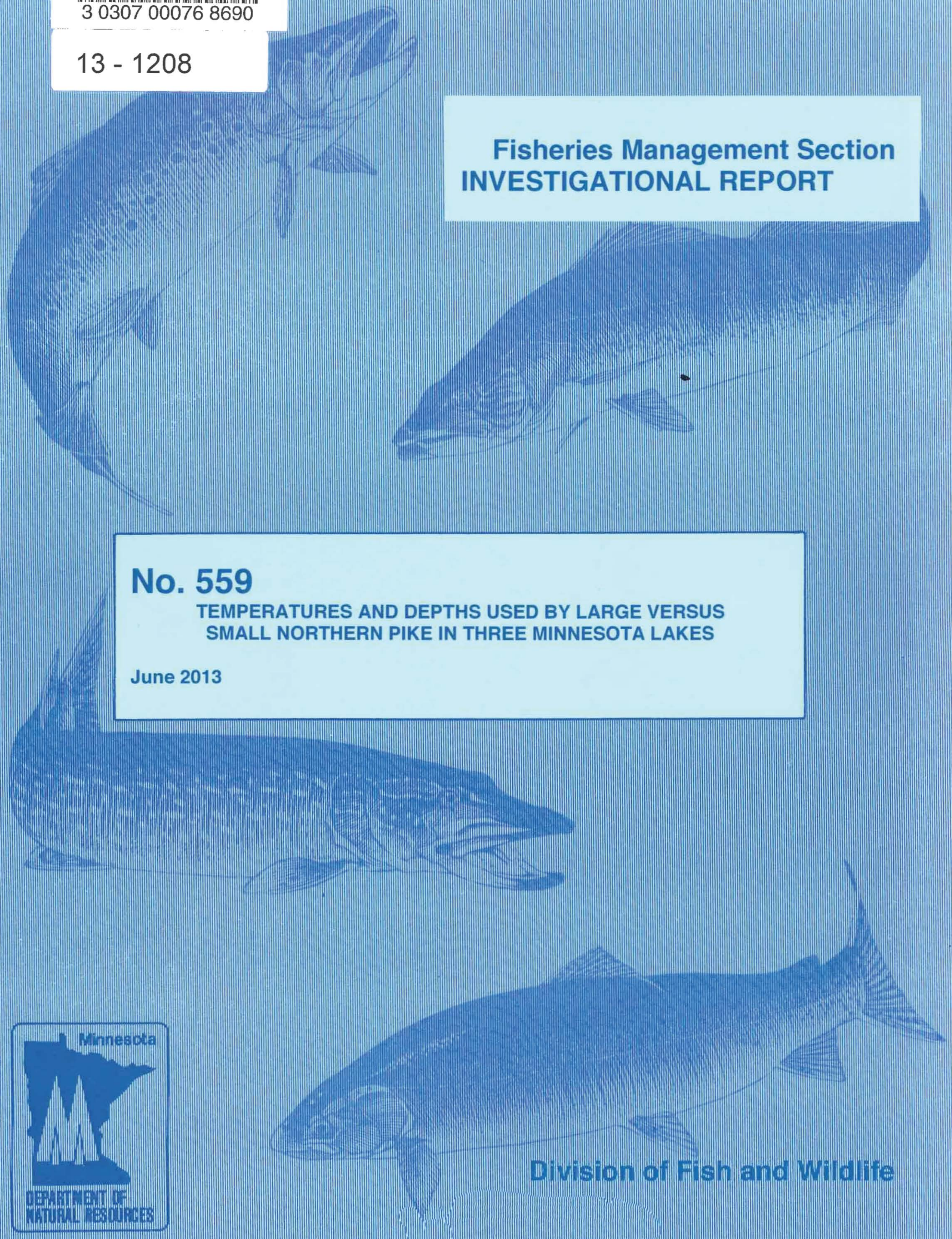

Fisheries Management Section
INVESTIGATIONAL REPORT

No. 559

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June 2013

Minnesota
DEPARTMENT OF NATURAL RESOURCES

Division of Fish and Wildlife

Minnesota Department of Natural Resources
Investigational Report 559, June 2013

TEMPERATURES AND DEPTHS USED BY LARGE VERSUS SMALL NORTHERN PIKE IN THREE MINNESOTA LAKES[1]

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Abstract.—We monitored depths and temperatures used by large versus small northern pike in three north-central Minnesota lakes with either acoustic telemetry or archival tags. Individual northern pike demonstrated flexibility in habitat use within a season and between years. The fish had some tolerance for low levels of dissolved oxygen but depth selection was generally constrained by low dissolved oxygen in summer and winter. The fish more fully exploited all available depths during cold water and thermal turnover periods. During the heat of the summer, large northern pike tended to follow the thermocline into deeper, cooler water as upper water layers warmed. Selection ratios indicated that large northern pike preferred water temperatures of 16°-21°C during August when temperatures up to 28°C were available. In two lakes providing dense overhead cover from water lilies in shallow water, small northern pike used warmer, shallower water compared to large fish during summer. In a third lake providing no such cover, small fish were more often in deeper, cooler water. For small northern pike, temperature seemed to be a secondary habitat consideration behind the presence of shallow vegetated cover. This study provided detailed temperature selection information that will be useful when considering temperature as an ecological resource for different sizes of northern pike.

[1] This project was funded in part by the Federal aid in Sport Fish Restoration (Dingell-Johnson) Program. Completion Report, Study 602, D-J Project F-26-R Minnesota.

The northern pike *Esox lucius* is valued principally as a sport fish in Minnesota and elsewhere, and provides a tremendous source of recreational fishing opportunities. Prior to the 1980s, the northern pike fishery was oriented primarily toward harvest of fish. During the 1980s and 1990s, an increasing number of anglers and fisheries managers were growing concerned about long-term declines in northern pike sizes and advocated for more special regulations designed to improve northern pike sizes or to manage for trophy fish (Pierce 2010). Minnesota now has 100 water bodies with slot length limits or high minimum length limits, and other states and provinces are also considering regulations designed to enhance populations of large northern pike. Evaluations of the effectiveness of these regulations depend on our understanding of habitat characteristics that help produce large northern pike. Furthermore, better information about habitat characteristics promoting good growth in large northern pike would have value in choosing future lakes for special regulations.

Recreational anglers and field biologists contend that large northern pike use deeper, colder habitats than small adult northern pike (Jacobson 1993; Diana 1996). Thermoregulatory behavior by the fish may serve to limit weight loss during the summer when surface water temperatures are too warm for good growth (Headrick 1985). In theory, shifts in preferred habitat could be related to shifts in temperature-linked metabolic processes that optimize growth at lower temperatures as fish attain greater mass, but shifts in thermal habitat may be difficult to decouple from intra-specific interactions (e.g. competition and cannibalism) or the availability of different types and sizes of prey fish. The primary issue, at present, is that shifts in thermal habitats used as northern pike grow to larger sizes have not been documented. Nor is it clear if thermal habitat constraints for large northern pike are extensive enough to limit the success of trophy fish management and development of fisheries containing larger sizes of northern pike.

Bioenergetics modeling is a tool that has become increasingly important for tracking the consequences of fisheries management activities to individual species as well as to fish communities. Combining energetics models with food web models can be an important step in understanding and forecasting how climate change will affect fish growth and population dynamics (Rose et al. 2008). Because they are top-level predators in fish communities, northern pike have the potential to heavily influence fish community-level energetic analyses. Assumptions about habitat use often underlie the thermal histories used in energetics models (Hartman and Kitchell 2008). If large differences in thermal habitat use by different sizes of northern pike exist, then size-based energy budgets should improve our ability to predict levels of predation on prey fishes and fish community dynamics.

Future management of northern pike throughout its circumpolar distribution may also be influenced by global climate change. According to climate change models, annual air temperatures in Minnesota will increase as atmospheric carbon dioxide levels rise, with increasing temperatures having consequences for thermal stratification and dissolved oxygen concentrations in lakes (Stefan et al. 1995). The magnitude of these effects on lakes depends on the lake's size, depth, and latitude, and the effects on fish such as northern pike are dependent on the temperatures they need to grow and persist (Stefan et al. 1995).

Better information about thermal habitat and depth preferences of different sizes of northern pike could clearly contribute to management aimed at restoring larger sizes of northern pike, to the development of more accurate bioenergetics models assessing northern pike population-level and community-level dynamics, and to more accurate projections of how climate change will influence northern pike populations, particularly large-sized fish. In this study, we monitored northern pike use of water depths and thermal habitat throughout the year in three natural temperate lakes. Our objective was to accurately measure how large and small northern pike selected water depths and temperatures in relation to available habitats in the lakes.

Study Lakes and Field Methods

Three natural lakes located in north-central Minnesota were selected for this study. Lakes were selected based on the presence of large northern pike and the availability of cool-water habitat during summer with enough dissolved oxygen to support northern pike. Therefore, in each of the lakes, northern pike could select from a wide range of available water temperatures that they could potentially use as habitat during the heat of the summer. Pillager Lake (46° 22' N latitude, 94° 29' W longitude) had a surface area of 83.0 ha and a maximum depth of 11.9 m. Little Wabana Lake (47° 24' N, 93° 30' W) had a surface area of 46.8 ha and maximum depth of 17.4 m. Shingobee Lake (47° 0' N, 94° 41' W) had a surface area of 62.4 ha and maximum depth of 12.2 m. All three lakes were second-order dimictic lakes having bottom temperatures well above 4°C in summer (Reid and Wood 1976). The primary difference in fish habitat among lakes was that Pillager and Shingobee lakes had more soft-bottom shoal areas, and therefore more extensive beds of shallow aquatic vegetation during summer than Little Wabana Lake. Shallow aquatic vegetation that was important in one or more of the lakes included wild rice *Zizania,* bulrush *Scirpus acutus*, cattail *Typha*, white water lily *Nymphaea odorata*, yellow pond lily *Nuphar variegatum*, muskgrass *Chara*, northern water milfoil *Myriophyllum exalbescens*, coontail *Ceratophyllum demersum*, bladderwort *Utricularia vulgaris*, naiad *Najas flexilis,* and several forms of pondweed *Potamogeton*. Soft-bottom shoal areas in Pillager and Shingobee lakes often had extensive surface coverage provided by water lily and pond lily pads whereas Little Wabana Lake had no lilies. These differences in shallow water vegetative habitat may be important for interpreting our results. Pillager and Shingobee lakes supported abundant cisco *Coregonus artedi* populations but Little Wabana Lake only had a trace population of cisco. The presence of cisco, a cold-water fish used as prey by northern pike, has been linked to catches of large-sized northern pike in Minnesota lakes (Jacobson 1993). Recreational fishing for northern pike occurred from mid May to the end of February in each lake, but the only lake with public access was Pillager Lake; the other lakes had private accesses and minimal exploitation of northern pike.

