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SEASONAL BATHYTHERMAL HABITAT USE BY  
LAKE TROUT AND LAKE WHITEFISH IN LAKE  
HURON AS MEASURED WITH IMPLANTED  
ARCHIVAL TAGS

presented by

Roger Allen Bergstedt

has been accepted towards fulfillment  
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**SEASONAL BATHYTHERMAL HABITAT USE BY LAKE  
TROUT AND LAKE WHITEFISH IN LAKE HURON AS  
MEASURED WITH IMPLANTED ARCHIVAL TAGS**

**By**

**Roger Allen Bergstedt**

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## **ABSTRACT**

### **SEASONAL BATHYTHERMAL HABITAT USE BY LAKE TROUT AND LAKE WHITEFISH IN LAKE HURON AS MEASURED WITH IMPLANTED ARCHIVAL TAGS**

By

Roger Allen Bergstedt

Temperatures occupied by 33 lake trout (*Salvelinus namaycush*) in Lake Huron were recorded with surgically implanted archival tags in 1999 and 2000. Objectives were to provide temperature data to refine bioenergetics models of sea lamprey (*Petromyzon marinus*) predation on lake trout, and to compare temperatures occupied by strains of lake trout. During seasonal periods of mixing, variability was low and followed surface temperature. During summer stratification, temperatures occupied varied substantially among individual fish and strains. Between June and mid August, upper Great Lakes origin (GLO) lake trout occupied warmer water than Finger Lakes, New York origin (FLO) lake trout, but both occupied temperatures below laboratory preferred temperatures. In October, both origins occupied warm or warmer water than that in summer, partially explaining the higher lethality of sea lamprey attacks during October.

The objectives of a second study with archival tags recording depth and temperature in 2002-2005 were to compare the observations with the 1999-2000 data, to examine whether GLO lake trout occupy both higher temperatures and lesser depths than FLO lake trout, and to examine changes in the temperatures occupied in light of concurrent changes in the prey community. Temperatures occupied by GLO0 lake trout were

significantly higher than by FLO lake trout, supporting the conclusion of the first study. The GLO lake trout also occupied significantly shallower depths than FLO lake trout. Compared to 1999-2000, both GLO and FLO lake trout occupied significantly lower temperatures. Concurrently, pelagic alewives (*Alosa pseudoharengus*) disappeared, demersal round gobies (*Neogobius melanostomus*) invaded Lake Huron, and prey biomass decreased by 90%. Switching to demersal prey and a retreat to temperatures below the optimum for growth in response to food scarcity are potential explanations of the movement toward lower temperatures.

Depth observations from tagged lake whitefish (*Coregonus clupeaformis*), recorded in 2003-2005, were used to examine whether seasonal depth differences could be exploited to reduce bycatch of lake trout in commercial gill net fisheries for lake whitefish. Both GLO and FLO lake trout occupied significantly deeper and colder waters seasonally, during both daylight and dark, than lake whitefish. Separation was greater between FLO lake trout and lake whitefish. Fishing to seasonal depth limits of 25 to 35 m could target half or more of the lake whitefish, yet relatively low percentages of lake trout. Percentages of lake trout targeted were lowest in late July (GLO = 8% and FLO = 11%) and early August (GLO = 4% and FLO = 7%). Feasibility depends on lake whitefish being available to gill nets. Modal depths of commercial gill net effort exceeded the modal depth in the lake whitefish archival tag data and suggested some lake whitefish were pelagic enough to not be vulnerable to gill nets. The possibility of using suspended gill nets was suggested.

## **DEDICATION**

This work is dedicated to my mother and father, Pearl and Roy Bergstedt, and to my wife Jocelyn, who patiently supported me as I resumed my education in pursuit of a doctoral degree.

## **ACKNOWLEDGMENTS**

I thank my graduate committee of Dr. William Taylor, Dr. Charles Krueger, Dr. Michael Jones, Dr. Mohamed Faisal, and Dr. R. Scott McKinley for their guidance.

Funding for this research was provided by the U.S. Geological Survey, the U.S. Fish and Wildlife Service through the Great Lakes Protection Fund, and the Great Lakes Fishery Commission.

I thank Mrs. Karen Slaght, Mr. David Keffer, Mr. Erick Larson, and Mrs. Mary K. Jones for their assistance in all phases of this research. Mr. Mark Ebener provided valuable assistance in obtaining the cooperation of tribal fishers. Dr. James Bence provided valuable assistance and advice on data analysis. I particularly thank Dr. Charles Krueger and Dr. Chris Goddard for their support in both my research and in my pursuit of a doctoral degree.

## PREFACE

Temperature is an important environmental variable affecting food consumption, growth, and the depth and spatial distribution of the genetic strains of lake trout (*Salvelinus namaycush*) stocked in Great Lakes. Studies of *Salvelinus* species have shown that temperature preference, depth preference, and thermal resistance are heritable characteristics of *Salvelinus* species and would likely vary among genetic strains. Temperature preference can be influenced by selective breeding of lake trout and the generation of hybrids between lake trout and brook trout (Goddard and Tait 1976). Tait (1970) showed that swim bladder gas retention of F<sub>2</sub> hybrids of lake and brook trout (*S. fontinalis*) was intermediate to either parent species. Gas retention was further demonstrated to vary between lake trout from two lakes, that interpopulation crosses were intermediate in gas retention, and that gas retention correlated with depth distribution of the parent populations (Ihssen and Tait 1974). The ability to tolerate thermal stress has also been identified as heritable (Ihssen 1973). The combined phenotypic expression of these multi-genic traits during summer periods of thermal stratification affects the temperature and depth distributions of lake trout. Clear genetic differences exist among the strains of lake trout stocked (Krueger *et al.* 1989), which suggest that strains may differ in their distributions across temperature and depth gradients.

Hutchinson (1957) was first to define “niche” in a strong quantitative sense and suggested that laboratory data could be used to describe the fundamental, or non-

interactive, niche of a species within a temperature gradient. Numerous laboratory studies have contributed to our understanding of the thermal behavior of lake trout, including preferred temperatures (*e.g.*, McCauley, and Tait. 1970; Peterson *et al.* 1979; Edsall and Cleland 2000), optimum temperatures for growth (*e.g.*, Elliot and Hurley 1999; Edsall and Cleland 2000), and temperature tolerance or lethal limits (*e.g.*, Ihssen 1973; Grande and Andersen 1991). Results of these studies tend to be consistent (Jobling 1981) and imply an innate component to the responses of lake trout to changes in temperature as suggested by Hutchinson (1957). However, description of a fundamental niche for temperature considers only one of a number of environmental variables affecting the distribution of fish and species are often found at temperatures outside the range indicated in laboratory studies (Magnuson *et al.* 1979). Describing the realized thermal niche based on assembled field observations, which incorporate the other variables affecting habitat will typically be of greater interest to fishery ecologists (Magnuson *et al.* 1979). As examples, Eaton *et al.* (1995) and Huff *et al.* (2005) used this approach to describe temperature tolerance and Huff *et al.* (2005) also described the center and width of the realized niche for some vertebrates.

Although the results of my research will be useful in describing temperatures occupied as one aspect of the realized niche of lake trout, my interest in describing the seasonal temperatures derived from experiences conducting fish stock assessment on Lake Ontario, 1978-1985, and my perception of the potential importance for management to have an accurate description of the seasonal temperatures occupied by lake trout. This interest was originally triggered by observations of losses of lake trout to sea lamprey

predation as documented by the collection of dead lake trout in bottom trawls (Bergstedt and Schneider 1988). Although intensive trawl surveys were conducted from late-April through October, dead lake trout were recovered only in October and early November, when the partial autumnal circulation placed lake trout at the highest temperatures of the year. This suggested that temperature could have a role through elevation of sea lamprey metabolic rate, and hence rate of blood consumption. Further analyses of collections of dead lake trout during 1982-1992 (Schneider et al. 1996) suggested that sea lamprey attacks on the Seneca strain of lake trout showed lower lethality than on other strains.

The seasonal depths and temperatures occupied by the various genetic strains of lake trout being stocked into the Great Lakes for rehabilitation and the commercially important lake whitefish (*Coregonus clupeaformis*) are known only as generalizations. Our knowledge is not based on continuous observations, but is deduced from captures in different fishing gears. These capture data only provide point estimates of abundance within the depths and temperatures sampled and suffer from the sampling bias of each gear. As such, existing data do not accurately reveal seasonal and diel rhythms, and are limited to the times of year when surveys are conducted in the Great Lakes. The ability to compare the seasonal distributions of lake trout and lake whitefish is of particular interest because lake whitefish are the primary commercial species in Lake Huron and loss of lake trout as bycatch affects achievement of lake trout rehabilitation in Lake Huron. Maintaining total annual mortality below 40% is critical to lake trout restoration and mortality due to bycatch is one of the components of mortality.

Development of archival, or data-storage, tags provided a new approach to collecting data on seasonal bathythermal habitat use by fish in the Great Lakes. Archival tags are considered a form of telemetry, but instead of transmitting data, they store it on flash memory. These tags can be either attached externally or implanted in the body cavity of fish. When a tagged fish is released, they record data at predetermined intervals. This was an important new advance in technology because investigators no longer were required to physically follow a fish to receive data transmissions. However, to retrieve the data fish must be recovered and the data from the tag downloaded. If a species is exploited at a reasonable rate, as are lake trout and lake whitefish, and if they are externally tagged with an offer of a substantial reward, recovery is not a problem.

Advancing the knowledge of bathythermal habitat selection by strains of lake trout (Chapters One and Two) provides an improved understanding of the mechanisms behind differences in attack frequency by sea lampreys and the lethality of sea lamprey attacks, a critical component of lake trout mortality. Great Lakes origin lake trout stocked in lakes Huron and Ontario have consistently higher sea lamprey attack rates than lake trout of Finger Lakes origin (Eshenroder et al. 1995; Schneider et al. 1996). Differences in attack rate and survival from individual attacks may be related to differences in seasonal bathythermal distributions among strains (Swink 1993; Schneider et al. 1996). If bathythermal distributions varied, then differential overlap with the bathythermal distribution of the sea lamprey could account for differing attack rates. Occupation of lower or higher temperatures could, through the effects of temperature on metabolic rate and blood consumption, also affect sea lamprey attack lethality.

The importance of lake trout restoration in the Great Lakes makes the data and analyses provided in this dissertation timely. For example, the recent signing of the 2000 Consent Decree in U.S. District Court, which governs fisheries management in the 1836 treaty-ceded waters of the upper Great Lakes for the next two decades, clearly demonstrated the strong commitment of the federal, state, and tribal fishery management agencies to rehabilitate lake trout. This commitment and, indeed, the Agreement itself require reductions in the mortality of lake trout caused by commercial and sport fisheries.

Lake whitefish are the principal target of commercial species in the Great Lakes, and lake trout are the principal bycatch in that fishery (Brown *et al.* 1999). Bycatch was defined by Crowder and Murawski (1988) as both the retained and discarded non-target organisms, including unobserved mortalities of fish that are released. Unobserved mortality includes delayed deaths caused by injury, stress, disease, or predation (Chopin *et al.* 1996). Lake trout gilled in the leads and pots of trap nets account for biologically significant bycatch mortality (Johnson *et al.* 2004), although not as high per lake whitefish harvested as gill nets. Johnson *et al.* (2004) also addressed the issue of post-release survival of lake trout released unharmed from the pots of trap nets. Using data from Chapters One and Two, they estimated that over 98% survived after release. In contrast, survival of live lake trout taken from gill nets was estimated at 72% (Gallinat *et al.* 1997). Recommendations to reduce bycatch losses of lake trout included limiting lake whitefish harvest to trap nets and reducing effort in summer when the ratio of lake trout to lake whitefish caught was highest (Johnson *et al.* 2004). Diel and seasonal

bathothermal habitat-use profiles for lake trout and lake whitefish provided in this dissertation increase our understanding of lake trout losses to sea lamprey predation and can contribute to consideration of options to reduce lake trout losses caused by commercial fisheries bycatch (Chapter Three).

In Chapter One, archival (or data-recording) tags implanted in lake trout that recorded the temperatures occupied during 1999 and 2000 and showed that different strains of lake trout inhabited waters of different temperatures. However, the archival tags used in that study only recorded temperature and could not reveal whether strain differences were due to differing depths or to occupying similar depths in different geographic areas where the depth of the metalimnion differed (*e.g.*, nearshore or offshore). Therefore, concurrent measures of depth and temperature were needed for the commonly stocked lake trout strains and lake whitefish to fully understand their interaction.

Subsequent to the first study (Chapter One), substantial progress occurred in miniaturization of electronics that made it possible to implant a smaller archival tag that recorded both depth and temperature. In Chapter Two, these newer tags were implanted in lake trout in 2002 and 2003 and used to assess the overlap of both temperature and depth distributions among strains of lake trout and to compare with results from 1999-2000. A similar approach was used for lake whitefish during 2002-2004, where the data were used to compare lake whitefish distributions to lake trout, and develop recommendations to reduce lake trout bycatch in lake whitefish commercial fisheries (Chapter Three).

The objectives in Chapter One were to:

1. Obtain seasonal temperature-use profiles for the strains of lake trout being stocked in Lake Huron
2. To examine whether the seasonal patterns vary significantly among strains.
3. To provide more realistic temperature data for bioenergetics models of strain differences in survival from sea lamprey attack and for models of prey consumption by lake trout.

The objectives in Chapter Two were to use archival tag data recorded 2002-2005 to:

1. Compare the temperatures occupied by lake trout strains in 2002-2005 to those reported in Chapter One for 1999-2000 with regard to strain and time interval.
2. Examine whether lake trout of Finger Lakes, New York origins consistently occupy both lower temperatures and greater depths during the summer months than lake trout of Great Lakes origin.
3. Examine whether changes in the temperatures occupied by lake trout have altered in light of recent changes in the abundance and composition of their prey.

The objectives in Chapter Three were to use archival tag data recorded 2003-2005 when data from both lake trout and lake whitefish were available to:

1. Describe the seasonal temperature and depth distribution of lake whitefish.
2. Compare the seasonal distribution of lake whitefish to lake trout of Finger Lakes and Great Lakes strain origins.

3. **Propose seasonal depth restrictions for commercial gear fished for lake whitefish for the purpose of minimizing lake trout bycatch.**

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## **CHAPTER ONE**

Bergstedt, R.A., Argyle, R.L., Seelye, J.G., Scribner, K.T., and Curtis, G.L. 2003. *In situ* determination of the annual thermal habitat used by lake trout (*Salvelinus namaycush*) in Lake Huron. *J. Great Lakes Res.* **29** (Suppl. 1):347–361.

## **Abstract**

Records of the temperatures occupied by 33 lake trout (*Salvelinus namaycush*) at large in Lake Huron were obtained for up to 14 months per fish, at 75-minute intervals, from surgically implanted archival temperature tags. The dataset covered nearly three years, from October 1998 to June 2001, and included 160,000 observations. The objectives of the tagging were to obtain temperature data to refine bioenergetics models of sea lamprey (*Petromyzon marinus*) predation on lake trout, and compare the temperatures occupied by strains of lake trout stocked in Lake Huron. The seasonal, thermal-use profiles of lake trout followed the general warming and cooling pattern of Lake Huron. During periods when the zone of surface water mixing extended below the depth range occupied by lake trout, variability among individual fish and strains was low and followed surface temperature. However, during the period of summer stratification, the average temperatures occupied varied substantially among individual fish and strains. Strains (Lake Superior and Lewis Lake) originating from the upper Great Lakes occupied similar temperatures. Between June and mid August, upper Great Lakes lake trout typically occupied water several degrees warmer than that occupied by lake trout of Finger Lakes, New York origin. Most of the lake trout occupied summer temperatures lower than the preferred temperatures suggested by laboratory studies. In October, all strains occupied water as warm as or warmer than that occupied in summer, which may partially explain the higher lethality of sea lamprey attacks during October.

## Introduction

Restoration of native lake trout (*Salvelinus namaycush*) in the Great Lakes continues to be a high priority for U.S. and Canadian fishery agencies. Although there is some natural reproduction in Lakes Huron and Ontario, restoration has only been successful enough to create self-sustaining stocks in Lake Superior. Possible impediments to restoration in the other lakes include a loss of genetic variability, effects of non-native species, habitat degradation, mortality from predation by sea lampreys (*Petromyzon marinus*), and mortality from fishing (Krueger *et al.* 1995; Ebener 1998). Research and assessment considered necessary to evaluate lake trout restoration in Lake Huron include community interactions, stocking strategies, and population and community modeling (Ebener 1998). A key information need in each category is seasonal, temperature-use profiles for the various hatchery strains of lake trout stocked.

Temperature is an important parameter governing food consumption and growth of both lake trout and sea lampreys, yet descriptions of temperatures occupied by lake trout as hosts are mostly derived from laboratory studies or based on captures in fishing gear. Temperature at capture in active gear reflects only the temperature occupied by the fish at that moment. For fish captured in passive gear, only the temperature at deployment or retrieval is known, which may not reflect the temperature at capture; in the Great Lakes that difference can be substantial due to internal seiches. In the absence of *in-situ* data, Stewart *et al.* (1983) assumed a preferred temperature of 10°C for lake trout in Lake Michigan, hypothesizing that lake trout occupy the warmest available water as long as it does not exceed the preferred temperature. The preferred temperature of 10°C was about

two degrees cooler than the temperatures preferred by yearling lake trout (11.7°C) in the laboratory (McCauley and Tait 1970). The lower temperature was used because field observations indicated that lake trout normally occupy temperatures about two degrees lower than in the laboratory (Spangler and Berst 1976; McCauley and Tait 1970). Madenjian *et al.* (1995) derived temperature regimens for lake trout from the mean temperatures in which lake trout were caught in gill nets and trawls.

Reduction and control of sea lamprey populations remains critical for restoration of lake trout, and justification for continued sea lamprey management ultimately rests on its expected benefits (Sawyer 1980; Koonce *et al.* 1993; Christie and Goddard 2003). Defining benefits requires estimating the damage done by sea lampreys to their host fishes. A promising approach to damage estimation has been bioenergetics modeling (Kitchell and Breck 1980; Kitchell 1990). The diurnal and seasonal temperatures occupied by sea lampreys when attached to lake trout (their preferred host in the Great Lakes) are necessary for developing and refining models of sea lamprey growth and for assessing the damage from attacks. Madenjian *et al.* (2003) integrated seasonal data on sea lamprey growth (Bergstedt and Swink 1995), energy density (Cochran *et al.* 2003), and temperature (this study) to construct a more realistic bioenergetics model of blood consumption by sea lampreys, and to examine some new hypotheses regarding the seasonal effects of sea lamprey predation on lake trout (Bergstedt and Schneider 1988; Schneider *et al.* 1996; Bence *et al.* 2003).

To better understand their seasonal bathythermal distribution and to provide data for bioenergetics models, archival (*i.e.*, data recording) temperature tags were surgically implanted in several strains of lake trout collected from Lake Huron during 1998-2000. The objectives were to obtain seasonal temperature-use profiles for strains of lake trout in Lake Huron, examine whether the seasonal patterns vary significantly among strains, and provide more realistic temperature data for bioenergetics models of strain differences in survival from sea lamprey attack and for models of prey consumption by lake trout.

## **Methods**

### **Tags and tagging**

The archival temperature tags used in this study were manufactured by Vemco Limited, Nova Scotia, Canada. Two types of archival tags were used, the standard TX Minilog, containing a single thermistor, and a customized TX Minilog with a second thermistor mounted on a 70-mm stalk. The purpose of the second thermistor was to provide capability for simultaneous collection of internal and external temperatures. Regardless of the tag used, all electronics were housed within the cylinder that was surgically implanted in the abdominal cavity of the fish. In order to obtain external temperatures, the stalk of the customized tag protruded through the body wall. External water temperatures are not reported in this paper, and all recorded temperatures refer to temperatures measured inside the abdominal cavity. The cylinder containing the electronics and battery measured 16 mm in diameter by 71 mm long. The tags were capable of measuring temperatures from  $-5$  to  $35^{\circ}\text{C}$  with  $0.2^{\circ}\text{C}$  resolution and  $\pm 0.3^{\circ}\text{C}$

accuracy. The calibrations were checked against a calibrated thermometer when tags were recovered; observed accuracy was always within the specified limits. The standard tag weighed 23.5 g in air and 9.0 g in water, and the modified tag weighed 26.8 g in air and 9.8 g in water. Fish were also marked externally with dart tags manufactured by Floy, Inc., Seattle, Washington, that advertised a \$100 (US) reward and provided contact information.

Tagging of adult lake trout was conducted from 1998 through 2000 (Table 1). In 1998, lake trout were tagged and released during October at Drummond Island and during November at the Hammond Bay Biological Station (HBBS). In 1999, tagging was at Drummond Island during May and November and at the HBBS during May, June, and August. In 2000, all tagging was conducted at the HBBS during May. The lake trout tagged at Drummond Island were obtained from gill nets fished by the Chippewa Ottawa Resource Agency (CORA) for lake trout assessment near Scammon Cove along the south shore of Drummond Island, MI. The lake trout tagged at HBBS were obtained from commercial trap nets fished by Gauthier and Spaulding Fisheries along the western shore of Lake Huron between the HBBS and Alpena, MI.

Lake trout obtained from gill nets were transferred to aerated containers and transported to shore and placed in 1000-L tanks supplied with a constant flow of aerated, ambient-temperature Lake Huron water. Lake trout from trap nets were placed in a floating pen adjacent to the trap net pot and then transferred in aerated containers—either directly by boat to the HBBS or indirectly by boat to shore and then by truck to the

HBBS. At the HBBS, they were held in raceways or in 1000-L tanks in aerated, ambient-temperature Lake Huron water. After transfer to the tanks

**Table 1.** Summary of lake trout tagged with surgically implanted archival temperature tags and released in Lake Huron, the number of lake trout tagged by date, location, and source, the number known to have been captured or died, the number from which data files were recovered, the number of fish used in the analyses, and (for the fish used in the analyses) the total days at large.

Date tagged	Tagging and release location	Source	Number released	Number reported captured or dead	Number of data files recovered	Number of fish used in analyses	Total days at large
Oct. 1998	DI	Gill net	90	13	11	9	6,303
Nov. 1998	HBBS	Trap net	13	3	2	1	268
May 1999	DI	Gill net	12	1	0	0	0
May 1999	HBBS	Trap net	56	10	9	8	1,549
Jun. 1999	HBBS	Trap net	34	5	5	0	0
Aug. 1999	HBBS	Trap net	8	0	0	0	0
Oct. 1999	DI	Gill net	43	7	7	7	3,648
May 2000	HBBS	Trap net	62	10	8	8	1,396
Totals			318	49	42	33	13,164

or raceways the lake trout were held from four hours to four days before undergoing surgery. Fish that were lethargic, appeared severely stressed, or showed visible injuries were not used in the study.

Fish were anesthetized with clove oil (Anderson *et al.* 1997). Once anesthetized, the fish were weighed, measured, and fin clips recorded. For the surgical procedure, lake trout were placed on a foam rubber-covered table and a small submersible pump was used to maintain a flow of water containing a maintenance concentration of anesthetic across the gills. A 2- to 3-cm incision was made about 1 cm to either side of the ventral midline anterior to the pelvic fins. The thermal tag was inserted through the incision, and, for the customized thermal tags, the external thermistor was threaded posteriorly out through a small hole in the body wall just behind the pelvic fins. Three or four monofilament sutures were used to close the incision and 3-M Vet-Bond® adhesive was applied to the knots. A numbered Floy tag was inserted just below the dorsal fin. The procedure generally took from 3 to 5 minutes, after which the fish were transferred to a recovery tank. For those fish tagged with the standard Minilog, the tag was simply inserted in the incision, the incision closed as described, and the fish double tagged (one tag on each side of the dorsal fin) with the numbered Floy tags. Following surgery, most fish regained equilibrium within 5 to 10 minutes and were held from 24 to 48 hours before release, except during fall 1998, when most fish were released when they appeared fully recovered from the anesthetic (generally within 3 to 4 hrs).

