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Pop-off data storage tags reveal niche partitioning between native and non-native predators in a novel ecosystem

Graham D. Raby¹  | Timothy B. Johnson² | Steven T. Kessel¹  | Thomas J. Stewart² | Aaron T. Fisk¹

¹Great Lakes Institute for Environmental Research, University of Windsor, Windsor, ON, Canada

²Glenora Fisheries Station, Ontario Ministry of Natural Resources and Forestry, Picton, ON, Canada

Correspondence

Graham D. Raby
Email: graham.d.raby@gmail.com

Present address

Steven T. Kessel, Daniel P. Haerther Center for Conservation and Research, John G. Shedd Aquarium, Chicago, IL, USA

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Abstract

1. Niche partitioning might be predicted to be particularly dynamic in 'novel ecosystems' characterized by human-altered environmental conditions and biological invasions. Restoration efforts for native species in such systems can be informed by detailed characterization of niche partitioning.
2. In Lake Ontario, fishery management agencies have been engaged in a long-term struggle to restore native top predators including lake trout (*Salvelinus namaycush*). Meanwhile, management agencies continue to stock non-native species like Chinook salmon (*Oncorhynchus tshawytscha*) into the lake to support a recreational fishery and to help control the abundance of a non-native forage fish, the alewife (*Alosa pseudoharengus*).
3. We used pop-off data storage tags to study fine scale (9.1M lines of data from 22 animals) behaviour and habitat use by lake trout (native) and Chinook salmon (non-native) in Lake Ontario in terms of depth and temperature, recorded at ≤ 70 s intervals for periods of up to 12 months.
4. Chinook salmon occupied warmer and shallower waters during summer than did lake trout, and their niche breadth was wider. They achieved greater niche breadth in part because they were much more active vertically, cumulatively traveling 103 ± 1 m/hour during summer (model-estimated median), whereas most lake trout were relatively inactive vertically (7 ± 1 m/hour). In each of our analyses, there was more inter-individual variation among lake trout than among Chinook salmon, driven by some lake trout that spent considerable time making forays into warmer, shallower waters.
5. *Synthesis and applications.* Our results illustrate the different foraging tactics used by two species in the Great Lakes and reflect their distinct life histories. Physical niche partitioning between Chinook salmon and lake trout helps to explain how these species can co-exist in a multi-species fishery even while having overlap in diet. The diversity of behaviours exhibited here by native lake trout have likely helped them persist during dramatic changes to the forage base in recent decades; that flexibility could help underlie their long-term prospects for restoration during future changes to the ecosystem.

KEYWORDS

behavioural thermoregulation, biologging, climate change, ecological restoration, restoration ecology, telemetry, thermal biology

1 | INTRODUCTION

Niche partitioning can in theory lead to equilibrium communities given a stable environment (Walker & Valentine, 1984). In reality, few ecosystems exist in a stable state, especially when considering that humans are manipulating ecosystems on unprecedented scales via habitat alteration, animal harvest, pollution, species introductions, and by changing the earth's climate systems (Steffen, Crutzen, & McNeill, 2007). Indeed, many ecosystems can now be described as novel (Hobbs, Higgs, & Harris, 2009), such that one might expect niche partitioning among species to be unusually dynamic (e.g., Layman, Quattrochi, Peyer, & Allgeier, 2007).

Biological invasions and the resulting competition between native and non-native species has added utility to the concept of the ecological niche (Jiménez-Valverde et al., 2011). Conservation practitioners interested in restoring native species in heavily disturbed landscapes may find that the historical niche previously occupied by the native species no longer exists, is occupied by non-native species, or some combination of both. Robust assessments of realized niche for native and non-native species in "novel" ecosystems undergoing restoration efforts could be useful in conservation triage (Bottrill et al., 2008); helping to prioritize restoration efforts for native species, and to assess whether changes to management of non-native species are needed.

Nowhere is this reality more evident than in the Laurentian Great Lakes of North America, the world's largest freshwater ecosystem. As a result of over-harvest of native fishes, destruction of spawning habitat, pollution, and introduction of >180 non-native aquatic species, the Great Lakes currently constitute a novel species assemblage that nonetheless continues to provide substantial ecosystem services (Bogue, 2000; Ives et al., 2019). In Lake Ontario, there is a vibrant recreational fishery for Chinook salmon (*Oncorhynchus tshawytscha*), a non-native Pacific salmonid introduced in the 1970s that continues to be stocked today because of its popularity among anglers and its capacity to suppress the abundance of a non-native forage fish, the alewife (*Alosa pseudoharengus*, Dettmers, Goddard, & Smith, 2012). At the same time, fishery management agencies that stock Chinook salmon into Lake Ontario are also engaged in long-term efforts to restore two native salmonids (OMNRF, 2018), lake trout (*Salvelinus namaycush*) and Atlantic salmon (*Salmo salar*), both of which, like Chinook salmon, are top predators as adults and may therefore ostensibly compete with Chinook salmon.

Chinook salmon and lake trout are both cold-water piscivores with similar gross morphology but distinct life histories and diet. Chinook salmon are semelparous (i.e., reproduce once and then die) and have a total life span in their native range that is typically 3–5 years, with the final 1–3 years consisting of a marine phase, or in the case of Lake Ontario a lake phase, where they rapidly increase

