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SPATIAL AND TEMPORAL DYNAMICS OF TOP PREDATORS IN A LARGE LAKE

By

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SPATIAL AND TEMPORAL DYNAMICS OF TOP PREDATORS IN A LARGE LAKE

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DECLARATION OF CO-AUTHORSHIP / PREVIOUS PUBLICATION

I. Co-Authorship

I hereby declare that this thesis incorporates material that is a result of joint research, as follows:

In all cases, the key ideas, primary contributions, experimental designs, data analysis, interpretation, and writing were performed by the author under the supervision of Aaron Fisk and Tim Johnson. Brent Metcalfe co-authored Chapter 2 and assisted with data acquisition and editing of the manuscript. Chapter 3 was co-authored by Graham Raby and Sarah Larocque, who provided data and assisted with writing the manuscripts.

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This thesis includes two original papers that have been previously published/submitted to journals for publication, as follows:

Thesis Chapter	Publication title/full citation	Publication status*
Chapter 2	Ivanova, S. V., Johnson, T.B., Metcalfe, B., Fisk, A.T., 2021a. Spatial distribution of lake trout (*Salvelinus namaycush*) across seasonal thermal cycles in a large lake. Freshw. Biol. 66, 615–627. https://doi.org/10.1111/fwb.13665.	Published

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ABSTRACT

Environmental degradation is the legacy of the Anthropocene era and maintaining ecosystem health is a major challenge for managers globally. Restoration ecology aims to improve ecosystem health through reintroduction and rehabilitation of important native species to maintain or increase biodiversity and achieve stable and resilient communities. Non-native species may affect reintroduction efforts through interactions in time and space. This dissertation proposes that understanding the spatio-temporal ecology of two species along with their energy demands and growth (i.e., bioenergetics), would provide key clues for untangling the complexities of species interactions and further the knowledge on influences of non-native species on native species rehabilitation. Lake Ontario has two native salmonids undergoing rehabilitation and four introduced salmonids and provided the ideal model system for this research. Here, I focused on lake trout (*Salvelinus namaycush*), a native top predator extirpated in the 1950s and currently under rehabilitation and the introduced Chinook salmon (*Oncorhynchus tshawytscha*).

Quantifying the spatio-temporal ecology of each species in Lake Ontario in the first two research chapters provided baseline information used in the last two research chapters for assessment of their interactions and their bioenergetics. Specifically, lake trout seasonal distributions showed inter-individual variation in home range size, winter and summer habitat preference, and long-distance movement behaviour. Chinook salmon showed moderate segregation occurring between immature and sub-adult individuals in both the horizontal and vertical planes, suggesting interactions with lake trout may vary by size-class. Spatial utilization overlap and fine-scale co-occurrence of the two species were assessed next, and the results revealed that the species segregated horizontally, except during the summer when segregation was vertical. The final research chapter showed that lake trout is occupying temperatures below the optimum and growing below its potential, while Chinook salmon occupied temperatures close to their optimum and their growth was nearing the species' potential under present conditions. Further, results from warmer temperatures and diet composition change scenarios revealed that prey quality was more important in determining growth than temperature (i.e., habitat).

Overall, this dissertation enhanced the understanding of lake trout and Chinook salmon spatial ecology, interactions and the relative influences of temperature and diet on their bioenergetics. Taken together, these results suggest that limited interactions occur between the two species and that Chinook salmon do not affect lake trout negatively, and thus are not an impediment to their restoration. Chinook salmon's presence in the lake appears to induce lake trout re-distribution and thus, limit their overlap and foraging on Alewife (*Alosa pseudoharengus*), a prey fish that impedes lake trout reproduction, suggesting that Chinook salmon indirectly facilitates lake trout restoration. Understanding the spatio-temporal ecology of these species together with their growth under varying scenarios, furthered our knowledge of the complexity of their interactions when the two species co-occur. The use of a multi-disciplinary approach (i.e., spatial ecology and bioenergetics) improved result interpretations, showcasing that this approach would provide a useful framework in any ecosystem where species interactions are poorly understood. These results provide relevant information on biodiversity targets aiming to improve ecosystem health that include seemingly conflicting objectives where restoration of native species is important, but the maintenance of non-native species is also highly desirable.

DEDICATION

To my family, friends, and colleagues for their faith in me, encouragement, and unwavering support to pursue my dreams.

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The use of experimental animals complied with the Canadian animal welfare laws, guidelines and policies as approved by the University of Windsor Animal Care Committee (AUPP 18_11) and the Ontario Ministry of Natural Resources and Forestry (Animal Use Protocol #135).

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AT – acoustic telemetry

CoA – centres of activity

D – depth

jPPA – joint potential path area

KUD – kernel utilization distribution

P – pressure

pDST – pop-off data storage tags

SUD – spatial utilization distribution

T – temperature

TL – total length

CHAPTER 1 – GENERAL INTRODUCTION

Introduction

Environmental degradation is observed in all ecosystems and biospheres on earth (Rapport et al., 2009) and with human population increasing exponentially, the era of the Anthropocene marks four main challenges for humanity: 1) food, water and energy security, 2) loss of biodiversity, 3) climate change, and 4) sea-level rise (Harris and Diggelen, 2006). All of these challenges are closely linked together, but the general overarching connection is the idea of improving ecosystem health through sustainability and conservation. Ecosystem health is a concept with varying definitions based on the context and use (O'Brien et al., 2016), however, for the purposes of management and, commonly, in environmental science, ecosystem health refers to the state of a system in light of a management goal as compared to a previous reference or a similar undisturbed system (Rapport, 1989; Schaeffer et al., 1988). An important emphasis when assessing ecosystem health is put on sustainability and resilience (Costanza et al., 1992), and thus, on the ability of the ecosystem to maintain structure and function when stressed (Mageau et al., 1995). Resilience suggests that the ecosystem is able to recover after a disturbance event (Walker et al., 2002). During prolonged stress, such as the constant and cumulative impacts of human activities, including the introduction of non-native species, a system may experience loss of species (extinction or extirpation), resulting in a change of the structure from trophic to spatial and temporal interactions between species. Extirpations could result in trophic cascades which could lead to further loss of species, resulting in an ecosystem that is no longer resilient. Biodiversity is probably the most important factor for achieving resilience, because it provides stability with redundancies and thus, a buffer against external stress (MacDougall et al., 2013).

The topic of biodiversity maintenance is at the basis of conservation and restoration ecology. Conservation is an idea that dates back centuries, but as a movement it began in the early 1900s with Aldo Leopold, and became established as a science in the second half of the 20th century (Vaughn et al., 2010). Restoration ecology is a discipline of conservation that aims to achieve resilient and sustainable ecosystems (van Andel and Aronson, 2006), through the reintroduction of native species, restoration of habitat, and even the assisted establishment of species in new territories (Hobbs et al., 2006; Vaughn et al., 2010). The latter is a proactive step with considerations for climate change, while the former two are reaction-based steps. Habitat restoration in a basic form has been employed for centuries by First Nation groups in North America in an effort to maintain natural ecosystem services, such as a suitable habitat for desired game animals (Stevens, 1997). Species reintroduction, also called repatriation, however, is a more recent concept that aims, as the name suggests, to bring back a species that was extirpated from an ecosystem. Reasons as to why reintroductions are undertaken vary from purely ecological to socio-economic. For example, a species may be highly valued economically or as an important food-source for local populations (Spraker, 1992), and/ or it may be important for the maintenance of ecosystem resilience and function, i.e., maintaining biodiversity (Stewart et al., 2017). More often than not, a variety of reasons are taken into account because species interact with their environment and with other species and thus, affect the health of the ecosystem they inhabit and its ecological services to humans.

Species reintroductions are influenced by biotic and abiotic factors, and understanding those influences is key to informing such efforts and their success. Abiotic factors include water temperature, water quality and contaminants (O’Gorman et al., 2002). Biotic factors include interactions with species in space and time. Interactions may include those with other species across the food web, or humans. Harvesting is a direct interaction between humans and animals and is well known for its effects on animal extirpation or extinction. The deliberate introduction of desirable species that are considered economically important is another human-animal interaction. In the latter, when the introduced animal is successfully established, that new species has the potential to affect the reintroduction efforts of a species of interest by adding a potential competitor. Inter- and intra-specific competition is known to influence animal movements in space and time (Nathan et al., 2008). Additional influences are the distribution of preferred prey and preference for certain environmental conditions. Interactions also affect an animal's bioenergetics, which ultimately influence their growth and reproductive output (Fry, 1947). Ultimately, understanding the spatial and movement ecology of species along with their energy budgets provides key information on the state of the species and their population: two important factors for informing reintroduction efforts.

Movement ecology

Animal movements have been studied by humans for centuries to inform food provision, however, active tracking of animals for scientific purposes began in the late 1900s, and movement ecology as a discipline is fairly new (Nathan et al., 2008). From migration and dispersal to foraging, movements of organisms are fundamental for their survival and thus, an integral part of any ecological process or question. Nathan et al. (2008) suggested four mechanisms for underlying movement: 1) internal state/ motivation, 2) motion capacity, 3) navigation capacities, and 4) external factors affecting movement. From the perspective of species reintroductions, however, interest is highly focused on the internal state or motivation and external factors affecting movements. Internal state or motivation can include the need to find a mate, dispersal, avoidance of predators, or hunger based on the metabolic requirements of the organism. External factors include environmental conditions of the occupied habitat, such as temperature, light, and depth for aquatic organisms, and interactions with other animals. Internal and external drivers are closely linked together and are highly influenced by one another. For example, choice and utilization of habitat could be influenced by density of conspecifics (Kawaguchi and Desrochers, 2018), and /or presence of predators or prey (Bled et al., 2015).

To understand internal and external drivers of movements, tracking an animal over prolonged periods of time in their natural habitat along with the collection of continuous environmental conditions data is crucial. Tracking of organisms has its challenges based on the size and longevity of the organism. Advances in technology have allowed researchers to tag and track animals in all environments, including the aquatic, and of all sizes, such as insects and small fish (Bangs et al., 2013; Hagler and Jackson, 2001). Satellite and acoustic telemetry are only two of the tracking methods, which have allowed scientists to penetrate the depths of the freshwater and marine environments. Satellite telemetry works well for organisms that are large and surface occasionally. Acoustic telemetry, however, is widely used for fish which don’t break the surface and due to the small size of the transmitters (hereafter tags), it allows for tagging juveniles and small species (Rechisky et al., 2013). Stationary receivers or active tracking from vessels allow for detection of the tagged fish to obtain time and location. Additional sensors in the tags provide the capability of transmitting environmental data, such as occupied water temperature and depth. Passive tracking through stationary receivers has the advantage of long-term year-round data collection. Such long-term data is useful for understanding diel activities, seasonal habitat preferences, preferred movement routes, energetics, behaviour, anthropogenic disturbance effects (Ivanova et al., 2018; Landry et al., 2018), etc. of a single species, but also potential competitive interactions of different species via spatial and temporal overlap of niches and home ranges (Fieberg and Kochanny, 2005). On a larger scale, the data obtained have dramatically increased our knowledge of animal migrations, dispersals and distributions contributing significantly to our understanding of ecosystem structure and function (Hussey et al., 2015). Thus, movements can provide valuable insights into an organism's ecology, as well as the ecology of species with which it interacts, and inform and aid reintroduction efforts.

Metabolism and energetics

All animals have a temperature range at which they function optimally and growth is maximized (Fry, 1947; Brown et al., 2004). Since fish are ectothermic and temperature is known to have great effects on chemical and biochemical reactions' rates, exposure to increasing water temperatures beyond their optimal temperature range is associated with exponential increase in metabolism and physiological stress (Gillooly et al., 2001). Metabolic rate is part of the generalized bioenergetics equation: Energy consumed = Metabolism + Waste + Growth (Brett and Groves, 1979). The difference between the standard metabolic rate, the minimum required for basic physiological function and maintenance, and the maximum, also called the active metabolic rate, is the metabolic scope within which an animal functions optimally (Fry, 1947). Thus, stress responses and increase in the metabolic rate associated with temperatures above the optimal thermal ranges, are directly responsible for fractions of energy budgeted away from somatic growth and/ or reproduction (Boisclair and Leggett, 1989; Rennie et al., 2009; Alfonso et al., 2021) both of which are dependent on surplus energy.

Metabolism is influenced by locale, such as temperature of the habitat, but also by diet, including feeding rate and energy density of the prey (Jobling, 1994) which directly affect energy budgets. Based on the degree of diet specialization of an animal, fluctuations in prey densities can have substantial effects on growth, reproduction and even survival. For example, Chinook salmon (*Oncorhynchus tshawytscha*), a diet specialist in the Great Lakes, showed poor body condition, was more susceptible to infection, and had an increased mortality when the populations of its primary prey Alewife (*Alosa pseudoharengus*) collapsed in Lake Michigan in the early 1980s (Jones et al., 1993; Rybicki and Clapp, 1996; Stewart and Ibarra, 1991). Yet, generalists are more resilient to such changes as they can switch to a different prey, minimizing any negative effects. For example, lake trout (*Salvelinus namaycush*) diet proportions shifted in favour of round goby (*Neogobius melanostomus*) as abundance ratios with Alewife changed in Lake Michigan in the mid-2000s (Brey, 2006). Lab studies have shown that at lower prey densities, fish would occupy lower temperatures than their optimum to regulate their metabolism and maximize growth under the available conditions, and only when fed to satiation would they occupy the optimum (Beitinger and Magnuson, 1975; Brett, 1971; Jobling, 1994). While the latter is true in lab studies where other influences are removed, in the natural world optimum temperature occupancy would also be affected by intra- and inter-species interactions, and the distribution of their prey among others (Jobling, 1994). Ultimately, all of these affect the body condition and thus, growth of individuals.

Energy density and its relationship with weight is an indicator of body condition, and energy deposits affect winter survival (Post and Evans, 1989; Post and Parkinson, 2001) and behaviour, such as migratory strategy (Brodersen et al., 2008; Jonsson and Jonsson, 1993) or frequency of spawning (Jørgensen et al., 2006; Thorpe, 1994). Energy density is a measure of the amount of macronutrients, i.e., carbohydrates, proteins, and lipids, deposited during body growth and resulting in new tissue and energy reserves (Jobling, 1994). Energy density is estimated indirectly by proximate composition analysis of proteins and/or lipids or through bomb calorimetry (Brett, 1995; Hartman and Brandt, 1995). Bomb calorimetry, while considered most accurate (Craig et al., 1978; Schloesser and Fabrizio, 2015; Weatherley and Gill, 1983) is time-consuming as it involves drying, pulverization, homogenization, and heat combustion of the whole body of the organism (Cummins and Wuycheck, 1971). Lipid extraction and conversion to energy density is another method employed that is less time-consuming. Lipid content is considered the primary determinant of available energy stores for fish (Anthony et al., 2000) because lipids are amassed when prey density is high and environmental conditions are optimum, and used up before other macronutrients when prey abundances are low and conditions are sub-optimal (Adams, 1999; Morgan et al., 2002). Regardless of the method used for obtaining energy density values, knowledge of those values through an animal's life provides important information on its growth potential in the environment it inhabits.

Climate change is increasing both the surface and hypolimnion water temperatures of lakes and marine ecosystems globally (Anderson et al., 2021; Dokulil et al., 2021; O'Reilly et al., 2015; Schneider and Hook, 2010) and, while those are predicted to lengthen the growing season (Brandt et al., 2002), a decrease in available habitat with optimum conditions is expected for cold-water species (Shuter and Lester, 2004). With the predicted further rise in temperatures (Seneviratne et al., 2014; Zhang et al., 2018), it is imperative to understand how different temperatures may influence the energy budgets of organisms. This information can be used to understand resource partitioning and the implications of climate driven environmental change on fish communities and the restoration of species.

Top predator interactions in space and time

Top predators interact in time and space and can modify each other's foraging or habitat use (Wootton, 1993) and thus, affect rehabilitation efforts (Stier et al., 2016). Interactions can be competitive, facilitative, or neutral in nature. Competition is often for resources, such as food or shelter, and when the two species' distributions continuously overlap, competition can result in interference or exclusion. On the other hand, co-occurrence of species may be purely driven by the similarity in habitat requirements, with varying ecological effects on one another, or with facilitation effects. The later occurs when one species provides a benefit for another (e.g., parasite removal or habitat enhancement resulting in increased survival and/or fitness; Silknetter et al., 2020), even if that benefit occurs indirectly in an interaction chain (Wootton, 1993). Interactions are often also complicated by species niche (Hammar, 2014), for example, if one species is a specialist and the other a generalist in their diet. For example, introduced Chinook salmon in the Laurentian Great Lakes is a specialist and lake trout a generalist suggesting a competition for the common resource Alewife where the two species co-exist. A diet rich in Alewife causes thiamine-deficiency in lake trout and induces fry mortality (Fitzsimons et al., 1999). One of the reasons Chinook salmon was introduced in the Great Lakes was to control Alewife populations. However, because of exploitative competition for the same resource and lake trout potentially supplementing a larger portion of their diet with other species to avoid competition, it has been hypothesized that Chinook salmon may have an indirect effect on lake trout populations by reducing thiamine deficiency and facilitating fry survival (Lantry et al., 2014). Competition, however, can also have negative effects when interference results in a reduced prey-capture success rate, or foraging efficiency (e.g., Cansse et al., 2020; Nakayama and Fuiman, 2010), affecting individual energy budgets. Thus, understanding the nature of the interactions between predators, and their complexities, contributes important information on the functionality of the top predator community and the interspecific dynamics influencing populations.

The Laurentian Great Lakes and Lake Ontario

Located between Canada and the United States of America (USA), the Laurentian Great Lakes (hereafter the Great Lakes) have been and are a major contributor to both countries' economies and humans have had great impacts on their ecology. The Great Lakes are one of the largest sources of freshwater in the world and include lakes Superior, Michigan, Huron, Erie, and Ontario. Since the mid 19-century, when European settlement was well underway, major changes have occurred in their ecosystems. For example, fish community structure was altered with non-native species introductions (deliberate and accidental, i.e., alien species), habitat degradation (such as dredging, contaminants and eutrophication) and overfishing, leading to population collapses of highly sought after species, such as lake trout and Atlantic salmon (*Salmo salar*) and their extirpation in Lake Ontario (Christie, 1972). In recognition of the economic importance of the Great Lakes, efforts have been put into controlling the water quality through reduction of nutrient and contaminant input, managing invasive species, and restoration of native species to contribute to biodiversity, and thus, ecosystem health.

As seen in the other Great Lakes, Lake Ontario's fish community has been dramatically changed over time due to the presence of non-native species, water quality degradation and overfishing. From two naturally occurring salmonid top predators (i.e., lake trout and Atlantic salmon), this number was increased to six through intentional introductions aiming to enhance recreational fisheries and control Alewife abundance. The appearance of Sea lamprey (*Petromyzon marinus*) in the 1870s contributed to the decrease of all top predator populations, including native lake trout and non-native Chinook salmon (Christie, 1972). Deepwater coregonids, including bloater (*Coregonus hoyi*), the preferred prey species for lake trout (Christie et al., 1987), declined due to overfishing and competition with other species in the early- to mid-1900s and were extirpated by the 1980s (Owens et al., 2003). Alewife, which invaded in the late 19th century, replaced bloater and declining native sculpin species in the diet of lake trout, creating thiamine-deficiency and negatively affecting fry survival (Fitzsimons et al., 1999). Lake trout was severely reduced to near extirpation by the 1950s due to overfishing, heavy predation by Sea lamprey and habitat degradation, and efforts to reestablish the species through stocking began in the 1970s (Schneider et al., 1983). Also in the 1970s, stocking of Chinook salmon and other Pacific salmonids was accelerated as a way to control Alewife abundance and help lake trout rehabilitation (Mills et al., 2003).

Sea lamprey control began around the same time and a decade later lake trout populations showed a positive response (Mills et al., 2003). Round goby was first recorded in Lake Ontario in 1998 (Owens et al., 2003) and are now part of lake trout's diet (Colborne et al., 2016; Dietrich et al., 2006; Rush et al., 2012). Bloater has recently been added to the list of native species to be restored and the species is now also being stocked. Currently, both lake trout and Chinook salmon are being stocked in Lake Ontario in an effort to maintain or increase their abundance and for lake trout to ultimately re-establish self-sustaining populations that allow for sustainable harvest (Stewart et al., 2017).

Study species

Lake trout, a native top predator in Lake Ontario, is currently under rehabilitation here and throughout the Great Lakes in both USA and Canada. Historically, lake trout was one of two pelagic salmonid top predators in Lake Ontario exerting stabilizing influence on the food web and key in the cycling of energy in the benthic and pelagic offshore zones (Ryder and Kerr, 1990). Today, lake trout are considered a key component of Lake Ontario's ecosystem health because they enhance biodiversity and help improve ecological function through top-down predation pressure. Because they are sensitive to ecosystem changes and stress, and thrive in pristine, oligotrophic systems, they are used as an indicator species of ecosystem quality (Ryder & Edwards, 1985). Evidence shows low levels of natural reproduction occurring in the current population in Lake Ontario and a failure of the species to establish a self-sustaining population (Lantry, Lantry, & Connerton, 2018). Currently, there is no commercial fishery for lake trout and recreational catch is regulated with angler possession limited at two individuals in New York state (NY Department of Environmental Conservation, 2018) and three individuals in Ontario (MNRF, 2018). Even though adults are present and population sizes appear stable (Lantry et al., 2014), there is a need to identify and quantify the factors that are limiting the establishment of a self-sustaining population.

Lake trout can achieve lengths of 1 m and live for more than 20 years (Scott and Crossman, 1973). Adults are piscivorous generalist in their diet and show preference for cold-water temperatures with thermal optimum ~10°C (Elrod et al., 1995). Lake trout are iteroparous, spawning in the fall at shallower depths (<10 m) on rocky reefs and offshore shoals, with rare examples in tributary rivers and streams, but generally occupy deep waters (Hansen, 1999; Stewart et al., 1983). A mark-recapture study in Lake Michigan found lake trout to return to the same location as they were tagged, thus exhibited site fidelity, and remained within a 80 km radius (Schmalz et al., 2002). In the same lake however, Rybicki (1990) showed that the species made cross-lake movements, and in Lake Opeongo, individuals did not return to the same shoal, but instead moved between shoals at spawning time (MacLean et al., 1981). Populations from the western and the eastern parts of Lake Ontario are believed to be spatially segregated, i.e. individuals stay in the respective basin and do not disperse out to the other basin (Raby et al., 2017; Ontario Ministry of Northern Development, Mines, Natural Resources and Forestry and U.S. Fish and Wildlife Service, pers. comm.). Currently, the size and preference of the habitat lake trout utilize in eastern Lake Ontario have not been examined in detail. Despite the longstanding fishery history and interest in reestablishment of lake trout, very little is actually known about their movements, spatial ecology or interactions with other salmonids (Dunlop et al., 2010; Morbey et al., 2006). Thus, quantifying the movements and residency of lake trout is an important step towards understanding their seasonal distribution, overall movement ecology and assessing any potential for interactions with other species in time and space.

Chinook salmon were first introduced in Lake Ontario in 1874 (Crawford, 2001) and have been stocked annually since 1968 (Stewart et al., 2013). Even though Chinook salmon are still being stocked annually by both USA and Canada, they have naturalized and have an established reproducing population (Connerton et al., 2009; Nack et al., 2011). The species bring both economic and ecologic benefits to Lake Ontario. With their large size, they attract recreational anglers from across North America (Melstrom and Lupi, 2013; Stewart et al., 2017) and bring hundreds of millions to the USA and Canadian economies (MNRF, 2021; Responsive Management, 2019). Their contribution to the lake ecology stems from regulating Alewife populations; sub-adults feed mainly on Alewife (Stewart et al., 2013) and its decline in Lake Huron was linked to the near collapse of Chinook salmon populations in the early 2000s (Roseman and Riley, 2009). Alewife over-abundance has been shown to cause a decrease in lake trout reproductive output and food availability for other prey species, including juvenile salmon and trout, thus negatively affecting a number of fish populations (Stewart et al., 2013). Therefore, Chinook salmon is also important for maintaining balance in the ecosystem.

Chinook salmon grow to more than 1 m and have a lifespan of 4 to 7 years (Ontario Fish Species, 2016). Their life history in Lake Ontario is similar to that in their native Pacific region. Spawning occurs once in rivers in the fall after which adults die off and smolts migrate to the lake in the spring to grow and mature (Kennen, 1993). The species have a cold-water preference ranging between 9°C to 14°C (Hinke et al., 2005; Stewart and Bowlby, 2009) and are found at maximum depth of up to 300 m in its native waters (Quinn, 2005) and ~200 m in Lake Ontario (Raby et al., 2020). With the short life span of only a few years and the large size obtained at maturity, this fish is reported to consume between 4 to 7 times more prey than lake trout (Negus et al., 2008; Schoen and Beauchamp, 2010). Extensive movements across Lake Ontario have been recorded for this species in the spring and summer (Haynes et al., 1986). Similar lake-wide movements in Lake Huron have been correlated to seasonal prey concentrations and water temperature (Adlerstein et al., 2007). In Lake Ontario, a data storage tag study showed that adult Chinook salmon had wide distribution based on the release of the fish compared to the retrieval location of the tags, and that the species' depth occupancy was highly variable (Raby et al., 2017). So far, however, seasonal distribution and movement activities by immature (age classes 1 and 2) and sub-adult (age classes 3 and 4) age class Chinook salmon in Lake Ontario and the rest of the Great Lakes have not been documented. Quantifying the spatial utilization, depth and temperature distributions for Chinook salmon across all seasons for different age classes would benefit not only the body of knowledge on their spatial ecology in freshwater ecosystems but would also contribute to understanding their interactions and resource partitioning with other species. As such this information would be useful to informing the rehabilitation efforts of lake trout in Lake Ontario.

Dissertation overview

While restoration of native lake trout populations is an important goal for both USA and Canada, maintenance of other top predator populations at high levels due to their recreational value may create competing interests. Chinook salmon is now being stocked not only to help control Alewife abundance, but also because its rapid growth and large body size make it the most sought-after salmonid species by anglers, whereas lake trout are less so. While Chinook may indirectly exert a limited positive influence on lake trout fry survival, through a decrease in the thiamine-deficiency in adult lake trout and through reduction in predation rates of juvenile Alewife on lake trout fry (Krueger et al., 1995; Madenjian et al., 2008), lake trout competition with Chinook salmon for the same prey, may be affecting the species' foraging success, behaviour and habitat use. As such, Chinook may also be affecting lake trout's growth and the re-establishment of self-sustaining populations.

This dissertation focused on the ecological dynamics influencing top predator rehabilitation in large lake ecosystems with an emphasis on spatial use and bioenergetics. Given Chinook salmon and lake trout are two top predators with differing life-histories and diet strategies, I specifically aimed to understand the movements and seasonal habitat use of lake trout (Chapter 2) and Chinook salmon (Chapter 3), how their overlap varies in time and space (Chapter 4), and the potential influences on lake trout growth (Chapter 5) and thus, on this species' rehabilitation potential.

Better understanding of the spatio-temporal ecology of species is useful for untangling the dynamics of their behaviours, such as those related to conspecifics and prey, and provides important clues on habitat exploitation. Seasonality is well known to affect the distribution of species due to thermoregulation requirements (Magnuson et al., 1979). Thus, Chapter 2 focused on quantifying the residency and home ranges of adult lake trout using acoustic telemetry and investigated their correlation to the temporal thermal cycles of the lake as a way to understand how the species respond to the spatio-temporal variation in the environment and assess potential thermal constraints.

Spatial use may vary with ontogeny as a mechanism of conspecific interaction avoidance or due to differing foraging or habitat requirements (Christiansen et al., 2012; Ross, 1986). Knowledge of such variation would improve our understanding of a species' general ecology, and aid in the assessment of intra- and inter-specific interactions. Chinook salmon exhibit size class segregation in their native region, the Pacific Ocean (Walker et al., 2007), but there is no knowledge of this in the Great Lakes. Thus, Chapter 3 focused on quantifying immature and subadult Chinook salmon seasonal spatial utilization distribution and depth and temperature occupancy as a way of assessing the potential for, and if so, the mechanism of segregation. Extensive lake-wide movements of each size class would suggest they both use the entirety of the lake with overlapping seasonal horizontal distribution, yet variation in the use of depth may act as a partitioning factor.

Spatio-temporal overlap in habitat utilization can be used as proxy for assessing the strength of inter-specific interactions between two species (Adams, 2001). This information provides useful insights into the partitioning of resources and minimizing competition and may offer clues to the type of interaction the species share (Adams, 2001). Thus, Chapter 4 focused on quantifying the habitat utilization overlaps and fine-scale paired-individual co-occurrence of lake trout and Chinook salmon as a way of estimating the potential for interactions between them. Horizontal and vertical distribution overlaps were expected to have season-specific variation based on the physiological needs of each species with segregation occurring in the vertical plane if the two species co-occurred in time and space.

Warming water temperatures affect the growth of ectotherm species by increasing their metabolic rate (Brett and Groves, 1979; Jobling, 1994; Magnuson et al., 1979). Thus, realized growth could be used as an indicator of the health of a species' population and in combination with predictions under various scenarios inform on the potential influences of interactions with other species. In Chapter 5, I used lake trout and Chinook salmon observed temperature preference in Lake Ontario to simulate their growth under present/baseline environmental conditions and predict growth rate potential under increasing water temperature scenarios and change in diet composition. The comparison of growth under the different environmental conditions aimed to assess each species' physiological state and thus, inform on the potential effects of climate driven environmental change and provide insights on the relative importance of diet as mitigator of sub-optimal temperature occupancy. Growth for lake trout and Chinook salmon was expected to decline under all future warming scenarios; for lake trout this trend was expected to reverse if consumption included higher quality prey.

Overall, this research provides key insights on the movement and spatio-temporal ecology of lake trout and Chinook salmon, an assessment of their interactions via co-occurrence, and the potential influences on each species growth rate potential in a warming climate. This type of information is considered key to successful restoration (Stier et al., 2016), thus the knowledge gained for lake trout would be useful for informing these efforts. This research also provides new understanding of the complexity of the two species' relationship in Lake Ontario and the functionality of the lake's top predator community.

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CHAPTER 2 – SPATIAL DISTRIBUTION OF LAKE TROUT (*SALVELINUS NAMAYCUSH*) ACROSS SEASONAL THERMAL CYCLES IN A LARGE LAKE

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Summary

1. Animal movements are influenced by the environment they inhabit and the need to maximize fitness and minimize cost. As such, seasonal thermal cycles in temperate lakes play an important role in the selection of habitat by species. Lake trout (*Salvelinus namaycush*) is a native top predator in the Laurentian Great Lakes and currently under rehabilitation in Lake Ontario. This cold, deep-water species is known to migrate to shallower depths in the autumn to spawn, but their spatial and seasonal distribution have not been examined in detail.

2. I quantified the residency and home ranges of 24 lake trout in eastern Lake Ontario across a full year using acoustic telemetry to assess the influence of seasonal thermal cycles. Specifically, I used three thermal logging stations in the eastern basin, 164 acoustic receivers, and a total of over 1,000,000 detections to describe seasonal distribution. I also documented occurrences of long-distance movements (via 130 acoustic receivers located in the western basin of Lake Ontario), and thus the potential spatial overlap of populations from the eastern and western basins.

