Title: Habitat selection of a migratory freshwater fish in response to seasonal hypoxia as revealed by acoustic telemetry

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Abstract (250 words)

Adaptive efforts to achieve water quality objectives by modifying nutrient loading can have attendant impacts on fish habitats and fisheries. Thus, coordinating fishery and water quality management depends on knowledge of fish behavioral responses to habitat change. This study combined acoustic telemetry of fish with water quality modeling to understand how water quality management might impact fishery management. We examined habitat use of a native demersal fish, lake whitefish *Coregonus clupeaformis*, in Lake Erie. We focused on the summer stratified period when habitat was expected to be most limiting and used a forecast model to predict temperature and oxygen in the hypolimnion when fish were detected. As hypothesized, lake whitefish occupied a subset of available conditions with occupied habitats characterized by a cool, normoxic, hypolimnion. On some occasions fish were detected when the hypolimnion was predicted to be hypoxic, suggesting that fish were either displaced vertically or horizontally into marginal habitats or uncertainty in model predictions was high. Still, when hypolimnetic conditions were hypoxic, fish tended to move toward normoxia as expected, but when initial conditions were cold with high dissolved oxygen, fish movements were toward lower oxygen (but still normoxic) conditions. We also observed a high affinity for fish to remain near the southern shore in eastern Ohio, Pennsylvania, and New York. If current nutrient reduction objectives are achieved and the extent and severity of hypoxia is reduced, an expansion of lake whitefish habitat and distribution may have significance to the spatial regulation of fishing effort in Lake Erie.

Keywords: habitat selection, coregonine, acoustic telemetry, dissolved oxygen, lake stratification

Introduction

Quantifying habitat use of migratory fish is especially important for spatial management of interjurisdictional species (Midway et al. 2016). When moving across an environment, fish are potentially exposed to different fisheries and variable exploitation rates (e.g., Liljestrand et al. 2019). Further, habitat quality may influence the duration of time spent in an area and the direction of movement in response to favorable or adverse cues. Complicating this situation, variations in habitat quality and the resulting effects on fish behavior may influence the vulnerability of fish to capture (Kraus et al. 2015, Chamberlin et al. 2020) or impaired health in suboptimal environmental conditions (Scott and Bollinger 2014). In this study, we employed acoustic telemetry to understand the influence of habitat availability on the habitat selection and movement of a fish targeted by an interjurisdictional fishery.

Acoustic telemetry has become a standard method for developing data on the spatial behaviors of fish (Cooke et al. 2013, Hussey et al. 2015), and extensive networks of passive acoustic receivers have provided novel insights on numerous species (Welch et al. 2002; Abecasis et al. 2018, Dembkowski et al. 2018, Ellis et al. 2019, Bangley et al. 2020). A key advantage of acoustic telemetry is the ability, passively and autonomously, to record the presence of tagged individuals wherever a receiver can be deployed. A researcher can then observe the locations of fish and identify areas and times when fish are absent (Kraus et al. 2018). When this information is combined with time series data on other variables, the researcher can evaluate whether occupied habitats represent a random sampling of available habitats to gain greater insights about habitat selection.

We examined movements and habitat selection of lake whitefish (*Coregonus clupeaformis*) in Lake Erie. Lake whitefish support an interjurisdictional fishery (cooperatively assessed by United States (US) state and Canadian (CA) provincial authorities, Figure 1) which has generated concerns about population decline, spatial patterns of exploitation, summer habitat refugia, and a need to improve stock assessment and management plan objectives (Brenden et al. 2010). Lake whitefish require cold, oxygenated, hypolimnetic conditions during summer for survival. Hypoxia is a recurring problem during the summer stratified period in the central basin of Lake Erie (Scavia et al. 2014). In recent decades, increases in dissolved phosphorous loading to Lake Erie have fueled algal blooms (Davis et al. 2019), which are associated with deoxygenated hypolimnetic conditions lagged by one year (Burns et al. 2005). Long-term increasing temperatures decrease the saturation level of oxygen and increase the summer stratified period, exacerbating hypoxia in the hypolimnion (Blumberg and DiToro 1990, Jane et al. 2021). Concerns about impacts on drinking water resources and fish habitats have prompted new attention to water quality objectives for nutrients, algal blooms, and the extent and severity of low oxygen in the central basin of Lake Erie through the renegotiated binational Great Lakes Water Quality Agreement (GLWQA 2012). For coldwater fishes such as lake whitefish, cisco (*Coregonus artedi*, Schmitt et al. 2020), and lake trout (*Salvelinus namaycush*), these water quality objectives have immediate significance to ongoing management, conservation, and restoration efforts.

To better understand the population structure, migration, survival, and summer habitat refugia of lake whitefish, fishery managers initiated acoustic telemetry studies in 2015 (MacDougall et al. 2019). Initially, arrays of passive receivers targeted boundaries between sub-sections of the lake to understand timing of walleye (*Sander vitreus*) movements in relation to spawning migration and the execution of fishery assessment surveys (Raby et al. 2018). Starting in 2016, a new, two-dimensional, systematic grid sampling design was gradually implemented to provide more information about movements and spatial distribution of multiple species (Kraus et al. 2018, Krueger et al. 2018). In parallel with this change to the passive telemetry receiver array, a physical model was developed to forecast depth-resolved temporal and spatial conditions of temperature and dissolved oxygen under seasonally stratified conditions in Lake Erie (Rowe et al. 2019). Here we utilized the physical model to hindcast hypolimnetic temperature and oxygen conditions at acoustic receivers during stratification for the first two years of full implementation of the two-dimensional receiver array (2017 and 2018). These years also corresponded with a peak in sample size of at-large, tagged lake whitefish, permitting an evaluation of seasonal movements and habitat use.

