Sveriges lantbruksuniversitet
Swedish University of Agricultural Sciences

Faculty of Forest Science

Evaluating lake charr (*Salvelinus namaycush*) temperature use in a mountain lake using acoustic telemetry

Utvärdering av kanadarödingens (*Salvelinus namaycush*)

temperaturanvändande med hjälp av akustisk telemetri

Johan Leander

Examensarbete i ämnet biologi
Department of Wildlife, Fish, and Environmental studies
Umeå
2015

Evaluating lake charr (*Salvelinus namaycush*) temperature use in a mountain lake using acoustic telemetry

Utvärdering av kanadarödingens (Salvelinus namaycush) temperaturanvändande med hjälp av akustisk telemetri

Johan Leander

Supervisor: Gustav Hellström, Dept. of Ecology and Environmental Sciences

Assistant supervisor: Hans Lundqvist, Dept. of Wildlife, Fish, and Environmental Studies

Examiner: Carin Magnhagen, Dept. of Wildlife, Fish, and Environmental Studies

Credits: 60 HEC
Level: A2E
Course title: Master degree thesis in Biology at the Department of Wildlife, Fish, and Environmental Studies
Course code: EX0595
Programme/education: -

Place of publication: Umeå
Year of publication: 2015
Cover picture: Rickard Linderot
Title of series: Examensarbete i ämnet biologi
Number of part of series: 2015:12
Online publication: http://stud.epsilon.slu.se

Keywords: Lake charr, acoustic telemetry, habitat selection, temperature

Sveriges lantbruksuniversitet
Swedish University of Agricultural Sciences

Faculty of Forest Science
Department of Wildlife, Fish, and Environmental Studies

Abstract

Bathythermal distribution of lake charr (*Salvelinus namaycush*) was surveyed in a boreal lake located in northern Sweden. Based on acoustic telemetry, a high resolution dataset was acquired with more than 630 000 observations from eighteen tagged lake charr. The study was conducted during 2013 and 2014 and covered spring, summer and autumn with their contrasting thermal conditions. I found that temperature was a limiting factor for lake charr habitat selection. When given the possibility to choose temperature, i.e. during the thermally stratified summer, they had a preferendum around 8.2°C stretching from 7.5°C to 10.5°C and less than 2% of all detections exceeding 12ºC. Activity of lake charr were, however, at a minimum at these temperatures and instead at maximum levels at depths corresponding to less than 7 and more than 12. Given that activity is correlated to search for prey, this suggest a trade-off between preferred temperatures vs. prey availability.

Key words: Lake charr; acoustic telemetry; habitat selection; temperature

Introduction

To describe movement and behavior of fish, temperature is of great importance. Almost all species of fish are obligate ectotherms which mean that they actively have to seek warmer or colder volumes of water to regulate their body temperature (Beitinger and Fitzpatrick 1979). This behavioral thermoregulation is necessary for the fish to optimize their metabolism, growth and gonad development (Johnston et al. 2011). The range of thermal optimum is species specific and extensively studied in many species. Most data on thermal optimums for fish have been acquired via laboratory studies. Temperature for optimum growth, thermal preferendum and upper and lower lethal limits can be described for a species as defined by Jobling (1981). Such thermal thresholds and ranges are thought of as physiological constrains of the fish, and are often assumed to be the main underlying factors determining habitat use and distribution of fish in nature (Wootton 1998). Given that assumption, laboratory data on thermal thresholds is often used in important ecological and conservational modelling, such as parameterizing models predicting risk of invasive species success in nature (Davis 2009). However, in contrast to the laboratory, nature is an immensely complex environment with a myriad of interacting variables with potential impact on fish behaviour. Access to food or protection may override temperature preferences for the fish as the most important factor driving behaviour. The trade-off between habitat selection (e.g. shelter, food availability) and temperature preference (e.g. metabolic optimum) may generate a temperature use that could differ from what is predicted by laboratory data. It is hence important to validate laboratory data with data of the actual temperature use of fish in the wild.

In order to acquire reliable data on fish temperature use in lakes, long-term, high resolution in-situ data is needed to cover both seasonal variation and short term diurnal variation. Such data, in combination with data on available temperatures in the lake, would give indications of the true importance of temperature in driving fish behaviour. Data would be strengthen even further if temperature use could be correlated with activity patterns of fish, as this would reveal information how the fish make trade-offs between optimum temperature and other needs, such as protection and search for prey.

Recently there has been a rapid development in fish telemetry, i.e. techniques used to track behaviour and movement of fish. Acoustic telemetry is the most promising of current techniques when it comes to generate position data with very high spatial and temporal resolution over long time. This study use acoustic telemetry to investigate temperature use of lake charr (*Salvelinus namaycush*), an invasive charr species, in a mountain lake located in northern Sweden. Previous studies have described this species as a cold-water stenotherm and laboratory studies (McCauley and Tait 1970; Peterson et al. 1979; and Edsall and Cleland 2000) have reported final temperature preferendum from 10ºC to 12ºC and highest growth rate at 12.5ºC (Edsall and Cleland, 2000). The study stretched over two years and covered spring, summer and autumn with all their contrasting thermal conditions. By overlaying this long term and very detailed data on temperature use with data on depth utilization and activity patterns, the study aim to shed light on the importance of temperature for behaviour and habitat selection in lake charr.

Four main questions are in focus. 1) Does temperature affect habitat selection of lake charr? 2) If so, what are the temperature thresholds limiting their habitat selection, and how does this affect the spatial distribution of lake charr in a lake? 3) What is the temperature preference of lake charr? 4) How is the temperature preference related to lake charr activity?

Methods

Study area

The study was conducted in Lake Gautsträsk situated in the county of Västerbotten, northern Sweden (65° 55.85' N, 16° 18.12' E) (Figure 1). This oligotrophic lake covers an area of 5.5 km^2 and has a mean and maximum depth of 20 and 58 m, respectively. In addition to the native fish populations of brown trout (*Salmo trutta*), grayling (*Thymallus thymallus*), arctic char (*Salvelinus alpinus*), northern pike (*Esox lucius*), white fish (*Coregonus lavaretus*), bourbot (*Lota lota*) and minnow (*Phoxinus phoxinus*) there is a reproducing population of the non-native species lake charr which was introduced from North America in 1966. Recruitment is supported by occasional catches in gill nets as well as direct observation of spawning behavior near shallow areas in the outlet of the lake during September and October. Otherwise, information regarding the lake charr population is very limited.