3. During stratification (Jul 01 to Nov 01), lake trout (n = 24) showed a horizontally restricted distribution in regions of deeper water in eastern Lake Ontario. A variable and broad distribution was observed around the shallower Kingston Basin shoals during isothermal (Jan 1 to Apr. 30), spring warming (May 1 – Jun. 30; spring mix), and autumn cooling (Nov. 02 – Dec. 31) periods. Home range sizes ranged from 0.1 to 3,966 km^2 among all thermal cycles, with the largest observed during cooling autumn mix conditions driven by four individuals. Large variation in home range area was observed among individuals, and thus, means were not statistically different between seasons.

Three individuals occupied shallower shoals even during stratified conditions, and another individual crossed the entire lake from the east to the west end of Lake Ontario, travelling over 200 linear km in 17 days.

4. Our results confirm that thermal regimes and spawning needs affect the spatial use of lake trout in Lake Ontario, but demonstrate that there are broad distributions during isothermal conditions, highly individualistic spatial utilization, and inter-individual variation in spatial distribution and exploratory behaviour. All of these behaviours are consistent with other top predator species.

5. Defining the spatial utilization and distribution of individuals are important steps toward a better understanding of reintroduced species ecology of freshwater ecosystems. The variation of individual lake trout distribution across seasons implies that individuals may have different influences on the overall ecosystem function and potentially different responses to increasing water temperatures. These results suggest an adaptive management approach is required when rehabilitating populations of this native fish where populating multiple habitats in an ecosystem is an objective in the face of a changing environment.

Introduction

Animal habitat use is influenced by the environment they inhabit and the need to maximize fitness and minimize cost, i.e. maximize habitat exploitation (Begon et al., 2006; Nathan et al., 2008). Animal movements and distribution across habitats represent efforts to optimize fitness (Magnuson et al., 1979), although these may be modified by other factors (Morbey, Addison, Shuter, & Vascotto, 2006). Predator home ranges are often large in extent, overlapping those of their prey, and areas considered good foraging grounds tend to be frequented more than areas where prey availability is scarce (Adlerstein et al., 2008). Spawning is another activity that influences fish movement and habitat use on a seasonal basis (Hunter et al., 2003). Spawning habitat is typically represented by specific features, such as substrate, depth and hydrology, which may differ from habitats used during non-reproductive times of the year. Preference and utilization of habitat could also be influenced by spatial competition based on density of conspecifics (Kawaguchi and Desrochers, 2018) and presence of heterospecifics (Vander Zanden et al., 1999). In all cases, thermal conditions constrain the choice of particular habitats for fish due to their thermoregulatory requirements as ectotherms (Magnuson et al., 1979), for example during stratification in lakes. The identification of distributions and home ranges throughout the year can inform our understanding of fish behaviour (Landsman et al., 2011).

It has been hypothesized that cold water species are more vulnerable to increasing temperatures in lakes associated with climate change, largely because of decreased suitable habitat within a lake due to alteration of the thermal structure and reduced oxygen concentrations (Collingsworth et al., 2017; Shuter and Lester, 2004). For large, deep lakes changes in the horizontal and vertical home ranges and distributions are expected to occur with seasonal changes in lake thermal structure (Cline, Bennington, & Kitchell, 2013; Magnuson, Meisner, & Hill, 1990). Prolonged stratification, either by delayed autumn turnover, early onset of spring stratification, or both, has the potential to delay habitat switching events, migrations, and autumn spawning, and/or impair egg survival due to physiological stress imposed by suboptimal conditions (Carlson and Siefert, 1974; Garside, 1959). Similarly, adult growth rate is shown to decrease with increases in temperature above the optimal (King et al., 1999). Thus, the quantification of the seasonal home ranges and correlations with thermal cycles provides an important baseline for prediction of climate change effects on species distributions and a necessary step to updating existing bioenergetic predictions.

Lake trout (*Salvelinus namaycush*) is a top predator native to all of the Laurentian Great Lakes (hereafter Great Lakes). The species declined in the mid 1900s due to a combination of overfishing, habitat degradation and predation by Sea lamprey (Christie, 1972; Fitzsimons, Brown, Honeyfield, & Hnath, 1999; Schneider, Kolenosky, & Goldthwaite, 1983) and is generally stocked to varying degrees for rehabilitation. As a native top predator, lake trout exerts a top down stabilizing influence on the food web and has a key role in the cycling of energy between the benthic and pelagic offshore zones (Ives et al., 2019; Ryder & Kerr, 1990). Further, because trout thrive in pristine, oligotrophic systems, individuals are sensitive to ecosystem change and stress, and are therefore used as an indicator species of ecosystem quality (Ryder & Edwards, 1985). Lake trout is thus considered a desired component of the Great Lakes fish community and a key indicator of Lake Ontario’s ecosystem health.

Lake trout is a cold-, deep-water species (Stewart, Weininger, Rottiers, & Edsall, 1983) and has been described as both pelagic and demersal (Guzzo et al., 2016; Riley et al., 2008) because individuals feed on both types of prey (Colborne et al., 2016; Mumby et al., 2018). Trout migrate to shallower depths (<10 m, rocky shorelines and offshore shoals) in the autumn to spawn (Hansen, 1999). In Lake Ontario, lake trout spawning behaviour has been studied and physical spawning habitat described (Fitzsimons, 1995; Goodyear, Edsall, Ormsby Dempsey, Moss, & Polanski, 1982; Thibodeau & Kelso, 1990), and recently, the temperature-depth niche has been quantified for spring, summer and autumn, but this has not been done for winter (Raby et al., 2020). Yet, lake trout home ranges throughout any season have never been quantified, and in particular, their sizes, locations and associated thermal conditions – a problem given the increasing warming of the Great Lakes (Zhong et al., 2019). In addition, trout from western and eastern Lake Ontario are believed to stay spatially segregated (Raby et al., 2017; Ontario Ministry of Natural Resources and Forestry and U.S. Fish and Wildlife Service, pers. comm.), yet new evidence suggests that may not be the case (Holden, 2019). Considering the variation of genetic strains stocked throughout the years in Lake Ontario with various habitat preferences (e.g. Seneca, Apostle Island, Klondike, etc.; Lantry et al., 2018), understanding the behaviour differences in strain performance would contribute valuable information to rehabilitation efforts, including the role of reintroduced fish in the ecosystem. In addition, understanding seasonal changes in lake trout distributions and home range sizes in Lake Ontario, and the potential for long-range movements between populations of the eastern and western basins of the lake, will, as a first step, provide a basis for predicting effects of lake trout on the lake ecosystem function as well as population responses to warming. On a broader scale, fit and function of reintroduced species in an ecosystem are important questions for any system in which species are undergoing rehabilitation or reintroduction, and contributions to this field are key to adaptive management.

With the growing use of acoustic telemetry in the Great Lakes, I had the opportunity to quantify the distribution and home ranges across seasons of an ecologically important top predator with history of rehabilitation. Since water temperature has a major influence on animal distributions and bioenergetics, I used the seasonal thermal cycles of the lake as a guide. Lake trout is a good cold-water model species and quantifying the residency and home ranges would contribute to: 1) understanding the among-season spatio-temporal ecology of a reintroduced cold-water predator in a large lake and provide clues on how such species respond to the spatio-temporal variation in the environment, 2) assessing potential thermal constraints to lake trout distributions at present, and, 3) ultimately, contribute to predictions about the impact of climate change on cold-water species, and in particular lake trout distributions in a warming climate. Thus, the objectives of this study were to quantify the thermal cycles of eastern Lake Ontario over a period of one full year, relate these to and quantify the home ranges and residency of individual lake trout using acoustic telemetry, and determine if any individuals dispersed to the western basin of Lake Ontario.

Methods

Study site

Lake Ontario is the 13th largest lake in the world with surface area >19,000 km^2, and a maximum depth of 244 m. It is home to six salmonid species, two of which are native, supporting a valuable recreational fishery (Stewart et al., 2017). Eastern Lake Ontario is characterized by shallow offshore areas (from hereon refered to as shoals or Kinsgton Basin) varying in depth from 0 to ~40 m (Figure 2.1) separated from the deep main basin of the lake by the Duck-Galloo Ridge. The larger St Lawrence Channel (~60 m deep) and two smaller Simcoe Island and Black River channels bisect the Duck-Galloo Ridge to provide deep water connections between the Kingston Basin and the main basin of Lake Ontario. The western basin of Lake Ontario is defined here as the area west of a line running north from the Niagara River mouth to Toronto (Ontario, Canada) (Figure 2.1). The main basin is generally considered the area between the Duck-Galloo Ridge and the western basin and for the purposes of this study the term would be used to identify these deeper areas (max depth 244 m) in eastern Lake Ontario. The term eastern Lake Ontario is used here to refer to the eastern basin, Duck-Galloo Ridge and eastern quarter of the main basin (as per extent shown in Figure 2.1). It is important to note I use lake bathymetry (i.e. restriction in the depth range available for occupancy in the shoals [0 to 40 m] versus the main basin [0 to 244 m]), and not position within the water column, to describe the two-dimensional horizontal spatial distribution of lake trout.

Description of thermal cycles

To describe the seasonal thermal dynamics in eastern Lake Ontario, three strings of temperature loggers (HOBO TidBit v2 Temperature Data Logger; Onset Computer

Corporation, Bourne, MA, USA) spaced every 2 m from 10 m depth to the lake bottom collected data over the study period of May 1, 2017 to April 30, 2018 (logger 1 coordinates: 43.979233, -76.49645; logger 2: 43.961675, -76.586484; and logger 3: 43.826748, -76.661223) (Figure 2.2). Temperature was recorded every 15 minutes, with a resolution of 0.02°C at 25°C, and accuracy of ±0.21°C from 0° to 50°C. To quantify the thermal seasons I calculated mean daily temperature at depth, examined temperature change in relation to depth to determine the position of the thermocline across locations, and used the following definitions: 1) stratified – when >5°C temperature differential occurred above versus below the thermocline; 2) autumn mixing and cooling (from here on referred to as autumn mix) – when the thermocline broke down, temperatures from the 10m logger and the bottom had <5°C difference, and the overall temperature was rapidly declining until it reached a relatively constant value; 3) isothermal – when temperatures varied <5°C among all loggers and were neither cooling nor warming; and 4) spring mixing and warming (spring mix) – when temperatures started to warm rapidly until a thermocline was established with temperature difference above and below the thermocline of >5°C.

Acoustic telemetry

A total of 164 fixed-station acoustic telemetry receivers (69-kHz VR2W, Innovasea, Bedford, Nova Scotia, Canada) in eastern Lake Ontario were used to track and record lake trout movements for one full year (Figure 2.1; May 1, 2017 to April 30, 2018). Receivers were spaced ~1 km apart in the St. Lawrence Channel. Receivers outside the channel and at the Duck-Galloo Ridge were spaced ~2.5 km apart, and in the Kingston Basin ~5-10 km apart. Receiver detection efficiency at 80% was ~1,600 m

(Klinard et al., 2019). Moorings consisted of concrete cylinders (~62 kg) as the anchors connected to two 28 cm (11”) trawl floats by a 3 m length of 1.1 mm (7/16”) polypropylene rope with inline galvanized swivels. Receivers were attached to the riser ~2m above the lake bottom with the hydrophone pointing upwards. An approx. 30 m weighted rope was attached to the concrete anchor at one end and a cinder block at the other end to serve as a drag line for grappling when retrieving the receivers for download. In addition, receivers (n = 130, 69-kHz VR2W) in the western end of Lake Ontario were used to identify any cross-lake movement. From here on, the receivers are collectively referred to as an ‘array’. Two tagging events took place in 2016: October 26 at Main Duck Island (43.927653, -76.618055, n = 9) and November 3 at Charity Shoal (44.042179, -76.483863; n = 21). In both cases, fish were caught using gill nets set overnight (30 m each of 64, 76 and 89 mm stretch monofilament mesh) and held in 600-L holding tanks continuously resupplied with aerated lake water until tagged; fish were held < 2 hours total following removal from nets. A tank filled with lake water and MS-222 mixture (4 g of MS-222 with 8 g of baking soda buffer per 10L of water) was used as anesthetic to prepare the fish for surgery. Once equilibrium was lost, fish were placed in a foam cradle and their gills continuously irrigated with lake water. Total length was measured, and fin clips and marks recorded (to confirm stocked or wild); 10 fish were female and 20 were male, all adult. A small incision (~ 20 mm) was made posterior of the pelvic fins, a V16 acoustic transmitter (hereafter tag; 68 mm length x 16 mm diameter; 10.3 g weight in water; nominal delay 180 s; estimated battery life 3650 d; Innovasea, Bedford, NS, Canada) was inserted into the peritoneal cavity, and the incision was closed with three Vicryl sutures (Ethicon VCP423, 2-0 FS-2 cutting). An external floy tag was also attached to provide angler awareness of the internally tagged fish. Surgery took < 3 minutes using aseptic techniques, after which fish were allowed to recover in a holding tank until able to swim upright, and then released within the receiver array in the St. Lawrence Channel in water > 20 m depth (Figure 2.1). All tagged fish were similar in size with mean total length of 766 ± 9 mm.

Data analysis

Data were analyzed for the period May 1, 2017 to April 30, 2018 during which all acoustic receivers were present. R statistical software (version 0.98.1103) was used for all analyses and ArcMap (version 10.3.1) for graphing. White-Mihoff filtering tools were used to filter out any false detections (White et al., 2014), where a detection range of 1,600 m was used based on 80% detection efficiency (Klinard et al., 2019). A total of six lake trout were removed from the analysis: IDs 16871 & 16875 were removed due to tag expulsion or death; four other individuals, although detected for a number of months after release, had no detections during the period of data analysis and were presumed to be either out of the array and/or dead. Of the remaining 24 individuals, partial data were used for IDs 16853, 16859 and 16876 due to eventual tag expulsion or fish mortality – this was determined based on the changed pattern of detections, where the tags were continuously detected by a single receiver for the remainder of the study; thus, any detections 24 h prior to the onset of such changed pattern were removed from analysis. A 24 h cut off was chosen based on examination of individual movement tracks and comparison to the other tagged fish in our study to ensure the observed behaviour included in the analysis was not out of the ordinary. Partial data inclusion is not likely to bias our results as all calculations were performed separately for each individual and then means taken where necessary (see below). A total of 1,050,469 detections were used for further analysis based on 24 individuals. Detection data were separated into four thermal seasons (defined in results) based on observed thermal cycles in eastern Lake Ontario.

The receivers in the eastern basin are not uniformly distributed and therefore may introduce bias based on density of spacing, and/ or if simultaneous detections occurred on different receivers. None of these were considered to be a problem for our residency index because calculations were based on presence/absence (not number of detections) per receiver and since fish move, the detections at a particular receiver would represent presence of the fish in the vicinity of that receiver within detection range. Thus, although some regions had more receivers than others, they all provide a general locality of the fish in a consistent manner (i.e., Kingston Basin versus St. Lawrence Channel versus main basin). For home range calculations that are based on density estimates, bias is more likely, especially when true spatial data (i.e., x, y positions) are not available. For this reason, I chose to calculate centers of activity (a position averaging calculation of all detections at receivers over a particular time interval) and use that for estimation of home ranges. To further verify that there was no bias based on receiver distribution, I examined the trajectories of each individual over time against the generated home ranges and confirmed the results. Inference has not been made, nor it should be, for areas without receiver coverage, or periods when the fish were outside the array.

Lake trout distribution preferences were determined using a residency index (Kessel et al., 2015). Individual residence was calculated as the number of days an individual was detected per receiver divided by the total number of days the same individual was detected in the array, and then mean residence index (RI) was obtained from the mean of all individuals' residence results. The numbers of detections used for RI calculations by thermal period were: stratified - 687,508, autumn mix - 59,539, isothermal - 86,347, and spring mix - 217,075. Centers of activity (Simpfendorfer et al., 2002), were used to approximate locations of individuals at a given time for the calculation of home ranges. For centers of activity, simultaneous detections on multiple receivers are not allowed, but only successive detections. Considering our tags had a large detection range of ~ 1,600 m at 80% detection efficiency (Klinard et al., 2019), receivers located in the St. Lawrence channel showed such tendency, thus I removed from analysis every second receiver and associated detections from this receiver array. Approximate locations were then calculated for each individual using position averaging of the detections occurring over a 30 min period. These locations were then used to infer individual home ranges using Kernel utilization distribution (KUD) at 50% (core) level (adeHabitatHR package (Calenge, 2006)). The numbers of locations and IDs used to infer home ranges by thermal period were as follows: stratified - 66,651 based on 24 IDs; autumn mix - 8,548 and 20 IDs; isothermal - 10,311 and 17 IDs; and spring mix - 18,583 and 22 IDs. CalcHR.R and Indices.txt (Fieberg and Kochanny, 2005) were used to quantify Hurlbert Index of overlap (Hurlbert, 1978) on core KUDs between all periods.

Results

The following four thermal cycle periods were identified for eastern Lake Ontario based on our temperature logger data: 1) stratified – Jul. 01 to Nov. 1; 2) autumn mix – Nov. 02 – Dec. 31; 3) isothermal – Jan. 1 to Apr. 30; and 4) spring mix – May 1 – Jun. 30.

Tags had a nominal delay of 180 s and maximum possible daily detections were ~ 480. Mean (± SD) of observed detections across individuals was 43,770 (± 3,314), with daily mean (± SD) 119.9 (± 9.1). There are a variety of reasons why the maximum detections per day were not observed, such as the spacing between receivers in the Kingston Basin for example, or individuals that spend time in the main basin but outside of the receiver range. Number of detections per individual were normally distributed (Shapiro-Wilk normality test p=0.98).

Based on the residence index (RI) method, lake trout showed a preference for the St. Lawrence Channel and the main basin during periods of thermal stratification. However, during isothermal, autumn and spring mix conditions, individuals dispersed throughout the shallower Kingston Basin and St. Lawrence Channel (Figure 2.3). The greatest RI values for the autumn mix period were observed at known spawning locations of Galloo Island and Charity Shoal, whereas RI values during the isothermal period were greatest at what I believe may be the wintering grounds throughout the Kingston Basin. The number of individuals that contributed to an RI calculation per receiver varied between 1 and 7 on any given date for all four periods (mean of 3.8 individuals per day for isothermal and autumn mix periods, and 4.1 for spring mix and stratification).

The core home ranges (50% KUD) showed similar pattern(s) to the residence index results. Nearly all individuals (21 of 24) showed a preference for the main basin and southern end of the St. Lawrence channel during stratification; whereas distribution of home ranges for the remaining three periods were spread throughout the shallower Kingston Basin (example shown in Figure 2.4). Three individuals (IDs 16855, 16856 and 16876) occupied multiple core home range areas during stratified conditions of which at least one was in the shallower (in comparison to the main basin) Kingston Basin (Figure 2.4), suggesting use of the shoals during that period. Seasonal individual core home range area sizes varied between 0.1 and 3,966 km^2 (Table 2.1) with the smallest and largest occurring during isothermal and autumn mix conditions, respectively. Home ranges averaged 72.5 km^2 (± 58.7 standard deviation) across the four seasons. While home range sizes were generally below 220 km^2, four individuals, namely IDs 16869, 16860, 16865 and 16867, contributed to the large mean and variance during autumn mix with core home range area sizes of 3966, 511, 283, and 279 km^2, respectively. Excluding these first two individuals' home ranges, there were no statistical differences between the mean home range sizes of any thermal periods ($p > 0.05$, ANOVA). The number of individuals with home range sizes falling within the 1st and 3rd quartile throughout all seasons varied and was approx. half or less of the total (Table 2.1). Hurlbert index of overlap of core home ranges was low between stratified and isothermal periods 0.008 ± 0.005 (mean ± S.E.), and between autumn and spring with 0.001± 0.0008.

A single individual (ID 16869) travelled from eastern Lake Ontario to the western basin (Figure 2.5). While the individual was consistently detected on receivers in eastern Lake Ontario during the stratified and autumn season (n=47,653 detections) it was last detected there December 5 before showing up on western Lake Ontario receivers 17 days later on December 22. The individual remained in the western basin until March 13 (a total of 556 detections) and was not detected again during the study period.

Discussion

Lake trout distribution and home ranges in eastern Lake Ontario determined using acoustic telemetry over the span of one year were generally correlated to the lake's seasonal thermal cycles based on the different basins examined providing novel insights into the species spatiotemporal ecology. Previous studies have largely relied on catch data to infer lake trout distribution in Lake Ontario (Olson et al., 1988a). Such data is often prone to spatiotemporal bias because the catchability of fish is dependent on the presence of gear in that location, vertical and horizontal, during that period and the gear's efficiency (Jagielo & Zimmermann, 2003; Thorson, Fonner, Haltuch, Ono, & Winker, 2017; Walker, Maxwell, Quesne, & Jennings, 2017; Walsh, 1996). Such bias may be amplified if the species of interest exhibit inter-population and/or inter-individual variation in habitat use and swimming activities. In this study, I also uncover and document important variation between individual lake trout based on multiple underlying factors when selecting habitat or in terms of exploratory behaviour. Such individualistic behaviour is consistent with other top predators, such as northern pike (*Esox lucius*), leopard seals (*Hydrurga leptonyx*), and sharks (Casselman and Lewis, 1996; Findlay et al., 2016; Hiruki et al., 1999; Wilson, 1905).

Residence index and home range results confirmed that lake trout generally used the main basin, the region with greater depth, during stratified periods, which has been suggested to be due to a physiologically driven need to inhabit colder, deep water below the thermocline, yet other factors have been cited to contribute as well. Thermoregulation requirements seem likely if I consider the broader distribution into the shallower Kingston Basin for the remainder of the year when no thermal limitation was occurring. However, Raby et al. (2020) reported that in October and November lake trout occupied waters with temperature ranging between 8-14°C, and suggested that thermal stratification may be only one of the factors driving their habitat use. Studies have reported dissolved oxygen and competition as other factors influencing lake trout distribution (Morbey et al., 2006; Sellers, Parker, Schindler, & Tonn, 1998; Vander Zanden et al., 1999). Dissolved oxygen has been used to define lake trout habitat quality (Evans, 2007; Plumb and Blanchfield, 2009), and lake trout perform better at higher dissolved oxygen levels (6-7 mg/L) (Evans, 2007). The lowest recorded dissolved oxygen level in the Kingston Basin during our study period occurred in August and was >5.9 mg/L. This is well within the preferred range recorded by Evans (2007) suggesting dissolved oxygen was not a driving factor for lake trout occupying areas outside the Kingston Basin. However, five other salmonid species and walleye (*Sander vitreus*) are present in Lake Ontario all of which forage on the same prey (i.e. Alewife, *Alosa pseudoharengus*) (Hoyle et al., 2017; Mumby et al., 2018), and lake trout prey consumption rates peak during adulthood (Negus et al., 2005). Given this, competition may be a plausible additional factor influencing lake trout distribution during the stratified period.

Species seasonal distributions may also be strongly influenced by their prey (Guzzo et al., 2016) and lake trout have the largest trophic (isotopic) niche of any of the six salmonid species of Lake Ontario, feeding on both pelagic and benthic species, with Alewife and round goby being the dominant prey (Colborne et al., 2016; Mumby et al., 2018; Rush et al., 2012; Yuille et al., 2015). Seasonal movement and distribution of Alewife and round goby are poorly quantified in the Great Lakes, yet inferences from other studies suggest variable horizontal seasonal overlap exists with lake trout. Alewife are found farther offshore in the autumn and winter when compared to other seasons to avoid stressfully low temperatures at shallower depths (Bergstedt and O’Gorman, 1989;

Colby, 1973; Smith, 1968), and in shallower regions to spawn in the summer (O'Gorman et al., 1991), suggesting a reverse horizontal distribution to that of lake trout. This is consistent with reports that lake trout consume Alewife in the spring, but partially replace them with other species in the summer due to their reduced availability in deep, cooler waters (Dietrich et al., 2006; Luo et al., 2019). Conversely, round goby in their native habitat are reported generally to occur at depth < 60 m (Miller, 1986) in the autumn and winter, and in southwestern Lake Ontario in April at depth < 130 m (Walsh, Dittman, & O'Gorman, 2007), whereas they migrate to nearshore areas (< 10 m) in the summer (Miller, 1986). Since the species is benthic, this likely means a distribution in the Kingston Basin when found at depth <40 m and the main basin when at greater depth. This is supported by previous studies (Dietrich, Morrison, & Hoyle, 2006) and more recently by trawl surveys (Walsh, Dittman, & O'Gorman, 2007). This implies that round goby horizontal distribution overlaps with that of lake trout during the colder months and partially during stratified periods. Raby et al. (2020) reported that the vertical/depth niche of lake trout measured using archival tags was small compared to other salmonids in Lake Ontario and suggested that lake trout likely focused their foraging in the area near the lake bottom with limited opportunistic foraging near the thermocline. Given all of the above and recent rebounding of deep-water sculpin (*Myoxocephalus thompsonii*) populations, a benthic species that was historically a major part of trout diet (DFO, 2016; Weidel et al., 2017), I suggest that different prey are available across all lake regions occupied by lake trout throughout the year and do not appear to be a critical driving force behind their distribution during stratified conditions. An incomplete understanding of seasonal prey distribution in eastern Lake Ontario prevents us from establishing this with certainty.

Lake trout had their largest mean home range core areas during the autumn, an unexpected finding for a period of spawning. However, this is also a period when individuals migrate from offshore areas of the main basin to spawning shoals closer to shore as water begins to cool and then likely to wintering grounds. Four individuals drive this large mean (two of which were statistically determined to be outliers) with much greater home range sizes than all others, including one that travelled to the western basin of Lake Ontario (ID 16869). The migration between basins occurs at the beginning of the autumn mix period, and over a short period of time (i.e. generally individuals complete the migration within a day; Ivanova et al. *In preparation*). Thus, the between-basin migration is not likely to have a great effect on core home range size. However, individuals visiting multiple shoals and exploring their quality and suitability for spawning may be the cause for the large home range cores during autumn – a plausible explanation given home range estimates are based on utilization density. Also, such behaviour is consistent with lake trout in Lake Opeongo, where fish move among multiple shoals at spawning time, visiting as many as 10 spawning shoals in a two-week period (MacLean et al. 1981). Lake trout are known to exhibit site fidelity, but in this study, I was unable to quantify this and parse the specific movements during this period to assess a potential pre-spawning exploration due to the distance between receivers in the array. However, travel to multiple wintering grounds away from the spawning areas may be a contributor to the observed home range sizes during the autumn. Three of the four individuals with the largest home ranges had two or three home range cores, and one had a single core, although still comparatively much larger in size than other conspecifics. There were however, four other fish that had two or more home range cores during this period but with smaller home ranges. This implies variation in the use of wintering grounds, including variation in size and/ or the use of multiple wintering grounds (the latter is also supported by observed multiple core areas during isothermal conditions for 12 fish). Thus, for the autumn mix period of our study, travel to different overwintering areas seem to be contributing to the larger home range area sizes, and I suspect that inter-individual variation plays an important role.

Home range size is often positively correlated to the number of home range cores observed and while this is generally true in this study as well, it was not always so, further suggesting the existence of inter-individual variation. For example, ID 16862 had a single core during the stratified period and a home range of 91 km^2, while ID 16853 had four cores and a home range of 14.7 km^2 during the same period. Multiple home range cores are not unusual, as many species are known to move between areas based on prey patch profitability. However, this is an especially interesting finding for the stratified period, when cores are located both in the shallower Kingston Basin and in the deeper main basin. Based on data during this period, temperatures at depths ~20-25 m can fluctuate greatly (by ~15°C) within days, and reach temperatures considered suboptimal for lake trout (i.e. >15°C; Olson et al., 1988). This implies that shallower areas (approx. <25 m) during the stratified period are likely to be avoided by lake trout, and deeper areas would provide more suitable cooler and stable environment, although frequent short movements into these shallower areas to forage are possible. This is supported by the observations of Olson et al. (1988a) and Raby et al. (2020) and their suggestion of individuals likely remaining near and below the thermocline, and may be a plausible explanation for the occurrence of cores in the two areas of the lake during this period. Thus, while it seems like some fish move from one area in the eastern basin to another possibly in response to temperature fluctuations, the majority remain distributed within the main basin. Overall, our observations of large variation in home range sizes and the number of cores imply the presence of inter-individual differences.

A single lake trout (out of 24) made a cross-lake movement from the eastern to the western basin of Lake Ontario (ID 16869), providing further evidence of inter-individual variation. Also, this is evidence that the eastern and western populations are are not entirely spatially segregated. Given the lack of coverage for the majority of the main basin, I was unable to estimate how far other individuals may venture into this region during isothermal conditions. However, 16 (of 24) individuals were continuously detected around the Kingston Basin during that isothermal period, suggesting this extensive movement behaviour is likely not common for lake trout. The drivers behind and significance of this cross-lake movement are not clear at present. Mark-recapture study done in Lake Michigan found lake trout remained within a 80 km radius (Schmalz et al., 2002). However, Rybicki (1990) showed that other lake trout in Lake Michigan made cross-lake movements of 120 km. The distance travelled by our lake trout from Duck-Galloo Ridge to the mouth of the Niagara River was > 200 km, which is greater than the distances reported by the above-mentioned studies. It should be noted that this one individual in our study, apart from this cross-lake movement, had behaviour similar to the majority of the tagged individuals with stratified home range exclusively in the main basin. Thus, while I observed variation in the spatial distribution among some lake trout during stratification, I believe that others may exhibit inter-individual variation in regard to exploratory behaviour.

On a broader scale, inter-individual variation is an important consideration for rehabilitation or reintroduction of species, because it provides the population with potential to use multiple habitats, aid in reestablishment efforts through adaptability, and perhaps even increase the impact of their function in the ecosystem. In this study, the home range sizes between seasons were not statistically different, suggesting observed inter-individual variation in home range location was a preference rather than a population level response to local conditions. The potential of fish using multiple habitats is seen in our study with fish occupying both deeper and shallower basins to various extents throughout all seasons, suggesting wide use of available and /or more profitable resources. Another major implication of such variation is related to the function a species has in the ecosystem. Lake trout, in particular, is considered key to the cycling of energy between offshore and nearshore zones (Ives et al., 2019; Ryder & Kerr, 1990). Considering our results, I could deduce that energy cycling is temporally correlated to the movement of the species from offshore (main basin) to nearshore (Kingston Basin) and vice versa. Thus, seasonal distribution variation between individuals may indicate that some play a larger and/ or slightly different role than others. For example, while most individuals link the nearshore and offshore in the spring, some individuals provide a link during summer stratification, and others may do so during isothermal conditions. Thus, our results underline the key role of inter-individual variation in species reintroduction efforts, and this being a crucial component when focus is on improving ecosystem function.

Conclusions

The existence of inter-individual variation in the distribution and movement behaviour of populations, as observed here for lake trout, has important implications for predicting the effects of increasing water temperatures driven by climate change on species distributions and their bioenergetics, the fit and potential function of reintroduced animals in the ecosystem, as well as better understanding of overall lake ecosystem function. This study also accentuates the importance of selecting for behavioural variation among stocked individuals as a key consideration for other species rehabilitations in ecosystems with a variety of habitats. Given the above, our results inform not only on the Lake Ontario and lake trout ecology but would also be useful for informing decision-making across all Laurentian Great Lakes, other freshwater ecosystems, and other species undergoing rehabilitation or reintroduction.

