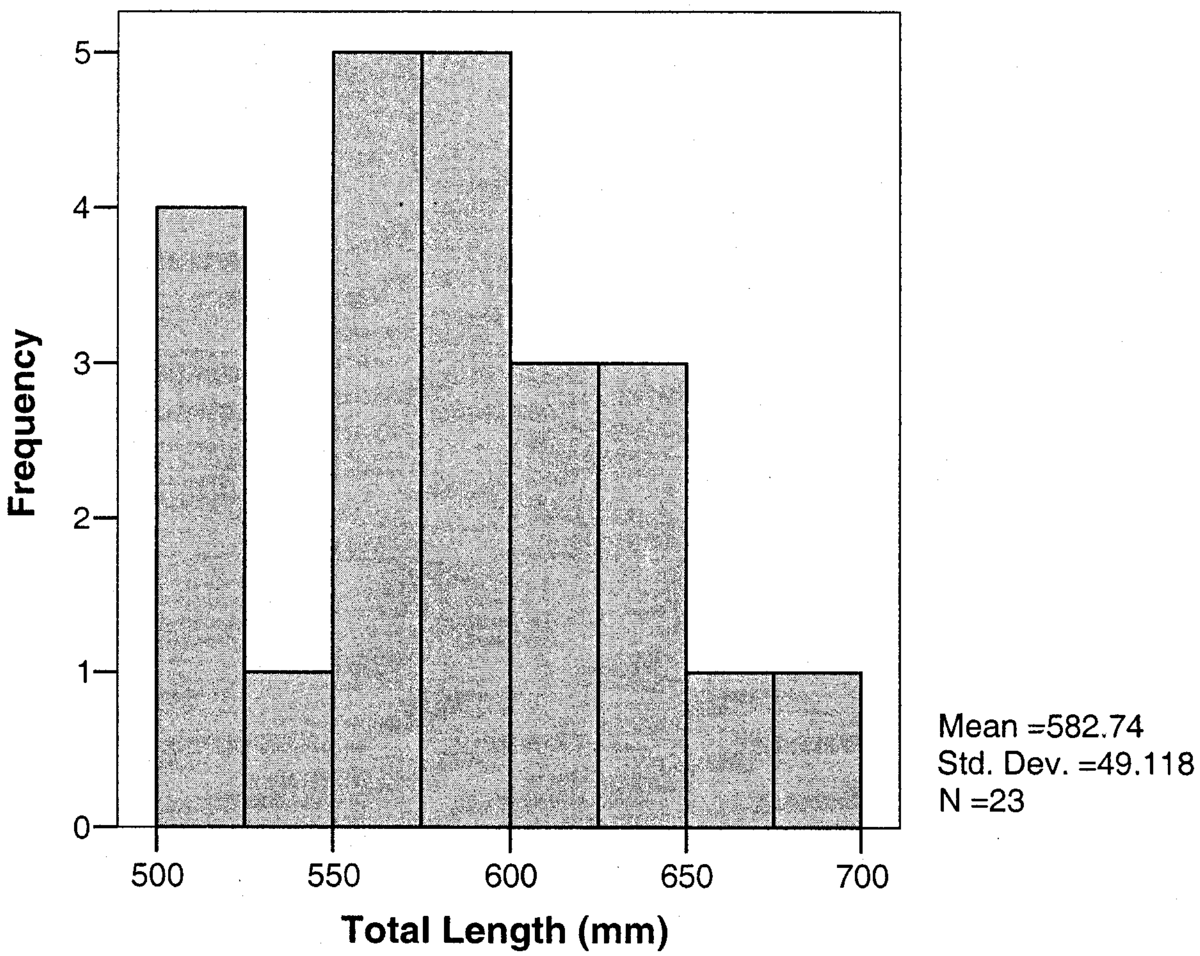

Figure 9. The frequency distribution of total lengths of tagged walleye from 2003 and 2004.

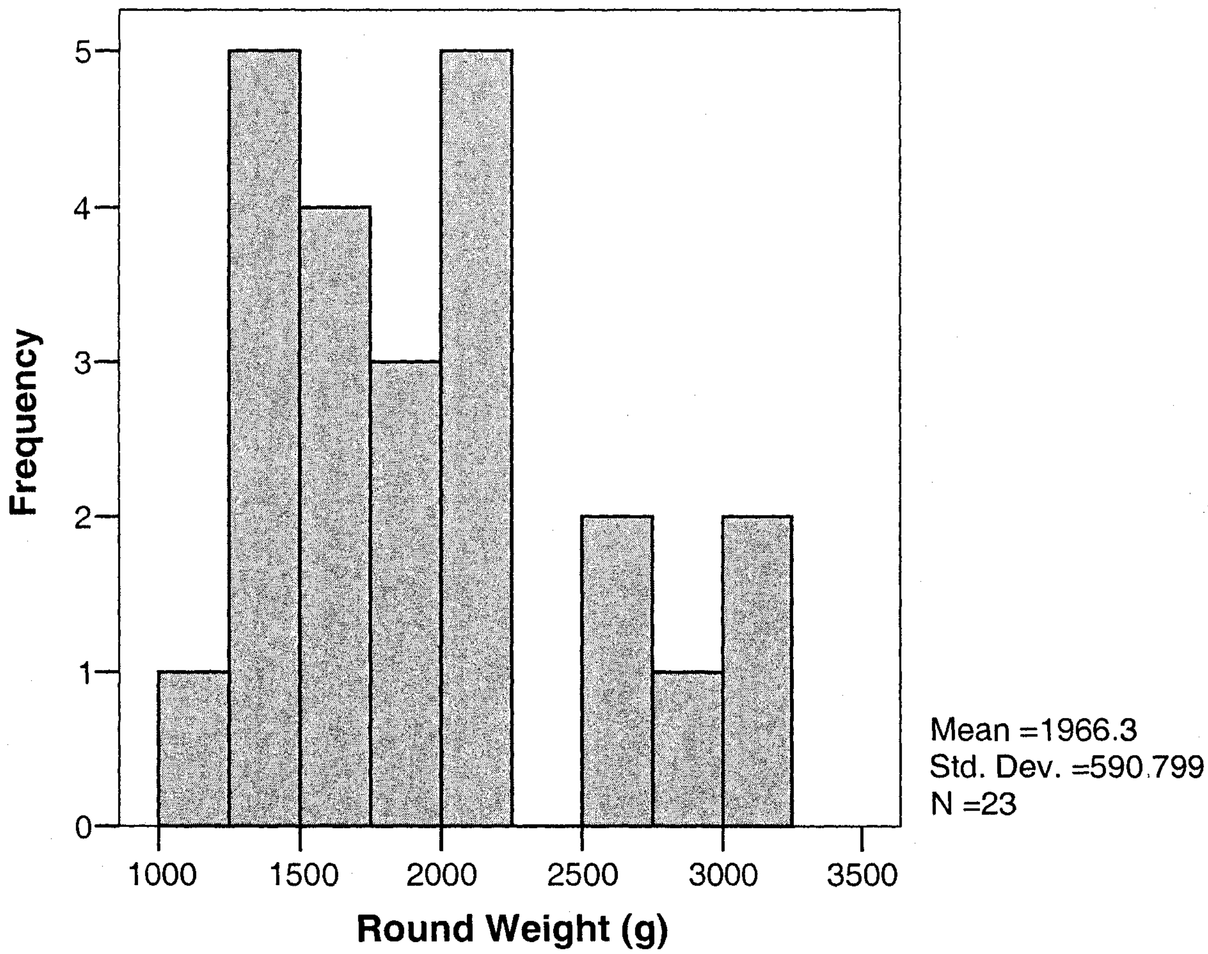

Figure 10. The frequency distribution of round weights of tagged walleye from 2003 and 2004.

disconnected from the antenna, and the receiver sensitivity was turned back up to maximum (the 5 m cable behaved as a short-range, omni-directional antenna). I would then move the boat in the direction I believed the fish was located until the transmitter could be picked up on the receiver (using only the cable as an "antenna"). Again, the receiver sensitivity was reduced until the strongest signal was obtained from the lowest gain. This procedure would usually put the boat within a 10 m radius of the tagged walleye.

Once a walleye's location was determined, the following measurements were made: water depth, fish depth, distance from shore, Universal Transverse Mercator (UTM) coordinates for the location, bottom structure present, adjacent shoreline structure, water temperature at fish depth, wave height, cloud cover, weather conditions, and a Secchi disk reading. Water depth was measured to the nearest 0.1 m, using a Hummingbird depth sounder. Fish depth was either read directly from the depth sounder (as the fish was occasionally detected by the depth sounder, often when the fish was suspended over deep water, or in a location free of submerged structure), or it was assumed to equal to the water depth. The distance to shore measurement was taken using a Bushnell 1000 Rangefinder. The UTM coordinates for the location were recorded using a Garmin 45 global positioning system. The bottom structure was determined using the depth sounder, after previous calibration using an Aqua-View submersible closed-circuit camera. The adjacent shoreline structure was determined visually.

Although walleye tracking usually began each day around 14:00, the time required to locate the fish that was to be tracked for the day was variable. Resulting data was rarely collected at the same time each day. Therefore, for ease of analysis, data was usually categorized into time intervals (the names of which corresponded with the hour in which the walleye location was determined; i.e., a walleye location determined between 20:00 and 20:59 would be placed in the category 20:00).

Multiple measures were made on each fish over the summers of 2003 and 2004, so data were averaged to produce a mean measurement per time interval, per fish (see Table 3 for a summary of numbers of locations recorded per time interval, per fish). Light-at-depth in each lake was estimated from surface illuminance using the Lambert-Beer law (see equation 1 in Introduction, page 7). Mean hourly values of ground-level solar radiation (I_o) for each day of the summers of 2003 and 2004 were used to calculate a mean hourly light-at-depth value for each hour, of each day, for both Upper and Lower Marmion lakes. To obtain a vertical extinction coefficient (ε) for each lake, a Li-Cor light meter was used to measure light intensity at 1 m intervals from 0.01 m below the surface to the bottom of the lake. The percent transmittance was then calculated and the negative slope of the light at-depth relationship plotted on a log-transformed axis was interpreted as the vertical extinction coefficient. This value was compared with theoretical values from the literature (Koenings and Edmundson 1991) for lakes of similar clarity to be sure that this method was accurate. The vertical extinction coefficient was calculated for each lake only once, in the middle of the summer, 2004.

The water temperature at fish-depth, at each fish location, was measured using a MK. II Digital Telethermometer. Once the fish's depth was determined, the telethermometer probe was dropped down to that depth and allowed to sit for approximately one minute to stabilize, before the reading was recorded.

To estimate foraging activity, I measured the distance from one walleye location to

Table 3. Number of walleye locations per individual, per hour, for the summer months of 2003 and 2004.

Fish ID	Year	Month	Time Interval 10:00	11:00	12:00	13:00	14:00	15:00	16:00	17:00	18:00	19:00	20:00	21:00	Total	Total/Fish
031A	2003	June														6
		July						1	1	1	1	1	1		6	
		August														
	2004	June														
		July														
		August														
052A	2003	June														6
		July														
		August						1	1	2	1	1			6	
	2004	June														
		July														
		August														
091A	2003	June														7
		July						2		1	1	2	1		7	
		August														
	2004	June														
		July														
		August														
132A	2003	June														30
		July				1			1	1	1	1	1		6	
		August														
	2004	June		1	1	1	1	1							5	
		July					1		1	2		1	1	1	7	
		August						2	1	2	2	2	3		12	
191A	2003	June			1										1	15
		July					1		1	3	1		1	1	8	
		August														
	2004	June						1	1	1	1	1	1		6	
		July														

Fish ID	Year	Month	10:00	11:00	12:00	13:00	14:00	15:00	16:00	17:00	18:00	19:00	20:00	21:00	Total	Total/Fish
								Time Interval								
		August														
251A	2003	June				2	2								4	36
		July					1	1		2	1	1		1	7	
		August								1	1	1	1		4	
	2004	June			1	1	2	1							5	
		July							3	2	2	2	1		10	
		August						1	2		1	1	1		6	
312A	2003	June														7
		July						1	1	1	1	1	1		6	
		August														
	2004	June			1										1	
		July														
		August														
331A	2003	June		1				2							3	21
		July														
		August							1	1	1	1			4	
	2004	June														
		July						3	1	2	2	2	2	2	14	
		August														
351A	2003	June			1	1	1	2							5	20
		July					1		2	2	1	1	1	1	9	
		August														
	2004	June														
		July						1	1	1	1	1	1		6	
		August														
431A	2003	June														27
		July						1	1	1	1	1	1		6	
		August														
	2004	June							1	1	1	1	1	1	6	
		July						1	1	2	2	2	1		9	
		August	1	1	1	1	1	1							6	

Fish ID	Year	Month	Time Interval 10:00	11:00	12:00	13:00	14:00	15:00	16:00	17:00	18:00	19:00	20:00	21:00	Total	Total/Fish
471A	2003	June														9
		July									2		1		3	
		August														
	2004	June														
		July				1			1	1	1	1	1		6	
		August														
562A	2003	June					1	1							2	24
		July														
		August						1	1	1	1	1	1		6	
	2004	June							2	3	1	3	1		10	
		July						1		2		1	1	1	6	
		August														
674A	2003	June			1										1	20
		July					1	1	2	3	2	2	2		13	
		August														
	2004	June														
		July					1		1	1	2		1		6	
		August														
695A	2003	June														21
		July														
		August														
	2004	June														
		July						1	2	2	2	2	2		11	
		August							2	2	2	2	2		10	
715A	2003	June														7
		July						2	1	1	1	1	1		7	
		August														
	2004	June														
		July														
		August														
734A	2003	June					1	1							2	29

Fish ID	Year	Month	Time Interval 10:00	11:00	12:00	13:00	14:00	15:00	16:00	17:00	18:00	19:00	20:00	21:00	Total	Total/Fish
		July														
		August					1	1	1		1				4	
	2004	June							1	1	1	1	1		5	
		July						1	2	2	2	2	1	1	11	
		August						2	1	1	1	1	1		7	
754A	2003	June														5
		July														
		August							1	1	1	1	1		5	
	2004	June														
		July														
		August														
774A	2003	June														12
		July														
		August														
	2004	June														
		July					1		1	1	1	1			5	
		August					1	1	1	1	1	1	1		7	
794A	2003	June														10
		July														
		August						1	2	2	3	1	1		10	
	2004	June														
		July														
		August														
811A	2003	June														27
		July						2		1	1	1	1	1	7	
		August						1							1	
	2004	June						1	1	1	1	1	1		6	
		July														
		August					1	2	2	2	2	2	2		13	
		Total	1	3	7	8	19	43	46	58	52	49	43	10	339	

the next subsequent walleye location and recorded this measurement as distance displaced. Every effort was made to locate walleye in exactly one hour intervals; however, this was not always possible. Typical tracking intervals were slightly longer or shorter. For this reason, the distance displaced between each walleye location was divided by the time that had elapsed to provide a standardized value: displacement rate. To see patterns more clearly, and avoid the misleading ability of highly active individuals, *change in* displacement rate was examined, rather than simply displacement rate. To do this, the displacement rate of an individual in one time interval simply had the displacement rate of the previous time interval subtracted from it, thus revealing the change (see Figure 11).

All statistical analyses of tracking data was carried out using SPSS 13.0 software for Windows. Full factorial analyses of variance (ANOVA) were used to compare dependent variables between lakes and among time categories (months or hours), and evaluate interaction terms. In order to convey as much information about the dataset as possible, I have chosen to [mostly] use boxplot graphs. Although they do not display the mean value (that the ANOVA tests use), they do give a good indication of the central tendency (median) and the distribution of the data points (25^{th}, 75^{th} quartiles, the range minus outliers and extremes, outliers, and extreme values). Natural-log transformations were used to better approximate normal distributions for some data, prior to analysis.

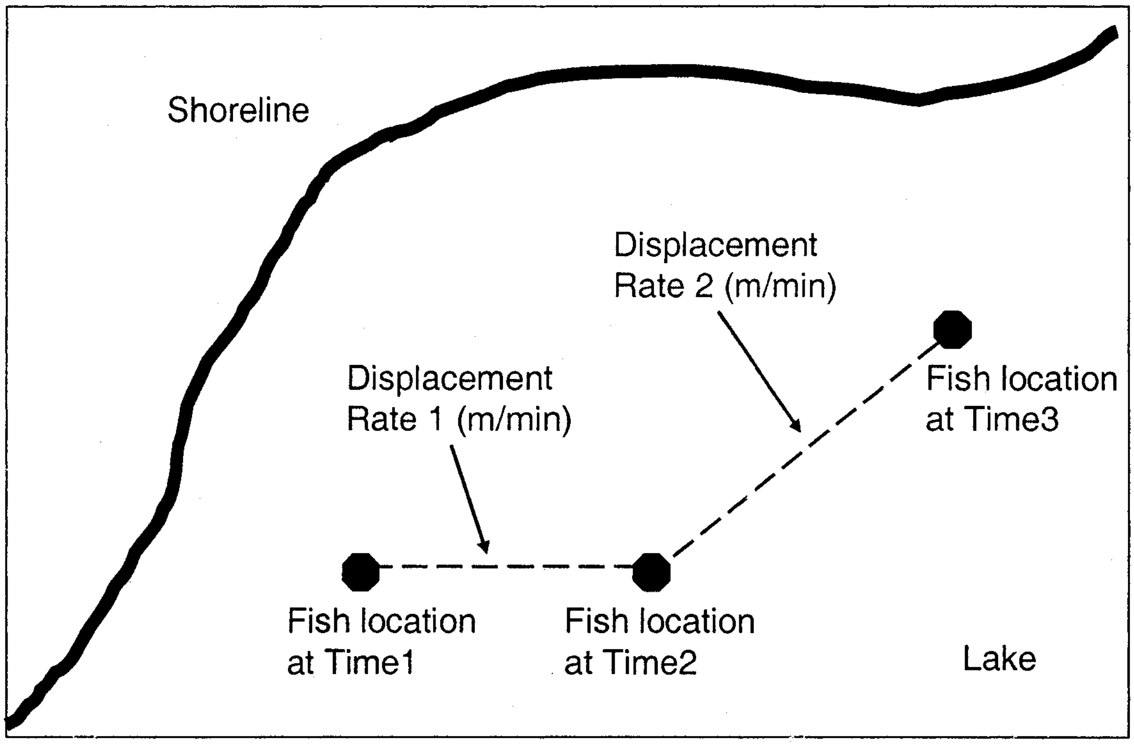

Figure 11. Diagram illustrates how the *difference* in displacement rate was calculated. The large dots represent a walleye's location at 3 consecutive time intervals. The broken lines represent the distance that a walleye displaced during each time interval.