their body mass by orders of magnitude while feeding primarily on forage fish (Healey, 1991). In the Great Lakes, adult Chinook salmon are known to forage almost exclusively on alewife (Dettmers et al., 2012). There is considerable variation in Chinook salmon across their range in life-history traits like diet (Healey, 1991), but that variation is low in comparison to that exhibited by lake trout (Scott & Crossman, 1973). Lake trout typically do not reach sexual maturity until 6–7 years of age, are iteroparous, and commonly live for 10–20 years throughout their range (Scott & Crossman, 1973). Adult lake trout are known to be extremely flexible in their diet, which can include contributions from crustaceans, freshwater sponges, plankton and fishes (Scott & Crossman, 1973). In Lake Ontario, the primary prey of adult lake trout have likely shifted a number of times over the past century (Dietrich, Morrison, & Hoyle, 2006; Rush et al., 2012). Lake trout prefer ciscoes (*Coregonus* spp.) and sculpin (*Myoxocephalus* and *Cottus* spp.; Scott & Crossman, 1973); the former and deepwater sculpin (*Myoxocephalus thompsonii*) collapsed in Lake Ontario in the 1940s because of introduced species, overfishing and habitat alterations (Christie, 1972). Since then, lake trout shifted their diet to focus on alewife and rainbow smelt (*Osmerus mordax*)—both of which are non-native pelagic forage fishes (Dietrich et al., 2006; Elrod & O'Gorman, 1991; Rand & Stewart, 1998). More recently, their diet has shifted to include more round goby (*Neogobius melanostomus*), a non-native benthic species (Colborne et al., 2016; Rush et al., 2012). However, the diet of lake trout in Lake Ontario remains diverse and continues to include substantial contributions from alewife and rainbow smelt; as such, their collective isotopic niche is larger than any of the other salmonids in the lake (Mumby et al., 2018; Yuille, Fisk, Stewart, & Johnson, 2015).

Here, we report an investigation into the thermal and vertical behaviours and niche overlap between native and non-native predators in Lake Ontario using animal-borne data loggers. We used pop-off data storage tags (pDSTs) with Chinook salmon (non-native, introduced) and lake trout (native, undergoing restoration efforts), the first application of this technology in freshwater fishes (Raby, Johnson, Kessel, Stewart, & Fisk, 2017). Prior knowledge about the depth and temperature occupancies of these species in Lake Ontario based on sporadic fishery surveys (Elrod, O'Gorman, & Schneider, 1996; Stewart & Bowlby, 2009), in combination with a broader knowledge base about their biology, led us to predict that lake trout would occupy colder and deeper waters than would Chinook salmon. The data presented here complement recently published stable isotope data about diet overlap between these species (Mumby et al., 2018; Yuille et al., 2015), and provide the best characterization to date of the thermal and vertical niche segregation/overlap between the two species. As such, this study is relevant to discussions among fishery managers and stakeholders in the Great Lakes about the intensity of competition for resources (physical space, prey, temperature)

between native and non-native predators. We predicted that our study would show that, despite known overlap in diet, lake trout and Chinook salmon effectively use different physical space in Lake Ontario, providing evidence that they can co-exist in a multi-species fishery.

2 | MATERIALS AND METHODS

2.1 | Study site and fish tagging

This study was conducted in Lake Ontario (Canada/U.S.A.), which is ca. 19,000 km² in surface area, has a maximum depth of 244 m, and is mesotrophic in some nearshore areas but oligotrophic offshore (Ives et al., 2019). The methods we used to catch fish and to tag them with data loggers (pDSTs) have been described in detail elsewhere (Raby et al., 2017). Briefly, between 2014 and 2016, we caught Chinook salmon ($N = 32$) and lake trout ($N = 40$) in one of three areas of Lake Ontario by trolling. We were also interested in tagging other salmonids including Atlantic salmon, brown trout (*Salmo trutta*) and rainbow trout (*Oncorhynchus mykiss*) but, primarily because of low catch rates for these other species and a limited number of tags to deploy, we focused most of our tagging (and all analyses for this study) on lake trout and Chinook salmon. We externally tagged fish with a pDST (G5 long-life 20 bar depth-temperature logger with a timed-release unit enclosed in a combination float; Cefas Technology Inc.) with a harness we attached to the fish through its dorsal musculature, posterior to the dorsal fin. During the tagging procedure we held the fish in a water-filled trough where its gills were continuously irrigated with fresh water. The pDSTs were programmed to record pressure (in dBar ~ depth in m, precision: 0.08 m, accuracy: ± 2 m) and temperature (nearest 0.03125°C, $\pm 0.1^\circ\text{C}$) every 70 s, with the exception of key 2–3 day periods of interest where logging occurred at 5 s intervals. We programmed the tags to ‘pop-off’ and float to the surface approximately one year after the fish were released, after which a subset was found by members of the public and returned for download in exchange for a reward. Some tags were also retrieved via anglers who captured fish with tags still attached (<1 year after release). In all, we recovered and downloaded 12 tags from Chinook salmon and 11 from lake trout. After data filtering (see Appendix S1), we were left with 9,157,335 animal-borne depth and temperature measurements from 22 animals (11 of each species).

2.2 | Modelling depth and temperature

We modelled depth (m) and temperature (°C) as separate variables using generalized additive mixed models (GAMMs; ‘mgcv’ in R; Wood, 2017). We were interested in assessing absolute differences between the species and whether the two species differed as a function of time of year or time of day. We focused on a continuous period when we had data for a minimum of six individuals of each species (total $N = 4,098,245$), which occurred from May 3 (year-independent; Julian date = 123) through September 5 (Julian date = 249). Within that period, we modelled temperature and depth separately

for late spring (49 days: May 3–June 20, $N = 1,238,653$) and for summer (78 days: June 21–September 5, $N = 2,859,592$).

Model fits were compared using Akaike Information Criterion (AIC) scores and likelihood ratio tests ($\alpha = .05$; following Zuur, Ieno, Walker, Savaliev, & Smith 2009). Assumptions were checked by plotting model residuals against fitted values and against all predictor variables, including variables not included in modelling (e.g., tagging location). Each model included a random effect of animal ID and a temporal autocorrelation structure (‘corARMA’ in the package ‘mgcv’, following Zuur, Ieno, Walker, Savaliev, & Smith 2009). Further details on fitting of GAMMs are given in Appendix S1.

2.3 | Thermal niche differentiation and diversity

To visualize the thermal niche of each individual and each species as a whole, we fitted four distribution types to each individual's temperature data (normal, log-normal, gamma, Weibull) and then chose the distribution that best fit the actual data based on AIC using the ‘fitdist’ function in the ‘fitdistrplus’ package in R (Delignette-Muller & Dutang, 2015). We used data from eight Chinook salmon and 11 lake trout for which we had full summer datasets for each fish (June 21–September 1; $n = 2,553,303$ data points; See Figure S1 in Appendix S2). For each animal, we calculated two thermal niche breadth metrics, which were simply the size of the temperature range spanning the middle 80% and middle 90% of their temperature record. To assess diversity in niche breadth within each species, we computed the difference between the niche breadth of each individual and the mean niche breadth for the species. We used the upper 90 and 95% percentiles for each individual as indices of upper thermal limits. Each of these variables (upper thermal limit, niche breadth, niche breadth divergence from the species mean) were compared between species using Welch's t test ($\alpha = .05$). Further details on thermal niche analyses are given in Appendix S1.