Future studies should consider incorporating environmental data into study designs, depth- and /or temperature-sensing acoustic tags, and metrics to assess competition with other species. Identification of strain of tagged fish would allow for detailed interpretation of plasticity in observed behaviours and whether there is evidence of an adaptive or genetic basis. Taken together, this information would provide major clues as to the drivers of the behaviours and selection of habitat, and identify constraints to species rehabilitation both currently and under potential climate change scenarios.

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Table 2.1. Lake trout mean, standard error, minimum and maximum core home range (50% KUD) area sizes (km^2) for eastern Lake Ontario. Also shown are the number of IDs with home range size within the 1st and 3rd quartiles out of the total number of IDs with the home range per thermal season. Two lake trout IDs with outlier values for the autumn mix period KUDs are also shown.

	KUD† **(mean +/- SE‡)**	**Min**	**Max**	**Number of IDs with KUD size between the 1st and 3rd quartile /all IDs**	**Mean number of HR cores between individuals** **(range)**	**Number of days**
Autumn mix*	297 +/- 195.1 81.2 +/- 20.9*	2.2	3966 282.6*	8/20	1.6 (1-3) 1.5 (1-2)*	60
Isothermal	74.1 +/- 16.4	0.1	215.5	9/17	2.05 (1-3)	120
Spring mix	77.8 +/- 9.5	3.2	178.4	8/22	1.05 (1-3)	61
Stratified	60 +/- 7.6	14.7	169.7	12/24	2.13 (1-4)	124
IDs with outlier KUD sizes for Fall mix						
16869	3966	--	--		2	
16860	510	--	--		3	

Note: † KUD – Kernel utilization distribution, ‡ SE – Standard error, * Mean and SE values calculated without outliers, which are shown in the bottom part of the table.

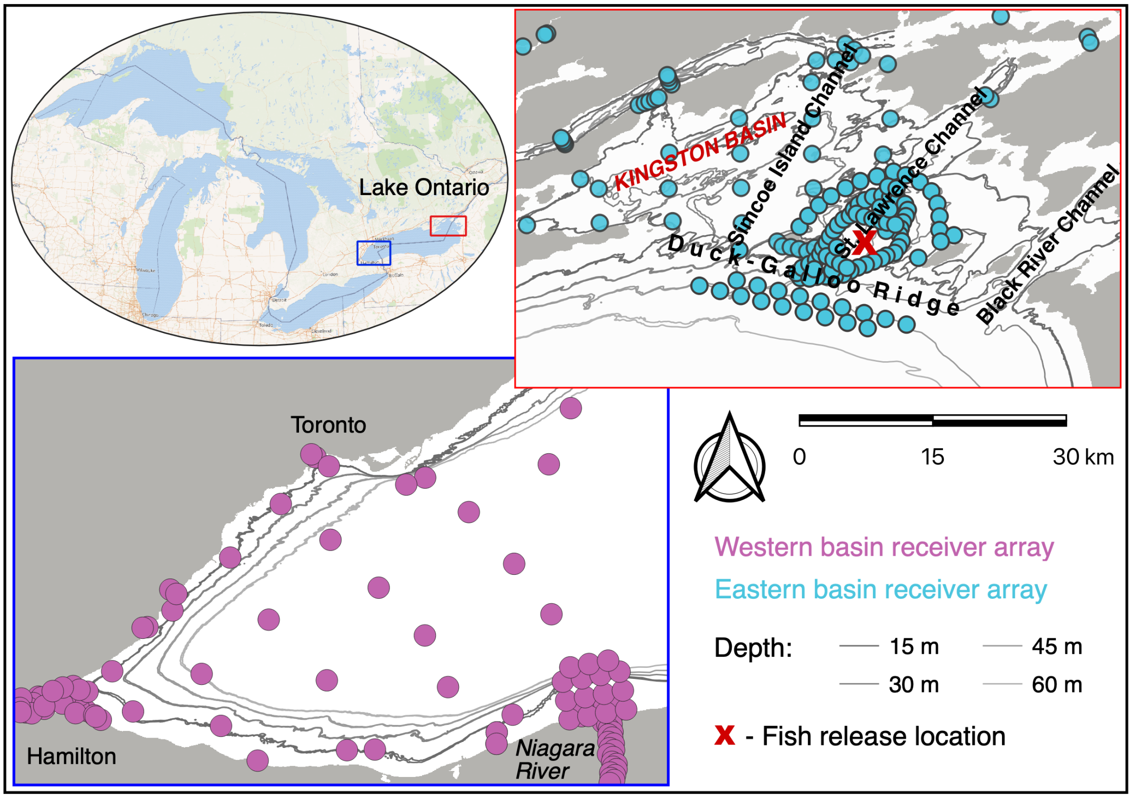

Figure 2.1 Map of receiver locations and bathymetric features for the western basin and eastern Lake Ontario used to examine the habitat use of lake trout.

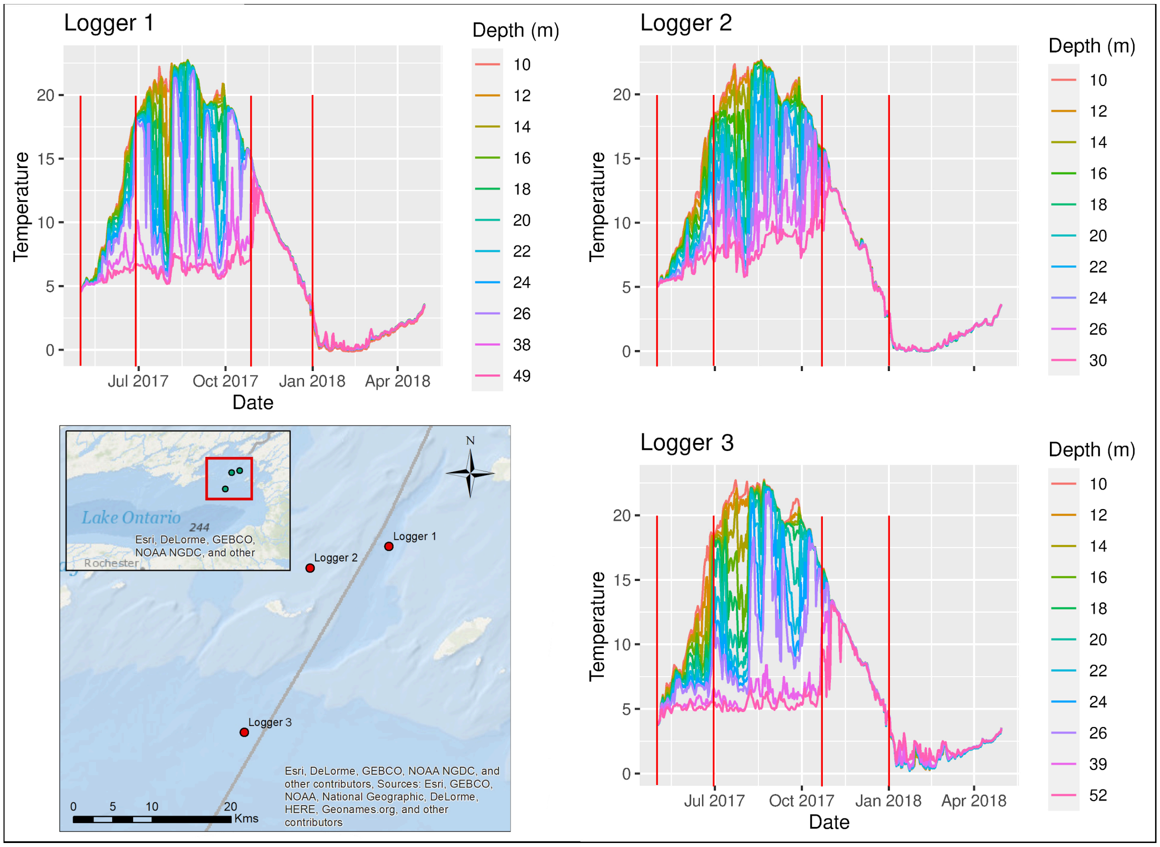

Figure 2.2 Eastern Lake Ontario thermal profiles (daily mean water temperatures) from May 1, 2017, to April 30, 2018 at three locations near the St. Lawrence Channel. Red vertical lines denote the starts and ends of the four thermal periods as follows: 1) stratified – Jul. 01 to Nov. 1; 2) autumn mix – Nov. 02 – Dec. 31; 3) isothermal – Jan. 1 to Apr. 30; and 4) spring mix – May 1 – Jun. 30.

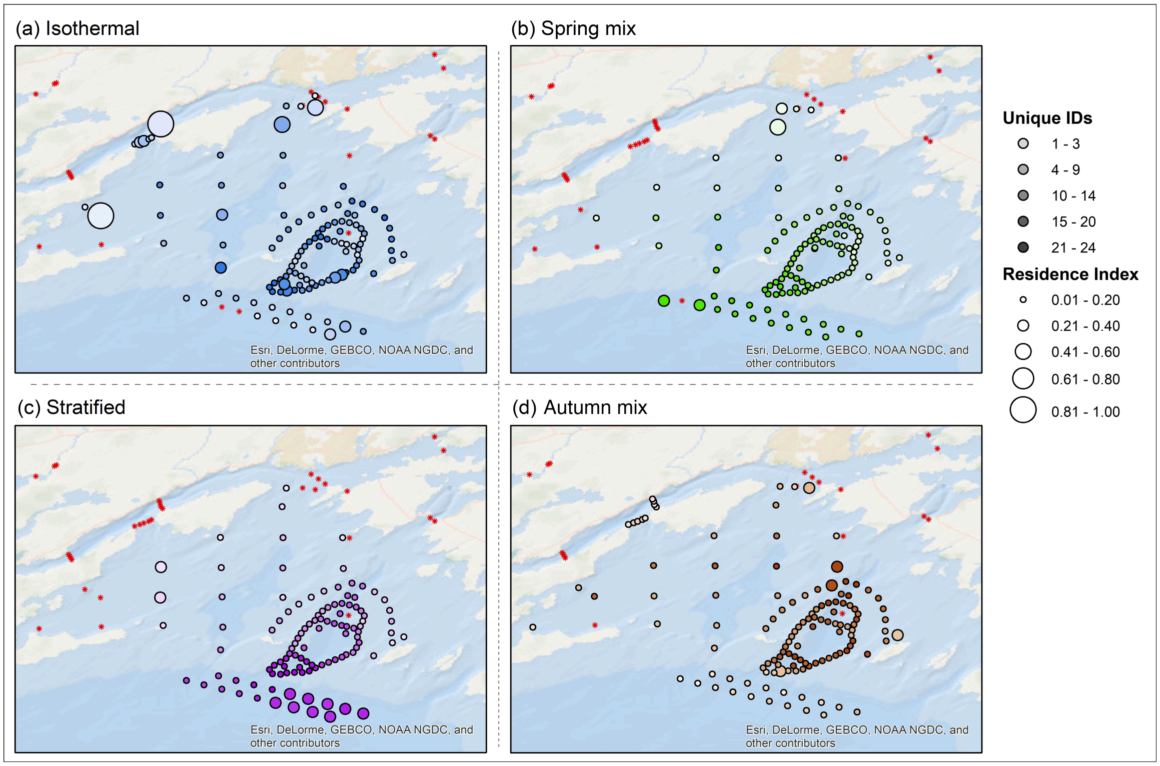

Figure 2.3 Mean residence index for all individual lake trout in eastern Lake Ontario for the period of May 2017 to May 2018. Hue and size represent the number of unique IDs and the residence index, respectively. Note, lake trout were not detected at all receivers (denoted with red stars).

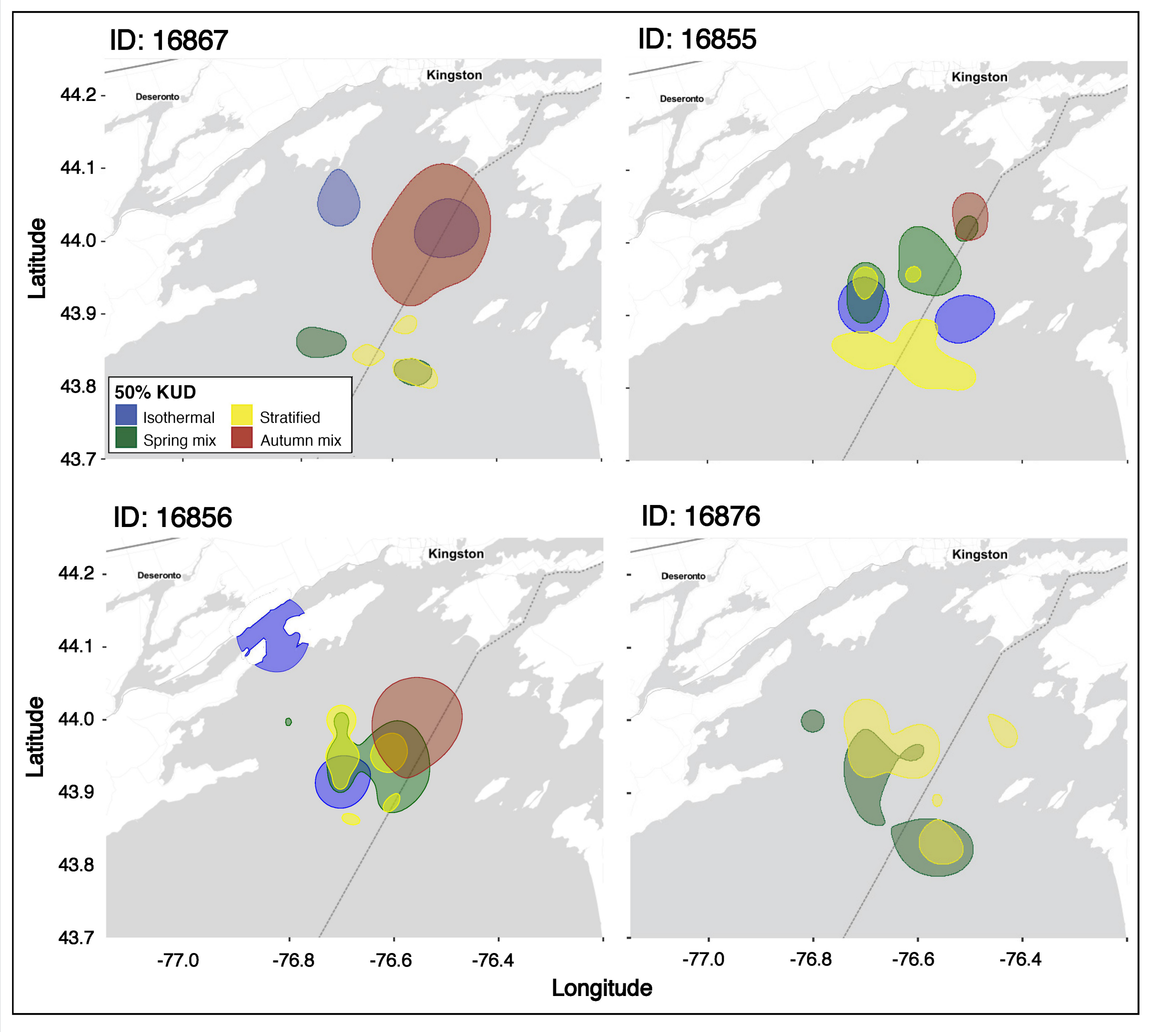

Figure 2.4 The home ranges of individual with ID 16867 are shown as a representative example for the majority of tagged lake trout. Shown are also the home ranges of the three lake trout individuals (IDs 16855, 16856 and 16876) that spent at least part of the stratified period into the Kingston basin shoals.

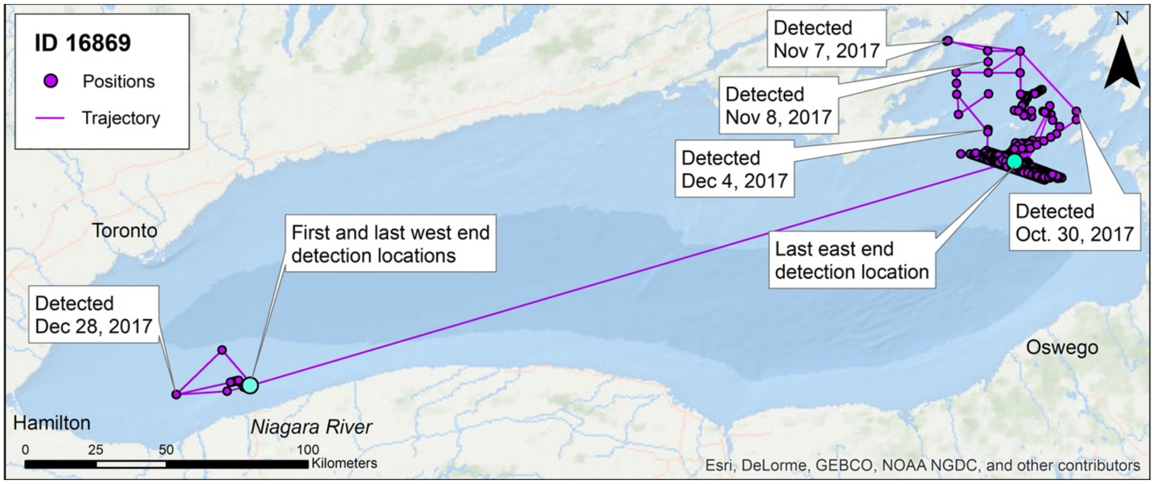

Figure 2.5 Lake trout ID 16869 Lake Ontario cross-lake movement. This individual left the eastern Lake Ontario arrays on Dec. 5, 2017 and was detected on the western basin at the mouth of the Niagara River on Dec. 22, 2017 – a distance of >200 km. The last detection for our study period (May 1, 2017 to April 30, 2018) occurred on March 13, 2018 in the west basin. A subset of dates and detection locations are also shown.

CHAPTER 3 – CHINOOK SALMON SEASONAL HORIZONTAL AND VERTICAL DISTRIBUTIONS BY SIZE CLASS IN LAKE ONTARIO

Summary

Chinook salmon (*Oncorhynchus tshawytscha*) have been observed to spatially segregate based on body size in the marine environment. In their introduced range in the Laurentian Great Lakes, where Chinook salmon support important recreational fisheries, very little is known about their seasonal habitat use, including effects of body size on horizontal and vertical distributions. This study quantified the seasonal spatial utilization, depth and temperature distributions of two age classes of Chinook salmon in Lake Ontario using pop-off data storage tags (pDST) from 2014 to 2016 and acoustic telemetry from 2017 to 2020. Moderate overlap occurred between immature (age classes 1 and 2) and sub-adult (age classes 3 and 4) individuals at the 50% spatial utilization distribution level, a measure of horizontal segregation, with the greatest segregation during the fall and spring. Depth and temperature occupancy for two immature individuals in the fall and winter also differed from those of sub-adults. This study is the first to examine the overlap in horizontal and vertical distributions between Chinook salmon age classes in the Great Lakes and contributes key information on their depth and temperature distributions.

Introduction

An important aspect of animal ecology is intraspecific interaction between size classes, which has implications for niche partitioning and lifetime growth patterns (Gouraguine et al., 2011; Moranta et al., 2008; Nelson and Dark, 1985). Conspecifics of different size/ age classes may exhibit segregation in habitat use and diet as a mechanism to avoid negative interactions, such as competition and cannibalism (Christiansen et al., 2012; Ross, 1986). For example, segregation between smaller and larger Arctic cod (*Boreogadus saida*) in the Beaufort Sea and the Arctic Ocean has been attributed to resource partitioning and avoidance of cannibalistic conspecifics (Benoit et al., 2014; Kessel et al., 2021). Quantifying conspecific size class segregation and associated drivers is useful for the management of fishes (Bell et al., 2015) and can help improve our understanding of interactions with other species (Christiansen et al., 2012). The dynamics of intra-specific competition are especially important from an applied perspective in systems in which the fish community is highly managed, such as in the Laurentian Great Lakes (hereafter Great Lakes; Sterner et al. 2017).

The Great Lakes includes five large lakes (Superior, Michigan, Huron, Erie and Ontario) that contain one of the richest fish communities among temperate freshwater systems, including a variety of native and introduced species (Christie, 1974; Cudmore-Vokey and Crossman, 2000). The six salmonid species residing in the Great Lakes provide substantial economic benefits to the region (Rand and Stewart, 1998) and influence the food webs as top predators (Mumby et al., 2018). Of the salmonids, arguably the most valuable recreational species is the Chinook salmon (*Oncorhynchus tshawytscha*), a fast-growing top predator first introduced in the Great Lakes, including

Lake Ontario, in the late 1800s (Wilmot 1878 in Crawford 2001) and stocked regularly since the 1960-70s (Stewart et al., 2013). Chinook salmon is now considered naturalized with approximately half of its Great Lakes population being from natural reproduction (Connerton et al., 2009; Marklevitz and Morbey, 2017; Tsehaye et al., 2014). Chinook were originally introduced with two purposes: to regulate the abundance of Alewife (*Alosa pseudoharengus*), an invasive species that had become hyperabundant with negative impacts on native species (Crowder, 1980; Fisher et al., 1996; Stewart et al., 1983) and to enhance the recreational fishery (Crawford, 2001). Chinook salmon is now the most sought-after recreational salmonid in the Great Lakes with the recreational fishery in Lake Ontario contributing approximately USD $450 million to the USA and Canadian economies taken together (MNRF, 2021; Responsive Management, 2019). Stocking of salmonids is coordinated between Canada and the USA and management now has a dual focus on i) maintaining Chinook salmon populations for recreational use and ii) restoring the native salmonids lake trout (*Salvelinus namaycush*) and Atlantic salmon (*Salmo salar*) (Stewart et al., 2017).

Despite their value to the fishery, high level of management, and role as a top predator, there is limited information on the movement ecology of adult and sub-adult Chinook salmon in their open water foraging phase, owing to the inherent difficulties in studying fish movement in large open systems (i.e., the Pacific Ocean or the Great Lakes). In Lake Ontario, the species was recently reported to occupy depths up to 180 m and temperatures up to 24°C throughout the year (Raby et al., 2020). However, it is unclear whether Chinook salmon use the entire lake, how they use the available vertical and horizontal spaces seasonally, and whether any differences exist in lake habitat use by size class. In the Pacific Ocean, vertical segregation has been observed offshore between Chinook salmon size classes, with immature fish (ages 1-2) found deeper than sub-adults (ages 3-4; Walker et al. 2007). Observations in Lake Ontario suggest that the species' size classes segregate vertically in the early summer, but all size classes move closer to shore and occupy similar depths in late summer prior to adults migrating up rivers to spawn (personal observations of the authors). Little is known of the size class distributions in the spring and winter in Lake Ontario; a current hypothesis is that both size classes are tracking their main prey, Alewife.

Considering past challenges to quantify the movement of ocean and lake fish species, especially those with large home ranges and propensity for great depths (Hussey et al., 2015), the lack of such information for Chinook salmon in the Great Lakes is not surprising. The development of novel technologies, including pop-off data storage (pDST) and acoustic telemetry (AT) tags, that track fish movements has reduced these challenges (Matley et al., 2021). Depth and temperature are recorded in detail (seconds to minutes, depending on the chosen settings) by pDSTs, but these tags do not give horizontal information (latitude and longitude). The tags are attached to the fish externally, archiving the data that can only be accessed if the tags are recovered. The AT tags are internally implanted transmitters that emit an acoustic signal and rely on stationary acoustic telemetry receiver arrays to record the signals and archive the data. Movement and habitat use can be derived from detections at strategically positioned receivers. These tags can also be equipped with sensors to provide temperature and/or depth but often provide fewer observations than pDST due to less frequent transmissions (every 60-180 s is most common) and the fact that AT-tagged fish may often be out of the detection range of receiver stations.

The objectives of this study were to quantify the seasonal spatial utilization, depth and temperature distributions of Chinook salmon size classes in Lake Ontario. This study combined the use of pDST and AT tags since these tag types have complementary strengths for assessing habitat use and movement. I hypothesized that Chinook salmon size classes would be spatially segregated as a mechanism of conspecific competition avoidance and because they feed on different sized prey. I predicted that (1) both, immature and sub-adult Chinook salmon would have extensive lake-wide movements, effectively using the entirety of Lake Ontario and overlapping horizontally, and (2) inhabit a wide range of temperatures and depths with size classes segregating along the vertical plane in all seasons except in the late summer. The results of this study will contribute to an improved understanding of how Chinook salmon spatial ecology and foraging tactics change with ontogeny.

Methods

Study site

Lake Ontario is 245 m deep with a surface area of 19,000 km^2 making it the 13th largest in the world, but the smallest by surface of the North American Laurentian Great Lakes. The lake is biodiverse, including over 120 fish species and home to a number of introduced species, including top predators Chinook and Coho salmon (*Oncorhynchus kisutch*), Rainbow trout (*Oncorhynchus mykiss*) and Brown trout (*Salmo trutta*), forage fish Alewife and Rainbow smelt (*Osmerus mordax*), and parasitic Sea lamprey (*Petromyzon marinus*). Lake trout (*Salvelinus namaycush*) and Atlantic salmon (*Salmo* *salar*) are the native top predators of the lake and are currently undergoing rehabilitation through stocking of hatchery-grown fingerlings and yearlings.

Telemetry

To obtain high resolution data on depth and temperature occupancy, I used pDST tag data from 11 Chinook salmon tagged between 2014 and 2016 (see Figure 3.1 for tagging locations and Table 3.1 for details). Detailed explanation of the tagging procedure is available in Raby et al. (2017). In summary, Chinook salmon were caught via trolling and angling in spring (April-May) and late summer (September) in 2014, 2015 and 2016. Using standard aseptic procedure, fish with a minimum fork length of 40 cm were tagged externally via harness through the dorsal musculature with a pDST tag (a time-release G5 long-life 20 bar depth-temperature logger with a float; Cefas Technology Inc.). Tagging involved two c. 2 mm incisions below the dorsal fin to accommodate a 3 mm stainless-steel needle. A plastic bracket and the harness (consisting of c. 10 cm long 135 kg 2 mm diameter monofilament fishing line threaded with 1 mm plastic washer) were inserted through the musculature of the fish (bracket was secured posterior of the harness) via the needle's sharp end. Extra space was left when securing the harness to allow for fish growth. Fish were held in lake water with continuous irrigation of the gills during the surgical procedure. The tags recorded pressure (in dBar; dBar approximates depth in m with precision of 0.08 m and accuracy of ±2 m) and temperature (precision 0.03125°C and accuracy ±0.1°C) every 70s. Tags were programmed to release after one year. A total of 12 tags from 32 tagged Chinook salmon were recovered, of which 11 had sufficient data for analysis, resulting in a total of 9,157,335 depth and temperature records.

A total of 419 permanent passive acoustic telemetry receivers were deployed in western and eastern Lake Ontario between 2016 and 2019 (69-kHz VR2W/VR2AR, Innovasea, Bedford, Nova Scotia, Canada; Figure 3.1). Receiver moorings are described in Ivanova et al. (2021a) and Chapter 2 here. Briefly, spacing among receivers was 2 to 15 km apart with maximum depth 163.5 m in the western part of the lake; receivers in the eastern end of the lake were arranged as a mixture of 'lines' and 'grids' along with strategic points of interest (Figure 3.1) and had a maximum depth of 102 m. In this study, it is important to note the gap in receiver coverage in the middle of the lake representing approximately 1/3 of the lake, thus all results and interpretations are made with this consideration.

A total of 45 Chinook salmon were tagged with acoustic telemetry tags in Lake Ontario for this study (see details in Table 3.1). A combination of Vemco V13 (45 mm length x 13 mm diameter; 6 g weight in water; nominal delay 180 s; estimated battery life 703 d; Innovasea) tags with and without sensors (temperature and/or depth) and V9 (24 mm length x 9 mm diameter; 2 g weight in water; nominal delay 180 s; estimated battery life 912 d; Innovasea) tags without sensors were used (Table 3.1). Full details of the tagging are available in Ivanova et al. (2021b) and Chapter 4. Briefly, Chinook salmon were caught via trolling in 2016-2019 and a tag was surgically implanted in the body cavity of the fish. Detection data from June 09, 2017, to April 30, 2020, were included in the analysis. Due to low detection histories (either due to tag expulsion, individual death or movements outside the detection range of our receivers), 16 of 45 individuals were removed from analysis. A total of 29 individuals (n=18 for each immature and sub-adult, with seven IDs including detections for both immature to sub-adult ages due to estimated growth during the detection period) generated 75,312 detections after false detections were filtered out of the dataset. False detection filtering removes false positive detections and here I used the *false_detections* function in the glatos package (see https://gitlab.oceantrack.org/GreatLakes/glatos) in RStudio (version 1.2.5033) with 3,600 s threshold. Eighteen individuals provided depth data (n=11 sub-adult and n=12 immature; five individuals had both immature and sub-adult detections due to growth during the detection period) while four fish had temperature data (n=4 sub-adult and n=2 immature, i.e., two individuals had detections encompassing both size classes due to growth during the detection period).

Data analysis

Chinook salmon length-at-age data for 1991-2019 (source: USGS) was used to approximate the age of the fish, extrapolate their body size throughout the study period (i.e., beyond the time when they were caught, tagged, and released), and to separate fish by size class, i.e., immature and sub-adult. Salmon jacks (i.e., early maturing males) are recorded at spawning areas at an approximate length of 600 mm and two years of age (Young et al., 2013). Since jacks may be considered sub-adults, I used the calculated minimum length of 540 mm for fish of age 2 to distinguish between immature (ages 1 and 2) and sub-adult (ages 3 and 4) size classes. The month of April was used for formal age switch where necessary due to growth during the detection periods.

All data were analyzed using RStudio statistical software (version 1.2.5033 running on Mac OS X 10.15.4). Acoustic telemetry data from June 2017 to April 2020 yielded 75,312 detections, including 44,594 depth (sub-adult n=22,437 and immature n=22,157) and 3,843 temperature (sub-adult n=2,214 and immature n=1,629) records.

Location was approximated from the acoustic tag detections of each individual using centres of activity (hereafter, 'CoA'; Simpfendorfer, Heupel, and Hueter 2002) at 15-min intervals (i.e., the ‘average’ position based on all receiver detections within each 15-min period). To quantify the horizontal spatial utilization distributions, all individuals were pooled together, separated by size class and kernel utilization distribution calculated for each season using the adehabitatHR() package (Calenge, 2006) at the 50% and 95% levels. Core spatial utilization distribution (i.e., 50% density level) represents the area(s) used most frequently and this core may change with season, whereas the 95% spatial utilization also includes habitat used for exploration (Burt, 1943). Seasons were based on lake thermal stratification as per Chapter 2 as follows: winter January through April (isothermal), spring May-June (transition to stratified), summer July-October (stratified), and fall November-December (transition to isothermal). Percent overlap between size classes was calculated at both spatial utilization levels.

A comparison between sub-adult AT and pDST depth and temperature was performed to understand any caveats of the use of each type of tag and their limitations. Considering the maximum depth to which our AT tag pressure sensors were calibrated was 68 m, pDST depth greater than that was excluded and modelled (using the same GAM method described below) and a Pearson *t*-test performed to assess any bias that depth limitation may have had on our results from the AT tags.