Results

Water Clarity

Upper and Lower Marmion Lakes are relatively large lakes (totalling approximately 10 000 ha), therefore, it was reasonable to expect variation in water clarity within each lake. Upper Marmion Lake has the main flow of the Seine River moving through it, contributing a large amount of dissolved organic material to the lake. Parts of the lake that were not directly in the river's current may have had reduced amounts of dissolved organic material present, and thus may have been clearer. For this reason, the water clarity data was divided into three categories depending on which general area of the lake the values were associated with (Figure 12). Lower Marmion Lake appeared to have two basins to it: Lower Seine Bay at the east end of the lake, and the remainder of the lake west of the Lower Seine narrows. However, due to the past history of the lake, I decided to partition the water clarity data into three groups depending on the general part of the lake the values came from (Figure 13). I suspected that there may have been increased turbidity, and reduced water clarity, at the west end of the lake (due to a near-by mining operation that deposited a slurry of materials into the shallows at the west end of the lake, in the last century). The geographical boundaries that I used to partition the water clarity data (the basins) were arbitrarily chosen to be where I felt they would best describe any spatial variation in clarity. I have also partitioned the water clarity data by month and year to see whether seasonal variation in clarity exists. Lastly, I partitioned the water clarity data by percent cloud cover to see if water transparency is affected by different weather conditions.

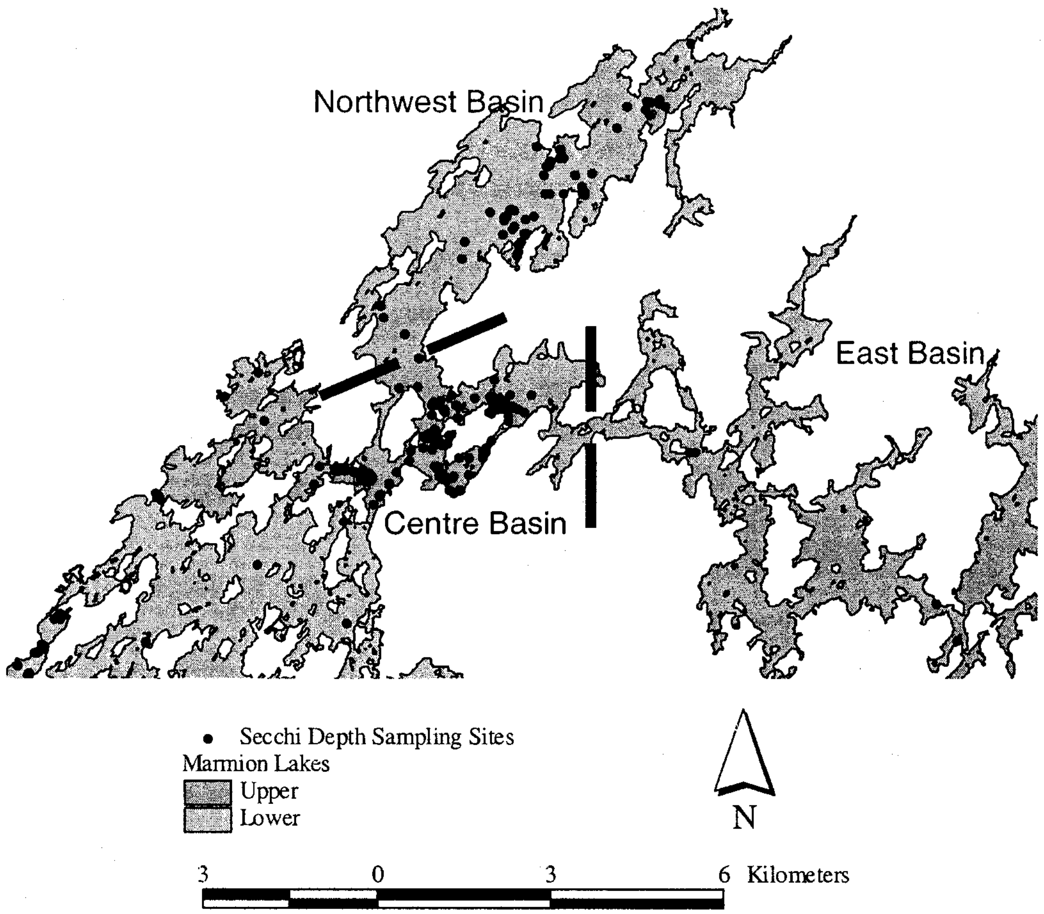

Figure 12. Location of Secchi depth sampling sites within each basin of Upper Marmion Lake. Dots represent sampling sites; broken lines represent basin boundaries.

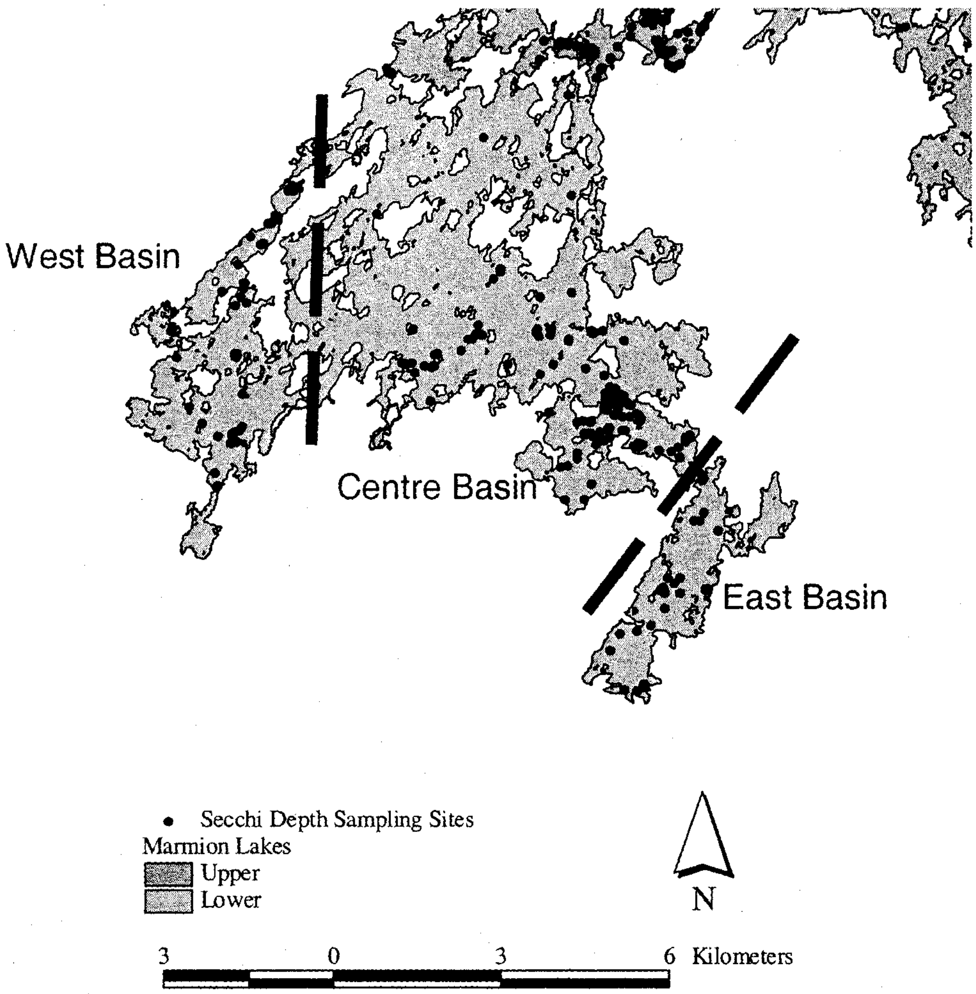

Figure 13. Location of Secchi depth sampling sites within each basin of Lower Marmion Lake. Dots represent sampling sites; broken lines represent basin boundaries.

Water clarity in Upper and Lower Marmion Lakes was evaluated using a Secchi disk and a submersible photometer. Lower Marmion Lake was approximately twice as clear as Upper Marmion Lake. Mean Secchi depths for Lower Marmion and Upper Marmion Lakes were 4.8 m ($n = 212$) and 2.4 m ($n = 171$), respectively. Mid-summer light extinction coefficients differed by a factor of 2.4 (Lower Marmion Lake vertical light extinction coefficient = 0.459; Upper Marmion Lake vertical light extinction coefficient = 1.138). Henceforth, Lower Marmion Lake will be referred to as the "clear" lake, and Upper Marmion Lake will be referred to as the "stained" lake.

Variation in water clarity was estimated using Secchi depth measurements. There was not much variation in median Secchi depths among months when all data was considered (Figure 14). However, when Secchi depths were examined by year, month, and basin, greater variation was apparent. In 2003, water clarity in the clear lake tended to decrease slightly as the summer progressed (Figure 15). The largest difference in median Secchi depth (approximately 1.0 m) over the summer months was between June and August, in the East basin. Because Secchi depth measurements can be influenced by a number of factors (cloud cover, sun height, water surface agitation, etc.), multiple Secchi depth measurements are preferable to a single reading when assessing water clarity. For this reason, the large difference in median Secchi depth observed in the East basin may not be reliable because the June value is based on a single observation. In subsequent months, with larger sample sizes ($n_{July} = 14$, $n_{August} = 8$), the difference was

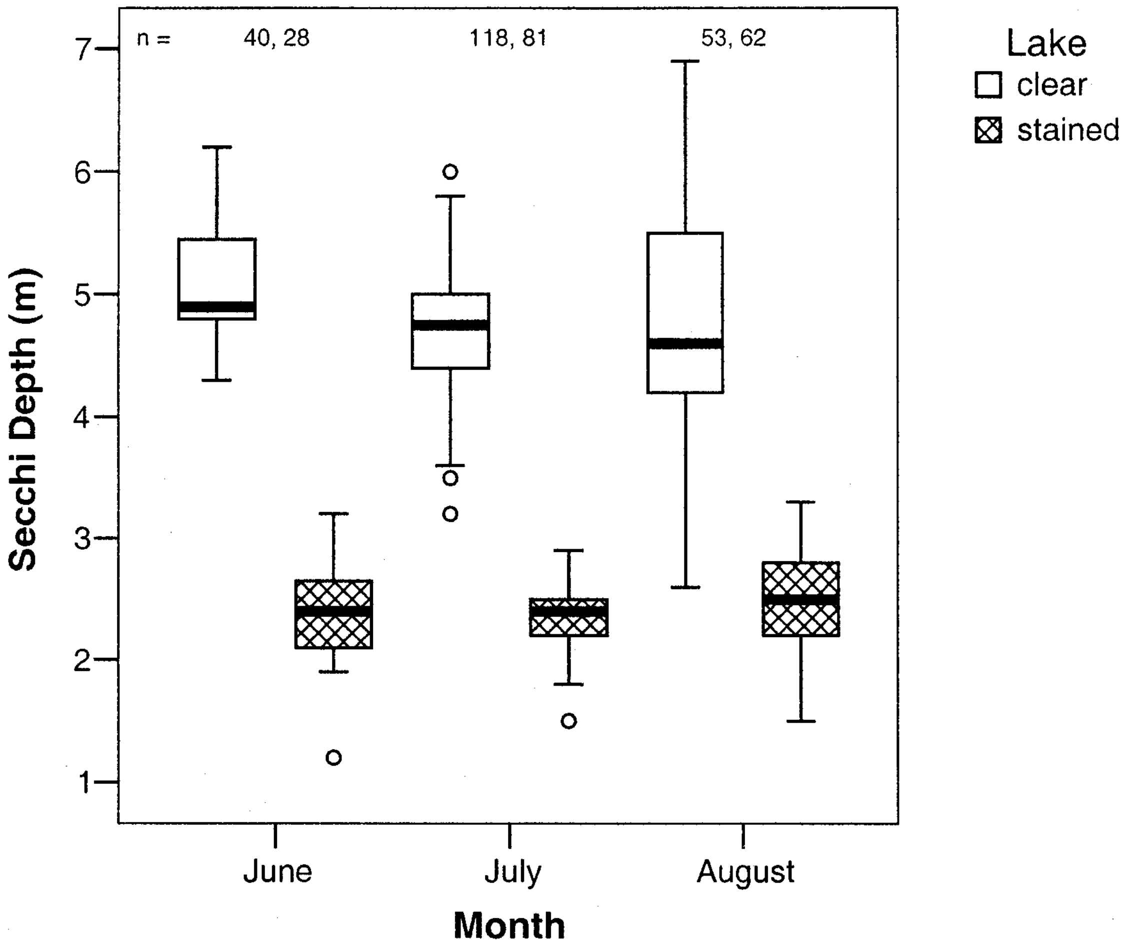

Figure 14. Secchi depths measured in stained and clear lakes from June to August, 2003 and 2004 (line = median; box = quartiles [25th and 75th]; whiskers = range minus outliers and extremes; circles = outliers; stars = extreme values).

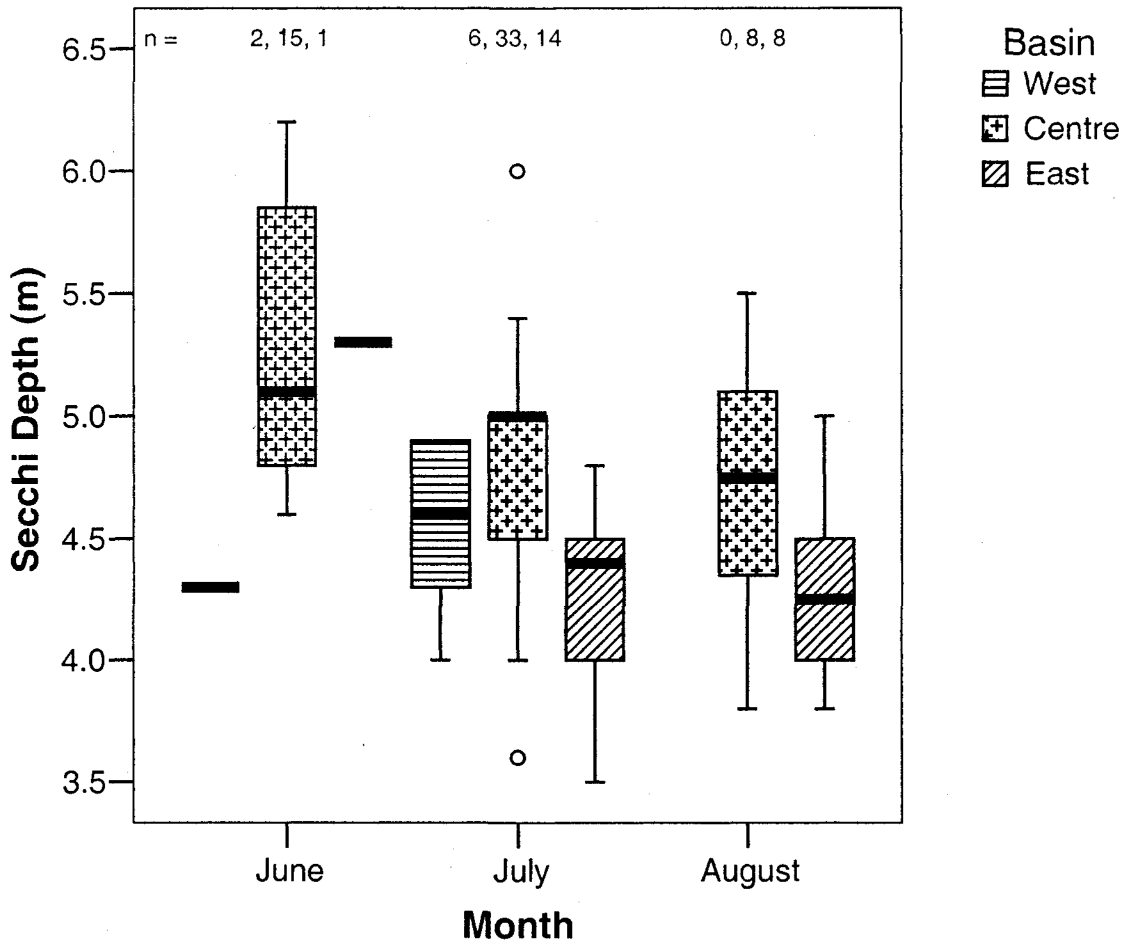

Figure 15. Secchi depths measured in the 3 basins of the clear lake for June to August, 2003 (symbols as in Figure 14).

much smaller (approximately 0.1 m). The greatest difference in median Secchi depth among the three basins was observed in July: the median Secchi depth in the Centre basin was approximately 0.6 m deeper than that in the East basin. In 2004, water clarity in the clear lake was variable among the three basins (Figure 16). Median Secchi depth was approximately 1.0 m shallower in the West basin in August than in June, while the median Secchi depth was approximately 0.6 m deeper in the Centre basin in August than in June. The largest difference among basins was in August when the Centre basin had a median Secchi depth approximately 0.7 m deeper than that in the West basin.

