Title: Spatio-temporal interactions of native and introduced salmonid top predators in a large lake: Implications for species restoration

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Abstract

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.

Keywords: salmonids, predator interactions, species management, acoustic telemetry, large lakes, ecosystem function, species co-existence

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., 1988), 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., 1988). 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, we 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. We 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, we tracked the species over a 2.5-year period in Lake Ontario.

MATERIALS AND 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 (Fig. 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, we 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; Fig. 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. (2020). 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 half 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; Fig. 1) and November 3, 2016 at Charity Shoal (44.04218º, -76.48386º; n = 21) and another 20 (implanted with pressure/temperature sensor tags) 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. 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, 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 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 we 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 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, we used the following timeframes established by Ivanova et al. (2020) 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, we used the *kde* function in the *ks* package (Chacón and Duong, 2018). We 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 (Fig. 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 (Fig. 2; see Supp Table S1 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 (Fig. 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 (Fig 3B; Supp Table S2). 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 (Fig. 4). Interactions occurred in 2017 between June and October, and in 2018 in May and July through October (Fig. 5a). Interactions were not significantly different between daylight hours and night ($p = 0.1$; Kruskal-Wallis rank sum test; Fig. 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; Fig. 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, we 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., 2020). 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, SV, Fisk AT, Johnson TB, *In Review*). 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, SV, Fisk AT, Johnson TB, *In Review*) 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, we gained valuable fine-scale insights 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. (1988), 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 Fig. 1) and homogeneity of bathymetric features in the western basin in comparison to the eastern, we 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, we 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), we 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.

Author Contributions

SVI, TBJ and ATF conceived, designed and planned the study. SVI, SML, TBJ, and ATF led and participated in the field work. SVI performed all analysis and wrote the manuscript. SVI, SML, TBJ and ATF contributed to and edited the manuscript.

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Data Availability Statement

Data from this project has not been made available or shared due to it still undergoing analyses for other projects.

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Table 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 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).

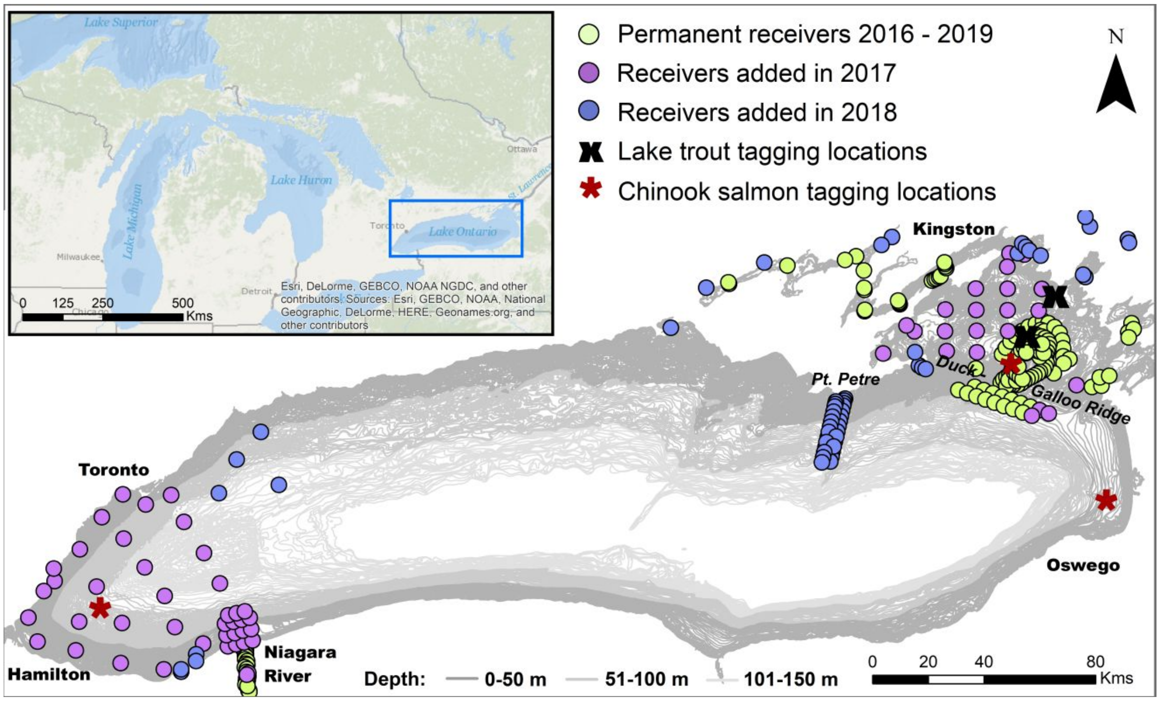


Figure 2. Eastern Lake Ontario lake trout (peach) and Chinook salmon (blue) 50% kernel utilization distributions and potential overlap (purple) in two-dimensions for winter, spring, summer/stratified and fall lake thermal seasons. Note: all IDs (with and without a depth sensor tag) were included in this 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.