2.4 | Bivariate niche size and overlap

We adopted methods designed for home range estimation to quantify the bivariate (depth and temperature) physical niche of our animals, using analysis tools in the R package adehabitatHR (Calenge, 2006). We focused on using data from summer, when we had 19 individuals with datasets that extended through most of summer (June 21 through September 1; same dataset as analyses of thermal niche, described above). First, we used the minimum convex polygon method (‘mcp’ function in adehabitatHR) to estimate the relative size of the ‘home range’ of each animal based on the 80% most central locations (in terms of depth in m, temperature in °C). Second, we estimated the kernel utilization distribution (KUD; ‘kernelUD’ function in adehabitatHR, ‘grid’ set to 300, ‘extent’ set to 1) for each animal as a form of home range estimation, which allowed us to estimate the proportion of each animal's ‘core’ home range (80% KUD) that was overlapped by each other animal in the sample (‘kerneloverlapHR’ function in adehabitatHR). For each animal, we then

calculated the mean proportion by which it overlapped the home range (80% KUD) of individuals of the same species and a mean for its overlap with individuals of the other species. We also repeated both analyses (home range size and overlap with others) at the species level (data from all individuals pooled). We then used Welch's *t* test to make comparisons between species for home range size and overlap ($\alpha = .05$).

2.5 | Patterns in vertical activity

We were interested in modelling species-specific diel patterns in vertical activity during the summer period when we had data for a sufficient number of fish to do so (eight Chinook salmon, 11 lake trout; Figure S1). We used the cumulative vertical travel for each hour for individual fish, by summing the absolute value of all changes in depth with each measurement (every 70 s). To build models that fit the data, we built separate time-of-day (24 hourly bins) models of vertical travel for each species (fitted with a poisson distribution for lake trout, log-normal for Chinook salmon). To ensure the datasets were small enough to allow models to converge, we fitted GAMMs on datasets that were made up of 24 data points per individual: 24 hourly medians of vertical travel (cumulative m/hour). Similar to our approach with absolute depth and temperature, we used GAMMs fitted with fish ID as a random effect and with a temporal autocorrelation structure. Our models provide estimates of hourly vertical travel for each species with 95% confidence intervals, allowing us to examine absolute species differences and diel trends within each species.

3 | RESULTS

3.1 | Upper thermal limits and niche breadth in summer

Chinook salmon realized a thermal niche in summer that was, on average, 54% wider than for lake trout (mean = 8.7 vs. 5.7°C wide) based on the middle 90% of each summer temperature record ($t_{15.5} = 3.9$, $p = .001$), and 39% wider (mean = 6.3 vs. 4.5°C wide) based on the middle 80% distribution ($t_{14.7} = 2.5$, $p = .03$; Figure 1). The upper limits of the thermal niche were also clearly higher in Chinook salmon than in lake trout based on both the 90th percentile (mean = 16.0 vs.

9.6°C; $t_{14.5} = 8.8$, $p < .001$) and the 95th (16.9 vs. 10.4°C; $t_{16.0} = 8.8$, $p < .001$). However, it should be noted here that these upper limits for lake trout were not the species' realized upper temperatures for the full year, because lake trout inhabited a higher and broader range of temperatures in October and November than in the summer months (Figure 2), presumably owing to the lake becoming thermally mixed and movement of the fish into shallower waters based on their depth recordings for the same time period (Figure 2).

Summer thermal niche breadth and upper temperatures were more variable in lake trout than in Chinook salmon (Figure 1). Mean absolute distance from the group mean for summer thermal breadth was 153% higher (1.74 vs. 0.69°C) in lake trout for their 80% realized thermal niche and 146% higher (1.69 vs. 0.79°C) for their 90% realized niche when compared to Chinook salmon ($t_{16.2} = -2.7$, $p = .02$; $t_{12.9} = -2.4$, $p = .04$, respectively). Likewise, the same measure of variance was higher in lake trout than in Chinook salmon for their upper 90th percentile temperatures (117% more variable; $t_{13.0} = -2.35$, $p = .04$) but not for their upper 95th percentile temperatures (74% more variable, not significant; $t_{14.1} = -1.94$, $p = .07$).

3.2 | Species-specific temporal patterns in depth and temperature

In spring and in summer, there were clear differences in the temperatures and depths occupied between Chinook salmon and lake trout. Our data suggested that lake trout were, on average, 10.8 m deeper (model intercepts \pm standard error: 25.2 \pm 3.3 m vs. 14.4 \pm 2.5 m; $p < .001$) and 3.3°C colder (6.4 \pm 0.5 vs. 9.75 \pm 0.4°C, $p < .001$) than were Chinook salmon in late spring and 12.5 m deeper (33.8 \pm 2.3 vs. 21.3 \pm 1.7 m, $p < .001$) and 6.3°C colder (6.9 \pm 0.5 vs. 13.2 \pm 0.3°C) in summer (Figure 3, full model details in Table S1 in Appendix S3), trends that were apparent when the raw data were plotted by month (Figure 2). Both species tended to occupy deeper waters in summer, but only Chinook salmon exhibited a change (increase) in their mean temperature from spring (Figure 3e) to summer (Figure 3g).