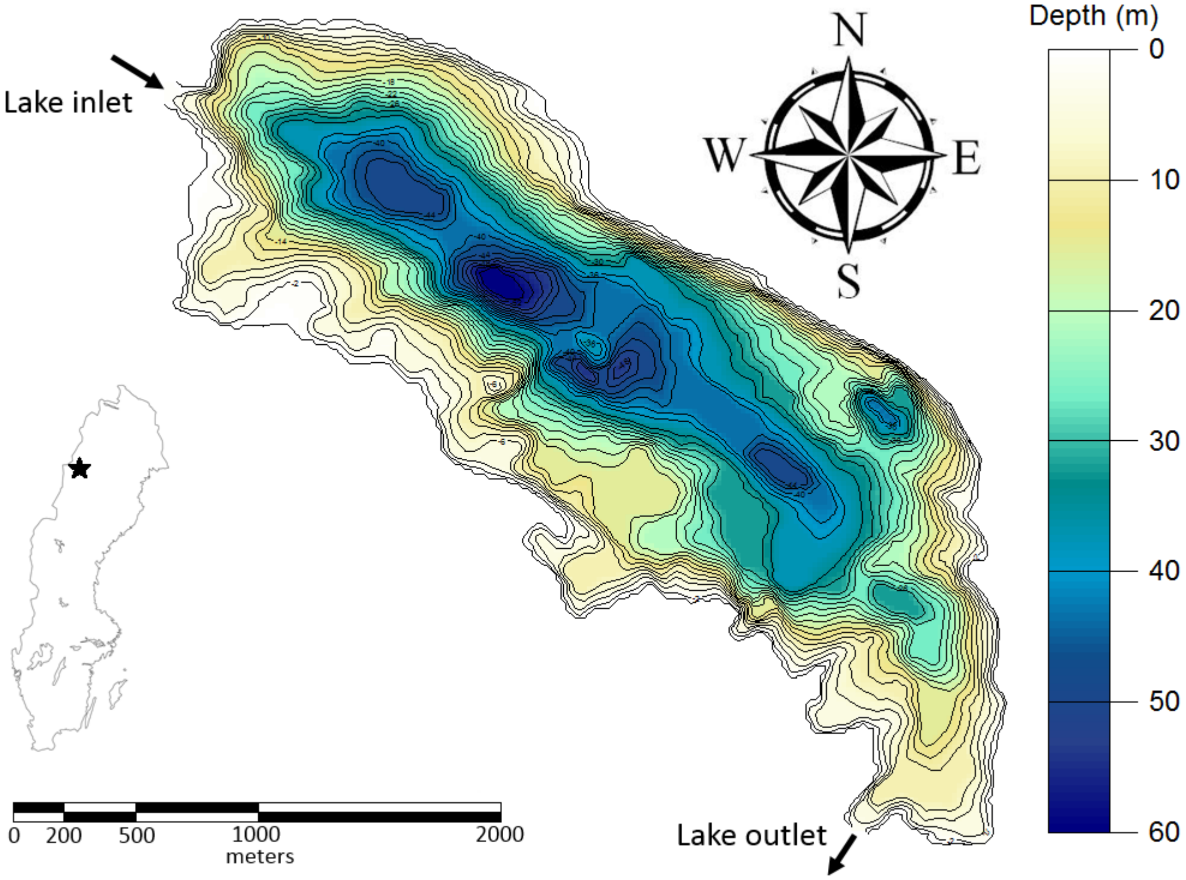


Figure 1. Inset map of Sweden showing the location of my study site (star) and a bathymetric map over Lake Gautsträsk.

Fish tagging and telemetry

Eighteen adult lake charr with a mean length of 720 mm (TL) (SD: ± 110 mm; range: 550 – 970 mm) were caught by angling and gill netting in Lake Gautsträsk and the lower part of the tributary River Tjulån during the summers of 2013 and 2014 and tagged with acoustic transmitters surgically implanted in the body cavity of the fish (see below) (Adams et al 2012). The transmitters recorded both depth and temperature and transmitted a signal in an average interval of 160 seconds the first 300 days and then every 200 seconds. The time between signals were randomized between 100 and 250 seconds to avoid systematic signal collisions (Webber 2009). The transmitters were 48 mm in length, had a diameter of 13 mm and weighed 13 g in air and 6.5 g in water (model V13TP – 69 kHz Vemco Ltd., Halifax, Nova Scotia). The temperature sensors had a range from -4 to 20 °C with an accuracy of ±0.5 °C and a resolution of 0.1 °C. The depth sensor had a maximum depth of 68 meters with an accuracy of ±3.4 meters and a resolution of 0.3 meters. Due to the internally placed tags the temperature records were not from the surrounding water but instead from the abdominal cavity of the fish. This resulted in a time lag when fish moved from one temperature to another for example during a dive through the thermocline or movement into an inlet area with deviating water temperature. Laboratory studies by Negus and Bergstedt (2012) demonstrated this time lag by moving lake charr with surgically implanted thermal sensors between water of different temperatures. After a rapid change in ambient temperature, internal temperature of lake charr moved in general 50% towards the new external temperature within

5 minutes and 90% toward the new temperature within 15 minutes. They also showed that the length of the time lag was positive correlated with fish size.

The fish was anaesthetized in a bath of water with a 0.5 ml/L concentration of 2-phenoxyethanol (Audun Richardsen, pers. comm. 2014). Depending on size and water temperature the fish were then kept in the bath up to three minutes until stage five of anesthesia was reached, i.e. absence of reflexes and slow, irregular opercular movements as defined by Summerfelt and Smith (1990). To measure and easily perform the surgically implantation the fish were then placed in a plastic half pipe with the ventral side up and continuously perfused with well oxygenated water over their gills. A 30 mm long incision was made between the pectoral and pelvic fins 2.5 cm to the right of the midline (Wagner and Stevens 2000) using a scalpel (Swann-Morton Surgical Scalpel Blade No.12). Each incision was only deep enough to penetrate the peritoneum without damaging the internal organs. After inserting the acoustic transmitter the incision was closed by three interrupted stitches tied 7-8 mm apart with surgeon knots. We used individually sterile packed, non-absorbable suture (Ethicon, Perma-hand size 2-0). New sutures and scalpel blades were used for each fish and the forceps were sterilized with ethanol between surgeries. After surgery the fish were transferred to a submerged holding cage where they were allowed to recover for two hours before released back to the lake or river.

A grid of 37 VR2W 69 kHz acoustic receivers (Vemco Ltd., Halifax, Nova Scotia) was used to track the movement, depth and temperature of the tagged lake charr. Receivers were held suspended three meters above bottom by rigs of weights, mooring lines and buoys. In addition to the receivers, 37 transmitters (model V16 – 69 kHz Vemco Ltd., Halifax, Nova Scotia) were also attached to the rigs which were used to synchronize the clocks of the receivers. Three stationary transmitters (model V8 – 69 kHz Vemco Ltd., Halifax, Nova Scotia) with known coordinates were also deployed as reference tags to which the performance of the receiver grid were calibrated (Webber 2009). Omnidirectional hydrophones on the receivers recorded the acoustic signals from the tagged fish and our range tests showed that each receiver could detect > 70 % of the transmitted signals within a spherical volume with a diameter of 1000 meters. The receivers were deployed with a mean distance of 460 meters from each other which resulted in overlapping detection areas of the receivers and hence high detection probability of transmitter signals. Each signal was on average detected by 3.4 receivers which made it possible to positioning the fish with a high accuracy (±5 meters on average). To avoid damages and loss of equipment due to moving ice, all VR2W receivers were collected in late October of both years, hence no winter data were collected.

After retrieving the receivers the data was sent to Vemco Ltd., Halifax, Nova Scotia and analyzed with their positioning service (VPS) where the differences between time of detection among the receivers was used in a time-difference-of-arrival (TDOA) algorithm to calculate the position of the fish (Webber 2009, Espinoza et al. 2011). After triangulation the data consisted of observation with time, coordinates and fish-ID together with depth or temperature. Since the tags switched between sending information on depth and temperature every other transmission an interpolation was made to fill the missing values.