To quantify seasonal vertical distribution, mean daily depth and temperature were calculated for each individual and the resulting values were pooled by size class and modelled using generalized additive models with a random effect (GAM; *mgcv* package (Wood, 2011)). Modelling was done separately for each tag type to avoid any biases from the limitation of depth of the AT tags and the placement of the receivers. The periods included for AT were June 2017 to April 2020 and for pDST October 2014 to September 2016. Correlation was tested for day, month, year, and id for depth and temperature. Month was strongly correlated to day (>0.6) and was thus removed from the models. Year and ID were both tested as random effects. For both AT and pDST data the models with lowest AIC value included day and size class and ID as a random effect, and these models were used to generate predictions. Immature pDST depth and temperature were only available for two fish with a total of 11,717 records for October-January and only these months were modelled and used for predictions. For comparison of immature pDST depth and temperature occupancy with that for sub-adults, predictions for the corresponding months (i.e., October-January) for sub-adults were extracted from the full year model. A similar approach was used for the AT dataset in which immature data were only available for September through March included. Predicted seasonal depth and temperature differences between size classes were tested using ANOVA.

Results

Chinook salmon sub-adult and immature spatial utilization distributions (SUD) were based on 7,287 and 7,740 CoA locations, respectively, for the entire study period. Sub-adults inhabited the western part of Lake Ontario during all seasons based on their core (50%) SUD, and more specifically the vicinity of the Niagara River mouth during the summer, fall, and winter seasons (Figure 3.2). Approximately half of the core SUDs of the sub-adults in the summer and fall were also in the eastern part of the lake near Pointe Petre (Figure 3.2). In the spring, sub-adult SUDs were distributed in the waters between the cities of Toronto and Hamilton (Figure 3.2). Although immature individuals showed an overall similar distribution to sub-adults, overlap between the two size classes core SUDs varied between 39.8 and 81.5% for the different seasons (Table 3.2). Sub-adult SUDs overlapped 81.5% of the immature core SUD during the summer, whereas immature cores overlapped sub-adult core SUDs the most during the winter (81.5%). The least overlap for both size classes was in the fall with 45.4% for immatures and 39.8% for sub-adults. At the 95% level, winter remained with the greatest overlap of immatures on sub-adult SUDs (99.9%), but sub-adults had greatest overlap on immature SUDs in the fall (95.8%).

Sub-adults were generally found deepest in the winter, and shallowest in the summer based on both AT and pDST tags (Figure 3.3a). For sub-adult pDST, the 68 m depth limitation removed 217,699 observations with the highest amount of data removed from the winter season (Table 3.3). Depth from the pDST data without limitation was significantly greater than depth of pDST data capped at 68 m for the period between October and June ($p < 0.001$; Figure 3.3a), but no difference was observed during the summer months of July through September. Significant differences were observed for all months of the year, except May, between AT and both unrestricted and restricted pDST depths, in which sub-adult AT depths were generally shallower than unrestricted pDST depths across the year except May (Figure 3.3a). The greatest mean depth difference between sub-adult AT and un-restricted pDST data were > 25 m observed during March, and smallest < 5 m in May.

Depth data from the pDST tags were available for two immature Chinook salmon for the months of October through January, and these two fish were at shallower depths than the sub-adults during the same period ($p < 0.001$; Figure 3.3b). During these months, minimum mean depth (and confidence intervals) for immature fish and sub-adult fish was 15.2 m (± 0.2 m) and 20.4 m (± 7.0 m) and maximum mean depth was 24.8 m (± 0.4 m) and 52.5 (± 7.2 m), respectively. The two immatures showed a largely flat mean distribution over time for this period, whereas sub-adults increased their mean depth distribution with the progression from fall to the winter season (Figure 3.3b).

Temperature curves for AT and pDST sub-adults were similar throughout the year, except for July through September (Figure 3.4a). The lowest daily mean temperature for AT and pDST sub-adults was 2.5°C and 4.1°C, observed in March and January, respectively. The highest sub-adult daily mean temperature for AT and pDST was 19.5°C in July and 15.7°C in October, respectively (confidence intervals $< 0.1°C$ and $< 0.05°C$ for all means). Temperature for immature individuals ($n = 2$ for each type of tag) was available for September-March and October-January for the AT and pDST datasets, respectively (Figure 3.4b). Overall, the two pDST immature individuals had a different mean temperature occupancy than the pDST sub-adults ($p < 0.001$, Welch two sample t-test). The two AT immature individuals occupied higher mean temperatures ($p < 0.001$, Welch two sample t-test) for this period compared to the four AT sub-adults with a mean difference of 3.4°C.

Discussion

Understanding how a species uses their environment is a key requirement for determining its ecological role and informing management decisions related to the conservation of the species or other species with which they interact. Here, I examined horizontal, vertical and temperature distributions and overlaps of Chinook salmon size classes in Lake Ontario using pDST and AT technology. Our results suggest moderate segregation is occurring based on the comparison of seasonal SUDs between immature (age 1-2, size range) and sub-adult Chinook salmon (age 3-4, size range), however depth and temperature distributions of immature individuals were significantly different from those of sub-adults during the fall and winter. These results are the first analysis of this type for the Great Lakes.

Limitations in this study included incomplete coverage of the lake by receivers and a cap on maximum depth recording capabilities of the AT tags. Acoustic telemetry positional data is based on receivers located at both the eastern and western ends of the lake, about 2/3 of the surface area, leaving the middle of the lake largely without coverage. Nevertheless, the results for the horizontal distribution of Chinook salmon show that the species move freely between the two ends of the lake during all seasons (Figure 3.2), thus a conclusion could be made that the species utilizes the middle of the lake more than it is represented by our SUD estimates. The second limitation is evident in the depth data of our AT tags. A comparison between our pDST depth data for sub-adults and the same data restricted to 68 m clearly shows that depths > 70 m are not captured in the restricted dataset for the winter and significantly biases our results for this period during the modeling. The same comparison indicates that tag type bias is not observed for the months of June through October. This leads us to believe that the winter depth results of our sub-adults with AT tags are not representative of the true distribution of this size class. In addition, based on our depth results for June through October, a difference between the pDST data and the AT data is evident, suggesting that the positioning of our receivers mostly captures the shallower use of these individuals within the lake and not the full extent of their depth occupancy. Given the above, I recommend that a more functional design be employed to improve receiver coverage of the entire lake, such as the grid design used in lakes Erie and Winnipeg (Kraus et al., 2018). In addition, I recommend that if AT tags with depth sensors are to be used, the maximum available depth recording capability is selected.

Home ranges are an important part of a species' ecology as these contain the resources and features in their environment that are of preference and thus, provide key information on areas used for various behaviours, such as optimal foraging (Powell, 2000). In this study, sub-adult Chinook salmon favored the western part of the lake in all seasons at the core SUD level. However, this may be due to sub-adults being tagged primarily in the western end of the lake. In addition, many of the receivers in the eastern part of the lake are positioned in locations < 40 m deep, and sub-adults showed preference for deeper offshore waters. In the summer and fall, approximately half of the core SUDs were distributed in the eastern part of the lake near Pointe Petre (Figure 3.2), suggesting that sub-adults as a population use the entire lake and thus had greater horizontal movement compared to winter and spring. Given this, core SUDs for spring and summer are likely larger and cover more of the middle of the lake than is represented by our results, since there were no receivers to quantify their presence in that part of the lake.

Understanding the depth and temperature occupied by animals within their horizontal SUDs contributes further insights of the resources and features they rely on and provides clues to their behaviour. Our pDST depth results showed individual Chinook salmon at depths > 150 m during the winter months. With only a few receivers positioned at depths greater than 130 m for this study (i.e., near the middle of the lake), the pDST maximum depth confirms that the AT arrays are not fully capturing the winter core SUDs of this species. Taken together, these two datasets indicate that the winter SUDs of Chinook salmon are more likely to be distributed further east towards the middle of the lake resulting in a larger SUD. It is unclear whether the western end of the lake near the Niagara River (hereafter Niagara bar) is likely to remain part of the core SUDs for sub-adults based on a more extended receiver coverage in the main basin. The structures formed by river mouths and the associated outflow of nutrients provide for richer foraging grounds and thus, greater species diversity (Janetski and Ruetz, 2015; Odum, 1990). Chinook salmon feed almost exclusively on Alewife, which are rarely caught near the Niagara bar in the spring and fall and are known to have an offshore distribution in these seasons and the winter (USGS, 2018; Weidel et al., 2017). Also, Chinook salmon distribution has been linked to that of Alewife (Clark et al., 2017), thus it is possible that the Niagara bar core SUD observed here may actually be an area of exploration rather than a favoured foraging locale. Also, considering the density of receiver spacing in that area, more detections would be recorded compared to the sparser placing of receivers in the deeper offshore areas where the detection ranges are not overlapping, detecting fish only when in range. The detection range for this study's tags was estimated at 1,000 m at 70% efficiency (Klinard et al., 2019) and receiver placement in the offshore areas was 10-15 km apart, resulting in large areas where fish could remain undetected. While calculating CoAs largely reduces bias of receiver spacing, even a minimal bias would result in a greater number of observations near the bar and thus, more weight during kernel calculations. Therefore, depth and temperature occupancy results interpreted in combination with horizontal SUDs, suggest sub-adults have a general preference for offshore waters during the winter, and highlight that more information is needed to understand the extent of reliance on resources in this part of the lake that is impacted by the Niagara River outflow.

Segregation of size classes of the same species may occur on the horizontal or vertical planes or both as a mechanism of resource partitioning and/or avoidance of negative interactions. Thus, knowledge of segregation can illuminate the intra-specific interactions between the size-classes. Based on the core SUD results, a moderate horizontal segregation occurred in Lake Ontario between size classes primarily in the fall and spring; segregation was negligible in the summer and winter. Results for vertical distributions showed that the two pDST-tagged immature individuals occupied shallower depths compared to the sub-adults during the fall and winter months. Incomplete information is available about horizontal, vertical and temperature distribution among Chinook salmon size classes in the marine environment. Studies suggest horizontal segregation mainly exists for juvenile (age 0) and larger immature/ maturing fish, as juveniles occur in coastal areas and maturing fish are in offshore areas (Quinn, 2005). To our knowledge, records are lacking for horizontal segregation of immature (ages 1 and 2) and sub-adult (ages 3 and up) Chinook salmon in offshore areas of the Pacific Ocean. Evidence for vertical distribution segregation is available from trolling surveys in southeast Alaska, which showed that younger Chinook salmon (age 0 and 1) were found shallower and larger fish (age 2) progressively deeper in waters of up to 36.6 m throughout the year (Orsi and Wertheimer, 1995). Walker at al. (2007), also presented trolling data from the Bering Sea for depths up to 350 m and reported that immature fish (ages 1 and 2) were distributed deeper than sub-adult fish (ages 3-5) in offshore waters.

Although the results presented here confirm segregation, the depths per size class contrast with the results of Walker at al. (2007). This is likely owing to the limited amount of data available for our immature individuals (pDST data includes only a few months for only two individuals). Another plausible explanation is that Chinook salmon in Lake Ontario exhibits predator-release apex predator behaviour (e.g., may occupy habitat they wouldn't when predators are present in the system), which may be more suppressed in the marine environment for certain size classes by the presence of predators. Fish-eating orcas (*Orcinus orca*) and salmon sharks (*Lamna ditropis*) both prey on Chinook salmon in the ocean (Ford and Ellis, 2006; Manishin et al., 2019) and specifically target Chinook of age class 3 and larger maturing fish (Manishin et al., 2019). As such, predator avoidance behaviour is employed by Chinook salmon in the marine environment, but that is unnecessary in Lake Ontario where they have no predators and their depth distribution is more likely driven by foraging and thermoregulation such as those shown for other salmonid species (Azumaya and Ishida, 2005; Quinn, 2005). Regardless of the differences in depths observed in this study in comparison to studies in the Pacific, the results presented here clearly show size class vertical segregation in late fall and early winter. Taken together with the moderate horizontal distribution overlap for the fall and winter, these results indicate that the immature individuals in this study segregate both vertically and horizontally from sub-adults in these two seasons. Whether this is representative of the entire population in Lake Ontario is a question that would require further study and the purpose here is to report our observations and provide the added benefit of informing future studies.

Conclusions

Chinook salmon is an important top predator in the Lake Ontario ecosystem exerting stabilizing influence on the Alewife populations and is one of the most sought-after species by recreational fishers. Even though it is a ‘managed’ species and has been stocked for over 50 years, relatively little is known about its spatial and thermal ecology in the Great Lakes. In this study, the data suggest that immature individuals segregate vertically from sub-adults in a season-specific context. The general depth and temperature results of the sub-adults in this study are consistent with the limited observations available from the native range of the species reported in the literature. This study presents the first comparison of Chinook salmon seasonal distributions in Lake Ontario by size class. These results would be useful for updating predictions for the species based on bioenergetics models and understanding how fluctuations in the environmental conditions and warming water temperatures would impact their growth and prey consumption. Overall, quantifying Chinook salmon size class distributions contributes to understanding their seasonal ecology and provides a basis for assessing their interactions with other species.

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Table 3.1. Summary of tagging information and total length for Chinook salmon in Lake Ontario. Abbreviations: AT – acoustic telemetry, pDST – pop-off data storage tags, T – temperature, P – pressure.

	Number tagged	**Length at time of tagging (m, mean ± SD)**	**Number used for analysis**	**Type of data recorded**
AT	11	0.61 ± 0.18	8	Location
	26	0.50 ± 0.079	17	Location, P
	8	0.51 ± 031	4	Location, T, P
pDST	32	0.70 ± 0.15	11	T, P

Table 3.2. Percent kernel utilization distribution (KUD) overlap at 50% and 95% for Chinook salmon size classes (immature: ages 1 and 2; and subadult: ages 3 and 4) in Lake Ontario based on acoustic telemetry observations from June 2017 to April 2020. Values shown are in percent of the respective spatial utilization distribution that is overlapped by the other size class.

	Immature		**Sub-adult**	
	Overlap KUD50 (%)	**Overlap KUD95 (%)**	**Overlap KUD50 (%)**	**Overlap KUD95 (%)**
Fall	45.44	95.78	39.77	83.44
Spring	51.67	87.58	59.39	62.02
Summer	81.51	94.96	75.87	94.41
Winter	45.59	67.73	81.45	99.97

Table 3.3. Mean seasonal percent of observations removed from pop-off data storage tags data capped at 68 m to assess the caveats of the depth limitation recording capability of the acoustic telemetry tags.

	Mean (±SD; %)
Fall	12.8 (5.3)
Spring	1.9 (1.7)
Summer	0.7 (1.2)
Winter	33.9 (8.1)

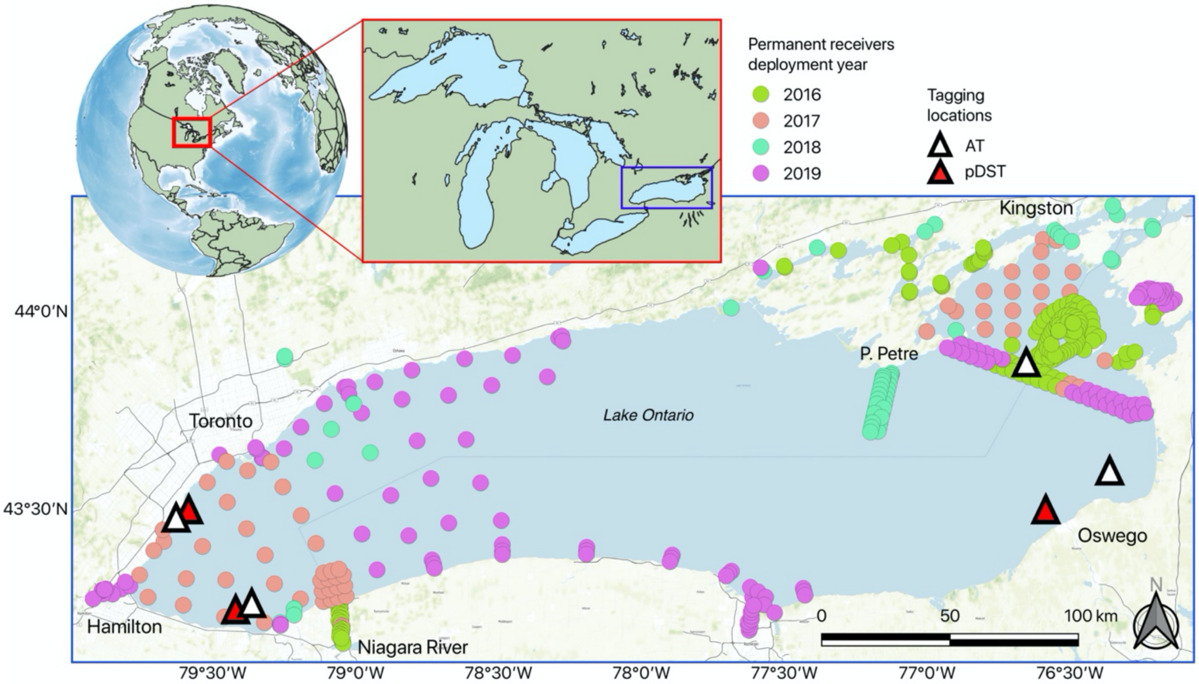

Figure 3.1. Map of Lake Ontario showing deployment of permanent receivers for the period 2016-2020 and Chinook salmon tagging locations with acoustic telemetry (AT) and pop-off data storage tags (pDST). Base map sources: Esri, DeLorme, GEBCO, NOAA NGDC, National Geographic, HERE, Geonames.org and the GIS User Community (ESRI, 2012), created using QGIS software; and Natural Earth – free vector and raster map data @ naturalearthdata.com.

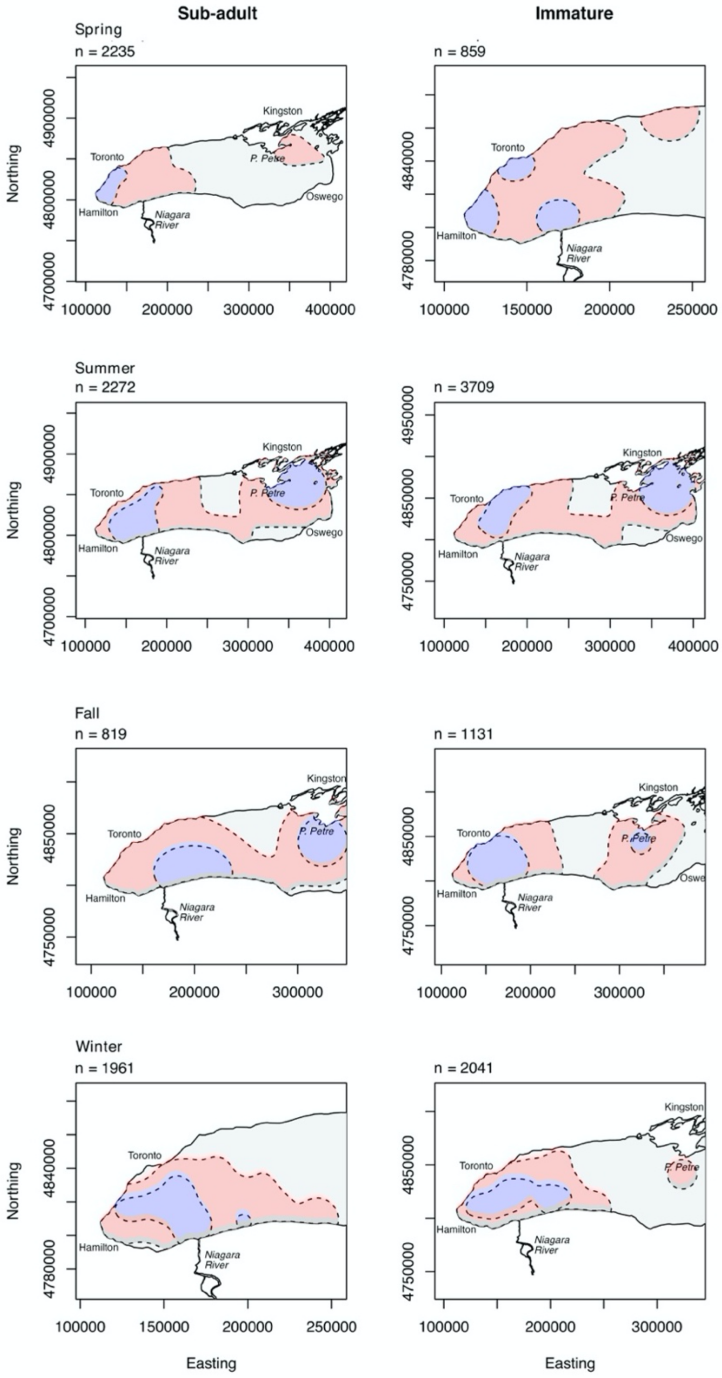

Figure 3.2. Chinook salmon kernel utilization distributions (50% in purple and 95% in pink; based on centers of activity) by size class (sub-adult – left panels; immature – right panels) and season in Lake Ontario. N = number of total centers of activity used in the seasonal analyses.

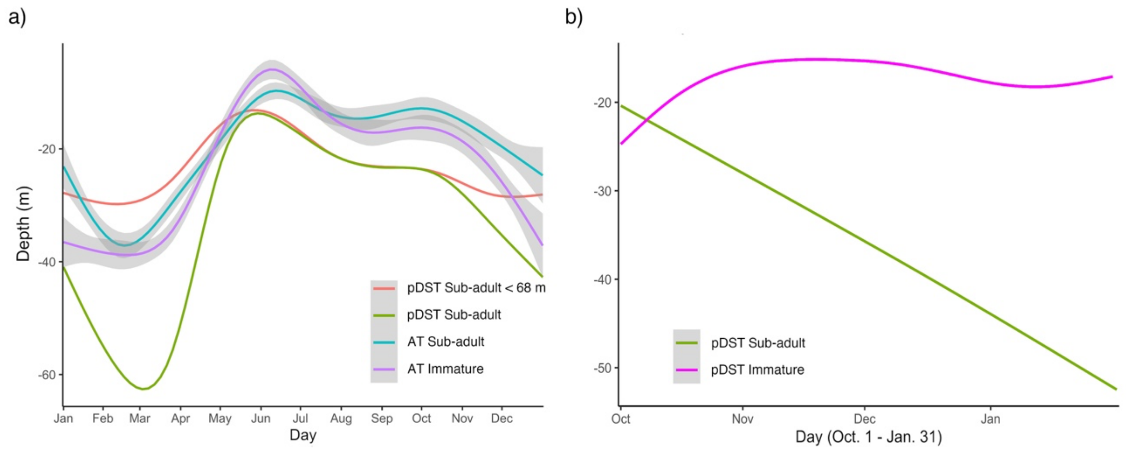

Figure 3.3. Generalized additive model depth results of Chinook salmon in Lake Ontario: a) acoustic telemetry (AT) and pop-off data storage tags (pDST) without and with 68 m restriction for sub-adults (immature fish shown for comparison) and b) immature and sub-adult pDST depth distributions from October through January. Grey ribbon represents the confidence interval around the mean.

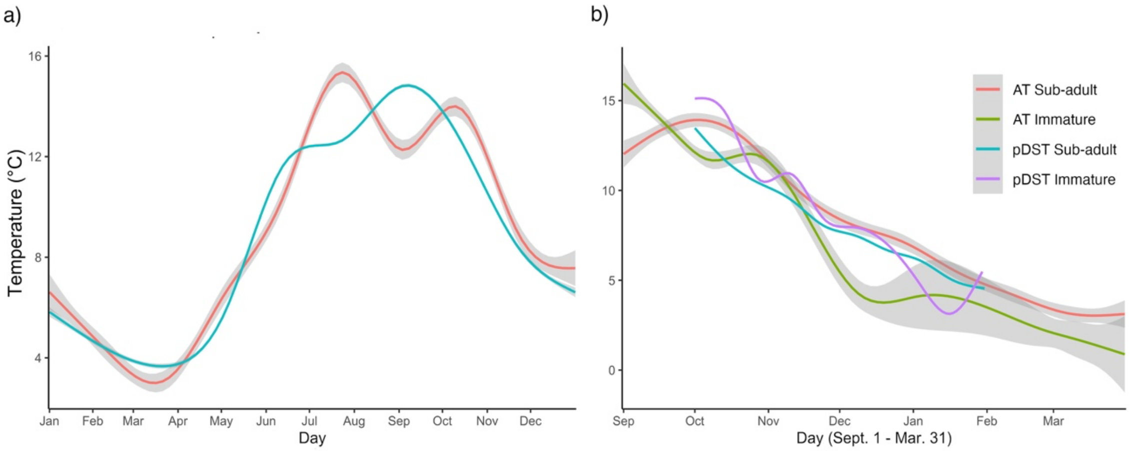

Figure 3.4. Generalized additive model temperature results comparison of immature to sub-adult Chinook salmon acoustic telemetry (AT) and pop-off data storage tags (pDST).

CHAPTER 4 – SPATIOTEMPORAL INTERACTIONS OF NATIVE AND INTRODUCED TOP PREDATORS IN A LARGE LAKE: IMPLICATIONS FOR SPECIES RESTORATION

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Summary

Animal interactions are an integral part of a community's function with influences ranging from the spatio-temporal habitat use of species to population effects to ecosystem management. Numerous non-native species are established or maintained through stocking in freshwater ecosystems with the potential to affect restoration of native species. Using acoustic telemetry, this study quantified the spatio-temporal co-occurrence of the native top-predator lake trout (*Salvelinus namaycush*) with non-native Chinook salmon (*Oncorhynchus tshawytscha*) in Lake Ontario over 2.5 years. Core home range overlap was observed during the summer with depth acting as a mechanism of segregation, but with potential for interactions during vertical exploration. Fine-scale individual pair-wise interactions confirmed the home range results. No horizontal overlap was observed during the winter and spring, but confidence was lower due to poor instrument coverage in deeper water which the two species may frequent in these seasons. These results demonstrate the importance of depth in understanding fish interactions and highlight the usefulness of considering pair-wise species interactions for understanding ecosystem community function to resource managers with multiple projects involving both native and non-native species.

Introduction

Ecosystem function is defined by the structure of its communities, with species interactions being a key component driving complexity (Lang and Benbow, 2013). As such, species interactions are an important aspect of the science of ecology, that can be relevant from individual to ecosystem scales, and knowledge of paired species interactions is necessary for understanding community function. Generally, species that co-evolved together co-exist successfully due to established niche partitioning (Hector, 2002; MacArthur, 1958). As a result of species range expansion and/or intentional or non-intentional introductions (Ewel et al., 1999), native species must now co-exist with non-native species with varying degrees of niche overlap, thereby creating new interactions that may be associated with explicit population-level outcomes. For example, the non-native Mediterranean mussel (*Mytillus galloprovincialis*) has been shown to induce declines in indigenous polychaetes and mussels (i.e., *Gunnarea capensis* and *Aulacomya ater*) and increases in the limpet *Scutellastra granularis* along the South African coast through recruitment facilitation based on habitat (Branch et al., 2010). Additional effects may be associated with realized niche shift in native only or in both native and non-native species, such as those observed for herbivores in Patagonia (Traba et al., 2017). Thus, non-native species in an ecosystem can present a challenge for native species, especially those undergoing rehabilitation and that are sensitive or vulnerable to new competitors in the system (Sharma et al., 2009).

When species interact in time and space they often modify each other's foraging or habitat use (Wootton, 1993) and may thus affect rehabilitation efforts (Stier et al., 2016). The end goal of restoration efforts is to bring the population of a species of interest to self-sustaining levels, but to accomplish this, understanding the basic ecology of the species is often insufficient. Knowledge of their pair-wise co-occurrence with other species and the spatio-temporal dynamics of any potential interactions are necessary to enable prediction of how foraging and habitat use may be altered and thus, detect and measure impacts on the populations and community. Rehabilitation efforts often employ more than a single strategy, for example habitat enhancement combined with control of predatory species and translocations of the species of interest, such as removal of introduced weka (*Gallirallus australis*) and translocation of skink (*Oligosoma spp*) and gecko (*Mokopirirakau spp*) populations in New Zealand (Hitchmough et al., 2016). At the same time other ecosystem enhancement and/or economic development efforts may be in place in regard to complementary non-native species, such as livestock which reduce rodent densities and thus predation on arboreal geckos (*Naultinus gemmeus*) in New Zealand (Knox et al., 2012), or competitive or predatory species, such as salmonids which predate on the razorback sucker (*Xyrauchen texanus*) in the Colorado River basin (Carpenter and Mueller, 2008). Given such concurrent interests exist, insights on the interactions between such species would be useful in guiding management of stocking and/or strategic decision-making.

Large lakes worldwide have and continue to endure a number of changes that affect their ecosystem function (Moiseenko et al., 2012; Taylor and Ferreri, 1999), and the North American Laurentian Great Lakes (hereafter Great Lakes) are no exception. The Great Lakes top predator community has experienced significant changes throughout the last century with species at all trophic levels declining and others invading or being introduced. For example, in Lake Ontario (the 13th largest lake globally, and fifth in area and third deepest of the Great Lakes) historically there were two native salmonids but now there are four additional non-native salmonids. Both native species, lake trout (*Salvelinus namaycush*) and Atlantic salmon (*Salmo salar*), employ iteroparous reproductive strategy, whereas two of the non-native species, Chinook (*Oncorhynchus tshawytscha*) and coho salmon (*Oncorhynchus kisutch*) are semelparous, thus introducing a novel life-history strategy to the top-predator community. While both native species are stocked annually by Canada and the USA as part of their rehabilitation, all of the non-native salmon are also stocked, and several (e.g. Chinook salmon) have now become naturalized (Connerton et al., 2009). Lake trout is high on the priority list for native species restoration, due to its importance for improving ecological function by coupling the offshore benthic and pelagic zones (Lantry et al., 2014), because it is used as an indicator species of ecosystem health due to its sensitivity to change (Ryder and Edwards, 1985), and because of its importance to the recreational fishers (Melstrom and Lupi, 2013). Similarly, Chinook salmon is highly valued by the recreational fishery (Melstrom and Lupi, 2013) and for exerting predatory control of invasive prey fish Alewife (*Alosa pseudoharengus*).

Large predatory species like lake trout and Chinook salmon tend to have large home ranges and thus monitoring interactions of two co-occurring species can be challenging. Further, large aquatic ecosystems pose significant challenges for sampling (physical size, weather, depth, etc.) which has been an impediment to studying interactions between species of the same trophic level *in situ*, and thus to furthering the understanding of fish community function. Species relationships existing in small lakes may not reflect the dynamics of large lakes, as the same species may not co-occur and/or the available habitat may not be equivalently heterogenous. Given this paucity in studies and in-depth understanding of the relationships that exist in large lake fish communities, it is difficult to monitor restoration efforts and predict environmental change influences on these efforts. In addition, the public clearly supports a diverse fishery including both Chinook salmon and lake trout, where Chinook dominate trophy-angling demand, yet native lake trout restoration is also important (Lantry et al., 2018). Considering this, and that Chinook salmon and lake trout have co-existed in Lake Ontario for ~ 50 years (Schneider et al., 1983) and restoration efforts have seen limited success (Lantry et al., 2018), better understanding of this pair-wise relationship would help inform management and decision-making regarding stocking strategies for each species. In addition, quantification of the interactions could provide clues to the nature and drivers behind those.