Information posters describing the study, advertising a \$100 reward for return of the tag and fish, and providing contact telephone numbers were displayed in tackle and convenience stores, at launch sites, and provided to commercial and charter fishers. The Michigan Department of Natural Resources and the Ontario Ministry of Natural Resources also publicized the study. In addition to the posters, the stalk of the external

thermistor on the customized Minilogs and the external Floy tags also carried reward notices and contact information.

### **Other data sources**

Seasonal surface water temperatures and measures of thermal stratification in Lake Huron were obtained from two sources. To describe the seasonal pattern of warming for surface waters, temperature data for spring through fall of 1998 through 2001 were obtained from a 3-meter discus buoy deployed by NOAA at station 45003 near the middle of Lake Huron (45.35° N, 82.84° W). Temperature at the buoy was measured at 0.6 m below the surface, and the buoy is deployed from April through November of each year. As an indication of the pattern of thermal stratification and the likely depths associated with observed temperatures, data collected with a bathythermograph during 16 to 18 August 1999 (Marc Tuchman, EPA Great Lakes National Program Office, Chicago Illinois, unpublished data) were averaged across seven sites in northern Lake Huron (Latitude > 44.5° N).

### **Genetic strains of lake trout**

In 1985 a study was initiated in Lake Huron to evaluate relative performance of the Superior Marquette Domestic (SMD) strain and several alternative strains. The fish included in this study were implanted with coded-wire tags (CWT) and marked externally by removing the adipose fin. Alternative strains included the Lewis Lake Wild strain (LLW), the Jenny Lake Wild strain (JLW), the Seneca Lake Wild strain (SLW), and the Lake Ontario Wild strain (LOW). The Lewis and Jenny Lake strains originated

from fry hatched from eggs collected in northern Lake Michigan and stocked in Shoshone and Lewis Lakes in Yellowstone Park in 1889 (Crossman 1995). The Lake Huron Technical Committee recommended JLW and LLW for Lake Huron because they might contain genes from original Great Lakes stocks (Ebener 1998). The Seneca Lake strain (SLW) originated from eggs taken in Seneca Lake (one of the New York Finger Lakes) and was a strain that showed evidence of being less vulnerable to sea lamprey attack (Schneider *et al.* 1996). The Lake Ontario strain (LOW) originated from eggs taken from feral fish of mixed strains in Lake Ontario. All of these strains are considered to be shallow water or “lean” forms of lake trout.

The LOW strain was included in Lake Huron stockings as a surrogate for the SLW strain because of a shortage of SLW eggs. Only the 1989, 1991, and 1992 year classes of the LOW strain were stocked. Several sources provide evidence that the LOW and SLW strains are genetically similar. Most of the LOW strain stocked were propagated from the 1983 year class of brood stock derived from gametes collected in Lake Ontario and held at the Allegheny National Fish Hatchery. Ninety percent of the 1989 year class, 100% of the 1991 year class (Elrod *et al.* 1996a), and 100% of the 1992 year class of LOW (D. Blick, Allegheny National Fish Hatchery, personal communication) were from this 1983 brood stock. Marsden *et al.* (1993) estimated that the parental contribution to the 1983 LOW brood stock was approximately 81% SLW, and that this strain provided the only statistically significant contribution among the six strains previously stocked into Lake Ontario. Krueger *et al.* (1989) compared allelic variation in 16 collections of lake trout, including SLW and the 1983 LOW brood stock, and concluded the two strains were

genetically similar. Therefore, the SLW and LOW strains were treated as one group. Because the lake trout in the New York Finger Lakes likely experienced some mixing over the years due to hatchery practices (Charles Krueger, Great Lakes Fishery Commission, personal communication), the combination of SLW and LOW is hereafter referred to as being of Finger Lakes Origin (FLO).

The genetic strains of fish in this study were identified from CWTs or a combination of fin clips and DNA analysis. Fish with CWTs were readily identified to strain if the fish was recovered along with the thermal tag. In a few instances, anglers had discarded the head but a tissue sample from a fillet was obtained for DNA analysis. For fish with only fin clips, strain could not be determined from fin clips because they were only year-class specific and all strains were usually marked identically. For 10 fish where the strain could not be determined from CWTs, individuals were assayed at eight microsatellite loci (Page 2001). For eight of those fish, the fin clips indicated the strain was either LLW or SMD, and for the other two, fin clips indicated either LLW, SMD, SLW, or LOW. Individual fish were assigned to hatchery strain of origin based on the likelihood of observing individual multilocus genotypes, given the expected frequency of occurrence in each strain in individual assignment tests (Paetkau *et al.* 1995). Estimates of statistical confidence in strain assignments for individual fish were derived from the posterior probabilities using a Bayesian approach (Pritchard *et al.* 2000, Topchy *et al.* in review) and considering the prior information on the possible strains associated with each fin clip. The tissue sample from one fish had deteriorated and strain could not be assigned. The other nine fish were assigned a strain based on the DNA analysis; the confidence in

correct assignment ranged from 0.74 to 0.98 with a mean confidence of 0.90 and median confidence of 0.91.

### **Data intervals and statistical tests**

The recording interval of the archival tags was set to 75 minutes, which resulted in a maximum temperature record of 424 days. When the memory filled, recording ceased and the data were retained until downloaded. For fish remaining at large until the memory filled, the 424-day record insured that data collected during the recovery period following surgery could be discarded while still retaining an entire year's record.

Temperature data were summarized by seasonal intervals of half-month duration. The first half of each month included the first 15 days and the second half the remaining days in the month. Half-month intervals were not initially combined across years. Because these data were intended to be used in bioenergetics models of sea lamprey growth (Madenjian *et al.* 2003), the arithmetic mean temperature (°C) in each half-month interval was used to best represent the average number of degree-days experienced by a fish. With each fish, there was a period following release when it was recovering from surgery and the diel temperature pattern was suspect. Each plot of temperature was inspected and a subjective judgment was made as to the date when behavior appeared normal. For fish captured within 424 days of release, when the tag was still actively recording, the date when the fish was caught in the fishing gear was evident from a cessation of diel temperature changes. Temperature observations before behavior appeared normal and after the fish was caught were not used in the analyses. Data for

each combination of fish and half-month interval were used only if there was more than seven days of data. To avoid pseudoreplication, subsequent analyses were based only on the means for individual fish by half-month interval. Analyses also considered the repeated nature of the measures among subsequent half-month periods for an individual fish.

The temperatures analyzed and reported in this study were only those recorded inside the abdominal cavity. At any instant, these could vary from the temperature of the surrounding water. However, over the temporal scale of a half-month interval, the mean internal temperature should approximate the average temperature of the water occupied by a fish. To simplify, these are hereafter referred to as temperatures “occupied.”

To initially determine if any of the strains did not differ in temperature use and could be combined, mean temperatures were compared in each of the possible two-way strain combinations within each half-month interval using *t*-tests. Significance was assumed at the  $\alpha = 0.05$  level, and a Bonferonni correction or other method of controlling the experimentwise error rate were not applied in these initial analyses.

The overall effect of strain on the temperatures occupied was evaluated with a mixed-model ANOVA (SAS 1999). The underlying model for the analysis was

$$T_{h,s,y,f} = \mu + \alpha_h + \beta_s + \gamma_{h,s} + \delta_{h,y} + \varepsilon_{h,s,y,f} \quad (1)$$

in which  $T$  is temperature and  $h$ ,  $s$ ,  $y$ , and  $f$  denote the half-month interval, strain, year, and individual fish. The fixed effects were the overall mean ( $\mu$ ), the seasonal or half-month adjustment ( $\alpha$ ), the strain adjustment ( $\beta$ ), and the interaction between half-month interval and strain ( $\gamma$ ). Potentially, the random components are a year by half-month variation ( $\delta$ ) and residual error ( $\epsilon$ ). Consecutive half-month means for the same fish were treated as repeated measures with a first order autocorrelation. Initially, three versions of the model were fit, first treating  $\delta$  as a fixed effect, second treating it as a random effect, and third treating it as a random effect with a first order autocorrelation. Each successive iteration was evaluated with a likelihood ratio test. The best of those three models were then reexamined to determine if there was any additional improvement by allowing separate errors by strain. The least-squares means and confidence intervals from the selected model were used to describe the temperature occupied by each strain in each half-month interval.

## **RESULTS**

### **Releases and Recoveries**

Sixteen of the 161 lake trout that underwent surgery at Drummond Island (10%) and one of the 174 at the HBBS (1%) died before release for a total initial mortality of about 5%. A total of 318 tagged lake trout were released during the study—145 at Drummond Island and 173 at the HBBS (Table 1), but a few of those likely died shortly after release.

Tagged fish (including those that died) ranged from 455 to 861 mm and averaged 657 mm in total length. The smallest fish weighed 0.87 kg and the average fish weighed 2.93

kg. The fish from the trap nets were significantly smaller ( $t = 10.23$ ;  $df = 333$ ;  $P < 0.001$ ) in length (average 618 mm) than those from the gill nets (average 700 mm). The wet weight of the tag never exceeded the suggested maximum of 1.25% of body weight (Winter 1996); the maximum was 1.1% for the smallest fish and 0.3% for the average fish.

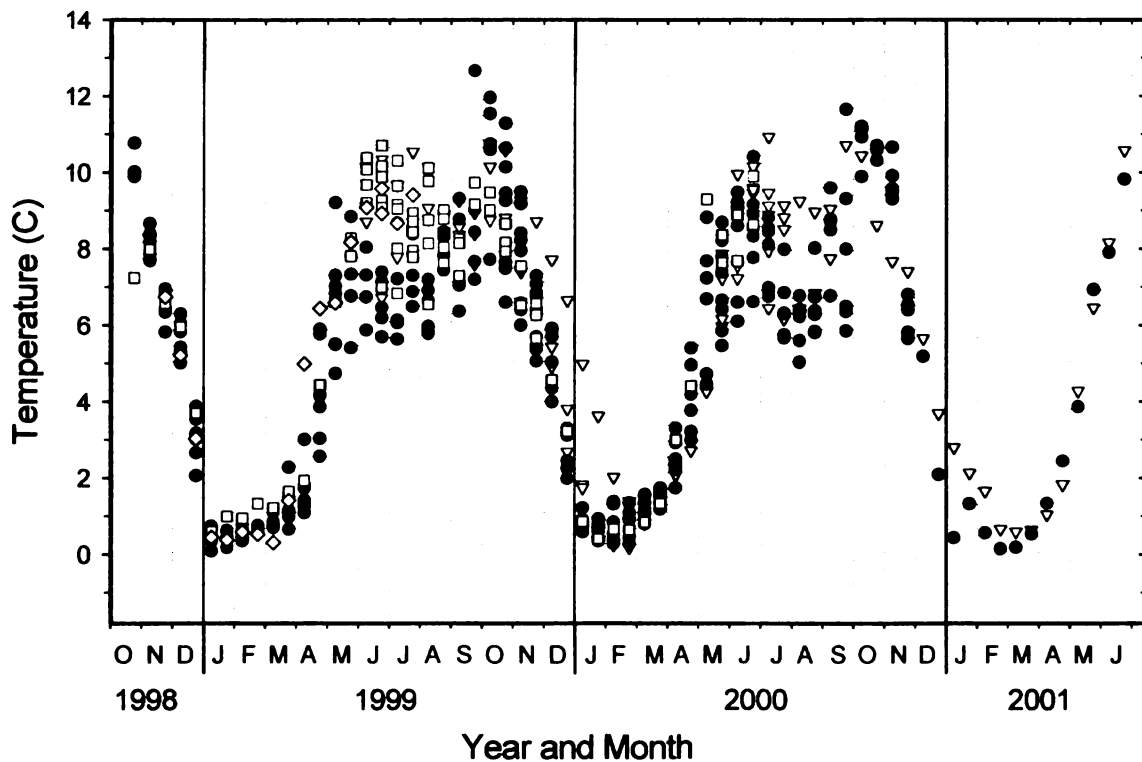
Of the 318 lake trout released, 49 (15%) were either captured or died. Three were caught in a trap net and released unharmed just a few days after tagging by the same commercial fisherman who initially caught them, one was caught in a gill net the morning after tagging, the external Floy tag from one was recovered from a commercial fish house (but no archival tag), one archival tag was found on a beach (indicating the fish had died), and one recovered tag had malfunctioned. Valid data files were recovered from 42 (13%) of the fish released (Table 1). Of those, strain could not be determined for two fish and seven fish had not been free long enough to meet the requirement for the minimum number of temperature observations (7 days). Thirty-three fish provided useable data from at least one half-month period and were included in analyses.

All recovered fish appeared healthy. Incisions showed no signs of redness and fish captured after about a month at large showed visible healing. There was never more than a slight redness where the tag rested against the body wall. The site where the external temperature probe passed through the body wall usually exhibited some irritation and redness. There was a small weight loss for many of the fish recaptured, but the loss (average, 135 g) was not significant (paired  $t$ -test;  $t = 1.569$ ;  $df = 21$ ;  $P = 0.131$ ). The

change in mean length of fish (-2 mm), measured at release and again at recapture, was also not significant (paired *t*-test;  $t = 0.328$ ;  $df = 23$ ;  $P = 0.745$ ).

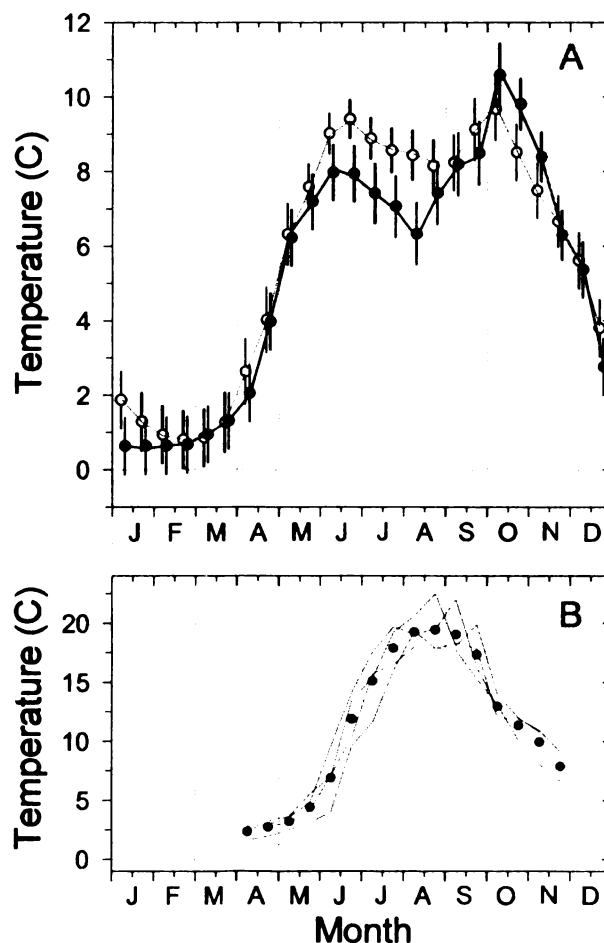
Between November and the following April, the mean recorded temperatures within half-month intervals varied little among individual fish (Fig. 1). There were no bathythermal profiles available seasonally for Lake Huron, but the general pattern of

Fig. 1. Mean water temperatures occupied by four groups of lake trout in Lake Huron, calculated by half-month interval from October 1998 to June 2002. Lake trout of Finger Lakes, New York origin (FLO) are denoted by solid circles, the Lake Superior Marquette Domestic (SMD) strain by open squares, the Lewis Lake Wild (LLW) strain by open triangles, and fish that could not be assigned to strain, but known to be either SMD or LLW strain by open diamonds.



increasing temperatures occupied by lake trout in spring and decreasing temperatures occupied in late autumn, irrespective of strain (Fig. 1 and 2A), approximated that of the surface temperature at the midlake buoy (Fig. 2B). From about June through October all lake trout occupied cooler water than was available near the surface. The FLO fish

Fig. 2. (A) Mean water temperatures occupied by lake trout of Upper Great Lakes origin (GLO; fine line and open circles) and of Finger Lakes, New York origin (FLO; heavy line and closed circles) from October 1998 to June 2001 in Lake Huron. The lines represent the mean temperatures occupied, calculated by half-month intervals pooled across years. Symbols and 95% confidence intervals are least-squares means from a mixed-model ANOVA treating the strain\*half-month interval interaction as a random effect and means for individual fish as repeated measures. (B) Average water temperatures 0.6 m below the surface at NOAA buoy 45003 near the center of Lake Huron (45.35° N, 82.84° W), calculated by half-month intervals, individually for 1998 through 2001 (lines) and pooled across years (symbols).



occupied their warmest waters of the year during late September through early November (Fig. 1). The SMD and LLW fish also occupied relatively warm waters in late September and early October, but occupied their warmest waters of the year during several half-month intervals earlier in the summer. By early December, lake trout were occupying water at temperatures averaging 6°C or less, and by late December they were in water around 3°C (Fig. 1, Table 2). From January through mid March, all lake trout occupied water that was 1°C or less (Fig 1, Table 2). Surface water temperatures were not available for comparison during the winter period because the buoys are removed each year.

The mean water temperatures occupied by each possible combination of strains were initially compared with *t*-tests in each combination of year and half-month interval (Table 2); the objective was to determine if any of the strains could be combined. Because the number of comparisons was large and the experiment-wise error not controlled, these tests were liberal and a number of significant differences were expected due to chance. However, none of the 26 comparisons between the LLW and SMD strains were significant. The LLW and SMD strains were therefore combined as being of Upper Great Lakes origin (GLO) for further analyses. Two of the fish for which genetic strain could not be determined had fin clips identifying them as either LLW or SMD and their strain was also assigned as GLO.

Analysis of all data collected from October 1998 through June 2001 in a single mixed-model, repeated-measures ANOVA, indicated there were significant seasonal

**Table 2.** Water temperatures (°C) occupied by lake trout in Lake Huron by year, half-month interval, and genetic strain. Labels for half-month intervals are the midpoints expressed as decimal months (e.g., 10.75 is the midpoint of the last half of October). Means and SEs are calculated from the individual means for the number (N) of fish contributing data in each cell. Pairwise t-tests were not corrected for experimentwise error. Blank cells denote no data, '-' denotes insufficient degrees of freedom, and '\*' or 'ns' denotes significance or non significance at the  $\alpha = 0.05$  level. Strain abbreviations are FLO, Finger Lakes origin; LLW, Lewis Lake wild; SMD, Lake Superior Marquette domestic; and GLO, Great Lakes origin (combines LLW, SMD and two fish that could not be assigned to strain, but could be identified from their fin clips as either LLW or SMD).

Year	Half-month interval	Genetic strain												Results of pairwise <i>t</i> -tests		
		FLO			LLW			SMD			GLO					
		Mean	N	SE	Mean	N	SE	Mean	N	SE	Mean	N	SE	FLO vs. LLW	FLO vs. SMD	LLW vs. SMD
1998	10.75	10.2	4	0.20				7.2	1	-	7.2	1	-		*	
1998	11.25	8.1	7	0.14				8.0	1	-	8.0	1	-		ns	
1998	11.75	6.5	7	0.16				6.6	1	-	6.7	2	0.09		ns	
1998	12.25	5.7	7	0.18				6.0	1	-	5.6	2	0.37		ns	
1998	12.75	3.1	7	0.22				3.7	1	-	3.4	2	0.33		ns	
1999	1.25	0.5	7	0.09				0.6	1	-	0.5	2	0.07		ns	
1999	1.75	0.4	7	0.07				1.0	1	-	0.7	2	0.31		*	
1999	2.25	0.5	7	0.05				1.0	1	-	0.8	2	0.18		*	
1999	2.75	0.7	7	0.02				1.3	1	-	0.9	2	0.40		*	
1999	3.25	0.9	7	0.07				1.2	1	-	0.8	2	0.46		ns	
1999	3.75	1.3	7	0.20				1.7	1	-	1.5	2	0.12		ns	
1999	4.25	1.7	7	0.24				1.9	1	-	3.5	2	1.53		ns	
1999	4.75	4.2	7	0.48				4.4	1	-	5.4	2	1.00		ns	

**Table 2.** Continued.

Half-month		Genetic strain												Results of pair-wise <i>t</i> -tests		
		FLO			LLW			SMD			GLO					
		Year interval	Mean	<i>N</i>	<i>SE</i>	Mean	<i>N</i>	<i>SE</i>	Mean	<i>N</i>	<i>SE</i>	Mean	<i>N</i>	<i>SE</i>	FLO vs. LLW	FLO vs. SMD
1999	5.25	6.6	7	0.56				6.6	1	-	6.6	2	0.01			ns
1999	5.75	7.4	6	0.49				8.0	2	0.24	8.1	3	0.14			ns
1999	6.25	7.9	6	0.65	9.2	2	0.50	9.8	4	0.26	9.5	7	0.22	ns	*	ns
1999	6.75	6.6	6	0.26	9.0	3	1.17	9.3	6	0.53	9.2	11	0.39	*	*	ns
1999	7.25	6.8	6	0.46	9.0	3	0.63	8.8	6	0.50	8.9	10	0.34	*	*	ns
1999	7.75	7.6	6	0.34	9.2	3	0.67	8.5	6	0.20	8.8	10	0.25	*	ns	ns
1999	8.25	6.4	6	0.24	9.3	3	0.42	8.6	4	0.82	8.9	7	0.49	*	*	ns
1999	8.75	8.2	6	0.21	8.3	3	0.07	8.4	4	0.32	8.4	7	0.17	ns	ns	ns
1999	9.25	7.7	5	0.56	8.7	3	0.27	7.9	3	0.30	8.3	6	0.26	ns	ns	ns
1999	9.75	9.0	5	0.97	8.3	3	0.39	9.5	2	0.29	8.8	5	0.36	ns	ns	ns
1999	10.25	10.5	5	0.74	9.9	3	0.59	9.2	2	0.23	9.6	5	0.37	ns	ns	ns
1999	10.75	9.2	9	0.45	9.4	3	0.62	8.2	3	0.21	8.8	6	0.38	ns	ns	ns
1999	11.25	7.7	9	0.41	7.8	3	0.79	6.9	3	0.34	7.3	6	0.43	ns	ns	ns
1999	11.75	6.3	9	0.26	6.8	3	0.98	6.2	3	0.27	6.5	6	0.48	ns	ns	ns
1999	12.25	5.1	6	0.34	6.0	3	0.86	4.6	1	-	5.7	4	0.71	ns	ns	ns
1999	12.75	2.7	6	0.23	4.4	3	1.18	3.2	1	-	4.1	4	0.88	ns	ns	ns

**Table 2.** Continued.

Half-month	Genetic strain												Results of pairwise <i>t</i> -tests		
	FLO			LLW			SMD			GLO			FLO vs. FLO	FLO vs. LLW	LLW vs. SMD
	Mean	<i>N</i>	<i>SE</i>	Mean	<i>N</i>	<i>SE</i>	Mean	<i>N</i>	<i>SE</i>	Mean	<i>N</i>	<i>SE</i>			
Yearinterval	Mean	<i>N</i>	<i>SE</i>	Mean	<i>N</i>	<i>SE</i>	Mean	<i>N</i>	<i>SE</i>	Mean	<i>N</i>	<i>SE</i>			
2000 1.25	0.8	6	0.09	2.9	3	1.07	0.9	1	-	2.4	4	0.90	*	ns	ns
2000 1.75	0.6	6	0.09	1.7	3	0.98	0.4	1	-	1.4	4	0.76	ns	ns	ns
2000 2.25	0.8	6	0.19	0.9	3	0.58	0.7	1	-	0.8	4	0.41	ns	ns	ns
2000 2.75	0.8	6	0.17	0.8	3	0.35	0.6	1	-	0.8	4	0.25	ns	ns	ns
2000 7.25	7.8	8	0.29	8.8	6	0.62				8.8	6	0.62	ns		
2000 7.75	6.5	7	0.30	8.2	4	0.68				8.2	4	0.68	*		
2000 8.25	6.1	6	0.26	7.3	3	0.96				7.3	3	0.96	ns		
2000 8.75	6.5	6	0.33	7.9	2	1.07				7.9	2	1.07	ns		
2000 9.25	8.5	6	0.38	8.4	2	0.64				8.4	2	0.64	ns		
2000 9.75	7.9	6	0.91	10.7	1	-				10.7	1	-	ns		
2000 10.25	10.9	5	0.25	10.4	1	-				10.4	1	-	ns		
2000 10.75	10.6	5	0.07	8.6	1	-				8.6	1	-	*		
2000 11.25	9.8	5	0.24	7.7	1	-				7.7	1	-	*		
2000 11.75	6.2	5	0.22	7.4	1	-				7.4	1	-	ns		
2000 12.25	5.2	1	-	5.7	1	-				5.7	1	-	-		
2000 12.75	2.1	1	-	3.7	1	-				3.7	1	-	-		