Our goal was to better understand how changes in oxygen and temperature during stratified conditions affected movements and habitat use of lake whitefish. The volume and location of suitable habitat (as defined by adequate oxygen and cooler temperatures) for lake whitefish and other species may shift rapidly (hourly) across large distances (several to tens of kilometers), mostly due to meteorological forcing (Kraus et al. 2015, Rowe et al. 2019). Lake whitefish tags were coded to allow tracking of individual fish, but did not provide additional information (e.g., estimated depth). Although we did not know whether individual fish were within depths encompassed by the hypolimnion, lake whitefish are demersal and we hypothesized that hypolimnetic temperature and oxygen conditions would be within reported ranges of suitability when fish presence was recorded on a receiver. As a corollary, we hypothesized that the range of bottom conditions from throughout the array would encompass supraoptimal temperatures and suboptimal dissolved oxygen values, such that fish would only be present at a restricted subset of available conditions.

While this exercise was itself valuable and typical of previous fish telemetry studies, we also considered that two dynamic processes were potentially interacting to produce the observed fish distribution. One process - already mentioned - was the short-term habitat changes caused by currents and meteorological forces. The second process was the movement of fish as they encountered changing conditions and chose either to stay in a location or seek out a different location. Here we developed an empirical linear model to predict conditions during the current detection, time t+1, based upon conditions at the previous detection, time t. We hypothesized that hypoxic (<1 mg/L) conditions at time t would result in a greater increase in dissolved oxygen values at the location at time t+1 than if initial dissolved oxygen conditions were normoxic (>4.0 mg/L). We also tested whether temperature could modify this response.

Our study provided important ecological information for the management of lake whitefish in Lake Erie and potentially other Great Lakes populations that are a focus of concern for declining recruitment (Ebener et al. 2021). Further, it elucidated some generalizable insights through comparative evaluation of i) habitat characterizations based upon conditions where fish were present, ii) habitat selection from a range of potential habitat conditions, and iii) habitat conditions that may cue movement. We discuss how this information could help develop or improve future studies of fish migration and habitat use.

Methods

Lake whitefish were tagged as part of an interagency field effort coordinated between Ohio Department of Natural Resources and Ontario Ministry of Natural Resources and Forestry. In the fall months (primarily November), historic spawning areas (Figure 1) were targeted with gillnets and electrofishing to capture adult fish for tag implantation. To obtain adult lake whitefish, standard gillnet assessment gears were deployed (Kraus et al. 2017), using overnight and short-term sets. Briefly, fish were captured, held in tanks, anesthetized with either continuous direct current or pulsed direct current (Vandergoot et al. 2011), implanted with acoustic telemetry tags, and released as soon as possible after regaining and maintaining equilibrium. The protocol for fish handling and tag implantation followed each agency's approved animal care policies, American Fisheries Society policies (Jenkins et al. 2014), and previous successful tagging studies on Lake Erie fish (Schoonyan et al. 2017; Reid et al. 2022).

Tags were a mixture of new tags and a small number of repurposed tags that were recovered by anglers from walleye in a separate project (Raby et al. 2018; Bade et al. 2019). Coordination through the Great Lakes Acoustic Telemetry Observation System (GLATOS, https://glatos.glos.us) ensured that sequential deployments of the same tag in different species were distinguished for this study. The tags were model V16-4H (16 mm diameter, 68 mm long, 24 g, estimated battery life = 2 to 5 years, power output = 158 dB; Innovasea, Halifax, Canada) and nominal delays had the same mean (120 s) across tags. Because tag supply and deployment were opportunistic, n=10, 37, and 105 tags were deployed, respectively in 2015, 2016, and 2017.

As GLATOS is a participatory system, detection histories of lake whitefish from 2017 and 2018 were compiled from receivers that were deployed and serviced by multiple individual agencies and researchers (Kreuger et al. 2018). Data were primarily recovered from a systematic grid of passive receivers (69 kHz VR2W, VR2TX, and VR2AR, Innovasea, Halifax, Canada) with 10-minute spacing in latitude and longitude across Lake Erie's central and eastern basins and slightly closer spacing (6-minute) in the western basin (Figure 2). Because the spacing was in minutes of longitude (or latitude) instead of arc-minutes of a circle, the longitudinal spacing decreased a small amount with latitude. Additional linear arrays from legacy projects during this period were more slowly decommissioned (e.g., from an area near Cleveland, OH, and along a division between the central and eastern sub-basins of Lake Erie; see https://glatos.glos.us). Because these other receivers had overlapping detection ranges with grid receivers, small portions of the lake had a substantial increase in detection probability, potentially skewing our view of habitat use. We excluded these redundant linear arrays from our analyses, focusing on the non-overlapping detection ranges provided by the grid design (Figure 2).