Temperatures and depths used by small versus large northern pike were monitored using either acoustic telemetry or archival tags. In Pillager and Little Wabana lakes, fish temperatures and depths were obtained using acoustic transmitters. The transmittters (V13TP; Vemco Ltd., Halifax, Nova Scotia[1]) sent coded acoustic pings to fixed station hydrophones (Vemco VR2 and VR2W) submerged in the lakes. The temperature and pressure sensing acoustic transmitters operated at 69 kHz and sent coded pings of sensor data at an average delay time of 4 minutes in Pillager Lake and 2 minutes in Little Wabana Lake. Transmitters were 45 mm in length, 13 mm in diameter and weighed 6 g in water and 12 g in air. Transmitters in Pillager Lake had only a temperature range of 0-20°C, so measurements of warmer temperatures were not obtained. In Little Wabana Lake, however, transmitters were capable of measuring temperatures up to 40°C, thus providing a more complete set of fish temperature data.

Northern pike were trap netted in Pillager Lake during April 2009 as the ice was receding from the lake and fish were staging for spawning. Transmitters were surgically implanted through abdominal incisions in five small females (487-607 mm total length), one small male (537 mm), three large females (827-1020 mm), and one large male (730 mm). Fish implanted with transmitters were not weighed, but weights from other trap-netted northern pike were used to develop a length-weight regression for predicting weights of fish implanted with transmitters. Predicted weights for northern pike with transmitters were 675-1,265 g for the small fish and 2,145-5,580 g for the large fish. Therefore, the transmitter weight in air accounted for 0.2%-1.8% of fish body weight in air. Survival of fish with transmitters in Pillager Lake was poor due to unrestricted access by recreational fishers. Only five fish survived to January 2010, and two of those were large fish that were subsequently harvested by

[1] Use of trade names does not imply endorsement of the products.

a single darkhouse spear fisherman in January-February 2010.

In Little Wabana Lake, northern pike were trap netted during April 2010. Northern pike implanted with transmitters in Little Wabana Lake included three small females (484-565 mm), three small males (495-557 mm), and five large females (807-975 mm). Predicted weights of northern pike with transmitters were 745-1,205 g for the small fish and 3,655-6,585 g for the large fish. Transmitter weight in air accounted for 0.2%-1.6% of fish body weight in Little Wabana Lake. The transmitter from an 892-mm northern pike was recovered (after the fish was killed in June 2010) and re-implanted in an 812 mm fish (unknown sex) caught by angling at the end of August 2010. Survival of the other fish with transmitters in Little Wabana Lake was better than in Pillager Lake because of limited public access to fishing. Ten transmitters were still broadcasting data in January 2011; two fish were harvested in June 2011; and the remaining eight transmitters broadcasted until mid September 2011 when their batteries stopped functioning.

Three data-logging hydrophones were deployed in Pillager Lake and two hydrophones were deployed in Little Wabana Lake. The omnidirectional hydrophones continuously recorded coded sensor data from fish transmitters, and transmitter records were downloaded from the hydrophones monthly. Hydrophones were submerged 3-5 m below the surface and spaced around the lake with the intent of maximizing coverage of northern pike movement in each lake. Range testing of the transmitters indicated that hydrophones received 65% to 82% of pings out to 300 m, but the percentage dropped off to 3% by 400 m during summer. Occasionally, when a fish was located between two hydrophones, simultaneous acoustic pings were recorded at both hydrophones. Such duplicate records were removed to achieve a dataset of unique values.

In Shingobee Lake, small and large northern pike were trap netted and surgically implanted with temperature and pressure sensing archival tags (LAT1100; Lotek Wireless, Inc., Newmarket, Ontario) during April 2011. The archival tags recorded temperature and pressure measurements at 30 minute intervals, storing the data directly to electronic memory within the tag. Archival tags were implanted in 4 small males (471-520 mm total length), 14 small females (468-508 mm), and 18 large females (728-942 mm). Predicted weights were 660-925 g for the small northern pike and 2,720-6,225 g for the large northern pike. Archival tags had a temperature measurement range of 0-35°C and were lighter than the acoustic tags, weighing just 1.7 g in water and 4.5 g in air. Therefore, archival tags accounted for only 0.5%-0.7% of the body weight of small fish and 0.07%-0.17% of the body weight of large fish. One 477-mm female died, presumably from our handling and tagging, within one month of release. The archival tag was re-implanted in a 517-mm fish of unknown sex caught by angling on 19 May. Similarly, a 942 mm female was caught and killed by angling on 23 July 2011, and the archival tag was re-implanted in a 722 mm fish of unknown sex on 23 August 2011.

A total of 20 archival-tagged fish were recaptured; 17 by ice-out trap netting during late March through early April 2012 and three more by angling during 7 June through 4 July 2012. Therefore, most archival tags recorded northern pike temperature and pressure measurements for nearly a year. Eight of the recovered tags were from small northern pike and 12 were from large northern pike. Data recorded on each tag were downloaded using Lotek's Tag Talk proprietary software. The tag from a 515 mm fish did not provide useful pressure data, and the tag failed completely after 30 October 2011. A second tag from a 487 mm fish failed to record data after 29 July 2011 but provided useful temperature and pressure data up to that date. A third tag from a 777 mm fish did not provide useful temperature readings.

Pressure readings for recovered archival tags were more closely calibrated to actual water depths by lowering the tags through a sequence of known depths. The calibration linear regressions of actual depths versus average pressure measurements for each individual tag were then used to compute the history of depths occupied by each fish. Tag calibrations indicated that actual tag depths were typically about 0.6 m deeper than the tag pressure readings near the water surface, and were about 1.2 m deeper than tag pressure readings 9 m below the water surface. We were not able to perform similar individual tag calibrations for acoustic transmitters in Pillager and Little Wabana lakes.

Quantifying Thermal Habitat and Habitat Selection

Thermal habitat available to northern pike in all three lakes was quantified by continuously monitoring water temperature throughout the water column at the deepest part of each lake. Hourly water temperature profiles were obtained using a string of data-logging thermistors (HOBO U22 Water Temp Pro v2; Onset Computer Corp., Bourne, Massachusetts) deployed at 0.5-m to 1-m depth intervals from the surface to the lake bottom in Little Wabana and Shingobee lakes. In Pillager Lake, which was open to public recreational use, thermistors were deployed from a depth of 3.2 m down to the lake bottom. Profiles of dissolved oxygen concentration with depth were obtained approximately weekly in each lake. Dissolved oxygen profiles were not obtained in early winter as the ice was forming on the lakes, nor as the ice was melting in the spring. Oxygen concentrations at each depth were measured using a luminescent dissolved oxygen probe and portable meter (LDO and HQ30d; Hach Company, Loveland, Colorado).

Volumes of water between 1°C isotherms were integrated over time to calculate thermal habitat volumes for monthly time intervals in each year. Isotherm depths were determined for each temperature profile (24 times per day) by interpolating depths for each 1°C temperature range. Volumes of water in each temperature range were further estimated from a hypsographic curve of lake volume in relation to lake depth (see the example in Figure 1). Finally, volumes from temperature profiles were summed over hourly time intervals to project the thermal habitat volume (expressed in cubic meter days) available to northern pike for each 1°C temperature range (Christie and Regier 1988).

Northern pike temperature preferences were evaluated using selection ratios, which are ratios of fish use of various habitats compared to the availability of those habitats. Rogers and White (2007) provided the following equations for calculating selection ratios for each habitat type (w_i):

$$\widehat{w}_i = u_{i+}/(\pi_i u_{++})$$

where u_{i+} is the number of observations in habitat type i for all fish, π_i is the proportion of available habitat in category i, and u_{++} is the total number of habitat observations for all fish. Selection for a particular habitat is indicated by $\widehat{w}_i > 1$ whereas avoidance is indicated by $\widehat{w}_i < 1$. Each fish was considered a primary sampling unit so that standard errors for selection ratios (SE($\widehat{w}_i$)) accounted for variation in resource selection among individual fish:

$$\mathrm{SE}(\widehat{w}_i) = \sqrt{\frac{n}{(n-1)(u_{++})^2}\sum_{j=1}^{n}\left(\frac{u_{ij}}{\pi_i} - \widehat{w}_i(u_{+j})\right)^2}$$

where n is the number of fish, u_{ij} is the number of observations in habitat type i for fish j, and u_{+j} is the total number of observations for fish j (Rogers and White 2007).

In each lake, temperature selection ratios were calculated for August when a relatively broad range of water temperatures was available to northern pike. Fish use of water temperatures was based on the number of observations of individual fish in 1°C temperature ranges. Available habitat was the thermal habitat volume calculated for each 1°C temperature range during August. Water layers with low levels of dissolved oxygen (<3 mg/l) were excluded from the thermal habitat volumes used in determining selection ratios because, after reviewing several studies of dissolved oxygen and northern pike, Casselman (1996) concluded that adult northern pike avoid oxygen concentrations of <3-4 mg/l.

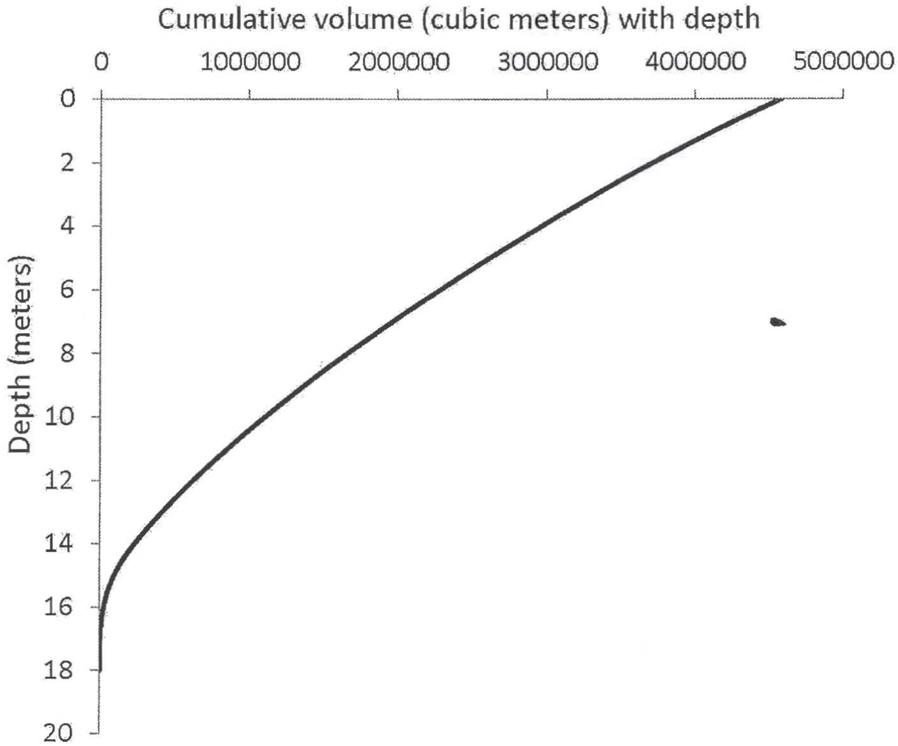


Figure 1. Cumulative volumes of water by depth, calculated from the deepest point in the lake to the surface, for Little Wabana Lake, 2010.