There were no significant effects of date on vertical habitat use in spring (Table S1) in either species (non-significant smoothing functions shown for illustrative purposes in Figure 3b), but both species did experience increasing temperatures throughout the spring (Figure 3f). Meanwhile, we documented clear differences between species in how their vertical habitat use changed throughout the

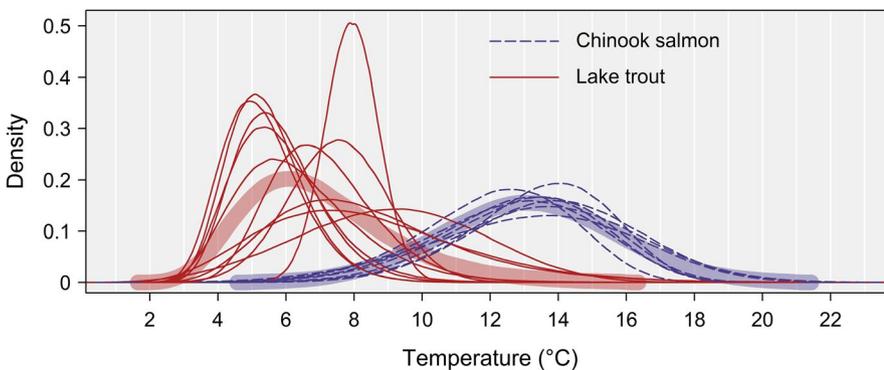


FIGURE 1 Density curves for the thermal records of 11 lake trout (red, solid thin lines) and eight Chinook salmon (purple, dashed lines) in Lake Ontario for which we had full temperature records from June 21 through August 31 based on externally attached data storage tags (see *Materials and Methods*). The thick, translucent lines in the background are based on all combined data for that species

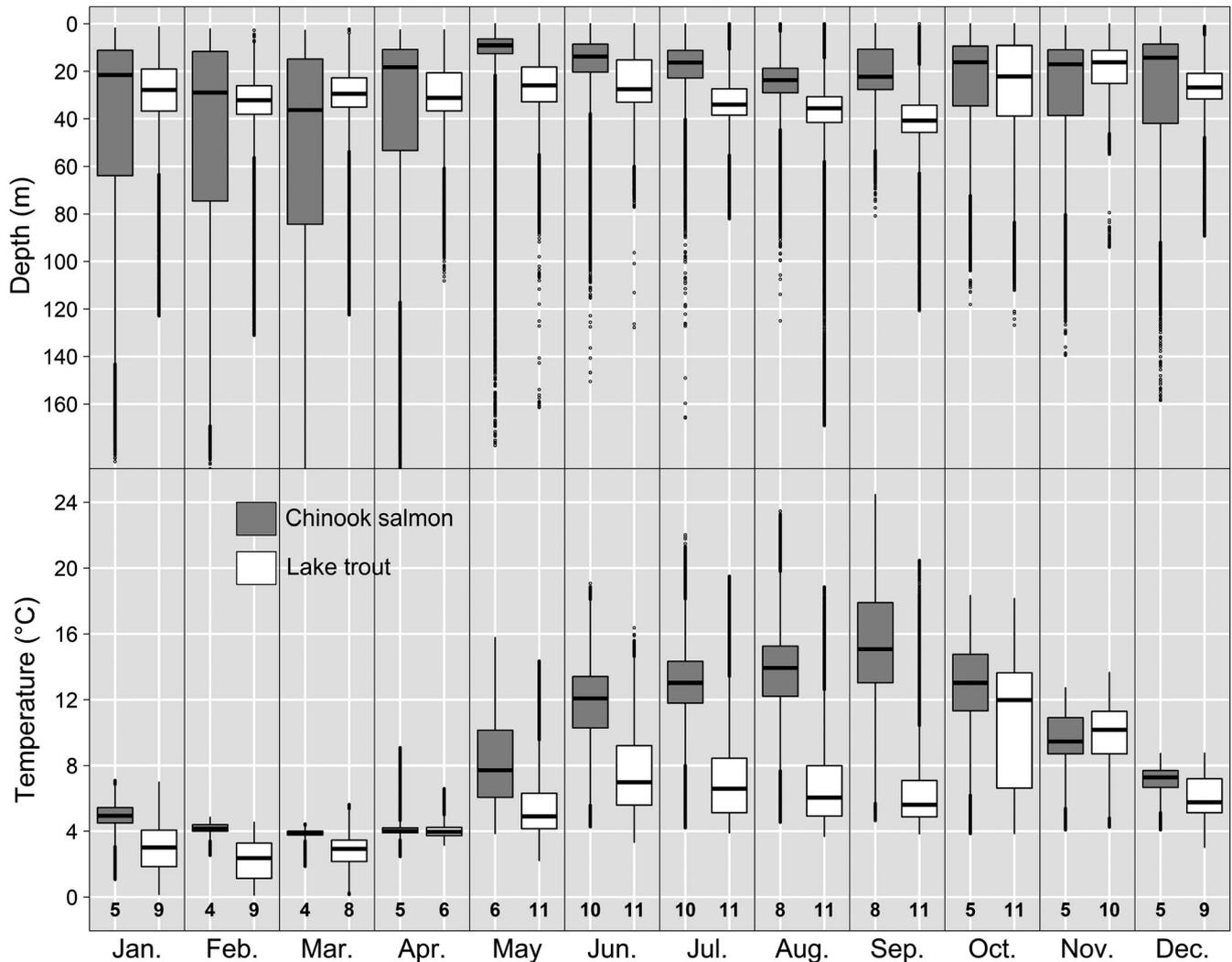


FIGURE 2 Month- and species-specific depth and temperature measurements from data storage tags attached to Chinook salmon (grey) and lake trout (white) in Lake Ontario ($N = 9,157,335$). Number of unique individual fish per species is shown along the bottom of the figure

day. As a species, lake trout exhibited negligible changes in depth or temperature across the 24-hr cycle in either spring or summer (Figure 3a,c). In contrast, the tagged Chinook salmon tended to show a crepuscular pattern in their vertical habitat use; using deeper waters in early morning (06:00–08:00) and in the evening (17:00–19:00; Figure 3a,c). Meanwhile, both species tended to occupy deeper waters as summer progressed (Figure 3d). At the same time, mean temperatures in Chinook salmon increased over the summer (by ca. 2°C) whereas there was a downward trend in our tagged lake trout (Figure 3h, Table S1).