Habitat analysis

The depth of Lake Gautsträsk was surveyed using an echo sounder (Hummingbird 798ci HD SI Combo) along transects forming a grid of depth measurements. A bathymetric map was then interpolated from that data (see Figure 1) using akima interpolation (Akima 1978).

Water temperature was continuously measured at 6 hours interval at three different locations in Lake Gautsträsk from September 8th to October 22nd in 2013 and June 2nd to October 17th in 2014 using temperature data loggers (HOBO TidbiT v2). Each location had a vertical mooring line with loggers attached to it every fifth meter from the surface and down to the bottom. The loggers stored date and time linked together with temperature measurement, forming a continuous temperature profile of the lake. The first two months of 2013 no data from temperature loggers was available, instead temperatures from fish was used to monitor thermal lake profile during this period.

Statistical analysis of bathythermal habiatat use

To evaluate the importance of temperature and depth on habitat selection by lake charr two methodological approaches were used. The first approach tested for differences in temperature use between lake charr and a null model. The null model consisted of a set of random walks (RW) where a number of simulated particles were allowed to move around the lake during the same time as the lake charr. The movement of the particles was constricted by a set of rules derived from the movement of the actual fish: 1) the particles moved every 200 second to mimic the average time interval of the real fish trajectories based on the signal delay of the acoustic transmitter 2) every time-step the particle moved a randomized distance between 0 m and the maximum observed distance a lake charr moved during one time-step 3) the direction of the movement was randomized between 0 and 360 degrees from the previous position 4) every time-step the particle made a randomized depth alteration between 0 m and the maximum observed depth alteration a lake charr made during one time-step 5) the particle could only move within the confines of the lake. These set of rules generated a dataset consisting of particle trajectories with coordinates and depth that followed the same physiological constrains as the lake charr. These positions were, however, assumed to be free of any habitat selection preference due to the randomized angle, distance and depth-alteration made between each time-step. For each RW-particle position, temperatures was extracted from the interpolated thermal profile of the lake and for each individual lake charr, one RW-particle was generated. To investigate whether lake charr moved based on temperature, difference in mean temperature between the RW-dataset and the observed lake charr data were tested using a two-way ANOVA, treating temperature as a response variable and type (fish or RW-particle) as a two level fixed effect and season as a three level fixed effect (spring, summer, autumn). Season was included to account for the variation in thermal profile due to stratification. If fish and the RW-particle differed significantly in temperature, it was concluded that lake charr temperature use was not random. To further explore any interaction effect, I used Tukey HSD test. Difference between fish and RW-particles in depth use was also tested, using an identical model structure as the temperature model, but with depth as response variable.

In the second approach I analyzed responses of bathythermal habitat use to changes in available temperatures over time. Each year was divided into spring, summer and autumn, defined by the time when the lake circulated. Differences in temperature and depth use between each period (i.e. spring, summer and autumn) and year (2013, 2014) was tested using a two-way ANOVA, treating temperature or depth as response variables, and season and year as fixed effects. In addition to the ANOVA I also used Tukey HSD test to explore any interaction effects. To avoid biased mean values I excluded individuals that only contributed with data during a restricted number of days of each season, e.g. individuals tagged in late spring was excluded from that season or individuals with transmitter battery failure in early summer was excluded from that season.

In addition to the two approaches for evaluating the importance of temperature on habitat selection I also analyzed the temperature and depth conditions associated with lake charr activity. Here I used the distance and time between each relocations from the fish trajectories to get an average speed (m/s) as a measure for activity. This analysis was done for the thermally stratified summers to capture both depth as well as temperature use in relation to activity.

Results

Thermal profile of Lake Gautsträsk

From the start of our measurements (7th of July 2013) Lake Gautsträsk was thermally stratified with temperatures stretching from 5°C to 17°C (figure 2). Epilimnion had temperatures between 10°C and 17°C and the thermocline was in the beginning of July at a depth of 17 meters and slowly dropping down to 20 meters and a short dip down to 22 meters just before the autumn circulation which occurred in the last days of September. Hypolimion had a temperature range from 5 to 7.5C. After the circulation the whole homogenous water column slowly cooled off down to 4°C in the end of October when we retrieved our equipment from the lake. The following year we started our measurements in the beginning of June when the lake had a homogenous temperature of 4°C (figure 3). A cold first month of the summer with air temperatures below 10°C resulted in a slow increase of temperature of the lake up to 7°C. Not until the last days of June, with increasing air temperatures, did the lake stratified into clearly defined epi-, meta-, and hypolimnion. Daily temperatures well over 20°C through July and most of August lead to high surface temperatures exceeding 20°C until middle of August. The epilimnion of 2014 had a temperature range from 10°C to 23°C but did not, however, stretch as deep as the epilimnion of 2013. 13 meters down in the water column, the thermocline with a temperature of 8°C to 10°C divided the warmer surface water from the 6.5 to 7.5°C hypolimnion. In the end of August the surface water had dropped down to 15°C and continued down to around 8°C in the end of September when the whole lake circulated.