Modeling Northern Pike Habitat Use

Patterns of northern pike habitat use were explored using linear mixed effects models of hourly averages of telemetry observations for individual fish. The models were used to establish if fish size or season influenced temperatures and depths used by northern pike, and if daily changes in temperatures and depths occurred. Each fish was a primary sampling unit with a random effect incorporated into the model to account for repeated measurements of temperature and depth from each individual. A one-step autoregressive (AR1) correlation process was included for temporal correlation among temperature and depth observations in successive hours. The correlation was modeled as a function of the observed time interval in hours between successive observations to account for times when the fish was not near a hydrophone (Rogers and White 2007). Seasonal changes in fish behavior were accommodated by running the model for each month's observations in each lake and year. All models included the random effect structure described above, and specific fixed effects compared in each month were 1) an intercept only model that provided an overall average of fish temperature or depth, 2) a model that only included the hour of the day, 3) models that only included the length or size category (large versus small) of the fish, 4) models that included both the hour of the day and the length (or size category) as additive fixed effects, and 5) a model that included an interaction between hour of the day and fish size. Models were fit using the "lme" function in the "nlme" package (Pinheiro et al. 2010) in the statistical program R (R Development Core Team 2012). Akaike's information criterion (AIC; Burnham and Anderson 2002) was used to choose among models fit for each month. Throughout this manuscript, time of day was reported as Central U.S. Daylight Savings Time to avoid interrupting measurements during spring and fall time changes.

Results

Automated acoustic telemetry and use of archival tags enabled us to measure northern pike use of available depths and temperatures in three lakes with a resolution not previously found in the literature. Even after filtering the data for duplicate records and erroneous transmissions, acoustic receivers still captured between 29,922 and 92,150 observations of temperature or depth from each transmitter per year. The average annual number of recordings per transmitter was 64,564 for temperature and 64,651 for depth. Those numbers were much higher than the recordings from archival tags, which collected 17,692 temperature and depth observations per year. Although archival tags recorded fewer observations, the temperature and depth observations were simultaneous and were obtained at regular 30 minute intervals regardless of where the fish was located. Therefore, archival tag data were not as subject to biases from factors reducing the signal detection efficiency of acoustic transmitters. Detection efficiency of acoustic transmissions depend on a fish's proximity to a hydrophone, background noise in the water, overlap (collisions) of simultaneous transmissions that interfere with each other when numerous transmitters are near a hydrophone, and attenuation of transmissions due to objects such as vegetation in the water column. In our study, acoustic transmitter observations were more sporadic (had longer time intervals and gaps in the data) when tagged fish were long distances from the receivers or were in thick, shallow vegetation. Percentages of the transmissions that were recorded at hydrophones were generally less than 46% (Table 1). The biggest potential source of bias in our acoustic transmitter data was from fish hiding in aquatic vegetation. For example, the two smallest northern pike in Pillager Lake (Figure 2) had fewer observations during summer than the other fish. During summer, we located those two individuals by tracking with a manual receiver; they were in a very shallow and heavily vegetated bay at the northwest end of the lake. Aquatic vegetation in the bay attenuated their acoustic transmission so that we had to be within about 5 m of the fish to obtain a signal. The percentage of transmissions received from small northern pike in Pillager Lake during August was smaller than the percentage of transmissions received from large northern pike in August (Table 1).

Table 1. Average percentages of the total possible transmissions of depth information received and recorded for individual fish in selected months at the hydrophone arrays in Pillager and Little Wabana lakes. Percentages of transmissions received are given for small versus large size categories of northern pike.

Lake and fish size	Percentage of transmissions received			
Pillager Lake	May	August	November	
Small pike (487-579 mm)	14.0%	21.0%	39.4%	
Large pike (827-842 mm)	13.7%	30.4%	45.9%	
Little Wabana Lake	May	August	November	February
Small pike (484-565 mm)	20.1%	26.5%	34.5%	30.9%
Large pike (807-975 mm)	16.0%	13.0%	19.2%	34.5%

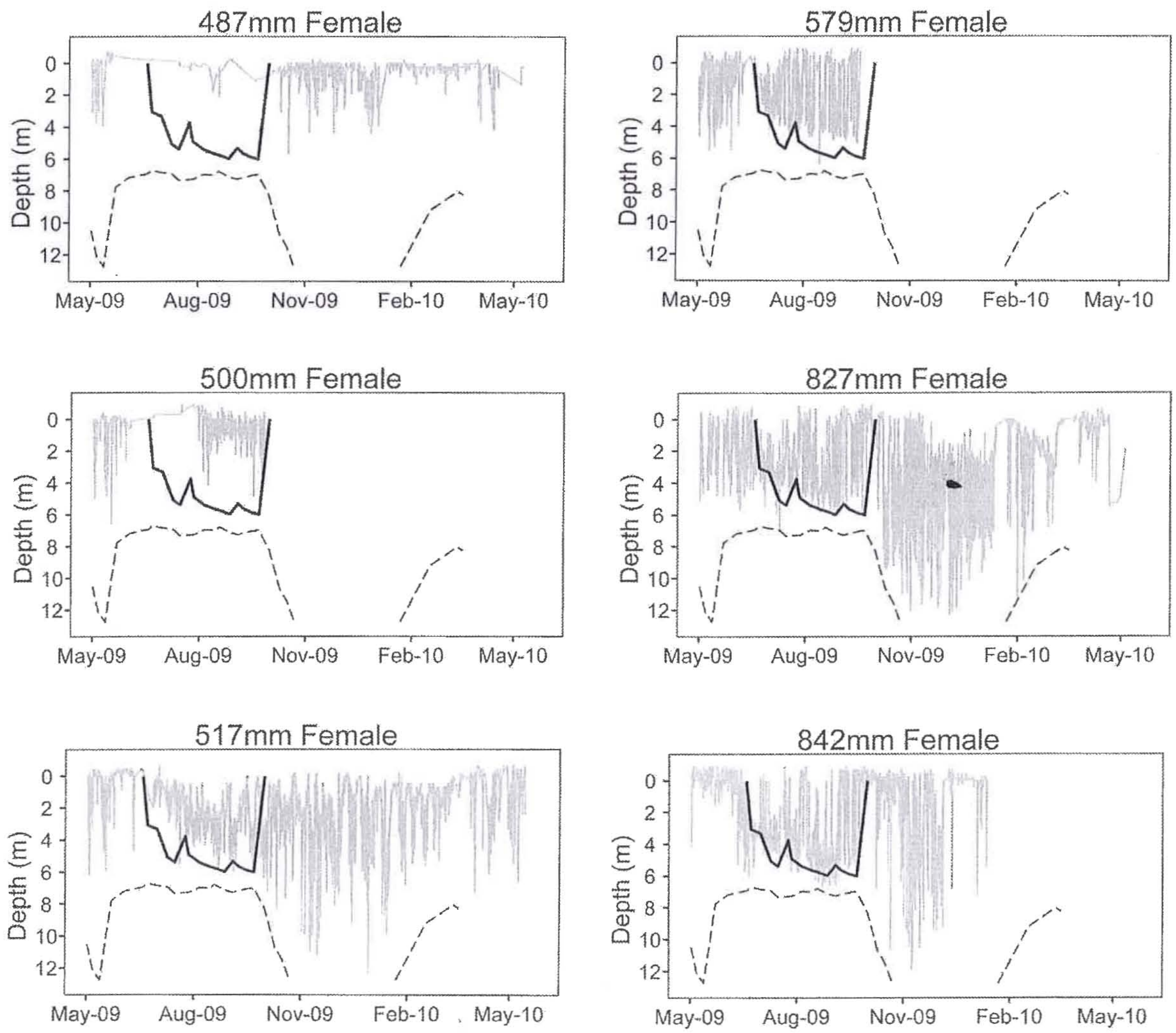


Figure 2. Sequential depth observations (gray lines) from individual northern pike in Pillager Lake during May 2009 to May 2010. Solid black lines are depths where water temperature = 21° C and dashed lines indicate depths where dissolved oxygen = 3 mg/l as measured from temperature and oxygen profiles in Pillager Lake. Each panel represents one transmitter.

Seasonal Depth Movements

Depth observations from individual northern pike throughout the year illustrated 1) that the deepest movements occurred during spring and fall turnover when dissolved oxygen in deep water increased; 2) behaviors (use of depths) throughout the year varied among individual fish; 3) a seasonal pattern was often observed in summer depth movements; and 4) behaviors of some individual fish changed from one year to the next. Examples of deep vertical movements during turnover periods were from 517-mm and 827-mm fish that went over 11 m deep in Pillager Lake (Figure 2), from 484-mm, 543-mm, and 557-mm fish that went as deep as 15 m in Little Wabana Lake (Figure 3), and from 735-mm and 866-mm fish that went over 11 m deep in Shingobee Lake (Figure 4).

Individual behaviors evident throughout the year included examples from Shingobee Lake of differences in depths used by small northern pike during the summer. Most of the depths used by small (471-502 mm) northern pike during summer were less than 2 m (Figure 4). However, one small (468 mm) fish used depths that were mostly greater than 4 m, and another individual (498 mm) spent most of its time in depths between 2 and 4 m (Figure 4). Fall and winter also provided examples of individual behaviors. In Little Wabana Lake, one large (975 mm) female spent most of the fall and winter in water between 1 and 3 m deep (Figure 3). In contrast, another large (807 mm) female spent most of the fall in moderate depth (2-6 m) water, but as the ice formed on the lake, that fish moved deeper (mostly 9-14 m) spending much of the winter in deep water (Figure 3). Moreover, that same fish spent much of its time in water that had low concentrations of dissolved oxygen; including at least 47 minutes in water depths with less than 0.5 mg/l dissolved oxygen (less than 4% saturation) during one February excursion that went into water over 12 m deep.