3.3 | Bivariate niche size and overlap

At the species level, there was very clear separation between lake trout and Chinook salmon in the bivariate niche space they occupied in Lake Ontario. The core of the Chinook salmon ‘home range’ during summer based on KUD estimates approximated 10–16°C and 10–30 m in depth. Conversely, lake trout displayed, overall, a narrower home range size (165 dimensionless units of niche space

vs. 276 on average for Chinook salmon; $t_{15} = 2.26$, $p = .04$) with a high density of physical habitat usage occurring between 4–6°C and 30–40 m depth. In general, it was evident that there was more variation in niche size among individual lake trout than among individual Chinook salmon; the six smallest home range size estimates were for lake trout, as were the two largest (the latter were fish 10398001, 10409001—see Figure 4). As with thermal niche size, there was more variation in lake trout than in Chinook salmon when considering their bivariate niche space (absolute coordinates). On average, the KUDs (home ranges) of individual lake trout overlapped only 40% of the KUDs of other lake trout, whereas among Chinook salmon, mean overlap was 67% ($t_{15} = 6.38$, $p < .001$; Figure 4).

3.4 | Patterns in vertical activity

There was clear separation in the overall rates of vertical travel for the two species, with a model intercept of 103 m for Chinook salmon and 7 m for our model of lake trout vertical travel (Figure 5). In Chinook salmon, there was a crepuscular pattern (GAMM time-of-day

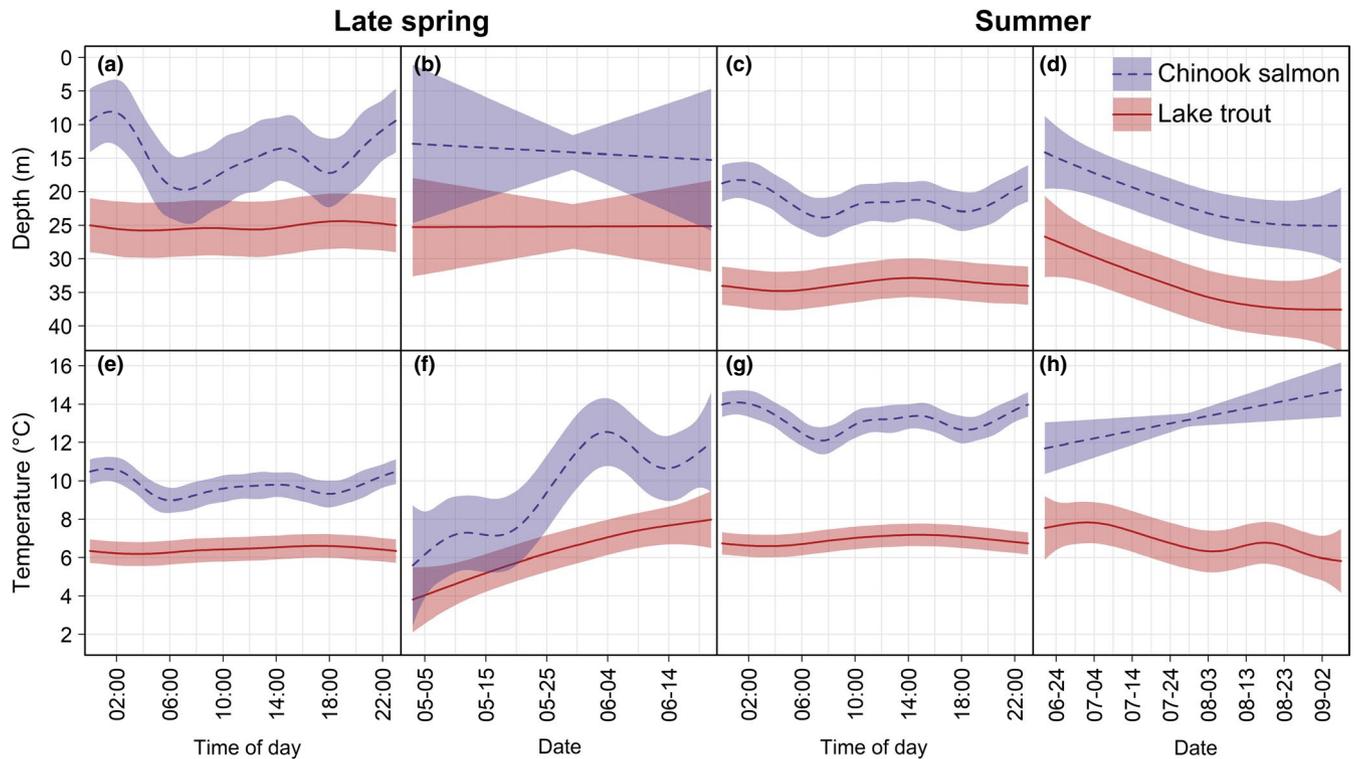


FIGURE 3 Smoothing functions for mean depth and temperature from four generalized additive mixed models (GAMMs) (Table S1) focused on temporal patterns and species differences (lake trout in red, Chinook salmon in purple): one GAMM for each of the two seasons and response variables (a,b = model for late spring depth; c,d = model for summer depth; e,f = model for late spring temperature; g,h = model for summer temperature). Note that the smoothers for effect of date on depth use in late spring (b) are shown here for illustrative purposes only; they were not statistically significant and were excluded from the final model for spring depth (Table S1). The areas shaded with either colour represent the 95% point-wise confidence intervals. Here, late spring encompassed May 3 through June 20, summer was restricted to June 21 through September 5. The summer models were developed using a sub-sampling (see electronic supplementary materials) of $N = 9,249$ data points from 21 unique individuals (11 lake trout, 10 Chinook salmon), while the late spring models were developed using a sub-sampling of $N = 5,248$ data points (11 lake trout, 10 Chinook salmon)

smoother, $p < .001$), with the highest activity occurring close to sunrise and sunset, and the lowest at night. For lake trout the least active period was also night (time of day smoother, $p < .001$), particularly from 22:00 to 05:00; median vertical activity increased through morning hours, peaked in late morning and declined gradually thereafter (Figure 5).

4 | DISCUSSION

We found Chinook salmon occupied a broader range of depths and temperatures than did lake trout in Lake Ontario, and there was clear niche segregation between the two species. In summer, lake trout inhabited a niche that was *ca.* 15 m deeper and 6°C colder than that of Chinook salmon. Chinook salmon realized a wider bivariate niche in large part due to their relatively high rates of vertical activity. A limitation to our ability to interpret the data was that we did not know the horizontal position (i.e., latitude and longitude) of the fish. A further caveat is that the potential effects of the bright orange, buoyant external tag on the behaviours of the fish were unknown; however, there was good evidence that fish survived, continued

growing, and (in the case of Chinook salmon), made spawning migrations into tributaries (Raby et al., 2017). Nevertheless, nearly all previous data on the vertical and thermal niche of these two species comes from angler catch records (but see Hinke, Watters, Boehlert, & Zedonis, 2005; Bergstedt, Argyle, Krueger, & Taylor 2012), an approach that is likely to suffer from the spatiotemporal biases associated with fishing effort (Thorson, Fonner, Haltuch, Ono, & Winker, 2016). Therefore, this study significantly improves our understanding of thermal and vertical niche segregation between lake trout and Chinook salmon in Lake Ontario.