In 2003, water clarity in the stained lake tended to decrease as the summer progressed (Figure 17). Median Secchi depth differed by approximately 0.7 m from June to August in the Centre basin. Between basins, median Secchi depth was approximately 0.4 m shallower in the Centre basin when compared to that in the Northwest basin. In 2004, water clarity in the stained lake was fairly consistent (Figure 18). In the Centre basin, the median Secchi depth varied only 0.2 m over the summer with no clear pattern of increase of decrease. The largest difference among basins was in August when the Centre basin had a median Secchi depth approximately 0.7 m shallower than that in the Northwest basin.

Variation in the median of Secchi depths recorded under differing cloud cover was not consistent among basins in the clear lake during July, 2003 (Figure 19). In the Centre basin, Secchi depths measured on sunny days had a median depth of approximately 0.5 m shallower than Secchi depths measured on overcast days. In contrast, Secchi depths measured in the East basin on sunny days had a median depth of approximately 0.4 m deeper than those measured on cloudy days. The medians of Secchi depth measurements

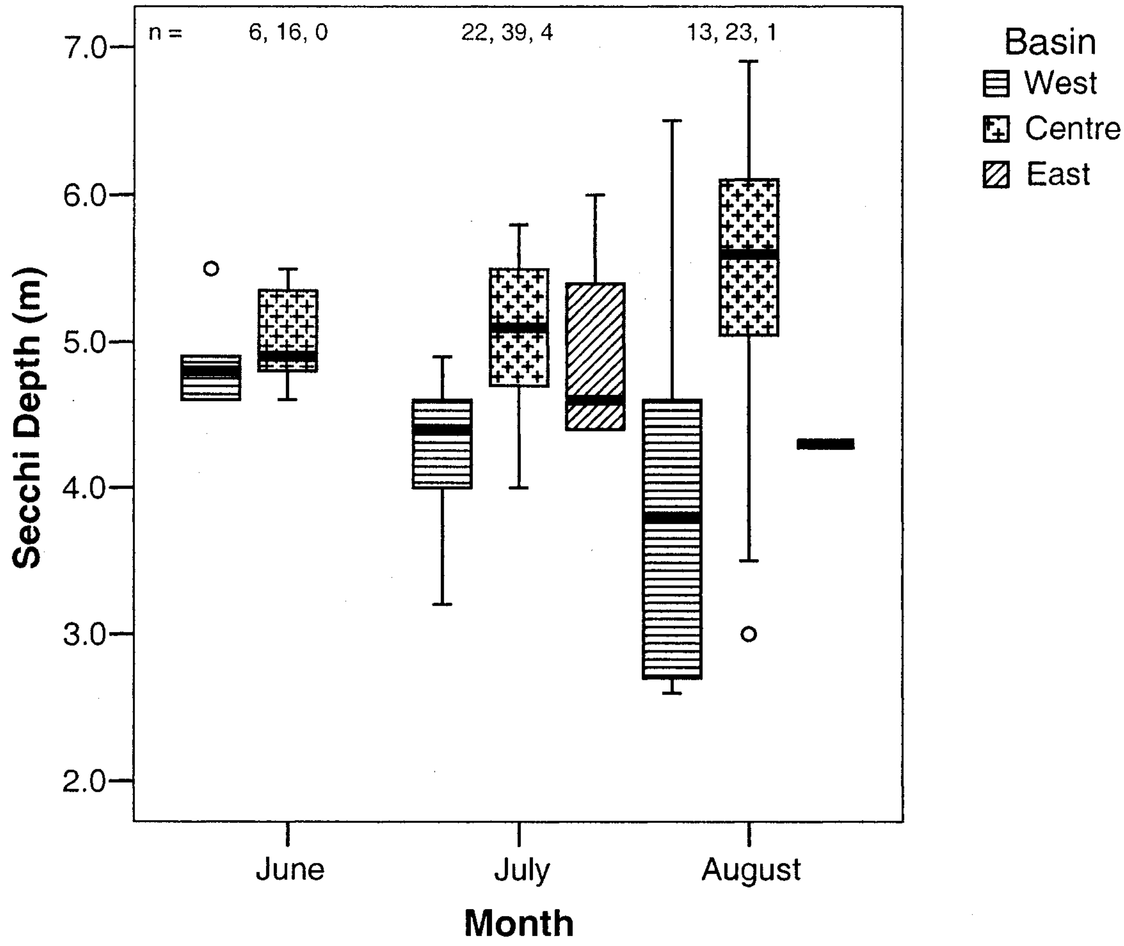

Figure 16. Secchi depths measured in the 3 basins of the clear lake for June to August of 2004 (symbols as in Figure 14).

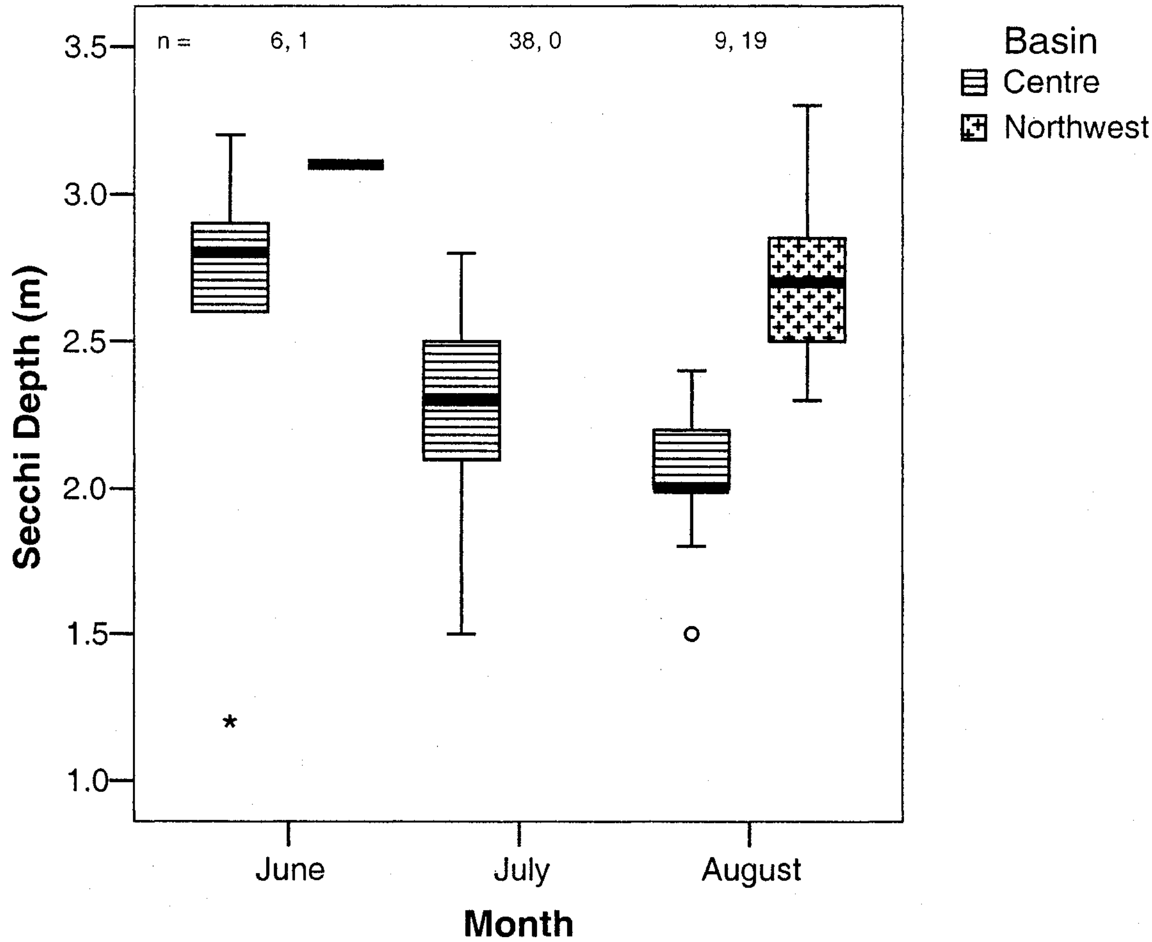

Figure 17. Secchi depths measured in 2 of the 3 basins (no measurements were made in the East basin) of the stained lake for June to August of 2003 (symbols as in Figure 14).

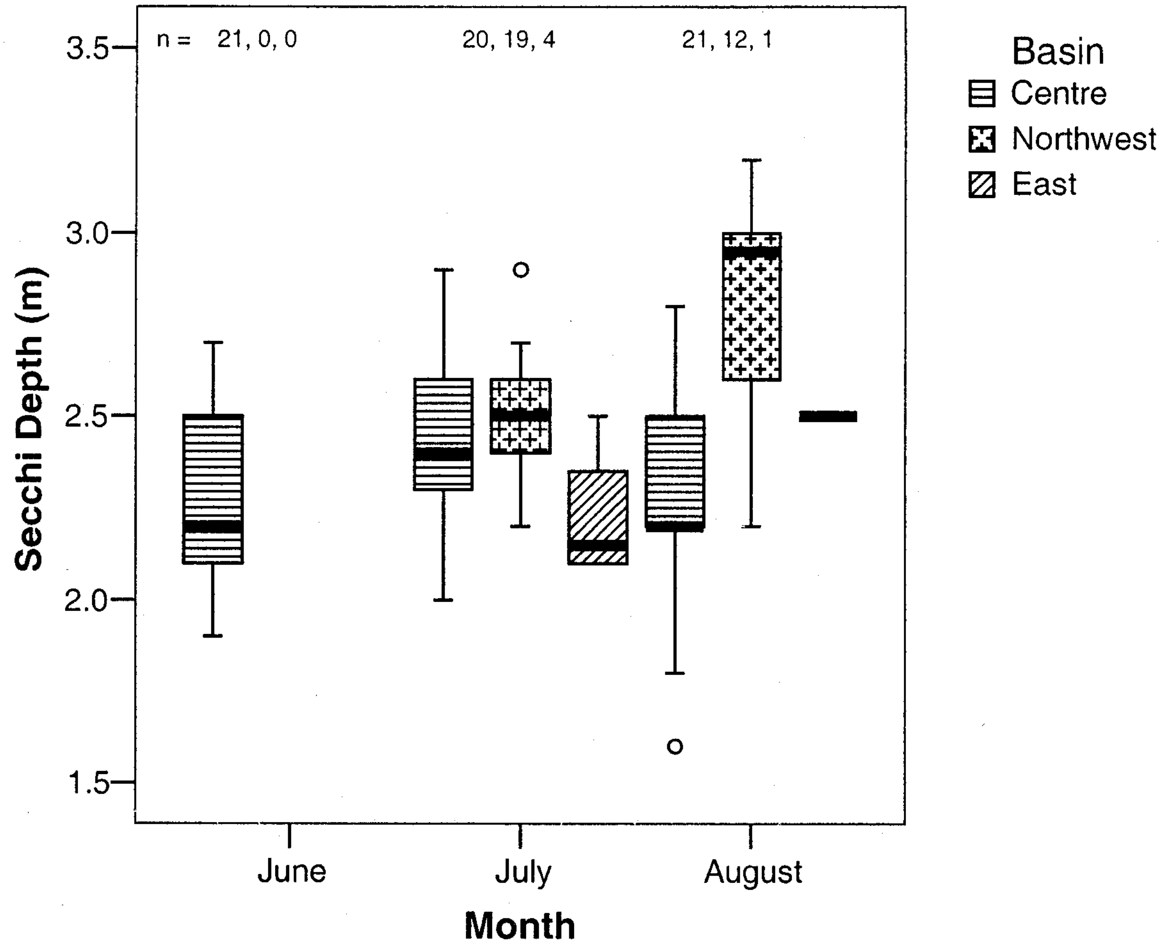

Figure 18. Secchi depths measured in the 3 basins of the stained lake for June to August of 2004 (symbols as in Figure 14).

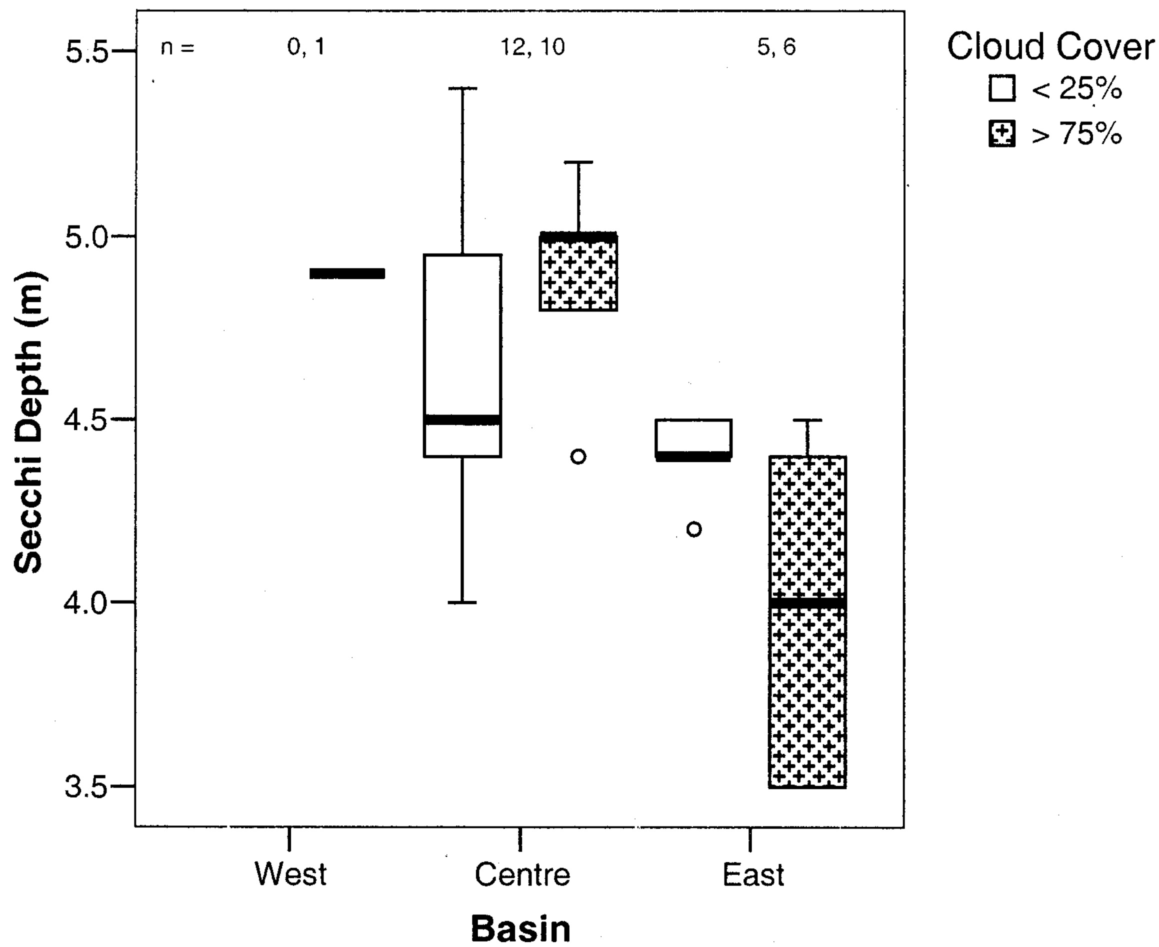

Figure 19. Secchi depths measured under varying cloud cover in the clear lake for July, 2003 (symbols as in Figure 14).

made in the clear lake in July, 2004, were more consistent than in 2003 (Figure 20). Regardless of basin, deeper Secchi depths tended to be recorded on sunny days when compared with overcast days. The magnitude of the difference in median Secchi depth between sunny and cloudy days was approximately 0.1 m in the West basin and 0.7 m in the Centre basin.

A very small number of Secchi depth measurements were made in the stained lake on cloudy days in July of 2003 and 2004. Therefore, no comparisons were possible. In August, 2003, Secchi depths recorded did not show a consistent pattern associated with cloud cover (Figure 21). Secchi depth measurements in the stained lake in August, 2004, tended to be more consistent than in 2003 (Figure 22). Regardless of basin, the medians of Secchi depths recorded on cloudy days tended to be deeper by approximately 0.1 or 0.2 m than the medians of those recorded on sunny days.