Lake trout is an offshore demersal/pelagic species known to opportunistically forage in the pelagic zone (Morbey et al., 2006) maintaining a depth below the thermocline during stratification (Olson et al., 1988b), while Chinook salmon is also an offshore pelagic predator, but forages near the thermocline (Raby et al., 2020). Adult lake trout move annually to shallower areas in the fall and spawn on shallow nearshore reefs, while Chinook (at ages 3 to 5) move near-shore late summer/ early fall in preparation to spawn and subsequently die in rivers. However, lake trout have shown limited dispersal distances (Binder et al., 2017; Elrod, 1987) while Chinook salmon move quite large distances (Adlerstein et al., 2008, 2007) in the Great Lakes. Thus, lake trout in Lake Ontario are believed to have western and eastern basin sub-populations, whereas this is not the case with Chinook salmon (Elrod, 1987; Raby et al., 2017). Lake trout are generalist, feeding on Alewife (ranging from 20 to 70% of the diet), sculpin (family *Cottidae*), round goby (*Neogobius melanostomus*) and Rainbow smelt (*Osmerus mordax*; Colborne et al., 2016; Mumby et al., 2018). In contrast, Chinook salmon diet consists of ~ 85% Alewife (Mumby et al., 2018; Olson et al., 1988b). It has been reported that individual Chinook salmon consume more prey per unit time than lake trout (Negus et al., 2008). In addition, lake trout are slow-growing with a lifespan of > 20 years, and a cold-water preference with optimal temperature between 7 and 10°C (Dillon et al., 2003; Raby et al., 2020), whereas Chinook salmon are fast-growing with a lifespan of 3-5 years and prefer cool water between 9 and 13°C (Hinke et al., 2005; Raby et al., 2020). Thus, there appears to be potential for competitive interactions based on habitat and diet overlap but also some distinction between the two salmonid species.

A recent study reported partitioning along the temperature-depth niches for the species during the summer season in Lake Ontario (Raby et al., 2020), yet, interactions across all seasons and in three-dimensions (latitude, longitude and depth) have not been examined. Considering the extremely low numbers of wild lake trout recruits (Lantry et al., 2018), understanding the extent of habitat overlap and potential interactions between these species would be an important step to informing lake trout restoration. Facilitated by the expanding usage of passive acoustic telemetry in the Great Lakes, I addressed this knowledge gap and examined the spatio-temporal interactions between lake trout and Chinook salmon in Lake Ontario. The objectives of this study were to: 1) quantify the overall and seasonal spatial use overlap for juvenile to adult Chinook salmon and eastern basin adult lake trout population; and 2) quantify co-occurrence on a finer scale (i.e. paired-individuals and 5-min interval time scale) through time, latitude, longitude and depth, and assess the potential for interactions. I predicted that: 1) general overlap in habitat would occur in the winter, spring and summer seasons, but not in the fall, when the fish are segregated by spawning preference and 2) species would segregate based on depth when co-occurring in time and space. Using acoustic telemetry, I tracked the species over a 2.5-year period in Lake Ontario.

Methods

Study site

Lake Ontario is one of the five Laurentian Great Lakes in North America and has a maximum depth of 245 m and surface area of 19,000 km^2. The lake's eastern basin covers 1,657 km^2 characterized by complex shoreline with shallower nearshore reefs and islands where maximum water depth is up to 40 m and is separated from the lake's deep main basin by the Duck-Galloo Ridge (Figure 4.1). The main basin is the area between Duck-Galloo Ridge and a Toronto-Niagara River line and encompasses the deepest parts of the lake. The western basin is the region west of the main basin.

Acoustic telemetry

To track the movements of the fish across the study period, I used a total of 278 permanent fixed-station acoustic telemetry receivers in Lake Ontario (a total of n=82 were located in the western basin and n=196 in eastern Lake Ontario; 69-kHz VR2W, Innovasea, Bedford, Nova Scotia, Canada; Figure 4.1). Receiver spacing varied between 2 to 15 km apart, with grid patterns used in the western and eastern basins, and a bathymetry driven design north of Duck-Galloo Ridge. For more details on the receiver moorings see Ivanova et al. (2021a) and/or Chapter 2. Maximum depth of receivers was

136 m in the western basin and 102 m in the east. A caveat in this study is the lack of receiver coverage in much of the main basin which represents over one third of the lake, thus it should be noted that the results presented here, and any interpretations are made with this in mind.

A total of 50 adult lake trout and 29 juvenile to adult Chinook salmon were tagged over the course of two years. Lake trout were tagged with V16 acoustic transmitters (hereafter tags; 68 mm length x 16 mm diameter; 10.3 g weight in water; nominal delay 180 s; estimated battery life 3650 d; Innovasea, Bedford, Nova Scotia, Canada) at two locations in the eastern basin; 30 on October 26, 2016 at Main Duck Island (43.92765º, -76.61805º, n = 9; Figure 4.1) and November 3, 2016 at Charity Shoal (44.04218º, -76.48386º; n = 21) and another 20 (implanted with pressure/temperature sensor tags; 71 mm length x 16 mm diameter; 11.7 g weight in water) on November 8, 2017 at Charity Shoal. Due to the challenges in acquiring large samples sizes of smaller Chinook salmon that were not going to spawn that year (to acquire year-round data), Chinook salmon were tagged in both eastern and western Lake Ontario as follows: in eastern Lake Ontario - eight individuals on August 17-18, 2017 (43.65350º, -76.28387º), and 10 individuals on July 2-5, 2018 (43.88546º, -76.53412º) both years using V13 pressure sensor tags (45 mm length x 13 mm diameter; 6 g weight in water; nominal delay 180 s; estimated battery life 703 d; Innovasea); and in the western basin six and 10 individuals on June 5, 2017 and July 12-13, 2018, respectively (at approximate coordinates 43.51335º, -79.49123º) using V13 tags without sensors. Minimum tagging sizes for lake trout and Chinook salmon were 60 and 38 cm, respectively. Lake trout were caught both years using multifilament gill nets set at 10-15 m for 20-24 h (30 m each of 64, 76 and 89 mm stretch monofilament mesh), and held for < 2 hrs during surgery in 600-L tanks in which aerated lake water was continuously delivered. A separate water tank (50 L) was filled with a mixture of lake water and anesthetic (4 g MS-222 and 8 g $NaHCO_3$ buffer per 10L of water) and used to prepare fish for surgery. Chinook salmon were caught using standard recreational angling techniques by boat trolling at 15-25 m. Size 2 barbed treble hooks were used for catch. Once unhooked, fish were transferred to a 50 L tank filled with lake water. Tank water temperature was continuously monitored with a thermometer and maintained at ~15° C to match lake water. Electro-sedation was chosen to anaesthetize Chinook salmon because it allowed for ~5 min recovery time based on our previous trials, compared to ~15-30 min using MS-222. Electro-sedation units consisted of conductive gloves and Ultima 3t Analog TENS Unit (PMT-U3T; Tensunits.com, Largo, FL, USA). Surgeries for both species were performed according to the following protocol. Fish were placed in a foam cradle and their gills continuously irrigated with lake water. Using aseptic procedures, an incision of 15 mm for Chinook salmon and 20 mm for lake trout was made ventrally, posterior of the pelvic fins and the acoustic transmitter implanted into the peritoneal cavity. Three Vicryl sutures (Ethicon VCP423, FS-2 cutting, size 3-0 for Chinook salmon and 2-0 for lake trout) were used to fasten the incision. To provide anglers with awareness that the fish is tagged, an external floy tag was attached in the dorsal musculature by the posterior margin of the dorsal fin. Surgery lasted < 3 minutes after which fish were placed in an aerated recovery holding tank until able to swim upright, and then released in the lake near to where they had been captured. Total length was measured and sex (if known) recorded. Mean total length for lake trout was 77.1 cm ± 5.8 (mean ± 1 SD) and for Chinook salmon 51 cm ± 13.2. It should be noted that western basin lake trout were not tagged in this study due to interest in the eastern basin sub-population. However, Chinook salmon is believed to be a single population in Lake Ontario traversing the lake often (Raby et al., 2017), thus tagging location (i.e. in the eastern and western basins) was considered to present no bias on the results.

Data analysis

All statistical analysis was completed using R statistical software version 3.6.1 (R Development Core Team, 2019) and graphing was done in R or ArcMap™ version 10.3.1 (ESRI, 2011) using base maps by Stamen Design (Stamen Design, 2020), Esri (ESRI, 2012), and NOAA Lake Ontario bathymetry (NOAA National Geophysical Data Center, 1999).

Collisions of the transmissions from two or more tags may result in a detection of a different tag ID code by an acoustic receiver, and these detections are deemed false-positive detections (Pincock, 2012). If these false detections are not removed from the data, they may lead to biased or erroneous results and interpretations (Simpfendorfer et al., 2015). False filtering is a type of quality control of the data to remove false-positive detections. White-Mihoff Filtering Tool (White et al., 2014) was used for false-positive detection filtering with a range of 1,500 m for lake trout and 1,000 m for Chinook salmon based on 70% detection efficiency of their respective tags (Klinard et al., 2019). Eight lake trout and 12 Chinook salmon were removed from analysis due to mortality, tag expulsion or lack of sufficient data (too few locations) to provide meaningful contributions for the purposes of this study. A total of 42 lake trout (2,846,749 detections) and 17 Chinook salmon (30,319 detections) were used for further analysis.

To approximate fish locations I used centers of activity (CoA) (Simpfendorfer et al., 2002). In particular, each detection was given a randomized position near the receiver on which it was detected based on probability from curves generated by range tests up until a 70% detection range (Klinard et al., 2019). From these, all positions, and if available, associated depth, occurring over a 30-minute period were pooled for each individual and averaged to calculate CoA, yielding 308,561 CoAs for both species, of which 97,115 had associated depth values (Table 4.1).

Seasonal home ranges and overlaps in two-dimensions (latitude and longitude; kernel utilization distribution, i.e. KUD) were calculated using the adehabitatHR package in R (Calenge, 2006) at the core level (50% KUD). The *gIntersection* function was used to calculate the overlap area for each species as a population and at the individual levels (including both sensor and non-sensor tags), and Hurlbert index (zero denotes no overlap and one complete overlap) was calculated to quantify the proportion of individual overlap between species (Hurlbert, 1978). To distinguish the lake's thermal seasons, I used the following timeframes established by Ivanova et al. (2021a) that represent different periods of thermal stratification of the lake: spring - May and June; summer – July to October; fall – November and December; winter – January to April. A generalized linear mixed model (glmmADMB R package version 0.8.3.3 (Fournier et al., 2012)) with negative binomial distribution was used to test for fish length per species, home range size, season and ID (as a random variable) influences on the Hurlbert index overlap results (n=1822).

To calculate and determine three-dimensional (3D; latitude, longitude and depth) kernel density estimates (KDE) for each species for the entire period, I used the *kde* function in the *ks* package (Chacón and Duong, 2018). I included both 50% (core) and 95% estimates, where 50% was used to indicate habitat of critical importance and 95% used to represent areas of non-critical importance and exploratory movements (vertical and/or horizontal) outside the core (Powell, 2000). Only fish tagged with sensor tags (lake trout n = 17; Chinook salmon n = 10) were used in this analysis. Overlap between the two species populations was calculated via Utilization Distribution Overlap Index (UDOI) 3D, a generalization of the Hurlbert Index of overlap based on Fieberg and Kochanny (2005). Individual depth values were pooled together and monthly means for each year calculated for the species. Overall mean of the depths for the species were tested for differences using Pearson's t-test, and a two-way ANOVA was used for between seasons with ID as random effect.

Joint potential path area (jPPA) represents a measure of where interaction between two individuals is possible by modelling co-occurrences as a potential spatial interaction (Long et al., 2015). The method involves the building of a time-geographic movement model and applying it to simulated biased correlated random walks of individuals. This method was used to estimate at a finer scale the spatio-temporal (latitude, longitude, time) likelihood of encounter and overlap of the movement trajectory between lake trout and Chinook salmon. All fish were used for this analysis (sensor and non-sensor tags). For this purpose, trajectories of each individual were calculated from the CoAs using the adehabitatLT (Calenge, 2006) package in R. For the jPPA calculation, a 5-min sampling interval was used for space-time prism projections constructed based on a starting and ending position generated from the trajectories for each individual. The areas of prism intersections of two individuals are termed the joint potential path areas, and thus areas of potential interaction. Each lake trout individual was compared to each Chinook salmon. Date, time, depth (if available) and coordinates were recorded, and areas mapped in R. Mean of the depths associated with jPPAs for the species were tested using Kruskal-Wallis rank sum test to establish if differences existed. Mean frequency of jPPA interactions based on time of day (where days were defined to be between the hours of 06:00 and 20:00 during which daylight is present in the summer months) was tested using a Kruskal-Wallis rank sum test.

Results

At the core (50%) home range level, seasonal latitude-longitude lake trout distribution was only in the eastern part of the lake, whereas Chinook salmon had distributions in the eastern and western basins of Lake Ontario (Figure 4.2). Core home range overlap between the species occurred only during the summer/stratified period and was 100% of lake trout's core home range area (Figure 4.2; see Appendix 1 Table S4.1 for results from the individual level). Volume of overlap between lake trout and Chinook salmon based on the 3D KDE at 95% was 1,025 km^3, with UDOI overlap for lake trout and Chinook salmon at 6.1 and 0.7%, respectively (Figure 4.3). Volume of overlap at 50% 3D KDE was 0 km^3. Depth for the entire period was statistically different between the species ($p<0.001$, Pearson's t-test) with mean (±1 standard error; SE) for lake trout 31.2 ± 0.05 m and Chinook salmon 28.6 ± 0.4 m and a seasonal flip in depth use ($p<0.001$, two-way ANOVA) observed between the two species. Chinook salmon appeared to occupy shallower depths in the summer and were found deeper in the winter, while lake trout were shallower in the winter and deeper in the summer (Figure 4.3B; Appendix 1 Table S4.2). Fish length, season and home range size did not significantly influence home range overlap between the species ($p > 0.15$ for all) based on the GLMM model results.

There were 88 unique individual interaction combinations between the two species, with a total of 1,565 jPPA interactions and mean number of interactions for lake trout of 40.1 ± 56.1 and Chinook salmon of 260.8 ± 368.1. Overall, 39 lake trout and 6 Chinook salmon were interacting with a mean number of individuals interacting monthly for lake trout 12.0 ± 7.9 and 1.5 ± 0.5 for Chinook salmon. Mean jPPA size was 12.0 km^2 ± 32.5. Interactions identified by jPPA did not always fall into the general core home range (Figure 4.4). Interactions occurred in 2017 between June and October, and in 2018 in May and July through October (Figure 4.5a). Interactions were not significantly different between daylight hours and night ($p = 0.1$; Kruskal-Wallis rank sum test; Figure 4.5b and c). Comparisons between depths occupied during the identified jPPAs indicated that lake trout were significantly deeper than Chinook salmon ($p = 0.004$, Kruskall-Wallis paired rank sum test; Figure 4.6).

Discussion

Understanding interactions between species within the same trophic level is important for unravelling the complexities of community function and informing ecosystem-based management that includes species restoration. Species interact in multiple dimensions and interactions are often observed at a variety of scales. Here, I quantified coarse scale spatio-temporal overlap (population) and finer scale (paired individuals) interactions over time, latitude, longitude and depth of the native top predator lake trout, currently undergoing rehabilitation, and the non-native perceived competitor Chinook salmon. Results showed that the species core home ranges overlapped during the summer season, but not the rest of the year, consistent with predictions for the summer and fall seasons but not for winter and spring. Depth use showed segregation of the species with a seasonal flip in depth preference. Fine-scale individual interactions showed that when individuals co-occurred in the same horizontal space in time, they were segregated vertically based on mean depth usage, in agreement with our prediction.

Spatio-temporal species interactions often vary seasonally along vertical and horizontal planes based on the habitat preferences and activity level of each species (McMeans et al., 2020). Our results revealed no three-dimensional overall overlap of core home ranges (50%) with depth segregating the species vertically, but some overlap occurring at 95%. Seasonally, two-dimensional overlap occurred only during the summer season between the two species, when lake trout largely occupy regions with deeper waters and where Chinook are mainly present. This was expected considering the cold-water preference of lake trout and the summer results of previous studies showing lake trout home ranges in the deeper main basin of Lake Ontario (Ivanova et al., 2021a). Based on previously reported temperature-depth niche partitioning between lake trout and Chinook salmon (Raby et al., 2020), it seems highly likely that the species are generally segregated in space and time while interacting only during exploratory vertical movements (i.e. 95% KDE).

There is however evidence that some lake trout individuals may have more overlap with Chinook salmon. Previous research has demonstrated the existence of contingents within this lake trout population associated with divergent migratory patterns in December/January and others during the spring or summer, suggesting that these individuals are also associated with different habitats during the winter and spring (Ivanova et al., 2021b). That study also reported four different individuals being detected at receivers in the western and north-western parts of the lake during the winter period, suggesting extensive use of the main basin by individuals associated with December/January post-spawning migration. Considering the lack of receiver coverage in the main basin of Lake Ontario, our lake trout results for the winter season are biased to areas with receivers, and that interactions and habitat overlap during this period are probable. Based on limited published data for the winter period, lake trout and Chinook seem to occupy similar depths (Raby et al., 2020), which is in contrast with our results for this period, suggesting that more information based on better receiver coverage of the lake is required to confirm whether this is the case. Thus, although our results showed home range overlap between the two species in the summer the lack of receiver coverage in the main basin of Lake Ontario and the existence of variable lake trout behaviour, suggest our results for the winter, and potentially spring season, are inconclusive.

The lack of interactions for fall was not surprising given the two species have different spawning behaviour with lake trout moving to shallower nearshore reefs (Ivanova et al. 2021b) while Chinook either remain offshore and do not spawn (semelparity) or spawn in tributaries. However, the lack of interactions for the winter and spring were not expected, and, as mentioned above, is likely a function of instrument positioning and the co-existence of lake trout contingents in the population. Lower number of unique lake trout detections in the winter and the observation of few detections of contingents that migrate to the main basin in early winter, suggest there is potential for interactions occurring between the two species during this period as well. The vast majority (>96%) of the Chinook salmon detections for the winter months (i.e., Jan-Apr) were recorded in the western basin with the rest recorded at the Pt. Petre array in the main basin (which was only deployed as of 2018), yet there were extensive periods during which individuals were not detected. Raby et al. (2020) reported a number of individuals registering depths >140 m and considering the maximum receiver depth in this study was 136 m suggests that the species likely occupy the deeper main basin of the lake where there is currently no receiver coverage. Also, Chinook salmon had a general preference for deeper water during this period consistent with Raby et al. (2020). This implies that Chinook salmon most likely co-occur and interact with lake trout contingents that use the main basin, something not captured here. Given our results for the summer period and that lake trout are mostly located in the main basin, some speculation can be made that potential interactions and overlap may also be happening in the winter. Thus, while additional studies are required to better assess the winter and spring interactions between lake trout and Chinook salmon, valuable fine-scale insights were gained into their summer interactions.

On a finer-scale, analysis of individual behaviours may be used to confirm the broader observations, but also often reveal details about the interactions not obvious from the larger scale perspective. From the jPPA analysis, possible interactions for the two species on the horizontal and vertical planes were evident when time was scaled down to minutes rather than seasons. These results suggest that when individuals of the two species are in proximity along the horizontal plane, depth acted as a partitioning factor. Most of these interactions were observed during the summer and paired depth during jPPA overlap was significantly different between individuals, thus largely confirming the lack of overlap in the overall 3D core home range results. These results are consistent with Olson et al. (1988b), who reported vertical segregation between lake trout and Chinook salmon in south-central Lake Ontario during the summer. In addition, such vertical segregation has been reported for a number of sympatric species globally (Lima et al., 2008; Ross, 1986).

The lack of tagged lake trout from the western basin in this study may have resulted in an underestimation of overlap between all lake trout and Chinook salmon in Lake Ontario. This would likely be true on the horizontal plane but based on the greater depth (see Figure 4.1) and homogeneity of bathymetric features in the western basin in comparison to the eastern, I speculate a similar vertical segregation of the fish species across the whole lake. Given Chinook salmon home ranges extended into the Kingston basin, the shallowness of this area (<40 m) would create more opportunities for vertical interactions between Chinook and the eastern lake trout population as the two species would be more confined on that plane, something that does not hold true for the western basin. Thus, I believe that including lake trout from the western basin in this study would not result in an increase in vertical overlap observed between Chinook salmon and lake trout in Lake Ontario, and the findings of this work reflect the interactions of these two species. Given this, and that there are two lake trout sub-populations (Elrod, 1987) while Chinook individuals utilize the entire lake (Haynes and Keleher, 1986; Raby et al., 2017), I believe that our findings provide a valid and valuable insight into the interactions of these two species in Lake Ontario.

More often than not resource managers juggle multiple projects involving a variety of species addressing different interests, from recreational angling to fish community function and ecosystem health, and oftentimes those projects influence the success of one another. In Lake Ontario, lake trout rehabilitation aims to recover historic ecological and economic function, whereas Chinook salmon stocking primarily supports the multi-million dollar recreational fishery while also aiding in regulating Alewife populations (Melstrom and Lupi, 2013). Competition for limited food and space is the major driver of interactions between native and non-native species of the same trophic level (Crowl et al., 1992). Thus, if a shared resource in Lake Ontario, Alewife, is limiting then managers must reconcile management decisions (Gaden et al., 2020; Negus, 1995). Many studies have been published reporting generally negative outcomes for the native species from reduction in abundance to displacement to extirpation (Arismendi et al., 2009; Bradley et al., 2019; Crowl et al., 1992). In this case, Chinook salmon consume more prey per unit time than lake trout (Negus et al. 2005) and lake trout are considered sensitive to competitors because they switch to other prey in the presence of competition (Vander Zanden et al., 1999). Thus, at first glance, lake trout rehabilitation may be challenged in the face of low Alewife abundance and competition with Chinook, but consumption of Alewife by lake trout induces thiamine deficiency which impairs lake trout recruitment success. Therefore, lake trout, a generalist in their diet, shifting to alternative prey (e.g. round goby and sculpins) may indirectly aid its rehabilitation through ecological facilitation (Lantry et al., 2014). This is plausible considering facilitation between non-native and native species has been reported for a number of taxa (Branch et al., 2010; Rodriguez, 2006). Furthermore, any value Chinook salmon may indirectly have in the restoration efforts of lake trout would also be influenced by the inter-individual behaviour variation in either species with contingents in the population of lake trout likely to be affected differently.

Ultimate success of lake trout rehabilitation depends on many factors, including adequate prey resources, water quality and control of parasitic lamprey. Our results suggest that while lake trout and Chinook salmon occupy similar core horizontal habitat in the summer season in Lake Ontario, vertical segregation minimizes spatio-temporal overlap except during exploratory vertical movements. Whether this vertical separation is driven by competitive avoidance versus physiological preference, the end result favours coexistence. Ultimately density-dependence and relative resource availability will dictate the magnitude of interactions, and thus managers should seek to balance the composition and numbers of fish stocked with knowledge of Alewife production. Thus, our results highlight the importance of considering pair-wise species interactions for understanding ecosystem community function and in systems where multiple, seemingly conflicting projects, are employed for management.

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Table 4.1. Summary of acoustic tagged lake trout and Chinook salmon in Lake Ontario including sample size (N), mean (±1 SD) total length (TL), number of centres of activity (CoAs), and CoAs based on depth sensor tags included in statistical analyses in this study for Lake Ontario.

Species	TL (cm)	N	CoAs	N (w/sensor)	Sensor CoAs
Lake trout (*S. namaycush*)	77.1 ± 5.79	42	7,222 ± 3,178	18	5,238 ± 1,684
Chinook salmon (*O. tshawytscha*)	51.0 ± 13.17	17	308.2 ± 242.8	10	282.5 ± 189.4

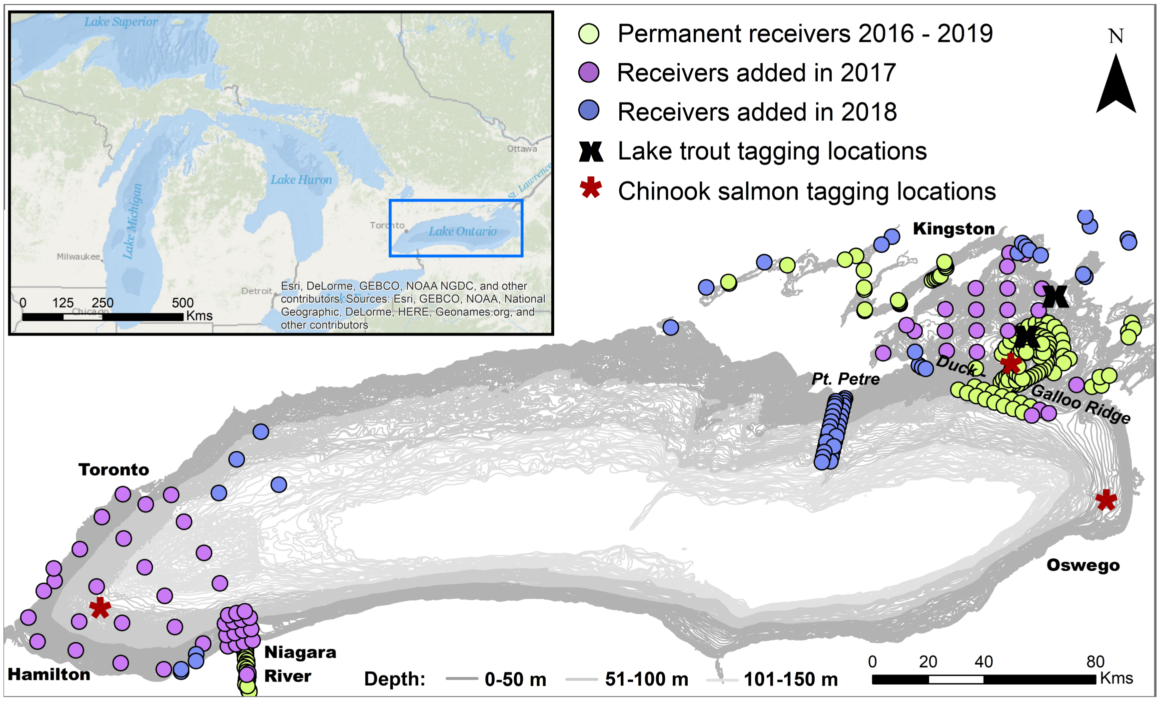

Figure 4.1. Map of study area with permanent acoustic receivers by year of deployment and fish release locations. Note: receivers are present in ~ 1/3 of the entire Lake Ontario and distributions are mainly at the western and eastern basins, leaving nearly the entire main basin without coverage and therefore detection data for our species. Inset base map sources: Esri, DeLorme, GEBCO, NOAA NGDC, National Geographic, HERE, Geonames.org and the GIS User Community (ESRI, 2012), created using ArcMap software by Esri. Depth contours are publicly available from GLAHF at https://www.glahf.org/data/ (Wang et al., 2015).

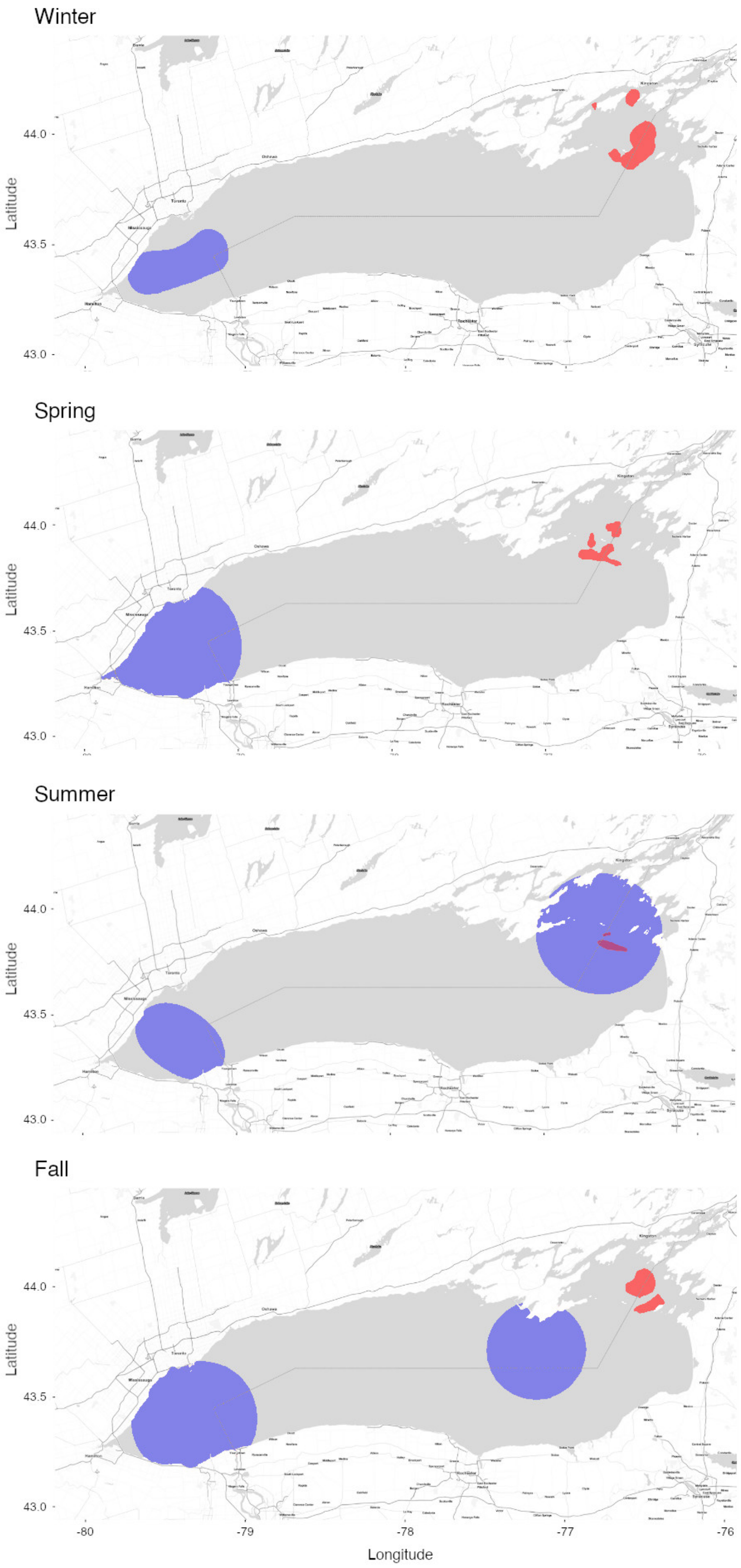
Winter
Spring
Summer
Fall
Latitude
44.0
43.5
43.0
-80
-79
-78
-77
-76
Longitude

Figure 4.2. Eastern Lake Ontario lake trout (peach) and Chinook salmon (blue) 50% kernel utilization distributions and potential overlap (purple) in two-dimensions for winter, spring, summer/stratified and fall lake thermal seasons. Note: all IDs (with and without a depth sensor tag) were included in this analysis. Base map tiles by Stamen Design used under CC BY 3.0 with data by OpenStreetMap under ODbL, see http://maps.stamen.com/#watercolor/12/37.7706/-122.3782 and https://www.openstreetmap.org/copyright.