For each of the receiver locations served by the GLATOS network, predictions of hypolimnetic temperature and dissolved oxygen were estimated with a forecasting model developed by NOAA-Great Lakes Environmental Research Laboratory (https://www.glerl.noaa.gov/res/HABs_and_Hypoxia/hypoxiaWarningSystem.html). The NOAA model produces three-dimensional, hourly, predictions of temperature and oxygen based upon the Finite Volume Community Ocean Model (FVCOM; Rowe et al. 2019) in which advection-diffusion and exchange of oxygen with the atmosphere were simulated, and oxygen depletion rates assigned to the sediment and water column were temperature-dependent but otherwise uniform through time. Model inputs were meteorological data (e.g., wind direction and speed) and recorded water levels. Extensive skill assessment of model-predicted bottom temperature and dissolved oxygen in comparison to observations indicated that the model simulated much of the observed spatial and temporal variance in hypoxia, although the model exhibited limited skill in some aspects, for example hypoxia was overpredicted on average in the south-eastern central basin (Rowe et al. 2019). To focus on stratified conditions when hypoxia typically occurs, we censored our analyses to the months of July, August, and September during focal years of the study. We further censored data to include only the central and eastern basins of the lake (Figure 1), where a seasonal hypolimnion develops every year and because no lake whitefish tags were detected in the western basin during the stratified months of July, August, and September. The model provided predictions at each receiver location in hourly time steps. We used time to match lake whitefish detections with temperature and dissolved oxygen estimates for the bottom layer (ca. 1 meter) of the model output.

Each year was analyzed separately because fall tagging events resulted in different individuals and total numbers of fish at-large in the following year. A few detection histories were truncated due to recapture by the fishery, short-term mortality, or unknown factors that resulted in only detections near the tagging sites immediately after tagging; these cases were removed from the data. To understand the geographic distribution and spatial extent of movements during stratified months, maps of lake whitefish detections were examined. We considered that a large fraction of detections from only one or two fish would restrict our ability to draw inferences for the broader population of lake whitefish in Lake Erie. We evaluated this possibility by summarizing detection counts for each fish at each receiver. Additionally, we examined detections on each receiver geographically.

To understand habitat use or avoidance by tagged fish, we constructed bivariate kernel density distributions of tag detections within dimensions of water temperature and dissolved oxygen. To accomplish this, detections were categorized hourly. We found no cases when an individual fish was detected on more than one receiver within a particular hour. Thus, hypolimnetic values for temperature and dissolved oxygen were determined by temporal matching of hourly model predictions with timestamps of tag detections. Bivariate kernel distributions were then estimated from proportions of detections at each observed combination of temperature and dissolved oxygen. The distribution of these variables was evaluated graphically by comparison with previously published habitat preferences for lake whitefish from other ecosystems, indicating an oxythermal habitat envelope of suitable conditions defined as <19.5°C and >3 mg/L (Jacobson et al. 2010). In our experience, the habitat envelope encompasses marginal values that are rarely observed when lake whitefish are captured during population assessment surveys (H.A. Cook, personal observations); therefore, we expected to detect fish in a more limited subset of oxythermal conditions. We described oxythermal conditions by estimating bivariate kernel densities of the proportions of temperature and dissolved oxygen observations from the entire data set of hourly model predictions at each acoustic telemetry receiver (including hours with and without a detection). The result was evaluated graphically by overlaying habitat use and oxythermal distributions.

We considered that comparisons of habitat use and availability are only one facet of habitat selection. The concept of habitat selection (or other types of ecological selectivity like diet selectivity; Chesson 1978) entails situations when habitat use is disproportionately higher than habitat availability. The opposite of this would be interpreted as avoidance, or when habitat use is disproportionately lower than availability. We examined habitat selectivity for each combination of temperature and dissolved oxygen (each variable was rounded to whole units) by the ratio of the proportion of tag detections to the proportion of observations from all acoustic receivers. This formula represents the most basic formula for selectivity indices (Manly et al. 2002). As the raw ratio was bound by zero on the left side, we took the natural log and centered (i.e., subtracted the mean) the index such that high positive values could be interpreted as selection and low negative values interpreted as avoidance. Because the index was based on a ratio of proportions, which would be highly influenced by small sample size, we censored cases with less than 10 observations. Though alternate formulations of selectivity can incorporate more restrictive assumptions (Jacobs 1974; Chesson 1978; Vanderploeg and Scavia 1979), none were appropriate to use without the ability to match model predictions more precisely with fish depth. Future applications of electronic tagging methods that would advance estimation of selectivity are suggested in the discussion.

Telemetry data provide an advantage over basic distributional occurrences in that a sequence of locations representing movement across a landscape (or, in this case, seascape) can be determined. When the underlying habitat is also dynamic and moving on a similar time scale (such as with temperature and oxygen in the hypolimnion), the researcher can develop additional complementary analyses to better understand the behavior of habitat selection. We tested whether movements of lake whitefish exhibited avoidance of low oxygen (or attraction to high oxygen habitats) by subsetting the dataset based on pairs of adjacent detections on different receivers. From this we estimated the change in dissolved oxygen, using a generalized linear mixed model with a Gaussian error distribution. Predictors were initial dissolved oxygen and temperature, and we were able to account for individual variations by treating unique fish as a random effect. Models with initial temperature, initial dissolved oxygen, both factors, and their interaction were compared using Akaike's Information Criterion (AIC) model selection with maximum likelihood estimation (Burnham and Anderson 2002). Once a best model was selected, we compared models with and without the random effect of individual fish using analysis of variance, and then we estimated marginal (least-squares) means with Restricted Maximum Likelihood (REML) to construct confidence intervals and graphically evaluate separate models for each year. Graphical inspection of residuals against time, initial dissolved oxygen, or temperature revealed no patterns for either year.