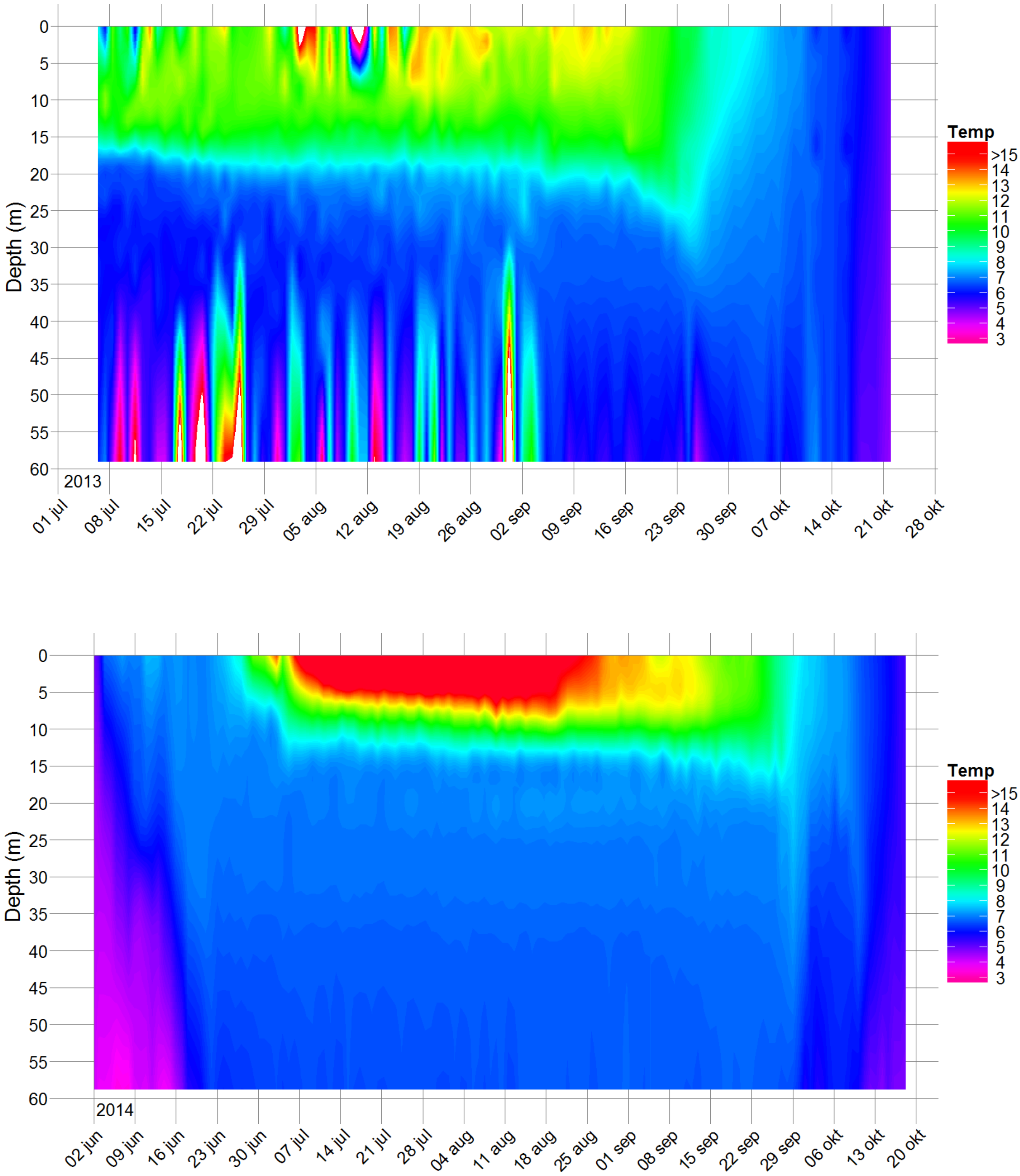
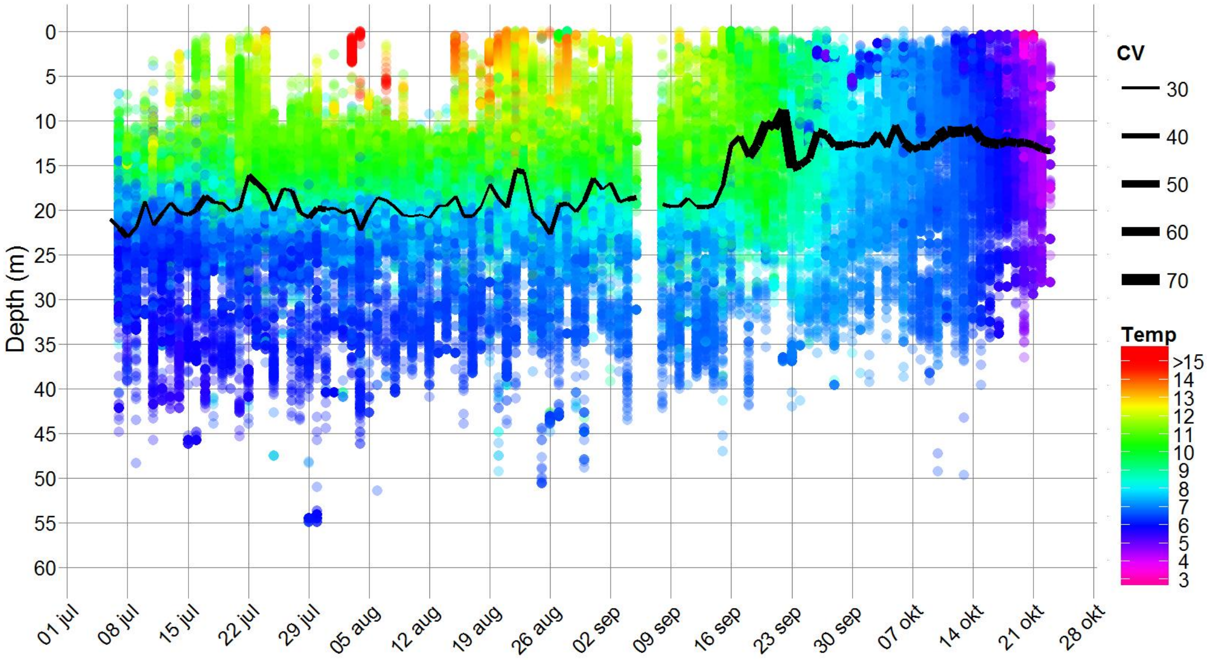


Figure 2. Thermal profile of Lake Gautsträsk from 2013 (top) and 2014 (bottom) interpolated from measurements recorded by temperature data loggers. No logger data was available from 7th of July to 5th of September 2013, instead fish records were used for this period. Low number of detections outside a range from 10 to 35 meters led to weaker interpolation at these depths, thus the high variance in temperatures.



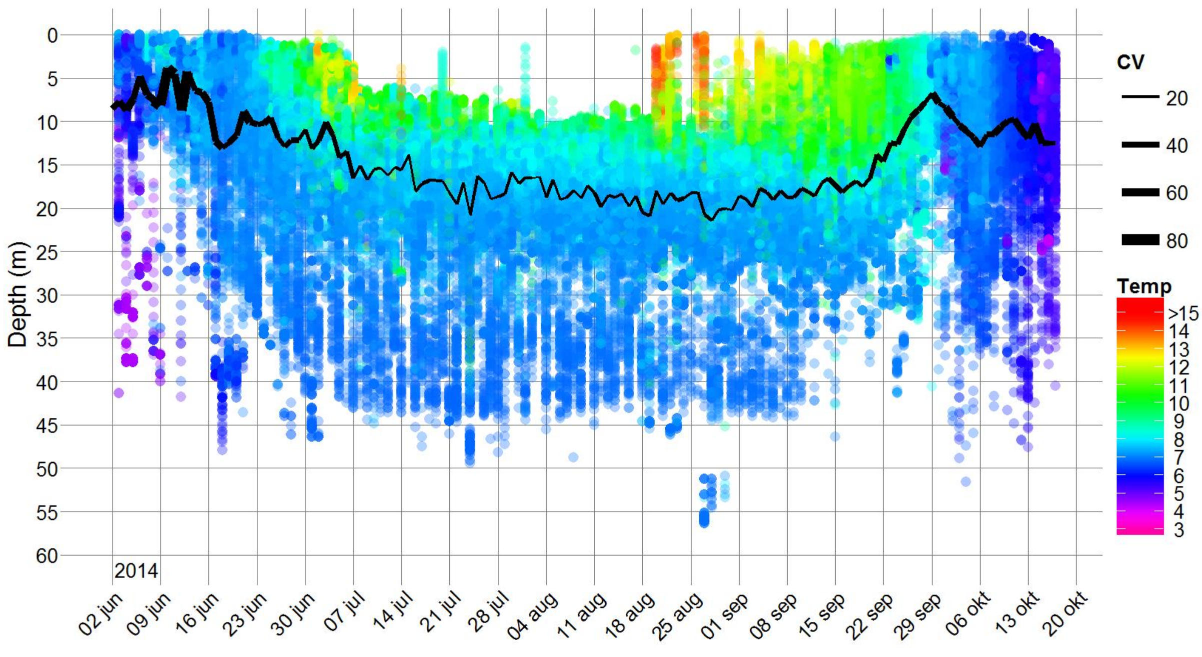


Figure 3. Bathythermal records of lake charr in Lake Gautsträsk from 2013 (top) and 2014 (bottom). Daily mean depth is plotted with black line with thickness representing coefficient of variance (CV).