Seasonal patterns in depth movements were most apparent during the summer and were somewhat dependent on fish size. In all three lakes, large northern pike tended to occupy deeper, cooler water associated with the thermocline, with summer depths being 3 to 8 m depending on the lake (Figure 5). Large northern pike followed the thermocline into deeper water as warming temperatures in shallow water layers progressively drove the thermocline deeper during July and August. In contrast, small northern pike could be found in either warm, shallow water (<2 m deep) or in the deeper water occupied by large northern pike (Figure 5). Figure 3 illustrates how a 557 mm fish and a 975 mm fish associated with the thermocline during two successive summers in Little Wabana Lake. Similarly, all of the large northern pike in Shingobee Lake maintained themselves in cooler water along the thermocline (Figure 4). Vertical movements of the northern pike in summer were generally constrained by low dissolved oxygen concentrations (<3 mg/l) in deeper water. However, two individuals (735 mm and 803 mm fish in Figure 4) from Shingobee Lake showed more extensive use of water with lower concentrations of dissolved oxygen during the summer.

Examples of fish switching their behavior from one year to the next were from Little Wabana Lake, where acoustic transmitter batteries lasted through two summers. Two fish (552 mm and 810 mm fish in Figure 3) exhibited more extensive use of shallower, warmer water during summer 2010 compared to summer 2011 when both fish used depths that more closely followed the thermocline into deeper water during July and August.

Diel Depth Patterns

Some individual northern pike showed strong evidence of daily depth movements while others did not. For example, an 865 mm female from Shingobee Lake demonstrated stark shifts between shallow water at night and deep water in daylight hours during January (Figure 6). That particular fish had similar diel depth changes during October, although the movements were not as decisive as in January. In August, the same fish remained mostly in deep water, but still showed small signals of moving a bit shallower during the day. In contrast, a 735 mm northern pike from Shingobee Lake did not exhibit as much vertical movement within the water column

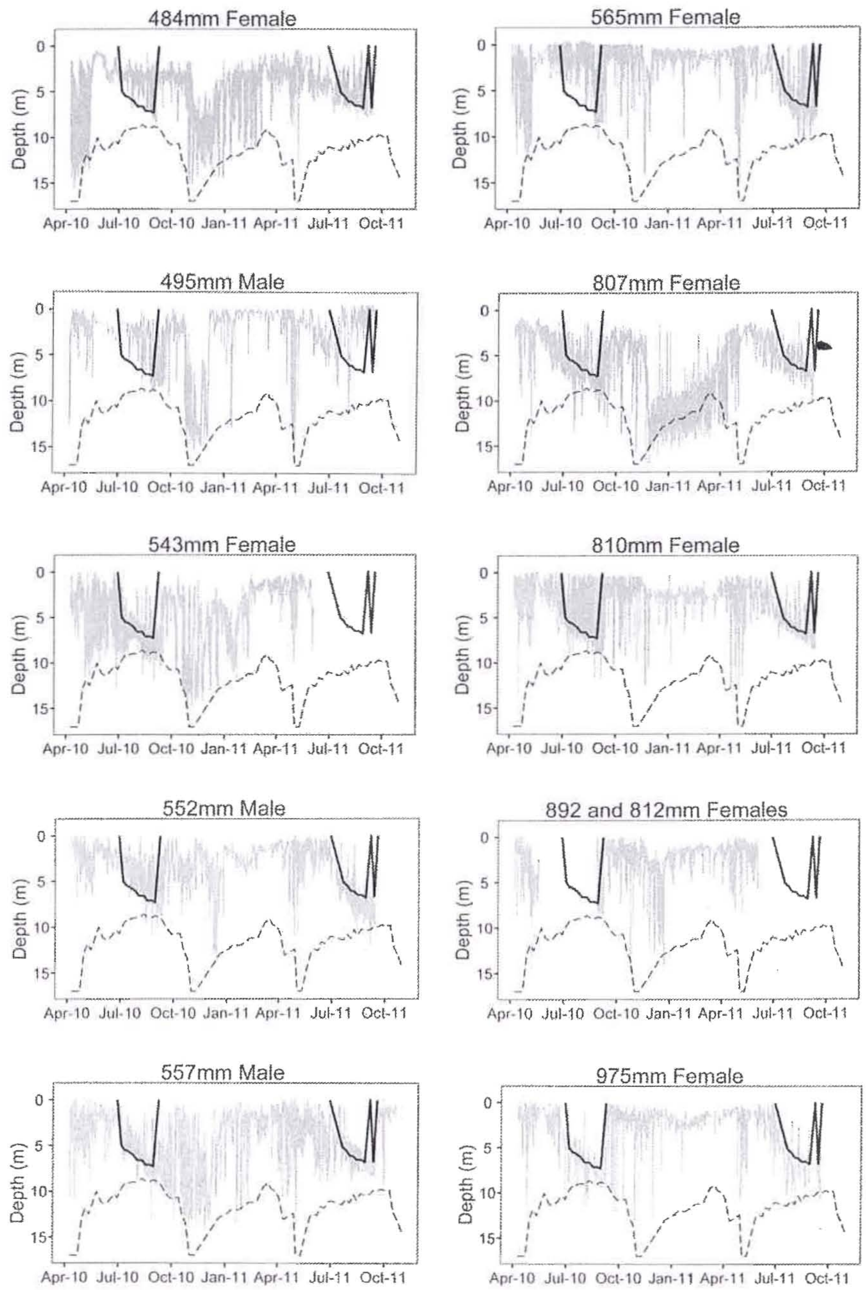


Figure 3. Sequential depth observations (gray lines) from individual northern pike in Little Wabana Lake during April 2010 to October 2011. Solid black lines are depths where water temperature = 21°C and dashed lines indicate depths where dissolved oxygen = 3 mg/l as measured from temperature and oxygen profiles in Little Wabana Lake. Each panel represents one transmitter.

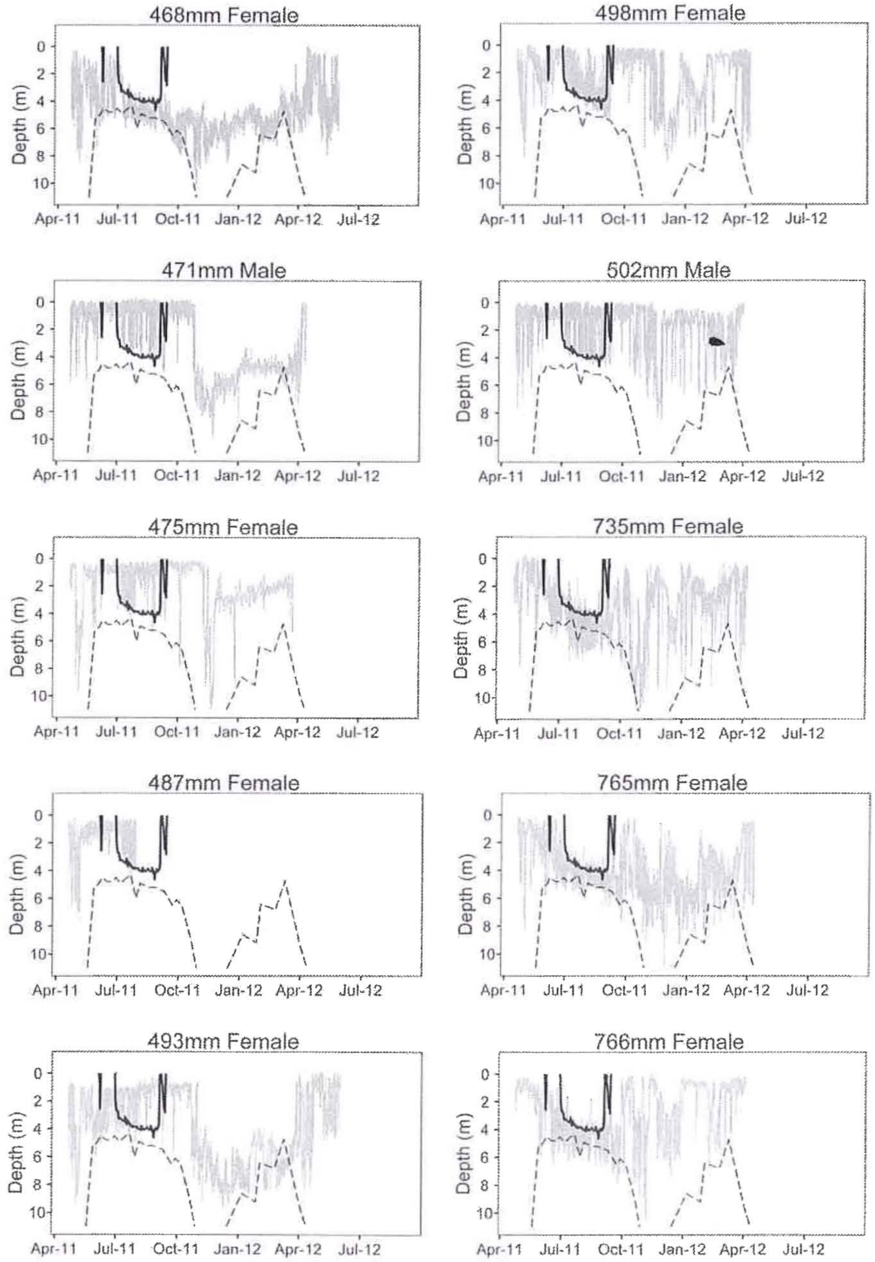
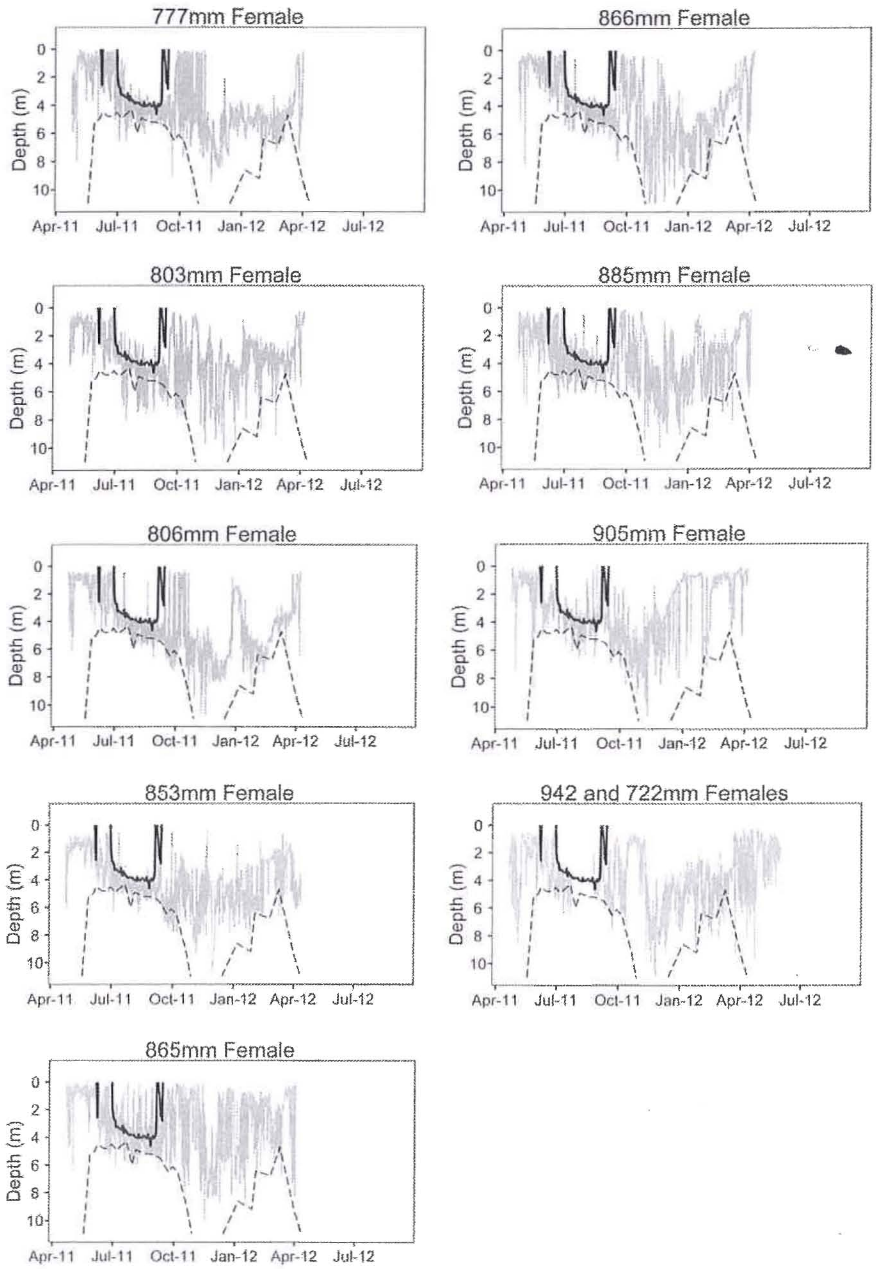