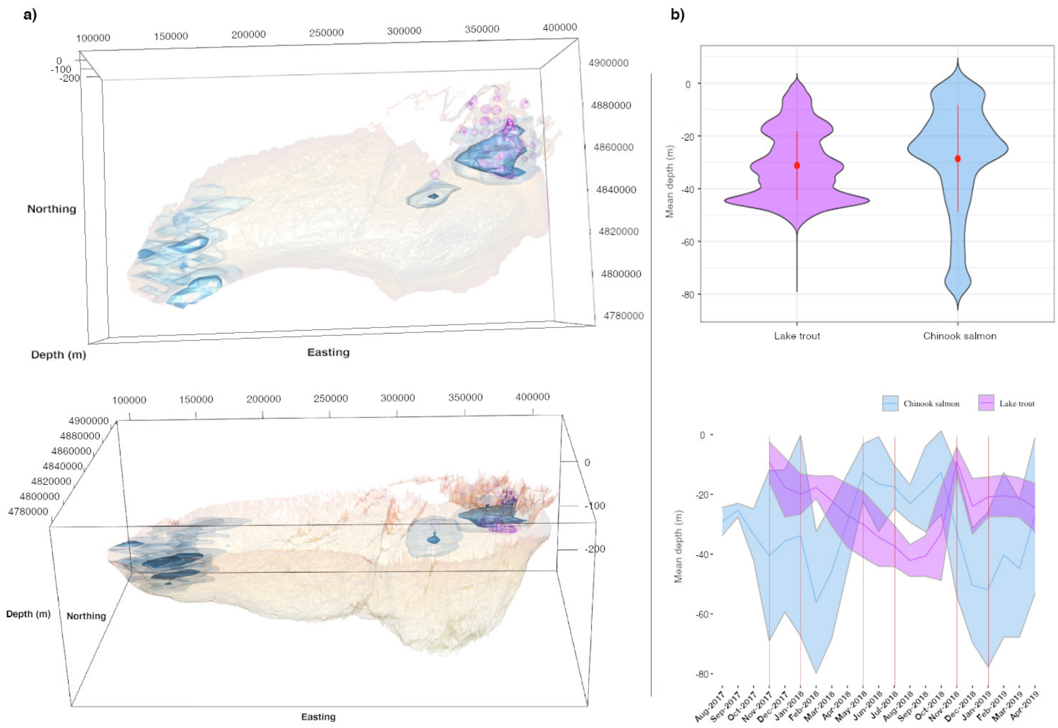

Figure 4.3. Three-dimensional home ranges and overall and monthly depths for lake trout (purple) and Chinook salmon (blue) in eastern Lake Ontario for the period of Dec. 1, 2016 to Apr. 30, 2019. **a)** General 3D (latitude, longitude and depth) kernel density estimates (KDE) at 95% and 50% (darker colour) for the two species overlaid on the bathymetry of Lake Ontario (see Appendix 1 Figure S4.1 for a zoomed in view). Base map source: NOAA Lake Ontario bathymetry (NOAA National Geophysical Data Center, 1999). **b)** (top) overall mean (± 1 SD) depth violin plots for the entire study period for were 31.2 m (± 13.1) and 28.6 m (± 20.32) for lake trout and Chinook salmon, respectively (see also Appendix 1 Table S4.2; red dot and lines represent mean and interquartile range, respectively); (bottom) mean depth and standard deviation binned monthly for the two species (red lines represent thermal season switches in the lake: spring - May and June; summer – July to October; fall – November and December;

winter – January to April). (Note: only individuals with a depth sensor tag were included in this analysis.)

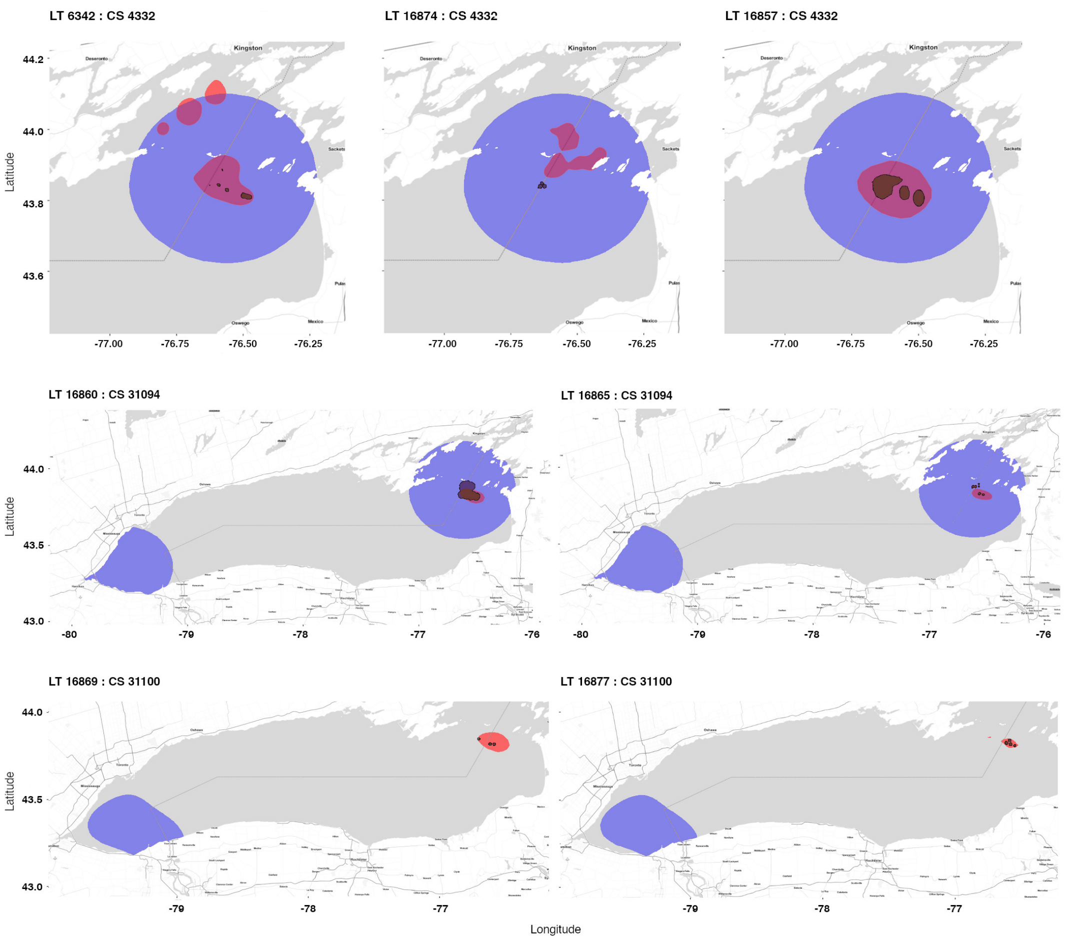

Figure 4.4. Examples of joint potential path area (jPPA; black outline with grey fill) for lake trout (LT) and Chinook salmon (CS) in Lake Ontario and 50% kernel utilization distribution (peach represents lake trout, blue Chinook salmon, and purple overlap between the species). Each panel shows a different pair of individuals with numbers at the top identifying the ID for each species. Note: jPPA identified interactions do not always fall into the general core home range; all fish (with and without a depth sensor tag) were included in this analysis. Base map tiles by Stamen Design used under CC BY 3.0 with data by OpenStreetMap under ODbL, see http://maps.stamen.com/#watercolor/12/37.7706/-122.3782 and https://www.openstreetmap.org/copyright.

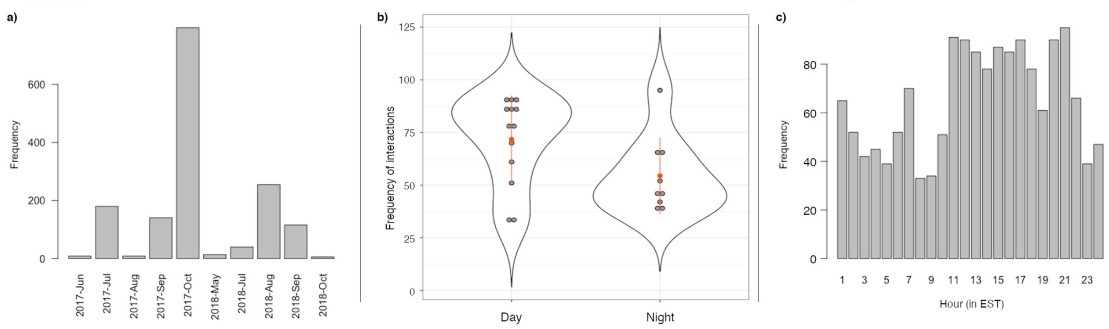

Figure 4.5. Joint potential path area (jPPA) for lake trout and Chinook salmon in eastern Lake Ontario based on a) month and year, b) time of day (days were defined as between the hours of 06:00 and 20:00 during which daylight is present; red circles in violin plots represent the means and whiskers the standard deviation, SD), and c) hour. There were 88 unique individual interaction combinations, a total of 1,565 jPPA interactions with total mean number of interactions for lake trout 40.1 (± 56.1) and for Chinook 260.8 (± 368.1). Total numbers of individuals interacting were 39 for trout and six for Chinook with mean number of fish interacting per month for trout 12 (± 7.94) and 1.5 (± 0.53) for Chinook.

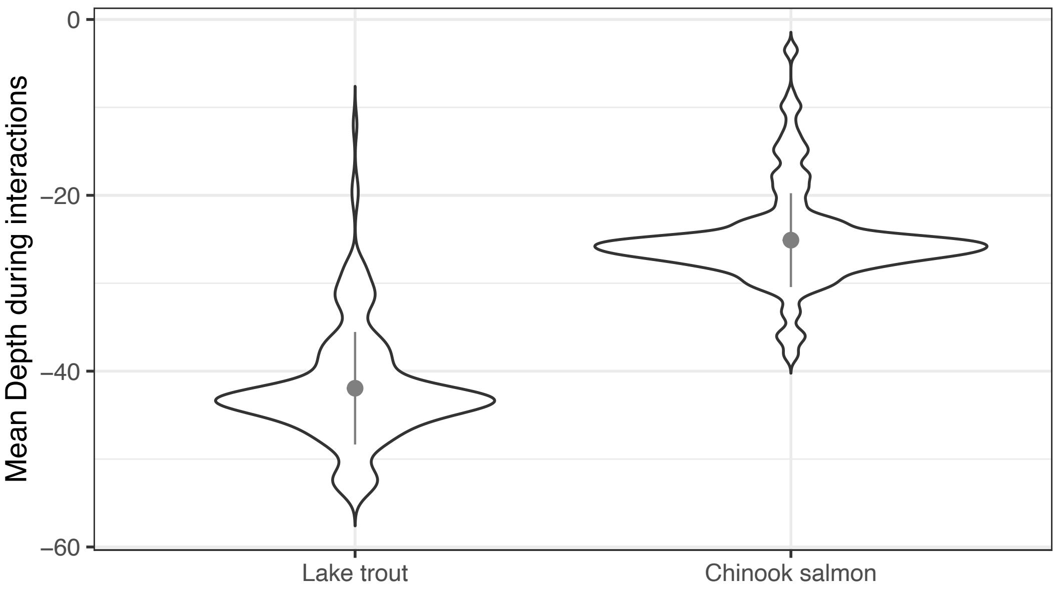

Figure 4.6. Mean depth violin plots for periods of identified joint potential path areas (jPPA) for lake trout and Chinook salmon in Lake Ontario. Gray circles represent the means, whiskers the SD and violin the distribution. Mean depth during the identified interactions were statistically different between the two species (p = 0.004, Kruskall-Wallis paired rank sum test). Note: only fish with a depth sensor tags were included in this analysis.

CHAPTER 5 – BIOENERGETICS AND PREDICTED GROWTH OF TWO TOP PREDATORS IN A WARMING FRESHWATER ECOSYSTEM

Summary

Warming water temperatures present challenges for ectotherm species in freshwater ecosystems through influence on their metabolic rate, i.e., bioenergetics. Diet, such as the inclusion of high energy density prey, can modify these influences. Existing bioenergetics models for ectotherms, such as those for growth, have relied on assumed thermal optimum temperatures and the known diet of the study species for modelling. Here, I modelled lake trout (*Salvelinus namaycush*) and Chinook salmon (*Oncorhynchus tshawytscha*) growth in Lake Ontario with *in-situ* observed year-round temperatures occupied by the species and examined the effects of diet switch on their growth for three time periods past (1983-1999), present (2010-2019) and future (2060; including low [+0.4°C] and high [+1.0°C] temperature increase scenarios). Temperature was obtained through acoustic telemetry and pop-off data storage tags deployed between 2016 and 2019. Effects of diet were examined with the inclusion of higher energy density re-introduced prey species bloater (*Coregonus hoyi*). Lake Ontario-specific energy density to weight equations were calculated and the species adult maximum weight potential, feeding rate and net weight change were modelled using the Wisconsin bioenergetics model. Results showed that the use of thermal optimum temperature introduced bias in the models and under- or over-estimated maximum adult weight potential and estimates of consumption. Under forecasted warming conditions, lake trout performed well, and fastest growth was observed with bloater re-incorporation in the diet (up to 40%). Chinook salmon performed poorly under all forecasted warming scenarios, but this effect was mitigated when bloater comprised ~33% of their diet. This study highlights the importance of using observational *in situ* data in system-specific bioenergetics models

and suggests that the negative effects of changing climate conditions on top predators can be better mitigated through improved growth predictions and strategic management of prey.

Introduction

As poikilotherms, fish are adapted to environmental temperatures that optimize growth and survival. Vulnerability to climate driven increases in water temperatures will depend on a fish species' thermal preferenda with implications for growth potential (Alfonso et al., 2021; Pörtner and Peck, 2010). A general premise of bioenergetics (a quantitative outline of energy budgets and influences of the environment; Madenjian, 2015) is that animals will occupy temperatures closest to their perceived physiological optimum (Hanson et al., 1997; Stewart et al., 1983a). Thus, with increasing water temperatures, a decline in the availability of optimal habitat would be expected for cold- and cool-water species with a reduction in the hypolimnetic volume due to deepening of the thermocline and prolonged stratification (Anderson et al., 2021; Brandt et al., 2002). If diet remained the same, the expected result would be an increased metabolic rate, reduced food conversion efficiency and slower growth (Brett and Groves, 1979; Jobling, 1994; Magnuson et al., 1979). Conversely, enhanced growth would be expected for warm-water species with increasing availability of optimal temperatures (Casselman 2002).

In addition to temperature, prey quality and density are also key to fish growth (Brandt et al., 2002) and prey availability and distribution may affect the final temperature preferenda of the predator (Quinn, 2005). For example, Coho salmon (*Oncorhynchus kisutch*) chose cooler temperatures than their optimum with decreasing prey availability (Brett et al., 1969). Similar to the effects on their predators, increasing water temperatures are expected to induce a shift in the prey habitat use, and based on their physiological optima this may similarly be reduced or expanded (Brandt et al., 2002). A reduction in habitat may result in greater prey aggregation, causing an increase in encounter rates for predators and thus in consumption rates. Whereas an increase in the available habitat for prey, may have the opposite effect and simulations have shown that this is the more likely scenario for the Great Lakes. For example, Brandt et al. (2002) predicted an overall increase in growth rate potential for Chinook salmon (*Oncorhynchus tshawytscha*), a cool-water species, with increasing temperatures in the Great Lakes when the species could feed to satiation; however, growth rate potential was reduced by 9% when prey density declined by 15% from the satiation levels. The effect of prey density is modified by the diversity of an animal's diet with generalists experiencing less effect than specialists due to their ability to switch from one prey to another (Clavel et al., 2011). Thus, ultimately, the magnitude of the effect on a predator's growth would be determined not only by the occupied temperature but also by the prey quality, diet diversity and consumption rates of the predator (Jobling, 1994).

Lake surface water temperatures are increasing at a faster rate than atmospheric temperatures resulting in an alteration of the length of the thermal seasons and temperatures at depth (Anderson et al., 2021; Austin and Colman, 2007; O'Reilly et al., 2015). While smaller shallower lakes are expected to have a reduced number of mixing events or become permanently stratified, changes in deep large lakes would be less severe due to their greater volume (Woolway and Merchant, 2019). Expected alterations include a decrease of periods with ice cover, compression of the cooling period (Jensen et al., 2007; Wang et al., 2012) due to earlier and later onset of spring and fall overturn, respectively, hypolimnetic volume decrease due to deepening of the thermocline, and a longer stratified period (Anderson et al., 2021; Austin and Colman, 2008; Brandt et al., 2002; Trumpickas et al., 2009). Presence of ice cover influences temperatures in subsequent seasons (Austin and Colman, 2007) and mean annual surface temperatures have already increased in the Laurentian Great Lakes (hereafter Great Lakes) (Anderson et al., 2021; Austin and Colman, 2008; Hook et al., 2012; Schneider and Hook, 2010) with the same trend also observed for the hypolimnion. Burns et al. (2005) reported a 0.04°C annual increase in hypolimnion temperatures between 1983-2002 in the central Lake Erie basin (depth 21-24 m). Similarly, Anderson et al. (2021) showed that the cooling period for Lake Michigan has fallen below 100 days since the late 1990s and the stratification period increased to >200 days resulting in an average warming of the hypolimnion (depth between 60-100 m) of 0.08-0.12°C per decade between 1990 and 2020. These increases were highly influenced by four colder winters during which minimum temperatures at depth fell below 2°C, thus the authors reported that the increasing temperature trend accelerated with repeated warmer winter conditions, i.e., short cooling period, and later fall turnover date, but it was slowed when natural weather variability was greater (Anderson et al., 2021). Given the observed increases in temperatures at depth, and that the entire water column temperatures are projected to increase up to 2°C by the second half of the 21st century (Lofgren, 2014), suggests that fish at all depths would be affected.

Shuter and Lester (2004) and Casselman (2005, 2002) predicted that the survival of cold-water species, such as lake trout (*Salvelinus namaycush*) and Chinook salmon, would be challenged under climate induced increases in water temperature, especially in Lake Ontario. Lake trout is a bentho-pelagic fish often found at temperatures between 4°C and 10°C (Stewart et al., 1983a), and with the hypolimnetic volume expected to decrease (Casselman 2002), the amount of preferred lake trout habitat is also likely to contract (Shuter and Lester, 2004). This suggests reduced foraging opportunities and/or an increase of the forays into warmer waters, and considering that lake trout metabolic rates and assimilated energy are sensitive to temperature increases (Morbey et al., 2006), the result would likely be higher metabolic cost and physiological stress and reduced growth rate potential. Contrary to this, simulations for Lake Michigan showed an overall increase in growth rate potential for this species attributed to a prolonged growing season (Brandt et al., 2002). Brandt et al. (2002) also modelled Chinook salmon growth in Lake Michigan based on the availability of habitat and showed an increase in growth rate potential. However, the reported temperature optimum for Chinook salmon is 14.3°C (Brett, 1952; Hasnain et al., 2010; Stewart et al., 1983a) and the species is known to stay near the thermocline (Raby et al., 2020). Thus, to maintain the above optimum, their distribution is expected to shift to deeper habitat further offshore where their foraging as a visual predator may be limited by light availability thus, also reducing feeding rate (Brandt et al., 2002). Based on this premise, Chinook salmon's growth rate potential is predicted to decline, or to maintain growth rate, the proportion of the maximum consumption rate would have to increase (Brandt et al., 2002). Any such increase would likely involve foraging in temperatures below or above the optimum, and/ or a change in diet composition.

Existing bioenergetics models for fish have used optimal growth temperatures observed in lab settings or extrapolated from limited field observations (e.g., Brandt et al., 2002; Stewart et al., 1983a; Stewart and Ibarra, 1991a). If these temperatures are not available in the ecosystem due to seasonality, the assumption is that maximum temperature up to but not exceeding the optimum would be selected for occupancy by the fish. The temperature used for lake trout has been 10°C based on the optimum from lab trials (Stewart et al., 1983a), whereas for Chinook salmon 11°C is used based on limited field observations (Brandt et al., 2002). Assumed temperatures, if different from the actual temperature occupied by the fish, could significantly bias estimates of growth rate potential and consumption rate. These estimates would also be biased if diet changes, and existing models do not account for potential changes in the prey community composition and associated diet proportions. Lake trout is a generalist predator that relied heavily on bloater (*Coregonus hoyi*) prior to the latter's extirpation in Lake Ontario in the early 1980s (Owens et al., 2003). Lake trout have now replaced bloater with Alewife (*Alosa pseudoharengus*) and round goby (*Neogobius melanostomus*) (Colborne et al., 2016; Mumby et al., 2018). Chinook salmon is considered a prey specialist in the Great Lakes with a diet primarily composed of Alewife (85-93% for adults; Jacobs et al., 2013; Mumby et al., 2018; Stewart et al., 1983b). An increased contribution of bloater to the Chinook's diet has been observed at decreasing Alewife abundances in Lake Michigan (Jacobs et al., 2013; Rybicki and Clapp, 1996). However, the species were reported to grow poorly, likely due to presumed limited overlap in the two species' depth distributions (Benjamin and Bence, 2003).

Given the already existing increasing of water temperatures in the Great Lakes (Anderson et al., 2021) and the contradictory predictions for these species' growth under the new conditions (e.g., Shuter and Lester, 2004; Brandt et al., 2002), more accurate predictions from bioenergetics models of lake trout and Chinook salmon are necessary. The newly available fine-scale year-round observational temperature data for these species enables the creations of such predictions. Knowledge of the growth potential of a species is important for fisheries management and the understanding of how this is altered by changing environmental conditions is key to adaptive and effective decision-making in the face of a rapidly changing climate. Growth is also strongly influenced by diet and the available prey in the community, therefore any changes in the diet composition may significantly impact how a species performs under the new environmental conditions. Other studies have modelled a shift to greater depths for thermoregulation (Brandt et al., 2002) but not how exposure to increasing water temperatures would affect growth – an oversight considering long-term warming is also occurring at depth (Anderson et al., 2021; Burns et al., 2005) suggesting that species would be exposed to greater temperatures. Thus, the objectives of this study were to i) understand the relative importance of using optimum thermal preferenda versus observed *in-situ* thermal occupancy on bioenergetic model predictions; ii) quantify the growth rate potential of lake trout and Chinook salmon at low and high future temperature increase scenarios; and iii) compare to a baseline period with the aim of examining the effects of a warming climate and any related influences of changes in the prey community, such as the establishment of bloater. I hypothesize that 1) use of optimum temperatures would bias prediction results; 2) both lake trout and Chinook salmon maximum attained adult weight would decline under all future temperature increase scenarios or would result in a higher consumption rate to maintain baseline body weight; and 3) bloater incorporation in the diet of the two species would be favourable to the growth, i.e., adult maximum weight potential, of lake trout, but not to Chinook salmon.

Methods

Telemetry

All methods for the acoustic telemetry and pop-off data storage tags (pDST) have been provided in detail in Chapters 2 and 3 of this dissertation, and in Ivanova et al. (2021a) and Raby et al. (2020), respectively. Briefly, 278 permanent acoustic telemetry receivers (69 kHz, VR2W, Innovasea Systems Inc, Bedford, Nova Scotia, Canada) spaced between 2 and 15 km apart were used to detect fish tagged with acoustic transmitters in Lake Ontario. Chinook salmon were tagged at both the eastern and western ends of the lake in 2017-2018 with V13 depth and temperature sensor tags (45 mm length × 13 mm diameter; 6 g weight in water; nominal delay 180 s; estimated battery life 703 days; Innovasea Systems Inc). Lake trout were tagged only at the eastern end of the lake during the same period with V16 depth and temperature sensor tags (68 mm length × 16 mm diameter; 10.3 g weight in water; nominal delay 180 s; estimated battery life 3650 days; Innovasea Systems Inc). Lake trout were gill-netted and Chinook salmon angled and kept in a 50L tank filled with lake water until surgery. Surgeries lasted <3 min and involved an incision posterior of the pelvic fins, implantation of the tag in the body cavity, three sutures to close the incision and tagging with an external Floy tag. For pDST tagging all fish were angled in 2014 to 2016 and the external harness was attached through the dorsal musculature. The pDST tags (a time-release G5 long-life 20 bar depth-temperature logger with a float; Cefas Technology Inc.) were programmed to log temperature (precision 0.03125°C and accuracy ±0.1°C) every 70s. Fish were allowed to recover in an aerated tank until upright swimming was restored prior to release for both types of tagging. A total of 10 Chinook salmon and 18 lake trout with acoustic telemetry tags and 11 of each species with pDST tags were included in the calculations of present temperatures.

Time periods, water temperature and future scenarios

Three time periods were used in this study for modelling the growth potential and net growth of lake trout and Chinook salmon: i) past – includes 1983 to 1999 prior to large temperature changes, bloater is extirpated, and round goby have not invaded; ii) present - includes 2010 to 2019 with round goby established and incorporated in the diet of lake trout; iii) future – year 2060 scenarios with low or high mean water temperature increase and with or without bloater re-establishment. The past and present periods used available data to provide understanding of the current growth of the two species and the effects of the use of assumed thermal occupancy on the results, and to serve as baseline for comparison with growth under forecasted warming.

Commonly, for multi-year analyses of fish growth rate potential, temperature at 30-day intervals throughout the year is used and the software interpolates the values between these days for smoothing purposes (Deslauriers et al., 2017). Modelling was done in Fish Bioenergetics 4.0 (Deslauriers et al., 2017). Even though daily mean temperature was available for the present period, this 30-day interval was used in all periods to avoid bias. Observed daily mean values were used for sensitivity analysis to estimate effects of temperature smoothing at 30-day increments on our results for the present period.

Observed thermal occupancy was not available for lake trout or Chinook salmon in Lake Ontario for our past period, thus assumed optimal thermal occupancy, i.e., 10°C

(Stewart et al., 1983a) and 14.3°C (Hasnain et al., 2010), respectively, or the closest available temperature in the lake (as per Stewart et al., 1983a) was used (Figure 5.1, Appendix 2 Table S5.1a and b).

For the present period, I used observed temperature occupied by individuals obtained via acoustic telemetry temperature sensor tags and pDST tags. Daily mean temperature for each species was calculated from the two datasets. From those daily values, an average temperature was calculated for every 30th day starting April 1 for lake trout and September 1 for Chinook salmon based on a 10-day mean before and after the 30-day mark. September 1 for Chinook salmon was chosen because juveniles would have descended from the tributaries and have become lake resident by this date, and because all data for weight-at-age was collected in August and September. The resulting temperatures were used as input values in the bioenergetics models.

To assess any influences of assumed thermal occupancy on model results and establish a period to use as a baseline, I simulated lifetime growth for each species with present diet composition and weight but used assumed optimum temperature occupancy as that of the past period (this model is hereafter referred to as 'present assumed'). A comparison was performed between the results for present assumed and those for the present with observed temperature occupancy (for the purpose of this comparison, hereafter referred to as 'present observed').

For the future scenarios, I used temperature increases as projected by Trumpickas et al. (2009) based on the Intergovernmental Panel on Climate Change (IPCC) high and low (A2 and B2) CO2 emission scenarios for the period 2011–2070 ([IPCC] Intergovernmental Panel on Climate Change, 2000) with earlier onset of spring and delay of fall. Both, low and high temperature increases were used for the year 2060, resulting in two general future temperature scenarios (Table 5.1 and Appendix 2 Table S5.1). Temperature increases of the hypolimnion were calculated as best- and worst-case scenario(s), i.e., high and low weather variability, for the low and high temperature changes, respectively. For the low temperature (best-case) scenario, the increase was 30% of the surface temperature (Anderson et al., 2021), and for high (worst-case which accounts for accelerated warming) it was 60% (Table 5.1). Temperature observations from the present period of each species were adjusted for each future scenario based on a mean increase (Table 5.1 and Appendix 2 Table S5.1) with earlier onset of spring, prolonged summer, and delay of fall. The lake's thermal seasons were defined in Chapter 2 in this disseration, and Ivanova et al. (2021b) Thus, the greatest temperature increases were assigned for the summer months (63% for months 7-10), followed by spring and fall (15% for each, months 5-6 and 11-12, respectively), and then winter (7% for months 1-4) (based on Trumpickas, Shuter, and Minns 2009; Figure 5.1 and Appendix 2 Table S5.1). These temperatures were presumed to remain steady throughout the lifetime of the modelled fish.

Predator energy density and equations used for modelling

To estimate energy density of lake trout in Lake Ontario, whole-body lipid data (source: Environment and Climate Change Canada) from 1977 to 2019 (n=5,766; Appendix 2 Table S5.2) were used with conversion of 39.5 kJ/g (Brody, 1945). These values were then compared to actual energy density values obtained by bomb calorimetry of whole animals (n=22; source: OMNRF) and the difference of the means between the two methods was converted to percentage and used to scale the lipid energy density values. Calorimetry values averaged 12.1% higher than lipid-based estimates and an adjustment of the lipid-based estimates was made.

For calculating the Lake Ontario-specific energy density equation, values of weight above 8,000 g were deemed outliers and removed from further analysis. Weight dependence of energy density was established using the piecewise.linear() function from the SiZer package (Sonderegger et al., 2009) in R with 1000 iterations and significance level of 0.001 to estimate the break-point for separating immatures from sub-adults and fit the two linear models. Based on the estimated break-point, the two linear models were fitted, and the equations of the lines used in the simulations.

Chinook salmon skinless, boneless filet lipid data (source: Ministry of the Environment, Conservation and Parks) from 1976-2018 (n=1,390) were used to calculate energy density based on the following lipid-energy density equation by Trudel et al. (2005):

$$\text{Energy density (kJ/g W)} = 3.60 + 0.047 * \text{Whole-body lipids (mg/g W)}.$$

Considering the above equation is for whole body lipids, the Chinook energy density values were compared to these of coho salmon for skinless, boneless filet and whole-body. Since the filet energy density values between Chinook and coho were not significantly different ($p = 0.25$), the difference of the means between the coho filet and whole-body energy density values was converted to percentage and used to scale the Chinook energy density values. Coho whole-body calorimetry values averaged 34.6% higher than the lipid-based estimates, thus the latter for Chinook were adjusted accordingly.

For calculating the Lake Ontario-specific energy density equation for Chinook salmon, values for regression were limited to fish of sizes 200 - 15000 g and since the number of observations for present period were lower, I combined the data for all periods together (Appendix 2 Table S5.2). The piecewise.linear() function did not yield a meaningful break-point for separating juveniles' from adults' energy density equations, so one equation was used for all ages for further analysis.

Prey energy density, diet composition and digestibility

Prey energy density was obtained from the literature (for details and associated references see Appendix 2 Table S5.3) and where multiple values for a species were available, a mean was calculated. Prey diet composition and proportions for the two predators used in the past scenario and associated references are provided in Appendix 2 Table S5.4, Appendix 2 Table S5.5 lists the proportions for present and future scenarios with no diet composition change, and Appendix 2 Table S5.6 contains the future scenario with diet composition and proportion changes. Prey digestibility was assumed to be the same across all prey species for both predators. Indigestible prey proportion used was 0.033 (Stewart et al., 1983a).

Modelling simulations

I used the Wisconsin bioenergetics model to simulate growth (Deslauriers et al., 2017; Kitchell et al., 1977). For each species, I replaced the energy density equations with those calculated from the available data for Lake Ontario. All other physiological parameters were kept as set in the software. Model sensitivity and assumptions are summarized in Bartell et al. (1986), Ney (1993, 1990), Brandt et al. (1992), and Madenjian et al. (2000).

