

SPATIAL AND THERMAL ECOLOGY OF LAKE TROUT (*SALVELINUS NAMAYCUSH*) IN
LAKE ERIE

By

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ABSTRACT

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Rehabilitation of lake trout (*Salvelinus namaycush*), which historically was the coldwater apex predator of much of the Laurentian Great Lakes, is a priority for fishery management agencies in the region. In Lake Erie, the shallowest and southern-most Great Lake, successful rehabilitation of lake trout has been hindered by limited wild recruitment, possibly related to the lake's warm temperatures and restricted oxythermal habitat. I used acoustic telemetry tracking technology to investigate how lake trout spatial and thermal habitat use varies seasonally in Lake Erie to better understand whether limited recruitment could be caused by thermal conditions in the lake. As expected, lake trout were restricted to the offshore region of the eastern basin of Lake Erie during summer stratification. During fall, lake trout tended to occupy the southern nearshore region of the eastern basin, suggesting the importance of focusing spawning habitat restoration in this part of the lake. Tagged fish dispersed long distances at much higher frequencies than other Great Lakes populations of lake trout. Lake trout in Lake Erie occupied thermal habitat similar to other Great Lakes populations during summer stratification. Following destratification in fall, fish were exposed to warm temperatures, in some years for extended periods. Lake trout hatchery strains of Finger Lakes, NY, origin occupied similar summer temperatures and warm temperatures for more days during fall than Great Lakes origin strains, contrary to findings from Lakes Huron and Ontario. These results reveal behaviors that can inform management of lake trout in Lake Erie and throughout the Great Lakes and could begin to explain recruitment failure observed in Lake Erie.

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INTRODUCTION

Lake trout (*Salvelinus namaycush*) historically were the native, coldwater apex predator of the Laurentian Great Lakes (Bronte et al. 2008; Muir et al. 2013). As an apex predator, lake trout exert top-down forces on lower trophic levels, which can play an important role in maintaining ecosystem function and diversity (reviewed in Sergio et al. 2014). The importance of a healthy apex predator population is exemplified in disrupted systems such as the Laurentian Great Lakes (Bence et al. 2008; Bunnell et al. 2014). Apex predators act as biotic resistance to invasions (Sergio et al. 2014), which is immensely important in a system like the Great Lakes, one of the most heavily invaded systems in the world (Ricciardi and MacIssac 2000; Ricciardi 2006). The role that apex predators play in providing resistance to invasions is heightened when the invader is a stronger competitor than native species (Carlsson et al. 2009; Juliano et al. 2010). This phenomenon has been demonstrated in many different systems and can often be attributed to changes in the behavior of the invasive species that limits competitive ability (Salo et al. 2008; Hollings et al. 2016) or the vulnerability of the invasive to predation due to a lack of coevolution with the predator (Juliano et al. 2010). Ecosystems with a top predator are known to generally have higher biodiversity than those without (Sergio et al. 2006). Additionally, the loss of a top predator threatens ecosystem stability and biodiversity (Edwards et al. 1990; Bronte et al. 2010; Hollings et al. 2016). For example, lake trout in Lake Superior are believed to function as a keystone predator that maintains diversity and stability of lower trophic levels by foraging on the most abundant forage fish species (Bronte et al. 2010). When lake trout populations collapsed due to overfishing and sea lamprey (*Petromyzon marinus*) predation (Lawrie and Rahrer 1972), shortjaw cisco (*Coregonus zenithicus*) populations similarly collapsed due to competition and predation from non-native fish species (e.g., rainbow smelt; *Osmerus mordax*) that had been

previously suppressed through lake trout predation (Bronte et al. 2010). Conversely, once lake trout populations recovered, the native forage base stabilized as lake trout primarily foraged on dominant invasive rainbow smelt (Gorman 2012).

In the Great Lakes, lake trout are important for energy transfer among profundal, pelagic, and nearshore habitats (Ives et al. 2019) and lake trout population status can be an indicator of overall ecosystem health (Edwards et al. 1990). However, lake trout were extirpated from most areas of the Great Lakes due to a combination of overfishing, predation by invasive sea lamprey, and habitat loss (Hartman 1973; Muir et al. 2013). Rehabilitation of this ecologically and economically important species is a high priority for several Great Lakes fishery management agencies (Krueger et al. 1995; Bronte et al. 2008; Zimmerman and Krueger 2009; Muir et al. 2013; Lake Erie Committee 2021). In Lake Erie, lake trout were extirpated by the 1960s (Moenig 1970; Hartman 1973), which led to the initiation of a lake trout stocking program in the 1980s with a goal of reestablishing a self-sustaining population (Cornelius et al. 1995; Markham et al. 2008). Reestablishment of a self-sustaining lake trout population in Lake Erie's eastern basin is deemed essential for ecosystem stability (Lake Erie Committee 2021). Successful achievement of a self-sustaining population is anticipated to promote reestablishment of native forage species including lake whitefish (*Coregonus clupeaformis*) and cisco (*Coregonus artedii*), which may be suppressed via competition and predation by invasive rainbow smelt and to a lesser degree alewife (*Alosa pseudoharengus*; Oldenburg et al. 2007). Rehabilitation efforts have successfully established a population of hatchery-origin, sexually mature fish but no significant natural recruitment to the population has been documented (Lake Erie Committee 2021; Coldwater Task Group 2022) despite limited evidence of spawning aggregations and gamete collection in the wild (Fitzsimons and Williston 2000). Currently, the population is primarily

comprised of three hatchery strains originating from Lake Champlain (Vermont), the Finger Lakes (i.e., Seneca Lake, New York), and to a lesser extent Slate Island (Lake Superior, Ontario; Coldwater Task Group 2022).

Restoration of lake trout and other coldwater fish species is ostensibly hindered by the geomorphological constraints of Lake Erie and anthropogenic nutrient loading that has reduced habitat availability (Francis et al. 2020). Lake Erie consists of three basins: (1) the shallow (mean depth 7.4 m), isothermal, eutrophic western basin; (2) the mesotrophic central basin (mean depth 18.5 m), which stratifies on an annual basis with a very narrow (< 2 m) hypolimnion that often becomes anoxic; (3) the deep (mean depth 24.4 m, max depth 64 m) oligotrophic eastern basin which stratifies on an annual basis and provides cold highly-oxygenated habitat year-round (< 10 °C, > 4 mg L⁻¹; Schertzer et al. 1987; Bolsenga and Hendendorf 1993). Historic fishery harvest and population assessment records indicate that lake trout and other coldwater species (e.g., burbot *Lota lota*, cisco, and lake whitefish) primarily used the eastern basin year-round, including to spawn along the shoreline (water depth < 15 m) during late fall. However, a smaller population contingent (Secor 1999) of lake trout was believed to use the western basin of Lake Erie and Detroit River during the fall to spawn (Moenig 1970; Cornelius et al. 1995; Cox 2013).

Lake trout are physiologically constrained to temperatures less than 15 °C and dissolved oxygen greater than 4 mg L⁻¹ (Evans et al. 1991), with an assumed preferred temperature range of less than 10 °C and dissolved oxygen concentration greater than 6 mg L⁻¹ (Dillon et al. 2003). However, recent research suggests previously assumed thermal occupancy ranges for lake trout (Bergstedt et al. 2003, 2012; Dillon et al. 2003; Jacobson et al. 2010) may not be a universal threshold; rather thermal occupancy may be more dependent on prey and habitat availability, at least in small inland lakes (Sellers et al. 1998; Plumb and Blanchfield 2009; Guzzo et al. 2017;

Challice et al. 2019; Binder et al. 2021). Previous research in the Great Lakes suggests lake trout generally occupy water temperatures less than the 10 °C preferred threshold throughout summer stratification. In Lake Ontario, lake trout occupied mean summer temperatures of 6.9 ± 0.5 °C with fish occupying temperatures below 8.8 °C 90% of the time (Raby et al. 2020). In Lake Huron, summer temperature occupancy ranged from 6.0 to 9.7 °C, but differed by stocking strain, with Finger Lakes origin fish ranging from 6.0 to 6.7 °C and Great Lakes origin fish ranging from 7.1 to 9.7 °C (Bergstedt et al. 2012). In large systems such as the Great Lakes, lake trout occupy the warmest water temperatures when the water column de-stratifies during fall turnover (October), which coincides with nearshore movements to spawn (Binder et al. 2021). Lake Erie is the shallowest, warmest, and located furthest south of the Great Lakes, at the southern edge of the native geographic range of lake trout, thus there is the potential for lake trout to be forced to occupy sub-optimal habitat for extended periods proximal to spawning.

Although lake trout are physiologically capable of tolerating warmer temperatures than previously assumed (Challice et al. 2019; Hébert and Dunlop 2020), exposure to warm temperatures may still impede rehabilitation efforts in several ways. Reproductive capabilities of salmonids decline when fish are exposed to elevated water temperatures for prolonged periods prior to spawning (reviewed in Pankhurst and King 2010; Servili et al. 2020). In Lake Erie, duration of summer stratification has increased in the last 50 years due to warming air temperatures (McCormick and Fahnenstiel 1999; Mason et al. 2016). Salmonid maturation and spawning timing are triggered at least partially via photoperiod (Bromage et al. 2001), suggesting that lake trout in Lake Erie could be exposed to warmer water temperatures for longer periods prior to spawning compared to historical conditions. Additionally, climate change will likely extend stratification periods even longer (Trumpickas et al. 2009; Woolway et al. 2021),

increasing the risk of excessive exposure to suboptimal temperatures by contemporary lake trout populations. Building on the theory relating high temperatures to a lack of successful natural recruitment, Bergstedt et al. (2003) found that increased exposure to elevated water temperatures by lake trout was likely linked to increased sea lamprey predation, which disproportionately affects larger fish (Swink 1991; Schneider et al. 1996; Rogers et al. 2019). Increased sea lamprey predation further hinders the reproductive capability of lake trout populations because larger, older females produce and deposit more eggs and spawn later in the year compared to smaller, younger females (Peck 1988), coinciding with cooler water temperatures and increased offspring survival (Casselman 1995).

Despite conducting annual population assessment surveys since 1992 (Coldwater Task Group 2022), little is known about the spatial and thermal ecology of contemporary Lake Erie lake trout populations, particularly outside the summer stratification period (Markham et al. 2008; Lake Erie Committee 2021). The purpose of this study was to begin to fill this knowledge gap and provide managers with descriptions of how lake trout use habitat, spatially and thermally, throughout the year. I used acoustic telemetry tracking technology to investigate the seasonal spatial ecology of lake trout in Lake Erie in Chapter 1 and the thermal ecology of lake trout in Chapter 2.

In Chapter 1, I addressed three research questions: (1) does Lake Erie lake trout habitat use vary spatially and temporally? (2) do distinct spawning populations in the eastern and western basins of Lake Erie exist and do these populations exhibit different seasonal movement patterns? (3) is lake trout habitat use related to fish size? In Chapter 2, the following three research questions were addressed: 1) What is the occupancy of thermal habitat by lake trout in Lake Erie? 2) Does thermal occupancy differ between stocking strains? 3) Do lake trout of

different sizes use thermal habitat differently? The results from this study will provide managers in Lake Erie and elsewhere with valuable information on the behavior of this ecologically important species. Additionally, a more thorough understanding of the spatial and thermal ecology of lake trout in Lake Erie could begin to explain observed recruitment failures and inform future studies designed to tease out important mechanisms at work in this system.

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CHAPTER 1: SEASONAL SPATIAL ECOLOGY OF LAKE TROUT (*SALVELINUS
NAMAYCUSH*) IN LAKE ERIE

Abstract

Lake trout (*Salvelinus namaycush*) are native, coldwater apex predators that play an important role in the Laurentian Great Lakes in maintaining ecosystem functionality and diversity. After Great Lakes lake trout populations collapsed, stocking was widely initiated to re-establish self-sustaining populations. Lake Erie may pose a challenge to the rehabilitation of lake trout due to limited availability of appropriate thermal habitat, which could impede successful recruitment. I used acoustic telemetry technology to investigate seasonal habitat use of adult lake trout in Lake Erie to better understand how to manage rehabilitation efforts. I found that 40% of tagged fish dispersed greater than 100 km from their tagging location, including 30% of fish tagged in the eastern basin and all fish from the western basin, which represents a greater proportion of the population moving long distances than what previously has been documented in the Great Lakes. During stratification, lake trout were detected almost exclusively in the offshore eastern basin in areas with deepest water depths, had relatively small home ranges, and large spatial overlap. Outside of stratification, fish used other regions of the lake, occupying areas of highly variable depths. During autumn, most fish tagged in the eastern basin occupied habitat along the south shore of the eastern basin. I found that fish tagged in the western basin returned to this region in the autumn of subsequent years despite occupying the offshore eastern basin during stratification, having similar depth occupancy, home range size, and overlap to eastern basin fish. Larger fish tended to be detected on deeper receivers during winter and spring and displayed higher space use overlap during spring and summer. The results of this study can inform

management decisions regarding stocking, harvest, and habitat restoration of this important native species.

Introduction

Understanding movement ecology of fish populations is important for effective management of exploited, threatened, and invasive species (Cooke et al. 2016). Recent advancements in tracking technologies, particularly acoustic telemetry, have greatly expanded the ability of researchers and managers to incorporate movement ecology into management policies and actions (McGowan et al. 2017; Crossin et al. 2017; Hays et al. 2019; Matley et al. 2022). Information on movement patterns is particularly beneficial for the management of species that cross jurisdictional boundaries during movement events. For example, Harrison et al. (2018) emphasized the need for inter-agency cooperation by revealing seasonal movement patterns and multi-jurisdictional residency of several marine predators, including species of tuna, sharks, pinnipeds, seabirds, and sea turtles. Many success stories exist highlighting the importance of applying movement ecology for sustainable management, including prohibiting harvest and adding habitat protection of lemon sharks (*Negaprion brevirostris*) on Florida's Atlantic coast (Kessel et al. 2014a; Reyier et al. 2014; Brooks et al. 2019) and facilitating the recovery and subsequent success of walleye (*Sander vitreus*) in Lake Erie, which are subject to different harvest regulations during annual migrations crossing state and provincial jurisdictional boundaries (Vandergoot et al. 2019; Matley et al. 2020).

Lake trout (*Salvelinus namaycush*) are an apex predator of high management and conservation priority in North America's Laurentian Great Lakes (Bronte et al. 2008; Muir et al. 2013; Lake Erie Committee 2021). Lake trout are a coldwater species with a preferred temperature of less than 10 °C and dissolved oxygen concentration greater than 6 mg L⁻¹ (Dillon

et al. 2003); lake trout are physiologically constrained to temperatures less than 15 °C and dissolved oxygen greater than 4 mg L⁻¹ (Evans et al. 1991). Where abundant suitable oxythermal habitat is available, prey availability dictates lake trout movement patterns and habitat selection (Binder et al. 2021). Lake trout typically spawn in late fall, though some spring spawning populations exist (Bronte 1993). Spawning site fidelity has been observed in many lake trout populations, for both wild and hatchery-origin fish (Krueger et al. 1986; Ellrott and Marsden 2004; Bronte et al. 2007; Binder et al. 2016). Additionally, recent studies suggest lake trout may exhibit fidelity to particular areas during non-spawning periods (Morbey et al. 2006; Binder et al. 2017; Riley et al. 2018). Experimental learning and memory may play a key role in repeated migration patterns of individuals (Binder et al. 2021). Long distance movements (> 100 km) have been noted in some Great Lakes populations (Schmalz et al. 2002; Kapuscinski et al. 2005; Riley et al. 2018; Ivanova et al. 2021), but seem to be rare as most individuals disperse less than 100 km (Schmalz et al. 2002; Kapuscinski et al. 2005; Bronte et al. 2007; Riley et al. 2018). Movements of Great Lakes lake trout tend to follow the shoreline, rarely crossing deep, open-water areas (Pycha et al. 1965; Krueger et al. 1986; Bronte et al. 2007).

Although historically abundant in Lake Erie, lake trout were extirpated by the 1960s (Moenig 1970; Hartman 1973) and presently are the focus of major rehabilitation efforts (Lake Erie Committee 2021). Reestablishment of a self-sustaining lake trout population in Lake Erie's eastern basin has been deemed essential for ecosystem stability and successful achievement of a self-sustaining population is anticipated to promote reestablishment of native forage species including lake whitefish (*Coregonus chupeaformis*) and cisco (*Coregonus artedi*; Oldenburg et al. 2007). After several decades of observed recruitment failure and extirpation, a lake trout stocking program was initiated on Lake Erie in 1980 with a goal of reestablishing a self-

sustaining population (Cornelius et al. 1995; Markham et al. 2008). Hatchery-reared yearling lake trout have been stocked in Lake Erie's eastern basin (i.e., New York, Pennsylvania, and Ontario jurisdictional waters) proximal to hypothesized historic spawning reefs and small cohorts of fish have also been stocked in the western and central basins in Ohio waters since 2012 (Lake Erie Committee 2021). Currently, the population is primarily comprised of three hatchery strains originating from Lake Champlain (Vermont), Finger Lakes (i.e., Seneca Lake, New York), and to a lesser extent Slate Island (Lake Superior, Ontario; Coldwater Task Group 2022). Although stocking efforts over the past 6 decades have successfully established a population of sexually mature fish, there has been little to no evidence of wild reproduction, in contrast to the other Great Lakes (i.e., Huron, Michigan, Ontario, and Superior; Muir et al. 2013). Although Fitzsimons and Williston (2000) and Ludsin et al. (2004) found limited evidence of natural recruitment, the lake trout population is believed to be sustained almost entirely by stocked fish (Lake Erie Committee 2021; Coldwater Task Group 2022).

In addition to competition and predation from non-native species (e.g., sea lamprey, *Petromyzon marinus*; steelhead, *Oncorhynchus mykiss*; rainbow smelt; round goby, *Neogobius melanostomus*), restoration of Lake Erie coldwater fish species is believed to be hindered by the geomorphological constraints of the lake and anthropogenic nutrient loading that has reduced habitat availability (Francis et al. 2020). Lake Erie consists of three basins: (1) the shallow (mean depth 7.4 m), isothermal, eutrophic western basin; (2) the mesotrophic central basin (mean depth 18.5 m), which stratifies on an annual basis with a very narrow (< 2 m) hypolimnion that often becomes anoxic; (3) the deep (mean depth 24.4 m, max depth 64 m) oligotrophic eastern basin which stratifies on an annual basis and provides cold highly-oxygenated habitat year-round (< 10 °C, > 4 mg L⁻¹; Schertzer et al. 1987; Bolsenga and Hendendorf 1993). Historic fishery harvest

and population assessment records indicate that lake trout and other coldwater species (e.g., burbot *Lota lota*, cisco, and lake whitefish) primarily used the eastern basin year-round, including to spawn along the shoreline during late fall (< 15 m). However, a smaller population contingent (Secor 1999) of lake trout was believed to use the western basin of Lake Erie and Detroit River during the fall to spawn (Moenig 1970; Cornelius et al. 1995; Cox 2013). Despite conducting annual population assessment surveys since 1992 (Coldwater Task Group 2022), little is known about habitat use and spatiotemporal movement patterns of contemporary Lake Erie lake trout populations, particularly outside the summer stratification period (Markham et al. 2008; Lake Erie Committee 2021).

The primary aim of this study was to provide fishery managers with information related to the seasonal habitat use of adult lake trout in Lake Erie. Using acoustic telemetry tracking technology, this study was intended to address the following research questions: (1) does Lake Erie lake trout habitat use vary spatially and temporally? (2) do distinct spawning populations in the eastern and western basins of Lake Erie exist and do these populations exhibit different seasonal movement patterns? (3) is lake trout habitat use related to fish size? Based on physiological constraints and observations in other populations, I hypothesized that lake trout would be spatially restricted to the offshore eastern basin during summer stratification due to thermal constraints and lake trout would occupy the deepest habitat, use the smallest spatial extent, and have the highest degree of space use overlap during summer compared to other, isothermal, seasons. During fall, I hypothesized that lake trout would make spawning migrations and would occupy the shallowest habitat, have relatively large space use extents, and high space use overlap. During winter and spring (i.e., periods when lake trout are not constrained by physiology or spawning behavior), I hypothesized that lake trout would use habitat at

intermediate depths over a large area, resulting in low space use overlap. If distinct western basin lake trout spawning populations exist, I expected fish to migrate to the western basin during fall but be constrained to the deep, cool areas of the eastern basin during thermal stratification.

Therefore, I hypothesized that western basin lake trout would differ in behavior from eastern basin fish exclusively during the fall (October-December). Considering that all lake trout used in this study were of mature size, I hypothesized that space use would not differ by fish size.

Methods

Fish capture and tagging

Lake trout used in this study were collected during spring and fall between 2016 and 2019. During spring (May) 2016 and 2018, lake trout were collected with overnight bottom-set gill nets (monofilament mesh, bar measure ranging from 10.2 to 25.4 cm) along the northern (Ontario) and southern (New York and Pennsylvania) shorelines of Lake Erie in proximity to areas believed to support historic spawning aggregations (Figure 1.1.1). Lake trout were captured in May, several months removed from when spawning was hypothesized to occur in this population (October-December), and thus were assumed to represent an admixture of fish (i.e., potentially comprised of individuals from different spawning locales). Following capture, fish were held aboard research vessels operated by the New York State Department of Environmental Conservation (NYSDEC), Ontario Ministry of Northern Development, Mines, Natural Resources, and Forestry (OMNDMNR), Pennsylvania Fish and Boat Commission (PFBC) and US Geological Survey (USGS) in recirculating tanks (378-576 L) supplied with fresh lake water until the tagging process could begin. Lake trout were immersed (range 180-300 s) in a solution (20 mg/L) of AQUI-S®2E (NYSDEC, PFBC, USGS) or Clove Oil (OMNDMNR) until reaching stage-4 anesthesia (Summerfelt and Smith 1990; characterized by a loss of equilibrium

and response to external stimuli). Once anesthetized, lake trout were transferred to a surgical v-board in the supine position with their gills irrigated with fresh lake water throughout the surgical procedure. An experienced surgeon implanted the acoustic transmitters (i.e., handling, surgery, and release) following the protocols described by Cooke et al. (2011). A small incision (15-20 mm) was made through the coelomic cavity with a sterilized scalpel along the ventral midline, posterior of the pectoral fins. A sterilized acoustic transmitter (i.e., immersed in betadine solution) was inserted into the coelom and the incision was closed with 2 or 3 interrupted sutures (Ethicon PDS-II size 2-0, monofilament). After the transmitters were implanted, total length was recorded, and an external loop tag (Lock-on TF-4, Floy Tag and Manufacturing, Seattle, Washington) was inserted through the dorsal musculature toward the posterior edge of the dorsal fin via a hollow piercing needle. Each external loop tag had a unique identification number, a contact phone number, and the verbiage “REWARD \$100” to encourage reporting and return of the transmitter if the fish was harvested. Prior to release, fish were held in recirculating tanks supplied with fresh lake water until they regained equilibrium and exhibited the ability to undergo sustained movement following the protocols described by Raby et al. (2012).