Water Temperature

The observed difference in water clarity between Upper and Lower Marmion Lakes was expected to create different thermal structures in each lake, as light would penetrate deeper in the clear lake than it would in the stained lake. Over the summer months of 2003 and 2004, water temperature profiles from one location in each lake (locations "D" and "L") were measured to monitor the thermal structures (Figure 8). In 2003, the clear lake appeared to warm earlier in the year than the stained lake did, and by early June was slightly warmer (Figure 23a), likely due to the increased penetration of light. The thermocline had begun to form by the second week of June (Figure 23b), and was approximately 2 m deeper in the clear lake than it was in the stained lake. By the end of

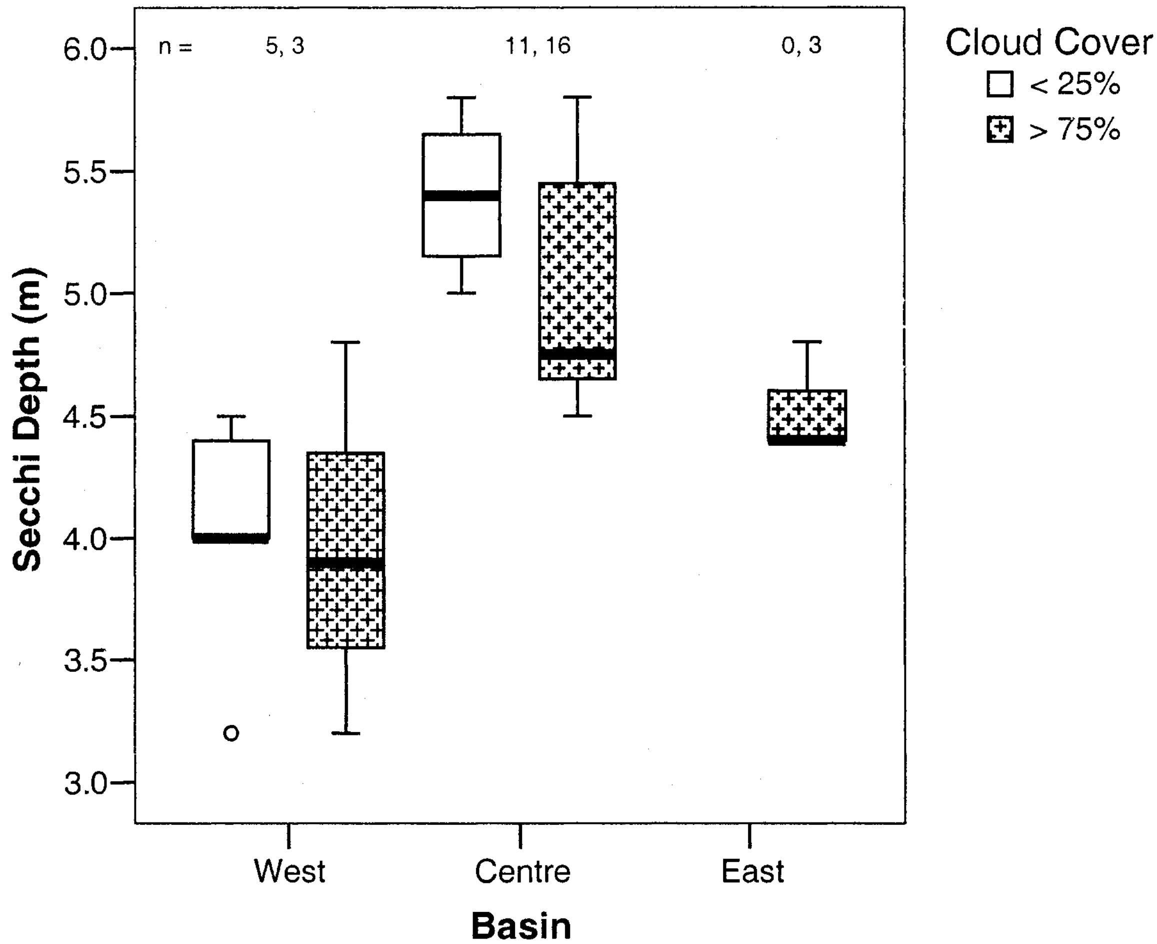

Figure 20. Secchi depths measured under varying cloud cover in the clear lake for July, 2004 (symbols as in Figure 14).

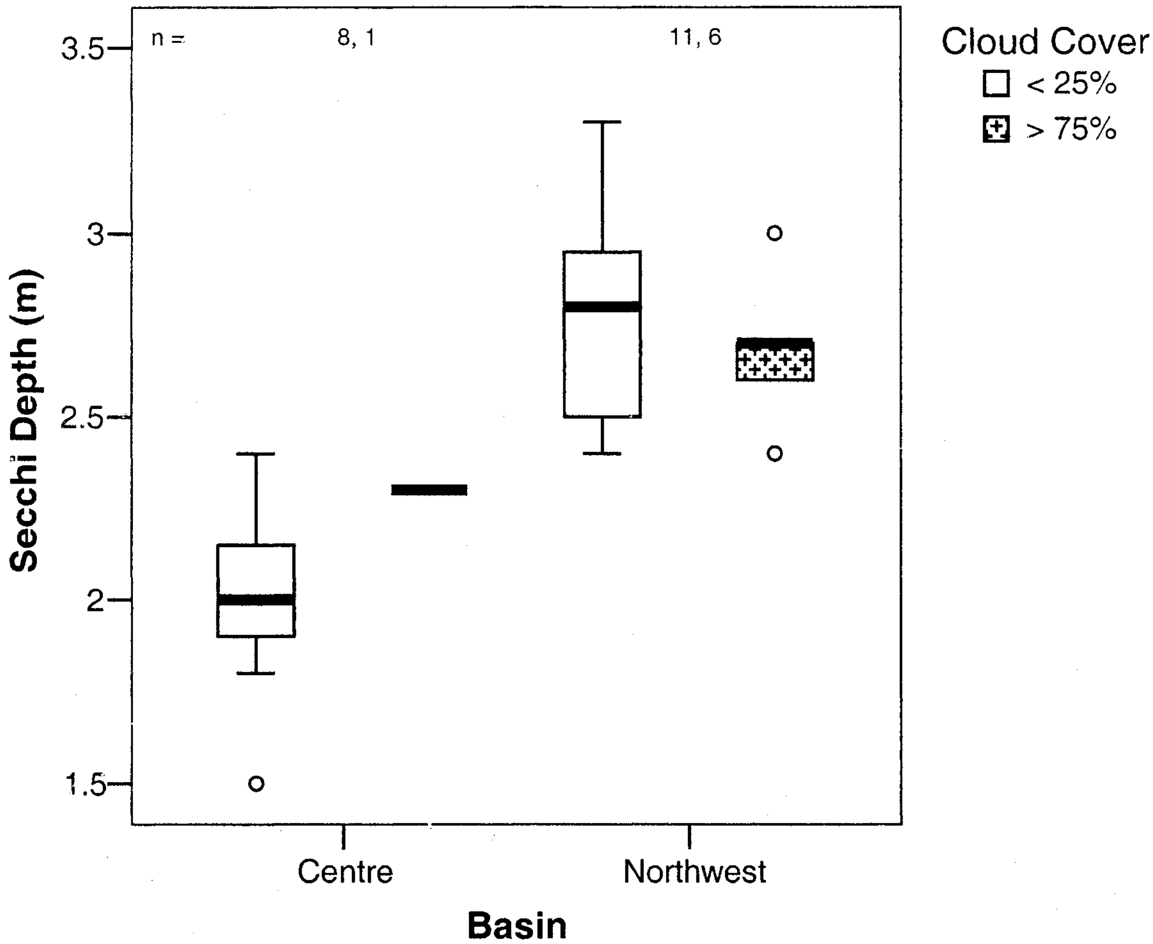

Figure 21. Secchi depths measured under varying cloud cover in the stained lake for August, 2003 (symbols as in Figure 14).

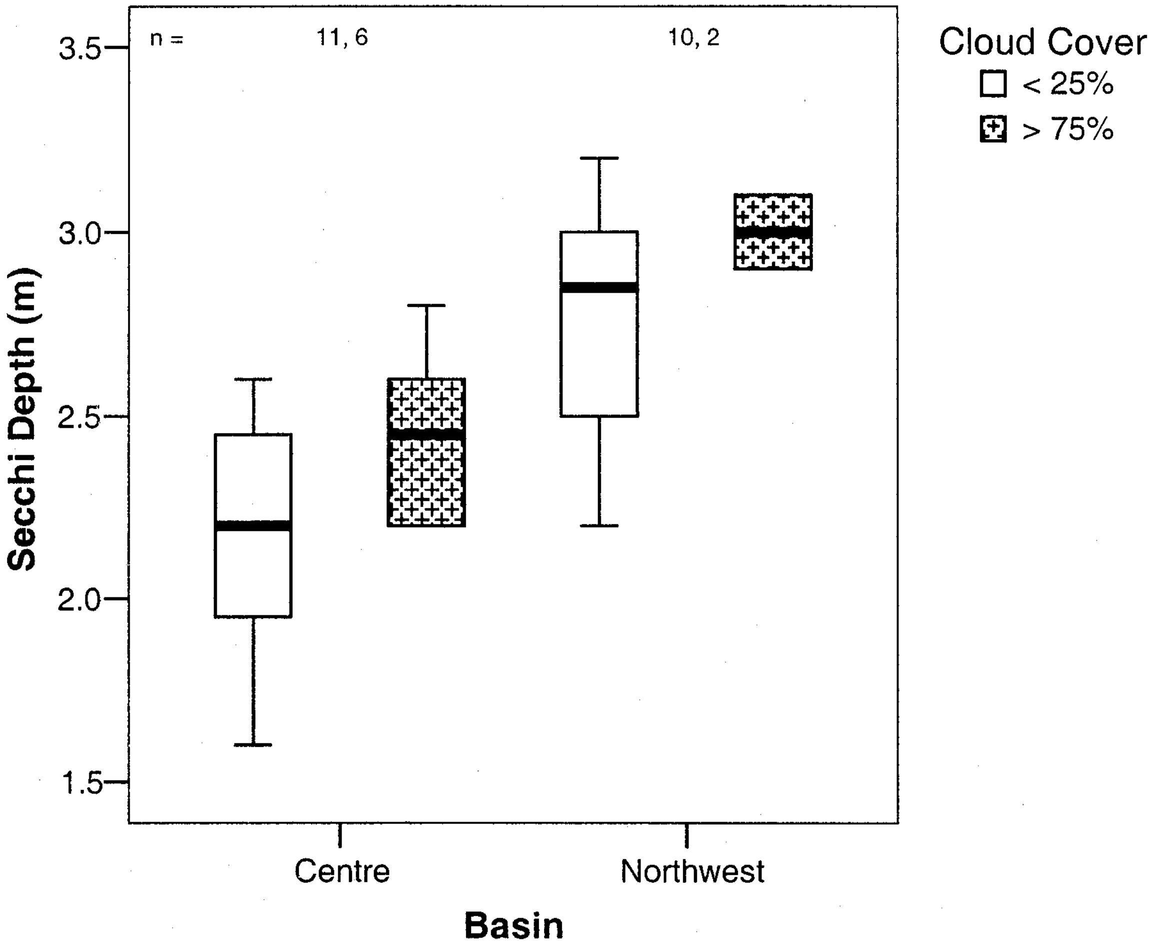

Figure 22. Secchi depths measured under varying cloud cover in the stained lake for August, 2004 (symbols as in Figure 14).

June the thermocline was established in the clear lake (Figure 23c). No thermal profile was measured in the stained lake in the last week of June, but it was assumed that the thermocline was established in that lake as well. Thermal profiles measured in early July verified that the thermoclines were well established in both lakes, and the clear lake had slightly warmer epilimnion and hypolimnion water temperatures (approximately 2 °C at the surface and 4 °C at 15 m; Figure 23d). By the later half of August, the epilimnion of the clear lake appeared to be slightly larger (by approximately 1 or 2 m deeper) than it had been previously (Figure 23e). The clear lake was still slightly warmer than the stained lake (approximately 1 or 2 °C).

In 2004, the thermocline was established in the clear lake by the latter part of June (Figure 24a). No water temperature data was available for the stained lake in June, however, it was assumed that the thermocline had also established in the stained lake. In mid-July, the epilimnion of both lakes appeared to have similar water temperatures (Figure 24b), while the hypolimnion of the clear lake was approximately 4 °C warmer than that the of the stained lake. By mid-August, the first 7 m of the epilimnia of both lakes were the same temperatures (Figure 24c). The epilimnion of the clear lake was, however, larger by approximately 4 m. The hypolimnion of the clear lake was approximately 4 to 5 °C warmer than that of the stained lake.

Due to the numerous sheltered back-bays and large open expanses in both Upper and Lower Marmion Lakes, variation in thermal structure within each lake was also expected to exist. In mid-July, 2004, numerous temperature profiles were measured at various locations (Figure 8) to observe the variation in thermal structure within each lake. These profiles showed that there was moderate variation in the thermal structures of each

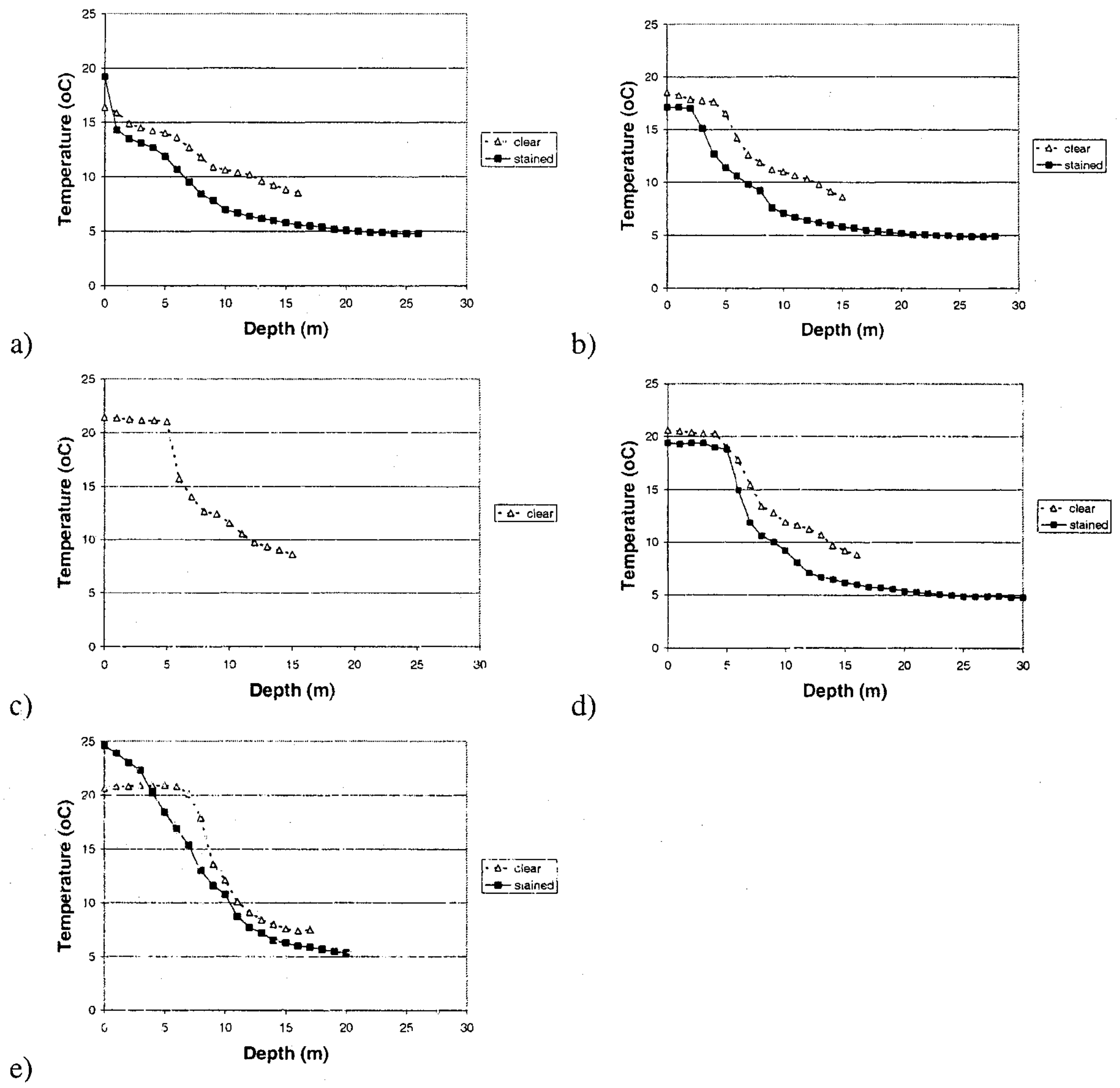

Figure 23. Water temperature at 1 m depth intervals from: a) June 02, 2003 (clear lake) and June 04, 2003 (stained lake); b) June 10, 2003 (clear lake) and June 11, 2003 (stained lake); c) June 25, 2003 (clear lake); d) July 02, 2003 (clear lake) and July 09, 2003 (stained lake), and; e) August 29, 2003 (clear lake) and August 14, 2003 (stained lake).