A summary of all scenarios, including past and present, is provided in Table 5.2. Two foraging scenarios were examined for the future periods: 1) prey base, prey energy density and prey diet composition and proportions remain the same as present/baseline (Appendix 2 Table S5.5), and 2) bloater becomes established in the lake and is incorporated into the diet (up to 40%) of both species at the expense of Alewife (Appendix 2 Table S5.6). Feeding rate, also known as P-value and defined as the proportion of the maximum consumption (Beauchamp et al., 2007), for past and present periods was calculated using lake trout start weight of 127 and 142 g, respectively, at age class 1 with simulations start day of April 1. Chinook salmon starting weight was 200 g at age class 0 for past and present and simulations start day was September 1.

To assess the growth rate potential of the species under each future scenario, lifetime growth was simulated for an individual's lifespan from age 1 through 15 for lake trout and 0 through 4 for Chinook salmon. Fit-to-weight (based on present weight) was modelled to assess how feeding rate would have to change if the present weight was to be maintained under the new conditions. Fit-to-feeding rate (based on present feeding rates) was modelled to assess how weight will change if present feeding rate was maintained under the new conditions.

Percent net change of weight and consumption at adult ages 14 and 4 for lake trout and Chinook salmon, respectively, were calculated using starting weight-at-age 13 for lake trout (6,573 g) and weight-at-age 3 for Chinook (9,742 g) from the present scenario and fitted to the feeding rate associated with the age from the respective period. The same approach was used to calculate the percent net change in feeding rate under the new conditions by fitting to the final weight of baseline age 14 and age 4 for lake trout and Chinook salmon, respectively. The ages of 14 for lake trout and 4 for Chinook salmon were chosen for the net change calculations as at these ages the species were considered adult and to have achieved full growth. Present weight, consumption and feeding rate were used as the baseline in the following general formula used for calculating percent net change ('value' in the formula denotes either weight, consumption or feeding rate):

$$\%\ \text{net change} = (\text{future scenario value} - \text{baseline value})/\text{baseline value} * 100$$

Results

Predator energy density

Lake trout exhibited a nonlinear relationship between energy density and weight resulting in biphasic dependency, with the transition between juveniles and adults occurring at 1,627 g ($p<0.001$, residual error of 1.762 and DF 5,762; Figure 5.2):

$$\text{Juvenile: } y = 2.21 + 0.00328 * \text{Weight}$$

$$\text{Adult: } y = 6.74 + 0.000501 * \text{Weight}$$

There was no distinction between juvenile and adult Chinook salmon in Lake Ontario, thus one equation was used for all ages (Figure 5.2):

$$y = 6.11 + 0.0000983 * \text{Weight}$$

Thermal occupancy

Occupied temperature (i.e., present period) based on acoustic telemetry and pDST tags for both species were different from the assumed thermal occupancy. Lake trout were found at lower temperatures than what would be assumed by thermal-optima during the year, except during April, October and November (thermal-optima is shown as past period and occupied temperatures as present period in Figure 5.1) when occupying shallower habitat (Ivanova et al., 2021b, 2021a; and Chapter 2). Chinook salmon were in cooler temperatures in the spring, but in slightly warmer waters in the mid-summer and during the fall (Figure 5.1), compared to assumptions and partially available (i.e., data has only been available for the summer season) field data (Brandt et al., 2002).

For the present scenarios, estimated weight-at-age 14 lake trout was 6,800 g under observed, and 6,271 g under assumed temperatures (Figure 5.3a) based on lifespan calculations. For Chinook salmon, estimated weight-at-age 4 (maximum age) was 10,387g under observed and 12,919 g under assumed temperatures (Figure 5.3c). Differences between assumed and observed temperatures for age-14 lake trout was 2.48% for net weight and 16.35% for net consumption, and for age-4 Chinook salmon were -8.28% and -5.84%, respectively.

Feeding rates-at-age were significantly different between present observed and assumed temperatures for each species ($p < 0.001$, Pearson's paired t-test, Figure 5.3b and d) with lake trout mean of 0.53 and 0.57, respectively, and for Chinook salmon 0.8 and 0.75, respectively. Total lifetime consumption between present assumed and observed temperatures was significantly different for lake trout ($p < 0.001$) but not significantly different ($p = 0.054$) for Chinook salmon (Pearson's paired t-test for both species). A single individual lake trout's total lifetime prey consumption for present assumed temperatures was 119 kg and for present observed 110 kg, whereas for Chinook salmon the total lifetime prey consumption was 114 kg and 109 kg, respectively. Net consumption rate for lake trout age-14 for assumed temperatures for a year was 7.5% higher compared to observed temperatures and significantly different ($p < 0.01$, Pearson's non-paired t-test), whereas for Chinook salmon age-4 it was 2.7% higher but not significant (p = 0.4, Pearson's non-paired t-test). Considering the above, the present period was considered more accurate due to the use of observed *in-situ* thermal occupancy and thus, chosen as the baseline to which future scenarios were compared.

Present/baseline and future scenarios

Feeding rate and weight were higher for the baseline compared to the past period for lake trout, while the opposite was observed for Chinook salmon (Figure 5.4a, b). Lake trout performed well under all future scenarios when compared to the baseline with growth potential increasing between 12 and 139%, if feeding rate remained the same (Figure 5.4c, and Figure 5.5d). The maximum adult weights of 87 and 139% above baseline were observed for lake trout during the future lifespan scenarios when bloater was incorporated into the diet (Figure 5.4c, and Figure 5.5d). Lake trout net weight increased 10% over baseline in the future high scenario with bloater relative to baseline, resulting in 20% higher prey net consumption (Figure 5.5a and b). The least net change for the future scenarios was observed in the low temperature scenario with no diet change at 1% for weight, 7% for consumption and -3% for feeding rate (Figure 5.5a, b and c). Chinook salmon growth during the future scenarios showed mixed results (Figure 5.4d). The main observation was the difference in the growth rate between scenarios that didn't include diet change compared to the baseline period. All scenarios in which diet remained unchanged from baseline had reduced adult weight potential (-11.5 to -29.6%) in the future compared to baseline (Figure 5.5h). Alternatively, to maintain similar weight to baseline with no diet change, Chinook salmon would need to increase their net feeding rate by 6.3 to 15.6% (Figure 5.5g). However, in the scenarios with bloater incorporated in the diet, Chinook adult weight potential was 5.5 to 30.3% higher (Figure 5.4d, and Figure 5.5h) with no change in feeding rate. Percent net weight change from baseline was highest in the low future scenario with bloater (7.6%) where hypolimnion temperature was 0.4°C higher overall (Figure 5.5e) also resulting in a 5.9% increase in prey consumption (Figure 5.5f). This was also the only positive value for net weight change for Chinook salmon, while in all other scenarios net weight values ranged between -3.1 and -16.2% (Figure 5.5e).

Discussion

Understanding the growth rate potential and thus, the attainable maximum adult weight, of a species provides important insights into the population's health and how those would be affected by changing environmental conditions. Cool- and cold-water species are more vulnerable to warming temperatures due to climate change because their optimal habitat is expected to contract in freshwater ecosystems and the exposure to higher sub-optimal temperatures to increase. From a bioenergetics point of view such changes affect growth potential through physiological stress (Brandt et al., 2002; Stewart et al., 1983a). Existing bioenergetics models for lake trout and Chinook salmon, have relied either on the assumption that the species would occupy the warmest temperature available up to that for optimal growth from lab trials and/or have been supplemented by limited observational temperature from their natural habitat (Brandt et al., 2002; Stewart et al., 1983a). Yet temperature is only one of the factors influencing growth. Prey quality and availability are others, and those directly affect growth and the final temperature preferenda (Jobling, 1994). Here, I modelled growth for these two species using observational data from the Great Lakes, specifically Lake Ontario, under different future scenarios. Our results suggest that the use of assumed optimal thermal occupancy introduces bias in bioenergetic model predictions of species consumption and growth with implications for management. Lake trout performed well under all future scenarios, whereas Chinook salmon maximum adult weight potential was inhibited under increasing temperature conditions but maintained or increased when bloater was present in its diet. These results, provide important insights into the effects of increasing water temperatures on the growth of two salmonid species in the Great Lakes, and the potential mediating effect of higher quality prey.

Due to lack of *in situ* observations, the use of lab trial data and the assumption that a species would occupy temperatures closest to their thermal optimum (see Stewart et al., 1983a) have been a normal practice for modelling species' physiology and ecology (e.g., Brandt et al., 2002; Madenjian et al., 1998; Stewart et al., 1983a). Testing the above assumption by comparing to the results with temperatures observed *in situ*, showed that maximum adult weight potential was underestimated for lake trout and overestimated for Chinook salmon under baseline environmental conditions. The calculated feeding rates for both species were significantly different for the two temperatures (Figure 5.3b and d) resulting in general underestimation of these for lake trout and overestimation for Chinook salmon under assumed thermal occupancy, while lifetime prey consumption and net consumption rate at age 14 were overestimated significantly for lake trout. These results suggest that use of assumed optimal thermal occupancy for different species may yield different biases and thus results, and studies that used such assumptions should be viewed with caution by management professionals.

With warming temperatures, spring lake turnover is expected to start sooner, summer stratification to last longer and fall turnover to be delayed (Trumpickas et al., 2009) as has been reported for Lake Michigan (Anderson et al., 2021), all resulting in a prolonged growing season and thus a predicted general positive influence on the growth of species (Brandt et al., 2002). Mason et al. (1995) showed a similar growth rate potential in Lake Ontario for both lake trout and Chinook salmon for the early 1990s and using individual growth as proxy for habitat quality suggested a similar availability of quality habitat for these species. If I employed the same proxy, our results from the baseline (2010-2019) and future scenarios suggest that under warming temperatures the available quality habitat for Chinook would decrease based on their decreased maximum adult weight potential, whereas for lake trout it would be somewhat similar. This could be attributed to Chinook observed occupied temperature being very close to that of their optimum, whereas lake trout's observed thermal occupancy was well below the optimum. Our results from the temperature-only change scenarios, i.e., lower net growth and overall lower lifetime growth potential, echo these of Brandt et al. (2002) that warmer conditions would be unsuitable for Chinook salmon growth. Brandt et al. (2002) presumed that Chinook salmon would occupy optimal temperature near the thermocline and observed increased overall mean growth rate but saw a dramatic decrease of 49% when they accounted for reduced light conditions affecting their ability as a visual predator. This study's lake trout results from the temperature-only change scenarios showed improved growth under all future conditions and supported those of Brandt et al. (2002). However, our baseline and future scenarios had lake trout occupy temperatures below their optimum, whereas Brandt et al. (2002) used the optimum temperature. Given this, warming environmental conditions and the prolonged growing season seem to be advantageous to lake trout growth and adult weight potential. However, it is clear that regardless of the longer growing season and whether Chinook salmon thermoregulated by remaining deeper longer or experienced increasing temperatures at the same depths, the species would face uncertain future if their diet remains unaltered (see paragraphs below).

Climate change is associated not only with increasing water temperatures but is also known to induce changes in the composition of the biotic community, affecting the availability of prey (Brandt et al., 2002). Thus, predictions based on different temperature and prey scenarios, would be useful for understanding population health and the combined effects of the two variables. Our results indicate that lake trout would experience better growth under increased temperature scenarios with the best when bloater is incorporated in their diet. This is plausible and supported by lake trout's historic preference for these species (Christie et al., 1987). This study's predictions show that Chinook salmon would only do well in the scenarios that include bloater and mean temperature increases under ~0.8°C. If bloater is incorporated to a lesser degree (i.e., <33%) in Chinook's diet, then the maximum adult weight values would drop. The greater weight increase for both species could be attributed to bloater's energy density exceeding that of Alewife (4,800 J/g compared to 6,427 J/g for bloater). This shows that Chinook salmon's poor growth when occupying warmer temperatures may be mitigated if the species consume more energy dense prey such as bloater. This agrees with studies in the Pacific Ocean that observed prey to be a better determinant of growth than occupied temperatures (Beauchamp et al., 2007). Thus, the predicted positive influence of bloater on both species' growth provides strong support for the ongoing efforts to re-establish bloater in Lake Ontario.

A diet change for Chinook salmon in the Great Lakes may be questioned considering the species specialist tendency (Jude et al., 1987; Mumby et al., 2018). In addition, Chinook salmon have been reported to follow their prey (Benjamin and Bence, 2003). For example, as Alewife populations collapsed in the early 2000s in Lake Huron, individual Chinook were found to move to Lake Michigan to feed (Clark et al., 2017). Considering the observed great variation in depth use of Chinook salmon in Lake Ontario (Raby et al., 2020), and a potential for a changed distribution of Alewife (Brandt et al., 2002), individuals in any future scenarios may simply follow Alewife to greater depths, and behaviourally thermoregulate to maintain preferred temperature exposure. If this happens, reduced light conditions are predicted to interfere with prey capture rate, as reported by Brandt et al. (2002), and result in declining overall growth and body condition. Alternatively, a switch to a more profitable prey species, such as bloater, may or may not necessarily happen in Lake Ontario, considering Chinook have shown a mixed preference in the Great Lakes for them. For example, Rybicki and Clapp, (1996) and Jacobs et al. (2013) reported a switch to bloater in Lake Michigan in the early 1990s, yet Bunnell et al. (2017) noted that this did not happen when bloater abundance was high in 2016. In the Pacific Ocean, salmonid diet and survival have been linked to changes in the availability and quality of prey and Chinook salmon show a greater diversity in their diet (Hertz et al., 2016; Hunt et al., 1999), indicating that diet plasticity exists in the species. Given the above, more studies are required to understand under what conditions Chinook would be more prone to include bloater in their diet. Alternatively, to maintain similar growth in elevated temperatures, Chinook salmon would need to increase their feeding rate between 6.3% and 15.6%. Considering their net consumption and mean feeding rate are already higher than lake trout's (mean of 0.74 for Chinook versus 0.53 for lake trout) for baseline, a change in the ratio of predator to prey would be required with no guarantee that it would help them maintain similar growth to the present period. Our results show that at age 2 and 3 Chinook salmon have a feeding rate of 0.90 and 0.79, respectively, suggesting they are already feeding very close to the theoretical maximum (Beauchamp et al., 2007). Thus, a conclusion could be drawn here that under warming conditions Chinook salmon would require to incorporate a more energy dense prey into their diet to maintain their baseline maximum adult weight.

Lake trout net weight change and lifetime adult weight potential may be enhanced with warming environmental conditions, yet some physiological stress may be experienced by the species in the critical period of their spawning. Lake trout migrate in October/November (Ivanova et al., 2021a) to shallower areas (~10 m depth) in Lake Ontario for spawning (Fitzsimons, 1995). The temperatures experienced by lake trout during these two months are clearly visible on the temperature curve for the baseline period (Figure 5.1) and peak at a mean of 10.6°C. Under the future high temperature increase, lake trout was modelled to experience waters of 11.9°C mean temperatures. It is unclear what the implications may be for the species and their reproductive potential under these conditions. Studies have shown that salmonids may delay migration due to warmer water temperatures in rivers and streams (Farrell et al., 2008) but these delays result in compromised reproductive output through poorer gamete quality if gamete formation is not delayed physiologically (Fenkes et al., 2016; Munkittrick and Moccia, 1987). Higher temperatures at the spawning grounds, especially at shallower sites, may delay spawning timing and affect egg development either due to poor quality, unfavourable conditions, or shorter development period under optimal conditions (Brown et al., 1993; Farmer et al., 2015). Thus, even though growth and maximum adult weight may not be reduced, the reproductive potential of lake trout may be affected.

It should be noted that for these simulations I used the default parameter settings of Fish Bioenergetics 4.0 for each species. Chinook consumption is modelled as a dome, increasing over moderate temperatures, and slowing before declining as temperatures exceed optimal. In contrast, lake trout consumption is modelled by an exponential function, allowing it to increase at an accelerating rate with no maximum. While in all of our scenarios, lake trout remained below or near the thermal optima and the default consumption model was appropriate, future scenarios in which lake trout are unable to thermoregulate behaviourally will require a different formulation of the consumption model.

Conclusion

Effective management relies on good understanding of species' bioenergetics, including metabolic rate, growth potential and the effects of diet, because these provide estimates of the predatory demand on the lower trophic levels. In addition, understanding the effects changing environmental conditions have on bioenergetics allows for better predictions and thus, more effective decision-making. Our results show that when assumed thermal occupancy is used, the models under-estimate maximum adult weight potential and over-estimate the proportion of maximum consumption, and thus, estimates of consumption. Lake trout grew better under all increasing temperatures with greatest adult weight attained under reduced Alewife and re-incorporation of bloater in the diet. Chinook salmon growth potential was maintained or increased only when bloater was incorporated in its diet. These results underline the importance of updating bioenergetics models with observational *in situ* data, provide insights on the differential effects increasing water temperatures have on species, and highlight the importance of species rehabilitation programs, such as that for bloater in Lake Ontario.

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Table 5.1. Mean temperature increases for the low and high future scenarios for modelling lake trout and Chinook salmon bioenergetics under new climate change conditions in Lake Ontario.

Scenario	**Mean surface water increase (°C)**	**Mean hypolimnion temperature increase (°C)**
Future Low	1.3	0.4
Future High	1.6	1.0

Table 5.2. Summary of scenarios used in the bioenergetics modelling of lake trout and Chinook salmon in Lake Ontario.

Scenarios	**Temperature used**	**Prey proportion change from present**
Past (1983-1999)	Assumed	NA
Present (2010-2019)	Observed	--
Future Low	Observed +0.4ºC	No
Future Low w/Bloater	Observed +0.4ºC	Yes
Future High	Observed +1.0ºC	No
Future High w/Bloater	Observed +1.0ºC	Yes

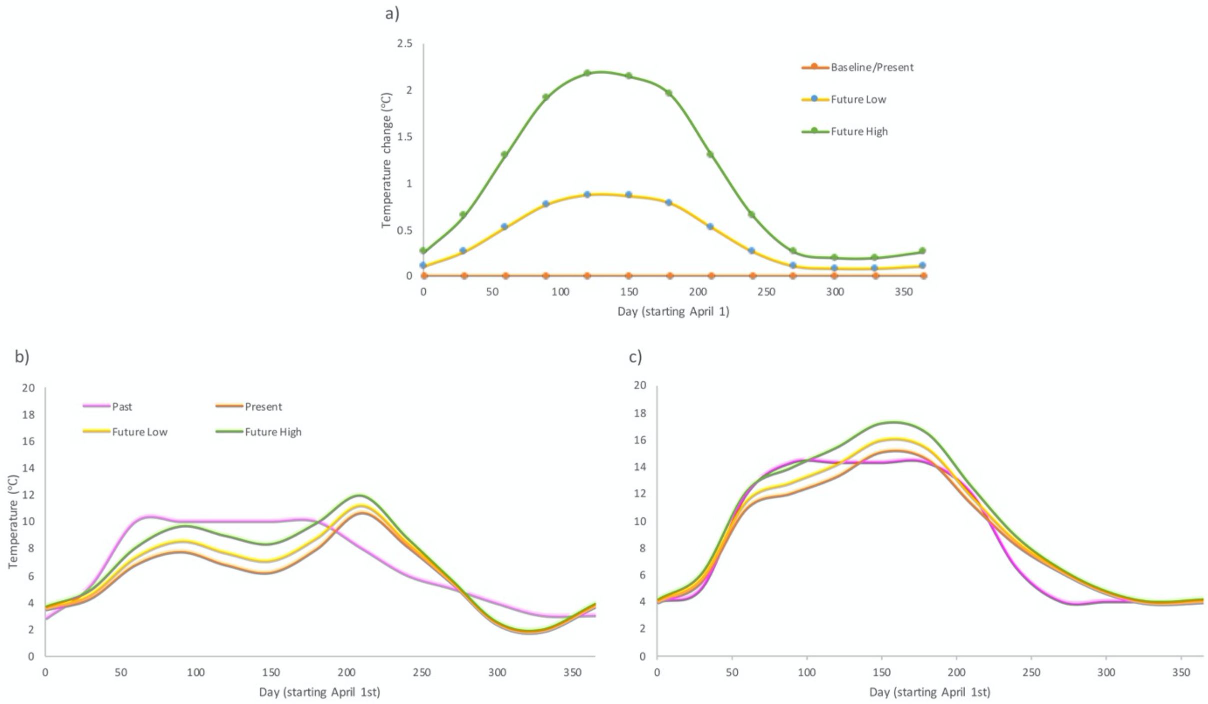

Figure 5.1. Monthly distribution of temperatures (increase above baseline where baseline is the present) for different scenarios (Table 5.2) in Lake Ontario (a), and monthly temperatures experienced by lake trout (b) and Chinook salmon (c) for the different scenarios. Note: ***Past*** represents the assumed thermal optima temperatures and the species occupying the warmest temperature available in the habitat up to but not exceeding the physiological optimum. ***Present*** represents the environmental conditions of 2010-2019 including observed temperatures occupied by the species. ***Future low and high*** scenarios, represent a mean annual increase of 0.4°C and 1.0°C, respectively added to the present temperatures.

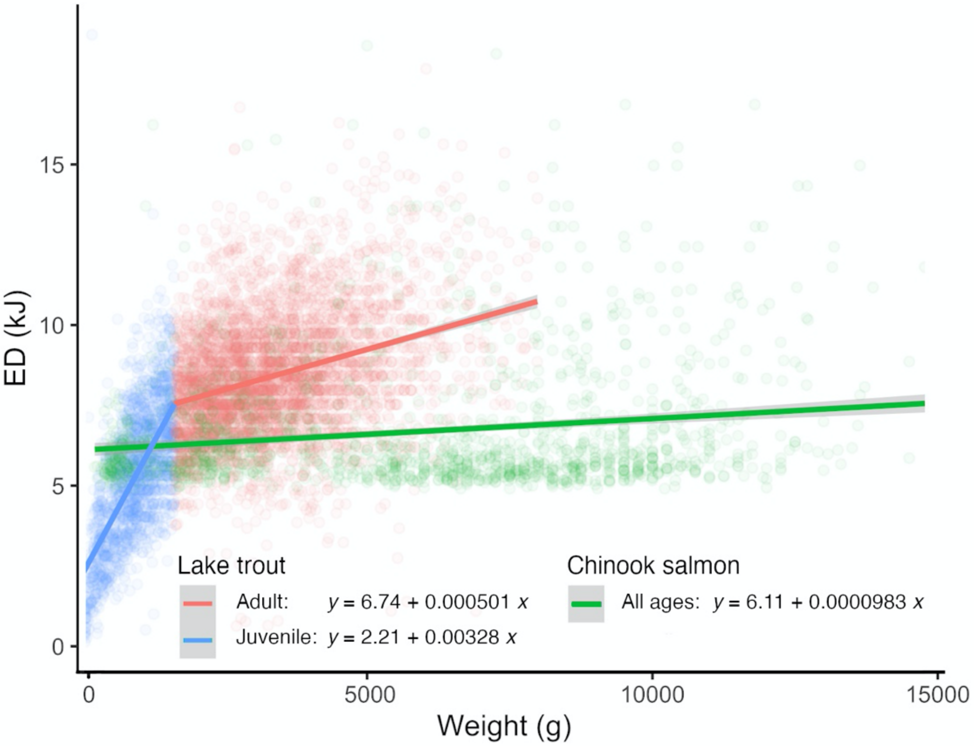

Figure 5.2. Energy density vs body weight for Lake Ontario lake trout and Chinook salmon. Calculations were based on 5,766 lake trout and 1,390 Chinook salmon.

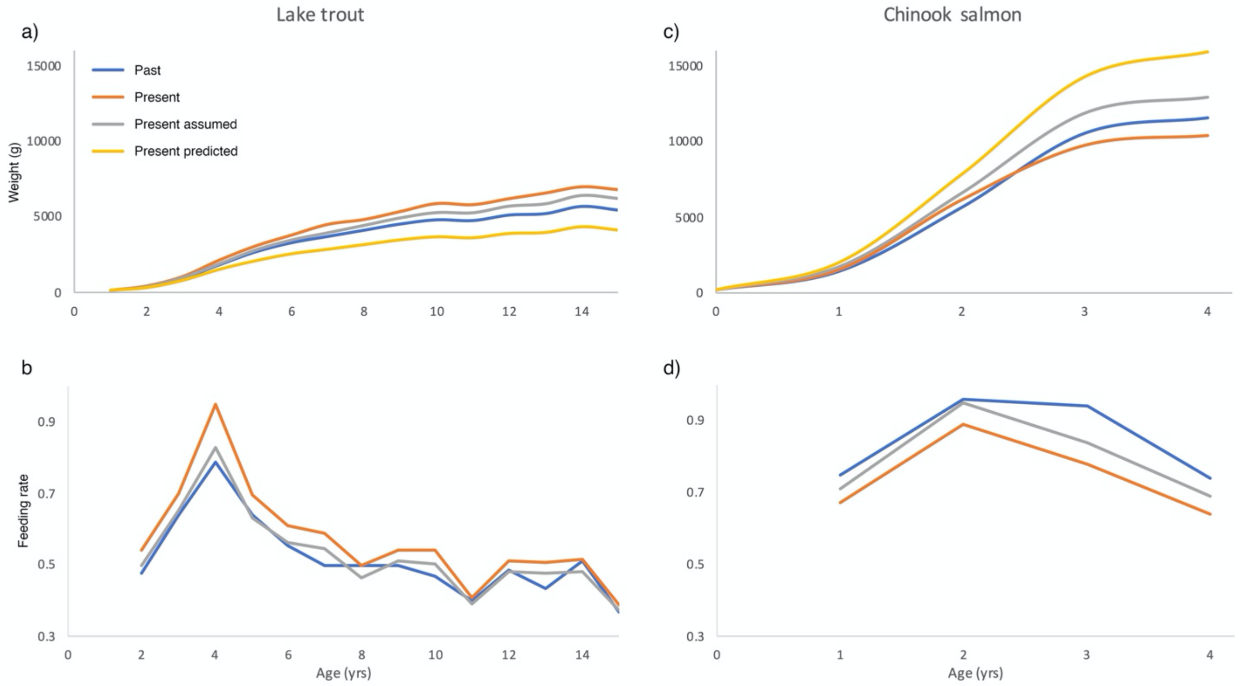

Figure 5.3. Lifetime growth rate (a, c) and feeding rate (b, d) for Lake Ontario lake trout (a and b) and Chinook salmon (c and d) under different temperature scenarios. Note: ***Past*** represents the assumed thermal optima temperatures and the species occupying the warmest temperature available in the habitat up to but not exceeding the physiological optimum, with weight-at-age values up to year 1999 and past diet composition. ***Present*** represents the environmental conditions of 2010-2019 including observed temperatures occupied by the species. ***Present assumed*** represents present diet composition, but with assumed optimal temperatures. ***Present predicted*** represents all present environmental conditions including observed temperature with present starting weight at age 1 fitted to past feeding rates across ages to obtain the predictions.

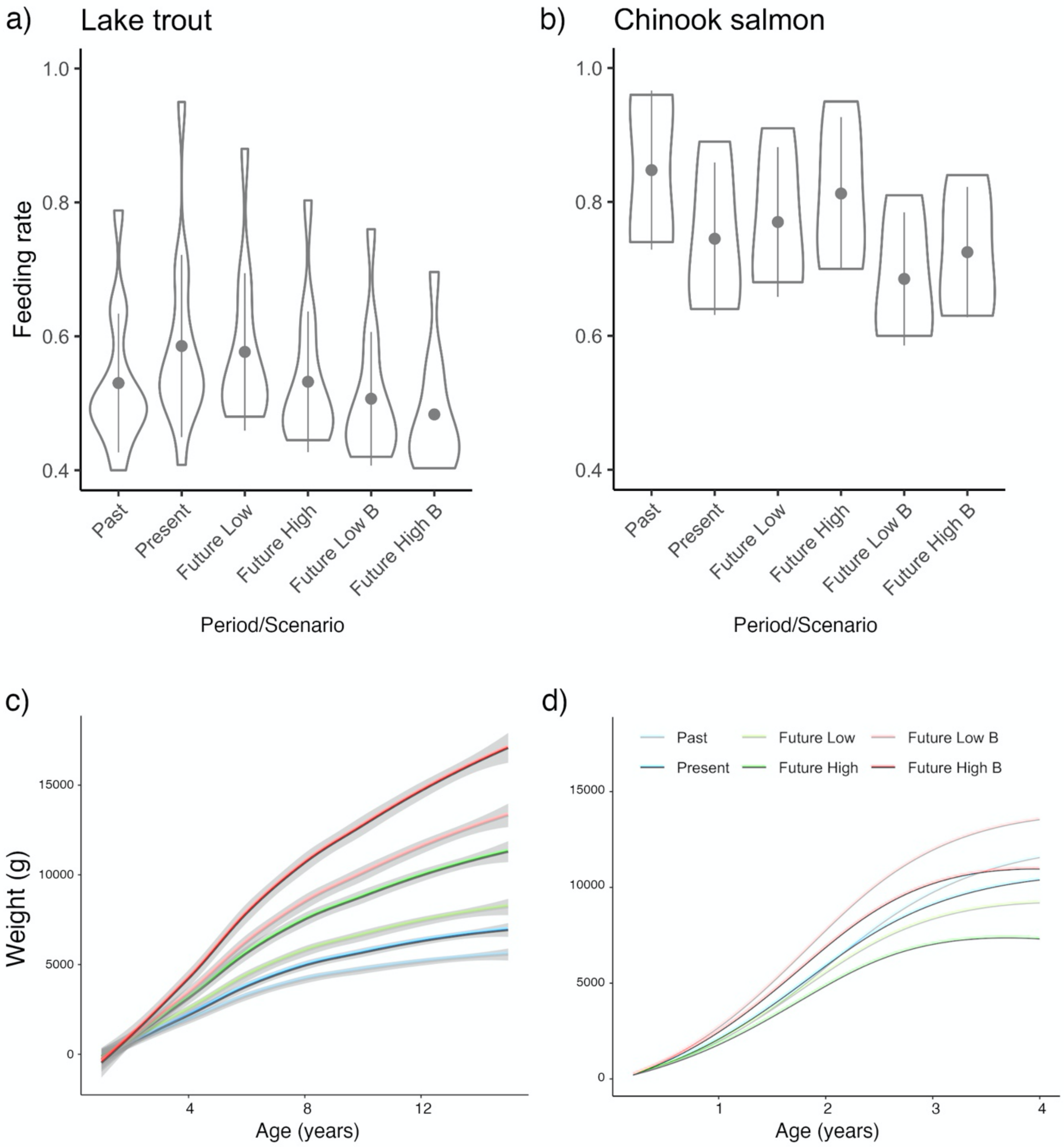

Figure 5.4. Proportion of maximum consumption (top row) and weight-at age (bottom row) depicting growth for lake trout (a and c) and Chinook salmon (b and d) in Lake Ontario for the past, present and future scenarios described in Table 5.2. Note: 'B' stands for diet change to include bloater.