Figure 4. Sequential depth observations (gray lines) from individual northern pike in Shingobee Lake during April 2011 to July 2012. Solid black lines are depths where water temperature = 21° C and dashed lines indicate depths where dissolved oxygen = 3 mg/l as measured from temperature and oxygen profiles in Pillager Lake. Each panel represents one archival tag.


777mm Female
866mm Female
803mm Female
885mm Female
806mm Female
905mm Female
853mm Female
942 and 722mm Females
865mm Female
Depth (m)
0
2
4
6
8
10
Apr-11
Jul-11
Oct-11
Jan-12
Apr-12
Jul-12

4b

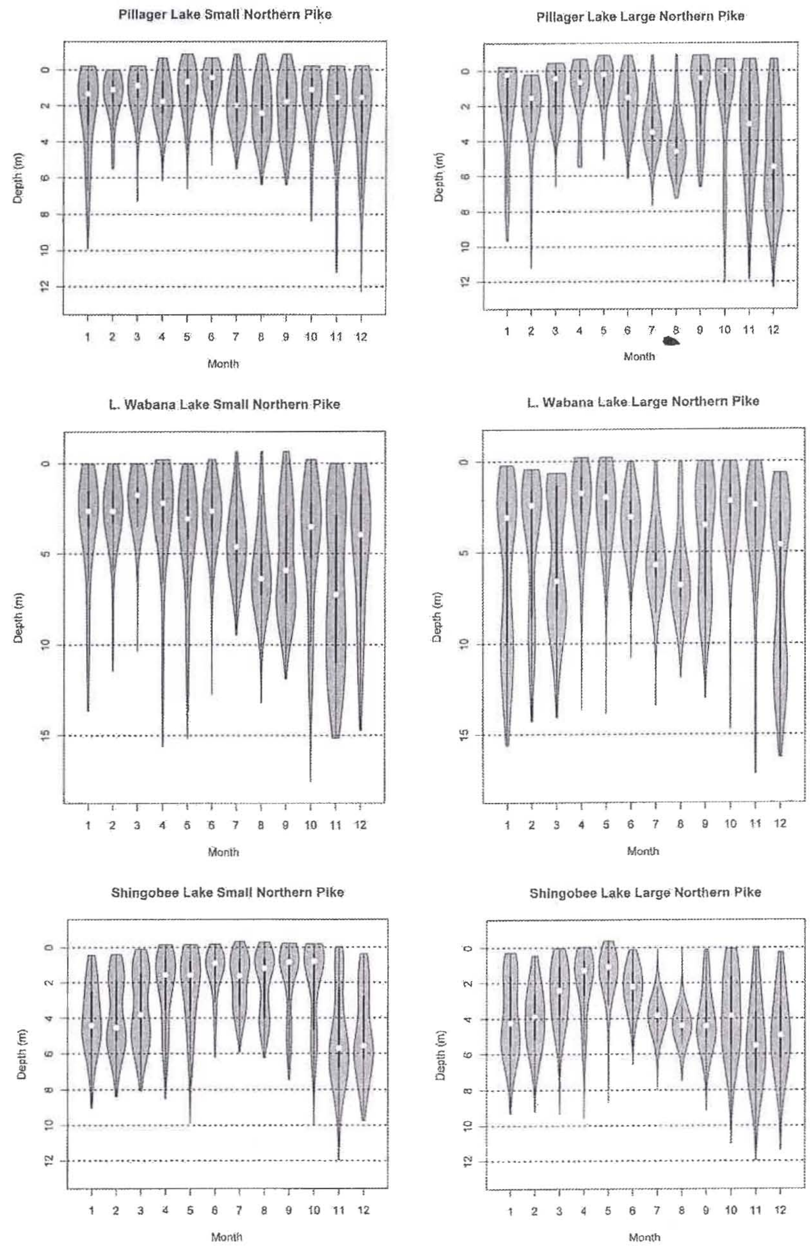


Figure 5. Violin plots of monthly fish depth observations from small versus large northern pike in all three lakes.

during October and February (Figure 6). Although the 735 mm fish had some vertical movement during August, movement that even included some time spent in water with low levels of dissolved oxygen, there was no modeling evidence for an "hour" effect for that fish in August. Moreover, the proportions of tagged northern pike showing evidence of diel depth patterns were different among lakes. In August, for example, seven of nine northern pike showed modeling evidence of diel movements in Little Wabana Lake, but only four of seventeen northern pike in Shingobee Lake had diel patterns. In February, the proportions of northern pike with evidence of diel movements were eight of ten in Little Wabana Lake and four of eighteen in Shingobee Lake. The habitat models projected that times-of-day when northern pike moved deepest in the water column were not consistent among individual fish, among the length categories, or among the lakes.

Temperature Selection in Oxygenated Water

Temperatures at which northern pike maintained themselves throughout the year did not differ much between the small and large northern pike except during July and August (Figure 7). In Little Wabana Lake, temperature observations in each month were similar across fish sizes, especially during the water temperature transition periods of spring and fall (Figure 7). The greatest difference in temperature observations between fish size categories in Little Wabana Lake was during July and August when there were a few more observations of warm temperatures among the small northern pike (mean=21.0°C) than the large fish (mean=20.1°C). In Shingobee Lake, temperatures of large and small northern pike were also similar among months except that larger differences were apparent between the two size groups during July and August (Figure 7). Mean temperatures for small versus large fish were 22.8°C versus 19.0°C in July and 22.2°C versus 19.1°C in August.

Selection ratios showed that large northern pike preferred to maintain cooler body temperatures of 16-21°C even though those water temperatures had somewhat limited availability to the fish during the heat of the summer. Large northern pike in Little Wabana Lake selected for 17-21°C during August 2010 and 16-21°C during August 2011 when temperatures of 7.9-27.5°C were available (Table 2). In Shingobee Lake, large northern pike also selected for 16-21°C temperatures during August 2011 when temperatures of 14.6-28.1°C were available. In Pillager Lake, where the acoustic transmitters limited selection ratio calculations to temperatures less than 20°C, temperature selection by large northern pike was apparent for 18-20°C during August 2009. Percentages of available thermal habitat less than 21°C were 23.3-34.6% of the August thermal habitat volumes in Little Wabana Lake and only 13.1% in Shingobee Lake. Water less than 20°C was only 11.2% of the thermal habitat volume available to northern pike in Pillager Lake during August. Selection ratios (Table 2) indicated that large northern pike in Little Wabana Lake avoided water greater than 22°C in both 2010 and 2011 even though 60.6-62.6% of the thermal habitat volumes were greater than 22°C. In Shingobee Lake, large northern pike avoided water greater than 22°C which was 75.2% of the available thermal habitat volume during August 2011. A few very high selection ratios at temperatures lower than 16°C were artifacts of a few fish observations in deep water at temperatures where the habitat was projected to be rare based on our calculations of habitat volume with a dissolved oxygen threshold of 3 mg/l. Large northern pike in Shingobee Lake did not use shallow springs with cold groundwater flow even though numerous springs were found near the shoreline at depths less than 1 m; simultaneous depths and temperatures from individuals (Figure 4) indicated that no large fish took advantage of shallow pockets of cold water near shore during summer.