Aproach 1: Comparison between lake charr and RW-particles

<u>Temperature</u>

The interaction term between season and type was significant (ANOVA: $F_{2,79} = 216.4$, $P < 0.001$, see table 1), indicating that the effect of type on temperature depended on the season. Mean temperature differed between fish and RW-particles only during the summer (Tukey HSD, $P < 0.001$, figure 4), with the fish having a lower mean temperature than the RW-particles (7.8°C for fish vs. 10.2°C for RW-particle). No difference in mean temperature between fish and RW-particles could be found for spring and autumn (Tukey HSD, $P > 0.05$), although there was a tendency of higher temperatures of fish in spring.

<u>Depth</u>

A significant interaction term between type and season (ANOVA: $F_{2,73} = 24.38$, $P < 0.001$, see table 1) indicated a dependency effect of type due to season. Tukey HSD tests concluded significant differences between fish and RW-particles in depth use for all three seasons (Tukey HSD, $P < 0.01$, figure 4). Compared to the RW-particles, fish showed a shallower use of depths in spring (9.2 m vs. 14.8 m) and autumn (11.9 m vs. 14.9 m), and deeper in summer (17.6 m vs. 14.8 m). The individual mean depths and temperatures for lake charr and RW-particles are illustrated in boxplots in figure 4.

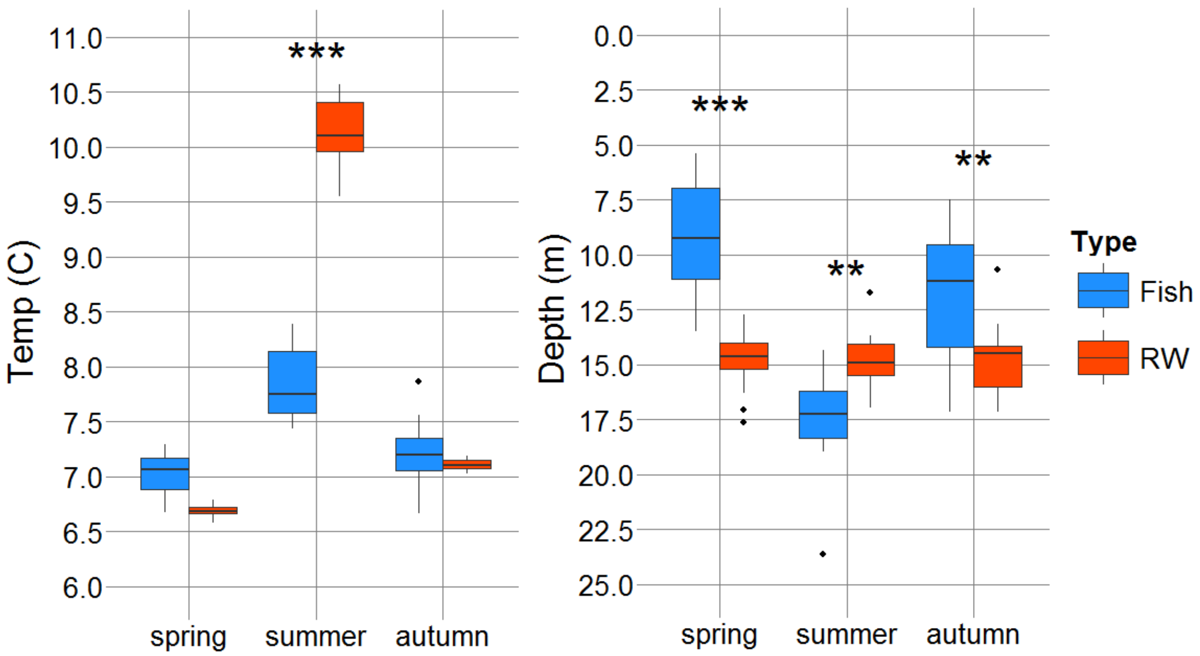


Figure 4. Boxplot showing individual mean depths and temperatures occupied by lake charr and random walk (RW) in Lake Gautsträsk during spring, summer and autumn 2014. Horizontal line within box = median; ends of box = 25th and 75th percentiles; ends of whiskers=10th and 90th percentiles; dots = outliers. Asterisks represent *P*-value if significant difference was found with ANOVA-test. *** = $P < 0.001$; ** = $P < 0.01$; * = $P < 0.05$

Table 1. Results of ANOVA-test examining factors influencing the mean temperature and depth occupied by lake charr and random walk in Lake Gautsträsk during 2014. The main effects were season (spring, summer, autumn), type (fish, random walk), and the season ×

Dependent variable	Fixed effect	df, residuals	*F*	*P*
Temp	Season	2. 79	752.4	<0.001
	Type	1. 79	159.6	<0.001
	Season × Type	2. 79	216.4	<0.001
Depth	Season	2. 73	9.60	<0.001
	Type	1. 73	7.50	<0.001
	Season × Type	2. 73	24.38	<0.001

Approach 2. Comparison between years and seasons

Temperature

When a warm epilimnion was present, lake charr avoided the shallow most depth of the lake. During the stratified summers less than 2% of lake charr observations recorded temperatures exceeding 12°C. Temperature use differed between 2013 and 2014 (ANOVA: $F_{1,46} = 4.245$, $P < 0.05$, see table 2), where lake charr (over the whole year) utilized slightly warmer water in 2013 compared to 2014 (7.9°C vs. 7.4°C). The effect of season on temperature use was dependent on year (ANOVA, interaction term "Season × Year", $F_{1,46} = 10.92$, $P = 0.0019$, see table 2). Temperature use in summer differed significantly from spring and autumn in both years (2013 8.7°C vs. 7.0°C; 2014 7.8°C vs. 7.1°C, Tukey HSD, $P < 0.05$, figure 5).

Depth

No difference in depth use was found between the years, there were however significant difference between seasons (ANOVA: $F_{2,40} = 18.58$, $P < 0.001$, see table 2). Tukey HSD tests revealed that depth use in summer significantly differed from spring and autumn within each year ($P < 0.05$, figure 5). No differences in depth between the summers nor autumns of 2013 and 2014 could be found.

The highest mean depths and temperatures of both years were recorded during the summer when the lake was stratified (2013 19.4 m, 2014 17.2 m). The summer period also had the lowest variance in depth but the highest variance in temperature. The opposite was true for spring and autumn with low mean depths and temperature, high variance in depth and low variance in temperature. The individual mean depths and temperatures for all seasons both year are illustrated in boxplots in figure 5.