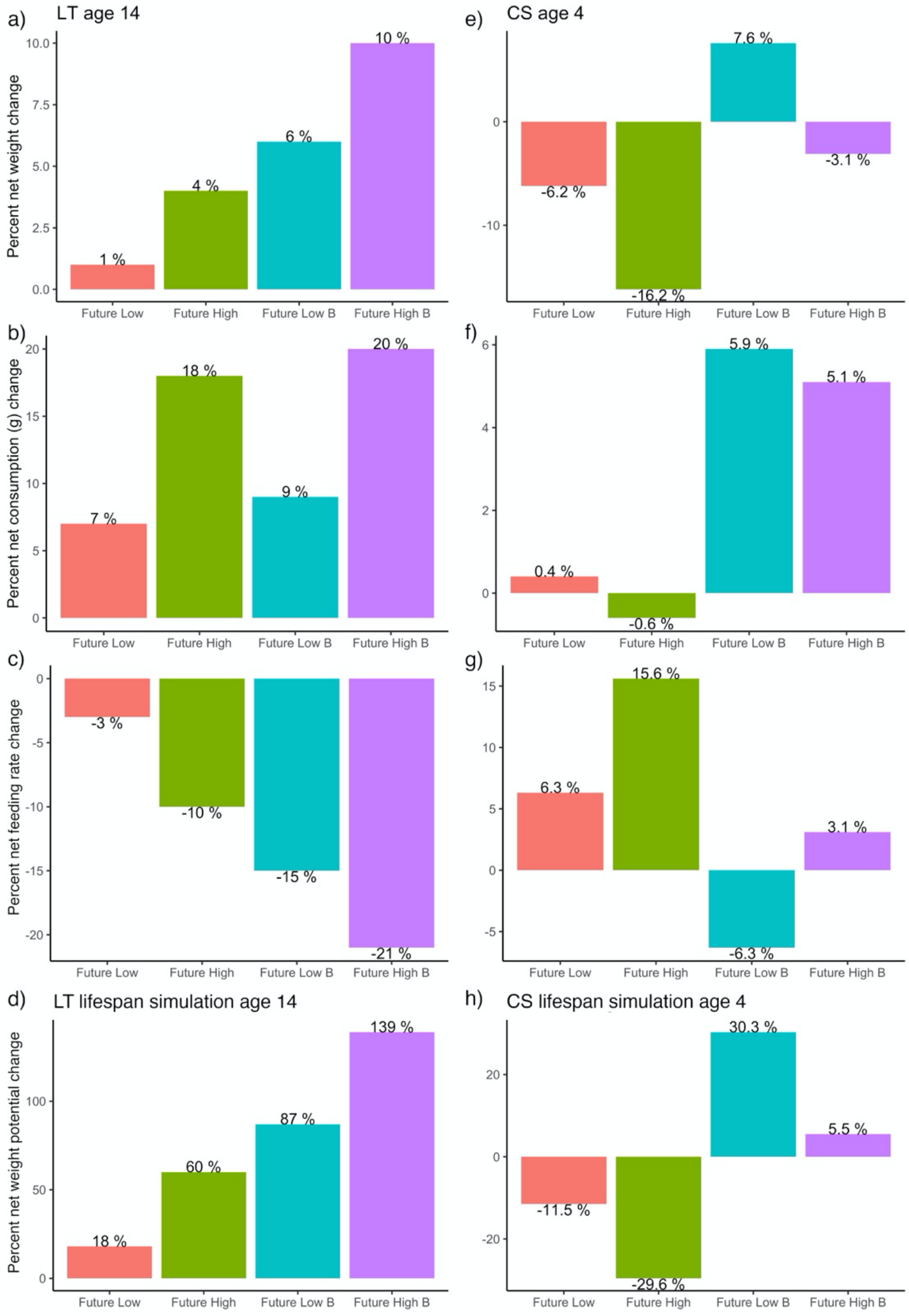

Figure 5.5. Net change in weight, consumption and feeding rate for lake trout (a-d) and Chinook salmon (e-h) in Lake Ontario for all future scenarios. Note: 'B' stands for diet change to include bloater; low and high future scenarios involve 0.4°C and 1.0°C mean water temperature increase, respectively; ***percent net weight change*** – present (used here

as baseline) scenario adult (age 13 lake trout (a) and 3 for Chinook (e)) starting weight is used to calculate an age 14 or 4 adult's weight under a future scenario by maintaining feeding rate, then the difference between the baseline and the future scenario weights is converted to percentage. ***Percent net consumption change*** (b and f) and ***Percent net feeding rate change*** (c and g) - Adult consumption and feeding rate at age 14 and 4 for lake trout and Chinook salmon, respectively, from baseline was compared to the same of future scenarios. ***Percent net weight potential change*** (d and h) – Adult weight at age 14 and 4 for lake trout and Chinook salmon, respectively, from the baseline lifespan simulation was compared to the same age of a future scenario lifespan simulation.

CHAPTER 6 – GENERAL DISCUSSION

Species restoration aims to reestablish native species that are often associated with ecologic and economic benefits (Spraker, 1992; Stewart et al., 2017). These types of benefits are closely linked together because a healthy biodiverse ecosystem is more resilient to changes and better able to sustain extraction of its resources (Costanza et al., 1992; MacDougall et al., 2013). A conflict of interest may be observed when a restoration of native species is accompanied by the stocking and maintenance of non-native species. While non-native species may also provide ecologic and economic benefits and increase biodiversity, if the two species share resources, competition may inhibit restoration efforts. Thus, understanding the distributions of both types of species and their spatio-temporal overlap would provide valuable insights on the potential for interactions between them. Furthermore, by quantifying their growth across scenarios, the relative population health of each species can be determined and potential impact of each on the other evaluated. This information provides insights on the function of the fish community and thus, informs its management.

The overall aim of this dissertation was to assess the extent of spatio-temporal overlap and interactions between native and non-native species with differing life histories and diet specialization and understand how their interactions may influence growth potential. This information would inform on a non-native species' contribution, if any, to the outcome of existing restoration efforts and on the potential influences of seemingly conflicting management projects on one another. Lake Ontario is highly managed and has a top predator community of salmonids that includes both native species under rehabilitation and introduced species that are established and largely self-sustaining yet still supplemented by stocking. Given this, I chose Lake Ontario as our study system and the native lake trout (*Salvelinus namaycush*) and introduced Chinook salmon (*Oncorhynchus tshawytscha*) as the model species for this study. While lake trout is a bentho-pelagic generalist and Chinook salmon a pelagic specialist in the Laurentian Great Lakes (Colborne et al., 2016; Mumby et al., 2018), these species share a common resource creating potential for competitive interactions. A result of competition may be a reduction in the foraging success and growth of lake trout and thus a negative impact on restoration efforts. Based on this, chapters 2 and 3 of this dissertation are devoted to better understanding the species seasonal spatial ecology and movements, and chapters 3 and 4 to assessing the potential for interactions between the species in a spatio-temporal context and their bioenergetics and growth potential, respectively.

To improve understanding of lake trout's distribution and their use of the available habitat chapter 2 quantified the species' seasonal home ranges and residency. The study was focused on the eastern Lake Ontario populations (considered separate from the western populations) because of the lack of reproductive evidence compared to the western population. Novel information on the species whereabouts was obtained by tagging and passively tracking individuals with acoustic telemetry, resulting in a yearlong dataset with observations for each lake season. Lake seasonality was established based on thermal structure. Inter-individual variation in the size of the home ranges, in the spatial distributions in winter and summer, and in exploratory long-distance movement behaviour were the defining results of the study. A limitation of this study was the lack of depth and temperature occupancy for the species to complement the positional data as those would have greatly improved our understanding of the response to thermal conditions in shallower areas and the use of the water-column. Overall, this chapter showed that lake trout utilized a wide range of habitats during all seasons, except in the fall when spawning occurs, suggesting that the seasonal overlap with Chinook salmon is likely high.

Spatial utilization distribution, depth and temperature occupancy were quantified for Chinook salmon in chapter 3 to better understand the species overall spatio-temporal ecology within the Great Lakes. Size-class (i.e., immature and subadult) distributions reveal aspects of the species' ecology associated with conspecific interactions and partitioning of resources. Yet, this information is lacking for the Great Lakes. Acoustic telemetry revealed that the size-classes had a similar habitat preference, yet their distributions overlapped only moderately at the 50% core spatial utilization distribution level. Segregation on the horizontal plane seemed to be more pronounced in the fall and spring. The integration of pop-off data storage tags (pDST) into the sampling protocol revealed that occupied depth by sub-adults was greater than the acoustic telemetry tags recorded. Based on the pDST results immature individuals were generally found shallower compared to the sub-adults in the fall and early winter months. A drawback for studying Chinook salmon was the lack of acoustic telemetry receivers in the middle part of Lake Ontario because according to the depth data and the observed movements, it could be deducted that the species utilize large parts of it horizontally and vertically, yet this was not completely captured here. Nevertheless, this chapter yielded important information on the spatial dynamics between Chinook salmon size classes, which indicates that any overlap and/or interactions with lake trout may vary with size-class.

Habitat overlap and co-occurrence of animals in space and time could be used as a proxy for interactions between them, and chapter 4 quantified the seasonal overlap between lake trout and Chinook salmon and examined individuals' pairwise co-occurrences. Advanced modelling techniques allowed the construction of joint potential path areas from movement trajectories to measure the potential for spatial interactions. Based on the three dimensions used for analysis (latitude, longitude, and depth) the species overlap horizontally mainly in the summer months yet are largely vertically segregated. Here, once again limited coverage with acoustic telemetry in the middle part of the lake prevented us from fully exploring the extent of the interactions and co-occurrence of the species in the winter months and at greater depths and thus with the different Chinook salmon size classes. While the drivers of the segregation remain unclear, these results indicate partitioning that favours coexistence given all other factors in the habitat are of adequate quality.

Animals' realized growth is an indicator of the state of their populations and the potential influences of interactions with other species, and chapter 5 modelled the bioenergetics of lake trout and Chinook salmon to discern these. Existing models relied on lab obtained temperature preferenda and the assumption that animals would choose the warmest temperatures available up to the laboratory defined optimum, and if available, were sometimes supplemented with limited *in-situ* measured temperature occupancy. Novelty in the bioenergetics modelling in this chapter was the use of fine-scale year-round multi-year temperature observations for both species from the telemetry data analyzed and interpreted in chapter 2, 3 and 4 from Lake Ontario. Simulations were performed for a period of the past (with assumed thermal optimum occupancy), present (with observed temperatures) and a total of four future scenarios to understand not only the current growth performance of each species but also any challenges or benefits they may experience under climate-driven environmental changes. The results showed that lake trout occupied temperatures well below the optimum whereas Chinook salmon's occupancy was lower but closer to that used in other studies. Present feeding rate was approximately half of the theoretical maximum for lake trout and close to the maximum for Chinook. Extended growing season in the future scenarios due to warmer winters and prolonged stratification period had an overall positive effect on adult' maximum attainable weight of trout, but negative on Chinook salmon, unless the species consumed a higher quality prey. Overall, these results indicate that lake trout at present is growing below their potential, whereas Chinook salmon seem to be near theirs under these environmental conditions. Considering lake trout's lower than optimum temperature occupancy, these growth results were not surprising, and it is clear that occupying habitat closer to their thermal optimum would be more beneficial to the species at similar feeding rates. However, the greatest benefit for both species was observed when diet included a more energy dense prey.

Taken together the results of these chapters suggest limited interactions are occurring between lake trout and Chinook salmon with depth being the main mechanism of segregation when spatial utilization distributions overlapped. Lake trout is known to shift their distribution in the presence of a strong competitor (Morbey et al., 2006), thus the presence of Chinook salmon may influence the lake trout distribution to deeper habitat and this may be the reason for their observed thermal occupancy being below their optimum. Lake trout is considered bentho-pelagic, feeding both near the bottom and in the water column with benthic species being a more common prey compared to pelagic species (Colborne et al., 2016). Thus, the observed temperatures are consistent with this behaviour. This suggests that Chinook salmon restrict the realized habitat niche of lake trout in Lake Ontario due to competitive interactions.

Both Chinook salmon and lake trout feed on Alewife (*Alosa pseudoharengus*), >80% of the Chinook diet consists of Alewife (Mumby et al., 2018), thus, if there is competition for prey, it would be mainly for this shared resource. Considering lake trout are generalist in their diet and the detrimental effects of Alewife on lake trout fry survival (Fitzsimons et al., 1999), if Chinook salmon indirectly influences diet in lake trout through depth redistribution, their interactions could be considered facilitative. However, this would hold only as long as lake trout have enough alternative prey and retain a body condition that allows for unaltered spawning. Recent studies show that lake trout aggregate and spawn in eastern Lake Ontario (although egg and fry survival are low) and that adult population numbers are stable (Lantry et al., 2014). Our growth simulations showed that the greatest benefit for lake trout was observed when diet included a more energy dense prey, such as bloater, their historically preferred prey (Christie et al., 1987). Thus, even though under the present-day conditions and fish community lake trout did not achieve the maximum adult weight of the modelled future scenarios, any effect Chinook salmon avoidance may have appeared to be secondary to the quality of prey consumed. Given prey quality showed to be a better determinant of growth for lake trout and current adult population stability, it can be deduced that competition with Chinook salmon does not have a negative effect on lake trout and results in an indirect facilitative interaction. As such, Chinook salmon do not impede or interfere negatively with lake trout restoration efforts in Lake Ontario and may actually enhance these efforts.

From management perspective there are many factors that are considered an impediment to the successful restoration of lake trout in Lake Ontario, and two of these are the maintenance of competing species such as Chinook salmon and the availability of quality prey at sufficient densities (Lantry et al., 2014). Considering that the availability of prey is a major determinant of the intensity of interactions between species (Crowl et al., 1992), the above mentioned two impediments are tightly linked together and thus, it is important to briefly consider prey availability here as well. Through bioenergetics modeling, I showed that prey quality (based on assumptions of a more diverse prey community that includes a healthy bloater population) is more important for lake trout growth than is depth redistribution due to interactions with Chinook salmon. However, bottom trawl surveys showed that by far the most abundant prey among all pelagic and benthic species is Alewife, comprising nearly 90% of the catches (Weidel et al., 2021). Also, Alewife abundance fluctuations have caused major issues for top predator populations in the Great Lakes (e.g., Jones et al., 1993, Rybicki and Clapp, 1996; Stewart and Ibarra, 1991). This current poor diversity of pelagic prey and dependence on Alewife have led management to initiate restoration of native deep-water coregonids, such as Bloater and Lake Herring (*Coregonus artedi*) in Lake Ontario (Lantry et al., 2014). Thus, based on this dissertation's prey quality importance results and the suggestion above regarding lake trout's need for alternative prey if avoiding interactions with Chinook salmon, a deduction could be made that a greater diversity of the prey community would greatly benefit lake trout restoration. As such, my interpretations of the results from this dissertation agree with these management decisions. However, until the restoration of these prey species is successful and greater diversity achieved, management should continue to reconcile salmonid stocking decisions with considerations for 1) the already existing salmonid abundances in the ecosystem, 2) the longevity of each species, 3) the age-class survival rates of stocked individuals, and 4) the fluctuations in alewife abundances.

Overall, the research in this dissertation assesses the spatio-temporal distribution and interactions between an introduced non-native species and a native species undergoing rehabilitation. The findings detailed here advance our understanding of the ecology of two salmonid species with wide distributions globally and contribute key insights on their relationship and influence on one another when co-occurring in freshwater ecosystems. Negative impacts of non-native species on native species are widely documented, and in many ecosystems managers balance projects that include the situation described in this dissertation in which maintenance of both is desirable (Carpenter and Mueller, 2008; Knox et al., 2012). As such, this dissertation shows the importance of using multiple approaches to examining a perceived conflict between species and emphasizes the complexities in species interactions. Based on this work, future research should focus on (1) better understanding paired species interactions because the influences they exert on each other would vary with the life-histories of each; (2) quantifying the distributions on seasonal and finer scales year-round in four dimensions (latitude, longitude, depth and temperature) for all species within a fish community to serve as a baseline for understanding behaviour and novel interactions; (3) modelling bioenergetics with observed temperatures in order to improve predictions and estimates of growth, consumption, and individual and population health.

Employing multiple approaches proved useful in understanding the interactions between the salmonids in this research and provided insights that otherwise would have likely yielded different conclusions. Thereby, while I recommend a focus on two species at a time, I also urge the use of various disciplines, such as spatial ecology and ecophysiology, as I have done here, to improve result interpretation. Ecosystems are in constant flux with new species being introduced incidentally or purposefully and species changing their distributions in response to climate warming. Thus, detailed baseline information is crucial to understating the extrinsic and intrinsic effects on a species once a system experiences change, and thus, is key to informing adaptive management. The health of a population is influenced by factors such as habitat quality, interactions with other species and life-history traits, thus, the health of populations in an ecosystem is a proxy of the health of this ecosystem. Enhanced understanding of the stability and state of populations in a community is necessary when improvement of ecosystem health is the goal. Bioenergetics modeling and the resulting estimates have a long history of being used for this purpose and if ecosystem health is to be improved, then management require more accurate and refined predictions. Thus, ultimately, the results presented in this dissertation inform future work and provide novel insights on salmonid ecology, interaction complexity, and effects of diet specialization on these interactions and thus, on rehabilitation efforts.

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APPENDICES

Appendix 1

Table S4.1. Individual lake trout and Chinook salmon mean (± SD) two-dimensional home range sizes (in km^2) at the 50 and 95% levels and mean (± SD) Hurlbert Index of overlap between individuals of the two species.

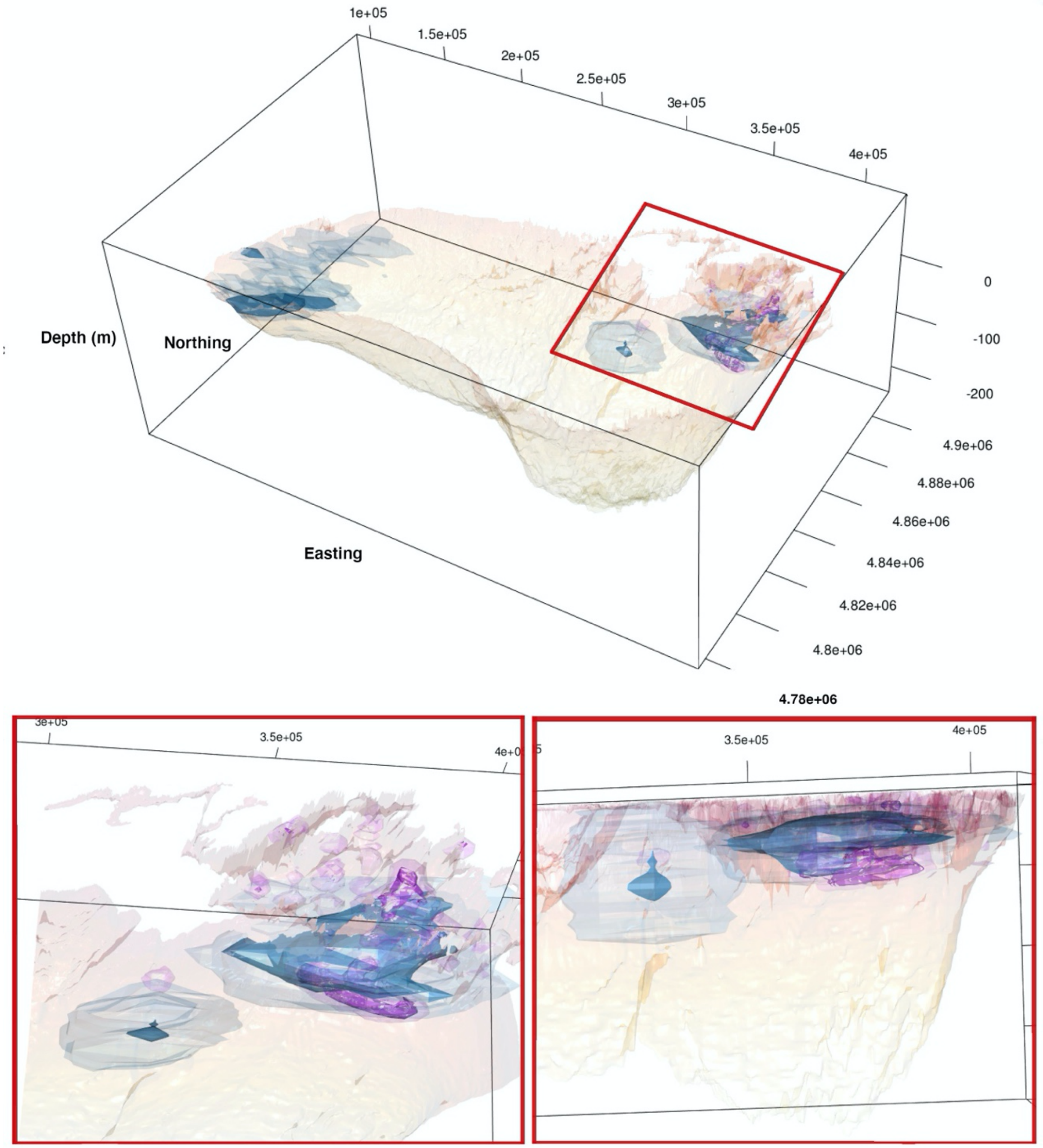
Home range size (km^2)	Fall		Winter		Spring		Summer	
	LT	CS	LT	CS	LT	CS	LT	CS
Mean (±SD) 50%	32.52 (46.12)	252.48 (310.79)	15.52 (13.55)	118.35 (135.23)	26.53 (17.92)	304.93 (553.89)	25.78 (14.32)	175.35 (182.90)
Mean (±SD) 95%	225.91 (232.10)	866.44 (877.58)	144.99 (118.24)	610.24 (526.05)	158.86 (98.51)	1304.86 (2242.17)	164.56 (78.46)	926.97 (882.44)
Mean (±SD) Hurlbert Index 50%	0.000 (0.004)		0.001 (0.012)		0.003 (0.021)		0.015 (0.043)	
Mean (±SD) Hurlbert Index 95%	0.001 (0.008)		0.002 (0.023)		0.015 (0.043)		0.116 (0.189)	

Table S4.2. Mean ± 1 standard deviation (SD) depth (m) of lake trout (LT) and Chinook salmon (CS) in Lake Ontario. Top part of table shows the values for the entire period, and the bottom part shows the calculations per month and year. N represents number of depth detections. Note: there were no tagged lake trout with depth sensors in the system August-October 2017; no depth detections for Chinook salmon in April 2018; and receivers (n=196) in Lake Ontario had mean, minimum and maximum depths of 30.1, 0.5 and 136.1 m, respectively.

	N	Mean depth ± SD	Min depth	Max depth
Lake trout	83606	31.2 ± 13.1	0	75.4
Chinook salmon	2576	28.6 ± 20.3	0.3	76.1

Year	Month	N		Mean (± SD) depth	
		LT	CS	LT	CS
2017	August	--	35	--	29.1 ± 4.6
	September	--	310	--	25.3 ± 2.3
	October	--	168	--	33.5 ± 8.6
	November	2703	2	9.2 ± 6.7	40.5 ± 28.5
	December	2275	46	17.7 ± 9.9	35.6 ± 23.8
2018	January	3270	12	19.9 ± 6.8	33.8 ± 33.6
	February	1536	41	17.7 ± 3.8	56.2 ± 23.7
	March	2026	49	22.2 ± 8.5	45.7 ± 22.5
	April	3337	--	27.1 ± 10.7	--
	May	8569	18	30.0 ± 11.1	12.8 ± 9.6
	June	3650	101	34.3 ± 9.8	16.6 ± 15.8
	July	9242	249	37.3 ± 6.9	17.5 ± 7.1
	August	13297	300	42.1 ± 5.3	23.1 ± 6.2
	September	12102	227	40.6 ± 6.8	18.2 ± 14.3
	October	7997	216	33.1 ± 15.7	12.7 ± 13.9
	November	2538	70	9.0 ± 4.8	32.6 ± 21.5
	December	2199	248	24.0 ± 9.3	50.4 ± 19.2
2019	January	1546	84	20.9 ± 6.7	51.8 ± 25.9
	February	1823	16	20.4 ± 6.9	40.2 ± 27.5
	March	2107	129	21.1 ± 6.6	44.8 ± 23.0
	April	3389	255	24.5 ± 8.2	27.2 ± 26.0

Figure S4.1. Three-dimensional home ranges for lake trout (purple) and Chinook salmon (blue) in eastern Lake Ontario for the period of Dec. 1, 2016 to Apr. 30, 2019. Kernel density estimates (KDE) at 95% and 50% (darker colour) for the two species overlaid on the bathymetry of Lake Ontario. Red square in top panel shows area of zoom and angle variation.



Appendix 2

Table S5.1. Temperatures used in Fish Bioenergetics 4 for modelling growth of Lake trout (a) and Chinook salmon (b) in Lake Ontario. Past period is considered between 1983-1999, and present 2010-2019. Mean low and high future temperature increases are +0.4°C and +1.0°C, respectively.

(a)

Day	Past	Present	Low	High
1 (Apr. 1)	2.8	3.45	3.554	3.71
30	5.2	4.26	4.52	4.91
60	10	6.77	7.29	8.07
90	10	7.74	8.507	9.657
120	10	6.76	7.631	8.937
150	10	6.2	7.058	8.345
180	10	7.94	8.72	9.89
210	8	10.64	11.16	11.94
240	6	8.16	8.42	8.81
270	5	5.38	5.484	5.64
300	3.9	2.33	2.408	2.525
330	3	1.79	1.868	1.985
365	3	3.63	3.734	3.89

(b)

Day	Past	Present	Low	High
1 (Sept. 1)	14.3	15.07	15.93	17.21
30	14.3	14.56	15.34	16.51
60	12	11.23	11.75	12.53
90	6.5	8.17	8.43	8.82
120	4	6.14	6.24	6.40
150	4	4.59	4.67	4.78
180	4	3.81	3.89	4.01
210	4	3.93	4.03	4.19
240	5	5.46	5.72	6.11
270	12	10.89	11.41	12.19
300	14.3	12.02	12.79	13.94
330	14.3	13.25	14.12	15.42
365	14.3	15.05	15.91	17.20

Table S5.2. Number of observations per size class per period from 1977 to 2019 for lake trout and from 1976 to 2018 for Chinook salmon used for calculating the energy density and equations.

Size class	Period	Lake trout	Chinook salmon
Juvenile	Historic (1983-1999)	1074	259
Adult	Historic (1983-1999)	2545	642
Juvenile	Middle (2000-2009)	204	119
Adult	Middle (2000-2009)	1358	185
Juvenile	Present (2010-2019)	94	80
Adult	Present (2010-2019)	491	105
Subtotal Juveniles	All	1372	458
Subtotal Adults	All	4394	932
TOTAL	All	5766	1390

Table S5.3. Prey energy density (ED; in J/g) used for modelling in Fish Bioenergetics 4.

	Alewife	Slimy sculpin	Deep-water sculpin	Rainbow smelt	Round goby	Bloater
Past period (source)	4600 (Rand et al. 1994)	5004 (Hondorp, Pothoven, and Brandt 2005)	5703 (Hondorp, Pothoven, and Brandt 2005)	4500 (OMNRF 2009-2011 ED data)	--	--
All other periods/scenarios (source)	4800 (OMNRF 2009-2011 ED data)	5004 (Hondorp, Pothoven, and Brandt 2005)	3695 (Pothoven, Hondorp, and Nalepa 2011)	4500 (OMNRF 2009-2011 ED data)	5800 (OMNRF 2009-2011 ED data)	6,427 (Steven A. Pothoven et al. 2012; Hondorp, Pothoven, and Brandt 2005)

Table S5.4. Past period diet proportions per size (weight was extrapolated from data based on length-weight relationship) used for the lifetime growth simulations to assess the growth/weight potential of an individual's lifespan from age 1 through 15 for lake trout and 0 to 4 for Chinook salmon. Lake trout diet proportions were obtained from Rand and Stewart (1998), Madenjian, Desorcie, and Stedman (1998) and Chinook salmon from Rand and Stewart (1998).

Lake trout	Length (mm)	Weight (g)	Alewife	Slimy sculpin	Deep-water sculpin	Rainbow smelt
	<399	< 572	0.3	0.25	0.25	0.2
	400-499	572 - 1224	0.35	0.15	0.15	0.35
	500-599	1224 - 2298	0.35	0.15	0.15	0.35
	>600	>2298	0.6	0.1	0.1	0.2
Chinook salmon						
	<399	<655	0.77	0.02	0.02	0.19
	400-499	655-1460	0.81	0.02	0.02	0.15
	500-599	1460-2271	0.84	0.03	0.03	0.12
	600-699	2271-3113	0.85	0.03	0.02	0.1
	700-799	3113-6000	0.84	0.04	0.03	0.09
	>800	>6000	0.85	0.04	0.03	0.08

Table S5.5. Present period and future scenarios without diet change in proportions per size from the present-day period (weight was extrapolated from data based on length-weight relationship) used for the lifetime growth simulations to assess the growth rate potential of an individual's lifespan from age 1 through 15 for lake trout and 0 to 4 for Chinook salmon. Lake trout diet proportions were obtained from Rand and Stewart (1998), Madenjian, Desorcie, and Stedman (1998) and Chinook salmon from Mumby et al. (2018).

Lake trout	Length (mm)	Weight (g)	Alewife	Slimy sculpin	Deep-water sculpin	Rainbow smelt	Round goby
	<399	< 572	0.31	0.1	0.1	0.21	0.28
	400-499	572 - 1224	0.39	0.1	0.09	0.17	0.25
	500-599	1224 - 2298	0.47	0.12	0.1	0.19	0.12
	600-699	2298 - 3736	0.47	0.1	0.09	0.18	0.16
	>700	>3736	0.42	0.1	0.09	0.19	0.2
Chinook salmon							
	<399	<655	0.66	0.02	0.02	0.08	0.22
	400-499	655-1460	0.74	0.02	0.02	0.08	0.14
	500-599	1460-2271	0.78	0.03	0.03	0.07	0.11
	600-699	2271-3113	0.82	0.03	0.02	0.07	0.06
	700-799	3113-6000	0.82	0.04	0.03	0.08	0.03
	>800	>6000	0.84	0.04	0.03	0.08	0.01

Table S5.6. Future scenarios with diet change in proportions per size (weight was extrapolated from data based on length-weight relationship) due to bloater incorporation in diet. Note that values were taken from the present period and for bloater were balanced with these of Alewife. For diet proportion references see Table S5.5.

* Based on Stewart & Ibarra (1991) bloater comprised ~35-40% of lake trout diet prior to 1978 and up to 1988. Bloater comprised ~33% of Chinook salmon diet after Alewife crash in Lake Michigan, compared to ~10% prior to that.

Lake trout	Length (mm)	Weight (g)	Alewife	Slimy sculpin	Deep-water sculpin	Rainbow smelt	Round goby	Bloater*
	<399	< 572	0.11	0.1	0.1	0.21	0.28	0.2
	400-499	572 - 1224	0.04	0.1	0.09	0.17	0.25	0.35
	500-599	1224 - 2298	0.07	0.12	0.1	0.19	0.12	0.4
	600-699	2298 - 3736	0.07	0.1	0.09	0.18	0.16	0.4
	700-799	>3736	0.02	0.1	0.09	0.19	0.2	0.4
Chinook salmon								
	<399	<655	0.33	0.02	0.02	0.08	0.22	0.33
	400-499	655-1460	0.41	0.02	0.02	0.08	0.14	0.33
	500-599	1460-2271	0.45	0.03	0.03	0.07	0.11	0.33
	600-699	2271-3113	0.49	0.03	0.02	0.07	0.06	0.33
	700-799	3113-6000	0.49	0.04	0.03	0.08	0.03	0.33
	>800	>6000	0.51	0.04	0.03	0.08	0.01	0.33

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