4.1 | Causes of niche segregation

Collectively, we found that lake trout occupied a smaller, colder and deeper niche than did Chinook salmon, but we also saw more variation among lake trout than among Chinook salmon. Lake trout sampled in this study appeared to mostly stay near to or below the thermocline (where some forage fishes can be abundant) and travel vertically very little; perhaps foraging mostly on round goby and other benthic species occurring on or near the lake bottom (which could include some pelagic species like alewife). Had these fish been

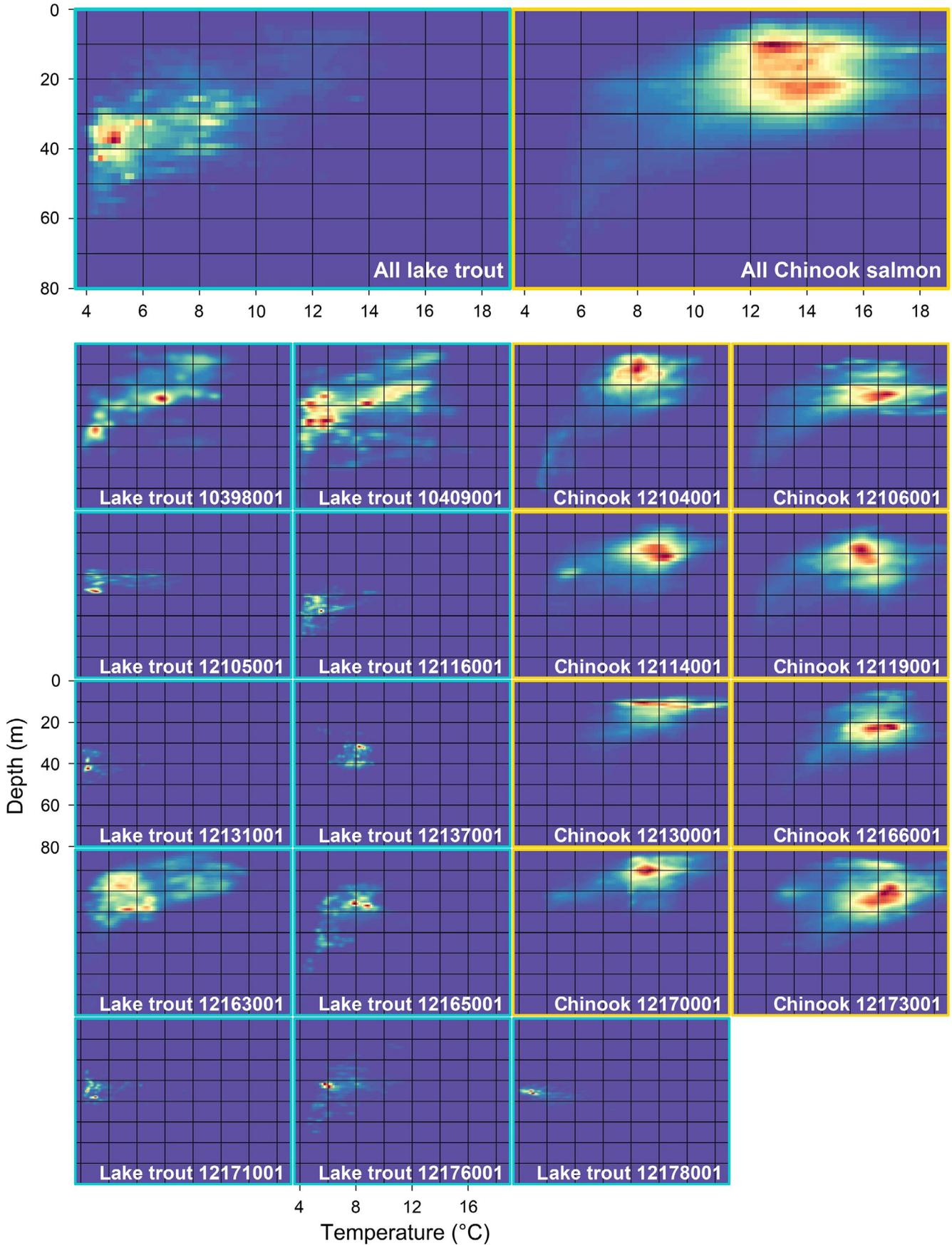


FIGURE 4 Bivariate kernel density estimates for the 19 fish for which we analysed summer bivariate niche size and overlap. For clarity, lake trout plots are outlined in light blue, Chinook salmon plots in yellow