Results

Tag detections from open-lake grid stations during stratified months of July, August, and September in 2017 and 2018 totaled n=457,737 (once dead individuals and false detections were filtered from the data; Simpfendorfer et al. 2015). Mortality was inferred either by lack of evidence of movement after release or by recaptures reported by the fishery. The filtered data reflected fish that were tagged and released in 2015, 2016, and 2017. A total of n=91 unique individuals were available for analysis, of which n=19 and n=87 were detected in stratified months during 2017 and 2018, respectively. As the tagging effort increased and more fish were at large in the second year of the study, more detections were recorded in 2018 (n=417,313) than 2017 (n=40,424). At the time of tagging, total length of these fish ranged from 436 to 721 mm (average TL = 608 mm), indicating that all were adults capable of spawning.

Detections during July through September occurred primarily south of the US-CA border in the eastern half of the lake (Figure 2). These detections were concentrated on relatively few receivers (primarily 7 or 8 depending on the year; Figures 2 & 3). To understand whether high levels of detections on a few receivers resulted from only a few individuals, we examined how detections were distributed with respect to individual fish and stations. Visual exploration did not reveal any prominent influence of a single or few individuals; rather, stations with high numbers of detections were spread across numerous individual fish (Figure 3). Further, stations with the highest detections were in the central basin in 2017 and the eastern basin in 2018 (Figures 2 & 3). For individual fish, the average number of detections per station was significantly higher in 2018, n=1304, than 2017, n=391 (ANOVA: F-statistic = 7.5, p-value = 0.007, with 117 denominator degrees of freedom).

Hypolimnetic oxythermal conditions (i.e., habitat availability) were more variable between years in August than July or September. In both years, oxythermal conditions in August peaked around 10°C and 7 mg/L (Figure 4). During July, hypoxia was present in 2017 but not in 2018. During August, conditions in 2017 were warmer with lower oxygen than in 2018 (Figure 4). In July of 2017, hypoxia was present and oxythermal conditions were diffuse without a prominent peak. By comparison in July of 2018, hypoxia was infrequent and oxythermal conditions showed a prominent peak at around 11°C and 5 mg/L (Figure 4). In both years, hypoxic conditions were well established in September, but oxythermal conditions peaked around 21°C to 22°C and 8 mg/L (Figure 4).

Peaks in habitat use of lake whitefish either overlapped or were shifted away from peaks in oxythermal conditions. For example, in 2017, some lake whitefish detections overlapped with hypoxia conditions (<2.5 mg/L) around 15°C in all three months (Figure 4). Other peaks in habitat use were either more diffuse (in July and August) or were concentrated at temperatures <20°C in normoxic conditions (Figure 4). By comparison, in 2018, peaks in habitat use did not overlap with oxythermal conditions in any month. During July of 2018, lake whitefish habitat use peaked at warmer (11°C) and included slightly lower oxygen (6 mg/L) levels than the primary peak in oxythermal conditions (Figure 4). In August, detections were more diffuse and completely separated from the primary peak in oxythermal distribution, with the majority of detections occurring where hypolimnetic conditions were around 12.5°C and 8 mg/L (Figure 4). In September of 2018 (similar to September of 2017), peak habitat use was shifted away from peak oxythermal distribution toward cooler (<20°C) normoxic conditions (Figure 4). The significance of adjacent but non-overlapping distributions of habitat use and peak oxythermal conditions are suggestive of an edge effect as explained in the discussion.

Selectivity index calculation provided a complementary view, emphasizing either selection or avoidance of hypolimnetic oxythermal conditions. Each year was somewhat different. In 2017, low sample size was a factor, and weaker values of selectivity or avoidance were mixed across the range of temperature and dissolved oxygen. In 2017, no prominent pattern of selection or avoidance was evident in August or September, but in July, two positive peaks in selectivity occurred: one at 17.5°C and 6 mg/L and a second at 15°C between 1.5 and 3.5 mg/L (Figure 5). Despite a larger sample, in 2018, all months showed wide variation in selectivity/avoidance across the ranges of temperature and dissolved oxygen. Although the categories were quite granular, there was a consistent region of weak selectivity from approximately 10°C to 20°C in normoxic conditions (5 to 9 mg/L). This somewhat diffuse area tended to be surrounded by a band of negative values indicating avoidance (Figure 5). A prominent peak in selectivity was only present in August in cold normoxic conditions (ca. 9°C and 9 mg/L).

Analyses of movement with paired detections supported the hypothesis that lake whitefish would tend to move toward sites with higher hypolimnetic oxygen conditions, but only when initial oxygen concentrations were very low or hypoxic. As with the previous analyses of static conditions, sample sizes were more limited in 2017 than in 2018. An important context was the time difference between paired samples in our analysis. In 2018, 90% (n=411,963) of paired detections were separated by 60 hours or less, but in 2017 when sample size was more limited, only 30% (n=677) of paired detections were separated by 60 hours or less. While this contributed to more variable results in 2017, the overall trend was similar between years, with the exception of the lowest temperature (10°C) case in 2017 when confidence intervals overlapped zero across a range of low oxygen conditions (Figure 6).