Small northern pike exhibited a more complex mix of thermal habitat preferences among the three lakes during August. Small northern pike tended to maintain their bodies at the same temperatures as large northern pike in Little Wabana Lake, but they often maintained warmer temperatures in the other two lakes. In Little Wabana Lake, selection

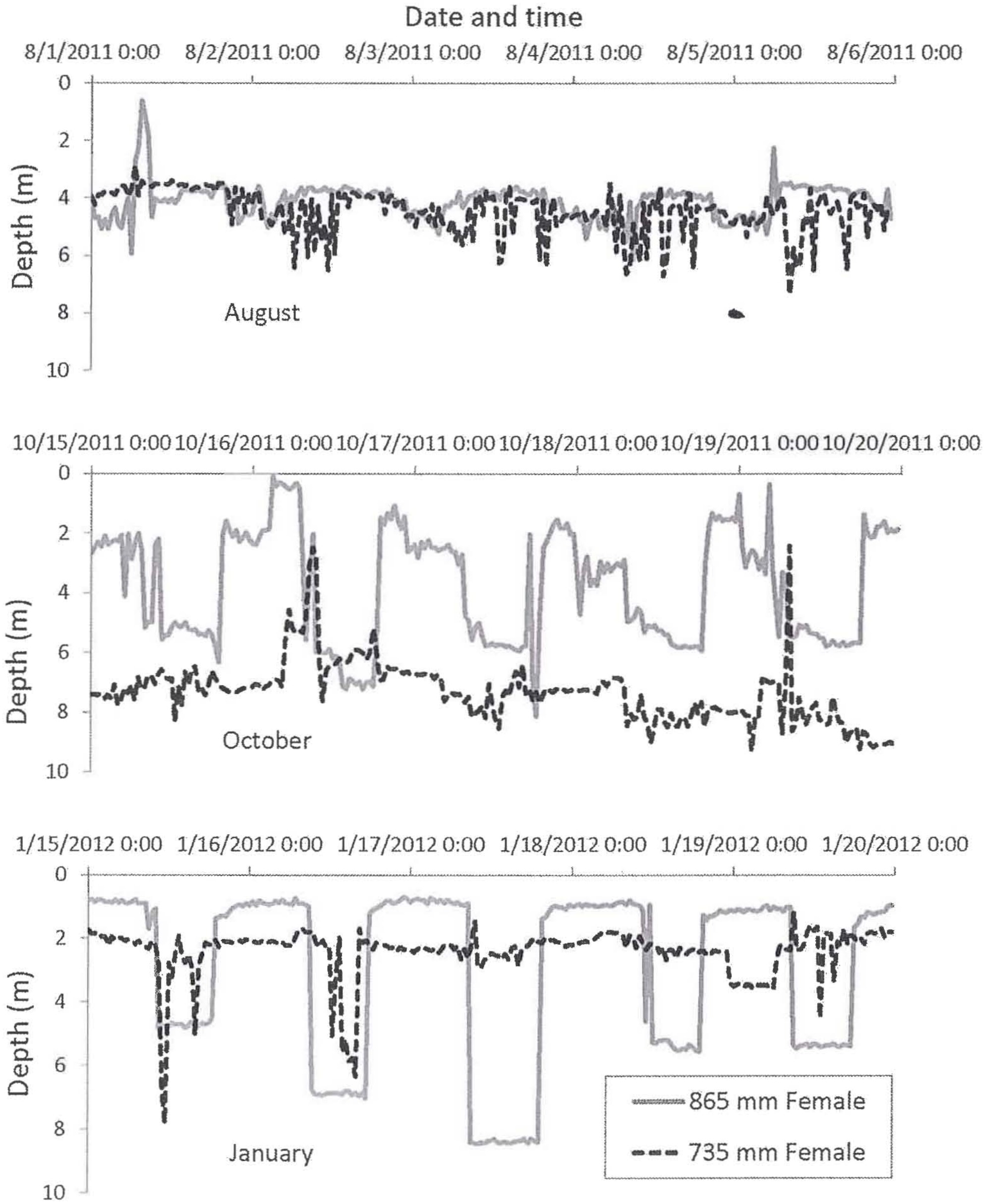


Figure 6. Diel depth observations from 865 mm and 735 mm northern pike in Shingobee Lake during five-day periods in August, October, and January.

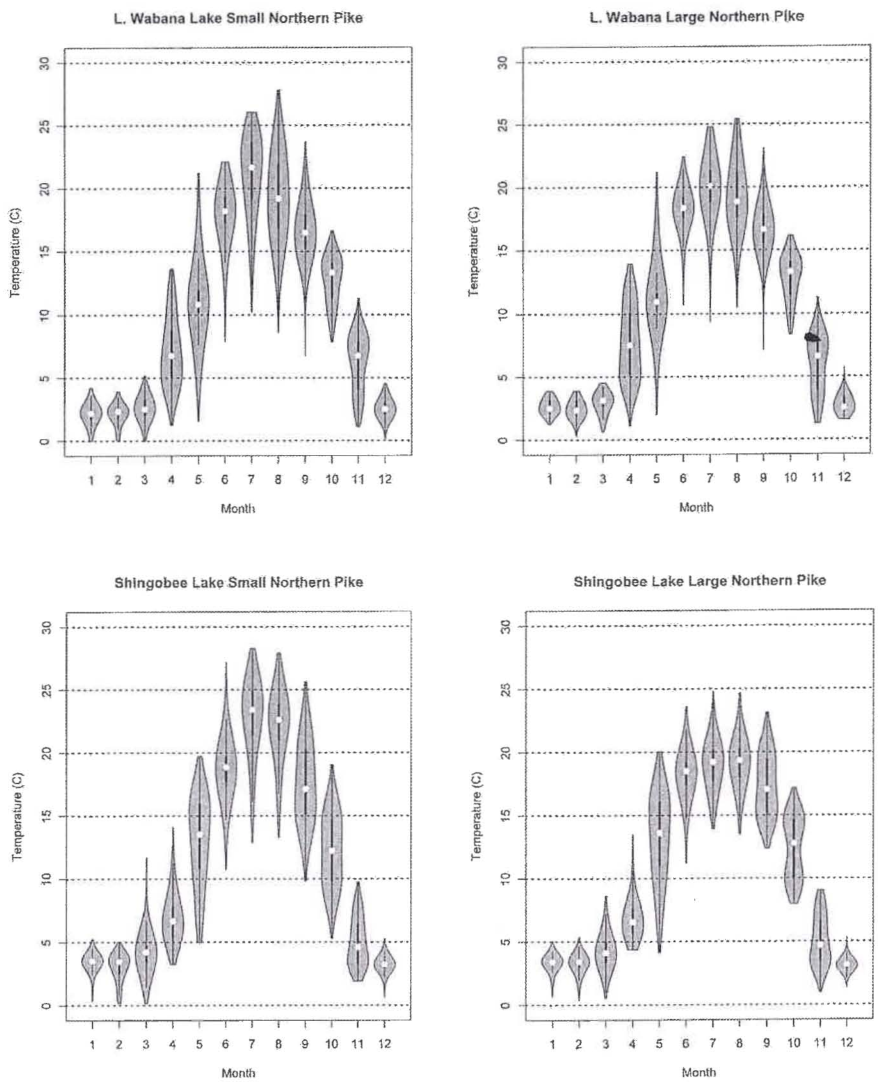


Figure 7. Violin plots of monthly fish temperature observations from small versus large northern pike in Little Wabana and Shingobee Lakes.

Table 2. Selection ratios (w_i) and standard errors for selection ratios (SE) calculated for 1°C water temperature ranges available to large and small Northern Pike during August in Pillager Lake (2009), Little Wabana Lake (2010 and 2011) and Shingobee lake (2011). Selection ratios for temperatures $\geq$20°C were not determined for Pillager Lake. Selection ratios with 95% confidence intervals that exceeded w_i=1.0 are highlighted in gray. Zeros indicate temperatures that were available but not used by Northern Pike.

Temperature	w_i(SE)							
	Pillager 2009		L. Wabana 2010		L. Wabana 2011		Shingobee 2011	
(°C)	Large	Small	Large	Small	Large	Small	Large	Small
7-7.9					0	0		
8-8.9					0	0		
9-9.9					0	0		
10-10.9					0.07(0.10)	0.03(0.02)		
11-11.9			0	0	0.30(0.43)	0.74(0.60)		
12-12.9			0.57(0.75)	0.06(0.06)	0.13(0.18)	1.37(1.08)		
13-13.9			239(316)	119(71)	0.13(0.18)	1.76(1.16)		
14-14.9	0	0	0.14(0.15)	0.83(0.45)	0.03(0.05)	2.15(1.09)	185(141)	66(59)
15-15.9	1.65(1.31)	0	1.65(1.56)	2.49(1.73)	2.08(0.81)	3.91(1.44)	6.39(2.47)	4.25(3.92)
16-16.9	2.33(1.30)	0	3.13(1.44)	3.47(1.33)	7.25(1.63)	5.04(2.26)	3.94(0.65)	1.72(1.63)
17-17.9	5.88(3.12)	0.01(0.01)	5.35(2.31)	4.18(1.36)	8.96(0.31)	4.91(1.53)	3.91(0.38)	1.10(0.90)
18-18.9	6.74(1.62)	0.16(0.07)	7.62(0.88)	4.29(1.13)	11.97(0.95)	5.09(1.16)	5.16(0.61)	0.81(0.38)
19-19.9	6.05(1.17)	1.72(1.23)	4.40(1.12)	3.35(0.93)	5.88(1.79)	4.42(1.71)	6.44(0.65)	1.11(0.48)
20-20.9	-	-	3.07(0.95)	2.93(1.25)	4.63(0.87)	3.98(1.85)	4.35(0.45)	1.72(0.48)
21-21.9	-	-	0.69(0.22)	0.66(0.22)	2.18(0.46)	3.83(2.30)	1.05(0.22)	1.85(0.16)
22-22.9	-	-	0.39(0.08)	0.43(0.20)	0.23(0.01)	0.49(0.25)	0.12(0.06)	0.75(0.11)
23-23.9	-	-	0.39(0.11)	0.30(0.10)	0.04(0.01)	0.21(0.13)	0.05(0.03)	0.81(0.16)
24-24.9	-	-	0.32(0.08)	0.65(0.31)	0.04(0.02)	0.18(0.14)	0.02(0.02)	1.13(0.23)
25-25.9	-	-	0.09(0.04)	0.32(0.13)	0	0.01(<0.01)	0	0.75(0.19)
26-26.9			0	0	0	0	0	0.69(0.19)
27-27.9			0	0.23(0.13)	0	0	0	1.55(0.70)
28-28.9							0	0

ratios showed small northern pike selecting for temperatures of 18-19°C (Table 2). In Shingobee Lake, however, small northern pike selected for warmer water of 21-22°C. Acoustic transmitters in Pillager Lake did not provide exact measurements for temperatures of 20°C and greater but the transmitter data still enabled us to count observations $\geq$ 20°C. Those counts provided strong evidence that small northern pike in Pillager Lake were using warm water; 94% of telemetered temperature observations from small northern pike during August 2009 were for temperatures $\geq$ 20°C compared with 37% from large northern pike. Similarly, 83% of temperature observations from small northern pike during August 2011 in Shingobee Lake were for temperatures $\geq$ 20°C. In contrast, observations $\geq$ 20°C for small northern pike in Little Wabana Lake were only 35-47% of the total telemetry observations during August in each year. Higher percentages of transmissions received from small northern pike than large northern pike in Little Wabana Lake in August (Table 1) help support the argument that small fish were not using warm, shallow beds of vegetation (where transmissions would be lost) to any greater extent than the large fish. Conversely, greater transmission losses from small northern pike in Pillager Lake during summer (Table 1) corroborate our manual telemetry observations that small northern pike were using warm, very shallow vegetated habitat. They were using shallow habitat like several of the small northern pike in Shingobee Lake where archival tag data was not subject to transmission loss biases.