Lake trout collected from the western basin (near Catawba Island, Ohio) along the shoreline (< 10 m) during the fall (October) of 2018 and 2019 were opportunistically obtained from a commercial fishing operation (Figure 1.1.1). Following capture, lake trout were transported to shore and held in recirculating tanks (378-576 L) supplied with fresh lake water prior to implanting an acoustic transmitter as described above. In contrast to the lake trout tagged in the eastern basin, western basin fish were immobilized with electrical current during the surgical procedure (Vandergoot et al. 2011) similar to the procedure described by Dembkowski

et al. (2021). In short, electrodes were wrapped around the dorsal musculature near the pectoral (anode) and anal (cathode) fins and held in place with current continuously supplied throughout the surgical procedure. Once immobilized, an acoustic transmitter was surgically implanted following the same procedure described above. Similar to the procedures described above, after the surgery was completed, fish were measured and tagged with an external loop tag, a fin-clip sample was taken, and fish were placed in a recirculating tank until deemed ready for release.

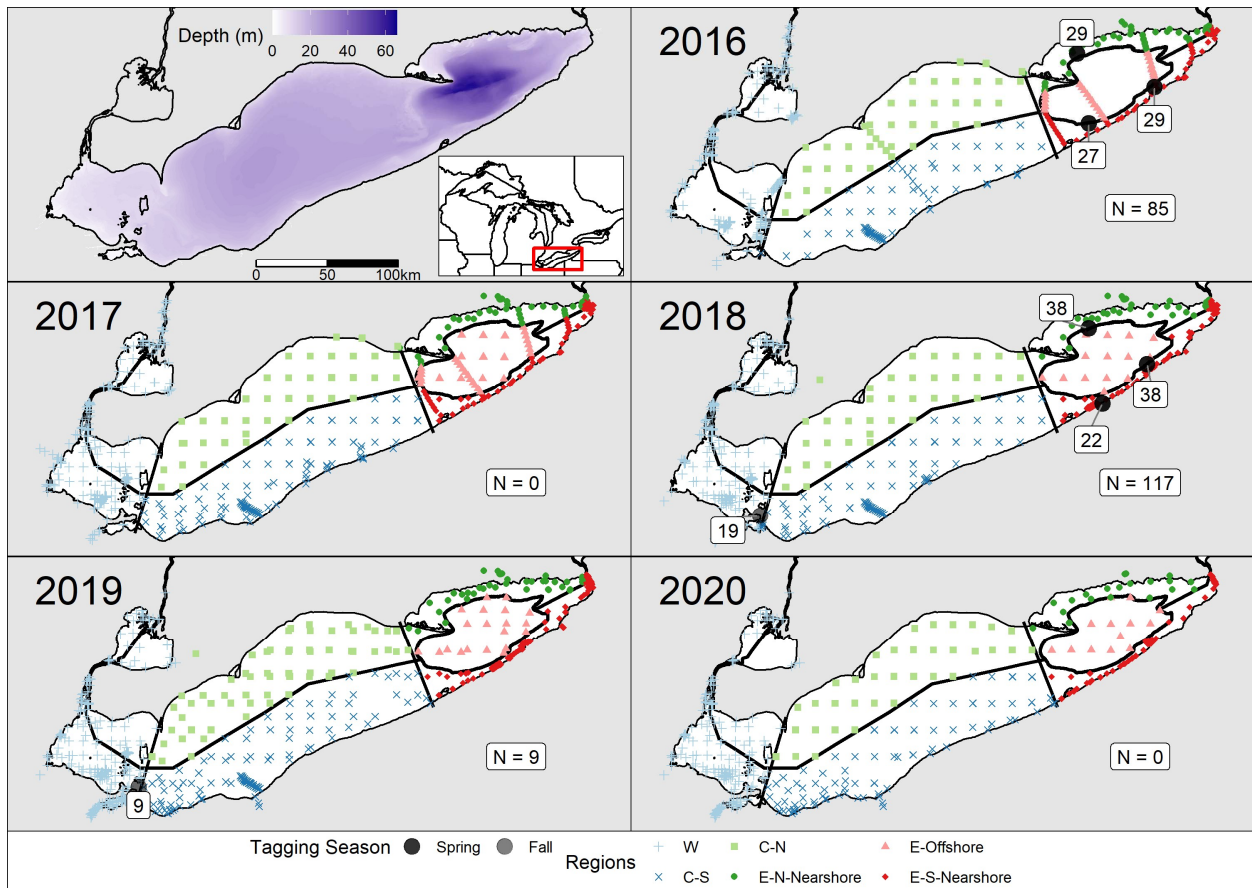


Figure 1.1. A) Bathymetric map of study area, Lake Erie, with inset of the Laurentian Great Lakes. B-F) Panels show the acoustic receiver array and tagging locations across years during the study period. Solid black lines indicate region divisions for consideration in residency index analyses. Colored points indicate acoustic receiver locations, with colors representing region (W: Western, C: Central, E: Eastern, S: South, N: North). Tagging release locations are represented by large black (spring tagging event) or grey (fall tagging event) circles and labelled with the number of fish released at each location. Tagging events took place in the eastern basin in 2016 (N = 85) and 2018 (N = 98) and in the western basin in 2018 (N = 19) and 2019 (N = 9).

Acoustic telemetry tracking

The acoustic transmitters (InnovaSea V16-4H, 158 dB; $n = 211$) surgically implanted in lake trout were programmed to emit a unique 69 kHz code at random time intervals between 60 and 180 s (120 s nominal delay). Acoustic receivers (InnovaSea VR2W, VR2TX, & VR2AR, 69 kHz) were deployed throughout Lake Erie in conjunction with other ongoing acoustic telemetry studies associated with the Great Lakes Acoustic Telemetry Observation System (GLATOS; Krueger et al. 2018) network. Receivers were deployed as either independent (i.e., designed to provide presence / absence information) or clustered (i.e., in close proximity of another receiver to better understand fine-scale movements) stations throughout the lake (Figure 1.1; Hussey et al. 2015; Kraus et al. 2018). Although the number and location of receivers varied throughout the study period, receivers were deployed annually in nearshore and offshore areas to provide broad-scale coverage. Lake trout movement information was collected immediately following release of the first cohort during May of 2016; however, movement data used for this study was left-censored (detections excluded from analysis) to coincide with acoustic receiver deployment and coverage corresponding with the type of analysis performed (see *Data Analysis* section). Based on field trials conducted in the central and eastern basins of Lake Erie prior to the current study, I assumed the acoustic transmitters used in this study had a detection range (i.e., >50%) of ~750 m (C. Vandergoot, Michigan State University, personal communication). The assumed detection range was used as a qualitative assessment to evaluate the likelihood of detecting a fish in a particular area as the probability of an acoustic transmitter being detected (i.e., coded) on an acoustic receiver varies spatially and temporally based on ambient lake conditions (e.g., water temperature, stratification, ice cover, wave action, productivity; Kessel et al. 2014; Hayden et al. 2016; Klinard et al. 2019; Kuai et al. 2021).

Description of seasons

To evaluate temporal differences in lake trout movement patterns, annual water temperature information was used to empirically identify spring, summer, fall, and winter seasons. Estimated water temperature data (i.e., surface and bottom) for Lake Erie were obtained for the study period 2017-2021 via the Great Lakes Operational Forecasting System (Chu et al. 2011). Water temperature data were modeled from surface temperatures and extrapolated throughout the water column using air temperatures and wind speed and direction. While these models have limitations (e.g., precision and fine-scale applicability), they provide the best available data source for describing lake-wide trends (e.g., periods of thermal stratification) and provide an opportunity to estimate available habitat over extensive areas. For example, modelled temperature data were cross-referenced (i.e., with respect to precision and accuracy) with observed data in the eastern basin where the majority of coldwater habitat in Lake Erie exists (Schmitt et al. 2020). Bottom water temperatures from ~10 m off Dunkirk, NY (42.499287, -79.356248) were compared to modelled bottom temperatures in the vicinity (P. Wilkins, New York State Department of Environmental Conservation, personal communication). From 2016-2018, the model was accurate within ± 3 °C throughout the year with the exception of occasional spikes during stratification, likely associated with upwelling events. During 2019-2020, the model severely underestimated bottom temperatures during stratification. However, accuracy at this nearshore area is only of interest when fish are likely to occupy nearshore habitat from mid-October through late-November. Between 2016 and 2018, the water temperature model tended to overestimate bottom temperature by approximately 3 °C. During 2019, ambient temperature was underestimated by approximately 2 °C; likewise, prior to early/ mid-November in 2020 ambient temperature was underestimated by approximately 3-5 °C. After early/mid-November 2020,

modeled ambient temperature was within approximately 1 °C of measured temperatures during the fall and winter. Because there was reasonable concordance between modelled and observed water temperature values, seasons (e.g., spring, summer, fall and winter) were defined using modeled surface and bottom temperature estimates from a fixed position located in the middle of the eastern basin (42.5359193, -79.78226437). For the purpose of this study, seasons were defined as: 1) spring warming – when bottom temperatures warmed past 2 °C until strong stratification was established where surface and bottom temperatures differed by > 15 °C (range: 51-87 days), 2) summer stratification – when surface and bottom temperatures differed by > 15 °C until stratification broke down where surface and bottom temperatures differed by < 5 °C (range: 104-119 days), 3) fall cooling – when surface and bottom temperatures differed by < 5 °C until bottom temperature cooled past 4 °C (range: 80-100 days) and 4) winter – when bottom temperature cooled past 4 °C until it warmed past 2 °C (range: 74-125 days).

Data analysis

One common issue to confront with acoustic telemetry detection data is the occurrence of false detections, which can arise from a variety of factors (e.g., acoustic signals colliding and/or erroneous interpretation of an acoustic signal) and lead to erroneous conclusions (Simpfendorfer et al. 2015). To remove false detections from the detection database, I used the “short-interval” procedure described by Pincock (2012). Specifically, potential false detections were removed if the time separating subsequent detections at a single receiver exceeded 3600 s (30 x the nominal delay of the tags; Pincock 2012). The lake trout detection dataset was also filtered to identify and remove fish presumed to be dead. Fish were assumed dead if they were detected on a receiver for a prolonged period of time (i.e., > 3 months) without being detected on another receiver during that period. When a fish was assumed to have died near a receiver ($n = 12$), all detections

subsequent to the first detection at that receiver were removed from the dataset to reduce the bias associated with including data observed from a dead fish (Klinard and Matley 2020). Fish were also assumed to be dead if they: 1) were never observed on a receiver following release, or 2) were not detected on any receiver for a prolonged period of time and were not reported as being harvested. The expansive receiver network in Lake Erie (see Figure 1.1) and the acoustic transmitters used in this study (approximate detection range 750 m) minimized the likelihood that a highly mobile species such as lake trout could go more than several months without being detected. The rationale for this assumption was based on the simulation study conducted by Kraus et al. (2018), where the authors estimated a walleye released in an acoustic array with 15 km grid spacing and a transmitter with an 800 m detection range would be detected on average once a week (range 3 days to 3 weeks), assuming correlated random walk movements. Individual detection histories indicated that no live fish (i.e., mobile, detected on more than 1 receiver) went more than 6 months between detections. Therefore, 38 of the fish released were considered dead after missing for more than 6 months prior to the end of the study period. Fish appearing to die within 30 days post-tagging ($n = 12$) were considered mortalities associated with the collection, handling, and tagging process and all detections from these fish were removed from analysis. After filtering, 188 fish (89% of 211 released) with valid detections remained in the dataset. Of those fish, 56 died (26%) during the study period, 6 of which were reported to be harvested by anglers (3%). Following release, acoustic transmitters could cease working (transmitter failure) or be expelled from the coelom of a fish; however, tag expulsion was not observed and is unlikely to have affected results or conclusions from this study.

Acoustic telemetry detection data were analyzed using regional residency index (RI), home range, and receiver depth occupancy. Lake trout movements observed on receivers

deployed between 1 January 2017 and 31 December 2020 were used to estimate RI and receiver depth occupancy as these analyses rely on presence / absence information observed over broad geographic scales (Figure 1.1.1). Whereas home range estimates (i.e., space use area estimates) were based on detections observed between 1 January 2018 and 31 December 2020 after the receiver grid array was deployed throughout the basin (Figure 1.1; compare 2017 vs. 2018 in the eastern basin). Regional RI, defined by the number of days a fish was detected at a group of receivers of interest divided by the total number of days that fish was detected (Kessel et al. 2016), was used to quantify seasonal spatial presence or absence. Receivers were grouped by regions of interest, by 1) basin (i.e., western, central, and eastern), 2) proximity within the central or eastern basins (i.e., north or south along the Canada/United States boundary) and 3) depth (i.e., deep ≥ 25 m vs shallow < 25 m) in the eastern basin, creating 6 total regions: western basin, central basin north, central basin south, eastern basin north nearshore, eastern basin south nearshore, eastern basin offshore (Figure 1.1.1). The grouping was used to provide general, broad-scale occupancy trends while accounting for yearly changes in the acoustic receiver array. Seasonal home ranges constructed for each tagged lake trout were used to quantify horizontal space use extent and space use overlap. To account for potential biases associated with time periods with a high number of detections in a short timeframe or in areas with fine-scale receiver coverage, centers of activity, which approximate animal locations within 30-minute time intervals (Simpfendorfer et al. 2002; VTrack package; Campbell et al. 2012), were used as inputs rather than raw detection data. Individual seasonal home ranges were calculated from centers of activity using Kernel utilization distribution (KUD) at the 95% level (adehabitatHR package; Calenge 2006). The utilization distribution overlap index (UDOI; Fieberg and Kochanny 2005) was used to quantify seasonal space use sharing of individuals (adehabitatHR package). The

UDOI considers the overlap as well as the utilization distribution of two individuals to create a metric that is between 0 and 1 for uniformly distributed and less than complete (100%) overlap, however the metric can be greater than 1 if space use has a high degree of overlap in more heavily used areas. Seasonal overlap estimates were obtained for a fish by averaging pairwise overlap values between that individual and all others. To construct meaningful seasonal home range estimations, fish must have had at least 10 centers of activity per season to be included in home range analyses. Acoustic telemetry transmitters were not equipped with depth sensors, thus analyses considered water depth of the receiver on which a fish was detected, as the actual depth that fish occupied was unknown. Bathymetric depth occupancy estimates were obtained by averaging observations from each fish, providing there were at least 3 observations in a day. To be included in analyses for weekly estimates, fish needed to be observed for at least 2 days with a minimum of 3 observations per day. For seasonal estimates, fish needed at least 4 days with a minimum of 3 observations per day. These filtering criteria were selected to ensure that estimates would not be biased by few extraneous observations from few individuals.

All statistical analyses were performed in R 4.1.2 (R Core Team 2021). To compare seasonal differences in behavior, linear mixed models (lme4 package; Bates et al. 2015) were fit to detection data from fish tagged in the eastern basin during 2017-2020 for depth occupancy and 2018-2020 for home range size and overlap. For assessing depth occupancy, season, year, and the interaction between these variables were considered as fixed effects and individual fish treated as a random effect. To assess home range size (\log_e -transformed), detection period and the number of centers of activity were also included as fixed factors to account for sensitivity in home range analyses to differences in detection histories. Similarly, to assess home range overlap, average detection period and combined number of centers of activity were calculated for

each pairwise comparison, then averaged by individual when individual overlap was calculated. For seasonal comparison of home range overlap of eastern basin fish, individual averaged overlap was calculated using only pairwise comparisons with other eastern basin fish. To evaluate potential differences in behavior between fish tagged in the eastern and western basins, linear mixed models were fit to detection data from 2019-2020, as the first cohort of western basin tagged fish were tagged in late 2018. Individual fish were treated as a random effect and season, year, tag basin, and associated interactions were considered fixed effects for assessing depth occupancy. Detection period and number of centers of activity were additional fixed effects in assessing home range size (log-transformed) and home range overlap as described for the eastern basin model. For tagging basin comparison of home range overlap, individual averaged overlap for fish from both basins was calculated using pairwise comparisons with all fish. Centers of activity and detection period were centered and Z-score scaled in all models in which they were included as fixed effects.

To assess potential behavioral differences across the length range of adult fish sampled, linear models or linear mixed models were fit to data only from eastern basin fish, due to the small sample and narrow range of lengths from the western basin sample. Since age samples were not collected, estimation of individual based growth was not applicable, therefore length at tagging was used and I considered only observations within the first year after a fish was released. To evaluate depth occupancy, a linear mixed model was fit considering season, length at tagging, and the interaction as fixed factors with tagging year as a random factor. Only fish tagged in 2018 were considered for length-based home range analyses as the receiver grid was not complete until after fish tagged in 2016 had been at large for over a year. To evaluate home

range size (\log_e -transformed) and home range overlap, a linear model was fit considering season, length at tagging, and the interaction, centers of activity, and detection period as fixed effects.

For all models, model fit was evaluated by observing model residuals. Residuals for all models describing home range area fit poorly with strong skews, suggesting the need for a \log_e -transformation of the response. The full model for each response variable considered all potentially relevant effects and all possible model subsets were considered as alternatives. Akaike Information Criterion corrected for finite sample sizes (AIC_c) was used to evaluate the various models; candidate models with a ΔAIC_c less than 2 were considered to have some evidentiary support as being the best performing model (MuMIn package; Barton 2020). If there were multiple models with ΔAIC_c less than 2, model predictions were averaged using the AIC_{modavg} package (Mazerolle 2020). If no other models had ΔAIC_c less than 2, only the best performing model was considered. Model effect sizes and uncertainty were calculated with the $ggeffects$ package (Lüdecke 2018).

Results

Seasonal basin occupancy

Broad-scale habitat occupancy of Lake Erie lake trout varied seasonally. Eastern basin fish on average had the highest residency index in the eastern offshore region in most seasons (winter: 63%; spring: 72%; summer: 94%; Figure 1.2) with the exception of fall (27%; Figure 1.2). Nearly all eastern basin fish (99%) occupied the eastern offshore region more than any other region during summer (Table 1.1), including 83% that occupied this region more than 90% of days during summer stratification. The proportion of time spent in the eastern offshore region varied widely on an individual level when the water column was isothermal (Figure 1.2). During fall, eastern basin fish had the highest occupancy in the eastern south nearshore region (mean RI:

68%; Figure 1.2) and 79% of fish occupied this region more than any other region during fall (Table 1.1). During winter and spring, individual variation in region occupancy was high, with highest average population occupancy in the eastern offshore region (winter: 63%, spring: 73%), followed by eastern south nearshore (winter: 24%; spring: 19%), eastern north nearshore (winter: 5%; spring: 12%), and central south (winter: 10%; spring: 2%; Figure 1.2). Fish utilized the central north region infrequently (> 1% every season) and none of the eastern basin lake trout were detected in the western basin during the study (Figure 1.2).

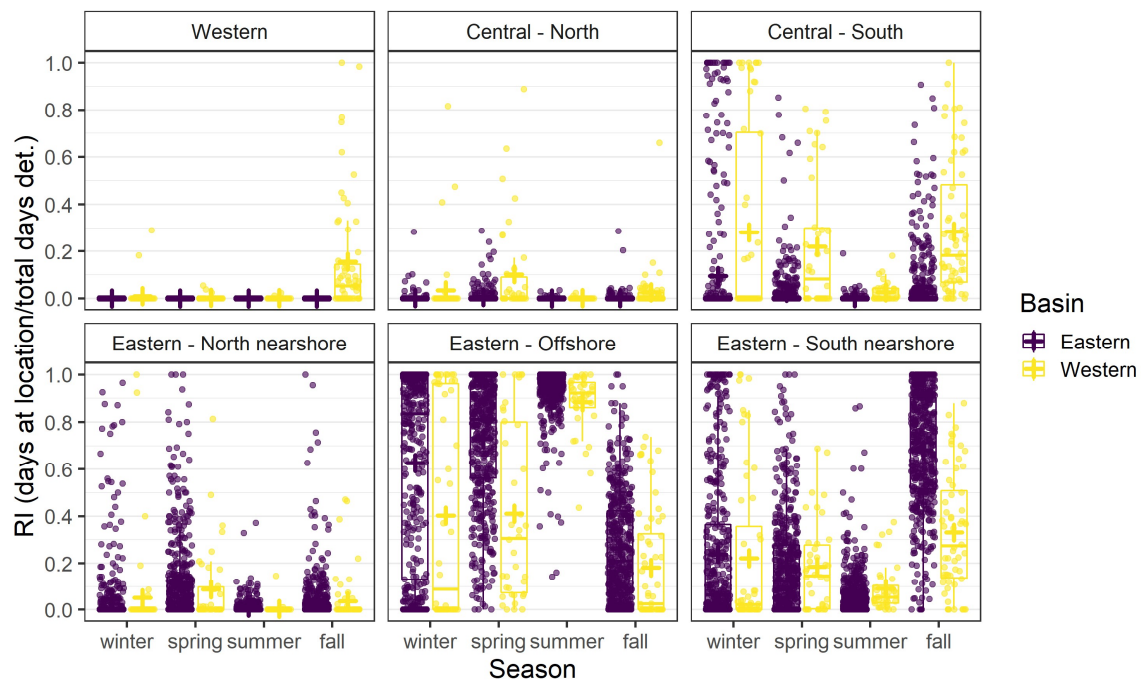


Figure 1.2. Seasonal residency index (RI; number of days detected in the region / total number of days detected) by region for fish tagged in the eastern (purple) or western (yellow) basin. Each data point represents one fish in one year. The underlying boxplots contains the box ranging from the first to third quartile, the solid line representing the median, the plus representing the mean, and whiskers extending up to 1.5 times the inter quartile range. See Figure 1.1 for region divisions.