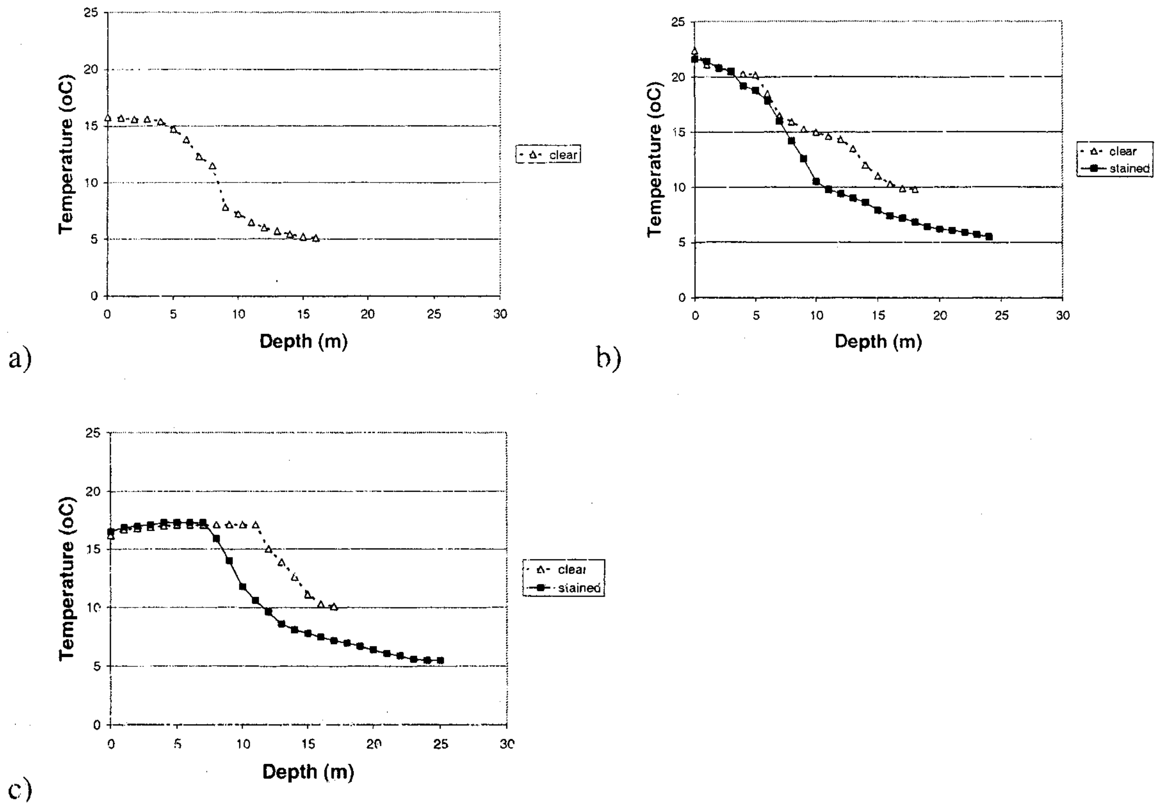

Figure 24. Water temperature at 1 m depth intervals from: a) June 24, 2004 (clear lake); b) July 14, 2004 (clear and stained lakes), and; c) August 19, 2004 (clear and stained lakes).

lake (Figure 25), with the largest variation in the temperatures of the metalimnion. Despite the internal variation, however, the median water-temperature profiles of both lakes were very similar. A second measure of internal variation in temperature profiles in mid-August, 2004, revealed a similar result (Figure 26).

Walleye Depth

When analyzing fish depth data from the two study lakes for the summer months of 2003 and 2004, I felt that any temperature differences between years that may have influenced the vertical distribution of fish would have been experienced in *both* lakes, and would thus have affected the fish in both lakes equally. For this reason, I decided to combine the data for both summers, rather than treat them separately.

Based on the hypothesis that subsurface illumination influences the spatial and temporal dimensions of walleye feeding habitat, I expected to see a difference in the depth distribution of walleye between the stained and the clear lake. Analysis of walleye depths showed that walleye were slightly shallower in the stained lake ('lake': $F_{1, 41} = 4.872$, $p = 0.034$, ln[*mean fish depth*]), during the summer months (median [*mean fish depth*] = 3.3 m [June], 5.0 m [July], 7.4 m [August]) when compared with walleye in the clear lake (median [*mean fish depth*] = 5.5 m [June], 6.0 m [July], 8.2 m [August]) (Figure 27). Walleye in both lakes were located in slightly deeper water as the summer progressed ('month': $F_{2, 41} = 6.373$, $p = 0.004$, ln[*mean fish depth*]). For the most part, walleye were not located at depths where the water temperature was less than 11 $^{\circ}$C.

By rearranging the Lambert-Beer Law (see page 7), the depth of the optimal light intensity range (68 to 8 lux) was determined for each hour of each day of the summer

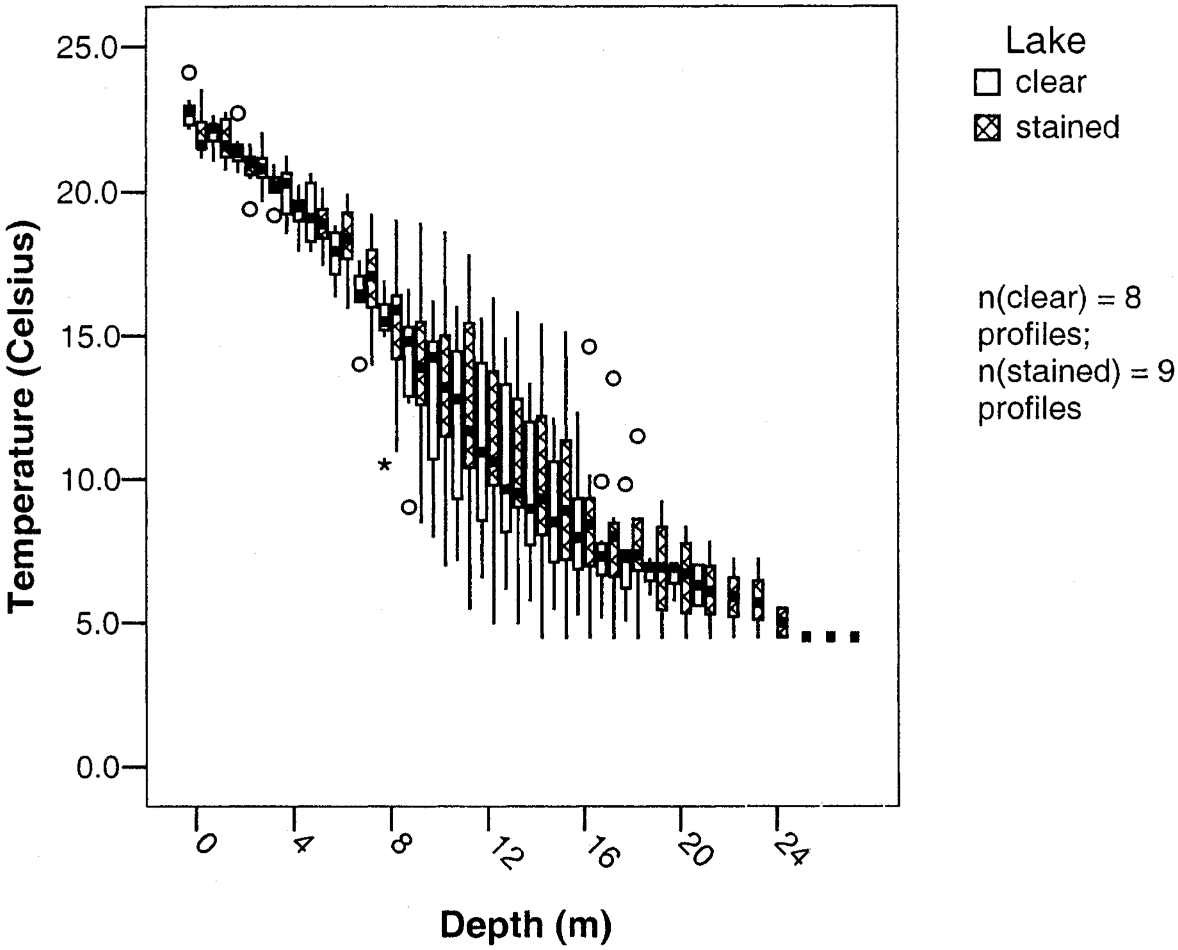

Figure 25. Water temperature at 1 m depth intervals from July 14, 2004. Thermal profiles were measured from 8 locations in the clear lake and 9 locations in the stained lake (see Figure 8 for locations; symbols as in Figure 14).

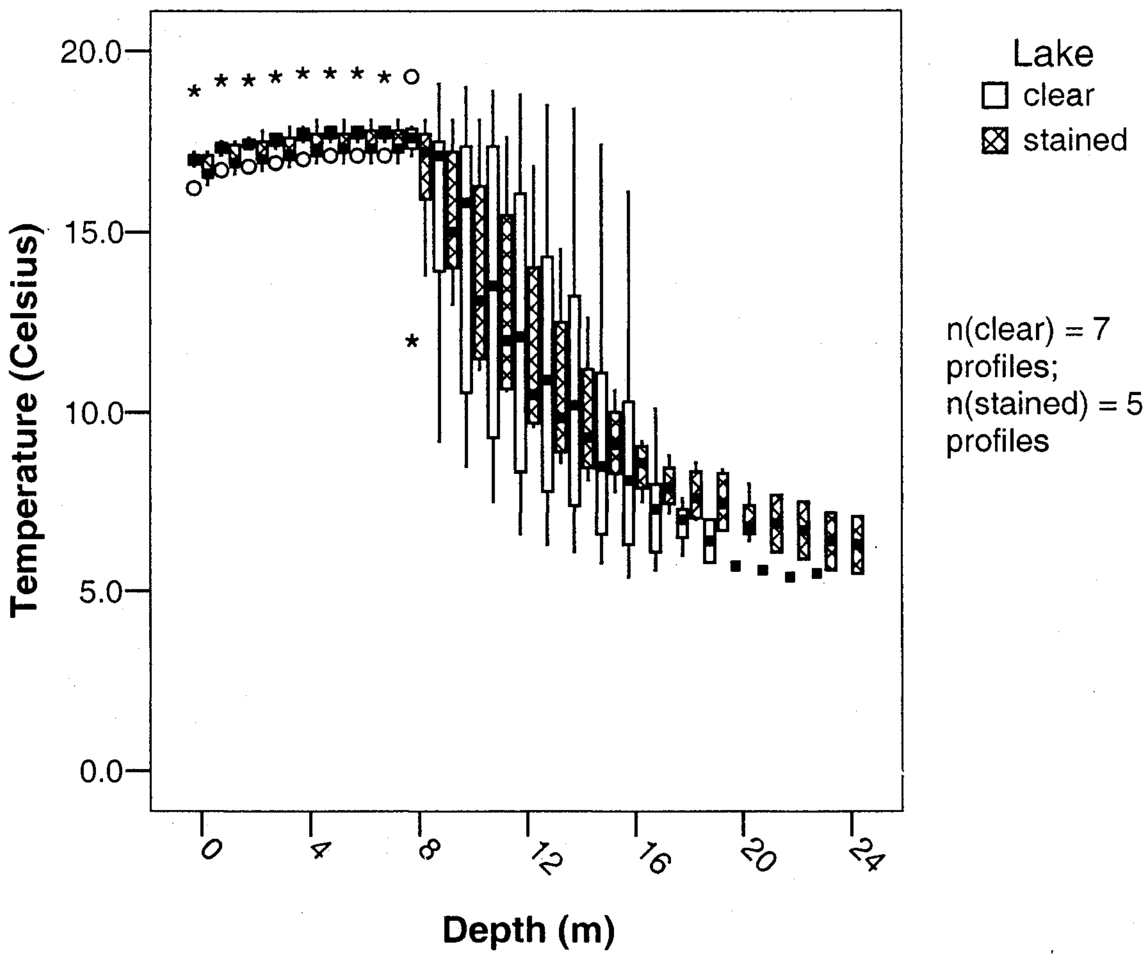

Figure 26. Water temperature at 1 m depth intervals from August 19, 2004. Thermal profiles were measured from 7 locations in the clear lake and 5 locations in the stained lake (see Figure 8 for locations; symbols as in Figure 14).

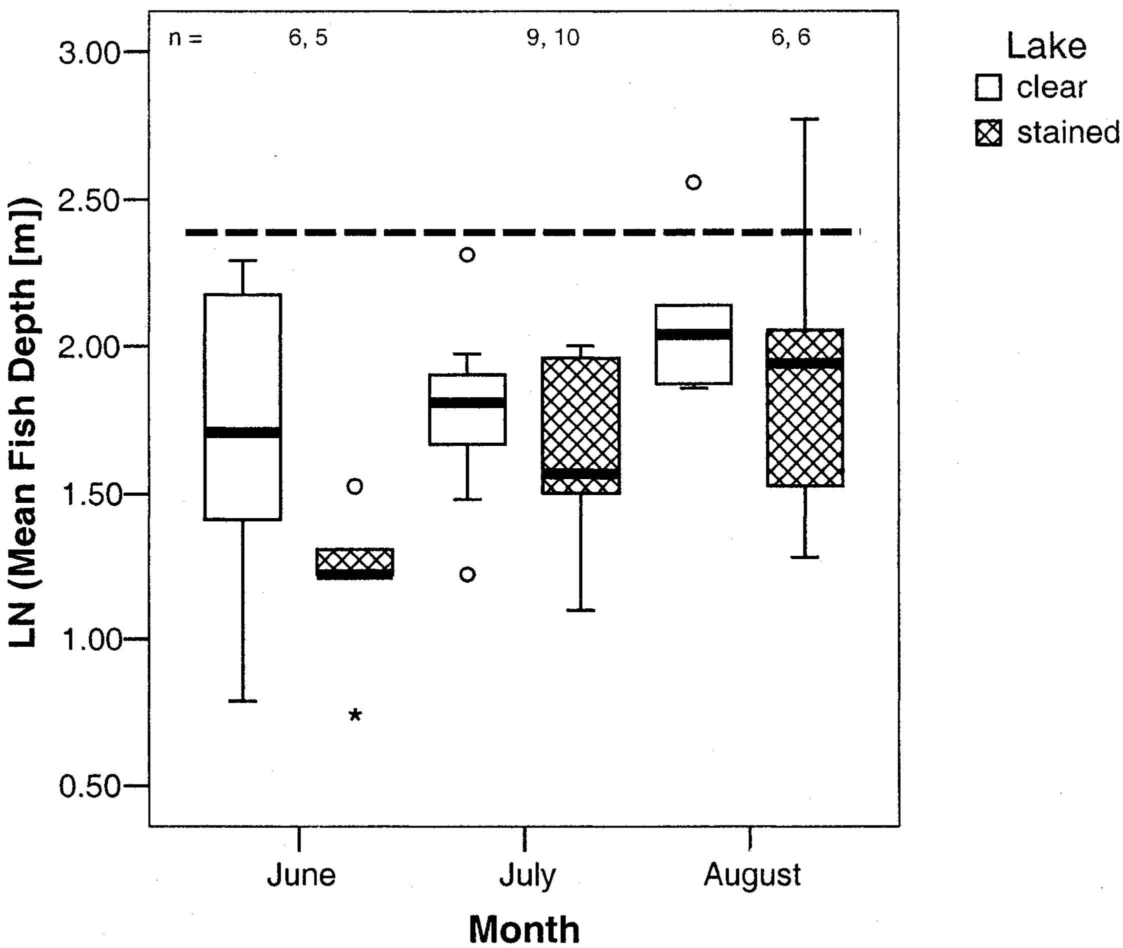

Figure 27. Mean depths of walleye for June, July, and August of 2003 and 2004, in both the stained and clear lake (symbols as in Figure 14). Horizontal broken line represents the mean location of 11 ^{o} C water: warmer water below the line, cooler water above.

months of 2003 and 2004, for both the clear and the stained lake. Based on the location of the optimal light intensity range, the predicted hourly walleye depth range (Figure 28) in the stained lake was approximately 5.0 to 8.0 m deep, in water with a mean temperature greater than 11 °C. The predicted hourly depth range for walleye in the clear lake was, however, located in depths of approximately 12.0 to 19.0 m, and was, for most of the day, in water that had a mean temperature below 11 ° C. The predicted depth range only came into waters above 11 ° C very late in the evening, after 20:00.

The observed hourly depth of walleye in the stained lake were, on average, approximately 1.9 m shallower throughout the afternoon and evening periods ('lake': $F_{1, 155} = 17.104$, $p = 0.001$, ln[*mean fish depth*]), when compared with the walleye in the clear lake (Figure 29). Some fish in both lakes were located in cold water (less than 11 ° C) throughout parts of the day. Within the stained lake, walleye were very near to, or at, the predicted depth range for most of the afternoon and evening (Figure 30). Within the clear lake, walleye were approximately 8.0 m shallower than predicted (Figure 31). Aside from a few individuals, most walleye in both lakes were located in waters where the temperature was greater than 11 ° C.