**Table 2.** Continued.

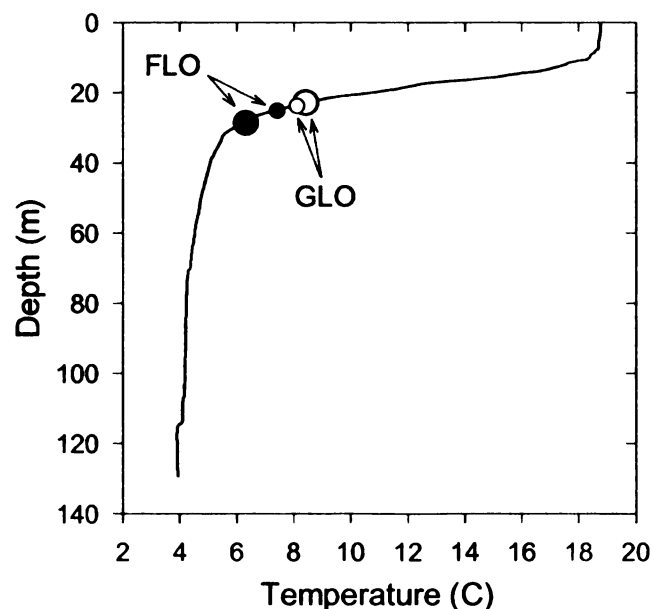
		Genetic strain										Results of pair-wise <i>t</i> -tests			
		FLO					LLW					GLO			
		Mean	N	SE	Mean	N	SE	Mean	N	SE	Mean	N	SE	Mean	N
Year	Half-month interval	Mean	N	SE	Mean	N	SE	Mean	N	SE	Mean	N	SE	Mean	N
2001	1.25	0.4	1	-	2.8	1	-	2.8	1	-	2.8	1	-	-	-
2001	1.75	1.3	1	-	2.1	1	-	2.1	1	-	2.1	1	-	-	-
2001	2.25	0.6	1	-	1.7	1	-	1.7	1	-	1.7	1	-	-	-
2001	2.75	0.2	1	-	0.7	1	-	0.7	1	-	0.7	1	-	-	-
2001	3.25	0.2	1	-	0.6	1	-	0.6	1	-	0.6	1	-	-	-
2001	3.75	0.5	1	-	0.6	1	-	0.6	1	-	0.6	1	-	-	-
2001	4.25	1.3	1	-	1.0	1	-	1.0	1	-	1.0	1	-	-	-
2001	4.75	2.4	1	-	1.8	1	-	1.8	1	-	1.8	1	-	-	-
2001	5.25	3.9	1	-	4.3	1	-	4.3	1	-	4.3	1	-	-	-
2001	5.75	6.9	1	-	6.5	1	-	6.5	1	-	6.5	1	-	-	-
2001	6.25	7.9	1	-	8.2	1	-	8.2	1	-	8.2	1	-	-	-
2001	6.75	9.8	1	-	10.6	1	-	10.6	1	-	10.6	1	-	-	-

differences between the FLO and GLO strains. The model (equation 1) was first fit with the year by half-month variation ( $\delta$ ) as a fixed effect. That model explained a significant portion of the variation (likelihood ratio test;  $P < 0.0001$ ). Treating  $\delta$  as a random effect resulted in a significant additional improvement (likelihood ratio test;  $P < 0.0001$ ) and both of these models provided a good fit to the data in Table 2. Treating  $\delta$  then as a random effect with first-order autocorrelation did not improve the model (likelihood ratio test;  $P = 0.09$ ), and the resulting model also yielded a questionable fit to the data, with predicted temperatures in winter below  $0^{\circ}\text{C}$ . Treating  $\delta$  as a random effect without autocorrelation, but allowing separate errors by strain, resulted in a further improvement (likelihood ratio test;  $P = 0.001$ ). In that model, the coefficients for strain ( $P = 0.009$ ), half-month interval ( $P < 0.0001$ ), and the strain by half-month interval interaction ( $P = 0.026$ ) were all significant. The least squares estimates of mean temperature and 95% confidence intervals in each strain by half-month interval combination were also calculated (Table 3). The confidence intervals for those estimates did not overlap between FLO and GLO lake trout from mid June to mid August (Fig 2A).

To assess how different the depths occupied by FLO and GLO lake trout might be, bathythermograph data (Marc Tuchman, EPA Great Lakes National Program Office, Chicago Illinois, unpublished data) collected during 16 to 18 August 1999 at seven locations in northern Lake Huron (Lat  $> 44.5^{\circ}\text{N}$ ) were used to calculate the average temperature by half-meter depth interval (Fig. 3). The seasonal locations of tagged fish were not known and bathythermal profiles can vary widely by location. Therefore,

plotting the least-squares mean temperatures occupied by FLO and GLO lake trout (Table 3) on the temperature-depth profile can only provide a general sense of how different the depths occupied might have been. The dates for the bathythermograph data are near the temporal boundary between the early and late August intervals. Because temperatures occupied by FLO and GLO fish in early August were different and those in late August were not (Fig. 2A), the means were plotted from both periods. Their locations on the depth-temperature profile suggest that the FLO fish were located near the lower boundary of the metalimnion. The GLO fish occupied shallower depths, although the maximum difference is only about 6 m (Fig. 3).

Fig. 3. Temperature by depth averaged across seven sites in northern Lake Huron (Latitude > 44.5° N) during 16 to 18 August 1999 and predicted mean temperatures occupied by Finger Lakes Origin (FLO; filled circles) and Upper Great Lakes Origin (GLO; open circles) lake trout during the first half of August (large circles) and the last half (small circles). Depth and temperature were collected with a bathythermograph (Marc Tuchman, EPA Great Lakes National Program Office, Chicago Illinois, unpublished data). Predicted temperatures for lake trout are least squares means from a mixed-model ANOVA using data from implanted archival tags collected during October 1998 through June 2001.



**Table 3.** Least square means (LSM), standard errors, and upper and lower 95% confidence intervals (CI) from a mixed-model ANOVA predicting water temperatures (°C) occupied by lake trout in Lake Huron by half-month interval, and genetic strain for combined data collected from mid October 1998 through June 2001. Labels for half-month intervals are the midpoints expressed as decimal months (e.g., 10.75 is the midpoint of the last half of October). Strain abbreviations are Finger Lakes origin (FLO) and Great Lakes origin (GLO). The GLO strain combines Lewis Lake wild (LLW), Superior Marquette domestic (SMD) and two fish that could not be assigned to strain, but could be identified from their fin clips as either LLW or SMD.

Half-month interval	FLO				GLO			
	LSM	SE	Lower CI	Upper CI	LSM	SE	Lower CI	Upper CI
1.25	0.6	0.39	-0.1	1.4	1.9	0.40	1.1	2.7
1.75	0.6	0.39	-0.1	1.4	1.3	0.40	0.5	2.1
2.25	0.6	0.39	-0.1	1.4	0.9	0.40	0.2	1.7
2.75	0.7	0.39	-0.1	1.4	0.8	0.40	0.0	1.6
3.25	0.9	0.39	0.2	1.7	0.9	0.40	0.1	1.6
3.75	1.3	0.39	0.5	2.1	1.3	0.41	0.4	2.1
4.25	2.0	0.39	1.3	2.8	2.6	0.44	1.7	3.5
4.75	4.0	0.39	3.2	4.8	4.0	0.44	3.1	4.9
5.25	6.2	0.39	5.5	7.0	6.3	0.42	5.5	7.2
5.75	7.2	0.38	6.4	8.0	7.6	0.32	7.0	8.2
6.25	8.0	0.38	7.2	8.7	9.0	0.28	8.5	9.6
6.75	7.9	0.39	7.2	8.7	9.4	0.26	8.9	9.9
7.25	7.4	0.41	6.6	8.2	8.9	0.28	8.3	9.5
7.75	7.1	0.42	6.2	7.9	8.6	0.30	8.0	9.2
8.25	6.3	0.42	5.5	7.2	8.4	0.34	7.8	9.1
8.75	7.4	0.43	6.6	8.3	8.1	0.36	7.4	8.9
9.25	8.2	0.43	7.3	9.1	8.2	0.38	7.5	9.0
9.75	8.5	0.43	7.6	9.4	9.1	0.42	8.3	10.0
10.25	10.6	0.43	9.7	11.4	9.7	0.42	8.8	10.5
10.75	9.8	0.35	9.1	10.5	8.5	0.38	7.8	9.3
11.25	8.4	0.34	7.7	9.1	7.5	0.38	6.7	8.2
11.75	6.3	0.34	5.6	7.0	6.7	0.36	5.9	7.4
12.25	5.4	0.38	4.6	6.1	5.6	0.39	4.8	6.4
12.75	2.8	0.39	2.0	3.5	3.8	0.39	3.0	4.6

## Discussion

There are no published accounts dealing specifically with the effects of internal tags on adult lake trout performance or behavior, and such an evaluation was not done in this study. However, the wet weights of the implanted tags were always a smaller percentage of fish weight than the upper limit of 1.25% suggested by Winter (1996). Furthermore, recent tests with rainbow trout (*Oncorhynchus mykiss*) suggest that the acceptable limit could be set higher without affecting performance (Brown *et al.* 1999). Adult Atlantic salmon (*Salmo salar*) with weights ranging from 1,021 to 2,388 g, showed no decline in swimming performance or blood physiology when tested 6 to 20 days after tagging with internal tags weighing 7.9 g in water and ranging from 0.3 to 0.8% of fish weight (Thorstad *et al.* 2000). In the present study, the wet weight of only nine tags were a larger percentage of the fish weight (max 1.1%), and the average (0.3%) was equal to the lowest percentage in their study. Mock tags adjusted to 1% (wet weight) of body weight did not affect the metabolic rate of sea bass (*Dicentrarchus labrax*), also indicating that small additions to body weight should not affect performance (Lefrancois *et al.* 2001). In the present study, the wet weight of only one tag exceeded 1% of the fish's body weight. It is always possible that tags could affect behavioral or physiological processes in ways that are difficult to anticipate. For example, in a study by Perry *et al.* (2001), juvenile Chinook salmon (*Oncorhynchus tshawytscha*) compensated for transmitter mass through changes in air bladder volume, but changes in depth affected the buoyancy of tagged fish (whose buoyancy depended on a larger gas volume) more rapidly than untagged fish. Perry *et al.* cautioned that reduced buoyancy at depth could affect behavior and physiology. Although questions

still remain about how internal tags affect fish, the available data suggest that for tags within weight guidelines, the effects are probably minimal.

Although interpretation of the data in the present study was hampered by a lack of depth information coincident with the temperature data from the tags, some inferences can be drawn about the winter depths occupied by lake trout from the temperatures they occupied and published winter bathythermal profiles for the other Great Lakes.

Regardless of the strain, lake trout remained at temperatures less than 1°C during winter, which suggested they did not move deeper in search of warmer water during the period of inverse winter stratification. If the winter thermal profile in Lake Huron was similar to that described for Lake Michigan during February 1964 (Wells 1968), they must not have been deeper than 40 to 50 m, although temperatures near 3°C were probably available at 100 m. Temperatures in Lake Ontario during February 1984 were 1°C at 15 m and 1.7°C at 35 m, with temperature rising to 1.9°C at 95 m and 3.7°C at 215 m (Bergstedt and O’Gorman 1989). Based on the Lake Ontario profiles, lake trout would have been shallower than 35 m during the winter months.

The variation in temperatures occupied was lowest among individual fish from late autumn through April. In autumn there is a partial circulation (Ruttner 1963) due to decreasing temperature in the epilimnion that reduces the stability of stratification and allows wind events to begin mixing the epilimnion into the hypolimnion. From October or November through the winter, surface waters can be homothermous to a considerable depth. For example, on October 14, 1964 in Lake Michigan, the temperature varied by

only 0.7°C in the upper 50 m of water (Wells 1968). Likewise, during February 1984 in Lake Ontario, there was only a 0.8°C difference in temperature throughout the upper 110 m of water. During this time of the year, lake trout are forced to occupy cold water within a narrow range of temperatures, unless they actively select a depth below the zone of partial mixing in autumn (Bergstedt and Swink 1995) or below the inverse stratification in winter (Wells 1968; Bergstedt and O’Gorman 1989).

The significance of the effect of strain and of the strain by half-month interaction in the ANOVA suggests that the strains occupied different temperatures, but not in all seasons. The pattern of overlap of the confidence intervals for the two strains (Fig. 2A) shows that the differences were the most apparent from mid June to mid August when stratification was strongest. Gill nets fished in Lake Ontario in September showed that the Seneca strain of lake trout, age-3 and older, was caught in deeper and colder water than the Superior strain (Elrod *et al.* 1996b). Temperature differences between strains had disappeared by early September in Lake Huron. This could be due to the more northern latitude of Lake Huron and an earlier breakdown of stratification, although a difference attributable to annual variation is also a possibility. Judging from the August 1999 bathythermal profile in Lake Huron (M. Tuchman, EPA, Chicago, IL, unpublished data), the difference in temperatures occupied by the strains implies a relatively small but consistent difference in depths occupied, unless these strains consistently occupied different areas of the lake with differing average depths of the thermocline. Archival tags that determine both depth and temperature would provide additional insights by providing concomitant measures of the depth and temperature occupied.

Differences in sea lamprey attack rates and mortality of lake trout from those attacks were thought to be related to differences in seasonal bathythermal distributions of strains of lake trout (Schneider *et al.* 1996). Mortality of lake trout induced by sea lampreys in Lake Ontario was documented using incidental recoveries of dead, wounded lake trout in bottom trawl catches—but only during a brief period from late September to early November (Bergstedt and Schneider 1988; Schneider *et al.* 1996). Also, the Lake Superior strain of lake trout was observed to suffer consistently higher rates of sea lamprey attacks in both Lakes Huron (Eshenroder *et al.* 1995a) and Ontario (Schneider *et al.* 1996). If the strains differed in their bathythermal distributions and one strain more closely approximated the bathythermal distribution of sea lampreys, it could explain the difference in attack rates and in any subsequent mortality per attack due to changes in metabolic rate and blood consumption (Swink and Hanson 1989; Madenjian *et al.* 2003). The FLO and GLO strains of lake trout do occupy, at least during portions of the year, different temperatures, and presumably, different depths.

Seasonal differences in the water temperatures available to lake trout may also explain the occurrence of most lamprey-induced mortality during a brief period in autumn (Bergstedt and Schneider 1988; Schneider *et al.* 1996) and the coincident rapid growth of sea lampreys during that same seasonal period (Bergstedt and Swink 1995). Bergstedt and Swink speculated that lake trout occupy the warmest water of the year during the partial autumnal circulation (Ruttner 1963). The archival tag data support that speculation. Higher temperatures and the resulting higher metabolic rates would

provide a partial explanation for the increased growth of sea lampreys in autumn (Bergstedt and Swink 1995) and partially account for the sharp increase in sea lamprey predation observed during that season (Bergstedt and Schneider 1988).

Although the data presented here advance knowledge of the actual temperatures occupied by two strains of lake trout, it is still unclear how “preference” for depth and temperature might interact. Because of that concern, the term “occupied” was intentionally chosen instead of “preferred.” When presented with a choice of temperatures, lake trout show a consistent preference for temperature in laboratory tests (McCauley and Tait 1970; Goddard and Tait 1976). However, native stocks of lake trout in the Great Lakes have historically inhabited a wide range of habitats and exhibited distinct phenotypic differences (Krueger and Ihssen 1995). There is evidence that other factors that would lead to differing selections of depth (and hence temperature) are heritable characteristics of *Salvelinus* species. Fat content is thought to affect depth distribution and vertical migration (Eshenroder et al. 1995b), and has been demonstrated to be a heritable characteristic, with hybrids having an intermediate fat content (Eschmeyer and Phillips 1965). Depth preference is also related to swim bladder gas retention, which determines the depth of neutral buoyancy. Gas retention can be controlled through selective breeding of lake trout with hybrids of lake trout and brook trout (Tait 1970; Goddard and Tait 1976). It has also been demonstrated that gas retention varied between lake trout from two lakes, that interpopulation crosses were intermediate in gas retention, and that gas retention correlated with depth distribution of the parent population (Ihssen and Tait 1974). During the period of stratification,

preference for depth could have a strong interaction with temperature preference in determining the actual temperatures occupied.

It is also possible the strain differences observed in this study were related to differences in geographic distribution of strains corresponding to differences in prey distribution and abundance. The temperature for optimal growth is affected by ration size (Brett 1971), and a positive effect of ration size on temperatures selected by lake trout has been demonstrated in the laboratory (Mac 1985). The relation of food availability to the temperatures occupied by Pacific salmon (*Oncorhynchus* spp.) is being considered as an important factor controlling their seasonal distribution (Welch *et al.* 1995). If food availability differed among lake trout strains, this could affect temperature selection. Separating the likely importance of various environmental and hereditary factors that might affect temperature selection will be a difficult task that initially requires collecting concomitant depth and temperature data and potentially assembling geo-referenced, strain-specific data on stomach contents and food habits.

Temperature selection influences the interaction of lake trout with other species by controlling metabolism (and the amount of prey consumed) and by determining spatial overlap with prey and with other predators. The thermal requirements of lake trout were formerly derived from laboratory studies or from temperatures at capture in various fishing gears. The data presented in this study indicate that during the period of summer stratification, lake trout tend to inhabit temperatures somewhat lower than the generalization of 10°C used in models such as that of Stewart *et al.* (1983) to predict

prey consumption or of Kitchell and Breck (1980) to predict predation of sea lampreys on lake trout. Bence *et al.* (2003) and Madenjian *et al.* (2003) found that the higher temperatures lake trout actually inhabit in October helped to explain the strong pulse of sea lamprey predation in October documented by Bergstedt and Schneider (1988). However, these differences do not appear to create large differences in model output. The predicted consumption of prey by lake trout in a model under development was reduced by only about 10% at the lower temperatures occupied by FLO fish (N. Dobiesz, Michigan State University, personal communication) and Madenjian *et al.* (2003) found a 7% increase in lake trout mortality from sea lamprey attack (assuming no change in sea lamprey growth) when the temperature regimes reported here were used. Although these differences are not large, they are the result of replacing generalizations with estimates based on actual thermal histories. Changes in model output likely reflect gains in accuracy, and replacing generalizations with observations certainly results in increased confidence in the output.

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## **CHAPTER TWO**

**Changes in bathythermal habitat use by lake trout in Lake Huron during a period when the prey base changed rapidly**

## **Abstract**

Before development of small archival (or data-recording) telemetry tags, knowledge of temperatures and depths of lake trout (*Salvelinus namaycush*) in the Great Lakes came from point estimates of abundance within the zones sampled with net gear. An initial archival tag study recording temperatures occupied by lake trout in Lake Huron during 1999 and 2000 (Chapter One) showed that lake trout strains of Great Lakes origin (GLO) occupied significantly higher temperatures than strains of Finger Lakes, New York, origin (FLO). The objectives of this study (Chapter Two) were to compare the temperatures recorded on tags recovered from 2002 through 2005 to those reported in 1999 and 2000, to examine whether lake trout of Finger Lakes, New York origin occupy both lower temperatures and greater depths than lake trout of Great Lakes origin, and to examine any changes in the temperatures occupied in light of changes in the abundance and composition of their prey. Archival tags recording depth and temperature were surgically implanted in 447 lake trout in Lake Huron in 2002 and 2003. Through 2005, 93 records of depths and temperatures occupied by GLO lake trout (38) and FLO lake trout (55) were recovered (21% of the tags deployed). Temperatures occupied by GLO lake trout were significantly higher than those occupied by FLO lake trout, supporting the conclusion of the first study. The GLO lake trout occupied significantly shallower depths than FLO lake trout, averaging 4.5 m shallower (range 2.3 to 8.3) across 24 half-month intervals. In comparison to the first study, both GLO and FLO lake trout occupied significantly lower temperatures; from May through August, GLO lake trout averaged 1.7°C lower temperatures and from May through early November FLO lake trout 1.6°C lower than in 1999-2000. Over the same

period, the prey fish community changed dramatically. The formerly abundant alewife (*Alosa pseudoharengus*), a key pelagic prey item, virtually disappeared and a new demersal species, the round goby (*Neogobius melanostomus*), invaded Lake Huron. Prey biomass also decreased by 90% during this period. Switching to more demersal prey and retreating to temperatures lower than optimum for growth in response to food scarcity could increase conversion efficiency could explain the movement toward lower temperatures.

## Introduction

Temperature is an important environmental variable that governs food consumption and growth, and hence affects the distribution of fishes in lakes (Fry 1947).

Temperature selection (Goddard and Tait 1976) and the ability to maintain position at different depths (Ihssen and Tait 1974) are known to be heritable characteristics in lake trout (*Salvelinus namaycush*). The combined expression of these multi-genic traits among fish species during summer periods of thermal stratification, along with other environmental variables (Fry 1947), yields the temperature and depth distributions of predators and their prey. Numerous laboratory studies have contributed to our understanding of the thermal behavior of lake trout, including preferred temperatures (*e.g.*, McCauley and Tait 1970; Peterson *et al.* 1979; Edsall and Cleland 2000), optimum temperatures for growth (*e.g.*, Elliot and Hurley 1999; Edsall and Cleland 2000), and temperature tolerance or lethal limits (*e.g.*, Ihssen 1973; Grande and Andersen 1991). The temperature relationships described by these studies tend to be consistent among each other (Jobling 1981), which suggests that a component of temperature selection is genetic and defines the fundamental niche axis as defined by Hutchinson (1957). However, description of a fundamental niche for temperature considers only one of a number of environmental variables affecting the distribution of fish; thus, a species is not necessarily found at temperatures indicated in the laboratory (Magnuson *et al.* 1979). Describing the realized thermal niche as recorded by field observations, and which incorporate these other variables, will be of greater interest to fishery ecologists (Magnuson *et al.* 1979). As examples, Eaton *et al.* (1995) and Huff *et al.* (2005) used this approach to describe temperature tolerance. Huff *et al.* (2005) also

described the center and width of the realized niche. Little is known about the depths and temperatures occupied by lake trout on a daily and seasonal basis in the Laurentian Great Lakes. That knowledge is deduced from captures in different fishing gears. These capture data only provide point estimates of abundance within the depths and temperatures sampled (*e.g.*, Elrod *et al.* 1996), and suffer from the sampling bias of each gear. Observations of temperature at capture are also limited to where gear is set, and do not necessarily reflect the range of habitats occupied.

During 1999 and 2000, archival tags implanted in lake trout of two genetic strains first enabled monitoring of the environmental conditions experienced by deep-ranging fish in the Great Lakes and provided the first reasonably continuous (75-minute intervals) seasonal measures of the temperatures occupied in Lake Huron (Chapter One). Although that information contributed substantially to our knowledge of lake trout behavior in the Great Lakes, the data were collected with tags that only measured temperature but not depth. The lack of depth data was problematic in that it was not possible to directly conclude that the higher temperature occupied by Great Lakes origin lake trout, compared to Finger Lakes origin lake trout, was due to the use of lesser depths. Uncertainty existed because the average thermocline depth can be affected by prevailing winds and bathymetry, and can vary geographically within one of the Great Lakes. Therefore, the temperature difference could have been due to a similar depth distribution but with differences in geographic distribution between strains (Chapter One).