Lake trout tagged in Ontario, Pennsylvania, and New York waters of Lake Erie (i.e., eastern basin) exhibited similar spatiotemporal habitat use patterns. Residency indices for fish tagged in Ontario waters were lower in the eastern north nearshore region (i.e., where they were

collected) compared to the other regions (e.g., offshore and south nearshore) in the eastern basin across seasons, which was a similar result to fish tagged along the south shore in New York and Pennsylvania (Figure 1.3d, e, & f). Pennsylvania fish had slightly higher occupancy in the eastern south nearshore region compared to New York and Ontario fish during winter (32% vs 21 and 19%, respectively) and spring (28% vs 16 and 12%, respectively, Figure 1.3f).

Conversely, Pennsylvania fish had lower occupancy in the eastern offshore region compared to New York and Ontario fish during winter (53% vs 69 and 65%, respectively) and spring (65% vs 77 and 77%, respectively, Figure 1.3e), though all three groups had a high degree of individual variability during these seasons (Figure 1.3). Most (range 78–86%) eastern basin fish spent >90% of the summer in the eastern offshore region (Table 1.1). Regardless of tagging location, during fall eastern basin fish spent the most time in the eastern south nearshore region (range 62–73%) followed by the eastern offshore region (range 21–31%). Since fish tagged from Ontario, Pennsylvania, and New York occupied similar habitats throughout the year, I combined all fish tagged in the eastern basin for further analysis.

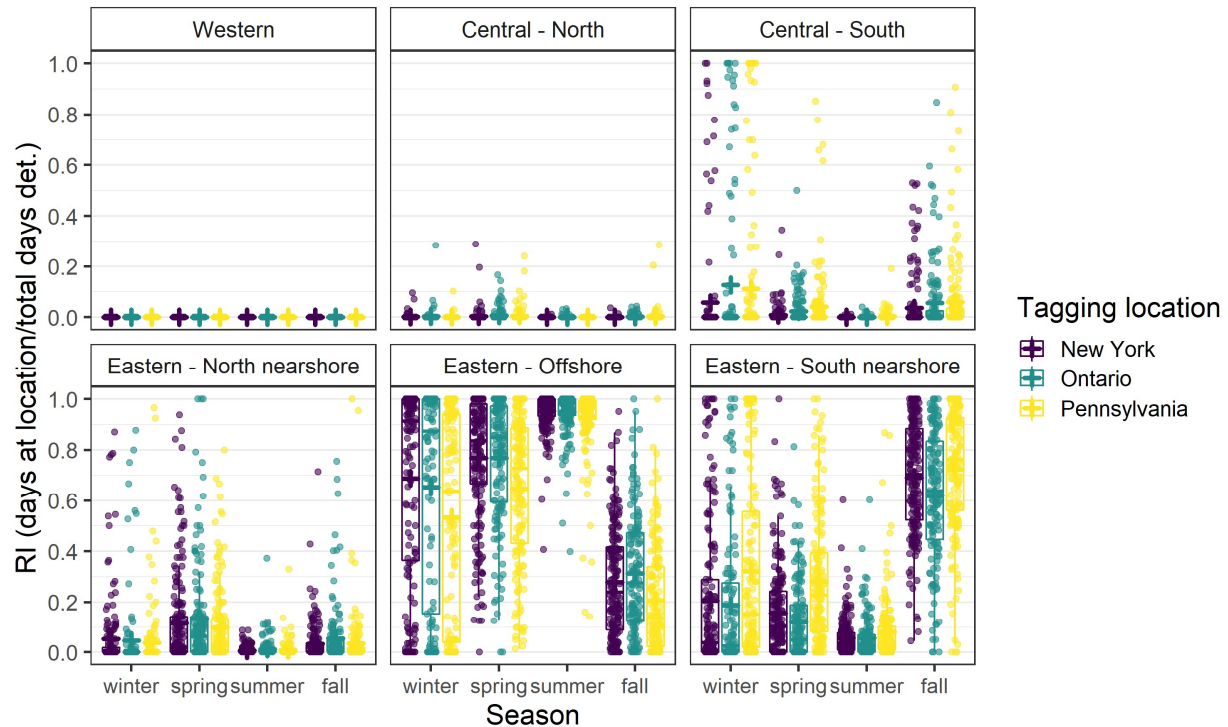


Figure 1.3. Seasonal residency index (RI; number of days detected in the region / total number of days detected) by region for fish tagged in the eastern (purple) or western (yellow) basin. Each data point represents one fish in one year. The underlying boxplots contains the box ranging from the first to third quartile, the solid line representing the median, the plus representing the mean, and whiskers extending up to 1.5 times the inter quartile range. See Figure 1.1 for region divisions.

Western basin lake trout had similar regional occupancy patterns to eastern fish for most of the year (i.e., winter, spring, and summer) but considerable differences in movement patterns and occupancy during the fall were evident. Similar to eastern basin fish, western basin fish had high eastern offshore occupancy on average during summer (88%; Figure 1.2) and all fish occupied the eastern offshore region more than any other region during summer (Table 1.1). During winter and spring, there was high individual variation among western basin fish. By evaluating each individual's most occupied region during each season, I found that at least 10% of western basin individuals occupied 5 different regions (all but western) most regularly during spring and at least 10% occupied 3 different regions during fall (Table 1.1). Compared to eastern

basin fish, western basin fish tended to have higher occupancy in the central south (Figure 1.2c) but lower occupancy in the eastern offshore basin (Figure 1.2e) throughout the year, particularly during winter and spring. Western basin fish spent 33% of the time during the fall in the eastern south nearshore region compared to 68% for the eastern basin fish (Figure 1.2f). Lake trout tagged in the western basin tended to reside along the southern shoreline of Lake Erie during the fall, as occupancy was highest in the eastern south nearshore region (33%), followed by the central south (28%), eastern offshore (18%), and western regions (16%; Figure 1.2).

Table 1.1. Percent of lake trout tagged from the eastern or western basin of Lake Erie occupying a region the majority of days during each season. Number indicates the number of fish having adequate data (detections on > 4 days in a season) to be included. Years were considered independently so each fish is often considered more than once. In a rare instance where a fish had a tie for the most occupied region, both regions were counted for that fish, resulting in the potential for a row to sum to slightly greater than 100%.

Season	Western	Central North	Central South	Eastern North Nearshore	Eastern South Nearshore	Eastern Offshore	Number
Eastern Basin							
Winter	0%	0%	11%	4%	21%	65%	457
Spring	0%	0%	1%	8%	11%	82%	505
Summer	0%	0%	0%	0%	1%	99%	519
Fall	0%	0%	3%	2%	79%	17%	500
Western Basin							
Winter	0%	6%	27%	4%	21%	42%	52
Spring	0%	13%	24%	11%	13%	42%	38
Summer	0%	0%	0%	0%	0%	100%	36
Fall	13%	2%	27%	2%	35%	23%	60

Long distance dispersal

Lake trout in Lake Erie frequently dispersed long distances from their tagging locations. Forty percent of all tagged lake trout were detected a maximum distance more than 100 km from their tagging location with a median maximum dispersal distance of 93.6 km (mean: 123.0). Fish tagged in the eastern basin had a median maximum dispersal of 91.3 km (mean: 93.5; range: 1.7–235.6 km) from their tagging location and 30% dispersed greater than 100 km. All fish tagged in

the western basin dispersed more than 100 km with a median maximum dispersal of 314.2 km (mean: 316.0; range: 296.7–349.7).

Western basin migrations

Lake trout tagged in the western basin during fall exhibited directed movements toward the central and eastern basins soon following release. All fish tagged in the western basin migrated to the eastern basin within 2 months of tagging, and most within a matter of days or weeks, with the exception of one individual that did not travel to the eastern basin until approximately 5 months post-tagging. Fish were detected on receivers within 50 km of the tagging site 71% (25 of 35) of the time during subsequent falls. Fish tagged in 2018 had a higher tendency to migrate than those tagged in 2019. For 2018 fish, 93% (14 of 15) of fish migrated back to the western at least once with an overall return rate of 78% (21 of 27) over both years, while 50% (4 of 8) of the fish tagged in 2019 migrated back the following year. These directed western migrations were typically rapid (median: 5.1 days, range: 3.0 – 18.6 days) and individuals generally spent little time in the area (median: 10.2 days); however, duration of stays were highly variable, and one individual spent several months in the western basin each year (range: <1 – 88.4 days). Migration back to the eastern basin was slightly longer than western directed migration (median: 6.5 days, range: 3.4 – 41.1 days). Additionally, outside of fall, several individuals appeared to make rapid migrations to the western basin or western central basin during late spring.

Depth occupancy

Using receiver depth as a proxy for the bottom depth eastern basin lake trout occupied while at liberty (i.e., 2017-2020), the model with the lowest AIC_c describing depth occupancy included season, year, and the interaction between these parameters as fixed effects and

individual fish as the random effect (Table S1.0.1). As predicted, each year eastern basin fish consistently occupied areas with deepest waters during summer (range 38–43 m) and shallowest during the fall (range 14–20 m; Figure 1.4a). Although considerable inter-annual variation was evident (Figure 1.5a), on average eastern basin lake trout occupied similar depths during the winter and spring [32 m (range 26–36 m) and 34 m (range 29–38 m), respectively; Figure 1.4a]. Nearshore (< 15 m) movement following thermal destratification during the fall (October/November) was sudden and consistent among years (Figure 1.5a). Following the nearshore movement during the fall (presumably to spawn), eastern basin lake trout tended to reside in areas of deeper water (>25 m) between December and March, headed back toward shore (20–35 m) during April, and then back offshore (>30 m) in May and as summer progressed and the eastern basin thermally stratified (Figure 1.5a).

Western and eastern basin lake trout occupied similar depths throughout the year; however, seasonal differences were evident. Of the candidate models evaluated, there was support for two of the models evaluated; these models included: season, year, basin, season×year interaction, season×basin interaction, and year×basin interaction as fixed effects, and individual fish as random effects (Table S1.0.2). Weighted averaging of the two supported models suggested little effect of an interaction between year and basin leading to very similar trends within each year. Western basin fish occupied shallower areas than eastern basin fish during winter [26 m (95% CI: 22.1–30.1 m) vs 32 m (30.0–33.6 m), respectively in 2019] and spring [31 m (27.0–34.4 m) vs 38 m (36.3–39.8 m), respectively in 2019; Figure 1.4]. Western and eastern basin fish had very similar depth occupancy during summer [37 m (33.3–40.9 m) vs 38 m (36.1–39.6 m), respectively in 2019] and fall [14 m (10.5–17.4 m) vs 15 m (13.0–16.4 m), respectively in 2019; Figure 1.4]. Similar to eastern basin fish, western basin lake trout moved

into shallow water (< 15 m) after thermal destratification during October and November, before then moving into variable mid-depth areas during January-May (Figure 1.5b).

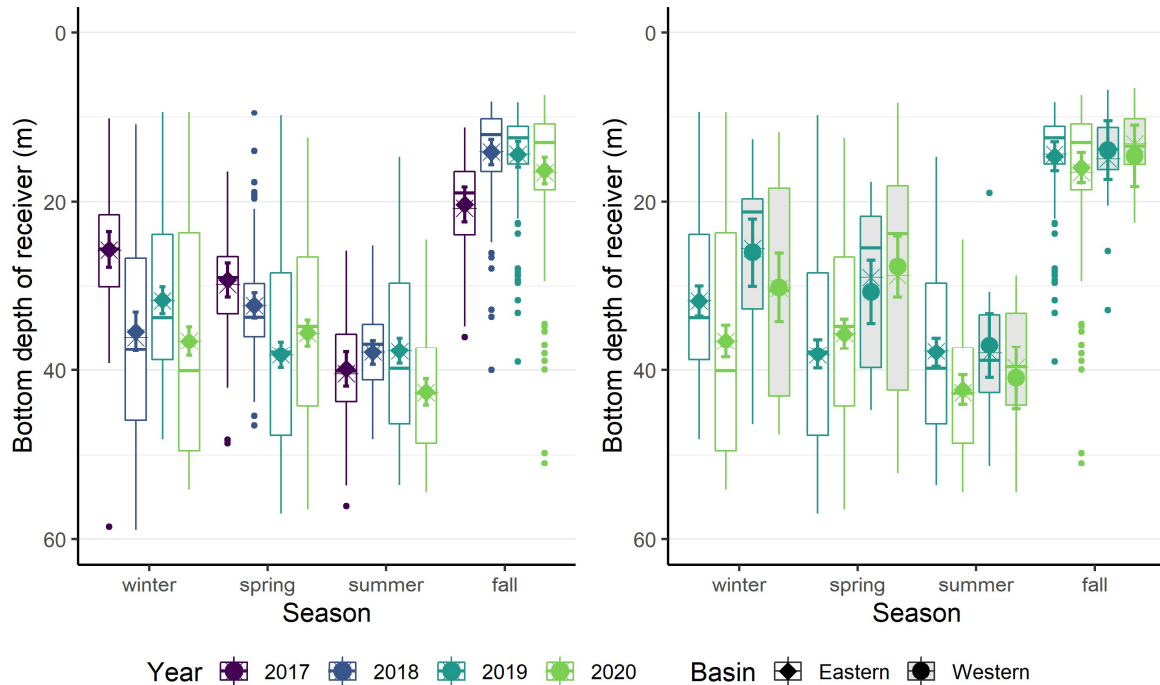


Figure 1.4. Average seasonal bottom depth of receiver detected on by year for eastern basin fish (left) and by year and tagging basin for eastern and western basin fish (right). Boxplots show raw data with the box ranging from the first to third quartile, the solid line representing the median, stars representing the mean, whiskers extending 1.5 times the inter quartile range, and outliers shown as small points. Large, filled shapes (diamond or circle) indicate model predictions with 95% confidence intervals of the predictions shown with error bars. Colors of boxplots and model predictions correspond to years and shading of the boxplot and shape of the large icon correspond to tagging basin.

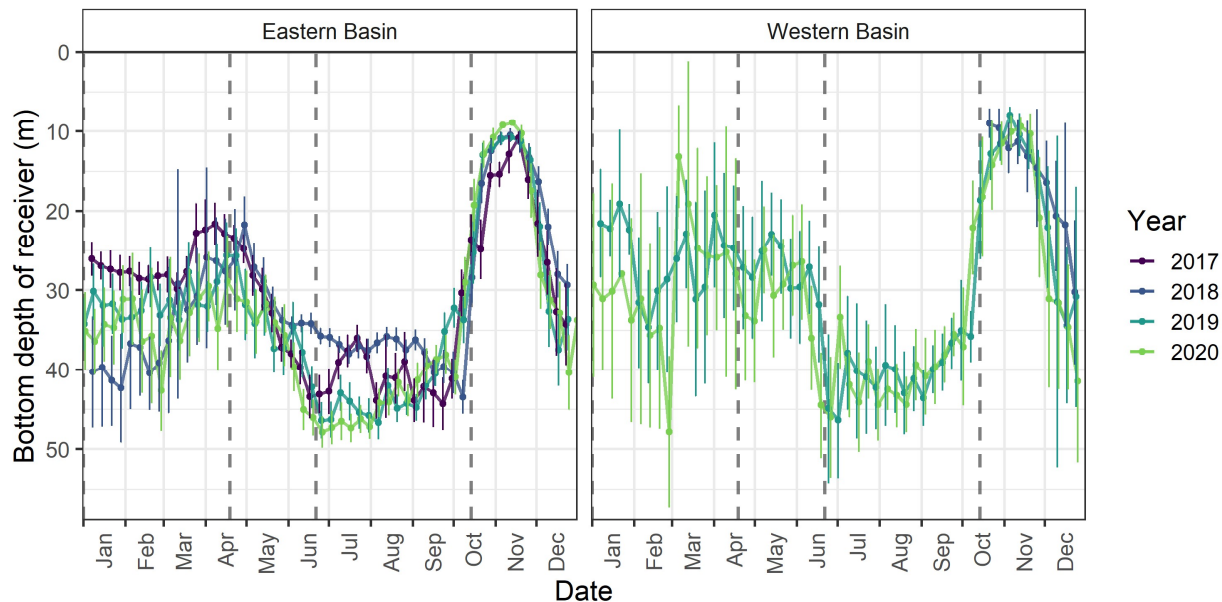


Figure 1.5. Weekly average bottom depth of receiver (m) detected on for fish tagged in the eastern basin (left) or western basin (right) by year. Each weekly average considers the average of the average depth of receiver from all fish having at least 2 days with at least 3 observations in a week. Error bars represent 95% confidence intervals of the weekly population average. Vertical dashed lines indicate average season breaks.

Space use extent

During the study period, space use extent, measured by home range estimates from KUDs at the 95% level, varied seasonally for Lake Erie lake trout with some inter-annual variability. Of the models evaluated, a model with season, year, season×year interaction, centers of activity, and detection period as fixed effects and individual fish as a random effect was the best performing based on AIC_c (Table S1.0.3). Eastern basin fish consistently had the largest horizontal space use extent during spring, though space use during this season was variable across years with smaller space use during the spring of 2018, compared to 2019 and 2020 [1806.5 km² (95% CI: 1635.1–1995.8 km²) vs 2335.2 km² (2142.9–2544.8 km²) and 2550.4 km² (2359.0–2757.4 km²), respectively; Figure 1.6]. Contrary to predictions, seasonal space use extent was smallest during summer only in 2020 [1105.5 km² (1006.3–1214.4 km²)], while in

2018 and 2019 space use was smallest during winter [918.8 km² (815.1–1035.7 km²) and 1078.7 km² (993.4–1171.3 km²), respectively; Figure 1.6].

Similar home range extent patterns existed for eastern and western basin fish based on model estimates from two candidate models with significant plausibility. Fixed effects for the first model included season, year, basin, season×year interaction, season×basin interaction, and individual fish as a random effect and the second model additionally included year: basin as a fixed effect (Table S1.0.4). Fish tagged in the western basin had similar space use extent size to eastern basin fish during winter [1053.4 km² (95% CI: 889.4–1247.6 km²) vs 1074.1 km² (986.8–1169.2 km²), respectively in 2019] and spring [2444.5 km² (2066.2–2892.2 km²) vs 2372.7 km² (2171.3–2592.2 km²), respectively in 2019], and insignificantly larger space use during summer [1639.4 km² (1376.5–1952.5 km²) vs 1307.0 km² (1184.1–1442.6 km²), respectively in 2019; Figure 1.6]. However, during fall western basin fish space use extent was nearly twice as large as that of eastern basin fish on average (2885.5 km² vs 1445.0 km², respectively; Figure 1.6).

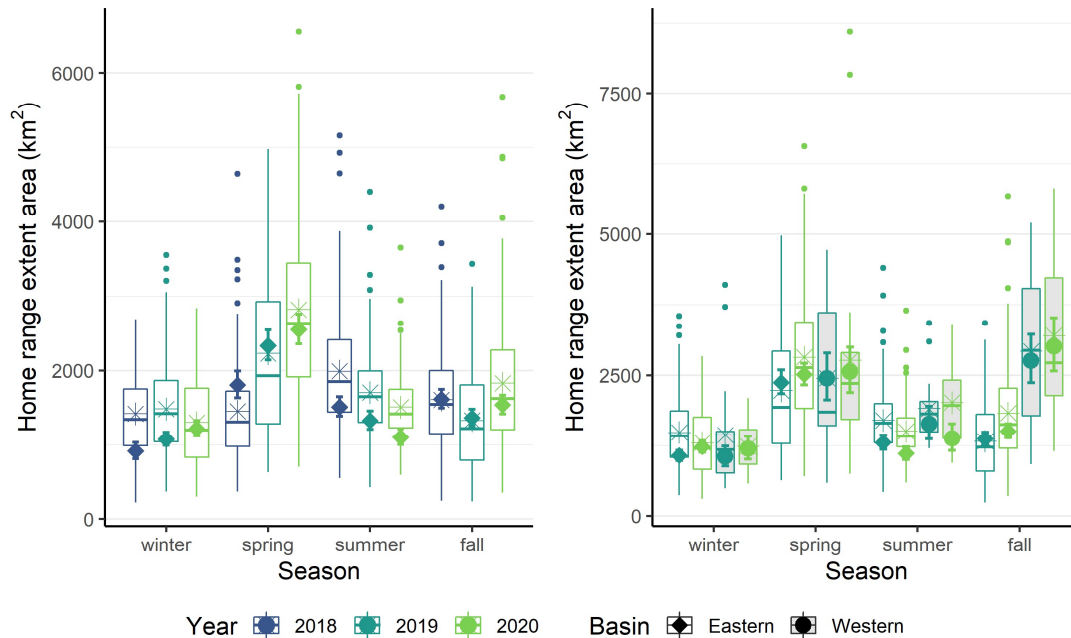


Figure 1.6. Average seasonal 95% KUD home range area (km^2) by year for eastern basin fish (left) and by year and tagging basin for eastern and western basin fish (right). Boxplots show raw data with the box ranging from the first to third quartile, the solid line representing the median, stars representing the mean, whiskers extending 1.5 times the inter quartile range, and outliers shown as small points. Large, filled shapes (diamond or circle) indicate model predictions with 95% confidence intervals of the predictions shown with error bars. Colors of boxplots and model predictions correspond to years and shading of the boxplot and shape of the large icon correspond to tagging basin.