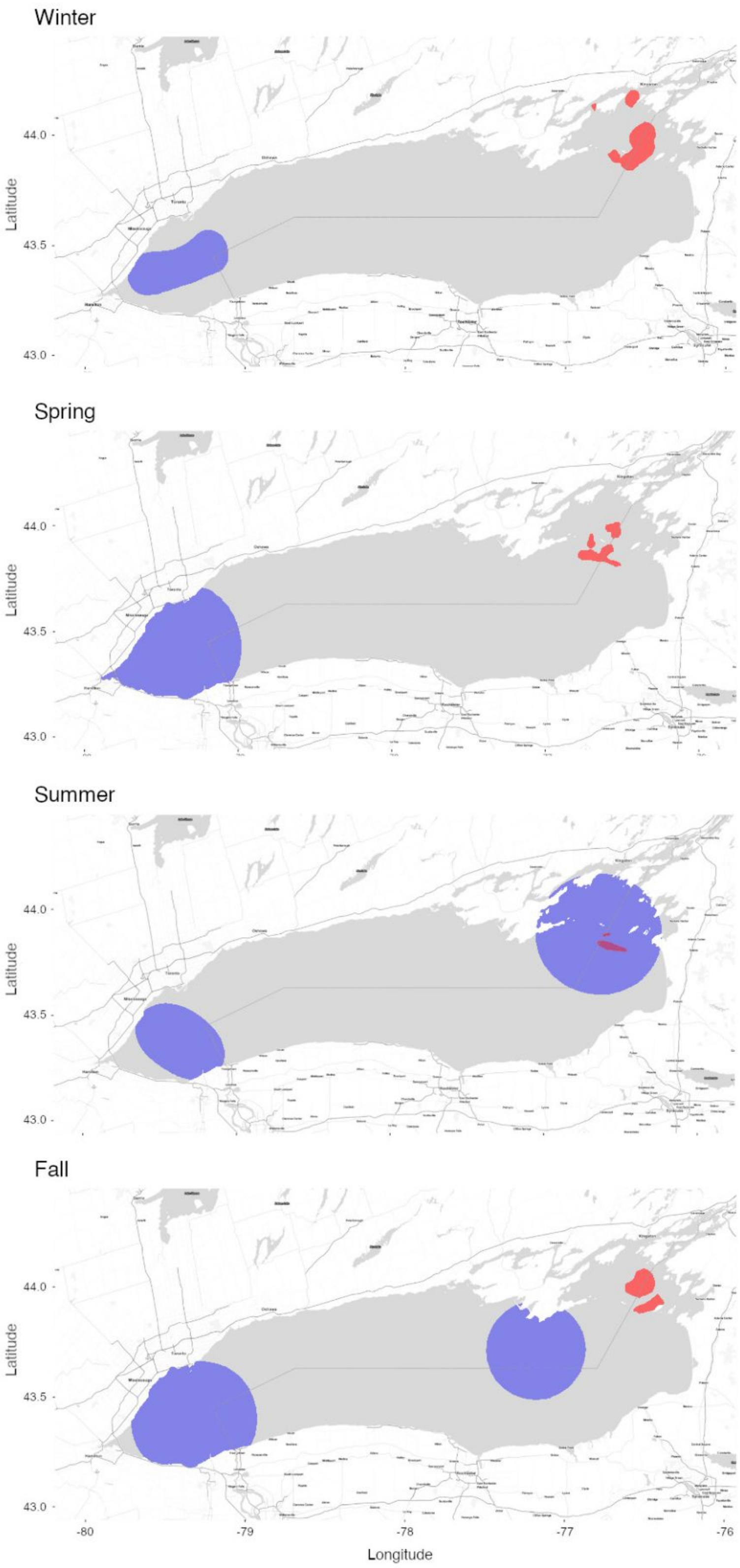
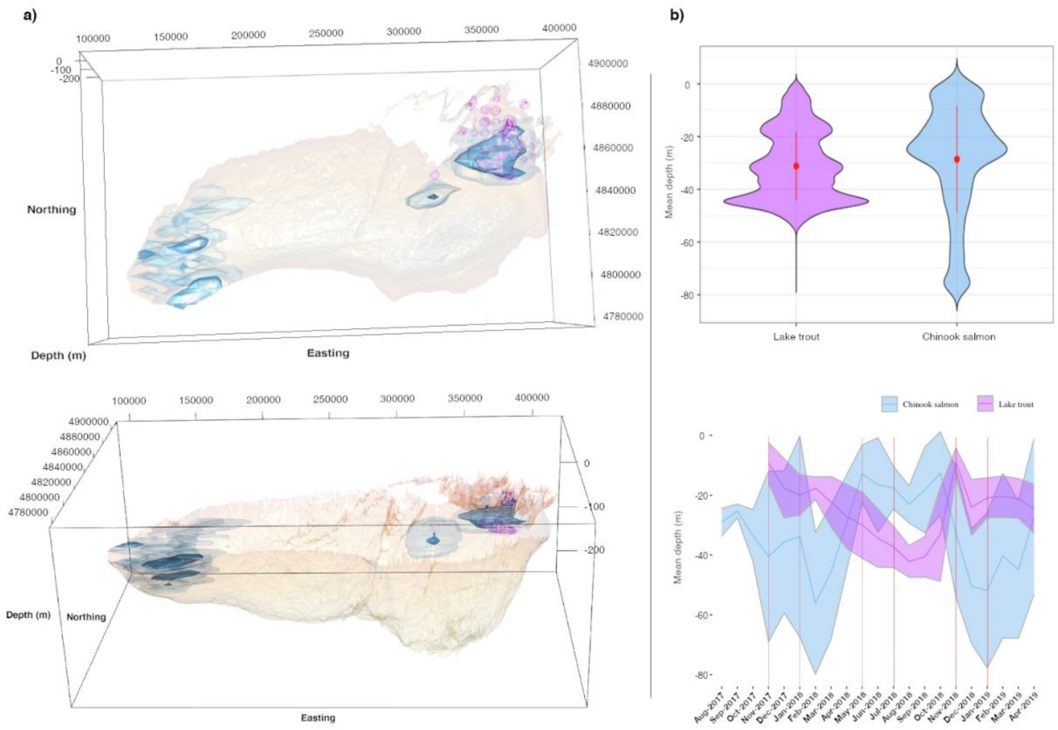