Habitat Modeling

Models of northern pike habitat use (monthly models for each lake) indicated that the habitat used was often best described by an interaction between the time of day and the size of the fish. Table 3 lists the types of models fit to our northern pike depth and temperature data for each lake-month combination, and the number of times each model option had the lowest AIC value (i.e., was the best-supported model). The intercept-only model was essentially an average fish depth or temperature for each month-lake combination and was the null model for comparisons with other models. In only seven cases was the intercept-only model the best-supported model. Intercept-only models were selected

Table 3. Numbers of population-level models of depths and temperatures used by northern pike that were the best-supported models (i.e. had the lowest AIC values) for each of the possible lake and month combinations. AIC model selection determined the best-supported model from seven potential models for each month's observations of fish depths and temperatures.

	Number of best-supported models for all lake-month combinations				
Data modeled	Intercept-only	Hour	Length	Additive (hour+length or hour+size category)	Interaction (hour*length or hour*size category)
Depth					
Pillager Lake	0	1	1	0	7
L. Wabana Lake	2	2	1	1	10
Shingobee Lake	1	0	0	4	6
Temperature					
L. Wabana Lake	2	5	1	1	7
Shingobee Lake	2	0	0	2	7

only during winter months that included December, February, and March for fish depth observations, and included November, January, and February for fish temperature observations. AIC values for other models were less than the null model by ΔAIC>2 but <10 in seven cases, and ΔAIC>20 in 48 cases. The largest numbers of best-supported models (Table 3) accommodated interactions between the time of day (hour) and the size of the fish (length or size category). The interaction models essentially allowed northern pike of different lengths to behave differently during different times of the day. Figure 8 illustrated the fish length by hour-of-the-day interactions for small and large northern pike during August. Most interesting were the graphs in Figure 8 of Pillager Lake in 2009 and Little Wabana Lake in 2011. In those two graphs, large and small northern pike illustrated opposite diel patterns, with the small northern pike tending to move a bit deeper during the day whereas the large fish moved shallower during the day.

Niche dimensions for temperature and depth in each month were presented graphically along with modeling results for individual fish from Shingobee Lake to illustrate how the fish distributed themselves seasonally in the available habitat (Figure 9). During the post-spawning period in May, as temperatures were rapidly warming, large northern pike stayed primarily in shallow water, but the small northern pike were more evenly distributed down to 4 m water depth. During August, large northern pike were associated with the thermocline and dissolved oxygen concentrations >3 mg/l. Two of the small northern pike were also in deeper water, but most were in shallow water during August. When water temperatures were colder during November and February, both large and small northern pike were distributed throughout water deeper than 1.5 m that still had oxygen.

Discussion

A salient feature of our results was the individualistic nature of northern pike behavior. Not only did individual fish demonstrate flexibility in their use of habitats within a season, but the Little Wabana Lake data also showed individuals changing the way they used lake habitats between one year and the next. In the population-level habitat modeling, our data supported a preponderance of behaviors in Table 3 that were interactions between individual fish lengths and time of day. One interpretation of those interactions is that they represent differences among individuals in their use of depths and temperatures. A radio telemetry study in two Danish lakes that had very different environments came to the same conclusion that northern pike behavior is extremely variable and that variation not only occurs between, but also within locations and populations (Jepsen et al. 2001). Moreover, the Danish study implied that individual behaviors may explain many of the discrepancies observed between results of various studies of northern pike ecology. In a small German lake, Kobler et al. (2009) concluded that behavioral diversification among northern pike reduced intraspecific competition in preferred habitats.

Although individual behaviors were important, some patterns of habitat use were apparent among our three natural lakes. Vertical movement by northern pike of all sizes was generally constrained by low levels of dissolved oxygen, with most tag depth readings in water with >3 mg/l dissolved oxygen. Large northern pike avoided shallow springs with cold groundwater flow presumably due to low levels of dissolved oxygen in the groundwater. When the water column became more fully oxygenated during spring and fall circulation and thermal overturn periods, northern pike more fully exploited all of the depths that became available to them.

Northern pike also demonstrated that they could tolerate lower concentrations of dissolved oxygen than many other fish species. Some of our winter fish depth measurements corresponded to portions of the water column with <0.5 mg/l of dissolved oxygen, confirming earlier observations that northern pike are relatively tolerant of winterkill conditions. Moyle and Clothier (1959) noted how northern pike were able to persist over winter in a shallow western Minnesota lake, the fish maintained themselves in Lake Traverse even

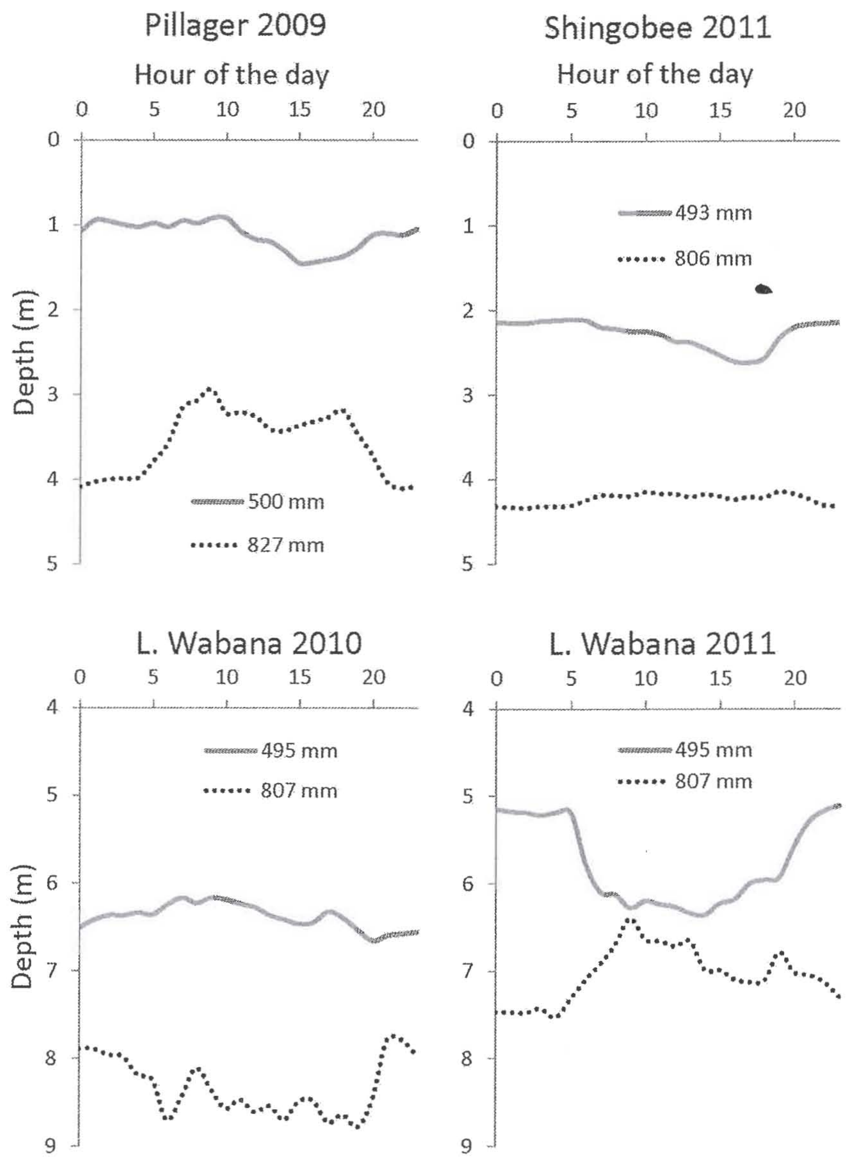


Figure 8. Mixed effects model predictions of hourly depths of small versus large northern pike during August in Pillager Lake 2009, Shingobee Lake 2011, and Little Wabana Lake in 2010 and 2011.

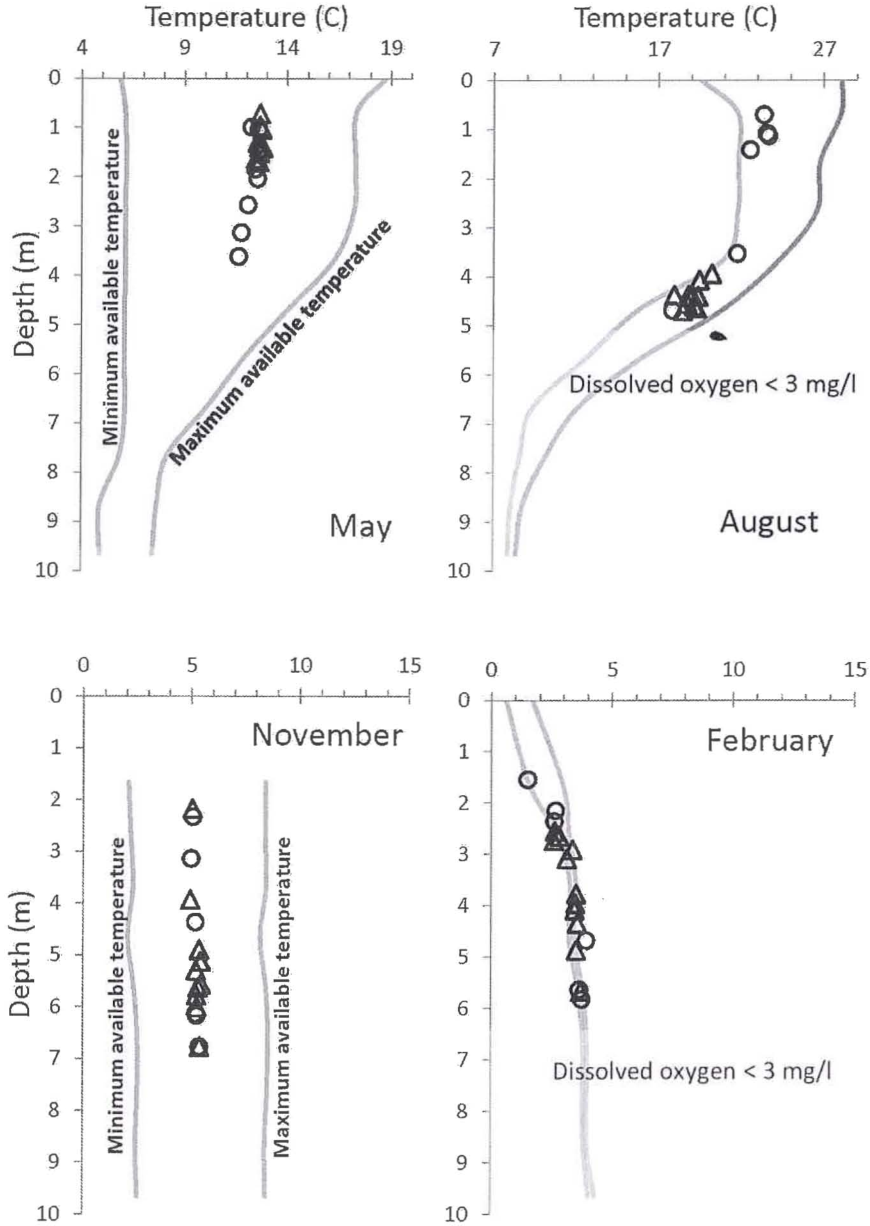


Figure 9. Dimensions of the temperature and depth habitats used by northern pike in Shingobee Lake during four months. Gray lines represent the minimum and maximum temperatures available at each depth during the month. Shaded areas are depths with low dissolved oxygen concentrations. Circles (small northern pike) and triangles (large northern pike) are predicted temperatures and depths from models for individual fish.