Subsequent to this first study (Chapter One), substantial progress occurred in miniaturization of electronics that made it possible to implant a smaller archival tag that recorded both depth and temperature. By 2001, an affordable tag became available that would measure both temperature and depth--and that also had substantially more memory. This newer tag could be implanted in lake trout and used to assess the overlap of both temperature and depth distributions among strains of lake trout and to compare with results from 1999-2000 (Chapter One).

Since the temperature distribution of lake trout reported in Chapter One (1999-2000) were collected, substantial changes have taken place in the food web in Lake Huron. Phosphorus reductions from pollution abatement (Nalepa *et al.* 2007), along with the probable effect of the zebra mussel (*Dreissena polymorpha*) and quagga mussel (*Dreissena bugensis*) colonizing Lake Huron (Nalepa *et al.* 2007; Hecky *et al.* 2004) have likely reduced pelagic plankton production and also food for benthos. Nalepa *et al.* (2007) reported that the densities of four key taxa (*Diporeia*, Oligochaeta, Sphaeriidae, and Chironomidae) had not changed substantially between 1970 and 2000, but then decreased significantly between 2000 and 2003. The decrease was greatest for *Diporeia* and Sphaeriidae, which dropped by 57 and 74% lakewide. The abundance of most prey fish species in Lake Huron also declined sharply in the early 2000s (Riley *et al.* in press), with alewives (*Alosa pseudoharengus*) virtually disappearing between 2003 and 2004 (Warner *et al.* 2005). The distribution of predators such as lake trout in Lake Huron would potentially shift after the loss of a key pelagic prey species, such as alewife.

The combination of the data presented in Chapter One and here bracket this period of sweeping changes in the biota of Lake Huron. The data collected provide an opportunity to examine the temperatures occupied by lake trout relative to a substantial shift in the prey-fish community, including the virtual disappearance of alewives between 2003 and 2004 and the appearance of a new invasive species, the round goby (*Neogobius melanostomus*). The objectives of this chapter were to compare the temperatures recorded on tags recovered from 2002 through 2005 to those reported in Chapter One (1999-2000), to examine whether lake trout of Finger Lakes, New York origin occupy both lower temperatures and greater depths than lake trout of Great Lakes origin, and to examine any changes in the temperatures occupied in light of changes in the abundance and composition of their prey.

## **Methods**

### **Tags and tagging**

In 2002 and 2003, LTD-1110 archival tags manufactured by Lotek Wireless Inc., Newmarket, Ontario, Canada, were surgically implanted in lake trout released to Lake Huron. Each tag recorded temperature (0 - 25 °C) and depth (0-500 m). With a battery life of two to three years, those tags provided temporal coverage from 2002 through 2005. The tags were cylindrical—11 mm in diameter by 32 mm long and rounded on one end. Weight was about 5 g in air and 2 g in water. Recording continued until tag recovery and download, or until the battery expired. Observations of date, time,

temperature, and depth were initially recorded at 15-second intervals until the memory was full. Software then replaced previous observations to maintain a complete set of observations from initialization to download, but with the intervals between observations gradually increasing. About 33,000 observations were recorded, with average intervals increasing from 15 seconds by about 1.3 minutes for each month after deployment and by 16 minutes for each year.

Tag specifications were 0.2°C resolution with  $\pm 0.3$  °C accuracy for temperature and 0.4% of the current depth scale with  $\pm 1\%$  accuracy. The potential depth range was 0 to 500 m, but, to improve resolution and accuracy, software initially set the range to one-quarter of that scale (0 to 125 m). If fish moved deeper than the initial scale, the range would progressively shift (permanently) to one-half scale (0 to 250 m) and then full scale (0 to 500 m). Resolution and accuracy (in parentheses) at those scales were 0.5 ( $\pm 1.25$ ) m, 1.0 ( $\pm 2.5$ ) m, and 2.0 ( $\pm 5.0$ ) m, respectively.

Recovery of archival tags depended on the recapture of fish by sport and commercial fisheries, and return of the tags. To promote returns, a reward of \$100 (USD) was offered. Tagged fish were also marked externally with orange dart tags. The external tags bore identifying serial numbers, reward advertisement, a contact telephone number, and instructions to not freeze the tag. The internal tags also bore a reward notice and contact information. Information posters describing the study and reward were displayed in tackle and convenience stores, at launch sites, and were

provided to commercial and charter fisheries. The Michigan Department of Natural Resources and the Ontario Ministry of Natural Resources also publicized the study.

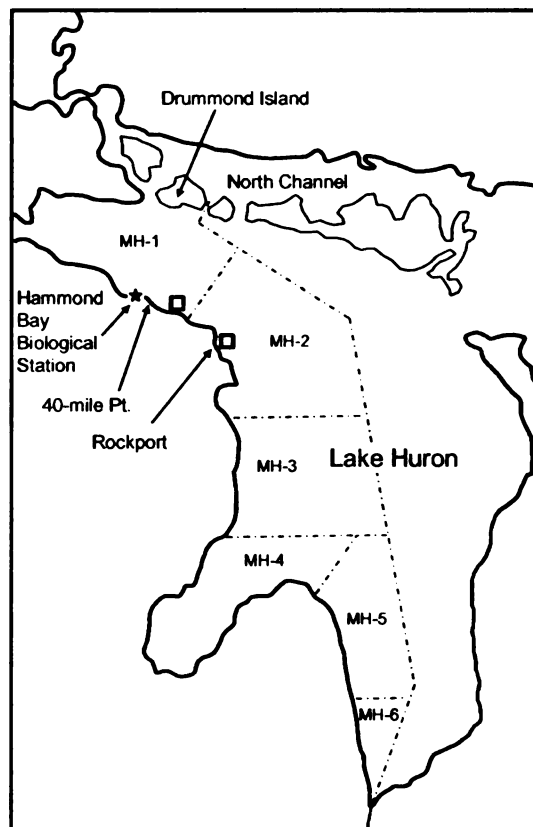
**Table 4.** Summary of lake trout tagged with surgically implanted archival temperature tags and released into Lake Huron, either at the Hammond Bay Biological Station (HBBS), at Drummond Island (DI), or on Lake Huron (LH), the number of lake trout tagged by dates, location, and source; the number recaptured; and the number and percent of fish used in the analyses.

Dates tagged	Re- lease loca- tion	Source (gill or trap net)	No. re- leased	No. recap- tured	% recap- tured	No. in ana- lyses	% in ana- lyses
15-30 May 2002	HBBS	trap	77	21	27	15	19
18-20 Jun. 2002	HBBS	trap	107	17	16	15	14
9-10 Oct. 2002	DI	gill	38	5	13	3	8
Subtotal			222	43	19	33	15
07-28 May 2003	LH	trap	64	24	34	20	28
15-16 May 2003	HBBS	trap	55	17	31	15	27
5-17 Jun. 2003	HBBS	trap	106	28	27	25	24
Subtotal			225	69	31	60	27
Total			447	111	25	93	21

All lake trout tagged were obtained from commercial trap nets fished during May and June of 2002 and 2003 along the Michigan shore of Lake Huron between Rockport and Forty Mile Point—with the exception of 37 lake trout from the Chippewa-Ottawa Resource Authority (CORA) assessment gill nets at Drummond Island, Lake Huron in October 2002 (Table 4; Fig. 4). Lake trout from gill nets were transported to shore in aerated containers and placed in 1000-L tanks supplied with aerated, ambient-

temperature Lake Huron water. Lake trout from trap nets were placed in a floating pen and either tagged and released at the capture site or transferred in aerated containers—either directly by boat to the Hammond bay Biological Station (HBBS) or indirectly by boat to shore and then by truck to the HBBS. At the HBBS, they were held in raceways or in 1000-L tanks in aerated, ambient-temperature Lake Huron water.

Fig. 4. Locations in Lake Huron of Drummond Island, the Hammond Bay Biological Station, Forty-mile Point, Rockport, sites where lake trout were tagged at the site of collection (squares), and boundaries of fishery statistical districts MH-1 to MH6.



Lake trout were anesthetized, weighed, measured, fin clips recorded, and a small piece of tissue taken from the upper lobe of the caudal fin for genotyping, as described in Chapter One. Archival tags were inserted through 1.5-cm incisions made slightly to

the side of the ventral midline anterior to the pelvic fins, the incisions closed with two monofilament sutures, 3-M Vet-Bond® adhesive applied to the knots, and a Floy tag inserted on each side of the dorsal fin. The procedure took about 3 minutes, during which the gills were continually irrigated. The fish were then transferred to a recovery tank or floating pen, where they regained equilibrium within 5 to 10 minutes. If tagging was done in the field, weights were not taken and they were immediately released. If tagged at the HBBS, they were held from 24 to 48 hours for observation before release from shore at the station.

### **Genetic origins of lake trout**

Lake trout used in this study were shallow water, or lean, lake trout of hatchery origin. A number of genetic strains have been stocked into Lake Huron, but all have origins either in Lakes Superior or Michigan or in the Finger Lakes of New York. No difference was found in temperatures occupied by strains derived from Lake Superior or Lake Michigan stocks, and therefore they were collectively designated as Great Lakes origin (GLO; Chapter One). All New York hatchery strains were designated as Finger Lakes origin (FLO). More detailed information on the sources of GLO and FLO lake trout is provided in Chapter One, Krueger *et al.* (1989), and Elrod *et al.* (1996).

Other than fish bearing a CWT, strain of a lake trout used in this study could not be determined directly from fin clips because marks were only year-class specific and all strains were marked identically. The genetic strains of fish in this study were therefore identified from coded wire tags (CWTs) after recapture or via a combination of genetic

analysis of tissue samples and fin clips (clips were used to narrow the set of potential strains).

Precautions were taken to equalize the releases and hence returns from the GLO and FLO groups, because of previous knowledge that temperatures and depths would likely differ with genetic origin (Chapter One). One strategy used was to tag fish with certain fin clips based on previous knowledge of the likely strain compositions. Fin clips and relative numbers to tag were chosen based on stocking records and previous genotyping (Chapter One). On 15-30 May and 8 October 2002, 114 lake trout were selected based on fin clips and tagged and released in the field. A second strategy used in 2002 relied on genotyping. Lake trout were transported to the HBBS, marked with the external Floy tags, and tissue samples were taken. Tissues from each fish were genotyped (Page 2001). Fish were held for about three weeks while genetic analyses were performed and strain assignments made. The results were used to choose another 107 fish for tagging. In 2003, information from the 2002 genotyping were combined with information from fin clips and coded wire tag data from Michigan Department of Natural Resources lake trout surveys in 2002 (Ji He, Alpena, Michigan Fisheries Research Station, personal communication). This information was used to choose which fin clipped lake trout to tag.

## **Statistical analyses**

Temperature and depth data from the tags provide an array of possibilities for their summarization. These data were summarized by half-month seasonal intervals (similar to Chapter One) -- an interval selected in consultation with potential users of the data for bioenergetics models of prey consumption (Charles Madenjian, USGS, Great Lakes Science Center; James Bence, Michigan State University; Ji He, Michigan Department of Natural Resources, personal communication). The first half of each month included the first 15 days and the second half the remaining days in the month. Because these data were likely to be used in bioenergetics models of growth or prey consumption, the arithmetic mean temperature (°C) in each half-month interval was used to best represent the average temperature experienced by each fish; this summary statistic, when expanded to the interval of interest, most accurately represents the number of degree-days experienced. For depth, the median depth occupied by each fish was used in each interval. With each fish, there was a period after release, during recovery from surgery, when the data were suspected to not represent normal behavior. Each plot of temperature was inspected and a subjective judgment was made as to the date when behavior appeared consistent with the remainder of the data. For fish captured when the tag was still actively recording, time of capture in the fishing gear was evident from a cessation of temperature and depth variation. Temperature observations before behavior appeared normal and after the fish was caught were not used in the analyses. Because of the expanding interval of observations over time and the greater number of observations per hour for fish recaptured sooner after release, and to give fish equal weight (the experimental unit used in this study was the individual fish), subsequent

analyses were based only on the mean temperatures and median depths for individual fish by half-month interval and considering the repeated nature of those measures. Mean temperature was chosen for the reason stated above, and their likelihood of use in bioenergetics models. The median depth was chosen as best representing the most common depth frequented.

The temperatures analyzed and reported in this study were only those recorded inside the abdominal cavity. At any instant, these could vary from the temperature of the surrounding water. Based on laboratory studies (HBBS, unpublished data), internal temperature after a rapid change in external temperature would move 50% toward the new external temperature within about 5 minutes, and 90% toward the new temperature within 15 minutes. Over the temporal scale of a half-month interval, the mean internal temperature should closely approximate the average temperature of the water occupied by a fish. To simplify, these mean temperature data are hereafter referred to as “occupied” temperatures, referring to both the approximation of a half-month average temperature occupied and the fact that these measures do not necessarily reflect a “preference,” but a realized niche as defined by Magnuson *et al.* (1979). The commonly used term “preference” only has meaning in the context of laboratory studies, where all other dimensions of the ecological niche are controlled. In this study, where temperature and depth are simultaneously measured, it is not possible to know along which of those niche axes a preference is being exercised or whether the controlling variable is along another axis.

To describe the variability in the observations, percent frequency distributions for temperature and depth were compiled by genetic origin. Because the time between release and recapture varied with individual fish, and because of the gradually increasing intervals between observations, and hence the changing number of observations per time interval, it was necessary to create a summary statistic to ensure that all fish contributed equally to the distribution. Therefore, the average temperature and median depth were calculated for combinations of genetic origin, individual fish, half-month interval, and hour and used to describe those statistics along with the 10<sup>th</sup>, 25<sup>th</sup>, 75<sup>th</sup>, and 90<sup>th</sup> percentiles by half-month interval.

The overall effect of genetic origin on the temperatures and depths occupied was evaluated with a mixed-model ANOVA (SAS 2001). The null hypothesis was that no difference existed between genetic origin of lake trout in temperatures and depths occupied. The underlying model for the analysis was

$$T_{h,s,y,f} \text{ or } D_{h,s,y,f} = \mu + \alpha_h + \beta_s + \gamma_{h,s} + \delta_{h,y} + \varepsilon_{h,s,y,f} \quad (1)$$

in which  $T_{h,s,y,f}$  or  $D_{h,s,y,f}$  is a half-month mean for temperature or depth and  $h$ ,  $s$ ,  $y$ , and  $f$  denote the half-month interval, genetic origin, year, and individual fish. The fixed effects were the overall mean ( $\mu$ ), the seasonal or half-month adjustment ( $\alpha$ ), the genetic origin adjustment ( $\beta$ ), and the interaction between half-month interval and genetic

origin ( $\gamma$ ). Potentially, the random components are a year by half-month variation ( $\delta$ ) and residual error ( $\epsilon$ ). Ten versions of the model were fit, testing each of five treatments of the random effects versus two treatments of the repeated aspect of the data. The repeated nature of the data was treated either as a first-order autoregressive structure or as a first-order autoregressive structure with the subjects identified as individual fish within genetic origin. For each repeated treatment, the random component ( $\delta$ ) was first treated as a fixed effect, second treated as a random effect, third treated as a random effect with a first order autocorrelation, fourth treated as a random effect allowed to differ between genetic origins, and fifth treated as a random effect allowed to differ between genetic origins and with a first order autocorrelation. These models were fit for depth and temperature and the Akaike Information Criterion (AIC) used to select the best model for each. The least-squares means (LSMs) and confidence intervals from the selected models were used to describe the depths and temperatures occupied by lake trout of each genetic origin in each seasonal, half-month interval.

The same procedure was used for model selection to compare temperatures occupied by lake trout of each genetic origin between 1999 and 2001 (Chapter One) to those occupied between 2002 and 2005 (current study). The null hypotheses were that for each genetic origin no difference in temperature existed between the two studies. The two intervals of years (studies) were substituted for genetic origin in the model above, with the analyses performed separately by genetic origin. Model selection was performed as described above, except that subjects were identified as individual fish rather than fish within origin. Because the tags used during 1999-2000 did not record

depth, the comparative analysis was only between occupied temperatures. Because these datasets were the first of their type for lake trout in the Great Lakes and to minimize type-2 errors, significance was evaluated at  $\alpha = 0.1$ . Where post-hoc *t*-tests were made comparing LSMs in each half-month interval, the intent was to describe the relative significance and pattern of differences throughout the year and Bonferroni corrections were not made.

Differences in recapture rates between genetic origins and tagging years were evaluated using Fisher's exact test. The deviation of numbers of GLO and FLO lake trout recaptures from the planned equal numbers to be recovered was evaluated with a Chi-square test assuming the expectation of equal proportions.

## **Model selection**

### ***Comparisons between genetic origins***

In the mixed-model ANOVA comparing depths and temperatures occupied by genetic origin during 2002-2005, the best treatment of the repeated nature of the data was a first-order, autoregressive structure that was allowed to differ for fish within genetic origin (Table 5). For both temperature and depth, the best treatment of the random effect was treating the coefficient for the year by half-month variation ( $\delta$ ) as a random effect, and allowing it to differ between genetic origins (Table 5).

**Table 5.** Results of model selection for a mixed-model ANOVA predicting the least-squares mean temperature and depth occupied by lake trout of two genetic origins in Lake Huron during 2002-2005. The AIC values are for two potential treatments of the repeated nature of the observations crossed with five potential treatments of the random components. The  $\Delta$  AIC values are based on the lowest AIC values (in bold) for analyses of temperature and depth. In one case the model did not converge (DNC).

Repeated statement	Random statement	AIC	$\Delta$ AIC
<b>Temperature</b>			
Type=ar(1)	None	8138.7	1194.2
	bimonth*year	8088.7	1144.2
	bimonth*year/ type=ar(1)	8090.7	1146.2
	bimonth*year/ group=origin	8042.7	1098.2
	bimonth*year/ type=ar(1)		
	group=origin	8045.1	1100.6
Type=ar(1), sub=fish(origin)	None	6984.0	39.5
	bimonth*year	6954.0	9.5
	bimonth*year/ type=ar(1)	6956.0	11.5
	bimonth*year/ group=origin	<b>6944.5</b>	<b>0.0</b>
	bimonth*year/ type=ar(1)		
	group=origin	6947.2	2.7
<b>Depth</b>			
Type=ar(1)	None	18092.5	2945.5
	bimonth*year	18070.2	2923.2
	bimonth*year/ type=ar(1)	18072.2	2925.2
	bimonth*year/ group=origin	18071.3	2924.3
	bimonth*year/ type=ar(1)		
	group=origin	18075.1	2928.1
Type=ar(1), sub=fish(origin)	None	15150.40	3.4
	bimonth*year	15149.4	2.4
	bimonth*year/ type=ar(1)	DNC	-
	bimonth*year/ group=origin	<b>15147.0</b>	<b>0.0</b>
	bimonth*year/ type=ar(1)		
	group=origin	-	-

### ***Comparisons between year intervals 1999-2000 and 2001-2005***

The mixed-model ANOVA options were evaluated separately for the GLO and FLO lake trout. For both genetic origins, the best treatment of the repeated nature of the data was a first-order, autoregressive structure that was allowed to differ within year intervals (Table 6). The best treatment of the random effect for GLO fish was treating the coefficient for the year by half-month variation ( $\delta$ ) as a random effect and allowing it to differ between year intervals. For the FLO fish, the random component providing the best fit was a first-order, autoregressive structure without separate coefficients for the two year intervals.

## **Results**

### **Tag returns**

Support from the commercial and sport fisheries in returning tags was strong, with 25% (111 tags returned of 447 released) returned through the end of 2005 (Table 4). Returns by tagging year were 43 of 222 tags deployed in 2002 (19%) and 69 of 225 (31%) deployed in 2003. The return rate for fish tagged in 2003 was significantly higher (Fisher's exact test,  $P = 0.035$ ). Data from 18 of the 111 returned tags could not be used due to tag loss (1 fish), due to tag malfunction and corrupted data (4 fish), recovery too soon after release for behavior to be representative (9 fish), or our inability to assign strain and genetic origin (4 fish). Analyses were therefore based on data from 93 fish, of which 38 were the GLO strain and 55 fish were the FLO strain. The lower return of GLO fish was different than the expectation of 46.5 (Chi-Square = 3.12,  $df=1$ ,

P =0.078), but likely due to the imprecision in predicting strain from fin clips and genotyping.

**Table 6.** Results of model selection mixed-model ANOVAs of temperatures occupied in Lake Huron during two studies, 1999-2000 and 2001-2005, run separately for Great Lakes and Finger Lakes origin lake trout. The AIC values are given for two potential treatments of the repeated nature of the observations and five potential treatments of the random components. The  $\Delta$  AIC values are based on the lowest AIC values for each genetic origin (in bold). In one case the model did not converge (DNC).

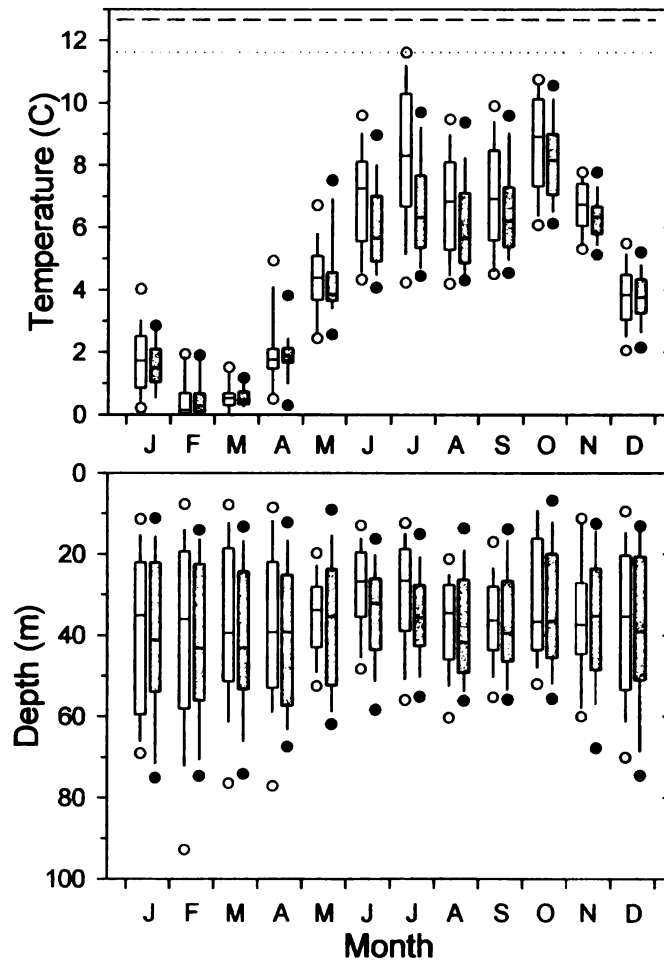
Repeated statement	Random statement	AIC	$\Delta$ AIC
<b>Great Lakes origin</b>			
Type=ar(1)	None	3505.3	526.5
	bimonth*year	3464.4	485.6
	bimonth*year/ type=ar(1)	3463.3	484.5
	bimonth*year/ group=study	3446.5	467.7
	bimonth*year/ type=ar(1) group=study	3448.0	469.2
Type=ar(1) sub=fish	None	2992.6	13.8
	bimonth*year	2986.9	8.1
	bimonth*year/ type=ar(1)	2987.8	9.0
	bimonth*year/ group=study	<b>2978.8</b>	<b>0</b>
	bimonth*year/ type=ar(1) group=study	2981.1	2.3
<b>Finger Lakes origin</b>			
Type=ar(1)	None	6270.5	830.6
	bimonth*year	6236.8	796.9
	bimonth*year/ type=ar(1)	DNC	-
	bimonth*year/ group=study	6236.9	797.0
	bimonth*year/ type=ar(1) group=study	DNC	-
Type=ar(1) sub=fish	None	5473.9	34.0
	bimonth*year	5442.5	2.6
	bimonth*year/ type=ar(1)	<b>5439.9</b>	<b>0</b>
	bimonth*year/ group= study	5443.6	3.7
	bimonth*year/ type=ar(1) group=study	5443.3	3.4

### **Individual variability**

Variation in hourly temperatures occupied among individual lake trout within half-month intervals was substantial overall and within strains (Fig. 5). The overall median hourly mean temperature for GLO fish was 5.3 °C. The range for the monthly medians was 8.8 °C—from a minimum of 0 °C in February and March (5.3 °C or 97% colder than the overall median) to 8.9 °C in October (3.6 °C or 68% warmer). The range in hourly mean temperatures observed for GLO fish in individual months (5<sup>th</sup> to 95<sup>th</sup> percentiles) was greatest in July, ranging from 4.2 to 11.6 °C and least in March, ranging from 0.0 to 1.4 °C. For FLO fish, the overall median hourly mean temperature was 4.8 °C. The range for the monthly medians was 7.9 °C—from a minimum of 0.3 °C in February (4.6 °C or 94% colder than the overall median) to 8.2 °C in October (3.3 °C or 69% warmer). The range in hourly mean temperatures observed for FLO fish in individual months was greatest in July, ranging from 4.5 to 9.7 °C and least in March, ranging from 0.0 to 1.5 °C.