Winter
Spring
Summer
Fall
Latitude
44.0
43.5
43.0
-80
-79
-78
-77
-76
Longitude

Figure 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 Supp Figure S1 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 Supp Table S2; 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.)


a)
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300000
350000
400000
0
-100
-200
4900000
4880000
4860000
4840000
4820000
4800000
4780000
Northing
Depth (m)
Easting
b)
Mean depth (m)
0
-20
-40
-60
-80
Lake trout
Chinook salmon
Chinook salmon
Lake trout
Aug-2017
Sep-2017
Oct-2017
Nov-2017
Dec-2017
Jan-2018
Feb-2018
Mar-2018
Apr-2018
May-2018
Jun-2018
Jul-2018
Aug-2018
Sep-2018
Oct-2018
Nov-2018
Dec-2018
Jan-2019
Feb-2019
Mar-2019
Apr-2019

Figure 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.

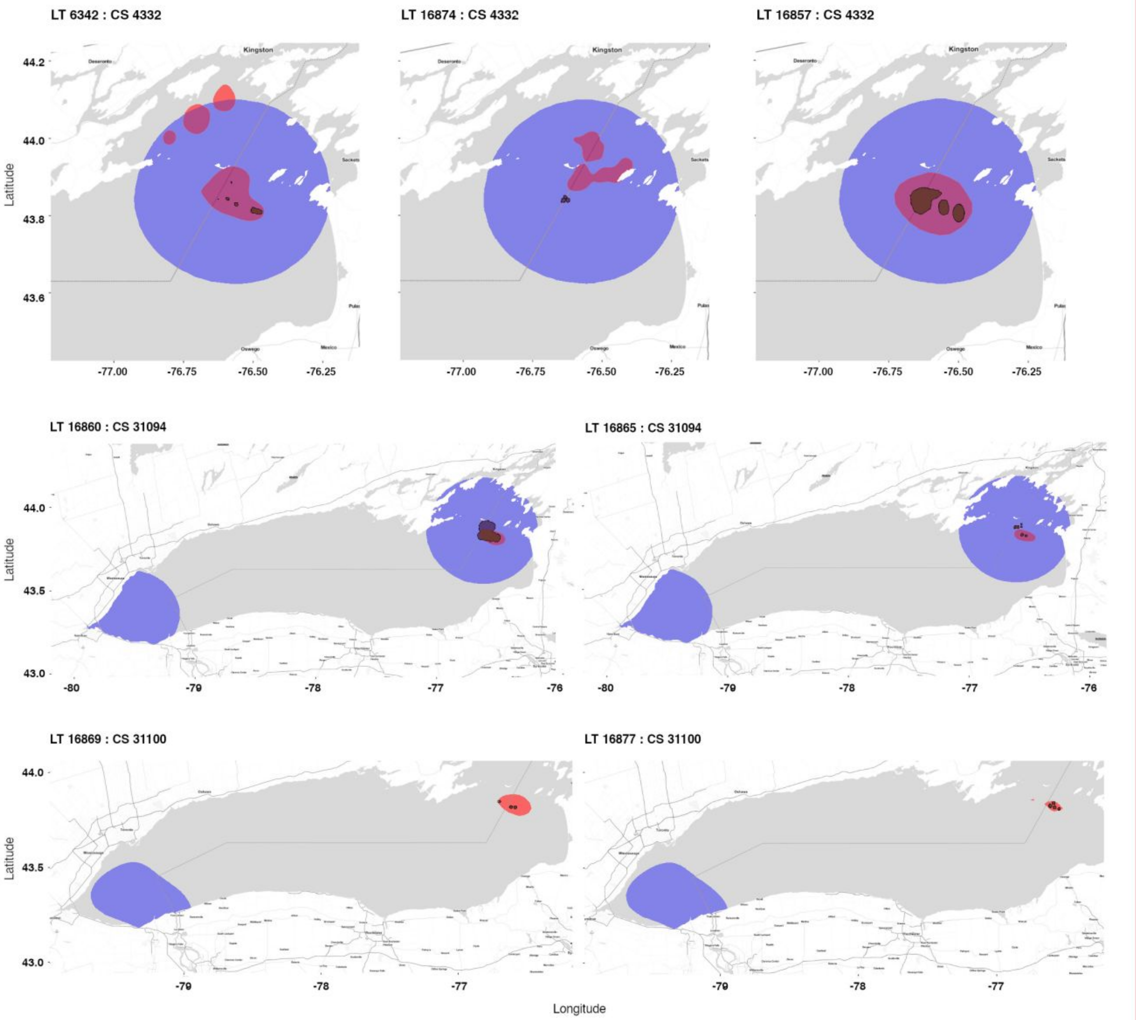