Light At Fish Depth

From the hypothesis that walleye have an optimal light intensity that they prefer, I expected to find walleye inhabiting areas where the light levels were close to, or in, the light intensity range of 68 to 8 lux. Walleye in the clear lake inhabited more brightly lit areas that were, on average, approximately 2 500 lux greater ('lake': $F_{1, 138} = 36.742$, $p = 0.001$, ln[*light at fish depth*]) when compared to the walleye in the stained lake (Figure

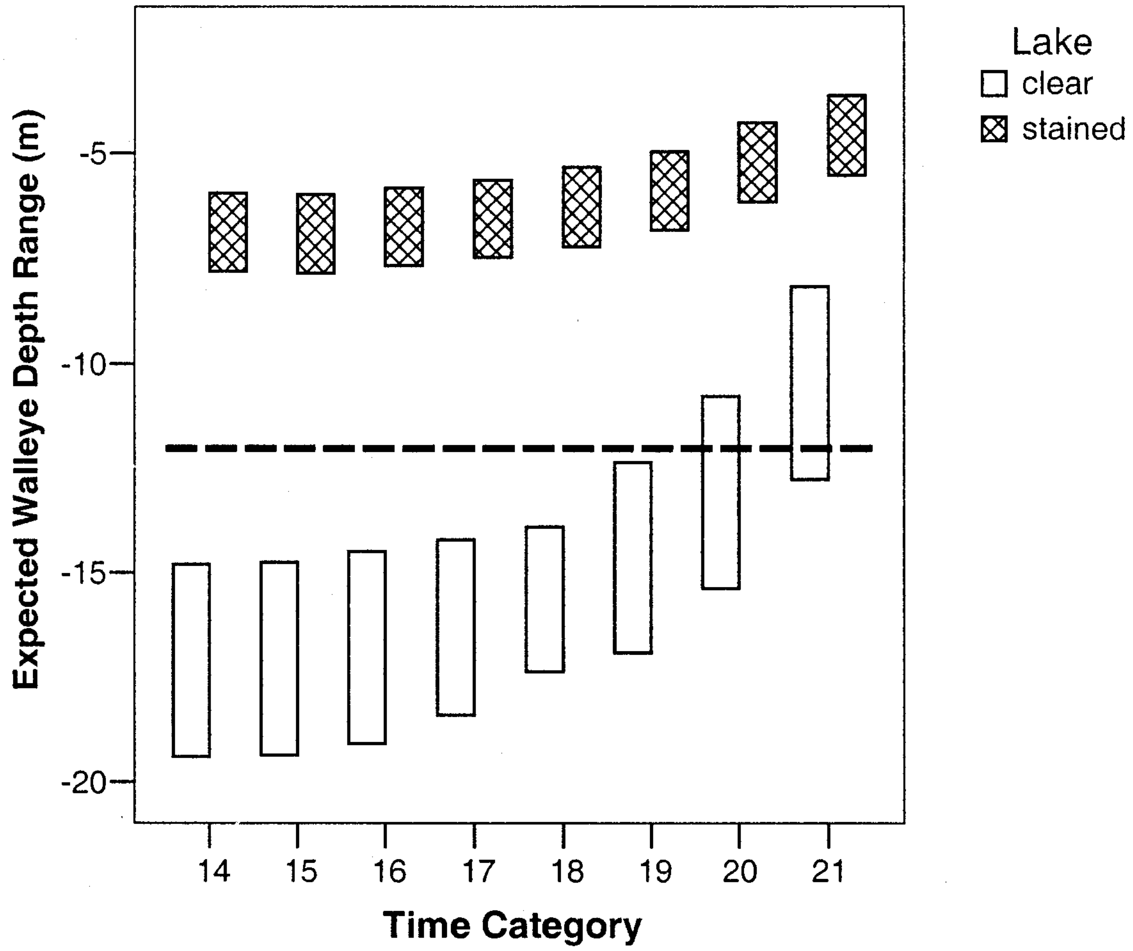

Figure 28. Range plots indicating the predicted hourly walleye depth (based on the hypothesized optimal light intensity range) for walleye in both lakes, for June to August of 2003 and 2004. The horizontal broken line represents the mean location of 11 °C water: warmer above the line, cooler below.

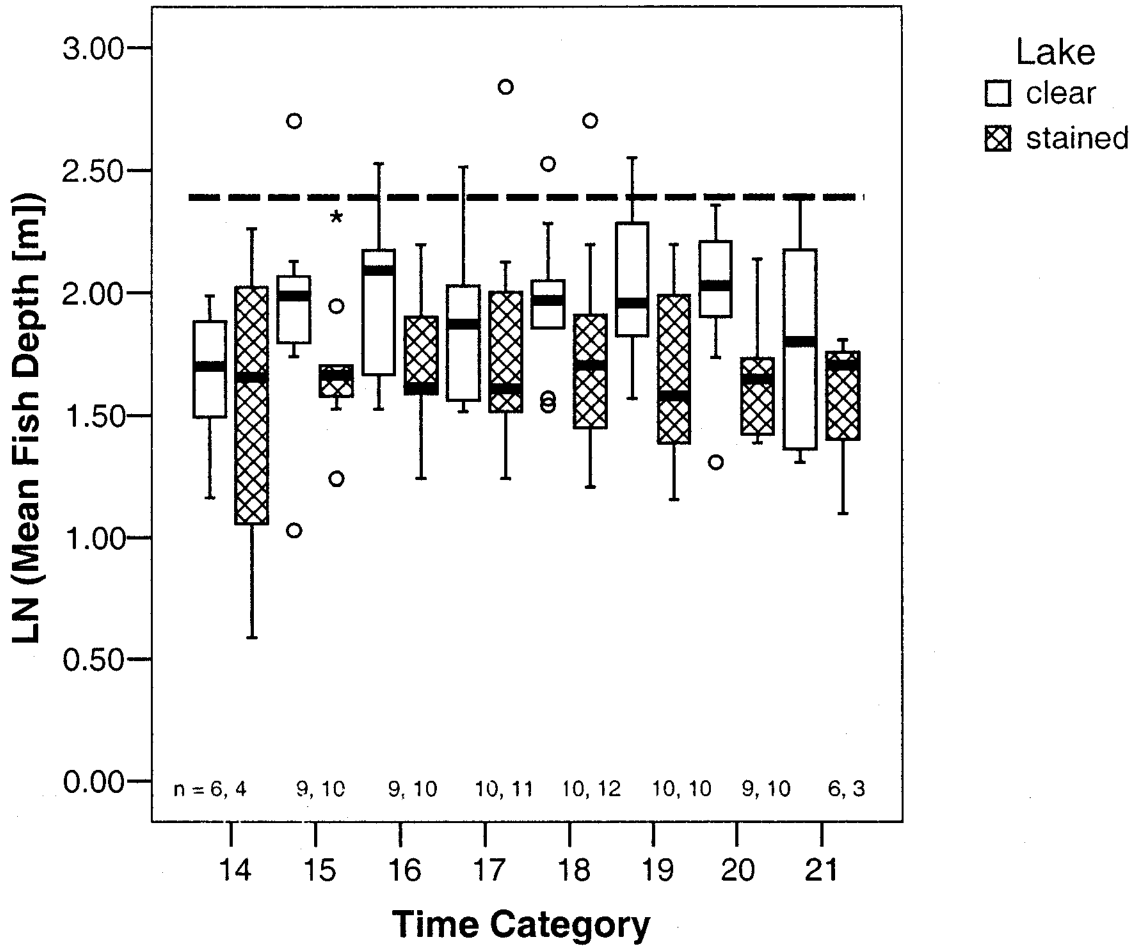

Figure 29. Mean hourly walleye depth for June to August of 2003 and 2004, in both lakes (symbols as in Figure 14). Horizontal broken line represents the mean locations of 11 °C water: warmer water below the line, cooler above.

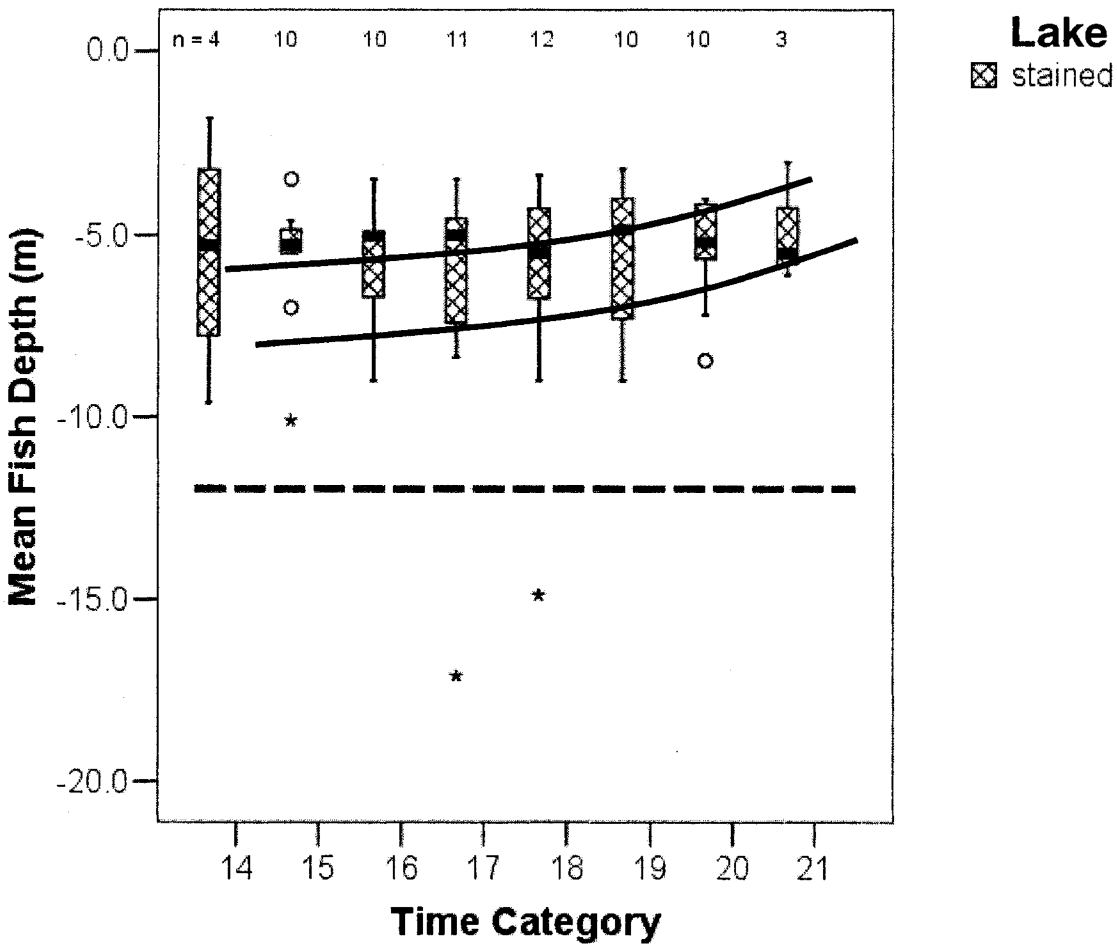

Figure 30. Mean hourly walleye depth in the stained lake, for June to August of 2003 and 2004 (symbols as in Figure 14). Horizontal broken line represents the mean location of 11 ° C water: warmer water above the line, cooler below. The solid upwards-sloping lines indicate the upper and lower bounds of the expected walleye depth (based on the location of optimal light levels [68 to 8 lux]).

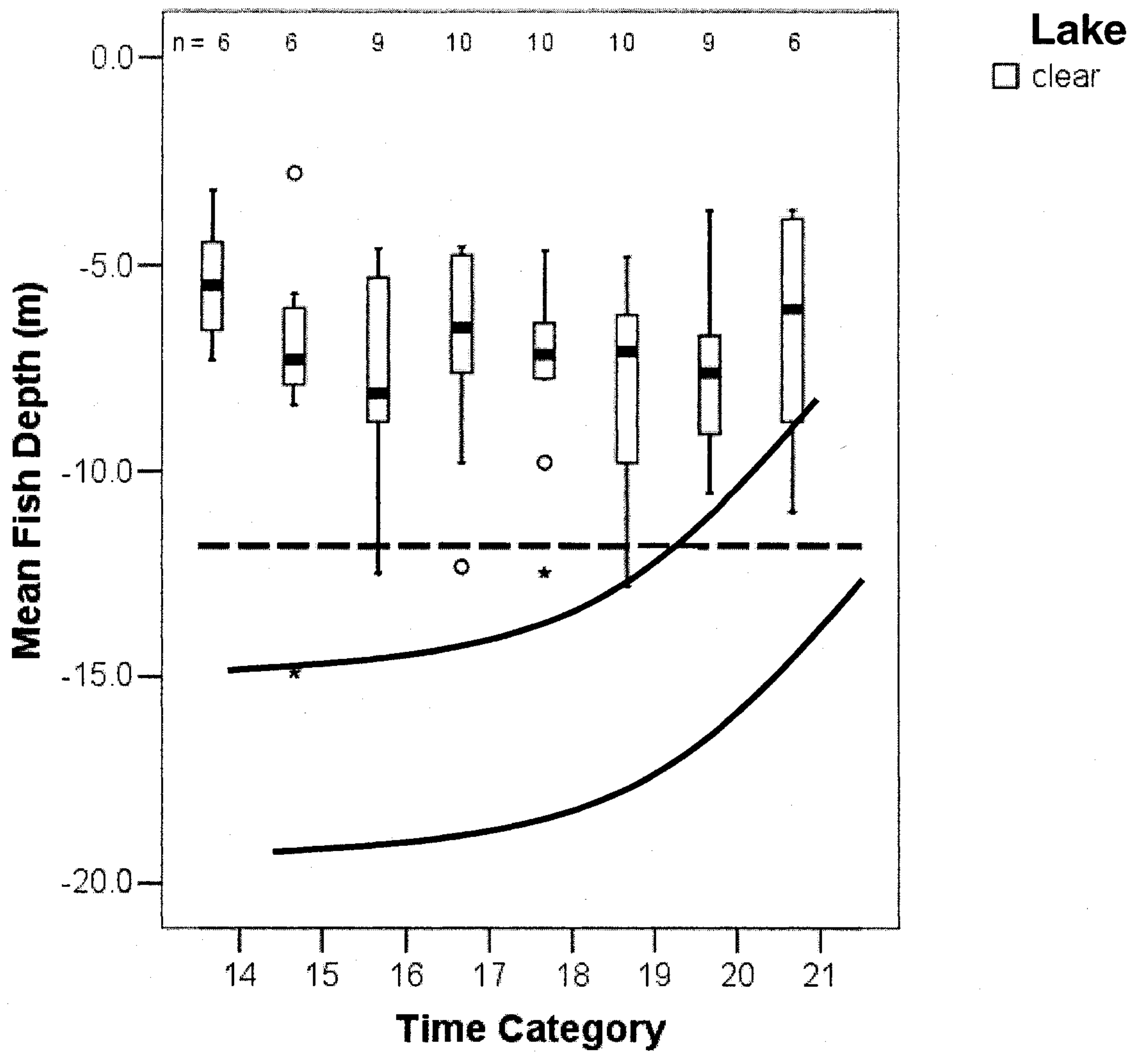

Figure 31. Mean hourly walleye depth in the clear lake, for June to August of 2003 and 2004 (symbols as in Figure 14). Horizontal broken line represents the mean location of 11 °C water: warmer water above the line, cooler below. The solid upwards-sloping lines indicate the upper and lower bounds of the expected walleye depth (based on the location of optimal light levels [68 to 8 lux]).

32). Light levels inhabited by walleye in both lakes were, on average, approximately 800 lux greater in the afternoon period ('time category': $F_{7, 138} = 2.348$, $p = 0.028$, ln[*light at fish depth*]) than in the evening. Walleye in the clear lake did not appear to be in areas where subsurface illumination was considered optimal (68 to 8 lux) for most of the afternoon and evening. Although some walleye in the stained lake inhabited this optimal area throughout the entire afternoon and evening, most of the tagged walleye in the stained lake were not located in areas with these light levels until the evening period (18:00 and beyond).

Temperature At Fish Depth

Since the optimal light levels were located at quite different depths between the clear and stained lake, I expected to find walleye inhabiting waters of quite different temperature. Walleye in the stained lake tended to be in warmer water (Figure 33), but the *mean temperature at fish depth* was highly variable and did not differ significantly between the lakes ('lakes': $F_{1, 42} = 1.406$, $p = 0.243$). For example, in the month of July *mean temperature at fish depth* ranged from 14.0 °C to 21.3 °C in the stained lake and 15.0 °C to 20.8 °C in the clear lake.