Individual space use overlap

Home range overlap among individual eastern basin lake trout, quantified using UDOI, varied seasonally, but exhibited inter-annual consistency. A model with season, year, season \times year interaction, centers of activity and detection period as fixed effects, and individual fish as a random effect was the most plausible among the candidate models evaluating home range overlap (Table S1.0.5). Seasonal space use overlap within eastern basin individuals was highest and consistent year-over-year during summer (average: 0.56, range: 0.54–0.60) and fall (average 0.56, range: 0.54–0.58; Figure 1.7). There was more than twice as much variability (i.e., based on inter quartile range) in home range overlap estimates for eastern basin fish during the fall compared to the other seasons (Figure 1.7). Eastern basin fish showed the lowest seasonal

overlap during winter (average 0.24, range: 0.21–0.25), followed by spring. Spring was the only season with notable inter-annual variability as overlap in spring 2018 was higher than 2019 and 2020 [0.45 (95% CI: 0.38–0.51) vs 0.28 (0.24–0.33) and 0.35 (0.31–0.38), respectively; Figure 1.7].

Western basin lake trout exhibited similar trends in seasonal home range overlap as eastern basin fish, although one notable difference was evident. Home range overlap was compared with a model where season, year, basin, basin: season, centers of activity, and detection period were fixed effects, and individual fish were treated as the random effect (Table S1.0.6). Similar to patterns observed for eastern basin fish, western basin fish home range overlap was highest during the summer and fall, and lowest during winter and spring (Figure 1.7). Western basin fish exhibited significantly lower space use overlap than eastern basin fish during spring [0.15 (95% CI: 0.10–0.20) vs 0.27 (0.25–0.30), respectively in 2019] and fall [0.30 (0.25–0.35) vs 0.50 (0.47–0.53), respectively in 2019; Figure 1.7]. Although lower, home range overlap for western basin fish was similar to eastern basin fish during the winter [0.14 (0.09–0.20) vs 0.20 (0.17–0.22), respectively in 2019] and summer [0.52 (0.47–0.58) vs 0.55 (0.52–0.58), respectively in 2019; Figure 1.7].

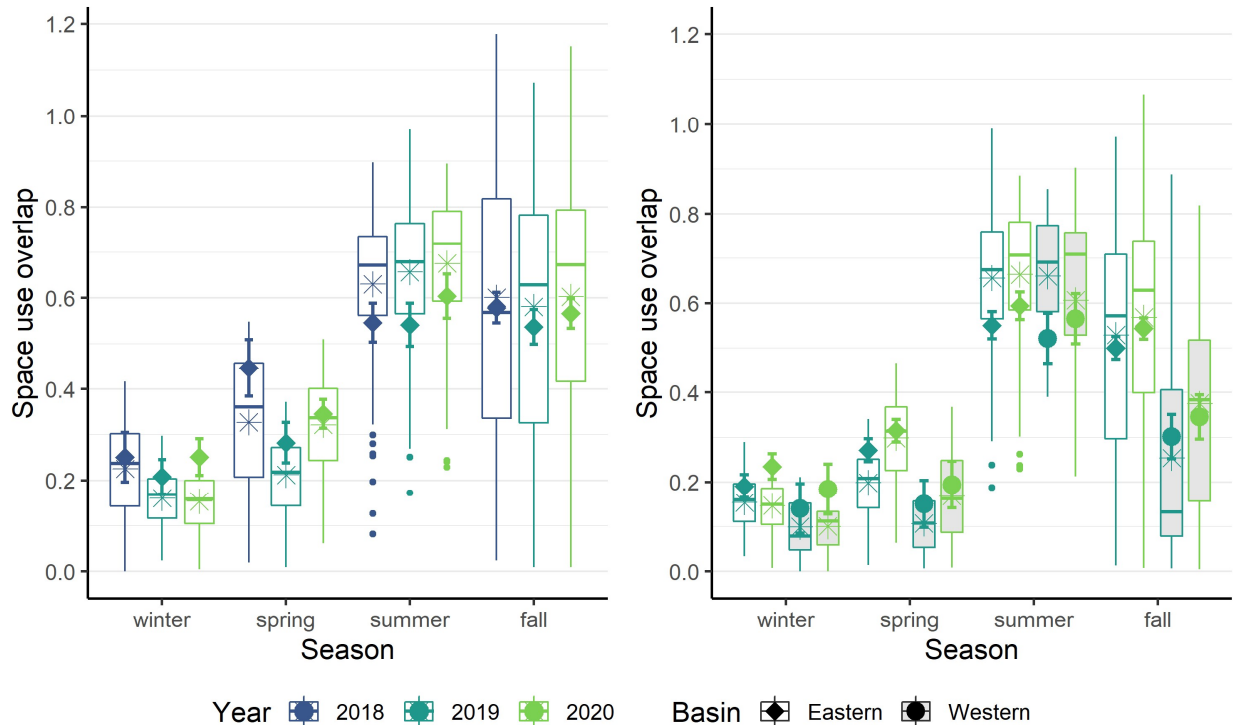


Figure 1.7. Seasonal space use overlap by year for eastern basin fish compared to other eastern basin fish (left) and by year and tagging basin for eastern and western basin fish compared to all other fish (right). Boxplots show raw data with the box ranging from the first to third quartile, the solid line representing the median, stars representing the mean, whiskers extending 1.5 times the inter quartile range, and outliers shown as small points. Large, filled shapes (diamond or circle) indicate model predictions with 95% confidence intervals of the predictions shown with error bars. Colors of boxplots and model predictions correspond to years and shading of the boxplot and shape of the large icon correspond to tagging basin.

Length

Seasonally, the depth of water fish occupied and space use overlap for lake trout originating from the eastern basin of Lake Erie was related to fish size (i.e., length at tagging), while space use extent size was not related to fish size. Fish depth (using receiver depth as a proxy for fish depth) was best described by two candidate models considering length and season, and their interaction as fixed effects and tagging year as a random effect (Table S1.0.7). Larger fish tended to be detected in deeper water (i.e., on average) than smaller fish during winter [0.017 m depth/mm increase in length (95% CI: -0.001–0.34); 6.38 m over range of observed

lengths, 510–892 mm] and spring [0.021 m depth/mm length (0.001–0.040); 7.85 m over range; Figure 1.8]. During summer [0.009 m depth/mm length (-0.007–0.024); 3.34 m over range] and fall [-0.003 m depth/mm length (-0.025–0.020); -0.97 m over range] there was no meaningful effect of length on depth occupied (Figure 1.9). To evaluate a potential effect of length on space use extent, log-transformed home range size was modeled considering various fixed parameters. Of the models evaluated, two models including season, centers of activity, and detection period (model 1) and season, length, centers of activity, and detection period (model 2) had the most support (Table S1.0.8). There was no relationship between fish length and space use extent [0.0002 (95% CI: -0.0004–0.0007)]. To evaluate a potential effect of length on space use overlap between an individual and the rest of the sampled population, the best model considered fixed effects of season, length, season: length, centers of activity, and detection period (Table S1.0.9). Larger fish had higher space use overlap with other individuals during spring [effect of length: 0.0009 /mm increase in length (95% CI: 0.0003–0.0014); 0.35 over range of observed lengths, 510–892 mm] and summer [0.0007 /mm length (0.0002–0.0012); 0.27 over range; Figure 1.8] than smaller individuals. However, length had no meaningful effect on space use overlap during winter [0.0002 /mm length (-0.0003–0.0007); 0.08 over range] or fall [-0.0001 /mm length (-0.0007–0.0004); -0.06 over range; Figure 1.8].

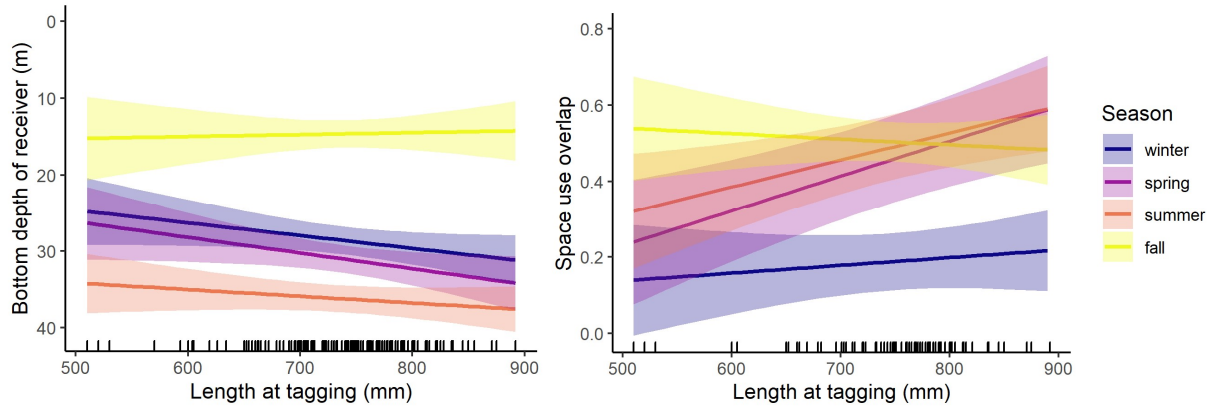


Figure 1.8. Seasonal average bottom depth (m) of receiver detected on (left) and space use overlap (right) by length. Model predictions are given by solid lines with 95% confidence intervals given by the shaded areas. Dashes at the bottom of each plot indicate the distribution of lengths across the sample.

Discussion

Lake trout in Lake Erie were observed frequently traveling large distances. While I expected that western basin tagged fish would disperse long distances to find suitable thermal habitat during summer stratification, surprisingly, 30% of fish tagged in the eastern basin dispersed over 100 km. These long distance dispersals were made by a much greater proportion of study organisms than what other studies in the Great Lakes have found. For example, in Lake Superior, 9% of fish were captured more than 160 km from the tagging site (Eschmeyer et al. 1953). In Lake Michigan, 90% of fish were recaptured within 69 km (Schmalz et al. 2002) of their initial tagging location. In Lake Huron, in a telemetry study of multiple populations, 3 to 9% of fish were detected at a maximum distance of over 100 km from their release location (Riley et al. 2018). Lastly, in Lake Ontario, one of 24 individuals (4%) was detected > 200 km from its release site (Ivanova et al. 2021). While lake trout in Lake Erie show stark differences in dispersal from previous studies, this could partially be a consequence of differences in methodology. Unintentional biases in methodology can lead to incorrect conclusions, particularly when studying movement (e.g., Gowan et al. 1994). Measures of lake trout dispersal from

previous Great Lake studies used mark recapture methods (Eschmeyer et al. 1953; Schmalz et al. 2002), where dispersal was inferred as distance between tagging and recapture locations, or acoustic telemetry studies relying on sparse receiver coverage (Riley et al. 2018; Ivanova et al. 2021). This study is the first in the Great Lakes to examine lake trout movements in a system with intensive coverage of acoustic receivers (i.e., grid, spaced ≤ 15 km). Dispersal measures from the previous Great Lakes studies likely represent minimum estimates of dispersal distances as it is conceivable that study organisms may have traveled much further distances undetected. However, I also cannot necessarily rule out that conditions in Lake Erie promote lake trout to move greater distances than in the other Great Lakes due to suboptimal habitat or limited prey availability. While exposure to suboptimal oxythermal habitat likely drives movement of fish tagged in the western basin, it seems unlikely that habitat quality drives long distance movement of fish tagged in the eastern basin, as these fish have access to preferred summer habitat within 15 km of tagging locations and historic spawning habitat. Additionally, because the fish used in this study were stocked, it is unlikely they would behave differently than stocked fish studied in the other Great Lakes. Considering that Lake Erie is the smallest of the Great Lakes, it seems likely that lake trout would undergo long distance dispersal and movements at similar, if not higher, rates in the other lakes compared to Lake Erie.

Similar to my expectations, tagged lake trout were primarily located in the offshore (> 25 m water depth) region of the eastern basin during summer stratification. During summer, fish typically occupied areas of deeper depths, had relatively small space use extents, and a large degree of space use overlap. Therefore, I can expect the most intense intraspecific competition for habitat to occur during stratification, compared to non-stratified seasons when fish had access to a larger area of suitable habitat. While being physiologically restricted during stratification,

lake trout displayed some inter-annual differences in behavior. Notably, in 2020 fish were located in areas with deeper depths than in 2018 and 2019; likewise, extent of space use was largest during 2018 and smallest during 2020. These patterns correlate with interannual differences found in August diets. In 2020, rainbow smelt, a pelagic prey species that typically serves as the primary prey item of lake trout, occurred in 94% of non-empty lake trout stomachs whereas round goby, a benthivorous species, only occurred in 4% of non-empty stomachs (Coldwater Task Group 2022). Conversely, in 2018 and 2019, occurrence of rainbow smelt in non-empty stomachs ranged from 57 to 61% whereas occurrence of round goby ranged 37 to 58% (Coldwater Task Group 2022). This suggests that inter-annual differences in space use may be influenced by availability and distribution of alternate prey species.

Following thermal destratification, lake trout made rapid, directed movements toward the nearshore zone presumably toward spawning habitat. During fall, eastern basin tagged fish occupied areas with the shallowest depths of the year, had small space use extents, and relatively large home range overlap. Nearly all eastern basin tagged fish spent most of their time during fall in the eastern south nearshore region, suggesting that fish could be spawning or staging to spawn in this region of the lake. Despite 37% of study fish being tagged in Ontario waters during the spring (presumably representing a mixed stock), only 3 fish (2%) spent the majority of time during fall along the north shore of the eastern basin. Lake trout are known to return to natal rearing or stocking locations (reviewed in Binder et al. 2021; Marsden et al. 2021) even over long distances (Binder et al. 2017; Riley et al. 2018). While some studies have found that the timing of spawning migrations is variable among years (Binder et al. 2016; Marsden et al. 2016), lake trout in the current study exhibited relatively consistent inter-annual nearshore movements. Given the aim of this study was to provide a general overview of the spatial and temporal

movements of Lake Erie lake trout, it would be worthwhile for future lake trout movement studies to focus more specifically on determining the timing of movement onto reefs, precise spawning locations, fine-scale searching behavior, and the extent of sex and strain differences in movement behaviors.

During isothermal seasons outside of stratification and hypothesized fall spawning, lake trout are not subject to temperature and oxygen constraints; consequently, it was unknown how fish would use available habitat in Lake Erie. Binder et al. (2021) hypothesized that prey availability and abundance would direct habitat selection and space use if lake trout were not constrained physiologically; however, in Lake Erie it is unclear how forage fish abundance influences lake trout habitat selection and use for most of the year as forage surveys are only conducted during the late spring and diet surveys are conducted during summer (Forage Task Group 2022). During winter, lake trout had the smallest spatial extent use and had the lowest degree of space use overlap. While Blanchfield et al. (2009) found that ice-cover during winter influenced habitat use in an inland lake, in Lake Erie this does not appear to be a driving force as fish did not appear to behave differently in years with little ice cover (2017: 35% maximum ice cover; 2020: 16%) compared to years with a high degree of ice cover (2018: 95%; 2019: 94%; Great Lakes Environmental Research Laboratory). While no trends in bottom depth of receiver or space use extent correlated with trends in ice cover, it is unknown how or if swimming depth within the water column was affected by ice cover. During spring, region and depth occupancy were highly variable among individuals and years. It is difficult to identify what may be contributing to annual differences in winter and spring behavior. In 2017 and 2019, fish were detected in areas of deeper water in spring than winter while in 2018 fish occupied areas of shallower water in spring and in 2020 depth occupancy was indifferent between spring and

winter. Additionally, it should be emphasized that depth occupancy measured here represents only the water depth of the receiver a fish was detected on and says nothing of where that fish was in the water column. From a very small sample of fish equipped with pressure-sensing tags, fish tended to be suspended in the water column during the spring months, while being near the bottom the remainder of the year (T.R. Funnell, unpublished data). A more thorough understanding of vertical habitat use of lake trout in addition to horizontal space use should be a priority for future studies. Space use extent sizes were largest during spring for eastern basin lake trout, suggesting that fish are most active and mobile over long distances during this season. Movements during this season are expected to be driven almost solely by prey availability. While I might expect that prey was most available or concentrated in spring of 2018 compared to 2019 and 2020, as space use extent was smallest and overlap was largest during 2018, this may be driven by the influx of newly tagged individuals which were released together at one of three stocking locations, rather than by yearly behavioral differences. Ultimately, outside of stratification, lake trout show the tendency to roam and disperse over considerable distances after facing thermal constraints during stratification.

Overall, western basin lake trout exhibited similar movement patterns and habitat use as eastern basin fish with a few notable exceptions. Similar to eastern basin fish, western basin fish were restricted to the offshore eastern basin during stratification as expected due to physiological constraints, specifically, cold well-oxygenated water only present in the eastern basin. These two tagging groups differed in that western basin fish occupied the central southern region more than eastern basin fish during non-stratified periods (i.e., fall, spring and winter) and western basin fish had larger home ranges and lower home range overlap than eastern basin fish during most

seasons. Fish tagged in the western basin showed strong fidelity to the region they were tagged, as 72% of western basin tagged fish migrated > 260 km to return to this area during fall.

Considering the fidelity of lake trout to their stocking locations (Binder et al. 2021) and the distance traveled, these fish were very likely to have been stocked in the western basin. The ability of these fish to return to hypothesized stocking locations considering the generally suboptimal conditions and substantial cost of migration to the western basin provides further evidence that stocking in suitable spawning locations is of extreme importance for the restoration of this species (Krueger et al. 1995; Muir et al. 2013; Riley et al. 2019). The migrations made by western basin fish were often rapid to and from the hypothesized spawning location and fish often spent little time in the area. Tendency to migrate did not seem to be dependent on year as of 12 individuals that were observed for two spawning seasons, 3 fish did not migrate in 2019 and 3 different fish did not migrate in 2020. It is unknown if these fish attempted to spawn elsewhere, such as with the eastern basin aggregation, or skipped spawning. Other Great Lakes lake trout have been found to skip spawning and this strategy would be plausible given the high cost associated with the long distance migration (Sitar et al. 2014). While it is unknown how lake trout home to rearing or stocking locations, a range of mechanisms have been proposed, including imprinted and conspecific olfactory cues, sound, bathymetry, hydrodynamics, solar cues, geomagnetic orientation, or learning and memory (Binder et al. 2021). Additionally, the tendency for fish tagged in the western basin to be more likely to utilize the south central basin and less likely to utilize the eastern north nearshore region during non-spawning, non-stratified periods could be attributed to a familiarity and prior exposure to the central basin during spawning migrations.

Fish size was positively related to receiver bottom depth during spring and winter, and positively related to space use overlap during spring and summer. Increased space use sharing by larger lake trout suggests the potential for a higher degree of intra-specific competition as compared to smaller individuals, which could be driven by large lake trout occupying more preferred habitat. Seasonal differences in space use overlap differ for large and small fish. Large fish followed the prediction that overlap will be highest during summer, while for smaller fish, overlap was highest during fall. While these trends are statistically meaningful, they should be interpreted with caution as lengths are taken from length at tagging during the spring, so length assignment will be most accurate during spring, but differential growth rates could cause true lengths to vary from length assignments following summer (i.e., fall and winter), when growth can be rapid. However, I assume that ranking will remain relatively stable, such that the smallest fish in the sample remain smallest and the largest remain largest, while I acknowledge that small fish are more likely to grow faster over the first year post-tagging.

Large female lake trout are of considerable importance to the successful rehabilitation of the species because larger females produce more eggs and spawn later in the year (Martin and Olver 1980; Casselman 1995) when water temperatures are cooler, which increases offspring survival (Casselman 1995). Delayed spawning is likely to be of increased importance in Lake Erie, considering its southern location, shallow bathymetry, and corresponding warm temperatures, as compared to other lakes within the range of lake trout. However, average age of females is much lower in Lake Erie than in other systems, possibly due to increased sea lamprey predation on older, larger fish (Stapanian and Madenjian 2007; Rogers et al. 2019). Future studies could consider sex, growth over time, and strain to build on our understanding of how groups within the population could be behaving differently to best inform rehabilitation and

management of this ecologically important species. These studies should focus on differential temperature occupancy, fine-scale timing and location of spawning, and sea lamprey interactions.

The tendency for lake trout to use areas of Lake Erie outside of the offshore eastern basin during non-stratified periods should promote ecosystem management and restoration efforts to be broadly focused on the basin or lake-wide level. Fish tagged on both the north and south shores exhibited high utilization of the southern shore of the eastern basin during the suspected spawning period, suggesting that habitat restoration efforts should be prioritized in this region. Additionally, restoration of offshore spawning reefs of historic importance could be beneficial in promoting spawning at cooler water temperatures. The frequent long distance movements of lake trout, often resulting in occupancy of several different jurisdictional waters across the U.S. and Canada, emphasize the need for inter-agency cooperation in management of this species. The Lake Erie Coldwater Task Group facilitates communication and collaboration among state, provincial, and federal (U.S.) agencies and continued success of this task group will be vital to the success of lake trout rehabilitation in Lake Erie. Additionally, management of this species in other Great Lakes could strongly benefit from inter-agency coordination. Continued growth of the Lake Erie lake trout population through stocking and promoting natural recruitment will be dependent on inter-agency cooperation, habitat restoration, and continued invasive species control. A healthy, self-sustaining lake trout population will be key to providing stability and rehabilitating the native coldwater fish community of Lake Erie.

APPENDIX

Table S1.1. Model selection table for candidate models fit to bottom depth of receiver detected on for eastern basin tagged fish only. All models were linear mixed models with individual fish as a random effect. Notation effect:effect indicates an interaction effect. A + indicates that the fixed effect was included in the model while - indicates it is not. DF is degrees of freedom and logLik is the log likelihood associated with the model.