For each year, we found unequivocal support for the interaction model (with temperature, starting dissolved oxygen and their interaction as main effects) as measured by delta-AIC and weight of evidence (Table 1). Fixed effects explained a moderate amount of variability: R^2_{model} = 0.45 and 0.52 in 2017 and 2018, respectively. Analysis of variance demonstrated the necessity of including individual fish as a random effect (Table 1), and conditional models (i.e., inclusion of random effects) explained only slightly more variability than fixed effects alone: $R^2_{conditional}$ = 0.55 and 0.66 in 2017 and 2018, respectively. The characteristics of the response (i.e., movement observed as a change in hypolimnetic dissolved oxygen) were significantly modified by temperature and substantially different between years.

To evaluate the model results with marginal means, estimates with confidence intervals were calculated for 5° increments of temperature and whole unit values of dissolved oxygen, limited to values within the observed ranges in the data. In 2017, under hypoxic initial conditions (<2.5 mg/L), lake whitefish moved to higher dissolved oxygen concentrations at 15°C, but not at

10°C (Figure 6). In 2017, when initial conditions were normoxic, lake whitefish moved to lower dissolved oxygen concentrations between successive detections and the decrease in dissolved oxygen was greater at 15°C than at 10°C (Figure 6). In 2017, there were not enough observations at 20°C to develop marginal mean estimates of the change in dissolved oxygen, but in 2018, it was possible to contrast three temperatures across a wide range of initial dissolved oxygen values. Significant increases in dissolved oxygen between successive detections were observed whenever initial hypolimnetic dissolved oxygen was <5.0 mg/L, and the magnitude of the change was largest at 10°C and smallest at 20°C (Figure 6). At initial conditions of 5.0 mg/L, the change in dissolved oxygen was positive but no effect of temperature was detected (Figure 6). The response shifted from increasing (positive values) to decreasing (negative values) at an initial dissolved oxygen value of around 6.0 mg/L (Figure 6). In other words, hypolimnetic dissolved oxygen tended to decrease between successive detections when initial values were > 6.0 mg/L, and the magnitude of the change was again largest at 10°C and smallest at 20°C (Figure 6).

Discussion

Fish habitat selection can be difficult to quantify and predict when there are multiple dimensions and contributing variables (Beck et al. 2001, Peterson 2003, Rice 2005, Larson et al. 2013, Elliot et al. 2016). Results presented here highlighted three interrelated perspectives on the habitat selection of a coldwater fish species in a large, temperate, lacustrine ecosystem. These perspectives a) concerned the geography of the ecosystem, b) involved correlation with two key abiotic variables, and c) elucidated cues to movement, resulting in the habitat selection process.

Each of these perspectives is addressed below, and taken together, they can provide a basis for improving acoustic telemetry studies as well as informing strategies for resource management under future climate scenarios.

At a fundamental level, it is often of interest to describe the habitat use of animals in terms of geography to identify where they spend most of their time. Such areas may represent territorial home ranges, breeding or foraging sites, or refugia, and often vary through time at scales that range from diel, seasonal, and annual (Kie et al. 2010). Designation of areas with high habitat utilization typically benefits from subsequent analysis of habitat variables, in which observations include both locations where animals were present and absent. The advantage of the passive receiver array in Lake Erie is broad, non-overlapping spatial coverage (Kraus et al. 2018). For lake whitefish, the grid sampling design revealed a pattern of concentrated habitat use in the southeastern portion of the lake during stratified conditions. In particular, US waters along the Ohio-Pennsylvania border and along the New York shoreline had most of the detections in both years (Figure 2). Despite the presence of lake whitefish in survey sampling and commercial fishing catches (Cold Water Task Group 2022), our tagged fish that rarely occupied waters in Ontario, CA, were not detected in the western end of the lake during stratification.

Reasons for the geographical pattern of detections are not immediately obvious but invite speculation. One hypothesis of interest is that historical patterns of fisheries exploitation have significantly reduced migratory or behavioral modalities that would have utilized more northern habitats of central and eastern Lake Erie. There is certainly evidence from other species that this can happen (e.g., Hilborn et al. 2003, Kess et al. 2019, but also see Turner et al. 2021), and since the most recent glacial recession, other species in Lake Erie have evolved divergent migratory behaviors to colonize new spawning habitat (Stepien et al. 2018, Euclide et al. 2021).

Coregonine (e.g., lake whitefish, and cisco) harvest in Lake Erie once supported the largest freshwater fishery in the world, but cisco harvest collapsed during the 1920s (Koelz 1926, Regier et al. 1969), and lake whitefish harvest collapsed shortly thereafter (Applegate and Van Meter 1970). Whether this extraordinary level of fishing pressure could have resulted in a loss of behavioral migratory diversity remains an open question, in part because almost nothing is known of the behavioral modalities that existed prior to commercial exploitation in Lake Erie. Further investigation to examine potential effects of exploitation on spatial distributions of lake whitefish may be warranted, but the recent pattern of exploitation has exhibited a shift toward the west in fall and winter where we obtained fish for tagging. The largest fractions of Ontario's annual lake whitefish harvest were taken in the central or eastern basin during 18 of 31 years from 1980 to 2010, (OMNRF 2020). Since 2011, Ontario's largest fraction of lake whitefish harvest was from the western basin as whitefish abundance declined during an extended period of low recruitment (Cold Water Task Group 2022). Lake whitefish harvest since 2014 was incidental in Ontario waters as quotas were reduced in response to declining abundance (Cold Water Task Group 2022). The limitation of the analysis in this study is that it lacks tagged fish from spawning aggregations other than those in the western basin. Spawning aggregations in or near the eastern basin are less well known, but some of these may represent alternative migration patterns or behavioral modalities (e.g., Kraus et al. 2004, or Gahagan et al. 2015) that occupy Canadian waters more frequently.