with winter oxygen concentrations that ranged as low as 0.9 to 2.7 mg/l. From a literature review, Inskip (1982) concluded that northern pike can tolerate dissolved oxygen as low as 0.1-0.4 mg/l for several days. Casselman (1996) described a curvilinear relationship between water temperature and incipient lethal oxygen concentration for northern pike that illustrated how northern pike can succumb from oxygen concentrations less than 2 mg/l during warm summer water temperatures, but lethal dissolved oxygen concentrations may be as low as 0.5 mg/l during winter water temperatures. Similarly, Privol'nev (1963) observed that critical low oxygen levels were 1.40 mg/l at 29°C and 0.72 mg/l at 15°C. Visual observations in very low oxygen conditions during winter (Magnuson and Karlen 1970) indicated that northern pike were less active than fish such as yellow perch *Perca flavescens* and bluegill *Lepomis macrochirus*. Casselman (1996) also noted that while adult northern pike attempt to avoid oxygen concentrations of <3-4 mg/l, live northern pike have been captured in nets where dissolved oxygen concentration was as low as 0.04 mg/l (0.3% saturation).

During summer, behavior of large northern pike was generally consistent among the study lakes with large northern pike following the thermocline into deeper, cooler water as upper water layers warmed through the summer. In Little Wabana and Shingobee lakes, large northern pike selected for temperatures in August that maintained their bodies at 16°-21°C even though 60%-82% of the available water volume (with dissolved oxygen concentrations >3 mg/l) in each lake was warmer than 22°C. The lower portion of their selected temperature range (16°-18°C) was lower than previously determined preferred temperatures and optimum temperatures for growth of northern pike. Preferred temperatures (temperatures selected under experimental lab conditions) have not been determined for the largest sizes of northern pike but were found to be higher (23°-24°C) for juveniles and subadults (McCauley and Casselman 1981). Casselman (1978) measured an optimum temperature of 19°C for growth in weight of lab-held yearlings and adults, and an optimum temperature of 21°C for growth in length. The adult fish ranged up to age 3 and were only 281-466 mm total length. In those studies, maximum swimming activity under lab conditions occurred at 19°-20°C. Comparing optimum temperatures for growth (in length) of 2- and 3-year-old fish between lab and field studies, Casselman (1978) found a very similar optimum temperature of 19.8°C in a lake.

In contrast to large northern pike, habitats used by small northern pike differred among the lakes during summer. Small northern pike in Pillager and Shingobee lakes tended to use warmer, shallower water than the large northern pike, but in Little Wabana Lake, the small fish were more often in deeper and cooler water. Temperatures selected by small northern pike in Shingobee Lake during August (21°-22°C) did not overlap with temperatures selected by large northern pike or even with temperatures selected by the small northern pike in Little Wabana Lake. The limited fish temperature information from Pillager Lake points to similar habitat preferences for small fish in both Shingobee and Pillager lakes.

The principal habitat difference among these lakes was the amount of shallow-water aquatic vegetation providing overhead cover for fish. Near shore areas in Shingobee Lake had soft bottom substrates so that the lake was nearly completely ringed with lily pads providing dense overhead cover from shore out to 2 m deep water. Pillager Lake had one large shallow bay (northwest end of the lake) that also had soft bottom substrates and dense overhead cover by lily pads. Furthermore, manual tracking of our small fish with acoustic transmitters showed northern pike residing in that shallow vegetation. Bottom substrates in near shore areas of Little Wabana Lake were predominantly hard sand and had more sparse aquatic vegetation (compared to the other two lakes) that provided no overhead cover for small northern pike. Little Wabana Lake also provided less of the other forms of aquatic vegetation that filled the water column underneath lily pads in the other lakes. Overhead cover provided by lily pads and vegetative structure from other plants in the water column in Shingobee and Pillager lakes likely provided some shading from direct heating by sunlight, habitat for forage fish and other potential food items, as well as hiding cover from larger northern pike and avian predators. The important conclusion, at least for small northern pike, is that temperature seemed to be a secondary habitat consideration behind the presence of shallow vegetated cover, and when cover was not available, small northern pike tended to follow the large northern pike into deeper and cooler water during the summer.

The scientific literature continues to explore relationships between northern pike sizes and their habitat choices, particularly with respect to availability of aquatic plants and intraspecific interactions (Bry 1996; Grimm and Klinge 1996; Pierce 2012). Experimental gill-net catches of northern pike in two shallow Ontario lakes were greatest at intermediate plant densities (35% to 80% of submerged vegetative cover; Casselman and Lewis 1996). The plants were primarily *Potamogeton* spp., coontail, and Canada waterweed *Elodea canadensis*. Small northern pike were usually caught in the densest beds of these plants, and large fish were in more sparse vegetation. Similarly, an inverse relationship was found between northern pike sizes and the density of aquatic plants in a small (27 ha) Swedish lake, suggesting that the small northern pike stayed in dense vegetation to avoid interactions with larger northern pike (Eklov 1997). What is not completely clear from our study is the role that northern pike density might play in the habitat choices made by small northern pike.

Because sample sizes were small, no attempt was made to determine sex-related differences in habitat use. Females dominate the large sizes of northern pike in most fish populations and all of our large northern pike for whom sex was determined were females. Our small northern pike represented a better mix of the sexes. In Little Wabana Lake, 50% of the small northern pike with transmitters were males. In Shingobee Lake, 33% of archival tags recovered from small northern pike were from males. In Pillager Lake, however, all four small northern pike tracked through the first summer were females.

Assumptions about what habitats are used by fish often underlie the thermal histories and activity levels used in developing bioenergetics models (Hartman and Kitchell 2008). Northern pike at the southern edge of their range react to mid-summer water temperatures by occupying the coolest available water that still has sufficient levels of dissolved oxygen. Headrick and Carline (1993) used temperature-sensitive radio transmitters to study habitat use of large (694-920 mm; mean length = 771 mm) northern pike in two southern Ohio impoundments where northern pike seem to be better adapted to warm water than our fish in north-central Minnesota. The large northern pike in the Ohio impoundments moved from inshore to offshore locations at the onset of thermal stratification, and when surface temperatures exceeded 25° C, they sought the coolest water available with oxygen concentrations exceeding 3 mg/l. No comparisons with smaller northern pike were made in the Ohio impoundments. A bioenergetics model developed by Headrick (1985) suggested that the combined effects of warm water temperatures and the rates at which they could consume prey items limited growth for large northern pike. Growth rates at warm temperatures were constrained more by food consumption than by temperature. In the warm Ohio impoundments, it was projected that large northern pike were not consuming enough food to reach their growth potential and even lost weight during midsummer. By occupying lower temperatures, large northern pike have lower metabolic needs and may be able to consume enough food to channel more energy into maintenance and growth. At temperatures above optimum, growth rates decrease rapidly and growth can be stopped altogether at about 27.5° C (Casselman 1978).

Previous bioenergetics models were simplified by assuming consistent summer habitat use within a population of northern pike. Diana (1987) added some complexity by incorporating four potential summer temperature regimes into a simulation model exploring mechanisms for poor growth rates. Results from our study suggest that population-level energetic studies also need to account for different patterns of temperature use within a population. Northern pike show important increases in metabolism with temperature (Diana (1996) so that, in our study, small northern pike occupying shallow water during the summer experienced important increases in metabolic rates compared to northern pike in deeper and cooler water. The additional detail from incorporating more behaviors into bioenergetics models should provide more realistic estimates of prey fish consumption and the role of northern pike as a top-level predator.

We studied temperature selection by northern pike under the assumption that fish select temperatures conferring energetic advantages to them. Applying relatively new technological advances in automated acoustic telemetry and archival tags, we were able to determine temperature selection with a degree of resolution that has not previously been available for natural lakes. Our temperature selection data could be used for predicting the influences that climate change may have on northern pike, particularly on larger sizes of northern pike. Stefan et al. (1995) provided an initial framework for predicting the effects of global climate change on fishes in Minnesota lakes. The approach integrated lake thermal stratification with area and volume calculations (following the approach of Christie and Regier 1988) for temperatures in which cold, cool, and warm water fishes grow best. Temperature ranges used for cool water fishes in their predictions were 16.3°C (range 13.2-18.2 °C) for the lower temperature of good growth, 28.2 °C (range 27.7-28.8 °C) for the upper temperature of good growth, and 25.1 °C (range 24.0-25.7) for the optimum temperature for growth. Temperature selection data from our study indicate that the upper and optimum growth temperatures used in such climate change models were too high for large northern pike. Temperatures selected by large northern pike in our study were intermediate between the cold water and cool water guilds proposed by Magnuson et al. (1979).

This study presented the most complete survey available to date of depths and temperatures used by large and small adult northern pike throughout the year, providing information about annual patterns of habitat selection, preferred temperatures, variation among individual northern pike, and contrasts in habitat use among natural lakes. The temperature selection results for large northern pike have important implications for comparing habitats among lakes, for bioenergetics studies of fish community relationships, and for future projections of climate change. Differences in optimal thermal habitat among lakes during summer may help explain how lakes differ in their capacity to produce large northern pike. Information from this study will be useful when considering temperature as an ecological resource for different sizes of northern pike.

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Acknowledgments

We thank Beth Holbrook, Melissa Drake, and Don Pereira for improving the manuscript. This study was funded in part by the Federal Aid in Sport Fish Restoration (Dingell-Johnson) Program (D-J Project F26-R, Study 685, Minnesota).