Substantial variation in the depths occupied existed among individual lake trout within strains (Fig. 5). However, seasonal median depths did not vary proportionally as much as the median temperatures. The overall median hourly mean depth for GLO fish was 34 m. The range for the monthly medians was 13 m—from a minimum of 27 m in July (7 m or 22% shallower, than the overall median) to 40 m in March (5 m or 16% deeper). The range in hourly mean depths observed within months (5<sup>th</sup> to 95<sup>th</sup> percentiles) was greatest in February, ranging from 8 to 85 m and least in May, ranging from 20 to 52 m. For FLO fish, the overall median hourly mean depth

Fig. 5. Frequency of hourly mean temperatures and depths occupied by individual fish of Great Lakes (open boxes and circles) and Finger lakes, NY, (filled boxes and circles) origin by month during 2002-2005. Horizontal lines are the median, boxes the 25th and 75th percentiles, vertical lines the 10th and 90th percentiles, and circles the 5th and 95th percentiles. The dotted horizontal line shows the final preferendum and the dashed line the temperature for optimum growth for lake trout, as summarized by Christie and Regier (1988).



was 38 m. The range for the monthly medians was 11 m—from a minimum of 32 m in June (6 m or 14% shallower) to 43 m in February (6 m or 15% deeper). The range in hourly mean depths observed for FLO fish was greatest in January, ranging from 11 to 75 m and least in September, ranging from 13 to 55 m.

## Temperatures occupied

Overall, GLO lake trout occupied significantly higher temperatures (mixed-model ANOVA;  $F_{[1,59]} = 9.22$ ;  $P = 0.004$ ) than FLO lake trout (Table 7; Fig. 6). Temperatures occupied differed significantly among seasonal periods, but more importantly, the interaction between genetic origin and seasonal period was not significant (mixed-model ANOVA;  $F_{[23,17]} = 0.80$ ;  $P = 0.696$ ). Together, these results indicate that the overall pattern of seasonal temperatures is similar between genetic origins, but with GLO fish occupying higher temperatures during periods of stratification.

**Table 7.** Results of a mixed-model ANOVA examining factors influencing the mean temperature (Temp) and median depth (Depth) occupied in Lake Huron during 2002-2005 by lake trout of two genetic origins—Finger Lakes, NY and the upper Great Lakes. Data were recorded with archival tags. The main effects were: Origin, Period (half-month seasonal periods), and the interaction of Origin and Period.

Dependent variable	Fixed effects	df	<i>F</i>	<i>P</i> > <i>F</i>
Temp	Origin	1, 59.3	9.22	0.0035
	Period	23, 16.8	32.91	<0.0001
	Origin*Period	23, 16.8	0.80	0.6960
Depth	Origin	1, 167	3.14	0.078
	Period	23, 34	3.90	0.000
	Origin*Period	23, 34	0.51	0.953

From the onset of autumnal mixing in Lake Huron through the onset of summer stratification, temperatures occupied varied little between genetic origins (Fig. 6a). Between those events, temperature varies little within the upper 100 m (see Bergstedt

and O’Gorman 1989), and choice is limited. As a consequence, little difference can exist between genetic origins with the temperature following the warm-up and cool-down of the lake. During stratification, the temperatures occupied by GLO fish were consistently higher. Within specific half-month periods, the LSMs differed the greatest in early July and in late August to late September (Tukey  $t$ -test,  $P < 0.1$ ), although the probability of a greater  $t$  in late July and early August were nearly as small (Table 8). Based on the least-squares means for temperatures expanded in each interval, the Great Lakes origin fish would annually experience 1,839 degree days versus 1,593 for the FLO fish—about 15 percent greater.

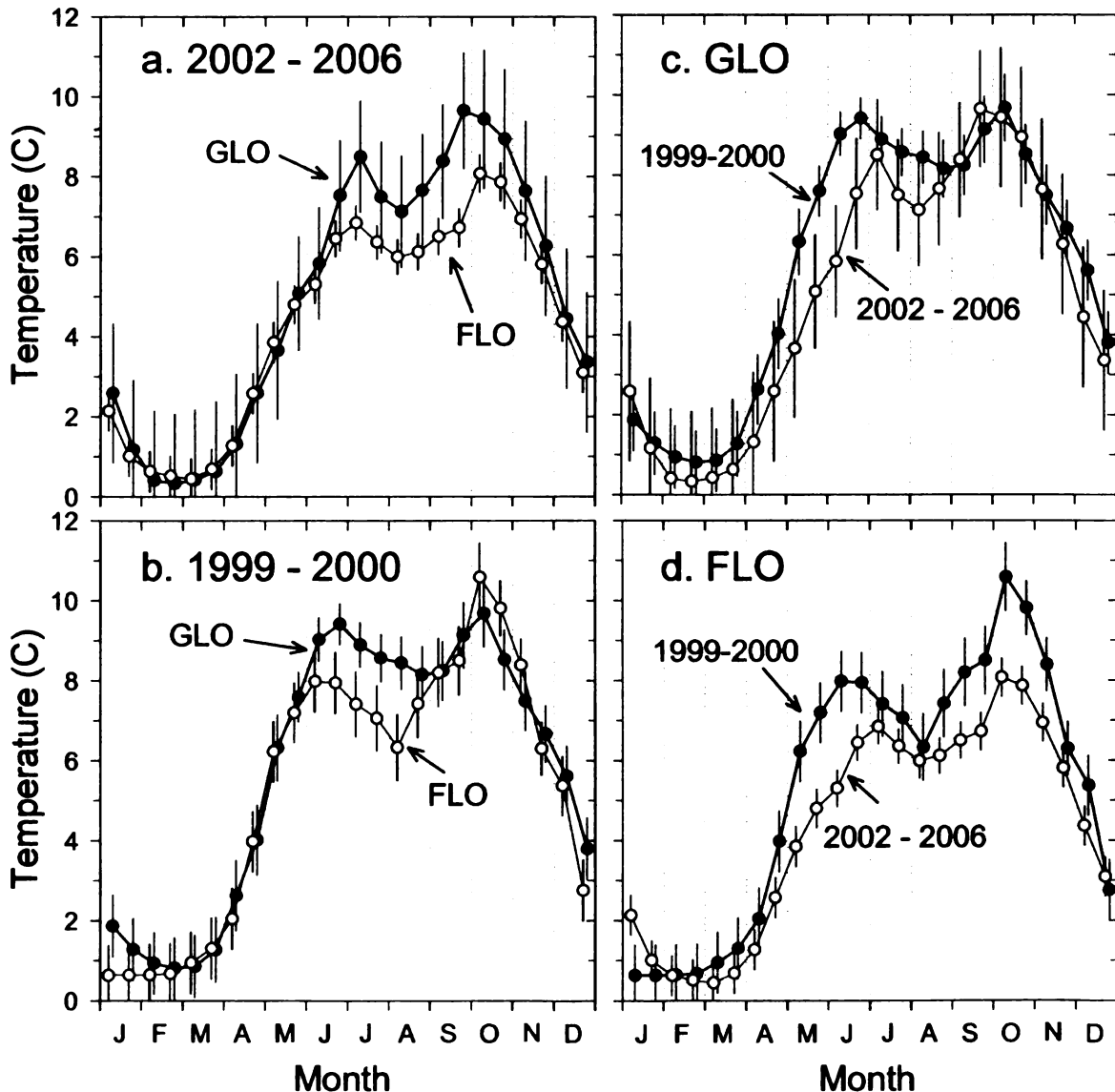
### **Depths occupied**

Median depths occupied were significantly different between genetic origins across the entire data set (mixed-model ANOVA;  $F_{[1,167]} = 3.14$ ;  $P = 0.078$ ). The LSMs for the median depths occupied were consistently lower for GLO than for FLO lake trout (Fig. 7). Within specific half-month periods, the LSMs differed significantly between genetic origins (Tukey  $t$ -test,  $P < 0.1$ ) in early June through early July, and in late September through early October (Table 9). The minimum difference between genetic origins was 2.3 m in late summer and the greatest difference was 8.3 m in early October.

### **Comparison of temperatures occupied in 1999-2000 versus 2002-2005**

The GLO lake trout occupied significantly lower temperatures in 2002-2005 compared to 1999-2000 (Table 10; mixed-model ANOVA;  $F_{[1,107]} = 5.77$ ;  $P = 0.018$ ).

Fig. 6. Seasonal internal temperatures by half-month intervals for tagged lake trout of Upper Great Lakes origin (GLO) and of Finger Lakes, New York origin (FLO) at large in Lake Huron as recorded with implanted archival tags. Symbols and 95% confidence intervals are least-squares means from a mixed-model ANOVA treating the origin\*half-month interval interaction as a random effect and half-month means for individual fish as repeated measures. The data were collected from May 2002 to September 2005. Data from 1999-2000 are from Chapter One. Panels a and b contrast GLO and FLO lake trout within each data-collection interval and panels c and d contrast the data-collection intervals for each genetic origin.

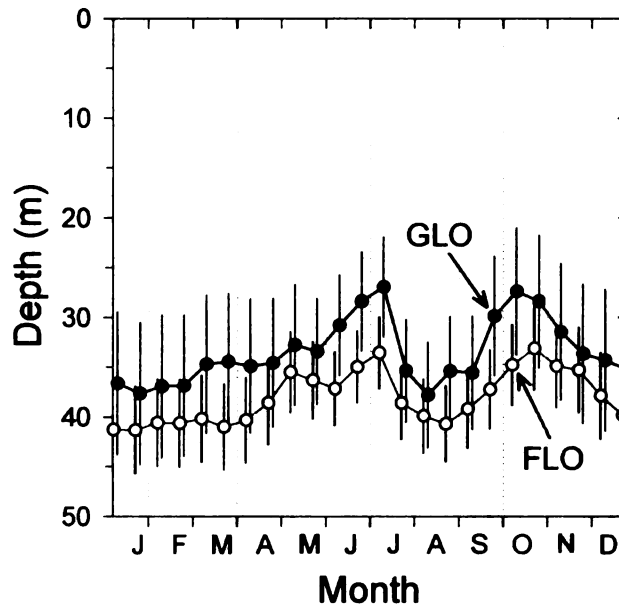


**Table 8.** Least-square means (LSM) of individual fish mean temperatures (°C) occupied and the degree-days (DD) experienced by Great Lakes and Finger Lakes origin lake trout in Lake Huron by half-month interval from a mixed-model ANOVA and results of post-hoc comparisons (Tukey *t*-tests) between origins within each interval

Half-month interval	Great Lakes Origin		Finger Lakes Origin		$\Delta$ LSM	df	<i>t</i>	$P >  t $
	LSM	DD	LSM	DD				
Jan	2.6	38.8	2.1	32.1	-0.4	21	-0.51	0.614
	1.2	18.6	1.0	16.2	-0.2	21	-0.18	0.861
Feb	0.4	6.1	0.6	9.4	0.2	21	0.25	0.804
	0.3	4.3	0.5	6.7	0.2	21	0.21	0.837
Mar	0.4	6.4	0.4	6.6	0.0	21	0.02	0.983
	0.6	10.0	0.7	10.9	0.1	21	0.06	0.952
Apr	1.3	19.7	1.3	19.0	0.0	21	-0.05	0.960
	2.6	38.7	2.6	38.7	0.0	21	0.00	0.999
May	3.7	54.8	3.8	57.7	0.2	20	0.23	0.822
	5.1	81.2	4.8	76.8	-0.3	22	-0.38	0.708
Jun	5.8	87.4	5.3	79.5	-0.5	20	-0.76	0.459
	7.5	112.9	6.4	96.6	-1.1	19	-1.57	0.134
Jul	8.5	127.5	6.8	102.6	-1.7	19	-2.40	0.027
	7.5	119.8	6.4	101.7	-1.1	19	-1.63	0.120
Aug	7.1	106.8	6.0	89.9	-1.1	20	-1.61	0.123
	7.7	122.4	6.1	97.8	-1.5	21	-2.17	0.042
Sep	8.4	125.7	6.5	97.5	-1.9	22	-2.61	0.016
	9.7	144.8	6.7	100.8	-2.9	24	-3.97	0.001
Oct	9.4	141.6	8.1	121.1	-1.4	20	-1.59	0.129
	8.9	143.1	7.9	125.8	-1.1	20	-1.26	0.224
Nov	7.6	114.6	6.9	104.0	-0.7	20	-0.81	0.428
	6.3	94.0	5.8	87.0	-0.5	21	-0.53	0.600
Dec	4.4	66.6	4.4	65.5	-0.1	21	-0.09	0.932
	3.4	53.7	3.1	49.5	-0.3	21	-0.30	0.767
Total		1 840		1 593				

The interaction between study and season was not significant (Table 10; mixed-model ANOVA;  $F_{[23,15]} = 1.19$ ;  $P = 0.372$ ), indicating that the seasonal pattern did not differ over all seasons between the two studies. Differences were greatest in May-June, and

Fig. 7. Seasonal depth by half-month intervals occupied in 2002-2005 by tagged lake trout of upper Great Lakes origin (GLO) and of Finger Lakes, New York origin (FLO) at large in Lake Huron as recorded with implanted archival tags. Symbols and 95% confidence intervals are least-squares means from a mixed-model ANOVA.



early August (Fig. 6c). Finger Lakes origin lake trout also occupied significantly lower temperatures in 2002-2005 than in 1999-2000 (Table 10; mixed-model ANOVA;  $F_{[1,66]} = 84.13$ ;  $P < 0.0001$ ). The interaction between studies and seasonal intervals was also significant (mixed-model ANOVA;  $F_{[23,65]} = 3.84$ ;  $P < 0.0001$ ), indicating that the seasonal pattern differed between the two studies. The greatest differences were in May-August for GLO and May-early November for FLO lake trout. Compared to 1999-2000 (Chapter One), GLO lake trout averaged  $1.7^{\circ}\text{C}$  lower temperatures from May-August and FLO lake trout  $1.6^{\circ}\text{C}$  lower from May through mid-November (Table 5; Table 2 in Chapter One).

**Table 9.** Least-square means of individual fish medians for depth (m) occupied by Great Lakes and Finger Lakes origin lake trout in Lake Huron by half-month interval from a mixed-model ANOVA and the results of post-hoc comparisons (Tukey *t*-tests) between origins within each interval.

Half-month Interval	GLO LSM	FLO LSM	$\Delta$ LSM	df	<i>t</i>	$P >  t $
Jan	36.6	41.3	4.8	298	1.06	0.291
	38.1	41.1	3.1	299	0.68	0.497
Feb	36.9	40.6	3.7	298	0.83	0.409
	36.1	40.4	4.3	297	0.96	0.338
Mar	34.3	40.1	5.9	293	1.33	0.186
	34.7	40.8	6.1	286	1.4	0.164
Apr	35.2	40.4	5.3	280	1.23	0.220
	35.2	38.4	3.1	261	0.75	0.452
May	31.5	35.0	3.5	229	0.88	0.382
	32.3	35.4	3.1	260	0.88	0.378
Jun	30.1	36.6	6.6	241	1.96	0.051
	27.2	33.6	6.4	216	1.96	0.051
Jul	24.9	31.0	6.1	224	1.86	0.064
	34.4	36.7	2.3	236	0.69	0.491
Aug	35.8	38.1	2.3	248	0.66	0.511
	33.6	38.8	5.2	263	1.47	0.143
Sep	34.1	37.5	3.4	281	0.91	0.363
	28.8	36.3	7.6	283	1.97	0.050
Oct	25.4	33.7	8.3	236	2.04	0.043
	27.1	31.2	4.1	260	0.98	0.328
Nov	30.5	33.9	3.4	277	0.79	0.430
	31.4	34.0	2.7	287	0.61	0.543
Dec	33.9	37.6	3.7	293	0.84	0.404
	35.6	39.2	3.7	297	0.81	0.416

**Table 10.** Results of a mixed model ANOVA testing whether the temperatures occupied by lake trout of Great Lakes (GLO) and Finger Lakes (FLO) origins in Lake Huron changed over time , as measured with archival tags. The main effects were study (two intervals of years; 1998-2001 and 2002-2005), season (24 half-month seasonal intervals), and the interaction of study and season.

Origin	Fixed Effects	df	<i>F</i>	<i>P</i> > <i>F</i>
GLO	Study	1, 107	5.77	0.0181
	Season	23, 15	19.09	<0.0001
	Study *Season	23, 15	1.19	0.3722
FLO	Study	1, 66	84.13	<0.0001
	Season	23, 65	124.60	<0.0001
	Study * Season	23, 65	3.84	<0.0001

## Discussion

An original concern leading to this study was the question of whether lower temperatures occupied by FLO lake trout in 1999 and 2000 might not be due to an innate difference in preference but rather related to geographic distribution and potential differences in thermocline depth as influenced by prevailing winds. The question was, could lake trout of one genetic origin or the other tend to be either inshore versus offshore or on the east or west side of the lake rather than in deeper or shallower water? The consistent depth difference reported here (Fig. 7) argues against that explanation and for the consistent selection of lower temperatures and greater depth by FLO lake trout, regardless of geographic location.

The results of Chapter One and this study provide new evidence to suggest that innate differences exist between the lake trout origins, which cause them to occupy different temperatures and depths. The difference in temperatures and depths occupied by GLO and FLO lake trout during summer stratification in 1999-2000 (Chapter One), here reported for the period 2002-2005, and reported in Lake Ontario in 1984-1993 by Elrod *et al.* (1996) were consistent. In all cases, the GLO lake trout occupied the higher temperatures. Additionally, lake trout of both origins appeared to respond similarly to the environmental variables responsible for the decrease in occupied temperatures between Chapters One and Two (Fig. 6). Swim bladder gas retention, which is related to depth distribution, has been demonstrated to be heritable (Ihssen and Tait 1974) and, thus, could affect depth preference and distribution observed in this study. Likewise, temperature preference in laboratory studies was shown to be heritable among *Salvelinus* species (Goddard and Tait 1976). Elrod *et al.* (1996) presented data from gill net surveys conducted in September 1984-1993, concluding that the Superior strain (SUP=GLO) was found significantly shallower and warmer than the Seneca strain (SEN=FLO). For GLO and FLO fish, Elrod *et al.* (1996) presented least-square, mean temperatures for September (interpolated from their Fig. 8) of about of 7.8 and 6.5 °C versus my results of 8.3 and 7.7 °C in Chapter One (Table 2) and 8.4 and 6.4 °C in Chapter Two (Table 8). The corresponding LSM depths for GLO and FLO were about 33 and 42 m in Elrod *et al.* (1996) versus my results of 34.1 and 37.5 m in Chapter Two (Table 9). These results were consistent despite spanning two lakes, two decades, and two degrees of latitude. In interpreting their results, Elrod *et al.* (1996) focused primarily on the potential for strains to reflect phenotypic traits selected for in the area

where they evolved, citing the example of the Clearwater Lake, Manitoba, strain, which were consistently captured at the shallowest depth and highest temperatures in Lake Ontario. Clearwater Lake is a shallow northern lake with a mean depth of 13 m and only 15% of its area greater than 24 m. This explanation of the difference between GLO and FLO lake trout is less plausible because Seneca Lake is slightly deeper than Lake Michigan based on average depth (85 versus 82 m), but is not deeper based on maximum depth (188 versus 282 m). Furthermore, Seneca Lake is much shallower than Lake Superior, which has an average and maximum depth of 147 and 406 m. It seems more likely that, if Seneca Lake strain has a preference for depths greater than selected by GLO lake trout, selection would have occurred along a niche axis other than depth.

The decrease observed in temperatures occupied between 1999-2000 and 2002-2005 coincided with recent changes in the food web in Lake Huron. Decreases in abundance of *Diporeia* spp. (Nalepa *et al.* 2007), and the abundance and species composition of the prey fish community (Riley *et al.* in press) could have influenced bathythermal habitat use. The most likely causes of the shift are changes in the distribution of available prey species, necessitating changes in search patterns for prey, or selection of lower temperatures to maximize conversion efficiency of food as prey availability becomes severely limited, as predicted by Mac (1985).

Changes in composition of the prey fish community could have put pressure on predators to move deeper. Since their ascendance as a dominant pelagic species in the Great Lakes, alewives became the most prevalent prey of salmonines (O’Gorman and

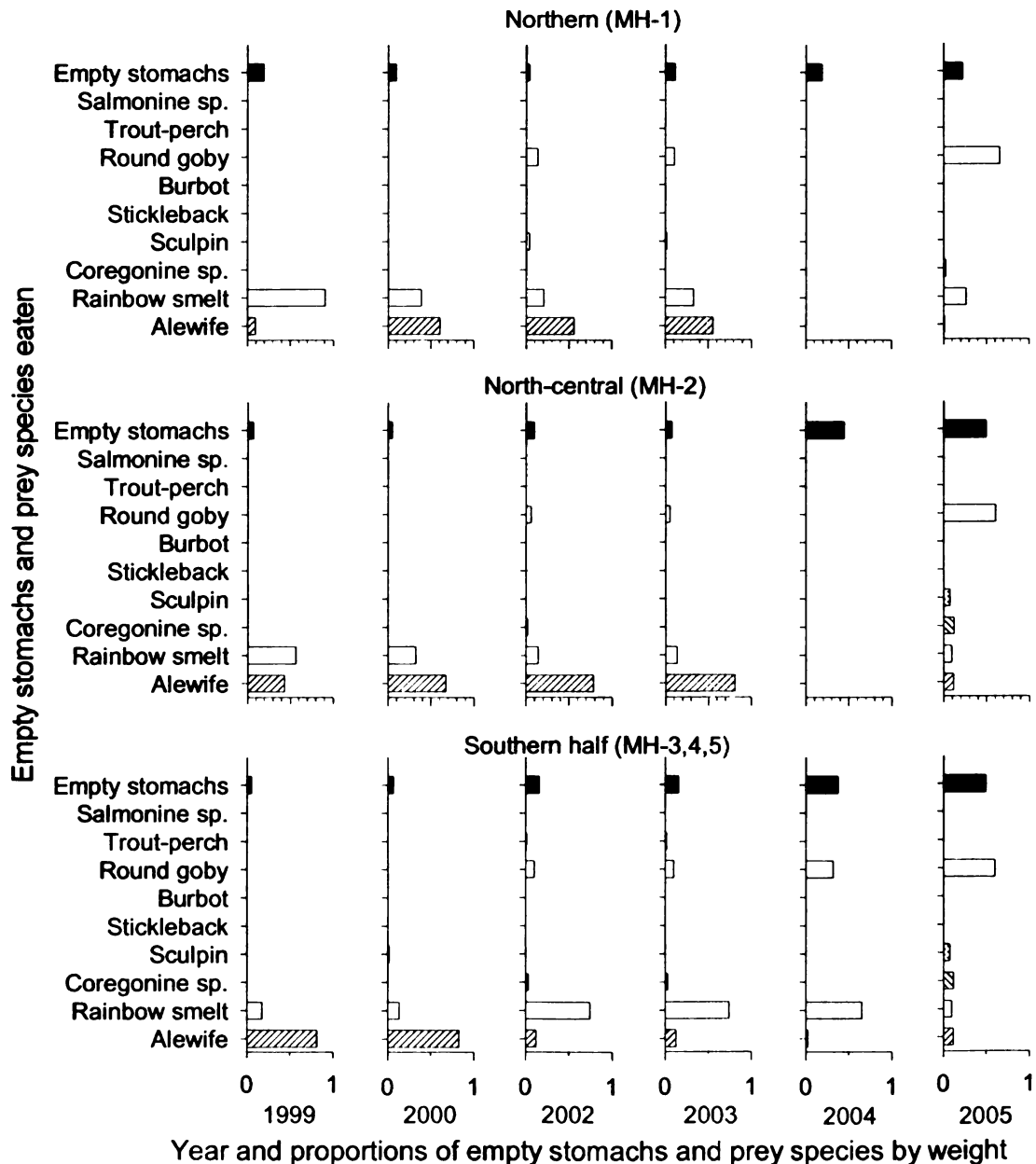
Stewart 1999). During the course of this study, alewife numbers dramatically declined in Lake Huron. Acoustic surveys by the USGS estimated their biomass at over seven  $\text{kg}\cdot\text{ha}^{-1}$  in 1997, but only  $0.002 \text{ kg}\cdot\text{ha}^{-1}$  in 2004 (Warner *et al.* 2004). In 2005, the estimate was  $0.012 \text{ kg}\cdot\text{ha}^{-1}$  (Schaefer *et al.* 2005), still almost two orders of magnitude lower than in 1997. In the absence of a key pelagic prey base, lake trout may have been forced to prey upon demersal species, and thus, used greater depths and lower temperatures in 2002-2005 than they did in 1999-2000, when pelagic prey were more abundant. Food habit data collected across U.S. waters of Lake Huron over this time period document a switch from pelagic to demersal prey species (Fig. 8). The pelagic species found in lake trout stomachs were primarily alewives and ninespine sticklebacks (*Pungitius pungitius*), with rainbow smelt (*Osmerus mordax*) important seasonally. Alewives systematically disappeared from the diet (Fig. 8). By 2004, alewives were largely absent from the diet except in MH1, which is nearest the connection with Lake Michigan, where alewives remained moderately abundant (Madenjian *et al.* 2005). The round goby, a recent invader and a strongly demersal species, has emerged as a major prey item of lake trout (Fig. 8).