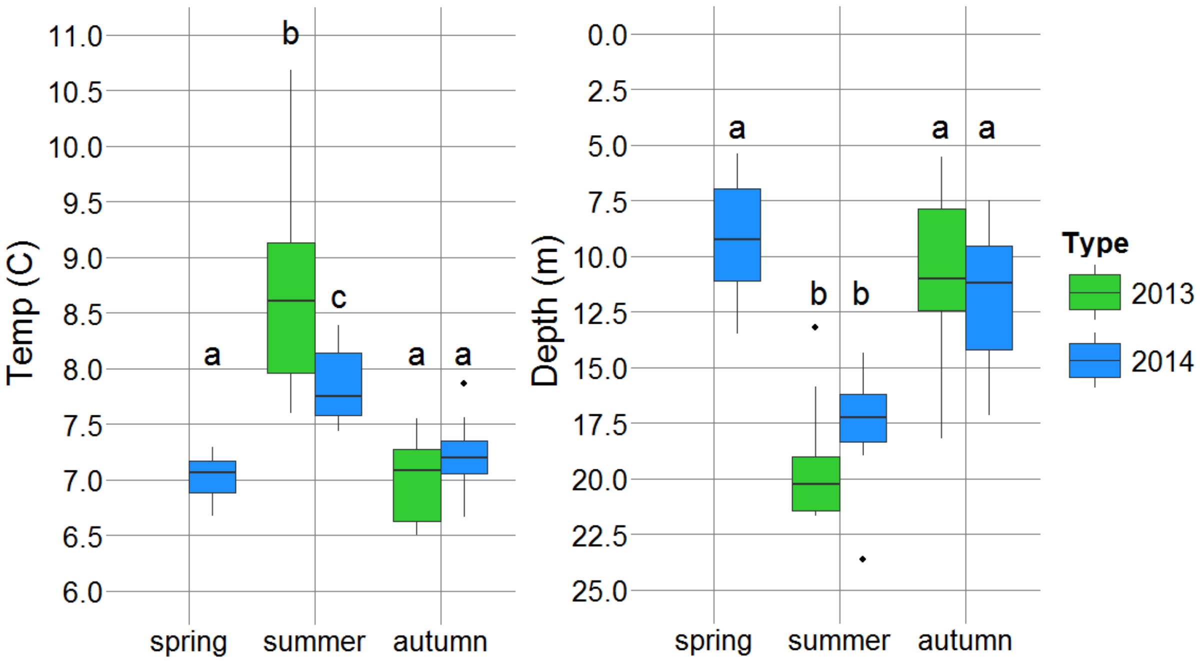


Figure 5. Boxplot showing mean depths and temperatures occupied by individual lake charr in Lake Gautsträsk during spring, summer and autumn 2013 and 2014. Horizontal line within box = median; ends of box = 25th and 75th percentiles; ends of whiskers=10th and 90th percentiles; dots = outliers. Letters represent significant differences found with ANOVA-test. **a** significantly differed from **b** and **c**, **b** significantly differd from **a** and **c**, *P*

Table 2. Results of ANOVA-test examining factors influencing the mean temperature and depth occupied by lake charr in Lake Gautsträsk during 2014. The main effects were season (spring, summer, autumn), year (2013, 2014), and the season × year interaction.

Dependent variable	Fixed effect	df, residuals	*F*	*P*
Temp	Season	2. 46	29.75	<0.001
	Year	1. 46	4.24	0.0452
	Season × Year	1. 46	10.92	0.0019
Depth	Season	2. 40	18.58	<0.001
	Year	1. 40	0.68	0.41
	Season × Year	1. 40	0.35	0.55

More than 75% of lake charr observations during the thermally stratified summers occurred at depths from 10 and 25 meters although this depth span only represents 35% of the lakes total water volume. The average swimming speed of lake charr at different depths showed a different pattern. The summers had a peak in activity in the shallow most water and high values in a range from 30 to 45 meters with a peak at 40 meters (figure 6).

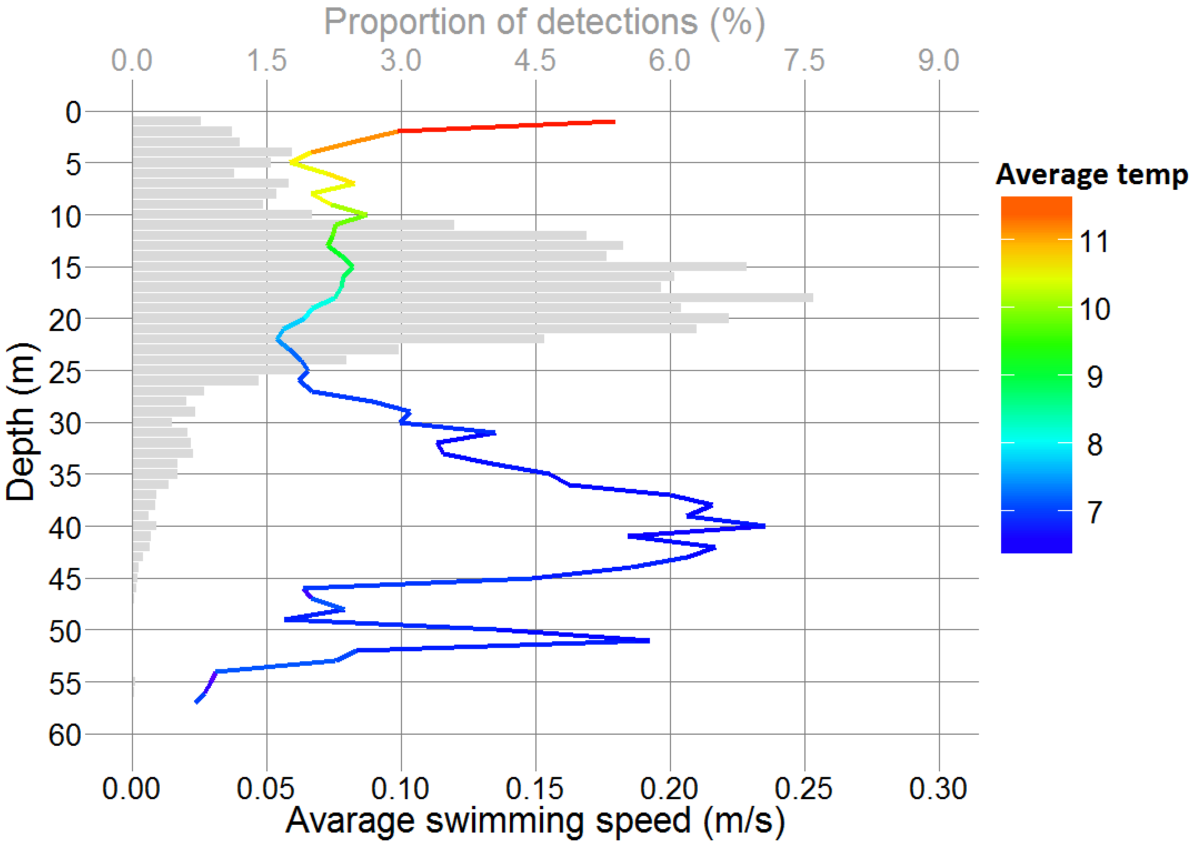


Figure 6. Depth diagram in one meters interval showing proportion of lake charr detections (bars) and average swimming speed (m/s) (line) with color representing average occupied

Discussion

This study shows that temperature use in lake charr is not random, as the observed temperature use by lake charr differed from that of a random particle. Seasonal differences in temperature and depth use strongly indicated that the spatial distribution of lake charr is influenced by temperature, and that an upper thermal limit exist (~12°C) above which lake charr rarely resides. Based on the time lake charr spent at different temperature regimes, lake charr have a temperature preference of 8.2°C ± 0.8°C. However, activity data show that this temperature range is not where the lake charr is the most active.