Model	Fixed effects			DF	logLik	ΔAIC_c
	Season	Year	Season:Year			
1	+	+	+	18	-5623	0.0
2	+	+	-	9	-5695	127.4
3	+	-	-	6	-5719	169.3
4	-	+	-	6	-6332	1394.7
5	-	-	-	3	-6343	1411.1

Table S1.2. Model selection table for candidate models fit to bottom depth of receiver detected on for eastern and western basin tagged fish. All models were linear mixed models with individual fish as a random effect. Notation effect:effect indicates an interaction effect, with S meaning season, B meaning tagging basin, and Y meaning year. A + indicates that the fixed effect was included in the model while - indicates it is not. DF is degrees of freedom and logLik is the log likelihood associated with the model.

Model	Fixed effects							DF	logLik	ΔAIC_c
	Season	Basin	Year	S:B	S:Y	B:Y	S:B:Y			
1	+	+	+	+	+	-	-	14	-3841	0.0
2	+	+	+	+	+	+	-	15	-3840	1.0
3	+	+	+	+	+	+	+	18	-3839	4.5
4	+	+	+	-	+	-	-	11	-3848	8.8
5	+	+	+	-	+	+	-	12	-3848	9.5
6	+	-	+	-	+	-	-	10	-3853	14.9
7	+	+	+	+	-	-	-	11	-3856	23.1
8	+	+	+	+	-	+	-	12	-3855	24.0
9	+	+	-	+	-	-	-	10	-3861	32.3
10	+	+	+	-	-	-	-	8	-3864	32.8
11	+	+	+	-	-	+	-	9	-3863	33.2
12	+	-	+	-	-	-	-	7	-3868	38.9
13	+	+	-	-	-	-	-	7	-3869	41.4
14	+	-	-	-	-	-	-	6	-3873	47.2
15	-	+	+	-	-	-	-	5	-4257	814.3
16	-	+	+	-	-	+	-	6	-4257	816.3
17	-	+	-	-	-	-	-	4	-4261	819.0
18	-	-	+	-	-	-	-	4	-4263	824.4
19	-	-	-	-	-	-	-	3	-4267	828.7

Table S1.3. Model selection table for candidate models fit to log-transformed space use area for eastern basin tagged fish only. All models were linear mixed models that included centers of activity and detection period as additional fixed effects with individual fish as a random effect. Notation effect:effect indicates an interaction effect. A + indicates that the fixed effect was included in the model while - indicates it is not. DF is degrees of freedom and logLik is the log likelihood associated with the model.

Model	Fixed effects			DF	logLik	ΔAIC_c
	Season	Year	Season:Year			
1	+	+	+	16	-698	0.0
2	+	-	-	8	-761	108.2
3	+	+	-	10	-760	110.1
4	-	+	-	7	-931	447.1
5	-	-	-	5	-934	448.9

Table S1.4. Model selection table for candidate models fit to log-transformed space use extent for eastern and western basin tagged fish. All models were linear mixed models that included centers of activity and detection period as additional fixed effects with individual fish as a random effect. Notation effect:effect indicates an interaction effect, with S meaning season, B meaning tagging basin, and Y meaning year. A + indicates that the fixed effect was included in the model while - indicates it is not. DF is degrees of freedom and logLik is the log likelihood associated with the model.

Model	Fixed effects							DF	logLik	ΔAIC_c
	Season	Basin	Year	S:B	S:Y	B:Y	S:B:Y			
1	+	+	+	+	+	-	-	16	-595	0.0
2	+	+	+	+	+	+	-	17	-595	1.8
3	+	+	+	+	+	+	+	20	-592	2.3
4	+	+	-	+	-	-	-	12	-608	17.1
5	+	+	+	+	-	-	-	13	-607	17.1
6	+	+	+	+	-	+	-	14	-607	19.0
7	+	+	+	-	+	-	-	13	-629	61.6
8	+	+	+	-	+	+	-	14	-628	62.2
9	+	+	-	-	-	-	-	9	-640	76.4
10	+	-	+	-	+	-	-	12	-637	76.4
11	+	+	+	-	-	-	-	10	-640	77.5
12	+	+	+	-	-	+	-	11	-639	78.4
13	+	-	-	-	-	-	-	8	-649	91.0
14	+	-	+	-	-	-	-	9	-648	92.0
15	-	+	+	-	-	-	-	7	-817	425.0
16	-	+	+	-	-	+	-	8	-817	426.5
17	-	+	-	-	-	-	-	6	-819	427.7
18	-	-	+	-	-	-	-	6	-824	437.2
19	-	-	-	-	-	-	-	5	-826	440.2

Table S1.5. Model selection table for candidate models fit to space use overlap, measured by UDOI, for eastern basin tagged fish only. All models were linear mixed models that included centers of activity and detection period as additional fixed effects with individual fish as a random effect. Notation effect:effect indicates an interaction effect. A + indicates that the fixed effect was included in the model while - indicates it is not. DF is degrees of freedom and logLik is the log likelihood associated with the model.

Model	Fixed effects			DF	logLik	ΔAIC_c
	Season	Year	Season:Year			
1	+	+	+	16	545	0.0
2	+	+	-	10	524	29.0
3	+	-	-	8	506	61.1
4	-	+	-	7	352	367.1
5	-	-	-	5	303	461.3

Table S1.6. Model selection table for candidate models fit to space use overlap, measured by UDOI, for eastern and western basin tagged fish. All models were linear mixed models that included centers of activity and detection period as additional fixed effects with individual fish as a random effect. Notation effect:effect indicates an interaction effect, with S meaning season, B meaning tagging basin, and Y meaning year. A + indicates that the fixed effect was included in the model while - indicates it is not. DF is degrees of freedom and logLik is the log likelihood associated with the model.

Model	Fixed effects							DF	logLik	ΔAIC_c
	Season	Basin	Year	S:B	S:Y	B:Y	S:B:Y			
1	+	+	+	+	-	-	-	13	562	0.0
2	+	+	+	+	-	+	-	14	562	2.0
3	+	+	+	+	+	-	-	16	563	5.1
4	+	+	+	+	+	+	-	17	563	7.1
5	+	+	+	+	+	+	+	20	564	10.3
6	+	+	-	+	-	-	-	12	550	22.7
7	+	+	+	-	-	-	-	10	547	24.5
8	+	+	+	-	-	+	-	11	547	26.4
9	+	+	+	-	+	-	-	13	547	29.8
10	+	+	+	-	+	+	-	14	547	31.8
11	+	+	-	-	-	-	-	9	533	49.9
12	+	-	+	-	-	-	-	9	533	50.7
13	+	-	+	-	+	-	-	12	533	55.8
14	+	-	-	-	-	-	-	8	519	75.4
15	-	+	+	-	-	-	-	7	379	353.8
16	-	+	+	-	-	+	-	8	379	355.2
17	-	-	+	-	-	-	-	6	371	366.8
18	-	+	-	-	-	-	-	6	359	392.5
19	-	-	-	-	-	-	-	5	351	404.8

Table S1.7. Model selection table for candidate models fit to bottom depth of receiver detected on for eastern basin tagged fish during their first year at liberty. All models were linear mixed models with tagging year (2016 or 2018) as a random effect. Notation effect:effect indicates an interaction effect. A + indicates that the fixed effect was included in the model while - indicates it is not. DF is degrees of freedom and logLik is the log likelihood associated with the model.

Model	Fixed effects			DF	logLik	ΔAIC_c
	Length	Season	Length:Season			
1	+	+	+	10	-1897	0.0
2	+	+	-	7	-1901	1.8
3	-	+	-	6	-1904	5.3
4	-	-	-	3	-2149	488.8
5	+	-	-	4	-2148	489.3

Table S1.8. Model selection table for candidate models fit to log-transformed space use extent for eastern basin fish tagged in 2018 during their first year at liberty. All models were linear models that included centers of activity and detection period as additional fixed effects. Notation effect:effect indicates an interaction effect. A + indicates that the fixed effect was included in the model while - indicates it is not. DF is degrees of freedom and logLik is the log likelihood associated with the model.

Model	Fixed effects			DF	logLik	ΔAIC_c
	Length	Season	Length:Season			
1	-	+	-	7	-157.5	0.0
2	+	+	-	8	-156.8	0.7
3	+	+	+	11	-155.2	4.0
4	-	-	-	4	-175.3	29.4
5	+	-	-	5	-174.7	30.2

Table S1.9. Model selection table for candidate models fit to space use overlap for eastern basin fish tagged in 2018 during their first year at liberty. All models were linear models that included centers of activity and detection period as additional fixed effects. Notation effect:effect indicates an interaction effect. A + indicates that the fixed effect was included in the model while - indicates it is not. DF is degrees of freedom and logLik is the log likelihood associated with the model.

Model	Fixed effects			DF	logLik	ΔAIC_c
	Length	Season	Length:Season			
1	+	+	+	11	109.4	0.0
2	+	+	-	8	104.5	3.3
3	-	+	-	7	99.6	11.0
4	+	-	-	5	76.7	52.6
5	-	-	-	4	72.1	59.8

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CHAPTER 2: THERMAL ECOLOGY OF LAKE TROUT (*SALVELINUS NAMAYCUSH*) IN
LAKE ERIE

Abstract

Understanding the thermal ecology of fish populations of concern is vital to their effective management, particularly in the face of climate change. In Lake Erie, lake trout (*Salvelinus namaycush*) are at the southern edge of their native geographical range and rehabilitation of self-sustaining populations is of high importance to managers. However, high water temperatures and lengthening periods of stratification could be hindering restoration efforts by contributing to unfavorable conditions for natural recruitment. The goal of this study was to determine the thermal ecology of Lake Erie lake trout using acoustic telemetry by evaluating behavior overall and by stocking strain and length. Lake trout occupied cool water during stratification at or below temperature occupancy of other Great Lakes lake trout populations; however, during fall lake trout were regularly exposed to temperatures above their preferred temperature range (< 10 °C). Compared to fish of hatchery strains originating from the Great Lakes, Finger Lakes strains occupied similar water temperatures during summer but spent more days in areas with water temperature above 10 °C during fall, which is different than what has been observed in other Great Lakes. Summer temperature occupancy decreased with increasing body size. The results of this study could identify potential mechanisms for observed recruitment failures to be evaluated in future studies. These findings reveal the thermal ecology of a coldwater species at the southern extent of its range and will provide vital information to fisheries managers on how to rehabilitate lake trout most effectively in Lake Erie and elsewhere in the face of climate change.

Introduction

Lake trout (*Salvelinus namaycush*) historically were the native, coldwater apex predators of the Laurentian Great Lakes and served a vital role in providing stability to coldwater fish communities (Edwards et al. 1990; Bronte et al. 2008, 2010). Lake trout were extirpated from most areas of the Great Lakes due to a combination of overfishing, predation by invasive sea lamprey (*Petromyzon marinus*), and habitat loss (Hartman 1973; Muir et al. 2013). Rehabilitation of this ecologically and economically important species is a high priority for several Great Lakes fishery management agencies (Krueger et al. 1995; Bronte et al. 2008; Zimmerman and Krueger 2009; Muir et al. 2013; Lake Erie Committee 2021). In Lake Erie, rehabilitation efforts have yielded a population consisting primarily of hatchery-produced adults; however no significant natural recruitment to the population has been documented despite the presence of spawning aggregations and gamete collection in the wild (Fitzsimons and Williston 2000; Lake Erie Committee 2021; Coldwater Task Group 2022). While multiple potentially compounding hypotheses exist as to why natural reproduction is not occurring in Lake Erie (Jones et al. 1995; Rogers et al. 2019), negative direct or indirect effects of water temperature are a common theme as Lake Erie is the shallowest and warmest of the Great Lakes (Muir et al. 2013; Lake Erie Committee 2021).

Improving the understanding of lake trout thermal ecology and habitat use in Lake Erie may provide beneficial insight regarding why rehabilitation efforts in Lake Erie have to date not contributed to establishment of a self-sustaining wild population (Markham et al. 2008; Zimmerman and Krueger 2009). Recent research suggests previously assumed thermal occupancy ranges for lake trout (< 10 °C; Bergstedt et al. 2003, 2012; Dillon et al. 2003; Jacobson et al. 2010) may not be a universal threshold; rather thermal occupancy may be more

dependent on prey and habitat availability, at least in small inland lakes (Sellers et al. 1998; Plumb and Blanchfield 2009; Guzzo et al. 2017; Challice et al. 2019). Previous research in the Great Lakes suggests individuals generally occupy water temperatures less than the 10 °C preferred threshold throughout summer stratification. In Lake Ontario, lake trout occupied mean summer temperatures of 6.9 ± 0.5 °C with fish occupying temperatures below 8.8 °C 90% of the time (Raby et al. 2020). In Lake Huron, summer temperature occupancy ranged from 6.0 to 9.7 °C, but differed by stocking strain, with Finger Lakes origin fish ranging from 6.0 to 6.7 °C and Great Lakes origin fish ranging from 7.1 to 9.7 °C (Bergstedt et al. 2012). In large systems such as the Great Lakes, lake trout occupy the warmest water temperatures when the water column de-stratifies during fall turnover (October), which coincides with nearshore movements to spawn (Binder et al. 2021). In Lake Ontario, pre-spawn lake trout occupied water temperatures in October between 8 and 14 °C (Raby et al. 2020), while in Lake Huron, thermal habitat use in October ranged between 7.9 and 9.4 °C (Bergstedt et al. 2012). Given that Lake Erie is the shallowest, warmest, and located furthest south of the Great Lakes, there is the potential for lake trout to be forced to occupy sub-optimal habitat for extended periods proximal to spawning, which could affect reproductive potential (e.g., gamete development or quality).

Although lake trout are physiologically capable of tolerating warmer temperatures than previously assumed (Challice et al. 2019; Hébert and Dunlop 2020), exposure to warm temperatures has the potential to negatively affect the rehabilitation of the species in several ways. Reproductive capabilities of salmonids decline when fish are exposed to elevated water temperatures for prolonged periods prior to spawning (reviewed in Pankhurst and King 2010; Servili et al. 2020). In Lake Erie, duration of summer stratification has increased in the last 50 years due to warming air temperatures (McCormick and Fahnenstiel 1999; Mason et al. 2016).

Given that salmonid maturation and spawning timing is triggered at least partially via photoperiod (Bromage et al. 2001), lake trout in Lake Erie are ostensibly exposed to warmer water temperature for longer periods prior to spawning compared to historical conditions. Additionally, with surface temperature expected to continue to rise, and fall cooling expected to occur up to two weeks later within the next 50-100 years (Trumpickas et al. 2009; Woolway et al. 2021), the risk of excessive exposure to suboptimal temperatures by contemporary lake trout populations is likely to increase over time. Building on the theory relating high temperatures to a lack of successful natural recruitment, Bergstedt et al. (2003) found that increased exposure to elevated water temperatures by lake trout was likely linked to increased sea lamprey predation, which disproportionately affects larger fish (Swink 1991; Schneider et al. 1996; Rogers et al. 2019). Increased sea lamprey predation further hinders the reproductive capability of lake trout populations because larger, older females produce and deposit more eggs and spawn later in the year compared to smaller, younger females (Peck 1988), coinciding with cooler water temperatures and increased offspring survival (Casselman 1995).

The goal of this study was to improve the understanding of the thermal ecology of adult lake trout in Lake Erie. Three research questions were addressed: 1) What is the occupancy of thermal habitat by lake trout in Lake Erie? 2) Does thermal occupancy differ between stocking strains? 3) Do lake trout of different sizes use thermal habitat differently? Temperature occupancy of lake trout was evaluated using lake trout captured in the eastern basin of Lake Erie and tagged with acoustic transmitters with temperature sensors ($n = 139$). I hypothesized that 1) lake trout would occupy habitat that conforms to their thermal optima ($<10\text{ }^{\circ}\text{C}$) throughout summer stratification, 2) fish would be exposed to the warmest temperatures during the month of October (i.e., post stratification), 3) fish would occupy temperatures greater than $10\text{ }^{\circ}\text{C}$ following

turnover for extended periods, 4) lake trout strains originating from Seneca Lake, or descendants of the Seneca Lake population (i.e., Finger Lakes origin; see *Strain assignment* in Methods) would occupy colder habitat during summer and fall than Great Lakes origin strains, 5) large lake trout would occupy colder temperatures than smaller lake trout during summer stratification and large fish would spend less time exposed to water temperatures $> 10\text{ }^{\circ}\text{C}$ compared to smaller fish.

Methods

Study site

Lake Erie is at the southern extent of the native geographic distribution of lake trout (Muir et al. 2021). Lake Erie is often divided by limnological and geomorphological characteristics into three distinct basins: western, central, and eastern (Figure 2.1). Contemporary lake trout are largely constrained to the eastern basin, particularly during summer (Chapter 1), due to its deep depths (mean depth 24.4 m, max depth 64 m), annual stratification, and oligotrophic state, which provides cold, highly oxygenated habitat year around ($< 10\text{ }^{\circ}\text{C}$, $> 4\text{ mg L}^{-1}$; Schertzer et al. 1987; Bolsenga and Herdendorf 1993). In contrast, during summer the shallow western basin (mean depth 7.4 m) becomes warm and isothermal, and the central basin (mean depth 18.5 m) stratifies but the narrow hypolimnion often becomes hypoxic (Hartman 1973; Schertzer et al. 1987; Bolsenga and Herdendorf 1993).

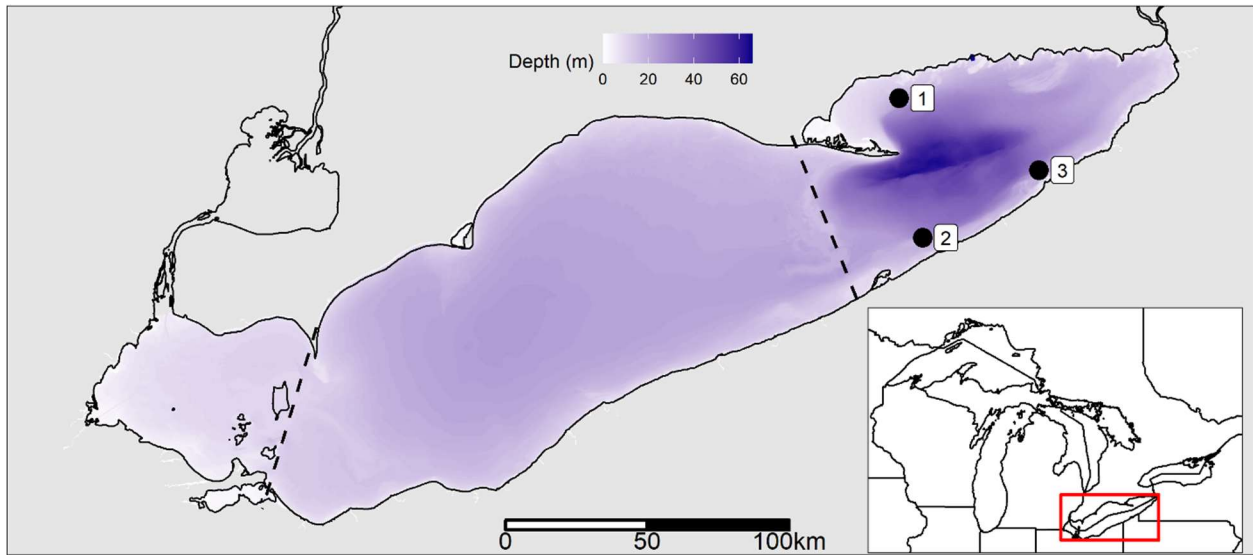


Figure 2.1. Bathymetric map of the study system, Lake Erie. Inset shows the position of Lake Erie, outlined in red, within the Laurentian Great Lakes. Black dots indicate tagging locations, numbered by agency performing tagging (1: OMNDMNRF, 2: PFBC and USGS, 3: NYSDEC). Dashed lines indicate approximate divisions between the western, central, and eastern basins (working left to right).

Fish capture and tagging

Lake trout were collected and tagged as previously described (Chapter 1). In brief, fish were collected with overnight bottom-set gill nets along the northern (N = 49) and southern (N = 91) shorelines of the eastern basin of Lake Erie in spring (May) 2016, 2017, and 2018 (Table 2.1; Figure 2.1). Fish were held aboard research vessels operated by the New York State Department of Environmental Conservation (NYSDEC), Ontario Ministry of Northern Development, Mines, Natural Resources, and Forestry (OMNDMNRF), Pennsylvania Fish and Boat Commission (PFBC) and US Geological Survey (USGS) in recirculating tanks (378-576 L) supplied with lake water prior to the tagging process. Lake trout were anesthetized by immersion (range 180-300 s) in a solution (20 mg/L) of AQUI-S®2E (NYSDEC, PFBC, USGS) or Clove Oil (OMNDMNRF) until reaching stage-4 anesthesia (Summerfelt and Smith 1990). Once anesthetized, lake trout were transferred to a surgical v-board in the supine position and the acoustic transmitter was inserted along the midline, posterior of the pectoral fins, by an experienced surgeon (Chapter 1).

Following surgery, total length was recorded, a clip of the pectoral fin was taken for genetic analysis, and an external loop tag (Lock-on TF-4, Floy Tag and Manufacturing) containing a unique identification number, a contact phone number, and the verbiage “REWARD \$100”, was inserted through the dorsal musculature using a hollow piercing needle. Prior to release, fish were held in tanks supplied with fresh lake water until they regained equilibrium and exhibited the ability to undergo sustained movement following the protocols described by Raby et al. (2012).