Prey availability decreased severely between the periods of data collection for Chapters One and this study. This decrease in prey could have caused a selection of lower temperatures than in the earlier study to conserve energy and make more efficient use of resources. The mean biomass of all demersal prey species taken in USGS bottom trawl tows in Lake Huron had declined since the mid 1990s, and dropped sharply to very low levels in 2003 (Riley *et al.* in press; Fig. 9). For all pelagic fish species

combined, biomass decreased by about 90% between 1997 and 2005 (Schaefer 2005).

In general during the present study (2002—2005), substantially fewer prey were available to lake trout, and empty stomachs were more prevalent (Fig. 8) than in the previous study (Chapter One).

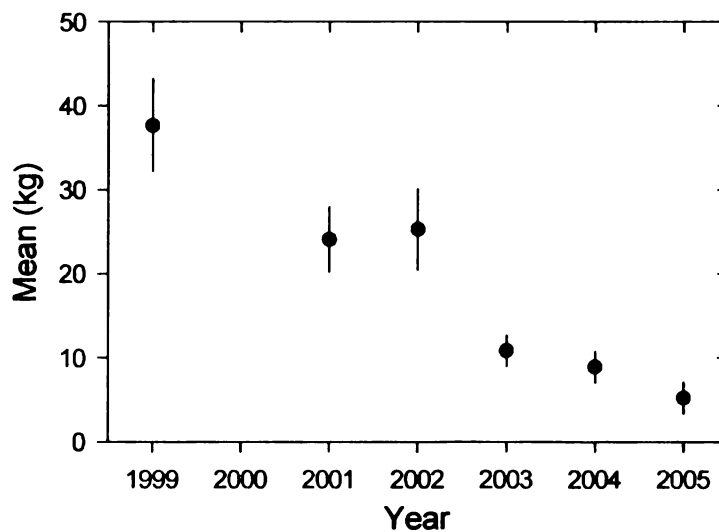
Fig. 8. The proportion of empty stomachs (dark fill) and the percent of diet by weight for nine prey items in stomachs of lake trout collected in three areas of the U.S. waters of Lake Huron (Fig. 4). Data were provided by the Michigan Department of Natural Resources, Alpena Fisheries Station.



The drastic reduction in prey availability over recent years could have triggered physiological responses affecting temperature preference. Good agreement exists between laboratory determinations of the final temperature preferendum and the optimal temperature for growth of many fish species (McCauley and Casselman 1981; Jobling 1981). Determinations of the optimal temperature for growth require feeding at an optimal or excess rate; however, piscivorous fish in oligotrophic lakes will rarely have prey supplies at excess levels and are hence not capable of supporting maximum growth. Brett *et al.* (1969) hypothesized that “the optimum temperature for growth would drop as the ration decreased.” The hypothesis was based on the assumption that decreased metabolic cost for maintenance at lower than optimum temperatures would make more energy available for growth when food was limited. By varying ration size for sockeye salmon (*Oncorhynchus nerka*), optimum temperature for growth decreased from 15°C at a ration of 6% of body weight per day to 5°C at a ration of 1.5% per day (Brett *et al.* 1969). This relation could be expected to have evolutionary significance and result in observable behavior. Such a behavior was demonstrated experimentally with juvenile lake trout, where a linear decrease in preferred temperature occurred when rations decreased from 5.0% to 0.3% of body weight (Mac 1985). The preferred temperature at the lowest ration tested was 9 °C, just slightly higher than observed for GLO lake in this study from mid June through September, and two to three degrees higher than observed for FLO lake trout. Citing unpublished data by D.V. Rottiers, Mac (1985) suggested that reductions in metabolic costs could be gained by using temperatures as low as 5 °C, which is identical to the results of Brett *et al.* (1969). Using techniques similar to Mac (1985), preferred temperatures were determined for

brown trout (*Salmo trutta*) and arctic char (*Salvelinus alpinus*) (Larsson 2005). The preferred temperature of brown trout (16 °C) was close to the optimum temperature for growth of 17 °C (Elliot and Hurley 1999), but the preferred temperature for Arctic char (11.8 °C) was 4.5 °C less than the optimum temperature for growth (Larsson and Berglund 1998). Reasoning that Arctic char typically inhabit low productivity waters, Larson (2005) speculated that char may tend to optimize conversion efficiency rather than growth. In Lake Huron, lake trout were rarely found near their optimum temperature for growth (Christie and Regier 1988; Fig. 5). Retreating to temperatures lower than optimum in response to a growing scarcity of food could increase conversion efficiency and partially explain the observed decrease in temperatures occupied by lake trout during this study.

Fig. 9. Mean biomass (kg) and 95% confidence limits in USGS fall trawl catches at five ports in the Michigan waters of Lake Huron, 1976-2006 (data from Riley *et al.* in press).



By occupying lower temperatures, lake trout may cause parasitic sea lampreys to reduce their blood consumption rate. Temperature data from Chapter One have already been incorporated into an individual-based model (IBM) of sea lamprey feeding and growth (Madenjian *et al.* 2003), where the summer-fall temperature regimes of GLO and FLO lake trout in 1999-2000 resulted in only a 3% increase in total blood consumption by sea lampreys feeding on GLO lake trout. However, sea lamprey growth surges in fall (Bergstedt and Swink 1995) and a disproportionate amount of blood consumption and mortality occurs then. The difference reported by Madenjian *et al.* (2003) was not great, but the number of predicted deaths was 7% greater under the GLO than under the FLO temperature regime. To explore how very low temperature regimes (such as might characterize the siscowet, or deep-water, form of lake trout in Lake Superior) might affect growth and mortality, the IBM was run not allowing seasonal temperature to exceed 4°C. Such a constant low resulted in a substantial decrease in predicted sea lampreys growth and blood consumption (Charles Madenjian, USGS, Great Lakes Science Center, personal communication). Growth of sea lampreys and predicted lake trout losses should be evaluated using the IBM and GLO and FLO temperature regimes from Chapter Two.

Summary statistics describing habitat dimensions such as the temperatures and depths occupied can obscure the tremendous individual variation and the potential for habitat overlap with other members of the fish community. During late fall through early spring lake trout were relegated to a narrow range of temperatures (Fig. 5). In the winter, temperature in the upper 100 m, or more, of the water column ranges from 0 to 2

°C, due to the small change in density over that range and wind-driven mixing. During the period of summer stratification, individuals occupied temperatures ranging from 4 to 12 °C. The pattern for variability in depth was related, but opposite, since lake trout during the winter could range widely in depth with little effect on temperature occupied. The difference in median depths occupied among seasons was not as striking as with temperature. The greatest variability in depth was recorded during winter, when temperature varied by a maximum of about 2°C, (Fig. 5). Unless lake trout moved deep enough in winter to enter the warmer layer below the winter mixing layer (greater than 100 m; Bergstedt and O’Gorman 1989), temperature varied little.

Archival tags can be a cost-effective tool for collecting data on lake trout in lakes and with species where sufficient exploitation will provide for the return of tags. At a return rate of 25%, our cost per returned tag was about \$1,200 (USD), including the reward. Although that cost is higher than a single acoustic or radio tag encoded for depth and temperature, the difference was offset by elimination of the need to keep a crew on the lake for extended periods and by the data not being interrupted by gaps due to weather or losses of contact. The cost also compares favorably with the extraordinary cost that would be needed for vessel operations to generate comparable data through netting. A key to encouraging the participation of sport and commercial fishers was the \$100 reward offered. By offering a substantial amount, most people encountering either the internal or external tag likely responded. In marine studies, where distance and effort required to return a tag can be much greater, substantially higher rewards have been offered (Block *et al.* 2005). Administrative approval of

suitably large rewards can be difficult to obtain, but when compared to the value of the data, a reward that increases recovery rate by even a few percent is warranted. In our case, most tags recovered within two years of deployment were redeployed, thereby compensating for the cost of the reward.

The increase from 19 to 31% in tag recovery between 2002 and 2003 (Table 4), likely reflected both the fact that in 2002, some fish tagged were captured in gill nets and experienced more stress during capture and that some fish were held for a long period (three weeks) to accommodate genotyping. The relatively small difference in recovery rate between lake trout tagged and released on the lake and at the HBBS suggests that the effect of capture and transport to the HBBS was minimal if the animals tagged were released quickly (Table 4). If possible, however, tagging immediately at the site of capture to eliminate as much stress from handling and transport as possible is recommended.

There was an initial constraint imposed by the lack of availability of archival tags small enough for lake trout. Tags of a suitable size only appeared in the late 1990s. By 2005, tags were available that are small enough for most freshwater game and commercial species and half the size of the LTD-1110 tag used here. Those seeking to collect similar data are encouraged to investigate the use of archival tags. I spent eight of the first ten years of my career working aboard a research vessel on Lake Ontario. I am convinced that no technique that I saw is capable of generating the quality and continuity of the data presented here at a similar cost.

## **Acknowledgments**

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## **CHAPTER THREE**

Seasonal and diel depth and temperature distributions of lake whitefish and of Great Lakes- and Finger Lakes-origin lake trout relative to exploitation and potential bycatch.

## **Abstract**

Depth and temperature data recorded during 2003-2005 in Lake Huron by archival tags implanted in lake whitefish (*Coregonus clupeaformis*) and two strains of lake trout (*Salvelinus namaycush*) were used to compare their seasonal depth and temperature distributions and to examine whether seasonal differences in depths could be exploited to reduce bycatch of lake trout in commercial gill net fisheries for lake whitefish. Both Great Lakes origin (GLO) and Finger Lakes origin (FLO) lake trout occupied during both daylight and dark significantly deeper and colder waters seasonally than lake whitefish. The temperature differences were greatest during periods of stratification when behavioral thermoregulation was possible. The greatest depth and temperature separation occurred between Finger Lakes lake trout and lake whitefish. Based on a comparison of the seasonal depth distributions of the two species, if the maximum depth of gill nets could be regulated seasonally from 25 to 35 m, one-half or more of the lake whitefish population would be vulnerable while avoiding most of the lake trout population. Percentages of lake trout targeted were lowest in late July (GLO = 8% and FLO = 11%) and early August (GLO = 4% and FLO = 7%). Feasibility of this approach depends on the shallower lake whitefish being available to the bottom-set gill nets and not suspended pelagically. Modal depths of commercial gill net effort for lake whitefish in Lake Huron exceeded modes from the lake whitefish archival tag data and suggested a portion of the lake whitefish population was pelagic and suspended far enough above bottom to not be vulnerable to the gill nets. Use of suspended gill nets to target those fish could increase their vulnerability and further avoid lake trout.

## Introduction

The structure of the fish community in Lake Huron has changed dramatically, influenced by fishing and the effects of invasive species over the past century. After decades of exploitation and combined with the effects of the parasitic sea lamprey (*Petromyzon marinus*), the abundance of the commercially important lake whitefish (*Coregonus clupeaformis*) was greatly reduced while the lake trout (*Salvelinus namaycush*) became nearly extinct (Berst and Spangler 1972; Hansen 1999).

A common requirement for restoration of both species was control of the sea lamprey. Beginning in the 1970s, Lake Huron's tributaries were treated with lampricides to reduce sea lamprey abundance (Smith and Tibbles 1980). These initial efforts reduced sea lamprey abundance substantially, but not to levels thought necessary for lake trout restoration. Stocked lake trout survived initially for the first few years of their lives, but did not survive to maturity (age 6+ years) in adequate numbers. It was not until a strategy to control a large remaining population of sea lamprey larvae in the outflow from Lake Superior was implemented in the late 1990s (Schleen *et al* 2003) that sea lamprey numbers approached levels thought to permit rehabilitation of the lake trout population.

In contrast to lake trout, initial sea lamprey control efforts were adequate for lake whitefish restoration, as harvest in the 1990s was the highest on record (Ebener 1997; Brown *et al.* 1999). When other hosts such as lake trout and Chinook salmon

(*Oncorhynchus tshawytscha*) were abundant, lake whitefish became a secondary host to the sea lamprey. More important than sea lamprey control, lake whitefish restoration was likely spurred by a number of changes in commercial fishing regulations and the fishing gear used. In the 1970s, the State of Michigan banned use of large-mesh gill nets and promoted adoption of trap nets as the preferred gear (Brown et al 1999). Trap nets, because of their capture of live fish, allow more flexible regulations. Bycatch in trap nets can be regulated to allow the release of non-target fish including small lake whitefish and species such as lake trout. Greater cooperation among State, Provincial, and Tribal fishery management agencies, and the adoption of quota management and strategies for setting total allowable catch restrictions have also aided in the lake whitefish recovery.

Management of the lake whitefish fishery affects lake trout restoration because the principal bycatch, regardless of the gear used, is lake trout (McNeil and deLaplante 1989; Johnson *et al.* 2004a). Bycatch consists of both the retained and discarded non-target organisms, including unobserved mortalities of fish that are released (Crowder and Murawski 1988). The observed portion of lake trout bycatch mortality are the fish harvested under quotas or discarded by the gill net fishery, and to a lesser-extent, gilled in the leads and pots of trap nets (Johnson *et al.* 2004b). Unobserved mortality includes delayed deaths caused by injury, stress, disease, or predation (Chopin *et al.* 1996). Johnson *et al.* (2004b) estimated the survival of lake trout after being released alive from the pots of trap nets as 98% (using in part data from Chapters One and Two). In contrast, the survival of live lake trout taken from gill nets was estimated at 72%

(Gallinat *et al.* 1997). Recommendations to reduce bycatch losses of lake trout included limiting lake whitefish harvest to trap nets and reducing effort in summer when the ratio of lake trout to lake whitefish caught in either gear was highest (Johnson *et al.* 2004b).

Fishery managers desire to reduce losses of lake trout due to bycatch so as to promote population rehabilitation. Less known and appreciated, is that commercial fishers also have an interest in the reduction of bycatch. Both gill net and trap net fishers found that as the lake trout population increased in the 2000s, sorting, handling, and releasing lake trout bycatch from their gear was a major task. Any viable strategy that maintained their access to lake whitefish, while reducing lake trout bycatch, would be welcomed.

One approach to reducing bycatch would be to exploit differences in the spatial distribution of species. In 1998 and 1999, a multi-agency effort occurred to determine if sufficient spatial separation existed at any seasonal period to permit a gill net fishery in areas of Lake Huron designated for lake trout rehabilitation (Johnson *et al.* 2004b). From October 1998 through December 1999, members of the Bay Mills Indian Community in Michigan made 260 monitored gill net lifts. The number of lake trout killed per lift decreased seasonally from 17.2 per lift during March-June, to 7.4 per lift during July-Oct 7, to 4.9 per lift during the remainder of October and November. Based on those results, a tribal small-boat gill net fishery in Hammond Bay has been allowed from October 1 to November 6 each year 2000-2007. Considering the change in lake

trout depth distributions since 1999 (Chapter 2), a reexamination of the seasonal overlap between lake trout and lake whitefish using more recent data is warranted.

The objectives of this chapter were to use data from archival tags implanted in lake whitefish and lake trout of two genetic origins to (1) describe the seasonal temperature and depth distributions of lake whitefish, (2) compare the seasonal and day-night temperature and depth distributions of lake whitefish and lake trout on a finer time scale and broader geographical scale, and (3) to estimate the likely relative effects on lake trout bycatch if the fishery was managed to have seasonal depth restrictions on gear placement. The key questions were: did the overlaps in depth distributions between the two species change by season or by day versus night and might any of the seasonal overlaps be exploitable to affect bycatch in the commercial fishery.

## **Methods**

### **Tags and tagging**

Archival tags, model LTD-1110 manufactured by Lotek Wireless Inc., Newmarket, Ontario, Canada, were surgically implanted in lake trout and lake whitefish released into Lake Huron. The tags were cylindrical—11 mm in diameter by 32 mm long and rounded on one end. Weight was about five g in air and 2 g in water. Each tag contained a thermistor and pressure sensor, and recorded temperature and depth. Recording continued until tag recovery and download, or until the battery expired

(battery life was two to three years). Observations of date, time, temperature, and depth were recorded at 15-second intervals until the memory was full. Software then replaced previous observations in a pattern that maintained a complete set of observations from initialization to download, but with gradually increasing intervals between observations. Nearly 33,000 observations were recorded with average intervals increasing from 15 seconds by about 1.3 minutes for each month deployed and 16 minutes for each year.

Tag specifications were for 0.2°C resolution and  $\pm 0.3$  °C accuracy for temperature and 0.4% of the current depth scale with  $\pm 1\%$  accuracy. The potential depth range was 0 to 500 m, but, to improve resolution and accuracy, software initially set the range to one-quarter of that scale (0 to 125 m). If fish moved deeper than the initial scale, the range would progressively shift (permanently) to one-half scale (0 to 250 m) and then to full scale (0 to 500 m). Resolution and accuracy (in parentheses) at those scales were 0.5 ( $\pm 1.25$ ) m, 1.0 ( $\pm 2.5$ ) m, and 2.0 ( $\pm 5.0$ ) m, respectively.

Recovery of archival tags depended on the recapture of fish by sport and commercial fisheries and return of the tags. To promote returns, a reward of \$100 (USD) per tag was offered. Tagged fish were also marked externally with orange dart tags. The external tags bore identifying serial numbers, reward advertisement, a contact telephone number, and instructions to not freeze the tag. The internal tags also bore a reward notice and contact information. Information posters describing the study and reward were displayed in tackle and convenience stores, at launch sites, and were

provided to commercial and charter fisheries. The Michigan Department of Natural Resources and the Ontario Ministry of Natural Resources also publicized the study.

All lake whitefish tagged were obtained from commercial trap nets (Table 11). In 2002, lake whitefish were transported to the Hammond Bay Biological Station (HBBS) for tagging. Unlike the lake trout, the lake whitefish appeared stressed after transport and tagging. Because of this observation, and the recovery of only one fish during summer 2002, the remainder of lake whitefish tagged in 2003 and 2004 were tagged and released immediately on removal from the trap nets to eliminate transport stress. Lake whitefish tagged in November 2003 were from shallow experimental trap nets set by the Chippewa Ottawa Resource Authority to collect fish for another tagging experiment and were in spawning condition.

Archival tags were inserted through a 1.5-cm incision made slightly to the side of the ventral midline anterior to the pelvic fins. The incision was closed with two slow-dissolving monofilament sutures, a veterinary-grade, isocyanate adhesive was applied to the knots, and an external tag inserted on each side of the dorsal fin. The procedure took about 3 minutes, during which the gills were irrigated. Lake whitefish tagged at the HBBS in 2002 were anesthetized, weighed, and measured before tagging. After tagging, the fish were transferred to a recovery tank and released the next day. When tagging was done in the field (2003 and 2004), fish were moved directly from the trap or gill net to a floating pen. After surgery, fish were placed in a recovery pen and released when they regained equilibrium.

There were two genetic origins of lake trout used in this study. One was of upper Great Lakes origin (GLO) and the other of Finger Lakes, New York (FLO) origin (Krueger *et al.* 1989; Elrod *et al.* (1996a, 1996b); Chapter One). The source, handling, and tagging of lake trout were identical to that described in Chapter Two.

### **Statistical analyses**

Temperature and depth data were summarized by half-month seasonal intervals as described in Chapter One. The first half of each month included the first 15 days and the second half the remaining days in the month. The arithmetic mean temperature (°C) in each half-month interval was used to best represent the average number of degree-days experienced by a fish. For depth, the median depth occupied by each fish in each interval was used. Because only one of the lake whitefish tagged in 2002 was recovered, only data from 2003-2005 from both lake trout and lake whitefish were included in the analyses.

With each fish, there was a recovery period after release during which the fish were likely still recovering from surgery and the data were suspected to not represent normal behavior. Each plot of temperature was inspected and a subjective judgment was made as to the date when behavior appeared consistent with the remainder of the data. For fish captured when the tag was still actively recording, the time of capture in the fishing gear was evident from a cessation of temperature and depth variation. Temperature observations before behavior appeared normal and after the fish was caught were not

used in the analyses. Because of the expanding interval of observations over time and the greater number of observations per hour for fish recaptured sooner after release, and to give fish equal weight (the experimental unit in this study was the individual fish), subsequent analyses were based only on the mean temperatures and median depths for individual fish by half-month interval and considering the repeated nature of those measures. Mean temperature was chosen for the reason stated above, and their likelihood of use in bioenergetics models. The median depth was chosen as best representing the most common depth frequented. However, in assessing exposure to capture by bottom-set gill nets, the maximum depths observed were also summarized.

The temperatures analyzed and reported in this study were only those recorded inside the abdominal cavity. At any instant, these measures could vary from the temperature of the surrounding water. Based on laboratory studies (HBBS, unpublished data), internal temperature after a rapid change in external temperature would move 50% toward the new external temperature within about five minutes, and 90% toward the new temperature within 15 minutes. Over the temporal scale of a half-month interval, the mean internal temperature should closely approximate the average temperature of the water occupied by a fish.

To describe the variability in the observations, percent frequency distributions for temperature and depth were compiled by group for lake trout and lake whitefish. Because the time between release and recapture varied with individual fish, and because of the gradually increasing intervals between observations, and hence the changing

number of observations per time interval, it was necessary to create a summary statistic to ensure that all fish contributed equally to the distribution. Therefore, the average temperature, median depth, and maximum depth occupied were calculated for combinations of group, individual fish, half-month interval, and hour and used to describe those statistics along with the 10<sup>th</sup>, 25<sup>th</sup>, 75<sup>th</sup>, 90<sup>th</sup>, and 90<sup>th</sup> percentiles by half-month interval.

Because catch and bycatch in gill nets occurs primarily at night, a variable was also added to account for light conditions. Times of sunrise, sunset, and twilight were downloaded from the U.S. Naval Observatory (<http://aa.usno.navy.mil/data>) for the span of the study. These data were used to classify each observation to one of three light conditions—daylight (sunrise to sunset), twilight (the morning and evening intervals when the sun is between 0° and 6° below the horizon, also termed civil twilight), and dark (when the sun is more than 6° below the horizon). Observations classified as being during twilight were eliminated in analyses that considered light conditions. The distributions of temperatures and depths occupied by lake whitefish and each lake trout genetic origin were determined by day and night. The cumulative percent frequency for depth was also determined by 3-m intervals and half-month period.