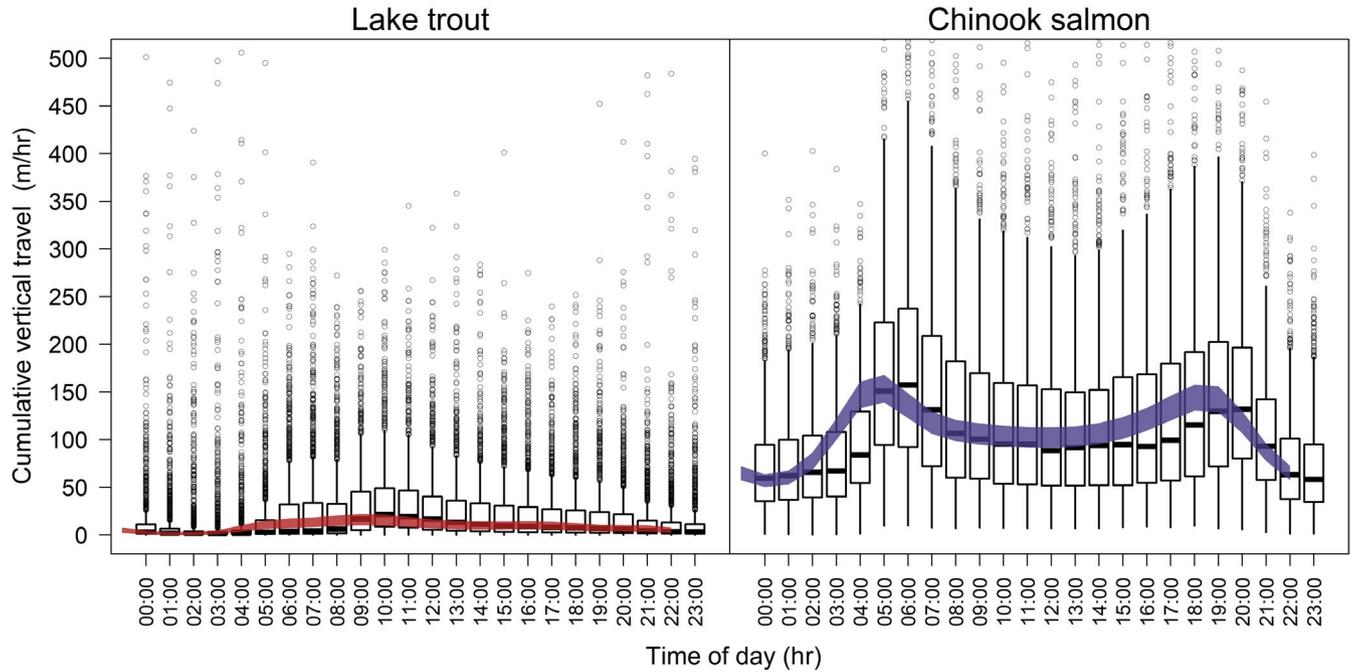


FIGURE 5 Cumulative changes in depth per hour per fish, with generalized additive mixed models (translucent coloured areas = mean \pm 95% confidence intervals) of the diel trends for both species. The boxplots represent all the raw data for both species. These data are based on eight Chinook salmon and 11 lake trout and cover a period of summer when we had full records of data for those individuals (June 21–September 1)

focusing on pelagic foraging, we might have expected to see more vertical activity (i.e., searching for prey in the water column). There were three lake trout (Figure 4) that clearly spent substantial time foraging above the thermocline, either in pursuit of alewife or rainbow smelt, or other prey nearer the shoreline, but these fish still appeared to remain primarily below the thermocline.

Chinook salmon are known to almost exclusively consume alewife in Lake Ontario (Jones, Koonce, & Gorman, 1993), and have one of the two smallest isotopic niche widths among salmonids there (Mumby et al., 2018; Yuille et al., 2015). In their native range, adult Chinook salmon forage primarily on another schooling pelagic fish, Pacific herring (*Clupea pallasii*; Healey, 1991). Perhaps reflecting their relative specialization for foraging on pelagic fishes, and unlike lake trout, there was low variation in physical niche dimensions and size among Chinook salmon in our study. They were vertically active, covering a wide range of temperatures and depths (presumably in search of pelagic fishes), but spent most of their time in warmer waters (cf. lake trout) above the thermocline. Overall, our data on the thermal and vertical niche of these species in Lake Ontario appear to corroborate what previous studies have shown regarding the diet of the two species, suggesting that they are currently, to some extent, partitioning the available foraging resources (Mumby et al., 2018; Yuille et al., 2015) in addition to occupying distinct vertical and thermal niche space (present study). It is possible that these two species naturally have little overlap in their fundamental habitat requirements, or that one species is ‘pushing’ the other into a more confined niche space than it otherwise would occupy – our study does not allow us to make a clear conclusion with respect to either possibility.

4.2 | Realized versus fundamental niche

Our data provide the first quantification of realized vertical and thermal niche based on animal-borne data for adult Chinook salmon in the Laurentian Great Lakes, and the first for lake trout outside Lake Huron (Bergstedt, Argyle, Krueger, & Taylor 2012). While our dataset quantifies realized niche, how do our findings compare with available evidence about the fundamental niches of both species?

In their native range, adult Chinook salmon are distributed throughout the North Pacific Ocean during the summer (Healey, 1991), and there are few historical data on their thermal and vertical niche. Ogura and Ishida (1995) manually tracked four Chinook salmon with depth-sensing acoustic transmitters in the central Bering Sea. In that sample, Chinook salmon depth data were evenly spread from the surface to ca. 50 m deep and averaged 29 m; only ca. 10 m deeper than in our study. Along the coastline of Oregon (U.S.A.), Chinook salmon apparently occupied a vertical niche of 0–150 m and a thermal niche of 9–12°C in summer (cf. 0–35 m, 10–16°C in the present study) based on externally attached data loggers (Hinke et al., 2005). Based on manual tracking of acoustically tagged Chinook salmon in the coastal environment of British Columbia during summer (Candy & Quinn, 1999), the average depth at which fish were detected was 70 m (range of 7–201 m) and all temperatures were between 9 and 10.5°C (i.e., the full range of temperatures available there). In Lake Ontario, a broad range of water temperatures exist during summer such that if it were a priority, Chinook salmon could behaviourally thermoregulate to remain close to the temperatures they are adapted to use in their

native range (i.e., 9–12°C, Candy & Quinn, 1999; Hinke et al., 2005). However, when Chinook salmon enter freshwater for spawning in their native range, they often experience warmer waters (Hinke et al., 2005) closer to the 10–18°C thermal window they occupied in our study. Therefore, their thermal niche in Lake Ontario likely falls within the same fundamental niche (i.e., physiological performance window) as the fish from which they descended on the west coast of North America.