LT 6342 : CS 4332
LT 16874 : CS 4332
LT 16857 : CS 4332
Kingston
Deseronto
Sackets
Oswego
Mexico
Pulas
44.2
44.0
43.8
43.6
-77.00
-76.75
-76.50
-76.25
LT 16860 : CS 31094
LT 16865 : CS 31094
44.0
43.5
43.0
-80
-79
-78
-77
-76
LT 16869 : CS 31100
LT 16877 : CS 31100
Latitude
Longitude

Figure 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.

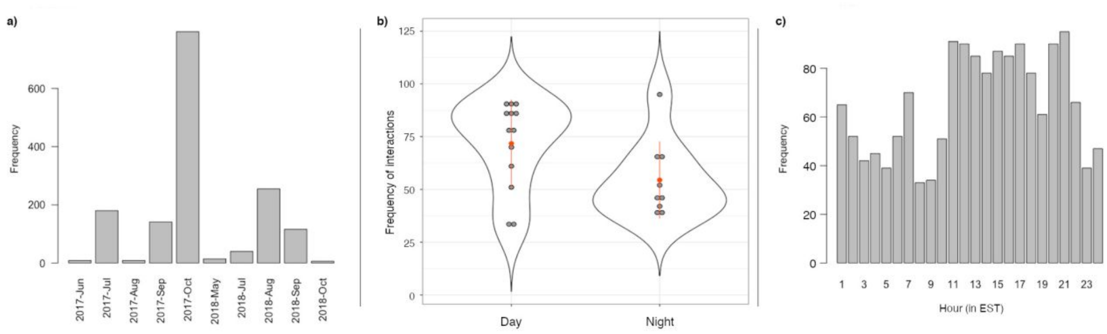

Figure 6. Mean depth violin plots for periods of identified joint potential path areas (jPPA) for lake trout and Chinook salmon in Lake Ontario. Gray circles represent the means, whiskers the SD and violin the distribution. Mean depth during the identified interactions were statistically different between the two species (p = 0.004, Kruskall-Wallis paired rank sum test). Note: only fish with a depth sensor tag were included in this analysis.