By combining the lake whitefish and lake trout data, three groups of fish were used in the analyses—GLO lake trout, FLO lake trout, and lake whitefish. The overall effect

of group on the temperatures and depths occupied was evaluated with a mixed-model ANOVA (SAS 2001). The underlying model for the analysis was

$$T_{h,s,y,f} \text{ or } D_{h,s,y,f} = \mu + \alpha_h + \beta_s + \gamma_{h,s} + \delta_{h,y} + \varepsilon_{h,s,y,f} \quad (1)$$

in which  $T_{h,s,y,f}$  or  $D_{h,s,y,f}$  is a half-month mean for temperature or depth and  $h$ ,  $s$ ,  $y$ , and  $f$  denote the half-month interval, group, year, and individual fish. The fixed effects were the overall mean ( $\mu$ ), the seasonal or half-month adjustment ( $\alpha$ ), the group

For the combined lake whitefish and lake trout data, the best treatment of the repeated nature of the data in the mixed-model ANOVA comparing depths and temperatures occupied, was a first-order, autoregressive structure allowed to differ for fish within group (Table 12). For both temperature and depth, the coefficient for the year by half-month variation ( $\delta$ ) was best treated as a random effect allowed to differ between groups (Table 12). This result was consistent with previous analyses of the lake trout data (Chapter Two). Because gill nets catches were primarily made at night, these analyses were also repeated separately by light condition (daylight or dark).

## Results

Recoveries of lake whitefish came entirely from the commercial fishery, because few lake whitefish are caught by Lake Huron sport fisheries. Thirty-six of the total 361

tagged fish (10%) were recovered through 2005 (Table 11). Only one of 73 fish (1%) tagged after transport to the HBBS was recovered and eight of 109 fish (7%) tagged in November 2003 while in spawning condition were recovered. In comparison, 25 of 179 (14%) lake whitefish tagged in May or June on the lake and immediately released were recovered. Returns of tagged lake trout were described in Chapter 2.

## **Temperatures and depths occupied**

### *Temperature*

The temperatures occupied seasonally differed between lake whitefish and each group of lake trout (mixed model ANOVA,  $F_{[2,214]}$ ,  $P < 0.0001$ ). The seasonal pattern of least-square mean (LSM) temperatures for lake whitefish was most similar to GLO lake trout (Fig. 10). Although the differences with GLO lake trout were relatively small, the LSM temperatures for lake whitefish were higher in 22 of 24 half-month intervals with one tie (Table 13). However, only in late July and early August, at the peak of summer stratification, did the difference in LSMs between GLO lake trout and lake whitefish exceed 2°C. In only three additional half-month intervals, October and early November, did the difference exceed even 1°C. The difference between the LSM temperatures occupied by lake whitefish and FLO lake trout was larger than with GLO lake trout and more consistent (Table 13; Fig. 10). In all 24 half-month intervals, lake whitefish occupied higher temperatures than FLO lake trout (Table 13). From July through early November, lake whitefish were at temperatures from 1.9 to 3.7°C higher than FLO lake trout. The greatest difference was in late July, when the LSM for lake whitefish was 10.2 °C but only 6.5 °C for FLO lake trout.

**Table 11.** Summary of lake trout and lake whitefish tagged with surgically implanted archival temperature tags and released into Lake Huron, including the number of lake trout tagged by date interval, species, location, source, the number released, the number and percent recaptured, the number and percent of fish used in the analyses, and (for fish used in the analyses) the total days at large.

Dates tagged	Species	Tagging and Release <sup>a</sup>		Source (net-type)	Number released	Number recaptured	Percent recaptured	Number of fish used in analyses	Percent used in analyses	Days of data contributed
		Location								
15-30 May 2002	LT	HBBS		trap	77	21	27	15	19	2 226
	WF	HBBS		trap	33	1	3	1	3	209
18-20 Jun 2002	LT	HBBS		trap	107	17	16	15	14	3 615
28 Jun 2002	WF	HBBS		trap	40	0	0	0	0	0
9-10 Oct 2002	LT	DI		gill	38	5	13	3	8	1 156
07-29 May 2003	LT	LH		trap	64	24	34	20	28	8 386
	WF	LH		trap	100	17	17	16	16	5 758
15-16 May 2003	LT	HBBS		trap	55	17	31	15	27	6 037
5-17 Jun 2003	LT	HBBS		trap	106	28	27	25	24	10 974
10-12 Nov 2003	WF	LH		trap	109	8	7	8	7	3 578
19-28 May 2004	WF	LH		trap	79	8	10	8	10	1 534
Total	LT				447	111	25	93	21	37 021
	WF				361	36	10	33	9	11 079

<sup>a</sup> Hammond Bay Biological Station (HBBS), Drummond Island (DI), and aboard boats on Lake Huron (LH)

**Table 12.** Results of model selection for a mixed-model ANOVA predicting the least-squares mean temperature and depth occupied by lake whitefish and lake trout of Great Lakes origin and Finger lakes, NY origin in Lake Huron during 2003-2005. The AIC values are for two potential treatments of the repeated nature of the observations crossed with five potential treatments of the random components. The  $\Delta$  AIC values are based on the lowest AIC values (in bold) for analyses of temperature and depth.

Repeated statement	Random statement	AIC	$\Delta$ AIC
<b>Temperature</b>			
Type=ar(1)	None	14396.5	4296.9
	bimonth*year	14206.9	4107.3
	bimonth*year/ type=ar(1)	14208.0	4108.4
	bimonth*year/ group=group	14054.7	3955.1
	bimonth*year/ type=ar(1) group=group	-	-
Type=ar(1), sub=fish(group)	None	10154.6	55.0
	bimonth*year	10108.2	8.6
	bimonth*year/ type=ar(1)	-	-
	bimonth*year/ group=group	<b>10099.6</b>	0
	bimonth*year/ type=ar(1) group=group	-	-
<b>Depth</b>			
Type=ar(1)	None	25512.7	4582.2
	bimonth*year	-	-
	bimonth*year/ type=ar(1)	25498.6	4568.1
	bimonth*year/ group=group	25458.1	4527.6
	bimonth*year/ type=ar(1) group=group	-	-
Type=ar(1), sub=fish(group)	None	20938.6	8.1
	bimonth*year	20933.7	3.2
	bimonth*year/ type=ar(1)	-	-
	bimonth*year/ group=group	<b>20930.5</b>	0
	bimonth*year/ type=ar(1) group=group	-	-

### *Depth*

The depths occupied seasonally also differed significantly among lake whitefish and the two groups of lake trout (mixed model ANOVA,  $F_{[2,183]}$ ,  $P < 0.031$ ). Because small

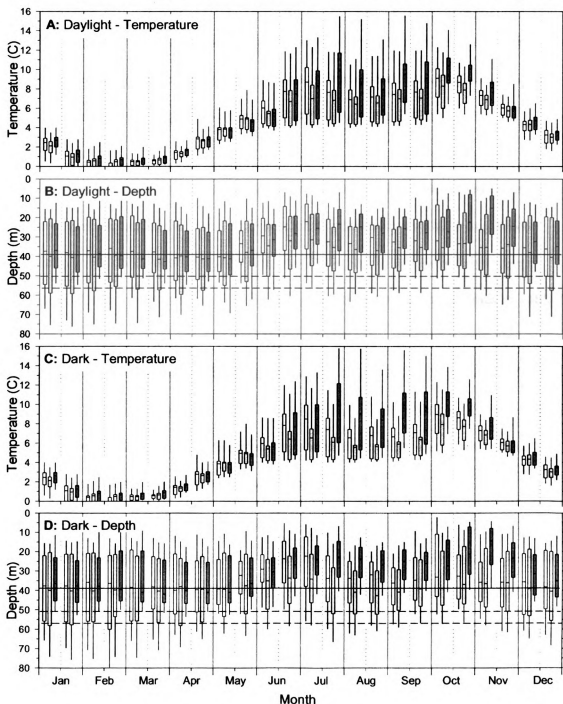
differences in depth can result in substantial differences in temperature if fish are located near the thermocline during summer stratification, the differences were less consistent than with temperature (Table 14). Judging from the relative size of the  $P$  values, the underlying data were also considerably more variable. The largest differences between lake whitefish and FLO lake trout occurred in late July, August, and early November, and with GLO lake trout in late July, early August, and early November (Table 14).

#### *Daylight versus dark*

In mixed model ANOVAs conducted separately by daylight and dark, temperatures occupied by GLO or FLO lake trout and lake whitefish differed in all comparisons ( $P < 0.001$ ) (Table 15). The interaction of group with seasonal period was significant ( $P = 0.063$ ) only in the comparison of temperature between lake whitefish and FLO lake trout at night. The interaction terms in all other comparisons of temperature were not significant ( $P > 0.67$ , Table 15).

In mixed model ANOVAs conducted separately by daylight and dark, comparisons of depths occupied between GLO or FLO lake trout and lake whitefish were all different ( $P < 0.01$  to  $P < 0.001$ ) (Table 15). The interaction of group with seasonal period was not significant in any of the depth comparisons ( $P > 0.67$ , Table 15).

**Fig. 10.** Frequency of hourly mean temperatures and hourly median depths by half-month interval during daylight (sunrise to sunset) and dark (excludes twilight) for Great Lakes origin lake trout (white fill), Finger Lakes origin lake trout (light-gray fill), and lake whitefish (dark-gray fill) in Lake Huron during 2002-2005. In the box plots, the horizontal line indicates the mean or median, the box the 25<sup>th</sup> and 75<sup>th</sup> percentiles, and the whiskers the 10<sup>th</sup> and 90<sup>th</sup> percentiles. Horizontal lines in panels B and D show modes for depths of tribal gill net effort in 2003-2005 (solid) and 2006-2007 (dashed). Effort data was provided by the Chippewa Ottawa Resource Authority, Sault Ste. Marie, Michigan.



### **Potential for reduced bycatch through depth restrictions of net gear**

Seasonal differences in the distributions of lake whitefish and lake trout exist in Lake Huron, but are those differences large enough to spatially separate the species and be useful in reducing bycatch? In the context of this question, differences in means become less important than the range of depths occupied. Comparison of the depth distributions (Fig. 10) indicated specific seasonal intervals existed when separation in depth could be potentially useful to fishery regulation. The most pronounced separation occurred during dark from mid-July through mid-September and again in November (Fig. 10).

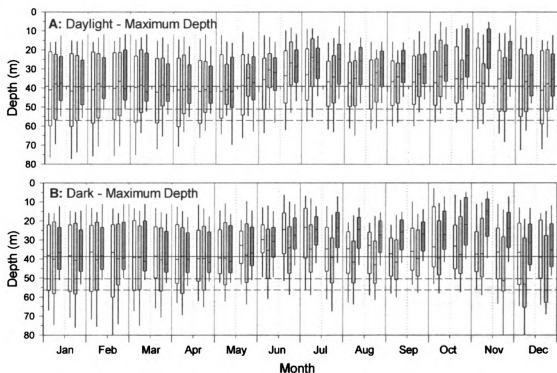
The cumulative percent frequency of observations with depth indicated the proportion of lake whitefish, and of GLO and FLO lake trout, potentially available to gill nets relative to a maximum depth limit for net sets (Table 16). From early July through November, fishing to a depth of 25 to 35 m (indicated by the horizontal lines in Table 16) could target half the lake whitefish population. At the same time, relatively low percentages of lake trout would be targeted—most notably in late July (GLO = 8% and FLO = 11%) and early August (GLO = 4% and FLO = 7%) (Table 16). Even at depths where 75% of the lake whitefish distribution is included in July-early September, only about 25% of lake trout would be targeted in most cases.

These data (Fig. 10-11; Table 16), suggest that depth regulations might be used to reduce lake trout bycatch by fishing depths that would target the median depth occupied by lake whitefish while avoiding 75% or more of the lake trout. This approach would

**Table 13.** Least-square means (LSM) of individual fish means for temperature (°C) occupied by Great Lakes origin (GLO) and Finger Lakes origin (FLO) lake trout and by lake whitefish (LWF) in Lake Huron by half-month interval from a mixed-model ANOVA and the results of post-hoc comparisons (Tukey *t*-tests) between origins within each interval.

Half month	LSM (°C)			FLO - GLO				FLO - LWF				GLO - LWF			
	FLO	GLO	LWF	Δ LSM	df	<i>t</i>	<i>P</i> >   <i>t</i>	Δ LSM	df	<i>t</i>	<i>P</i> >   <i>t</i>	Δ LSM	df	<i>t</i>	<i>P</i> >   <i>t</i>
Jan	2.1 1.0	2.7 1.2	3.2 1.9	-0.5 -0.2	14 14	-0.47 -0.20	0.64 0.84	-1.1 -0.9	133 145	-1.76 -1.52	0.08 0.13	-0.6 -0.7	19 19	-0.47 -0.60	0.65 0.56
Feb	0.6 0.5	0.5 0.4	1.4 1.2	0.2 0.1	14 14	0.14 0.11	0.89 0.92	-0.8 -0.7	148 149	-1.29 -1.17	0.20 0.24	-1.0 -0.9	19 19	-0.80 -0.72	0.43 0.48
Mar	0.4 0.7	0.5 0.7	1.2 1.3	0.0 0.0	14 14	-0.03 0.00	0.98 0.99	-0.7 -0.6	148 145	-1.16 -1.03	0.25 0.30	-0.7 -0.6	19 19	-0.58 -0.54	0.57 0.59
Apr	1.3 2.6	1.3 2.6	2.0 3.0	-0.1 0.0	14 14	-0.06 0.00	0.96 0.99	-0.7 -0.4	139 135	-1.12 -0.72	0.27 0.47	-0.6 -0.4	18 18	-0.53 -0.38	0.60 0.71
May	3.9 4.8	3.6 4.9	3.9 5.0	0.2 0.0	13 12	0.21 -0.03	0.84 0.97	-0.1 -0.1	144 123	-0.14 -0.24	0.89 0.81	-0.3 -0.1	16 15	-0.27 -0.08	0.79 0.93
Jun	5.3 6.5	5.9 7.2	5.9 7.8	-0.6 -0.7	12 12	-0.55 -0.70	0.59 0.50	-0.6 -1.3	105 105	-1.19 -2.47	0.24 0.02	0.0 -0.6	14 14	-0.03 -0.49	0.97 0.63
Jul	7.0 6.5	8.4 7.6	9.0 10.2	-1.4 -1.1	12 12	-1.29 -1.05	0.22 0.31	-1.9 -3.7	112 118	-3.61 -6.87	0.001 <0.001	-0.6 -2.6	15 15	-0.50 -2.31	0.62 0.04
Aug	5.9 6.0	7.3 8.3	9.3 8.7	-1.4 -2.3	13 13	-1.28 -2.08	0.23 0.06	-3.3 -2.7	131 142	-5.98 -4.69	<0.001 <0.001	-2.0 -0.4	16 16	-1.72 -0.36	0.11 0.72
Sep	6.4 6.8	8.9 10.7	9.5 9.6	-2.5 -3.9	14 15	-2.30 -3.46	0.04 0.01	-3.1 -2.9	157 175	-5.31 -4.74	<0.001 <0.001	-0.6 1.1	17 19	-0.49 0.90	0.63 0.38
Oct	8.0 7.6	9.5 8.9	10.8 10.7	-1.5 -1.3	11 11	-1.00 -0.89	0.34 0.39	-2.8 -3.0	185 194	-4.58 -4.90	<0.001 <0.001	-1.3 -1.7	13 13	-0.88 -1.13	0.40 0.28
Nov	6.9 5.9	7.4 6.1	8.9 6.9	-0.5 -0.3	11 11	-0.34 -0.18	0.74 0.86	-1.9 -1.1	189 174	-3.13 -1.76	0.002 0.08	-1.4 -0.8	13 13	-0.94 -0.53	0.37 0.60
Dec	4.6 3.1	4.4 3.3	5.7 4.4	0.3 -0.2	11 11	0.18 -0.14	0.86 0.89	-1.1 -1.3	169 161	-1.79 -2.10	0.08 0.04	-1.4 -1.1	13 13	-0.89 -0.71	0.39 0.49

**Fig. 11.** Frequency of hourly maximum depths by half-month interval during daylight (sunrise to sunset) and dark (excludes twilight) for Great Lakes origin lake trout (white fill), Finger Lakes origin lake trout (light-gray fill), and lake whitefish (dark-gray fill) in Lake Huron during 2002-2005. In the box plots, the horizontal line indicates the mean or median, the box the 25<sup>th</sup> and 75<sup>th</sup> percentiles, and the whiskers the 10<sup>th</sup> and 90<sup>th</sup> percentiles. Horizontal lines in panels B and D show modes for tribal gill net effort in 2003-2005 (solid) and 2006-2007 (dashed). Effort data was provided by the Chippewa Ottawa Resource Authority, Sault Ste. Marie, Michigan.



appear to particularly protect FLO lake trout. If observations from the archival tags could be directly converted to estimates of vulnerability, as in Table 16, restrictions variable by month specifying the maximum depth gear could be fished would be a valuable tool for management to reduce bycatch of the commercial fishery. The distribution of hourly median depths from tagged fish did not match the depth-effort data provided by the Chippewa-Ottawa Resource Authority (Fig. 10). During daylight in June through November, less than 25 percent of lake whitefish were as deep as the

**Table 14.** Least-square means of median depths (m) occupied by Great Lakes origin (GLO) and Finger Lakes origin (FLO) lake trout and by lake whitefish in Lake Huron by half-month interval from a mixed-model ANOVA and the results of post-hoc comparisons (Tukey *t*-tests) between origins within each interval; Bonferroni corrections were not applied.

Half month	LSM (m)			FLO minus GLO			FLO minus LWF			GLO minus LWF					
	FLO	GLO	LWF	Δ LSM	df	t	P>  d	Δ LSM	df	t	P>  d	Δ LSM	df	t	P>  d
Jan	41.4	37.2	34.1	4.2	159	0.94	0.35	7.3	525	1.83	0.07	3.1	224	0.61	0.54
	41.2	38.6	35.4	2.6	165	0.58	0.56	5.8	547	1.44	0.15	3.2	238	0.63	0.53
Feb	40.7	37.3	34.8	3.4	166	0.76	0.45	5.9	562	1.45	0.15	2.5	242	0.49	0.63
	40.5	36.6	34.3	4.0	164	0.89	0.38	6.3	576	1.55	0.12	2.3	241	0.46	0.65
Mar	40.2	34.8	34.2	5.4	160	1.22	0.23	6.0	588	1.50	0.13	0.6	237	0.13	0.90
	40.8	35.2	35.3	5.6	154	1.27	0.21	5.5	598	1.39	0.16	0.0	229	-0.01	0.99
Apr	40.6	35.8	35.7	4.8	151	1.10	0.27	4.9	600	1.26	0.21	0.1	221	0.03	0.98
	38.4	36.0	36.3	2.4	143	0.57	0.57	2.1	593	0.55	0.58	-0.3	206	-0.07	0.95
May	35.1	32.3	36.4	2.8	132	0.68	0.50	-1.3	550	0.37	0.71	-4.1	183	-0.91	0.37
	35.6	33.8	34.7	1.7	118	0.44	0.66	0.9	479	0.26	0.80	-0.8	157	-0.2	0.84
Jun	36.7	29.8	32.2	6.9	107	1.82	0.07	4.5	422	1.36	0.18	-2.5	142	-0.59	0.55
	33.8	28.5	28.1	5.3	101	1.41	0.16	5.7	416	1.73	0.08	0.4	138	0.09	0.93
Jul	30.6	24.3	26.4	6.3	106	1.65	0.10	4.2	444	1.24	0.22	-2.1	150	-0.5	0.62
	37.0	36.9	25.1	0.1	111	0.02	0.98	11.9	458	3.45	0.001	11.8	158	2.72	0.01
Aug	38.8	36.5	28.8	2.4	115	0.59	0.56	10.0	492	2.81	0.005	7.7	168	1.72	0.09
	39.2	32.9	30.3	6.3	121	1.55	0.13	8.9	515	2.44	0.015	2.6	177	0.58	0.57
Sep	37.0	33.6	30.6	3.5	126	0.82	0.41	6.4	546	1.70	0.09	3.0	188	0.63	0.53
	36.1	26.9	30.6	9.2	115	2.09	0.04	5.5	583	1.40	0.16	-3.7	175	-0.75	0.46
Oct	33.7	24.7	28.3	9.1	67	1.93	0.06	5.4	595	1.37	0.17	-3.6	100	-0.69	0.49
	29.9	28.2	22.8	1.8	75	0.37	0.71	7.1	610	1.75	0.08	5.3	111	0.99	0.32
Nov	32.0	33.6	18.9	-1.6	79	-0.32	0.75	13.1	590	3.23	0.001	14.7	114	2.72	0.01
	33.1	31.7	23.8	1.4	81	0.29	0.77	9.3	536	2.31	0.02	7.9	111	1.46	0.15
Dec	37.7	34.0	30.9	3.7	79	0.76	0.45	6.8	516	1.70	0.09	3.1	108	0.58	0.57
	39.3	34.9	32.2	4.3	73	0.89	0.38	7.1	502	1.77	0.08	2.8	102	0.52	0.61

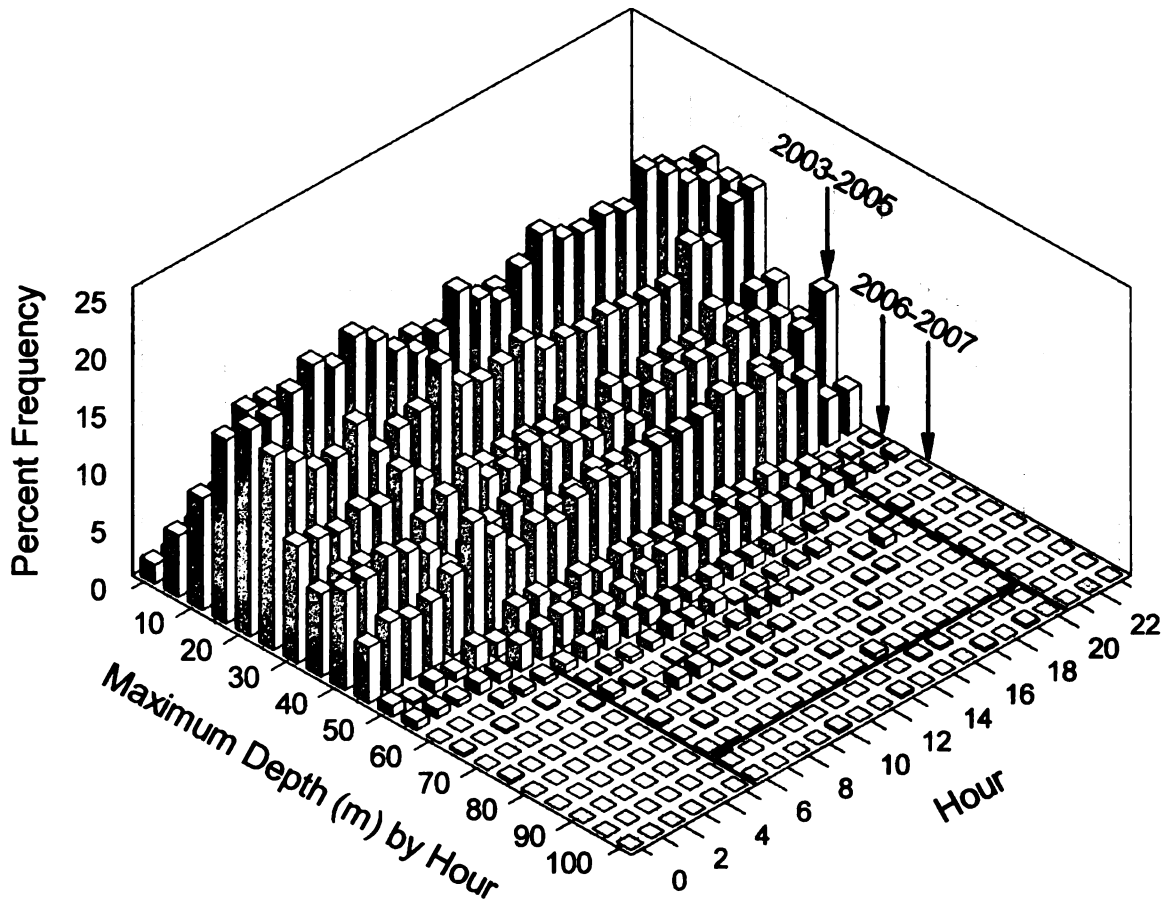
**Table 15.** Results of mixed-model ANOVAs assessing differences by light condition (daylight or dark) in the mean temperatures (Temp) and median depths (Depth) occupied in Lake Huron during 2002-2005 by lake trout of two genetic origins, upper Great Lakes origin (GLO) and Finger Lakes, New York origin (FLO), and lake whitefish LWF. Data were recorded with archival tags. The main effects were: Group (GLO vs. LWF or FLO vs. LWF), Period (half-month seasonal periods), and the interaction of Group and Period.