Strain assignment

All fish used in this study were determined to be of hatchery origin by either a clipped adipose fin and/or the presence of a coded wire tag. While coded wire tags are implanted into fish stocked in the Great Lakes to identify origins of the fish (i.e., stocking year, strain, and location), this information is only accessible upon lethal sampling the fish, while the presence of a tag can be detected without lethal sampling. Therefore, stocking strain was identified by genetic assignment from a pectoral fin sample taken at the time of tagging. Three primary strains have been stocked into Lake Erie in the last 20 years, originating from Seneca Lake (NY), Lake Champlain (NY/VT), and Slate Island (Lake Superior, ON), with minor contributions from Manitou Lake (ON), and various origins within Lake Superior (i.e., Apostle Island, Klondike, Michipicoten). Additionally, although Lake Huron strains (i.e., Big Sound, Parry Sound, and Iroquois Bay) have never been stocked in Lake Erie, I included these strains as potential assignments as to not rule out the possibility of fish immigrating into Lake Erie through the Huron-Erie Corridor (i.e., through the St. Clair River, Lake St. Clair, and Detroit River, which drains into the western basin of Lake Erie).

Table 2.1. Tagging summary table indicating the number of fish tagged, number with valid detections after the removal of potential tagging mortalities, and length at tagging, given as the mean (min-max) in mm. Each category is broken down by all fish (N), fish of Finger Lakes origin strains (FLO; Seneca, Lake Champlain), fish of Great Lakes origin strains (GLO; Slate Island, Apostle Island, Klondike, Michipicoten, Manitou, Huron Parry Sound, Iroquois Bay), and fish of unknown strain (Unk) due to lack of genetic samples (2016) or inability to assign stocking strain (2017 and 2018). Tagging total by shore: south (United States) = 91, north (Canada) = 48. Note that 2017 transmitters were set at a nominal delay of 2 seconds rather than 120, resulting in much shorter tag battery life.

Year	Location	Number tagged				Detected				Length at tagging (detected only); mean (min-max) (mm)		
		N	FLO	GLO	U	N	FLO	GLO	U	All	FLO	GLO
2016	South shore-PA	7	0	0	7	7	0	0	7	753 (685-800)	NA	NA
2017	South shore-PA	24	16	2	6	24	16	2	6	743 (614-891)	744 (614-837)	816 (740-891)
	North shore-ON	18	16	0	2	17	15	0	2	771 (710-830)	773 (710-830)	NA
	2017 total	42	32	2	8	41	31	2	8	754 (614-891)	758 (614-837)	816 (740-891)
2018	South shore-PA	22	8	5	9	22	8	5	9	718 (510-871)	771 (600-836)	672 (510-790)
	South shore-NY	38	22	7	9	36	20	7	9	761 (652-892)	760 (662-845)	775 (652-892)
	North shore-ON	30	19	6	5	24	18	2	4	753 (475-875)	773 (682-875)	572 (475-669)
	2018 total	90	49	18	23	82	46	14	22	747 (475-892)	767 (600-875)	709 (475-892)
	TOTAL	139	81	20	38	130	77	16	37	750 (475-892)	763 (600-875)	722 (475-892)

Pectoral fin clips were taken from each fish following the surgical implantation of the acoustic transmitter; these samples were dried and stored in paper coin envelopes prior to genetic strain assignment. Fin clip samples from fish tagged by the PFBC, NYSDEC, and USGS during 2017 and 2018 in US waters ($n = 84$) were sent to the US Fish and Wildlife Service (USFWS)

Northeast Fishery Center and clips from fish tagged by OMNDMNRF from Canadian waters ($n = 48$) were sent to the Aquatic Research and Monitoring Section of OMNDMNRF. Fin clips were not taken from fish tagged in 2016. Strain assignment varied slightly between the two labs as each was only able to assign samples to strains that were stocked in each respective country. At the USFWS lab, fish were assigned to potential strains including Seneca Lake, Lake Champlain, Apostle Island, Klondike, Parry Sound, and Lewis Lake (Lake Michigan descendants) using 11 loci. Baseline samples included 50 to 292 individuals and self-assignment scores were 62-85%. Due to the generally low self-assignment, pooling of strains into larger groups was performed. Strains were grouped as either Finger Lakes Origin (FLO) or Great Lakes Origin (GLO). Strains originating from Seneca Lake or Lake Champlain were considered FLO, as the Lake Champlain population consists of primarily Seneca Lake strain fish, or wild descendants of Seneca Lake strain fish (Ellrott and Marsden 2004). Additionally, Seneca Lake and Lake Champlain samples had a pairwise F_{st} (i.e., differences in allele frequencies) of 0.012, compared to pairwise values ranging 0.027-0.044 between FLO and non-FLO strains, further suggesting strong genetic similarities between these strains. All other strains, originating from Lakes Superior, Huron, and Michigan, were considered GLO. This broad grouping was selected because 1) there was a very low sample size of Great Lakes fish outside of Slate Island and Apostle Island strains, 2) there is very high confidence in baseline self-assignment using these groups (FLO: 95%, GLO: 96%), and 3) Bergstedt et al. (2003, 2012) found no behavioral differences between stocking strains originating from the Great Lakes and used similar FLO and GLO groups. Unknown study fish were assigned to these strain groups with relative assignment scores and all assignments with greater than 90% assignment confidence were used (60 of 84 fish; 71%). At the OMNDMNRF lab, fish were assigned to potential strains including Seneca

Lake, Slate Island, Manitou, Manitou Wild Caught, Michipicoten, Big Sound (Lake Huron), and Iroquois Bay (Lake Huron) using 17 loci. Baseline samples included 154-775 individuals and self-assignment scores were greater than 90% for all strains except Manitou and Manitou Wild Caught, which were 52 and 62%, respectively, with nearly all misidentification occurring within these two assignments. Since self-assignment confidence was high, fish were assigned to strain and then strains were grouped based on the FLO/GLO criteria described above. All assignments with greater than 90% confidence were used (41 of 48 fish; 85%). Fish with less than 90% confidence in their strain assignment were likely a stocking strain not included in the baseline of the lab at which the fish was analyzed. Future studies will include collaborations between the Canadian and US labs to provide each with a baseline that includes all potential stocking strains present in Lake Erie, which should bolster the ability to accurately assign strain.

Acoustic telemetry

Acoustic transmitters (InnovaSea V16T-4H, 158 dB, 1342 days estimated tag life; N = 139; Table 2.1) implanted in fish in 2016 and 2018 fish were programmed to emit a unique 69 kHz code at a nominal delay of 120 s (random time intervals between 60 and 180 s); additionally, these transmitters were equipped with temperature sensors which emitted a temperature reading of the transmitter with each acoustic signal transmission (± 0.5 °C). Transmitters implanted in fish in 2017 ($n = 42$) were mistakenly programmed to transmit with a nominal delay of 2 seconds; thus, to standardize the detection data collected from 2017 fish to the intended format of a nominal delay of 60-180 seconds (i.e., transmitters released in 2016 and 2018), detection data from 2017 tags were filtered. Starting from the first detection of a fish, the next detection was sampled from all detections occurring within 60-180 seconds following the previous detection. If no detection occurred within 60-180 seconds, the next detection occurring

more than 180 seconds from the previous was used. This procedure was intended to keep as many detections as possible while sampling randomly within the intended nominal delay framework so that detections from 2016, 2017, and 2018 transmitters were consistent. Due to the programming glitch, the transmitters released in 2017 ceased emitting acoustic signal transmissions within 5 months post-tagging (average: 142 days), typically during mid-October 2017.

Acoustic receivers (InnovaSea VR2W, VR2TX, & VR2AR, 69 kHz) were deployed throughout Lake Erie in conjunction with other ongoing acoustic telemetry studies that were a part of the Great Lakes Acoustic Telemetry Observation System (GLATOS; Krueger et al. 2018). A specific description of receiver coverage throughout the lake is provided in Chapter 1. While the receiver network began collecting data when the first cohort of fish was released (i.e., May 2016), the low sample size of tagged fish ($n = 7$) and sparse receiver coverage limited data acquisition prior to the release of the first large cohort in May 2017. Additionally, due to the early expiration of 2017 tags the available sample size from November 2017 to May 2018 was too low to include these data in any analyses. Therefore, data collected from May 2017 to October 2017 and May 2018 to December 2020 were analyzed as part of this project. Based on field trials conducted in the central and eastern basins of Lake Erie, I assumed the acoustic transmitters used in this study yielded a detection range (i.e., >50% probability of detection) of approximately 750 m (C. Vandergoot, Michigan State University, personal communication).

Data analysis

With acoustic telemetry studies, transmitter code collisions can occur when numerous tagged individuals are in close proximity to each other, which can result in mistaken detections of tagged fish and affect study results (Simpfendorfer et al. 2015). As a result, lake trout

detection data were filtered to remove potential false detections. False detections were removed using a filtering procedure similar to the “short-interval” procedure described by Pincock (2012). A detection was removed from the dataset using the R *glatos* package (Holbrook et al. 2021) if the time threshold separating the detection and any previous or subsequent detections at a single receiver exceeded 3600 s (i.e., 30 times nominal delay of 120 s). Mortality events also have the potential to occur during long-term telemetry studies and can bias results if these events are not considered (Klinard and Matley 2020). Mortality events were identified when a fish was detected at a single receiver (or two receivers < 1500 m apart) for a period greater than 4 months without ever being detected on another receiver outside of the potential range of the mortality event. This time period was used because no fish was confirmed to be alive by mobile detection history following stationary detections spanning more than 4 months. When a fish was declared dead at a receiver, all detections subsequent to the first detection at that receiver were removed from the dataset to reduce the effect of including detections from a dead fish (Klinard and Matley 2020). Additionally, some fish were detected for a much shorter period than the expected tag life and were assumed to have died outside the range of all receivers. The transmitter settings and expansive receiver network in Lake Erie minimized the likelihood that a fish could go undetected in Lake Erie for more than several months (Kraus et al. 2018). The longest period a lake trout went undetected before being confirmed to be alive via mobile detection history was 6 months. Therefore, fish were considered to have died if they went undetected for more than 6 months prior to the end of the study period. Fish assumed to have died within 30 days post-tagging were considered to be mortalities associated with the collection, handling, and tagging process and all detections from these fish were excluded from further analysis. Of 139 tagged fish initially released, all were detected at least once, 9 fish (7%) were assumed to have died due to the

tagging process and were subsequently removed from analyses, and a single fish tagged in 2016 was not detected after May 2017. Eighteen fish were identified as having died during the study period (13%; 1 reported angler or commercial harvest, 4 dead at a receiver, and 13 undetected); all detection data from these fish prior to their estimated time of death were included in subsequent analyses. Due to the conservative filtering criteria (4 months at a single receiver or 6 months undetected) and short detection period of 2017 tagged fish, it is possible that mortalities of 2017 fish were underestimated or missed, however this was unlikely to affect results.

All analyses were performed in R 4.1.2 (R Core Team 2021). The final dataset from May 1, 2017 to October 30, 2017 and May 1, 2018 to December 31, 2020 contained 2,934,775 detections from 129 fish. To estimate temperature occupancy, monthly average temperature ($^{\circ}\text{C}$) was calculated for each fish. To be included in analyses, a fish needed to be detected at least 5 times on at least 4 different days in a given month. This was done to prevent undue influence from individuals with just a few observations. Monthly means were taken as an average of all fish monthly means and 95% confidence intervals (CI) were used to quantify uncertainty about the population-level mean. To determine if fish were selecting constant or variable temperatures during a given day, as a potential means to investigate the occurrence of pronounced diel vertical movements, individual fish daily temperature ranges (max-min) were averaged when the lake was thermally stratified (June-September) and averaged over the total sample. To understand how bottom depth of the receiver detected on influences temperature, monthly temperature occupancy for June-September was fit to several linear mixed models. To be included in this analysis, only detections including both temperature and bottom depth of the receiver were considered and, as described above, a fish needed to be detected at least 5 times on at least 4 different days. All candidate models considered fish ID as a random effect and month and mean

day of detection as fixed effects. Additionally, models contained potential fixed effects of bottom depth, year, month by year interaction, month by bottom depth interaction, and year by bottom depth interaction. The full model contained all these effects; alternative models included all possible subsets of the effects. Average day of detection was included in models to account for water temperature changing throughout a month. For example, during spring and summer, fish detected exclusively late in a month were likely to be exposed to warmer temperatures than fish detected early in a month.

To further investigate temperature occupancy proximal to hypothesized spawning, the number of days that fish had a daily average temperature greater than 10 °C from the period of September 1-November 30 was calculated. These analyses were restricted to detections from 2018 to 2020, as during 2017 the large cohort of tags expired during this time period and the remaining fish gave an inadequate sample size. All fish detected at least five times in a day were included in daily temperature analyses. Due to heightened occupancy of nearshore regions of the eastern basin during fall (Chapter 1) and the increased density of receivers in these areas targeted toward capturing spawning activity, the probability of being detected was expected to be increased compared to other seasons when fish occupy offshore areas with sparser receiver coverage (Chapter 1). To estimate the timing and duration of the period when nearly the entire population was exposed to warm water, number of days when more than 90% of fish occupied a mean water temperature greater than 10 °C was used.

To address if stocking strain influences temperature occupancy, fish of FLO and GLO strains were compared (see *strain assignment*). To determine monthly temperature differences during summer and fall months, average monthly temperature was modeled using a linear mixed model for summer months (June-September) and linear models for October and November

independently. Summer monthly temperature occupancy was fit with fish ID as a random effect and month and average day of detection as fixed effects. Additional models included year; strain; year and strain; strain and strain: month; and year, strain, and strain: month. October and November data were each fit individually using linear models with possible effects of average day of detection only; average day and year; average day and strain; or average day, year, and strain. Number of days that fish had a daily average temperature greater than 10 °C from the period of September 1-November 30 was considered using strain as a possible effect. Due to the format of the data (counts) and evaluation of model residuals, generalized linear mixed models assuming a Poisson error distribution were fit to the number of days fish averaged over 10 °C during fall. All models included a random effect of fish ID and candidate models considered fixed effects of strain, year, strain and year, and strain, year, and strain×year.

To address if fish length influences temperature occupancy, strain analyses were repeated considering length at the time of tagging in place of strain as a potential effect with few discrepancies. Since length at tagging was used, only detections from the spring, summer, and fall following tagging was considered for length analyses (Chapter 1). November data did not include an adequate sample size from 2017 and therefore were fit to linear models with possible effects of average day of detection only, or average day and length. The number of warm days occupied during fall (September 1-November 30) was analyzed for 2018 only, given the small sample in 2016. Generalized linear models were fit to number of days with mean temperature occupancy over 10 °C with length as a fixed effect or as an intercept-only (null) model. Lastly, to determine whether large (≥ 750 mm) and small (< 750 mm) fish differed in the timing of occupying warm temperatures, I considered daily percent of fish occupying average temperatures over 10 °C. For this analysis, lengths were binned at 750 mm as this provided an approximately

even split of the slightly bimodal length at tagging data. Additionally, this approximate length may incorporate biological significance as sea lamprey have been found to select for large individuals, often considered greater than 737 mm (Eshenroder and Koonce 1984; Rutter and Bence 2003).

Linear models, linear mixed models, and generalized linear mixed models were evaluated for adequate fit by observation of model residuals (lme4 package; Bates et al. 2015). Model selection was performed by considering AIC_c differences of candidate models, always additionally considering a null, intercept-only model. An AIC_c difference of greater than 2 units was considered to be meaningful support of the top performing model exclusively (bbmle package; Bolker and R Development Core Team 2021). Confidence intervals for model parameters (95%) were calculated by likelihood profiling.

Results

Summer temperature occupancy

Lake trout monthly mean temperature occupancy during the summer (June to September) ranged from 5.5–8.2 °C. Monthly temperature occupancy was similar between 2018 and 2019 (5.6–6.6 °C and 5.5–6.8 °C, respectively), slightly higher in 2017 (6.1–6.9 °C), and highest in 2020 (6.8–8.2 °C; Figure 2.2). Throughout the summer, temperature occupancy was relatively similar between June and July before slightly increasing in August (August-July: 2017=0.53 °C, 2018=0.20 °C, 2019=0.54 °C, 2020=0.29 °C) and further increasing in September (September-August: 2017=0.26 °C, 2018=0.49 °C, 2019=0.73 °C, 2020=1.07 °C; Figure 2.2). Lake trout occupied relatively uniform daily temperatures during summer months. On average, individual daily temperature range was between 0.6 and 1.0 °C from June through September (Jun: 0.7, Jul: 0.6, Aug: 0.7, Sep: 1.0) and was similar across years. Furthermore, few individuals (3–11%)

experienced daily temperature ranges exceeding 3 °C for more than 10% of summer (June-September) days while only 1 fish experienced ranges exceeding 3 °C for more than 25% of summer days over the 4-year study period.

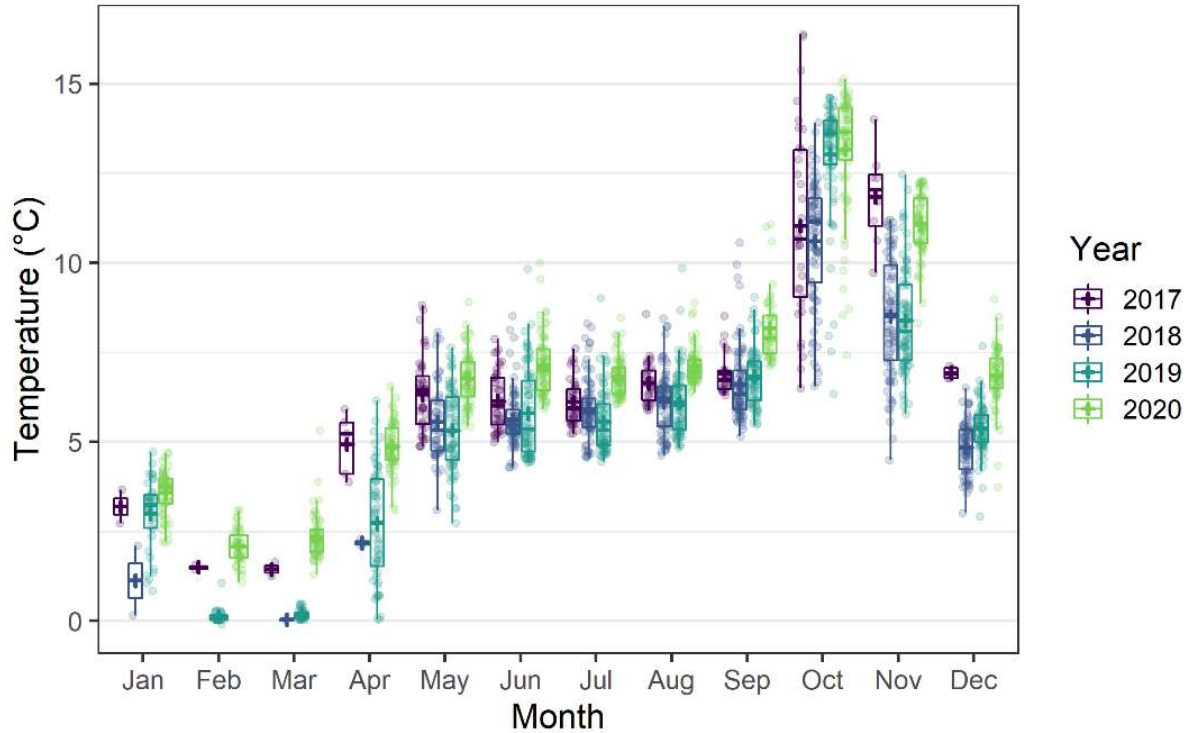


Figure 2.2. Average monthly temperature (°C) occupied by year. Each point shows the monthly average from an individual fish. Boxplots show sample-level summary statistics with the box ranging from the first to third quartile, the solid line representing the median, the plus representing the mean, and whiskers extending 1.5 times the inter quartile range.

Bottom depth of receiver was negatively correlated with fish temperature occupancy during summer months (Figure 2.3). The best fitting model for explaining temperature occupancy considered fixed effects of receiver depth, month, mean day of detection, year, depth×month interaction, depth×year interaction, and month×year interaction with fish ID as a random effect (Table S2.0.2). While the slope of this trend varied slightly by year and month, model fit was generally very tight (conditional $R^2 = 0.77$), with few observations far below the model average (Figure 2.3). The slope of the relationship between temperature and bottom depth

was strongest in 2018 and weakest in 2020 (Figure 2.3). This effect, in combination with the coolest average occupancy occurring in 2018 and warmest occupancy in 2020, resulted in the largest yearly temperature differences occurring at the deepest occupancy and smallest yearly differences at the shallowest depths (Figure 2.3).

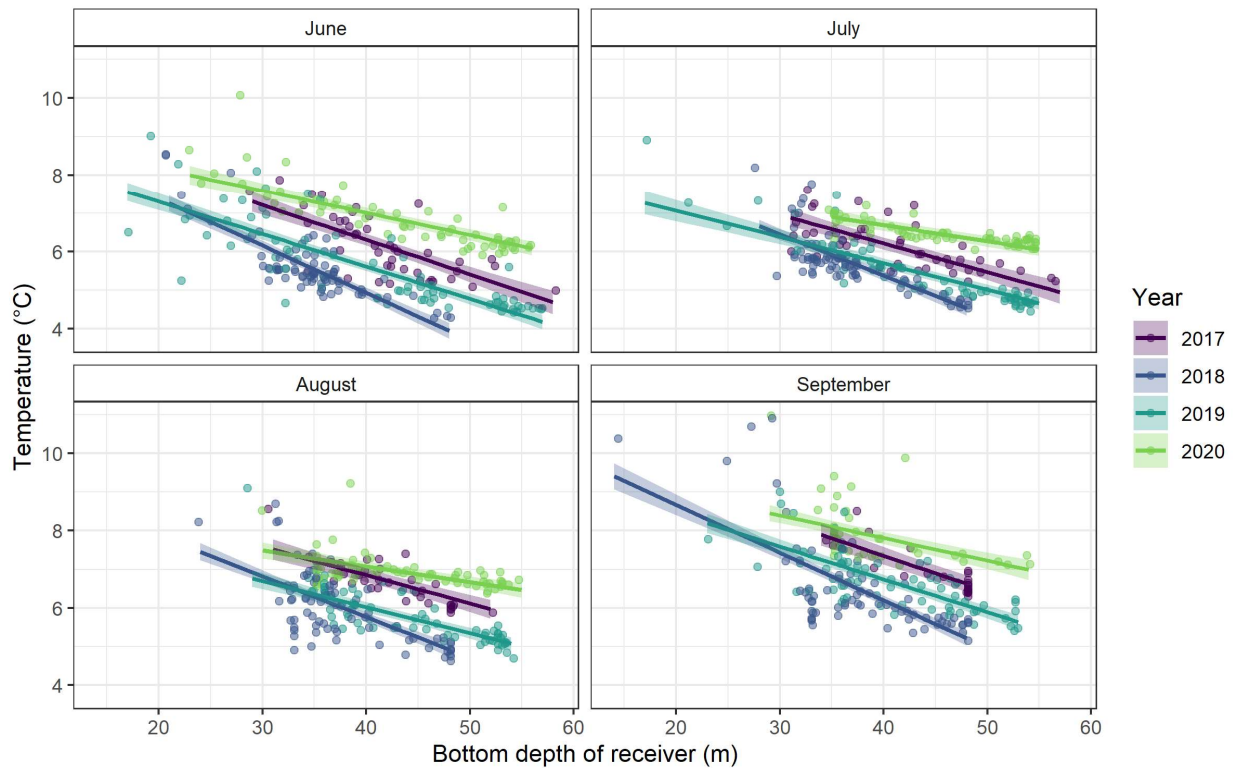


Figure 2.3. Monthly average temperature (°C) by average bottom depth of receiver (m) detected on. Each point indicates the monthly average of an individual. Lines indicate model predictions and shaded regions indicate the 95% confidence intervals.