Change In Displacement Rate

Based on the hypothesis that optimal thermal-optical habitat may exist at different times of the day depending on lake clarity, I expected that walleye activity would differ between the clear and the stained lake. Walleye activity appeared to be quite high during time category 16 (14:00 to 16:00) in the clear lake (Figure 34). However, this apparent

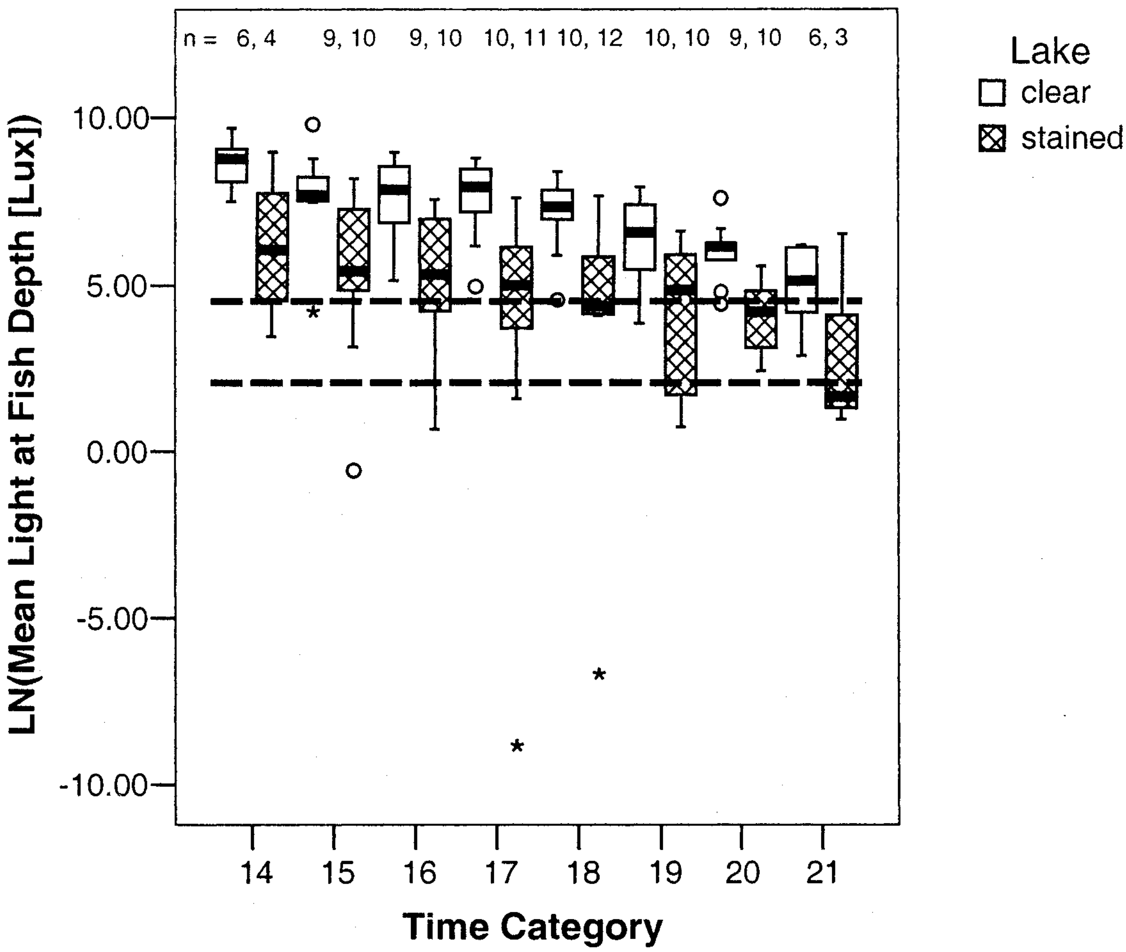

Figure 32. Mean light levels at walleye depth for June to August, 2003 and 2004, in both lakes (symbols as in Figure 14). Horizontal broken lines indicate the upper and lower bounds of the optimal light levels (68 to 8 lux).

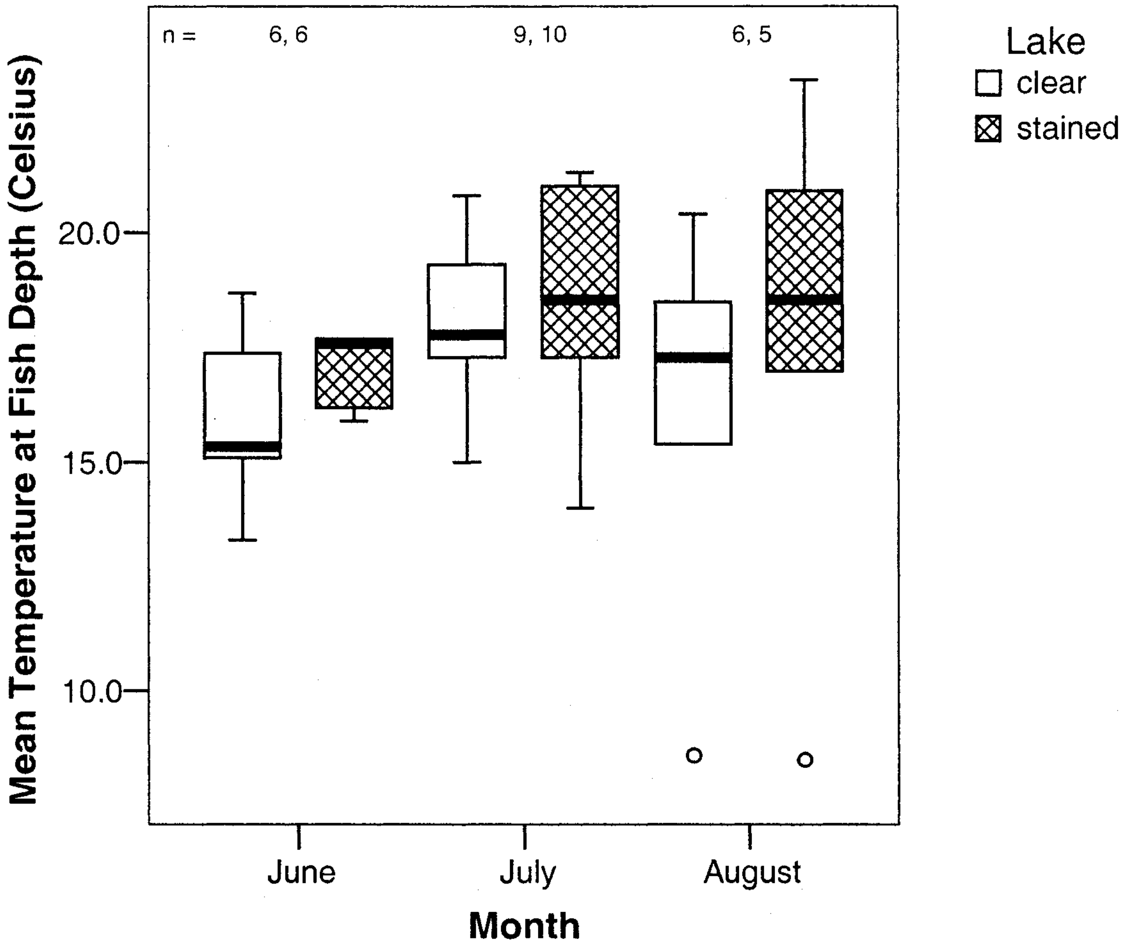

Figure 33. Mean water temperatures at walleye depth for June, July, and August, 2003 and 2004 (symbols as in Figure 14).

spike in activity was largely due to the movements of one fish. To prevent this single point from potentially having a large impact on the trends in walleye activity, time category 16 was omitted from the analysis. Walleye displayed very similar activity patterns, regardless of which lake they were in ('lake': $F_{1, 88} = 0.076$, $p = 0.784$): very minimal *mean percentage change in displacement rate* in the afternoon (approximate average of 30 % change in displacement rate), followed by an increase (approximate average of 300 to 800 % change in displacement rate) in the late evening ('time category': $F_{4, 88} = 2.416$, $p = 0.056$).

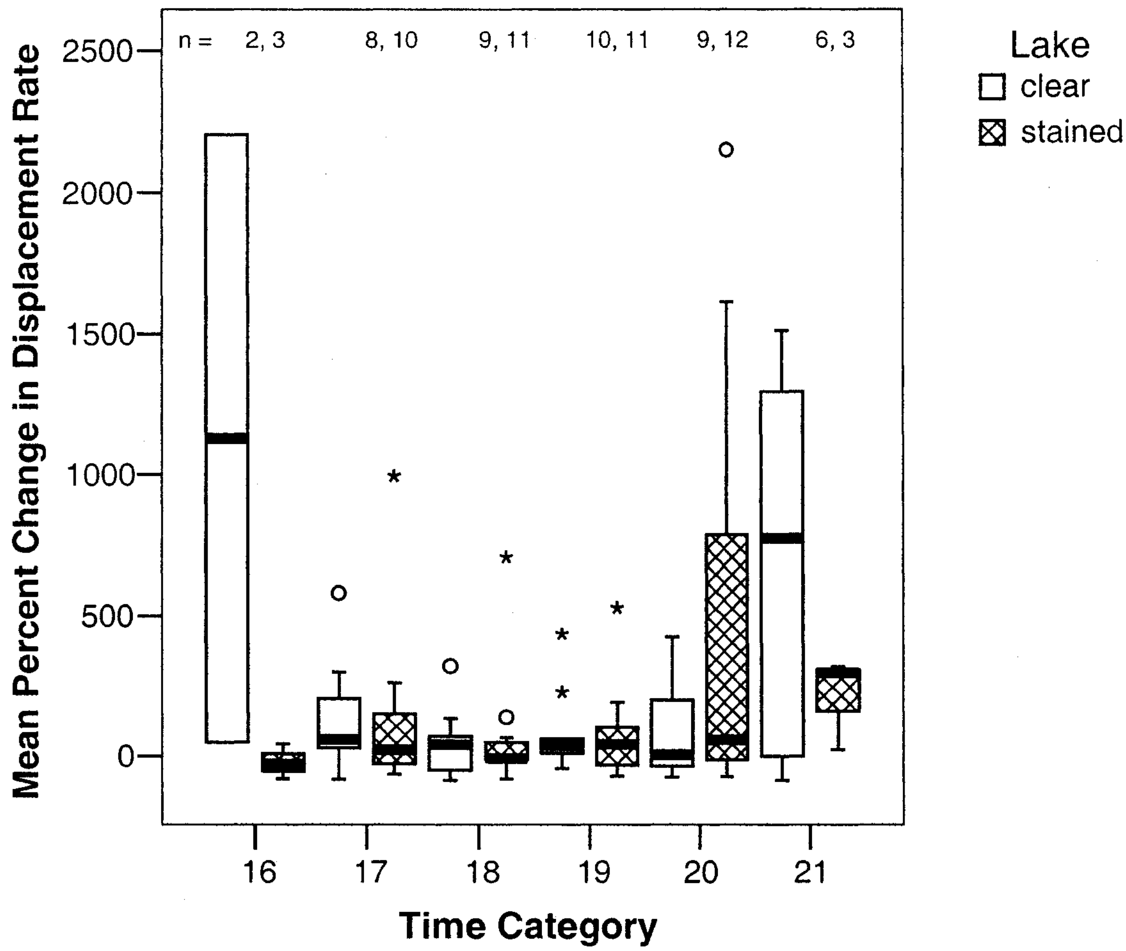

Figure 34. Mean percent change in displacement rate for walleye in both lakes, for June to August, 2003 and 2004 (symbols as in Figure 14).

Discussion

Although there was a great deal of variability in walleye locations and movement patterns, water clarity appeared to influence the depth distribution of walleye. Walleye did not, however, behave exactly like the Habitat Suitability Model (HSM) (Lester et al. 2004) had predicted. If subsurface illumination is, in fact, the primary abiotic controlling variable that determines the spatial and temporal dimensions of walleye feeding habitat, then walleye inhabiting lakes with different subsurface light regimes should differ in their behaviour and depth distribution. The HSM predicts that walleye will utilize waters where light intensities are within the hypothesized optimal range, barring other constraints. Therefore, in lakes of different water clarity, I predicted that walleye in stained lakes would be located in shallower, warmer water when compared to walleye in clear lakes. Lastly, I predicted that walleye in stained lakes would feed throughout the day, and not show pronounced diurnal activity patterns, when compared with walleye in clear lakes. Because walleye behaviour did not exactly follow the predictions made based on the HSM, it is likely that other factors are contributing to walleye behaviour patterns.

The two lakes used in the study had different water clarities, but were similar in most other aspects. They were similar in surface area, underlying geology, turbidity levels, and had the same predator and prey fish species. Vertical light extinction coefficients and mean Secchi depth measurements for Upper and Lower Marmion Lakes identified that Upper Marmion Lake (vertical extinction coefficient = 1.138; mean Secchi depth = 2.4 m) was approximately half as clear as Lower Marmion Lake (vertical extinction coefficient = 0.459; mean Secchi depth = 4.8 m). Extensive Secchi depth sampling showed that water clarity varied temporally over the summer season, and varied spatially within each lake. Although water clarity differed by as much as 0.7 m among basins in each lake, and as much as 0.7 m over the summer season, the differences in water clarity were much smaller in magnitude than the difference in clarity between the lakes. The difference in water clarity between the lakes was expected to create different thermal structures between the lakes. The epilimnion of the clear lake appeared to extend deeper (approximately 1.0 to 1.5 m) than that of the stained lake; however, there was considerable variation in thermal structure within each lake, and the median temperature profiles were similar. Based on their general similarities, apart from a large difference in water clarity, I assumed the lakes would be ideal to test the effect of light on walleye feeding habitat and activity.

The HSM hypothesized that walleye have an optimal subsurface light intensity range (8 to 68 lux) that they will occupy, all other factors being equal. Based on the location of this optimal light intensity range, I expected to find walleye in the stained lake in depths of approximately 5.0 to 8.0 m throughout the afternoon, moving slightly shallower in the evening. In the clear lake I expected walleye to be between 12.0 to 19.0 m throughout the afternoon, moving shallower in the evening. The light intensities in the areas inhabited by the walleye differed between the two lakes and also differed among time intervals. Walleye in the stained lake were in, or very close to, the expected depths (observed median depths: 3.3 to 7.4 m; predicted depths: 5.0 to 8.0 m), in areas that had light levels close to the optimal range throughout the afternoon, and were in the optimal range in the evening. The walleye in the clear lake were in much shallower depths than predicted by light levels alone (observed median depths: 5.5 to 8.2 m; predicted depths:12.0 to 19.0 m), in areas where light intensities were much greater than expected (8 to 100 times) throughout both the afternoon and evening periods. Although walleye in the clear lake were located approximately 10 m shallower than predicted simply by the location of optimal light levels, they were, on average, about 1.5 to 2.0 m deeper than walleye in the stained lake, suggesting that light levels may have partially influenced their vertical distribution. With the preferred light and temperature levels being available throughout the entire afternoon in the stained lake, I expected that the walleye in the stained lake would forage intermittently throughout the day, and not show as large an increase in foraging activity in the evening compared to walleye in the clear lake. However, the walleye in the stained lake displayed a very similar activity pattern to those in the clear lake: low activity in the afternoon and increasing in the evening at dusk.

A number of factors may have contributed to a potential underestimate of walleye foraging activity. Walleye were located in one hour intervals, from mid-afternoon until dark. Because walleye were only located each hour, any activity that occurred between hours was not measured. Additionally, any activity that occurred nocturnally was not measured due to the many navigational hazards that rendered night tracking unsafe. A number of studies have reported observing crepuscular or nocturnal activity maxima in walleye (Swenson and Smith 1973; Ager 1976; Kelso 1976; Holt et al. 1977; Swenson 1977), suggesting that limiting tracking to daytime periods only likely underestimated actual walleye activity. My inability to measure small walleye movements may have also contributed to the potential underestimate of walleye activity. The tagged walleye were located within a 10 m radius of their actual location, but it was often difficult, and very time consuming, to narrow a fish's location down any further. Thus, small movements by walleye were not measurable, and walleye activity may have been underestimated. Kelso (1976) noted that the majority of the walleye movements he observed were very small, but often continuous throughout the tracking period. These shortcomings were, however, not biased to one lake or the other, and walleye activity in both lakes had an equal opportunity to be underestimated.

A lack of detailed bathymetry information for the two lakes also hampered the interpretation of the data. Without a good knowledge of the availability of optimal walleye habitat, I was unable to conclude whether the walleye in the clear lake were not in the expected depths because they chose not to be, or whether the depths where optimal light levels would be found simply did not exist, thus forcing walleye to inhabit other depths. Radio-tagged walleye were seldom observed in areas of the lake where there was deep water and little doubt that optimal light levels existed. Future studies would benefit from detailed bathymetric maps which would allow the calculation of habitat availability based on factors such as light and temperature.

Despite limitations to the precision of the data collected, the difference in clarity and light between the two lakes was large and deviation of walleye behaviour from that predicted by light levels alone suggested other factors were involved. The HSM states that a walleye's light preferences may be modified by their water temperature preferences. Ryder and Kerr (1989) promoted the idea that fish satisfy their life requirements in a hierarchal fashion, and temperature requirements would likely be satisfied before light requirements. This may have been the case in the clear lake: walleye were in warm waters where mean light levels were approximately 8 to 100 times brighter than predicted. Perhaps walleye were avoiding cold temperatures where optimal light levels existed (approximately 8 °C). The walleye were in depths where the water temperature was much closer to their optimum (18 to 22 °C), in the range of 15 to 21 °C. Scherer (1971) observed walleye abandon their light avoidance behaviour in order to satisfy their dissolved oxygen requirements. Like dissolved oxygen, temperature is also a *limiting* variable and thermal preferences likely take greater priority over subsurface illumination preferences when it comes to satisfying life requirements (Ryder and Kerr 1989). Ager (1976) reported that tagged walleye remained in waters where the temperature was greater than 12 °C, and that water temperature likely played an important role in habitat selection. Kelso (1976) reported that tagged walleye remained in the epilimnion, within a very narrow temperature range, throughout the entire observation period. All of these observations suggest that water temperature may be of greater significance in determining the spatial extent of walleye feeding habitat than light. Visual piscivores appear to have species-specific differences in prey detection capabilities under different optical conditions (Vogel and Beauchamp 1999), and thus, light levels likely affect foraging success (Aksnes and Giske 1993; Sweka and Hartman 2001; Sweka and Hartman 2003; Gadomski and Parsley 2005). Brighter-than-optimal light levels may reduce foraging efficiency in walleye by reducing their ability to visually identify prey. If, however, walleye can satisfy their food requirements during the short times of the day when optimal thermal and optical conditions co-exist, the need to be in optimal light conditions at other times of the day may not be important. Because temperature affects metabolic processes and growth efficiency in fish (Shuter and Meisner 1992; Kershner et al. 1999; Quist et al. 2002), the desire to be in optimal water temperatures most of the day is likely a higher priority than being in optimal light levels most of the day. For this reason, light may have a greater role in determining the temporal dimensions of walleye feeding habitat, and somewhat less of a role in determining the spatial extent of walleye feeding habitat.