A second potential explanation for the geographical pattern of lake whitefish detections involves gradients of primary productivity in Lake Erie. First, while most of the freshwater supply to Lake Erie comes from the Detroit River on the Michigan-Ontario border, nutrient loading is highest from the Maumee River followed by smaller but significant contributions from other Ohio tributaries (Scavia et al. 2014). The Detroit River ultimately drains the highly oligotrophic waters of Lake Huron (by way of the St. Clair River and Lake St. Clair), which contrasts sharply with the more turbid, eutrophic outflows from Ohio tributaries. Combined with a predominantly west-to-east flow of river plumes, an additional north-south gradient of increasing turbidity, nutrient concentration, and algal blooms is present. Lake whitefish may favor the combined advantages that low visibility waters provide as protection from predators and the increased zooplanktonic food supply fueled by higher nutrient and algal concentrations along the southern shore (Nieman et al. 2018). Clearly, trade-offs exist as eutrophic conditions may also bring increased levels of hypoxia that fish must contend with (Almeida et al. 2022). Linking water quality to lake whitefish habitat is indirect because this species is demersal and tends to feed on benthic macroinvertebrates (Lumb et al. 2007). Areas with lethal durations of hypoxia have a lower abundance of benthic organisms (Karatayev et al. 2017), but benthic macroinvertebrate abundance response to limiting nutrients and pollution along the US shoreline is more variable and instead results in a change in species composition (Krieger 1984, Scharold et al. 2015). Because the north-south gradient of visibility, nutrients, zooplankton diminishes and benthic macroinvertebrate prey availability changes toward the eastern end of the lake, spatially explicit diet analysis (beyond the scope of this study) would be needed to understand how macroinvertebrate communities influence lake whitefish habitat use.

A third hypothesis to explain the geographic concentration of detections partially involves the second hypothesis regarding productivity. Although north-south productivity differences diminish toward the eastern end of the lake, conditions of temperature and oxygen may limit lake whitefish habitat utilization in more productive regions in the western part of the lake. The obvious endpoint for this third hypothesis is the supra-optimal temperatures and lack of hypolimnion that occur seasonally in the western basin of the lake. High temperature and absence of a cold hypolimnion explains the seasonal summer absence of lake whitefish in the west despite the higher concentration of food (i.e., behavioral thermoregulation, *sensu* Raby et al. 2018). By comparison, the central basin of the lake is deeper (Figure 1), and the abiotic conditions are more variable. Greater depth permits development of a seasonal thermocline, which isolates a cold hypolimnion as the season progresses. Isolation also limits replenishment of oxygen from surface water diffusion and mixing; therefore, oxygen depletion is another characteristic of the hypolimnion in the central basin (DeLorme 1982). Linked to increased nutrient loading, oxygen depletion leading to hypoxia has become more intense and widespread in recent decades (Zhou et al. 2013, Jabbari et al. 2021). Recent modeling work has demonstrated that hypoxic zones can shift rapidly on short time scales from meteorological forcing (Rowe et al. 2019). Although, upwelling events have been quantified on both the north and south shores of the central basin (Rao et al. 2014, Beletsky et al. 2012), the hypolimnion is thinner along the US coastline and tends to be more variable (Rowe et al. 2019). The eastern end of the central basin is slightly deeper and less frequently affected by hypoxia (Ludsin et al. 2001). Prevailing southwest winds in Lake Erie may contribute to a sustained, imbalanced north-south hypolimnetic distribution in the central basin, offering more habitat volume in the east-central basin for lake whitefish. In addition, a deep channel north of Pennsylvania's shoreline connects the variable habitat of central Lake Erie with more stable, oligotrophic conditions of eastern Lake Erie. This passage may represent an important conduit for lake whitefish movement, making them less susceptible to upwelling-induced mortality. Thus, the combination of a small increase in productivity near the south shore combined with unfavorable hypolimnetic conditions in the rest of the central basin, may account for the high frequency of detections near the Ohio-Pennsylvania-New York border.

Clearly, more definitive tests of the third hypothesis are needed. Moreover, the third hypothesis contributes little explanation to why only a small number of receivers accounted for the vast majority lake whitefish detections (Figures 2 & 3). As noted above, no single individual or sub-group of individuals accounted for the high numbers of detections on these receivers; thus, we can posit that this may represent a population-level phenomenon or at least a phenomenon of the tagged population of adult lake whitefish. Some fine-scale factors may exist that account for a high habitat preference near these few receivers, but data from this study do not provide information to examine whether local resources can explain the detection histories. Alternatively, detection efficiency of acoustic telemetry receivers can vary greatly through time and space (Binder et al. 2016; Huveneers et al. 2016; Klinard et al. 2019). While a comprehensive evaluation of acoustic transmitter detection efficiency is lacking for Lake Erie compared to other Great Lakes systems (e.g., see Hayden et al. 2016), acoustic receivers deployed offshore (i.e., > 10 km) in Lake Erie exhibit high annual detection efficiency (>80%) along the northern and southern shorelines of the central basin (Vandergoot, unpublished). Although the thermocline can be variable on time scales of minutes to hours in Lake Erie, the receivers in this area straddled the typical depth of 15 m. This arrangement could have reduced detection efficiency up to 50% if the tag and receiver were on opposite sides of the metalimnion (Kuai et al. 2021), highlighting the need for depth resolved telemetry information. Currently, data are not available to evaluate the specific receivers or locations in question for this study; thus, we cannot completely rule out variation in detection efficiency among receivers to account for the pattern.