Light Condi- tion	Depen- dent variable	Fixed effect	df	<i>F</i>	<i>P</i> > <i>F</i>
<b>GLO lake trout vs. lake whitefish</b>					
Daylight	Temp	Group	1, 63.2	34.12	<.001
		Period	23, 62.5	21.77	<.001
		Group*Period	23, 62.5	0.55	0.94
	Depth	Group	1, 30.9	7.38	0.01
		Period	23, 30.9	2.14	0.03
		Group*Period	23, 30.9	0.56	0.71
Dark	Temp	Group	1, 50.6	45.26	<0.001
		Period	23, 49.5	24.57	<0.001
		Group*Period	23, 49.5	0.86	0.67
	Depth	Group	1, 30.4	15.83	<0.001
		Period	23, 30.4	2.56	0.01
		Group*Period	23, 30.4	0.82	0.68
<b>FLO lake trout vs. lake whitefish</b>					
Daylight	Temp	Group	1, 51.9	57.07	<0.001
		Period	23, 51.6	22.11	<0.001
		Group*Period	23, 51.6	0.84	0.67
	Depth	Group	1, 73.6	30.55	<0.001
		Period	23, 73.2	2.05	0.01
		Group*Period	23, 73.2	0.43	0.99
Dark	Temp	Group	1, 52.6	83.08	<0.001
		Period	23, 52.3	24.75	<0.001
		Group*Period	23, 52.3	1.67	0.06
	Depth	Group	1, 71.2	45.56	<0.001
		Period	23, 70.8	1.94	0.02
		Group*Period	23, 70.8	0.57	0.93

modal depth of effort in 2003-2005. Hence, it would appear that gear was set deeper than most of the occupied depths recorded by the tags in lake whitefish. At night the percentage was even smaller, approaching 10 percent during some seasonal intervals. In 2006-2007, the modal depth for gill net effort was even deeper than in 2003-2005 and deeper even than the 90<sup>th</sup> percentile for hourly median depths of lake whitefish (Fig. 10). The distributions of the hourly maximum depths occupied by lake whitefish (Fig. 11) differ only slightly from the distributions of hourly median depths (Fig. 10) and also failed to match the reported depths of gill net effort.

The hourly distribution of maximum depths in early August by 5-m depth interval (Fig. 12) showed a pattern of diel movement which might explain the difference between the modal depth of gill net effort and the depth distribution of lake whitefish based on the archival tag data (Fig. 10-11). During daylight, a higher frequency of observations occurred at the outer range of the lake whitefish depth distribution than at night (Fig. 12). During dark, 1.9% of observations were in the 46- to 50-m depth range, compared to 7.3% during daylight. The lower percentage at night indicates that a group of fish must be moving, either horizontally or vertically, in and out of deep waters in a diel pattern. The archival tags lacked a means to establish horizontal position, so it was not possible to say which direction of movement was responsible for the pattern.

**Fig. 12.** Percent frequency of observations of maximum depth for combinations of individual lake whitefish, day, and hour during the first half of august 2003-2005. Percents add to 100% within each hour. The area between the lines at 05:30 and 20:30 is the approximate period of daylight. Arrows show the modal depths for tribal gill net effort during the study and the following two years.



## Discussion

### Ecological factors affecting depth and temperature distributions

Lake whitefish and lake trout are both native residents of the Great Lakes, yet seasonally show clear differences in depth and temperature distributions (Fig. 10). From a review of the literature, Christie and Regier (1988) listed ranges for laboratory studies of

**Table 16.** Cumulative percent frequency by half-month interval and upper limits of 5-m depth intervals for Finger Lakes origin (FLO) lake trout, Great Lakes origin (GLO) lake trout, and lake whitefish (LWF) in Lake Huron, based on maximum depths observed with archival tags for combinations of individual fish and hour during 2003-2005.

Depth (m)	Early July			Late July			Early August			Late August			Early September		
	GLO	FLO	LWF	GLO	FLO	LWF	GLO	FLO	LWF	GLO	FLO	LWF	GLO	FLO	LWF
5	3	1	3	3	0	0	3	0	3	3	0	0	3	0	0
10	5	3	4	3	0	5	3	0	7	3	0	3	3	0	3
15	14	3	4	3	0	11	3	1	12	3	0	3	3	1	3
20	19	5	11	3	1	16	3	2	28	4	2	7	3	3	8
25	29	7	29	4	4	34	4	7	48	4	6	21	3	8	20
30	37	11	46	8	11	48	11	9	64	10	13	33	3	13	39
35	43	18	61	15	17	58	20	13	68	16	18	52	8	15	58
40	48	25	68	23	20	69	27	18	80	32	22	62	21	22	69
45	59	33	80	35	26	79	34	25	89	44	25	76	34	27	78
50	63	37	87	45	34	90	49	35	94	47	30	85	42	34	91
55	72	44	93	55	39	94	59	43	97	54	39	89	48	49	97
60	82	58	99	60	49	96	64	55	98	66	53	94	61	59	99
65	85	66	100	74	58	97	72	63	100	73	68	96	72	68	99
70	88	73		79	65	98	80	69		78	76	99	79	79	100
75	93	79		81	71	99	85	78		79	81	100	84	85	
80	94	85		83	76	99	85	81		81	86		88	86	
85	95	87		89	82	99	91	85		86	88		89	89	
90	97	89		91	82	100	91	85		89	90		90	91	
95	98	90		93	84		93	89		90	92		94	93	
100	98	91		94	85		93	95		92	92		95	94	
105	100	92		97	86		94	96		94	94		97	95	
110		92		97	87		94	97		95	95		97	97	
>115		100		100	100		100	100		100	100		100	100	

**Table 16. Continued.**

Depth (m)	Late September			Early October			Late October			Early November			Late November		
	GLO	FLO	LWF	GLO	FLO	LWF	GLO	FLO	LWF	GLO	FLO	LWF	GLO	FLO	LWF
5	4	0	0	5	1	0	0	0	0	0	0	8	0	0	0
10	4	0	5	8	2	8	1	1	18	1	1	23	0	0	7
15	4	2	6	11	5	21	8	4	23	5	5	30	2	5	8
20	5	3	8	14	7	24	12	12	30	6	10	33	12	12	12
25	12	10	23	18	18	32	13	18	37	12	18	43	13	16	23
30	19	16	35	21	22	39	13	29	50	21	26	48	15	19	39
35	25	22	50	25	27	54	29	35	61	31	31	58	25	28	53
40	33	25	59	32	30	64	39	37	70	37	37	69	40	31	66
45	44	30	75	37	38	75	50	41	77	44	42	81	42	39	84
50	55	39	88	52	46	81	62	50	87	60	53	84	54	51	88
55	65	51	93	58	54	90	72	60	89	68	60	90	58	59	93
60	75	62	98	72	63	96	79	69	91	76	70	98	65	66	96
65	83	73	98	81	74	97	88	75	92	78	80	100	70	74	96
70	89	78	99	82	84	97	90	81	92	84	87		75	80	96
75	90	83	100	88	89	97	93	88	92	86	89		81	81	96
80	91	88		89	93	97	95	91	94	91	92		89	89	99
85	92	89		97	95	97	97	91	97	95	93		91	92	99
90	93	92		98	96	97	99	92	100	100	95		93	96	100
95	95	95		98	96	98	100	93			95		94	98	
100	98	97		98	98	98		97			95		95	98	
105	98	98		98	98	100		97			95		99	99	
110	98	100		98	98			98			95		99	99	
>115	100			100	100			100			100		100	100	

temperature preference of lake whitefish of 12.7 to 13.5°C (ignoring one value of 14 °C they reported from a study of larval lake whitefish) and optimal temperatures for growth of 12 to 15.1°C. For lake trout, the values listed were 10.8 to 12.7 °C and 10 to 16 °C. As discussed in Chapter Two, lake trout were rarely found at those temperatures and were likely responding to other variables. Similarly, lake whitefish were rarely found between 12.7 and 13.5°C at any time of year (Fig. 10). In July-September, when strong thermal stratification is in place in Lake Huron and behavioral thermoregulation is possible, the mean temperatures occupied by lake whitefish ranged from 8.7 to 10.2 °C, about two degrees lower than laboratory values. The most likely causes of a separation in depth or temperature are related to differences in diet and separation of prey items, and more speculative issues related to life history and evolution of temperature preferences.

Diet and food availability might be the most important variables currently controlling depth distributions of lake trout (Chapter Two) and lake whitefish. Despite the importance of lake whitefish as a commercial species in the Great Lakes for more than a century, the best diet information is recent and related to changes in their diet in Lake Michigan—believed to be the result of changes in the food web caused by the invasion of Dreissenid mussels (Pothoven 2005). Similar changes in food webs have occurred in Lake Huron (Nalepa *et al.* 2007) and elsewhere in the Great Lakes (Hecky *et al.* 2004); hence, the data of Pothoven (2005) are likely indicative of current diets in Lake Huron. Except for one group of unusually large lake whitefish sampled in northwestern Lake Michigan in 2002-2005, fish were a rare item in the diet of lake

whitefish (Pothoven 2005). Lake whitefish were predominantly benthivores, with Dreissenid mussels recently becoming a prominent part of their diet. By comparison, lake trout in Lake Huron are primarily piscivores (Fig. 8 in Chapter Two). Differences in diet undoubtedly have affected, and continue to affect, the relative depth and temperature distributions of lake trout and lake whitefish.

The food web has changed throughout most of the Great Lakes due to effects of phosphorus reductions and interception of nutrients by invasive Dreissenid mussels (Hecky *et al.* 2004). The disappearance of *Diporeia* spp., formerly a key food item of lake whitefish has been notable in several lakes (Nalepa *et al.* 2007). The recent offshore movement of the commercial fishery for lake whitefish was thought to relate to these changes in the food web (Mohr and Ebener 2005). Increasing dependence on Dreissenid mussels would shift the lake whitefish distribution closer to the depth of greatest density of quagga mussels (*Dreissenia bugensis*), the more abundant and deeper ranging of the Dreissenids. Quagga mussels were most abundant in 2003 at depths of 31-50 m (Nalepa 2007), consistent with modes of gill net effort in the tribal fisheries (Fig. 10-11). In this study, the least-square mean depths occupied by lake whitefish were generally around 30 m at the lower end of that depth range (Table 14). Key changes in the prey base of lake trout in Lake Huron (Chapter Two) that might also have influenced their depth distribution were the reduced importance of rainbow smelt (*Osmerus mordax*) in the diet, the disappearance of alewife (*Alosa pseudoharengus*) a former important diet item, and the appearance of a new prey item, the invasive and demersal round goby (*Neogobius melanostomus*). During the period of this study, the

depth distribution of round gobies peaked at 37 m (Edward Roseman, USGS, Great Lakes Science Center, unpublished data), similar to the least-square mean depth for lake trout in late summer (Chapter Two; Table 16). The depths of both lake whitefish and lake trout are consistent with recent measures of the distributions of their major prey items, lending support to a hypothesis that prey availability and distribution is an important variable affecting lake whitefish and lake trout depth distributions.

Innate differences arising from post-glacial evolution undoubtedly exist in the behavior of lake whitefish to fill a niche as a short-lived planktivore/benthivore, and of lake trout to fill a niche (primarily) as a long-lived piscivore. As suggested by Larsson (2005), species regularly encountering low prey availability might evolve to occupy lower temperatures and maximize efficiency of using food resources. As a long-lived predator facing variation in both year-class strength and variability in prey availability in the Great Lakes, lake trout might favor low temperatures and deep water more than a lake whitefish, which feeds on a more consistent diet of benthos and zooplankton (Pothoven 2005). Lake whitefish can feed either on plankton or benthos, but shift mainly to benthos if lake herring (*C. artedii*) are present (Carl and McGuinness 2006). Lake herring historically supported the largest commercial fishery catch in Lake Huron, with lake whitefish making up only 35 % of the total catch. Lake herring have been decreasing in abundance in the main basin of Lake Huron since 1970 (Ebener and Mohr 2005) and currently are uncommon. Since the disappearance of lake herring, plankton could be an increased part of the lake whitefish in Lake Huron diet. But because plankton abundance is low in the hypolimnion, feeding on plankton in metalimnion or

epilimnion would be expected to result in a decrease in depth and increase in temperature, which is contrary to the results presented in this chapter.

### **Diel movement and availability**

Availability is one of the key variables governing catch per effort. Marr (1951) defined availability as “variations in catch not associated with abundance or fishing intensity, but rather with variations in environmental factors.” The effect of those environmental factors is to change the distribution of a population over time, such that the proportion located in areas where they are vulnerable to the fishing gear changes. Because his definition focuses on variation in catch, the concepts of spatial availability are connected to vulnerability. To be spatially available to gill nets, lake whitefish must be within the range of bottom depths fished and within a distance from bottom covered by the height of the net. The distributions of lake whitefish based on archival tag data (Fig. 10-11; Table 16) suggested that larger catches of lake whitefish and less bycatch of lake trout could be achieved by fishing shallower bottom depths than are currently targeted by tribal gill net fisheries. This would be true if all lake whitefish were closely associated with bottom. The distribution of gill net effort realized in the fishery is a result of trial and error by the fishers and it seems highly unlikely that they would fish in deep waters, and bypass a high density of fish if they could be caught closer to shore in shallower waters. A more likely situation is that the population of lake whitefish is dispersed horizontally over a broad range of depths with a large portion suspended at some distance above the bottom. Considering the small portion of the distribution at depths consistent with the bottom depth being fished with gill nets, most of that

population might be suspended. In that case, the potential benefits for decreasing bycatch in Table 16 would be exaggerated unless an approach to fishing gill nets at controlled depths above the bottom were employed. The potential cause for the lack of discovery of this distribution by the commercial fishery could be due to the difficulty in setting suspended nets well off the bottom.

The apparent pattern of diel movement from shallow to deep waters in daylight (Fig. 12) might also partially explain the depth range being fished. To be caught in passive gear like a gill net, a fish must move to intersect the gear. Because no information exists on geographical position of the tagged fish, it is unclear whether the movement observed (Fig. 12) was a local descent to the bottom by a group of fish remaining in the same general location or an oblique movement up and down the slope along bottom by a group of fish that remains within the height of the gill nets. In the case of vertical movement, random foraging movements would result in capture during the time spent near bottom, which is during daylight, inconsistent with the general belief that gill nets primarily catch at night. In the case of movement along the slope, movement would be directional between depths, and near the bottom, where fish might be intercepted by gill nets. Intercepting such a movement could be particularly effective if nets were not oriented directly down the slope. Catch in this case could occur in twilight or darkness, when fish are leaving from, or returning to, shallower depths. In either case, based on the analysis presented here, a relatively small proportion of the population was using the depths being fished and providing the catch to the fishery (Fig. 12).

Day and night bottom and midwater trawl catches made along contour during 2004 and 2005 at depths of 30, 60, and 120 m in the Apostle Islands area of Lake Superior provide evidence that diel movements up and down the slope occur (Yule *et al.* 2008). Bottom trawls fished at 30 m during the night caught a wide range of lengths of lake whitefish. At the same depth during the day only a few small and no large lake whitefish were caught (Yule *et al.* 2008). At 60 m, trawls caught primarily large lake whitefish (> 300 mm) at night in contrast to primarily small lake whitefish during the day. The implication is that movement between those depths occurs between day and night. Using the Lake Huron archival tag data presented here, vertical versus horizontal movement could not be ruled out. The relative catches in day and night bottom trawls in Lake Superior (Yule *et al.* 2008) and previous nighttime acoustic and midwater trawl surveys at the same sites and years (reported in greater detail by Yule *et al.* 2007), showed that few lake whitefish were pelagic (Yule *et al.* 2008). This suggests that lake whitefish moved up and down the slope and were associated with bottom. Yule *et al.* (2008), however, did not comment on the possibility of suspension of lake whitefish during the day, as suggested by the archival tag data of the present study (Fig. 12). The slope in the Apostle Islands area of Lake Superior is steeper and the distances associated with a change in depth less than is typical in northern Lake Huron and these may be variables that could cause differences in the lake whitefish behavior between the two lakes.

### **Management recommendations**

A number of management actions have been adopted in Lake Huron to regulate gear type and use to restrict bycatch or reduce mortality of lake trout (Brown et al 1999). Since the late 1970s, the State of Michigan has banned large-mesh gill nets and has only permitted the use of trap nets (Brege and Kevern 1978). Under the year 2000 consent decree governing fishing in 1836 treaty waters, the tribes agreed to fish only trap nets south of the Hammond Bay Refuge Harbor, which includes Hammond Bay (U.S. District Court 2000). All lake trout caught in trap nets must be released. Dead lake trout not retained by the gill-net fishery would be wasted, and a quota was set for retention by the tribal gill-net fishery. Because lake trout are the principal bycatch in gill nets set to capture lake whitefish (McNeil and deLaplante 1989; Johnson *et al.* 2004a), managers in Lake Huron conducted studies to examine both the survival of fish released after capture and ways to minimize bycatch (Johnson *et al.* 2004b).

The number retained or discarded dead was measured in 260 monitored gill net and 96 trap net lifts in the Hammond Bay area in 1998 and 1999 (Johnson *et al.* 2004b). In both gear types, the ratio of lake trout to legal lake whitefish was highest in summer and lowest in fall. Bycatch mortality expressed as lake trout killed per lift was highest in spring for gill nets and in the summer for trap nets. The fates of lake trout collected from Lake Huron trap nets for use in Chapter One were used to assess delayed mortality of lake trout released alive from the Lake Huron trap net fisheries. Only three of 186 lake trout taken from trap nets and transported to the HBBS, implanted with archival tags, and held for a day before release did not survive the transport and handling resulting in an estimate of only 1.6% delayed mortality for fish taken alive from the trap

net pot (Johnson *et al* 2004b). Even though percent mortality of lake trout released from trap nets was low, the number caught can be seasonally high and hence the catch in gill nets and trap nets can make an important contribution to total mortality. Using rates for losses from gill nets and trap nets in the study, Johnson *et al.* (2004b) estimated that 10 150 kg of lake trout would be killed in a gill net fishery catching 100 000 kg of lake whitefish and 4 900 kg in a 345 00 kg trap net fishery. Either loss was deemed substantial.

One management option to reduce losses to bycatch would be to switch entirely to trap nets. However, tribal fishers are afforded the right to use gill nets under the year 2000 consent decree (U.S. District Court 2000) and therefore this strategy is not viable unless tribal fishers choose independently to do so. A second option is to reduce fishing effort, but the lake whitefish population in Lake Huron is strong and restricting effort is not needed to protect stocks (Ebener 1997). The most palatable means to reduce bycatch was to redirect effort toward seasons and depths where fishing is economically feasible and the overlap of lake whitefish and lake trout distributions is small. Based on results from Johnson *et al.* (2004b), a limited small-boat gill net fishery was permitted October 1 through November 8, and again in December in Hammond Bay south of the regular boundary for gill nets.

The data presented here and in Chapter 2 suggest that depth distributions of lake trout and, most likely, lake whitefish have changed since 1999 and that the benefits of seasonal and depth restrictions should be reexamined. From early July through

November, fishing at a depth between 25 to 35 m could target 50% of the lake whitefish population while exposing less than 25% of the lake trout populations to the fishery (Fig. 10-11; Table 16). However, concern remains that the measures of depths from the archival tags may not have distinguished between fish that are suspended versus those closely associated with bottom and vulnerable to gill nets. For lake trout, this issue is not a concern, because fish located deeper than gill net sets would not be available to those nets regardless of their vertical distribution. Viability of the depth and season regulations suggested above could be determined through an experimental fishery to answer whether lake whitefish could be caught in economically viable numbers at those depths, while avoiding lake trout.

Based on archival tag data (Fig. 10-12), a considerable portion of the lake whitefish population was located shallower in summer than the depths currently being fished with bottom-set gill nets, suggesting that lake whitefish may be predominately suspended. If lake whitefish are more pelagic in Lake Huron than previously thought, new opportunities for exploitation with suspended gill nets could exist—if a logistically feasible method of achieving that could be found. Suspended gill nets have been used in research to target pelagic coregonines (*e.g.*, Milne *et al.* 2005). In the Great Lakes, the lakewide assessment plan for Lake Michigan fish communities (Schneeberger *et al.*; available on the Great Lakes Fishery commission web site, <http://www.glfc.org/pubs/SpecialPubs/lwasses01.pdf>), gives specifications for the suspended gill nets being used to sample Chinook salmon and rainbow trout, although it is noted that the suspended nets are bulky, require a net reel, and may not be adaptable

to some commercial vessels. On suitable vessels, commercial use of suspended gill nets can be viable, as evidenced by their use in the late-fall fishery for herring roe on Lake Superior (Stockwell *et al.* in review).

Feasibility of this suggestion rests both on the depth distribution of lake whitefish and on their geographical distribution, which was not measured in this study. If pelagic lake whitefish are dispersed broadly, densities may be too low to support a fishery. Additional research would be required to determine whether there are concentrations of suspended lake whitefish spatially dense enough to support a commercial fishery.

#### **Use of archival tags**

The continuity of data collected with archival tags led to production of new types of information, such as the plots of the distributions of individuals in Fig. 10-12 and Table 16. Because records are not interrupted by fish going too deep or because of weather, as with conventional telemetry, complete data sets were available from release to recapture. The continual recording eliminates the uncertainties that exist in net captures, where the knowledge is limited to the presence of a fish in the area of a single trawl tow or over the duration of a gill-net set. Within the limitations of archival tag capabilities versus information needs, archival tags can provide much more complete and unambiguous descriptions of behavior than net surveys.

A further suggested use of these data is to improve models of fish behavior, growth, or food consumption into the more realistic form of an “Individual Based Model” or IBM. MacKay (1992) first used an IBM approach to improve the Kitchell and Breck (1980) and Kitchell (1990) models of sea lamprey feeding and host mortality. This model was further improved when Madenjian *et al.* (2003) incorporated more specific information on individual variability in sea lamprey growth (Bergstedt and Swink 1995) and seasonal temperatures occupied by lake trout hosts (Bergstedt *et al.* 2003). Similar improvements in models of fish growth and energy or prey requirements are possible using the data from Chapters Two and Three. Temperature is an important variable affecting metabolism and food conversion (Brett *et al.* 1969) and summary statistics can mask broad variation in thermal behavior (Fig. 10-11). It is now possible to create IBMs of growth and prey needs of lake whitefish and lake trout that incorporate the documented behavior from tagged individuals and relate that variation to documented weight, sex, and maturity at tagging and capture. Measures of observed growth of individual fish combined with a record of the temperatures they occupied while at large in the Great Lakes have not previously been available. The data in this dissertation should be exploited for this purpose.

Lake whitefish, in this study, were more susceptible to the stress of handling and tagging than lake trout. The poor return of lake whitefish tagged at the HBBS in 2002 suggested that lake whitefish were not capable of surviving the combined stresses of capture, transportation, surgical procedures, and release. As with lake trout (Chapter 2) the best approach was to tag them at the site of the trap net. This approach limited

tagging to days with light winds, but also minimized stress to lake whitefish caused by implantation of the tags. Minimizing stress will be critical to success with future lake whitefish studies using archival tags.

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