Thermal profile of Lake Gautsträsk

The thermal profile of Lake Gautsträsk differed from 2013 to 2014. Most profound was the differences during the summers when the lake was thermally stratified. There was on average colder temperatures 2013 than 2014 but the deep thermocline of 2013 allowed warm surface water to circulate down to 20 meters. The opposite situation occurred 2014 where on average warmer temperatures was recorded in the lake but a shallow thermocline prevented the warm surface water from circulating deeper than 13 meters.

Bathythermal habiatat use of lake charr

Approach 1: Comparison between lake charr and RW-particles

With the results from my ANOVA-analysis between fish and RW I can discard my null hypothesis that lake charr choose temperature randomly. Lake charr differ significantly in bathythermal habitat use from RW, i.e. they actively avoid or exploit certain habitats of the lake in regard to depth and temperature. The average depth of the RW was approximate 15 meters during all seasons. Compared to the RW, the observed depths of the fish was significantly deeper during summer. The mean difference in depth was 2.8 meters which resulted in temperature difference of around 2.4°C. While the RW used all of the water column, both the deep cold water and the warm surface water, the fish avoided the epilimnion during the warmest part of the summer and therefore ended up with a colder mean temperature. The mean depths of fish during spring and autumn was significantly shallower compared to RW but this did not result in any significant difference in temperature since the lake had a more homogenous temperature profile during these periods. The homogenous temperature profile during spring and autumn also affected the variation of depth used by the fish. With little or no thermal stratification of the lake, lake charr moved more freely in the vertical axis. The higher variance in use of depth was true both on a daily basis within each individual (figure 3) and over the whole seasons between individuals (figure 4). The result hence confirms that temperature is a driver in lake charr behaviour. Random walk theory is a powerful method when investigating the importance of environmental factors on habitat selection (Manly 2001) as it take into account the availability of different temperatures in the lake, in contrast to a more descriptive approach (e.g. approach 2 in this thesis) which just focus on the utilized temperatures of the fish in the lake. By concluding that temperature use is not random in lake charr, the more descriptive data from approach 2 in this study gains more relevance.

Approach 2. Comparison between years and seasons

During the thermally homogenous periods of the year, i.e. spring and autumn, the lake charr resided in the shallow parts of the water column with an individual mean depth of 11.5 m (SD ± 4.7 m) and a temperature of 7.1°C (SD ± 0.3°C). Fish records from the stratified summer had greater individual mean depth, 18.5 m (SD ± 2.8 m) and higher mean temperature (8.2 ± 0.8°C) with few positions of lake charr recorded above metalimnion. These long term data on depth and temperature utilization indicate that when there is no variation in temperature present, i.e during spring and autumn, and hence no options for the fish to choose a preferred temperature, lake charr resides in shallower water. When variation in temperature is present, i.e during the stratified summer, lake charr choose to reside in deeper, colder water. Moreover, in the homogenous spring and autumn, variation in depth use is considerably larger than during summer as indicated by the larger standard deviation, as well as the coefficient of variation seen in figure 3. This point to the importance of temperature as the lake charr seem to 1) adjust depth to regulate temperature 2) become more confined within a narrower depth zone when a temperature gradient is present. Their most frequently utilized temperature of 8.2°C during the stratified periods of this study is in the lower margin of preferred temperature range of 10°C ± 2°C reported from previous studies (Ferguson 1958, Coutant 1977, Christie and Regier 1988) and well below the optimum growth temperature of 12.5°C described by Edsall and Cleland (2000). These temperatures are however derived from laboratory experiments or very limited sampling in field. More recent studies with data collected from fish tagged with archival temperature tags (Bergstedt et al. 2003), data storage tags (Bergstedt et al. 2012) and acoustic tags (Plumb and Blanchfield 2009, Mackenzie-

Grieve and Post 2006) have reported temperatures occupied by lake charr more similar to those I have observed in this study with temperature preferendum ~ 8°C. Long term, in-situ studies consistently reports colder temperature preferendum than those derived from laboratory studies. My results also support this and suggesting that temperature preferences acquired from laboratory studies does not match the temperatures lake charr prefer in nature. This discrepancy may be due to lake charr having to trade-off optimal temperature use to other needs, such as foraging. However, as seen below, activity data does not support this hypothesis.

Temperature in boreal lakes varies over the year and variation is most profound at the vertical axis. Temperature use of fish in boreal lakes is hence often closely correlated to their vertical distribution. Depth preferences in fish may, however, not be determined by temperature per se, as depth itself may provide both protection and food resources. Disentangle the effect of depth and temperature on fish behaviour is needed to evaluate importance of temperature. My method of evaluating bathythermal habitat use of lake charr by comparing their residence during different thermal conditions was facilitated by the different thermal conditions of 2013 and 2014. The differences in lake temperatures between seasons within each year was expected but the differences between summers of 2013 and 2014 was however not predicted. Because of the altered thermocline depth from one year to another, preferences of depth could be separated from preferences of temperature which otherwise can be hard to distinguish since they are strongly correlated in a thermally stratified lake. The comparisons between summers of 2013 and 2014 showed no significant differences in depth utilization, the observed temperatures of 2013 was however significantly colder than those from 2014. This is explained by the mean depths of the fish in relation to the thermocline which in 2013 occurred at around 20 meters compared to 12 meters in 2014 (see figure 1). The mean depths of fish in 2013 was slightly deeper than those in 2014 but not enough to compensate for the difference in depth of thermocline and its corresponding temperature. In 2013, fish resided on average at the lower margin of the thermocline compared to five meters below thermocline in 2014, thus explaining the lower temperatures of the fish in 2014. This similar use of depth in contrasting thermal regimes suggests that, to some extent, lake charr adapt to different temperatures. Bathymetric structure and bottom substrate could override the absolute temperature preferendum of 8.2°C as long as temperatures stay within an, to lake charr, acceptable range. I would argue that a span around 8.2°C stretching from 7.5°C to 10.5°C would best describe lake charr temperature preferendum given the individual mean temperatures from the summer periods shown in figure 5. The results however also shows that during time when warm epilimnic water is present, less than 2% of lake charr observations have recorded temperatures exceeding 12°C. This is evident also when looking at the summer months in figure 3 where temperatures > 12°C (yellow and red) is clearly underrepresented indicating this as an upper thermal limit.

Distribution of lake charr during the stratified summers, i.e. when they have the possibility to choose temperature, concluded 8.2°C as their preferendum. 75% of fish observation during this period occurred at depths between 10 and 25 meters which corresponded to temperatures from 7.5°C to 10.5°C. The level of activity at these temperatures were however at minimum, suggesting that these water volumes were mostly used for shelter and food digestion. High level of activity was instead found at depths between 30 and 45 meters and in the surface water, most likely related to search for prey. Thus, there is indication for a trade-off between habitat with high prey density, but less favorable temperatures and habitat with low prey density, but more favorable temperatures as described for other species of fish (Garner et al. 1998, Wildhaber 2001)

This study concludes that temperature has a strong effect on behaviour and habitat use in lake charr. My results support earlier studies describing lake charr as a cold water stenotherm with a temperature preference of 8.1°C and an above limit of 12°C. I also conclude that lake charr temperature preference in nature is slightly lower than that reported from laboratory studies which is important to consider when designing ecological and conservational models for risk assessment of invasive species success or habitat loss in predicted climate scenarios.