Acknowledging that small-scale, site-specific factors may increase variation, the observed correlations of habitat use in dimensions of hypolimnetic temperature and dissolved oxygen remained evident. The distribution of hypolimnetic temperature and oxygen values that were matched to fish detections showed more variability than expected based upon habitat requirements reported in the literature. While the majority of detections occurred at suitable hypolimnetic temperatures <19.5°C and dissolved oxygen values >3 mg/L (Jacobson et al. 2010), there were a substantial number of detections in hypoxic conditions in 2017 (Figure 4). This result in part may be due to inaccuracies of predicted hypolimnetic conditions. In the southeastern region of the central basin, the water quality model tended to overpredict hypoxia (Rowe et al. 2019), which may have led to erroneous associations of lake whitefish and hypoxic conditions. In addition, uncertainty in depth of habitat of tagged fish and the possibility of tag detection at a distance in part explains why lake whitefish were sometimes associated with hypoxic hypolimnetic conditions. Previous research using bottom trawls and hydroacoustics for other species has shown that fish may occupy the metalimnion adjacent to hypoxia through horizontal or vertical displacement (Roberts et al. 2009, Vanderploeg et al. 2009, Kraus et al. 2015). This hypothesis could be tested in future tagging studies of lake whitefish through the application of tags that record or report depth (e.g., V16P-6H acoustic transmitters equipped with depth-pressure sensors, 69 kHz; InnovaSea, Bedford, Nova Scotia, see Gorman et al. 2019).

Although depths of tagged fish were unknown, it remains illustrative to estimate hypolimnetic conditions when fish were detected and compare these values with the range of oxythermal conditions from throughout the telemetry receiver array. The mismatched distributions of fish habitat versus peak oxythermal conditions supported the hypothesis that lake whitefish would occupy only a subset of available habitats (rather than a random sampling of available habitat). As fish seek preferred habitats and avoid unfavorable ones, this result is simply confirmatory of a general aspect of fish behavior. Rather, shifts in peak habitat use relative to peak habitat availability remind us that lake whitefish habitat selection involves other variables that are not completely represented in the space of temperature and oxygen. As mentioned above, some of these other factors may include spatial uncertainty in fish position, water quality model uncertainty, and lack of understanding in fish responses to gradients in turbidity and prey. Despite being coarse-grained and limited by sample size, habitat selection was apparent. Future tagging efforts in Lake Erie would benefit from the addition of vertical data logger strings on buoys or acoustic receivers to provide depth-matched observations with fish tags. More importantly, understanding habitat selection for summer refugia provides valuable information for managing lake whitefish fisheries near the southern extent of their range.

To extend the analysis further, comparison of paired detections provided an indication of how lake whitefish may behaviorally respond to hypolimnetic conditions. Without the benefit of depth measurements, fish could have been within or adjacent to the hypolimnion, but they responded predictably by moving toward areas with higher oxygen. The movement toward areas with lower hypolimnetic oxygen when initial conditions were normoxic is more difficult to explain. Some insight can be obtained from 2018, when our results showed that the highest initial oxygen levels were associated with the lowest temperatures (Figure 6). For lake whitefish, movement toward lower oxygen, but still normoxic, conditions would place fish in warmer conditions. This situation could provide a metabolic advantage especially in the early part of the stratified season when the hypolimnion is colder, but hypoxia has not become widespread. Bioenergetics modeling could be one way to investigate this idea but was beyond the scope of this present study.

Additionally, some of the variation could be attributed to seasonal warming and overall oxygen depletion in the hypolimnion (Burns et al. 2005). If sufficient time passed between paired detections, hypolimnetic oxygen will decline no matter where the fish is detected. This effect is unlikely to account for the pattern in lake whitefish because the oxygen depletion rate for Lake Erie's hypolimnion is typically constant around 2.5 mg/L per month (Conroy et al. 2011) compared with a decline ≤ 5 mg/L over the course of <60 hours (in 2018, see Figure 6 and notes on paired detection intervals above). The interactive effect of temperature lends indirect support for the hypothesis that fish habitat selection (rather than an underlying abiotic process) is driving the pattern. During the stratified season, hypoxia spreads throughout the central basin to encompass a larger volume of hypolimnion (Zhou et al. 2013, Rowe et al. 2019), naturally reducing spatial variation in dissolved oxygen as temperature increases. This can be observed in the fish detection data when comparing the reduced range of oxygen differences at 20°C with 10°C (Figure 6).