Fall temperature occupancy

Lake trout consistently occupied the warmest temperatures of the year during the month of October (i.e., post-stratification). During October of 2017 and 2018, mean temperature occupancy was 11.0 °C and 10.6 °C, respectively, while temperature occupancy was much higher during October 2019 (13.0 °C) and 2020 (13.2 °C; Figure 2.2). Temperature occupancy during the month of November decreased from the October peak and exhibited yearly trends similar to those from summer months, with 2020 occupancy being warmer than 2018 and 2019

(Figure 2.2). The highest degree of individual variation was apparent during October and to a lesser extent November (Figure 2.2).

Lake trout spent an average of 14.1 days in 2018, 13.8 days in 2019, and 22.6 days in 2020 occupying temperatures greater than 10 °C. Approximately 20 to 30% of fish in 2018 and 2019 spent less than 10 days exposed to average temperatures of greater than 10 °C [2018: 22% (18 of 81 fish); 2019: 27% (21 of 77 fish)], but in 2020 that fraction dropped to 6% (4 of 72). Conversely, 40% (29 of 72) of the population spent greater than 25 days exposed to temperatures greater than 10 °C in 2020, whereas 0 fish in 2018 and 3 fish in 2019 (4%) were exposed to warm temperatures for a greatly extended period. Considering the proportion of fish that occupied an average temperature greater than 10 °C on each day from September-December, greater than 90% of fish occupied warm temperatures for 12 days in 2018 spanning October 20-November 7, 15 days in 2019 spanning October 17-November 7, and 22 days in 2020 spanning October 15-November 15 (Figure 2.4).

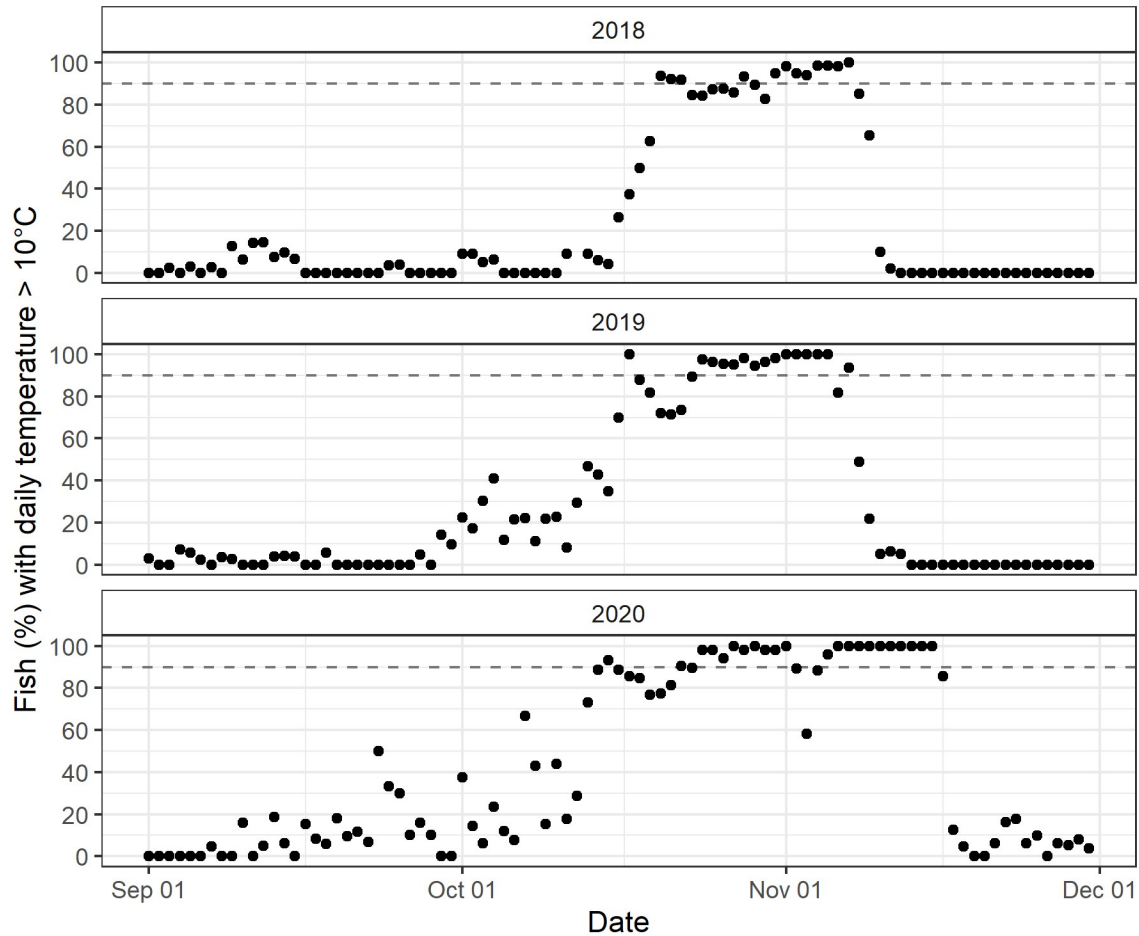


Figure 2.4. Percent of fish with recorded mean daily temperature greater than 10 °C for September 1-Novemeber 30 during 2018, 2019 and 2020. The dashed lines reference 90% of the sampled population.

Strain effect

Hatchery strain of lake trout had little effect on the average monthly temperature fish occupied. For the summer months (June-September), two candidate models were considered plausible and were averaged (Table S2.0.3). The best performing model (Model 1; AIC weight 72%), did not include strain as an explanatory factor. After model averaging, the coefficient for the strain effect was positive (0.02 °C), however, the 95% confidence interval estimate for the parameter encompassed both positive and negative values (-0.14 – 0.17). Similar to the summer months, for October, a model that did not include hatchery strain was the most plausible, while

the second-best performing model was within 2 AIC units and included strain (Table S2.0.4); however, in the averaged model confidence intervals describing the effect of strain overlapped zero [-0.07 °C (95% CI: -0.44 – 0.30); Figure 2.5]. Hatchery strain was not included in the best performing model for water temperatures occupied by lake trout during November (Table S2.0.5).

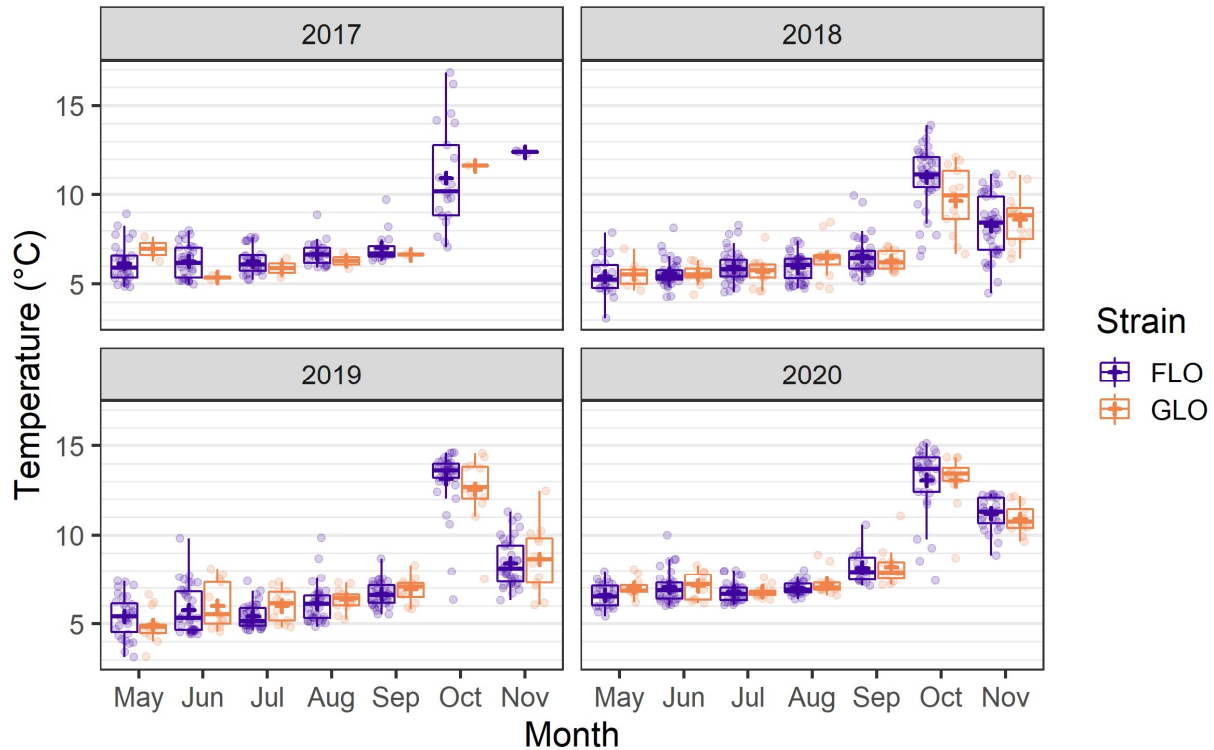


Figure 2.5. Average monthly temperature (°C) lake trout occupied by strain (FLO: Finger Lakes Origin, GLO: Great Lakes Origin) during 2017, 2018, 2019 and 2020. Each point shows the monthly average from an individual fish. Boxplots show summary statistics with the box ranging from the first to third quartile, the solid line representing the median, the plus representing the mean, and whiskers extending 1.5 times the inter quartile range.

Hatchery strain did influence the number of days fish occupied warm water (10 °C) during fall (Sept 1- November 30). The best performing model for describing the average number of days lake trout were observed in water temperatures > 10 °C considered fixed effects of strain, year, and strain×year interaction with a random effect of fish ID (Table S2.0.6). FLO

fish experienced more days with a mean over 10 °C than GLO fish during 2018 [14.1 days (12.7–15.6) and 11.0 days (9.0–13.5), respectively] and 2019 [15.1 days (13.6–16.8) and 10.3 days (8.4–12.7), respectively], but not during 2020 [20.2 days (18.2–22.4) and 22.4 days (19.0–26.4), respectively; Figure 2.6].

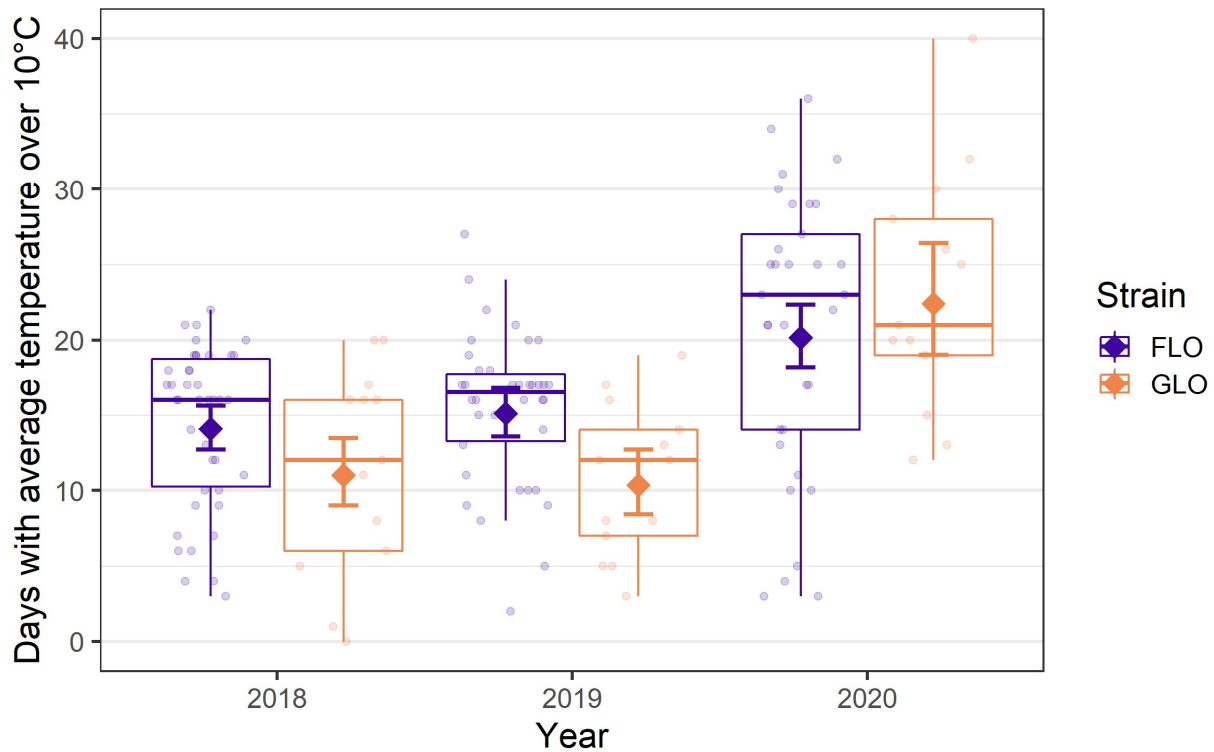


Figure 2.6. Number of days from September 1–November 30 that fish had a mean daily temperature of greater than 10 °C by strain (FLO: Finger Lakes Origin, GLO: Great Lakes Origin) and year. Diamonds and associated 95% confidence intervals indicate model average predictions and boxplots (median, 1st and 3rd quartiles and whiskers 1.5 times the interquartile range) represent the observed observations from strain-specific individual lake trout.

Length effect

Based on the movements of fish observed during the study, lake trout length at tagging influenced temperature occupancy during the first year at liberty during the summer. The model with the most support included temperature with month, year, length, and mean day of the month as fixed effects and fish ID as a random effect (Table S2.0.7). Larger fish occupied cooler water

temperatures during each month from June through September [-0.00279 °C/mm (95% CI: -0.00428 – -0.00128); -1.06 °C over range of observed lengths, 510–892 mm; Figure 2.7]. Summer temperature occupancy was 0.43 °C (95% CI: 0.20–0.66) warmer during 2017 compared to 2018, and this effect was independent of length or month. During October, the best performing model did not include length as a fixed effect (Table S2.0.8); however, during November, the best performing model included length at tagging and mean day of the month (Table S2.0.9). During November, larger fish occupied cooler temperatures than smaller fish [-0.00401 °C/mm (95% CI: -0.00578 – -0.00224); -1.53 °C over length range; Figure 2.7]. Fish length at tagging was not a meaningful predictor of number of days spent over 10 °C [effect of length: 0.00016 °C/mm (95% CI: -0.00049 – 0.00080); Table S2.0.10] and the daily percent of fish occupying temperatures greater than 10 °C did not differ between fish 750 mm and larger and fish less than 750 mm, with percentages differing by greater than 20% only 1 day.

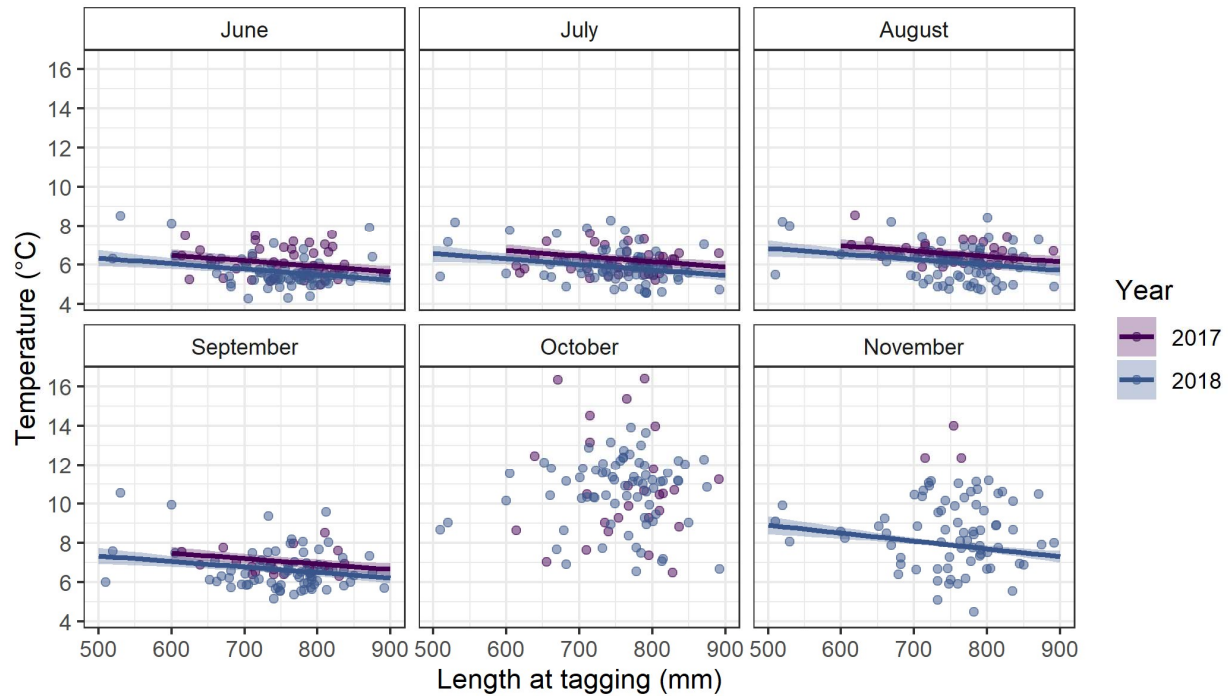


Figure 2.7. Average monthly temperature (°C) by length at tagging (mm) during June–November of the first year after tagging for 2017 and 2018 tagged fish. Trend lines show population-level model averages with the 95% CI shaded.

Discussion

We found that lake trout in Lake Erie occupied similar, and in some years cooler, thermal habitat compared to previous studies in the Great Lakes (Bergstedt et al. 2003, 2012; Raby et al. 2020). I observed this despite Lake Erie presumably having a greater availability of warmer temperatures given the lake’s location and depth. While the limnological characteristics of Lake Erie provide abundant habitat close to the thermal optimum of lake trout (10 ± 2 °C; McCauley and Tait 1970; Christie and Regier 1988), fish occupied habitat below the lower extent of the thermal optimum during summer stratification. This observation was expected, as in many lake trout populations fish tend to primarily occupy temperatures below the laboratory determined thermal optimum, both within (Bergstedt et al. 2003, 2012; Raby et al. 2020) and outside of the Great Lakes (Mackenzie-Grieve and Post 2006; Plumb and Blanchfield 2009; Jacobson et al.

2010; Guzzo et al. 2017). This discrepancy between laboratory and wild behavior is often considered to be due to decreasing metabolic costs and maximizing food conversion efficiency as temperature preference decreases with decreasing ration size (Brett et al. 1969; Mac 1985). While habitat use at temperatures below the thermal optimum could be driven by responses to food scarcity, prey availability and distribution likely act as drivers of equal or potentially greater importance (Marsden et al. 2021).

The forage base in the eastern basin of Lake Erie is primarily comprised of rainbow smelt (*Osmerus mordax*) and round goby (*Neogobius melanostomus*), with the former thought to be the preferred prey of lake trout during periods of stratification (Coldwater Task Group 2022; Forage Task Group 2022). In most years since 2001, rainbow smelt composed more than 75% of the diet of lake trout during August (e.g., 88% in 2017 and 94% in 2020; Coldwater Task Group 2022), though the occurrence of rainbow smelt in lake trout diets in 2018 (57%) and 2019 (61%) was low relative to previous years (Coldwater Task Group 2022). During years of low rainbow smelt abundance, composition of round goby in lake trout diets generally increases suggesting it may provide a buffer when preferred prey resources are less abundant. For example, in 2018 and 2019, round goby occurrence in diets increased to 58% and 37%, respectively, before decreasing to 4% in 2020 when rainbow smelt abundance and occurrence in diets returned to high levels (Coldwater Task Group 2022). Adult rainbow smelt typically occupy cold, hypolimnetic water during the day with populations varying in temperatures of maximum occupancy from 4-8 °C, while at night rainbow smelt occupy highly variable habitat, ranging from 4-20 °C, with the species often making diel migrations to warmer water either vertically or horizontally (Brandt et al. 1980; O’Gorman et al. 2000; Simonin et al. 2012). Consequently, lake trout summer thermal habitat selection could be partially driven by rainbow smelt daytime distribution. Future studies

should address thermal habitat use of rainbow smelt in Lake Erie and investigate predator-prey habitat selection more directly.