Acknowledgment
First and foremost I would like to thank my supervisor Gustav Hellström, not only for advice with data analysis and comments on writing but also for including me through the whole process of this study. Many thanks to Ammarnäs FvO, the local fishing organization, for providing logistical support throughout the field work. The study was dependent on several parts to succeed and I highly value the expertise assistance from Rickard Linderot with capture of fish and Johnny Norrgård with fish tagging. I would also like to thank Micael Jonsson for bringing clarity on data analysis and statistics in moment of doubts.

References

Adams, N. S., Beeman J. W. and Eiler J. H., editors. (2012) Telemetry techniques: a user guide for fisheries research. American Fisheries Society, Bethesda, Maryland.

Akima H. (1978) A method of bivariate interpolation and smooth surface fitting for irregularly distributed data points. ACM Transactions on Mathematical Software 4(2), 148-159

Beitinger T.L. and Fitzpatrick L.C. (1979) Physiological and ecological correlates of preferred temperature in fish. American Zoologist 19(1), 319-329.

Bergstedt R. A., Argyle R. L., Krueger C. C. and Taylor W. W. (2012) Bathythermal habitat use by strains of Great Lakes- and Finger Lakes-origin lake charr in Lake Huron after a change in prey fish abundance and composition. Transactions of the American Fisheries Society 141(2), 263-274

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 use by lake charr (*Salvelinus namaycush*) in Lake Huron. Journal of Great Lakes Research 29(1), 347–361

Christie G.C. and Regier H.A. (1988) Measures of optimal thermal habitat and their relationship to yields for 4 commercial fish species. Canadian Journal of Fisheries and Aquatic Sciences 45(2), 301-314.

Coutant C.C. (1977) Compilation of temperature preference data. Journal of the Fisheries Research Board of Canada 34(5), 739-745.

Davis M.A. (2009) Invasion Biology. Oxford University Press. New York

Edsall T. A. and Cleland J. (2000) Optimum temperature for growth and preferred temperatures of age-0 lake charr. North American Journal of Fisheries Management 20, 804–809

Espinoza M., Farrugia T.J., Webber D.M., Smith F. and Lowe C.G. (2011) Testing a new acoustic telemetry technique to quantify long-term, fine-scale movements of aquatic animals. Fisheries Research 108(2-3), 364-371

Ferguson R.G. (1958) The preferred temperature of fish and their midsummer distribution in temperate lakes and streams. Journal of the Fisheries Research Board of Canada 15(4), 607-624.

Garner P., Clough S., Griffiths S.W., Deans D. and Ibbotson A. (1998) Use of shallow marginal habitat by *Phoxinus phoxinus*: a trade-off between temperature and food? Journal of Fish Biology 52(3), 600-609.

Jobling M. (1981) Temperature tolerance and the final preferendum—rapid methods for the assessment of optimum growth temperatures. Journal of Fish Biology 19, 439–455

Johnston I.A., Bower N.I. and Macqueen D.J. (2011) Growth and the regulation of myotomal muscle mass in teleost fish. Journal of Experimental Biology 214(10), 1617-1628.

Mackenzie-Grieve J.L. and Post J.R. (2006) Thermal habitat use by lake charr in two contrasting Yukon Territory lakes. Transactions of the American Fisheries Society 135(3), 727-738

McCauley R. W., and Tait J. W. (1970) Preferred temperature of yearling lake charr, *Salvelinus namaycush*. Journal of the Fisheries Research Board of Canada 27, 1729–1733

Manly B.F.J., McDonald L., and Thomas D. (2001) Resource Selection by Animals: Statistical Design and Analysis for Field Studies. Springer.

Negus M. T. and Bergstedt R. A. (2012) Rates of intraperitoneal temperature change in lake charr implanted with archival tags. Transactions of the American Fisheries Society, 141(2), 383-391

Peterson R. H., Sutterlin A. M. and Metclife J. L. (1979) Temperature preference of several species of *Salmo* and *Salvelinus* and some of their hybrids. Journal of the Fisheries Research Board of Canada 36(9), 1137-1140

Plumb J. M. and Blanchfield P. J. (2009) Performance of temperature and dissolved oxygen criteria to predict habitat use by lake charr (*Salvelinus namaycush*) Canadian Journal of Fisheries and Aquatic Sciences. 66, 2011–2023

Summerfelt R.C. and Smith L.S. (1990) Methods for fish biology. pp. 213-272, American Fisheries Society, Bethesda, Maryland.

Wagner G.N. and Stevens E.D. (2000) Effects of different surgical techniques: Suture material and location of incision site on the behaviour of rainbow trout (*Oncorhynchus mykiss*). Marine and Freshwater Behaviour and Physiology 33(2), 103-114.

Webber, D. (2009). VEMCO Acoustic telemetry new user guide. Vemco Inc. Amrix Systems. DOC-004934-01

Wildhaber M.L. (2001) The trade-off between food and temperature in the habitat choice of bluegill sunfish. Journal of Fish Biology 58(5), 1476-1478.

Wootton R. J. (1998) Ecology of Teleost Fishes. Springer.

SENASTE UTGIVNA NUMMER

2014:15 The Secret Role of Elephants - Mediators of habitat scale and within-habitat scale predation risk
Författare: Urza Flezar

2014:16 Movement ecology of Golden eagles (Aquila crysaetos) and risks associated with wind farm development
Författare: Rebecka Hedfors

2015:1 GIS-based modelling to predict potential habitats for black stork (Ciconia nigra) in Sweden
Författare: Malin Sörhammar

2015:2 The repulsive shrub – Impact of an invasive shrub on habitat selection by African large herbivores
Författare: David Rozen-Rechels

2015:3 Suitability analysis of a reintroduction of the great bustard (Otis tarda) to Sweden
Författare: Karl Fritzson

2015:4 AHA in northern Sweden – A case study
Conservation values of deciduous trees based on saproxylic insects
Författare: Marja Fors

2015:5 Local stakeholders' willingness to conduct actions enhancing a local population of Grey Partridge on Gotland – an exploratory interview study
Författare: Petra Walander

2015:6 Synchronizing migration with birth: An exploration of migratory tactics in female moose
Författare: Linnéa Näsén

2015:7 The impact of abiotic factors on daily spawning migration of Atlantic salmon (Salmo salar) in two north Swedish rivers
Författare: Anton Holmsten

2015:8 Restoration of white-backed woodpecker *Dendrocopos leucotos* habitats in central Sweden – Modelling future habitat suitability and biodiversity indicators
Författare: Niklas Trogen

2015:9 BEYOND GENOTYPE Using SNPs for pedigree reconstruction-based population estimates and genetic characterization of two Swedish brown bear (Ursus arctos) populations
Författare: Robert Spitzer

2015:10 Hot, hungry, or dead: how herbivores select microhabitats based on the trade-off between temperature and predation risk
Författare: Kristina Vallance

2015:11 Habitat diversity and composition among growing wild boar (*Sus scrofa L.)* populations in Sweden
Författare: Sebastian Olofsson

Hela förteckningen på utgivna nummer hittar du på www.slu.se/viltfiskmiljo