Another possible explanation for why walleye in the clear lake were not located at depths where optimal light levels were predicted to exist is that perhaps walleye were able to find refugia from bright light levels in areas where water temperatures were more preferable. I was not able to determine the actual light intensities that entered the tagged walleyes' eyes. Subsurface illumination was estimated from incoming solar radiation using the Lambert-Beer Law, and from this, light at walleye depth was determined. Ryder (1977) reported observing many walleye utilizing submerged structure possibly to shelter their eyes from bright light intensities during his many SCUBA diving investigations. In both lakes, but particularly in the clear lake, there is a very large amount of submerged timber (resulting from the flooding process undertaken in the 1920s). Often when walleye were located in the clear lake, they were found at locations with submerged trees and logs. Because no thermal refugia exists at the predicted optimal depths, walleye may have been using the submerged timber to modify their light environment in shallower, warmer waters.

The behaviour of the forage-fish species in Upper and Lower Marmion Lakes may have influenced walleye activity. The main walleye forage-fish species in these two lakes are herring (*Coregonus artedi*) and perch (*Perca flavescens*). By day, herring and perch tend to remain in protective schools, but in the evening the schools break up (Scott and Crossman 1973). Herring disperse and feed nocturnally, while perch, a daytime feeder, spend the night in shallow waters, inactive and often laying on the lake bottom

(Scott and Crossman 1973; Hasler and Villemonte 1953: in Ali et al. 1977). In the evening when the herring schools are breaking up and the visual acuity of perch is decreasing (Ali et al. 1977), the visual performance of walleye is approaching its optimum, and thus both herring and perch likely become more vulnerable to predation in the late evening, night, and early morning. It seems possible that for the walleye in this study, foraging activity may have been more dependent on the behaviour of the prey species available, and less dependent on the amount of time throughout the day that optimal light conditions existed. Even though optimal light conditions existed throughout the afternoon in the stained lake, walleye foraging activity appeared to be greatest during late evening periods when perch and herring were most vulnerable.

The relative abundance of walleye and the relative abundance of prey-fish in each lake may have also influenced walleye activity. The results of Fall Walleye Index Netting (FWIN) done on the two lakes (Lower Marmion Lake in 2003; Upper Marmion Lake in 2001) indicated higher walleye density (approximately 15 walleye per hectare) and lower prey-fish density in the stained lake, when compared to the clear lake (approximately 5 walleye per hectare) (Jackson 2002; Bio-Consulting 2003). The activity of the walleye in these two lakes may have been influenced by the different community dynamics that arise from predator-prey density differences.

In future research on this topic, a few key changes would need to be made in order to answer some additional questions raised by this study. First, what were walleye doing during the night and morning periods? I have documented the behaviour and depth distribution of the walleye in these lakes from mid afternoon until dusk. However, more information on walleye activity during the night and dawn times would fill gaps in our knowledge about what walleye do over the entire 24 hour period. As mentioned previously, many studies have reported increased crepuscular and nocturnal activity in walleye (Swenson and Smith 1973; Ager 1976; Kelso 1976; Holt et al. 1977; Swenson 1977). Second, had submerged timber (and, thus, potential light refugia) not been so readily available to these walleye, would they have utilized deeper, colder depths? Kelso (1976) reported that his tagged walleye utilized the homothermous epilimnion and never observed them straying into the colder waters of the hypolimnion. And third, if walleye densities had been similar between the two lakes, would walleye activity have noticeably differed between lakes? Addressing these emergent questions would add to the knowledge acquired in this study about how subsurface illumination influences habitat use and activity of walleye.

The more we know about the habitat selection process of fish, the better our ability to anticipate ecological impacts as many lakes and rivers in Ontario (and elsewhere) have recently experienced changes to their water clarity, and many will undergo changes in the future. On a local scale, invasive species and land-use practices have caused a change in water clarity. In the past two decades, reductions of nutrient inputs coupled with the invasion of the European zebra mussel (*Dreissena polymorpha*) throughout the lower Great Lakes has caused some locations to experience mean Secchi disc transparencies doubling in a two year period (Herbert et al. 1989; Neary and Leach 1992). As these exotic bi-valves continue to spread inland from the Great Lakes, so too will changes to subsurface light regimes. In contrast, in northern parts of the province, land-use activities such as forest management may result in a decrease in water clarity. In many lakes, light transmission is primarily a function of the amount of dissolved organic matter (DOC) in the water (Dillon et al. 1988; Koenings and Edmundson 1991; Fee et al. 1996; Perez-Fuentetaja et al. 1999; Bukaveckas and Robbins-Forbes 2000; Patrick 2003), and changes in DOC concentrations impact water clarity. Carignan et al. (2000) observed that DOC levels and light attenuation coefficients for 22 boreal shield lakes experienced a three-fold increase following deforestation events. Steedman (2000) concluded that an increase in DOC levels in three Northwestern Ontario lakes following logging disturbances was probably responsible for a 25 % reduction in water clarity. Similarly, France et al. (2000) found that DOC concentrations in 116 boreal lakes increased following forest removal. As forest management will no doubt continue in the future, so will localized changes to the clarity of many boreal lakes.

On a much broader scale, global warming is expected to indirectly cause changes in water clarity. Global circulation models (GCM) predict that increased air temperatures will likely result in increased evaporation and reduced precipitation (summer) for large parts of Ontario (Magnuson et al. 1997; Lofgren et al. 2002). It has been predicted that these drier watersheds will lead to reduced inputs of dissolved organic matter to lakes and rivers (Schindler et al. 1996; Schindler 2001), and this reduction in DOC will lead to increases in water clarity and greater penetration of visible and ultraviolet radiation. The future impacts of these changes to water clarity on walleye will be difficult to predict. The increasing transparency of waters in southern Ontario may lead to less optically preferential walleye habitat (Chu and Minns 2004), while the increased DOC staining in northern Ontario may locally create more optically preferential habitat. As global warming causes air temperatures to warm, the thermocline of many lakes may develop earlier and shallower, as time to stratification is inversely correlated with the mean air temperature (Snucins and Gunn 2000; Cahill et al. 2005), resulting in smaller epilimnia, and potentially less thermally preferential walleye habitat early in the summer. However, the predicted clearing of waters associated with global warming will also allow sunlight to penetrate further, likely pushing the thermocline deeper over the summer, resulting in a larger epilimnion by the end of the summer season (Perez-Fuentetaja et al 1999; Cahill et al. 2005), and potentially more thermally preferential walleye habitat.

If the behaviour of the walleye in this study is representative of walleye behaviour elsewhere, one might speculate as to how changing water clarity would affect other walleye populations. If lakes and rivers clear as predicted by global warming scenarios, walleye may move somewhat deeper, into slightly cooler waters. However, it appears as though the walleye response to changing light conditions may be specific to each lake, depending on the availability of refugia from bright light levels and the amount of thermally preferential habitat available. In Pigeon Lake, a shallow, weedy lake in southern Ontario, optimal light levels almost never exist in open water. The only parts of the lake where light levels approach the optimal range are within dense vegetation. Radio telemetry showed that walleye in Pigeon Lake remained in heavy vegetation during daylight hours, and were almost never observed in the weed-free areas of the lake (Holden, personal communication). The Pigeon Lake walleye may be behaving similarly to the walleye in the clear lake of this study, in that it appears as though they were using submerged structure to modify their light environment.

What is obvious from the results of this study is that light is not the only environmental factor that determines the spatial and temporal dimensions of walleye feeding habitat. It is more likely a combination of factors: light, temperature, structure, and prey behaviour; each one more or less important depending on the specific conditions existing in each waterbody that influence habitat use and foraging behaviour of walleye. As changes to water clarity are expected to continue in the future, it will be difficult to predict how those changes will affect walleye habitat. The walleye in this study did not behave quite as predicted, indicating that we still need to learn more about how light and other environmental factors influence the behaviour and habitat use of walleye. Continued study of this pervasive environmental variable would provide further, much needed insight into its importance in shaping the habitat selection of fish.

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Appendix I: Study Site Background

Upper and Lower Marmion Lakes were the result of flooding from three hydroelectric projects on the Seine River system in the mid-1920s (Ecological Services for Planning Ltd. 1992). The flooding resulted in one large lake (approximately 10 000 ha) known simply as Marmion Lake (or the "Floodwaters"). At that time, the main flow of the Seine River came in from the northeast and flowed southward out through the southwestern corner of Marmion Lake, at Moose Lake (now "Moose Bay"). In the early 1940s, Steep Rock Iron Mines Limited dewatered Steep Rock Lake, located approximately 2 km southwest of Marmion Lake, to extract iron ore from beneath the lake-bed (Ecological Services for Planning Ltd. 1992). This required re-routing the flow of the Seine River to bypass the mining operations. The old outlet of Marmion Lake (at Moose Bay) was blocked off, and a new channel was cut through the western shoreline of Marmion Lake to Raft Lake, and then on through to Finlayson Lake. Water level control structures were created at the junction of Marmion and Raft Lakes to provide adequate water flows to hydroelectric projects downstream.

By the mid 1940s, Steep Rock Iron Mines Limited and the Caland Ore Company were using the southern portion of Marmion Lake as a disposal site for the spoils (clay, silt, sand, and gravel) of the Steep Rock Mine. Between 1955 and 1960, approximately 112 000 000 m^3 of spoils were deposited in Marmion Lake (Ecological Services for Planning Ltd. 1992). At this same time, a series of weir structures were constructed to separate the southern portion of the lake (now *Lower* Marmion Lake [or the "Caland Silt Basin"]) from the northern portion (now *Upper* Marmion Lake), to prevent the spoils from being carried downstream in the main flow of the Seine River (now confined to the upper portion of the lake). One of the weirs had a channel through it so that water levels in Lower Marmion could fluctuate with those of Upper Marmion. At that time, water levels generally fluctuated up to 2.7 m per year (Ecological Services for Planning Ltd. 1992).

In the mid 1980s, Ontario Hydro built a thermal generating station (Atikokan Thermal Generating Station) on the southwestern shore of Lower Marmion, next to the old outlet at Moose Bay. The station used Lower Marmion (as well as adjoining Snow, Icy, and Abie Lakes) as part of its cooling-water circuit. The station's pumps required relatively stable water levels, so the channel linking the two lakes was filled (all except for a small navigational sluice that has its stop-logs removed in the summer months when the two lakes' water levels equalize), reducing the water fluctuation in Lower Marmion to approximately 0.4 m per year (Ecological Services for Planning Ltd. 1992).

Prior to the 1980s, little information existed on fish populations in Upper and Lower Marmion. The construction of the thermal generating station resulted in a number of fish population studies being conducted on Lower Marmion. The results of these early studies were contained in the Atikokan Generating Station Environmental Effects Report (Ecological Services for Planning Ltd. 1992). The report summarized a number of changes in the cooling circuit lakes, including changes in water temperature, water flow, water quality, and timing and location of walleye spawning. The report also concluded that more studies were required to fully assess the impacts of the generating station on the fish population in Lower Marmion. In the mid-1990s, Ontario Hydro agreed to implement further monitoring programs for the fish populations of Lower Marmion; this led to index netting assessments in 1996, 2001, and 2003. Additionally, the Ontario

Ministry of Natural Resources (OMNR) conducted an index netting assessment in 2001 and several angler surveys throughout the late 1980s and 1990s. The OMNR also conducted an assessment of the walleye population in Upper Marmion in 1994 and 2001 to be used for comparison purposes.

Results of the mid-1990s index netting indicated a very low density of walleye (1.5 walleye/ha; essentially dominated by one year class, with very few young fish) in Lower Marmion (Bio-Consulting 1996), when compared to Upper Marmion (18.4 walleye/ha; good representation of all year classes) (Jackson 1995). It was hypothesized that the generating station's warm water output was disrupting normal walleye spawning routines, leading to the extremely low density of walleye in Lower Marmion. Subsequent measures were taken to prevent walleye from entering the cooling circuit lakes. Additionally, the sport-fishery for walleye was closed indefinitely in Lower Marmion Lake in 1998.

Since that time, follow-up assessments in 2001 and 2003 indicated a continued low density of walleye in Lower Marmion (3.8 walleye/ha), but suggested it may be slowly increasing. Northern Pike (*Esox lucius*) and Coregonids showed an increased catch-per-unit-effort as well (although the index netting method used has only been standardized for walleye) (Bio-Consulting 2003). Smallmouth Bass (*Micropterus dolomieu*) catch-per-unit-effort decreased in the most recent netting assessment; however, angler catch rates of bass are increasing (personal communication, Brian Jackson).

Appendix II: Transmitter Implantation Methods

Early in the summers of 2001 and 2002, after spawning had concluded, 6-foot trap nets were used to generate a sample of 25 walleye in Lower Marmion Lake. These fish were used in a walleye telemetry study being conducted by the Ontario Ministry of Natural Resources, Atikokan Area Office. By May, 2003, 14 of these radio transmitters were still functional. In June, 2003, an additional 10 radio transmitters were implanted in walleye from Upper Marmion Lake, bringing the total number of operational transmitters available for this study in both lakes to 24. The locations where trap nets were set were limited to the western half of Upper Marmion Lake in the hopes that the walleye would remain in the western portion of the lake: the entire lake was too large to monitor each day (approximately 20 km long across the land; approximately 50 km long following the water). The trap net locations were selected using a map and numbered grid system, and a set of randomly generated numbers to identify the part of the lake where the net would be set.

The transmitters used were supplied by Advanced Telemetry Systems (Isanti, Minnesota), and were model F1850 (formerly known as model 6AA). For transmitter specifications, see Table 4.

The surgery techniques used to implant the radio transmitters were adapted from Hart and Summerfelt (1975) and Ross (1982), by Darryl Mcleod and Brian Jackson (Ontario Ministry of Natural Resources). After walleye were removed from the trap net, they were measured for length and weight. Although recent research suggests that peritoneal transmitters up to 12% body weight: transmitter weight can be used without affecting

Table 4. Operating specifications of Advanced Telemetry Systems F1850 radio transmitter.

Model	F1850
Pulse rate	40 pulses per minute
Pulse width	20 milliseconds
Weight	25 grams
Battery	AA Lithium
Warranty life	633 days
Battery capacity	1266 days
Operating frequency	048.001 - 048.990 MHz

swimming performance (Brown et al. 1999), I adhered to the generally accepted guideline of 2% body weight: transmitter weight. The ATS F1850 radio transmitters weighed 27. 2 grams, therefore, only walleye equal to or greater than 1.2 kg received transmitters. Walleye were anaesthetized using a mixture of 9.6 grams of tricane methane sulfonate (MS-222) to 32 litres of lake water. Walleye remained in the anaesthetic bath until the fish lost equilibrium and all body movement (except for respiratory movement) ceased. Fish were then placed ventral side up on a V-notched measuring board such that the fish's gills remained submerged, while the incision area was out of the water. All surgical equipment was rinsed in a 1:1 mixture of 70% alcohol and distilled water, prior to each usage. Surgical gloves were worn at all times, and were replaced at the beginning of each surgery. After the incision site was rinsed with alcohol, a 3 cm long cut was made using a scalpel. Care was taken to ensure that no internal organs were damaged, and the cut was just deep enough to expose the body cavity. The incision site was located approximately 2 to 3 cm posterior to the pelvic fins. Next, a 30 cm shielded-needle was inserted into the body cavity. The needle was used to create a small opening in the body wall beside the anal pore that the shielding-tube could pass through. The needle was withdrawn from the shielding-tube and was replaced with the wire antenna of the transmitter unit. The tube was then removed from the fish via the small hole next to the anus, drawing with it the transmitter antenna. The transmitter itself was placed into the body cavity at this time. The main incision was stitched 3 times using a surgical knot technique. The antenna exit hole was small enough that it did not require stitching. Using a hypodermic needle, 3 mL of an antibiotic (oxy-tetracycline) was then injected into both wounds. Just prior to being placed in the recovery tub, each walleye had a yellow disc tag (with a unique 6 digit identification number on it) sewn into its back just anterior to the dorsal fin. The fish was then returned to a tub of fresh water, where it was allowed to recover from the anaesthetic. After a recovery period of approximately 30 minutes, the walleye was released back into the lake at the initial capture site. Each surgery took approximately 5 minutes to complete.