Lake trout in some populations have been shown to undergo diel vertical migrations in pursuit of prey (Sellers et al. 1998; Bergstedt et al. 2016; Binder et al. 2021). However, in the current study lake trout were rarely detected over wide daily temperature ranges, suggesting that diel vertical migrations into the metalimnion or epilimnion may not occur in Lake Erie. However, methodological constraints may have limited the ability of this study to detect partial vertical migration including vertical movements within the hypolimnion. First, acoustic transmitters equipped with temperature sensors fail to convey precisely where the fish reside vertically within the water column, particularly within the hypolimnion as temperature changes little from the bottom of the thermocline to the lake bottom. Acoustic transmitters equipped with depth (pressure) sensors, in addition to temperature sensors, could identify diel vertical migration more directly. Second, internal temperature sensors can fail to detect rapid forays into warmer water. Negus and Bergstedt (2012) found that intraperitoneal temperature of a 2.2 kg lake trout took nearly 20 minutes to approach within 2 °C of the ambient temperature for a 5 °C change and nearly 35 minutes for a 10 °C change. Additionally, the time to approach ambient temperature increased linearly with mass, roughly doubling from 0.8 to 2.2 kg fish. The fish used in the present study ranged from 2.8 to 7.0 kg, suggesting that intraperitoneal temperature adjustment times for fish in this study likely exceed those studied by Negus and Bergstedt (2012). Third, detection range decreases by approximately half when the transmitter (in the fish) and the receiver (the hydrophone moored to the lake bottom) are separated by a large temperature gradient (Wells et al. 2021). This decreases the probability of detecting a fish

making a vertical migration into the epilimnion or metalimnion, though it is unlikely that all detections in the upper water column would have been missed.

Lake trout showed notable annual variation in temperature occupancy, both in average monthly temperature occupancy and number of days occupying warm water (>10 °C). Consistent annual trends were observed despite average summer bottom depth of receiver being deepest during 2020, shallowest during 2018 and 2019, and intermediate during 2017 (chapter 1). This mismatch between temperature occupancy and bottom depth of the areas of the lake where lake trout inhabited suggests that during 2020, and to a lesser extent 2017, fish were either forced to occupy warmer water due to ambient lake temperatures or fish suspending vertically within the water column over deeper water. In 2020 and 2017, model fit of temperature based on depth was very tight, particularly at deep depths, suggesting that fish likely occupied demersal habitat. Further, August bottom temperature at depths between 30 and 50 meters (i.e., hypolimnion), the depth range of greatest summer lake trout occupancy (chapter 1), was higher in 2017 and 2020 (7.6 and 7.3 °C, respectively) than in 2018 and 2019 (6.1 and 5.9 °C, respectively; J. Markham, NYSDEC, personal communication). These data, in combination with summer bottom depth occupancy presented in chapter 1, suggest that fish occupied warmer habitat during summer due to water conditions, more so than through selection of warmer habitat, during 2017 and 2020. Similarly, during fall, water temperatures taken nearshore (~10 m water depth on bottom, off Dunkirk, NY) near areas of high fall occupancy showed warmer temperatures in 2020 compared to 2018 and 2019 (October: 20.6, 14.8, and 17.7 °C, respectively; November: 13.4, 7.8, and 10.9 °C, respectively; P. Wilkins, NYSDEC, personal communication). This provides further evidence that yearly differences in temperature occupancy are driven by water temperature to a greater extent than observed behavioral differences. Resultingly, if warm temperature prior to or

during spawning are hindering wild recruitment in this population, relative recruitment success could be dependent on frequency of cooler water years, with years like 2020 potentially leading to recruitment failure.

Fish of different hatchery strains did not show meaningful differences in monthly average temperature occupancy during summer or fall months. This finding was surprising, considering that previous studies within the Great Lakes found that FLO fish occupied cooler temperatures, particularly during summer, than GLO fish (Elrod et al. 1996; Bergstedt et al. 2003, 2012). FLO strain lake trout have typically been found to be the most successful strain stocked in Lakes Huron (Scribner et al. 2018), Michigan (Larson et al. 2021), Ontario (Marsden et al. 1989), and Erie (Lake Erie Committee 2021), which is attributed to lower sea lamprey mortality rates compared to GLO lake trout strains. The relative success of the FLO strains both in the Great Lakes and Lake Erie motivated the Lake Erie Committee in the most recent lake trout rehabilitation plan (Lake Erie Committee 2021) to devote all stocking efforts to only these strains (Seneca Lake and Lake Champlain) moving forward. The exact mechanism for why FLO strains may have lower sea lamprey mortality rate is not known with certainty but has been attributed to lower spatial overlap with sea lamprey and a greater ability to survive a sea lamprey attack compared to GLO strains (Elrod et al. 1996; Lantry et al. 2015; Scribner et al. 2018; Coldwater Task Group 2022). The lack of temperature occupancy differences across these groups of strains suggests that increased survival of FLO strains may be more likely due to the strain being more able to survive sea lamprey predation. In support of this hypothesis, during 2020 and 2021, the Coldwater Task Group (2021, 2022) found that 40-61% of Finger Lakes origin fish had a healed lamprey wound (A4) and 3-13% had a fresh wound (A1-A3), whereas no Slate Island strain fish were captured with a healed or fresh wound. The Coldwater Task Group (2021, 2022) considered

the low observed marking rates of the Slate Island strain to be due to either high avoidance behavior or low survival rate following an attack. While the results found in this study did not identify behavioral differences in temperature occupancy when considering monthly average, differences were found for time spent in warm water.

Contrary to the previous findings suggesting that FLO lake trout have a heightened affinity to cold water compared to GLO strains, I found that FLO fish occupied warm water for more days than GLO fish during 2018 and 2019. These differences can likely be attributed to FLO fish beginning to occupy warm water earlier in the fall than GLO fish during these years. The increased time spent in warm water by FLO lake trout could be contributing to the heightened lamprey marking rates of FLO strains found by the Coldwater Task Group (2021, 2022; Swink 1993). Despite these behavioral differences and the increased marking rates found in FLO fish, FLO fish are thought to maintain higher survival than GLO fish in Lake Erie (Lake Erie Committee 2021). However, excess occupancy of warm water by FLO fish may pose alternative problems. For example, Hébert and Dunlop (2020) found that the Seneca lake strain juveniles exhibit a lower aerobic scope temperature optimum than several Great Lakes strains and suggested this could result in increased susceptibility of the Seneca strain to anaerobiosis and reduced reproductive investment resulting from exposure to high temperatures. Warm water temperatures nearshore at suspected spawning locations in Lake Erie could explain, in part, why substantial recruitment has not yet occurred in Lake Erie, in contrast to the other Great Lakes where FLO-derived natural recruits tend to dominant wild cohorts.

Large lake trout were found to occupy cooler temperatures than small lake trout during summer months and November. During summer (i.e., June-September), the largest and smallest fish in the study differed in temperature occupancy by approximately 1 °C, a potentially

meaningful difference across the wide size range of mature fish. Occupancy of deeper areas of the lake is likely the driver of these differences, as there is a strong negative relationship between occupied temperature and bottom depth. This observation of depth occupancy increasing and temperature occupancy decreasing as fish increase in size and age is common in marine systems and often termed Heincke's law (Heincke 1913, as cited in Lindmark et al. 2022). Though contention exists over the mechanisms at play in heavily exploited marine fisheries displaying this phenomenon, primarily regarding the influence of fishing pressure (e.g., Frank et al. 2018; Audzijonyte and Pecl 2018), the very low fishing pressure on the lake trout population in this study (Coldwater Task Group 2022) provides three potential explanations for this behavior. First, Lindmark et al. (2022) found that optimum growth temperature decreases with increasing body size, suggesting that the trends shown here could be attributed to maximizing metabolic efficiency. Second, while fisheries exploitation is minimal in Lake Erie, predation from sea lamprey could dictate the size-structured distribution of lake trout through the preferential predation of large individuals and increased mortality rate of lake trout following a sea lamprey attack as water temperature increases (Swink 1991; Schneider et al. 1996; Rogers et al. 2019). Third, differences in diet across the range of sizes observed here could drive habitat selection, though this explanation seems least likely given that all fish were of a mature size and gape limitations are unlikely to be a significant factor in prey selection. While mean temperature occupancy during the hypothesized spawning month of November was cooler for larger fish, individual variability was high and length was not a meaningful predictor for the month of October or the number of days fish spent in warm (>10 °C) water during fall. The general lack of a relationship between length and fall warm water occupancy occurred contrary to my predictions. This could be due to sex-specific spawning behavior, as males typically arrive on the

spawning grounds earlier than females and are therefore expected to be exposed to warm temperatures for much longer periods (Binder et al. 2021). Resultantly, a balanced sex ratio in the sample would explain the high observed variability and absence of a length-dependent trend. Additionally, while larger females are expected to spawn later when water temperatures are cooler, this does not preclude them from arriving on the spawning grounds and occupying warm water for week to month long periods prior to spawning (Binder et al. 2021).

The results of this study confirmed the availability of suitable thermal habitat for lake trout in Lake Erie, particularly during summer. Jacobson et al. (2010) found that lake trout utilize the coldest and most restricted oxythermal habitat of four coldwater species native to Lake Erie, including lake whitefish (*Coregonus clupeaformis*), cisco (*C. artedi*), and burbot (*Lota lota*). Lake whitefish and burbot are present in Lake Erie and are of management concern (Coldwater Task Group 2022), while cisco are considered extirpated and are only recently being considered for reintroduction (Schmitt et al. 2020). The thermal habitat occupancy of lake trout found in this study confirms the availability of adequate habitat to support the continued rehabilitation of other coldwater species in Lake Erie (Schmitt et al. 2020). The continued efforts to rehabilitate the Lake Erie lake trout population will assist in the rehabilitation efforts of other native coldwater species of ecological, economical, and cultural significance (Oldenburg et al. 2007).

The study of lake trout in Lake Erie provides an opportunity to evaluate the behavior of a coldwater species at the southern extent of its native geographic range in the face of a climate change. Somewhat surprisingly considering the bathymetry and southern location of the lake, thermal ecology of lake trout in Lake Erie was not considerably different than in Lakes Huron and Ontario. Lake trout were found to occupy cold water during summer but warmer water during fall, in some years for extensive periods. Warm water occupancy of fish, particularly

during the fall proximal to spawning, has been considered one of the more prominent hypotheses for explaining the lack of wild recruitment in Lake Erie (Lake Erie Committee 2021). Indeed, I did find differences in adult temperature occupancy between Lake Erie and Lake Huron (to a lesser extent Lake Ontario) to build support for this hypothesis. Of particular concern could be the heightened warm water occupancy of FLO strain fish. While FLO strain fish are believed to have greater survival than GLO strains, they are exposed to warm water for longer periods of time, which could result in decreased reproductive potential (Hébert and Dunlop 2020). Managers should continue to consider alternatives such as continuing to stock GLO strains, despite their generally lower survival, that may be less hindered by exposure to warm water. Stocking on and restoration of offshore spawning reefs could also benefit rehabilitation efforts by promoting spawning at deeper depths that could allow for spawning at cooler temperatures (Krueger et al. 1995; Dawson et al. 1997). Lastly, continued effective sea lamprey control could allow for an increased average age of female lake trout, which could result in spawning later at cooler temperatures. Ultimately, the management of this population could benefit from any combination of the above suggestions, as well as continued research into still largely unknown mechanisms of continued lack of wild recruitment in Lake Erie lake trout.

APPENDIX

Table S2.1. Average monthly temperatures for lake trout with at least 3 days with at least 5 detections in a month. For each year, 2017-2020, monthly sample mean (°C) with 95% confidence intervals (CI), range (maximum–minimum, °C), and number of fish included in the sample, are given. To be included, a month needed at least 3 fish with ample data, explaining the missing data in winter and early spring of 2017 and 2018. Months with low samples (less than 10 fish; April, November, and December 2017) are italicized to be interpreted with caution.

	2017			2018		
Month	Mean (95% CI) °C	Range (Min-Max) °C	N	Mean (95% CI) °C	Range (Min-Max) °C	N
Jan						
Feb						
Mar						
Apr	<i>4.93 (3.82-6.04)</i>	<i>2.03 (3.88-5.9)</i>	<i>5</i>			
May	6.31 (5.99-6.63)	3.95 (4.86-8.81)	43	5.55 (5.23-5.87)	4.95 (3.1-8.05)	47
Jun	6.14 (5.9-6.38)	2.88 (4.98-7.87)	45	5.62 (5.44-5.8)	4.24 (4.28-8.52)	78
Jul	6.1 (5.91-6.3)	2.39 (5.22-7.6)	43	5.91 (5.73-6.1)	3.74 (4.55-8.29)	81
Aug	6.64 (6.44-6.83)	2.68 (5.88-8.56)	35	6.11 (5.91-6.31)	3.83 (4.62-8.44)	78
Sep	6.9 (6.64-7.15)	2.21 (6.29-8.5)	23	6.6 (6.37-6.83)	5.41 (5.15-10.56)	80
Oct	11.03 (10.08-11.98)	9.88 (6.5-16.38)	33	10.6 (10.21-10.99)	7.36 (6.55-13.91)	78
Nov	<i>11.83 (10.72-12.95)</i>	<i>4.29 (9.71-14)</i>	<i>8</i>	8.51 (8.13-8.88)	6.71 (4.49-11.2)	78
Dec	<i>6.92 (6.63-7.22)</i>	<i>0.37 (6.76-7.12)</i>	<i>4</i>	4.83 (4.67-5)	3.5 (3-6.5)	76
	2019			2020		
Month	Mean (95% CI) °C	Range (Min-Max) °C	N	Mean (95% CI) °C	Range (Min-Max) °C	N
Jan	2.99 (2.66-3.31)	3.87 (0.84-4.71)	38	3.58 (3.42-3.73)	2.52 (2.17-4.69)	62
Feb	0.12 (0.05-0.19)	1.15 (-0.09-1.06)	34	2.07 (1.93-2.22)	2.03 (1.07-3.09)	45
Mar	0.18 (0.13-0.22)	0.46 (0.02-0.48)	40	2.34 (2.17-2.52)	4.04 (1.28-5.32)	56
Apr	2.72 (2.31-3.12)	6.12 (0.03-6.15)	59	4.87 (4.71-5.04)	3.45 (3.09-6.55)	63
May	5.33 (5.05-5.61)	4.91 (2.72-7.63)	68	6.75 (6.57-6.93)	3.48 (5.42-8.9)	67
Jun	5.79 (5.51-6.06)	5.4 (4.42-9.82)	76	7.12 (6.92-7.32)	4.08 (5.91-9.99)	70
Jul	5.55 (5.35-5.74)	4.56 (4.44-9.01)	76	6.81 (6.69-6.94)	2.4 (6.04-8.45)	71
Aug	6.09 (5.88-6.3)	5.02 (4.83-9.85)	73	7.1 (6.99-7.22)	2.51 (6.37-8.88)	70
Sep	6.82 (6.64-7)	3.58 (5.46-9.04)	72	8.17 (7.89-8.45)	3.94 (7.13-11.07)	46
Oct	13.02 (12.63-13.41)	8.28 (6.33-14.61)	73	13.17 (12.77-13.56)	7.71 (7.42-15.13)	70
Nov	8.38 (8.05-8.72)	6.68 (5.78-12.46)	76	11.06 (10.84-11.27)	3.97 (8.32-12.29)	65
Dec	5.37 (5.2-5.53)	4.77 (2.9-7.67)	70	6.83 (6.62-7.04)	5.25 (3.73-8.98)	63

Table S2.2. Model selection table for candidate models fit to average monthly temperature, May-September. All models were linear mixed models that included mean day of the month as an additional fixed effect with individual fish as a random effect. Notation effect:effect indicates an interaction effect, with D meaning depth, M meaning month, and Y meaning year. A + indicates that the fixed effect was included in the model while - indicates it is not. DF is degrees of freedom and logLik is the log likelihood associated with the model.

Model	Fixed effects							DF	logLik	ΔAIC_c
	Depth	Month	Year	D:M	D:Y	M:Y	D:M:Y			
1	+	+	+	+	+	+	-	26	-697	0.0
2	+	+	+	+	+	+	+	35	-690	3.7
3	+	+	+	-	+	+	-	23	-704	6.9
4	+	+	+	-	+	-	-	14	-726	33.0
5	+	+	+	+	+	-	-	17	-725	35.8
6	+	+	+	+	-	+	-	23	-739	77.8
7	+	+	+	-	-	+	-	20	-747	87.8
8	+	+	+	+	-	-	-	14	-759	98.3
9	+	+	+	-	-	-	-	11	-764	101.6
10	+	-	+	-	+	-	-	11	-959	491.9
11	+	-	+	-	-	-	-	8	-968	504.4
12	-	+	+	-	-	+	-	19	-1039	668.4
13	-	+	+	-	-	-	-	10	-1053	677.3
14	+	+	-	+	-	-	-	11	-1133	840.8
15	+	+	-	-	-	-	-	8	-1141	850.8
16	-	-	+	-	-	-	-	7	-1185	936.6
17	-	+	-	-	-	-	-	7	-1227	1020.6
18	+	-	-	-	-	-	-	5	-1231	1023.3
19	-	-	-	-	-	-	-	4	-1310	1179.2

Table S2.3. Model selection table for candidate models fit to average monthly temperature, May-September. All models were linear mixed models that included month and mean day of the month as additional fixed effects with individual fish as a random effect. A + indicates that the fixed effect was included in the model while - indicates it is not. DF is degrees of freedom and logLik is the log likelihood associated with the model. Models within 2 AIC_c units of the best model were averaged and weight of each model in that average is provided.

Model	Fixed effects			DF	logLik	ΔAIC_c	Weight
	Strain	Year	Month:Strain				
1	-	+	-	10	-796	0.0	0.72
2	+	+	-	11	-796	1.9	0.28
3	+	+	+	14	-795	6.1	
4	-	-	-	7	-926	254.0	
5	+	-	-	8	-926	255.5	
6	+	-	+	11	-925	260.1	

Table S2.4. Model selection table for candidate models fit to average October temperature. All models were linear models that included mean day of the month as an additional fixed effect. A + indicates that the fixed effect was included in the model while - indicates it is not. DF is degrees of freedom and logLik is the log likelihood associated with the model. Models within 2 AIC_c units of the best model were averaged and weight of each model in that average is provided.

Model	Fixed effects		DF	logLik	ΔAIC _c	Weight
	Strain	Year				
1	-	+	6	-305	0.0	0.69
2	+	+	7	-304	1.6	0.31
3	-	-	3	-350	85.3	
4	+	-	4	-350	86.6	

Table S2.5. Model selection table for candidate models fit to average November temperature. All models were linear models that included mean day of the month as an additional fixed effect. A + indicates that the fixed effect was included in the model while - indicates it is not. DF is degrees of freedom and logLik is the log likelihood associated with the model.

Model	Fixed effects		DF	logLik	ΔAIC _c
	Strain	Year			
1	-	+	5	-140	0.0
2	+	+	6	-140	2.0
3	-	-	3	-226	167.6
4	+	-	4	-226	169.6

Table S2.6. Model selection table for candidate models fit to number of days an individual occupied an average temperature greater than 10 °C each year from September-November. All models were generalized linear mixed models assuming a Poisson error distribution that included individual fish as a random effect. A + indicates that the fixed effect was included in the model while - indicates it is not. DF is degrees of freedom and logLik is the log likelihood associated with the model.

Model	Fixed effects			DF	logLik	ΔAIC _c
	Year	Strain	Year:Strain			
1	+	+	+	7	-542	0.0
2	+	+	-	5	-552	15.5
3	+	-	-	4	-553	15.6
4	-	-	-	2	-604	114.2
5	-	+	-	3	-603	115.0

Table S2.7. Model selection table for candidate models fit to average monthly temperature, May-September, for each individual's first summer following release. All models were linear models that included mean day of the month as an additional fixed effect. Notation effect:effect indicates an interaction effect. A + indicates that the fixed effect was included in the model while - indicates it is not. DF is degrees of freedom and logLik is the log likelihood associated with the model.

Model	Fixed effects				DF	logLik	ΔAIC_c
	Month	Length	Year	Month:Year			
1	+	+	+	-	9	-479	0.0
2	+	+	+	+	12	-479	5.9
3	+	-	+	-	8	-486	10.5
4	+	+	-	-	8	-486	11.2
5	+	+	-	+	11	-486	17.1
6	+	-	-	-	7	-491	19.9
7	-	+	+	-	6	-531	96.7
8	-	+	-	-	5	-535	102.4
9	-	-	+	-	5	-538	108.9
10	-	-	-	-	4	-541	113.3

Table S2.8. Model selection table for candidate models fit to average October temperature during the first year following release. All models were linear models that included mean day of the month as an additional fixed effect. A + indicates that the fixed effect was included in the model while - indicates it is not. DF is degrees of freedom and logLik is the log likelihood associated with the model.

Model	Fixed effects		DF	logLik	ΔAIC_c
	Length	Year			
1	-	+	4	-198	0.0
2	+	+	5	-198	2.1
3	-	-	3	-206	13.9
4	+	-	4	-206	16.0

Table S2.9. Model selection table for candidate models fit to average November temperature during 2018 for fish tagged during the spring of 2018. Both models were linear models that included mean day of the month as an additional fixed effect. A + indicates that the fixed effect was included in the model while - indicates it is not. DF is degrees of freedom and logLik is the log likelihood associated with the model.

Model	Fixed effect			
	Length	DF	logLik	ΔAIC_c
1	+	4	-61	0.0
2	-	3	-70	16.4

Table S2.10. Model selection table for candidate models fit to number of days an individual occupied an average temperature greater than 10 °C from September-November of 2018 for fish tagged during this year. Both models were generalized linear mixed models assuming a Poisson error distribution. A + indicates that the fixed effect was included in the model while - indicates it is not. DF is degrees of freedom and logLik is the log likelihood associated with the model. Models within 2 AIC_c units of the best model were averaged and weight of each model in that average is provided.

Model	Fixed effect		DF	logLik	ΔAIC_c	Weight
	Length					
1	-		1	-271	0.0	0.63
2	+		2	-271	1.1	0.37

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