Specific to Lake Ontario, there are a few previous reports of the temperatures and depths used by Chinook salmon. Wurster, Patterson, Stewart, Bowlby, and Stewart (2005) used analysis of otolith microchemistry to estimate summer temperatures for Chinook salmon during their pelagic feeding phase in Lake Ontario. They estimated that the mean temperature occupied by Chinook salmon was 19°C for July and August, which was at the extreme upper end of the temperatures our fish occupied (Figure 1). Our mean summer temperature for Chinook salmon was 13.2°C (Figure 3g,h), which is more in line with reports of temperatures occupied by this species in Lake Ontario based on fishing surveys (14.4°C in Olson, Winter, Nettles, & Haynes, 1988; 11–14°C in Stewart & Bowlby, 2009). Based on angling data from 1997 to 2005, Chinook salmon were caught by anglers at average depths of 13–14 m in Lake Ontario (Stewart & Bowlby, 2009), which is shallower than our model's estimated mean depth in summer of 21 m (Figure 3c,d).

Lake trout were historically thought to prefer 10°C and generally remain below the thermocline in stratified lakes (Scott & Crossman, 1973); the latter appears to hold true based on our data but by staying below the thermocline, lake trout in our study mostly remained well below 10°C (model estimated species mean = 6.9°C) with the exception of three individuals that occupied a niche closer to that of Chinook salmon (Figure 4). The median summer temperature for lake trout based on the best distribution fit of the full dataset was closer to 6°C (Figure 1). Olson et al. (1988) found lake trout were restricted to depths of 45 m or less, and that they were most commonly found at $10.1 \pm 2.8^\circ\text{C}$ (mean \pm SD) and 25.4 ± 8.9 m in Lake Ontario; shallower and warmer than in our study. Bergstedt, Argyle, Krueger, and Taylor (2012) implanted data loggers into lake trout in Lake Huron and found similar summer temperature occupancy as in our study, with means ranging from 5.3–8.4°C through July and August. Their depths were also comparable, with time- and strain-specific means for July and August ranging from 25–39 m (cf. model estimated mean depth of 34 m in summer in our study). Bottom trawling data collected for Lake Ontario in September (1979–1993) suggested mature lake trout were most commonly caught at depths of 25–45 m, and temperatures of 6–9°C (Elrod et al., 1996), in good agreement with our study. Thus, our data do not conflict with existing reports about the vertical and thermal distribution of lake trout in the Great Lakes, suggesting that, at least for Lakes Huron and Ontario, lake trout may have maintained a similar realized bivariate niche space over recent decades, despite changes to their diet (Dietrich et al., 2006; Rush et al., 2012).

Although we focused on a species comparison during summer when we had sufficient data to do so, our data for October and

November (Figure 2) show that lake trout moved into shallower waters (perhaps in the nearshore), possibly associated with spawning activity, after the lake became thermally mixed and occupied much warmer waters (ca. 8–14°C) than during the summer. Those temperature data for October and November (Figure 2), for the same individuals as in summer, show quite clearly that their fundamental niche extends well above their realized niche in summer.

4.3 | Application and future research

Lake Ontario is a novel ecosystem (Hobbs et al., 2009) due to a long list of species extirpations and introductions as well as physical modification of habitat (Christie, 1972; Ives et al., 2019; Mills et al., 2003). The ecosystem is also somewhat unique because, in addition to stocking native salmonids like lake trout as part of a restoration effort, Chinook salmon and other non-native salmonids continue to be stocked into the system owing to their popularity among anglers despite the possibility that their abundance could challenge the restoration of naturally reproducing populations of native species (OMNRF, 2018; Scott, Judge, Ramster, Noakes, & Beamish, 2005; Mumby et al., 2018). Stocking levels for both species were reduced in the early 1990s following work that showed predator demand and prey supply were unbalanced (Jones et al., 1993). Despite some year-to-year variance, stocking levels have remained relatively unchanged since 1993: lake trout and Chinook salmon have been stocked in similar numbers (data available via the Great Lakes Fishery Commission, <http://www.glfsc.org/fishstocking/>). Given that it was not possible for us to use a before-after control-impact design in our study, our data cannot be used to assess whether Chinook salmon are occupying thermal and vertical niche space that would otherwise be filled by lake trout were the former species not present. Despite some overlap in diet and space use, these two species are currently occupying distinct niche space in Lake Ontario in terms of depth, temperature (this study, and Elrod et al., 1996; Stewart & Bowlby, 2009) and diet (Mumby et al., 2018; Yuille et al., 2015). The data presented here may be useful for fishery managers when considering how to manage the system and communicate with stakeholders (Stewart, Todd, & LaPan, 2017), who may view lake trout and Chinook salmon as inherently being in conflict. In reality, along with previous work (Mumby et al., 2018; Yuille et al., 2015), the evidence here helps explain how Chinook salmon and lake trout can co-exist while sharing some of the same forage base (i.e., in part by exploiting alewife at different times and places).

The new temperature data presented here could be used to update the bioenergetics models that fishery managers use to assess the consumptive demands of predators, informing decisions about how many individuals of each species to stock. In addition, the new finding that Chinook salmon increase their vertical activity and average depth around sunrise and sunset during summer could be relevant to interpreting diel trends in catch-per-unit effort data from fishery surveys. Future research using telemetry tracking of these species will help to 'complete the picture' of niche partitioning given in this paper by providing the horizontal dimension to habitat use

(i.e., spatial segregation in terms of onshore-offshore, east-west). There appear to very few data on the thermal preferences of adults of either species (based on laboratory experiments, e.g., Edsall & Cleland, 2000), or on their thermal optima for key performance traits like growth or swimming performance (but see Stewart, Weininger, Rottiers, & Edsall, 1983 and references within). Such experiments (e.g., Kelly, Burness, McDermid, & Wilson, 2014) would be useful for defining the fundamental thermal niche of both species, which will be necessary to project whether fish will be able to use their 'built-in' thermal plasticity to take advantage of warming habitats (Magnuson, Meisner, & Hill, 1990).

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AUTHORS' CONTRIBUTIONS

A.T.F., T.B.J. and T.J.S. conceived the study and designed the data collection methods. All authors were involved in data collection. G.D.R. analysed the data and wrote the manuscript. All authors gave input on the manuscript and their approval for publication.

DATA AVAILABILITY STATEMENT

Data are publicly archived via the Dryad Digital Repository <https://doi.org/10.5061/dryad.kn02d60> (Raby, Johnson, Kessel, Stewart, & Fisk, 2019).

ORCID

Graham D. Raby  <https://orcid.org/0000-0002-0549-4017>

Steven T. Kessel  <https://orcid.org/0000-0001-7729-7701>

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