For lake whitefish, results presented here illustrated novel linkages between fisheries management and efforts to improve water quality through nutrient reduction. Binational nutrient reduction goals are aimed both at reducing algal blooms and hypoxia in Lake Erie (IJC 2012). Results from this study demonstrated that the success or failure in achieving nutrient reduction may have attendant consequences for the distribution of lake whitefish during a period when normoxic hypolimnetic habitats represent important refugia (Schmitt et al. 2020). An important consideration in the context of habitat change is how Lake Erie fisheries are managed according to spatial management units. Nutrient reductions could expand available habitat further west during stratification, and this could change the vulnerability of lake whitefish as incidental catch in percid fisheries (i.e., walleye and yellow perch *Perca flavescens*) if they spend more time in other management units. Because Lake Erie is a dimictic lake (i.e., seasonally stratified), it is not clear whether this speculative outcome would elevate concern for managing lake whitefish.

In more general terms, these results reinforce advancements in acoustic telemetry technology and electronic tagging methods to develop more detailed information about fish habitat use. These advancements allow for field testing of hypotheses related to habitat selection as well as evaluation of potential environmental cues to understand movements more precisely. As we demonstrated, in combination with hydrographic modeling and an appropriate sampling design for passive receivers, directional predictions of fish movement can be tested. Although prior research indicated that lake whitefish are likely in the hypolimnion during stratification, detections during hypoxic conditions calls this assumption into question. Application of depth and temperature sensors to tagged fish would not only address this assumption, but also extend our analyses to three-dimensions. It has long been recognized that accounting for dynamic aspects of habitat selection in telemetry studies could transform current concepts of fish habitat (Jacoby et al. 2012). Future work toward improving concepts of fish habitat, either functional or theoretical, has the potential to improve management adaptation to long-term environmental change.

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Table(s)

Table 1. Generalized linear mixed model selection results based on AICc. Delta-AICc (Δ) values <2.0 and weight of evidence (*ω*) values > 0.99, provided support for choosing the interaction model as the best alternative. A Chi-squared (χ^2) test of the random effects was conducted once the best model was chosen. Model details are described in the text.

2017 Models:	K	AICc	Δ	*ω*	LL
Interaction	6	1057	0.00	>0.99	-522.44
T + DO	5	1070	13.24	<0.0001	-530.12
DO	4	1073	16.15	<0.0001	-532.61
T	4	1170	113.4	<0.0001	-581.24
	Interaction model test of random effects: $\chi^2 = 4.937$, d.f. = 1, p-value = 0.026				
2018 Models:					
Interaction	6	8068	0.00	>0.99	-4028.37
T + DO	5	8117	48.68	<0.0001	-4053.71
DO	4	8137	68.96	<0.0001	-4064.86
T	4	9079	1010.6	<0.0001	-4535.70
	Interaction model test of random effects: $\chi^2 = 469.12$, d.f. = 1, p-value <0.001				

T = water temperature; DO = dissolved oxygen; K = number of fixed factors; LL = log-likelihood.

Figures

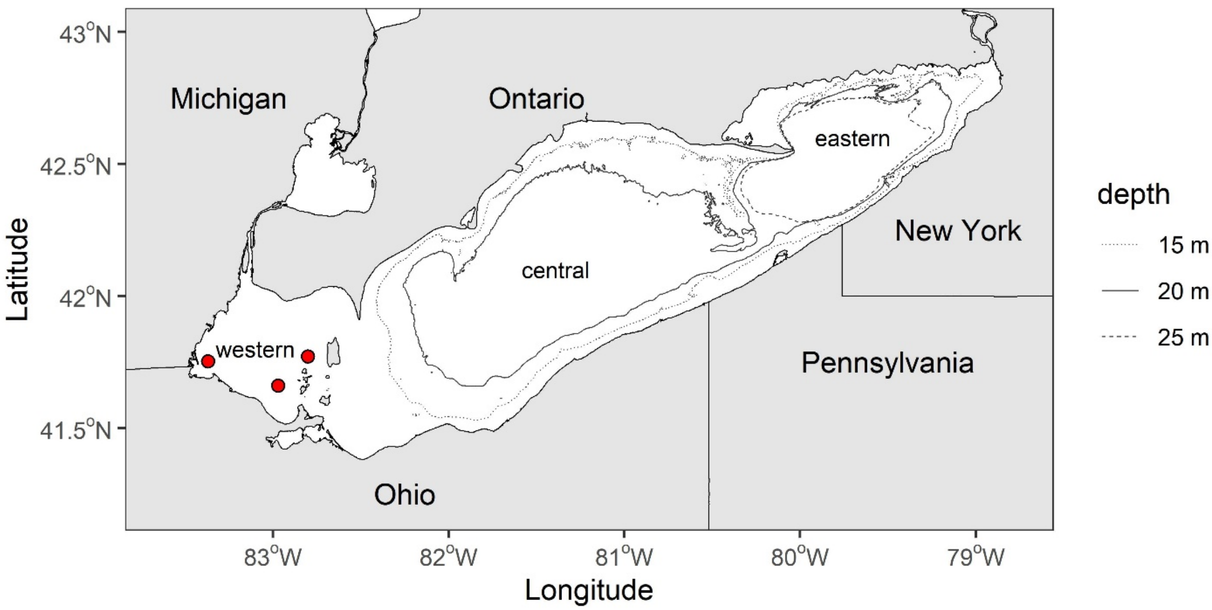

Figure 1. Reference map of Lake Erie depicting US states and the province of Ontario (gray-shaded land areas), important depth contours (see key), approximate locations of basin subdivisions (annotated on the lake) and tagging locations for lake whitefish (red dots in the western basin).

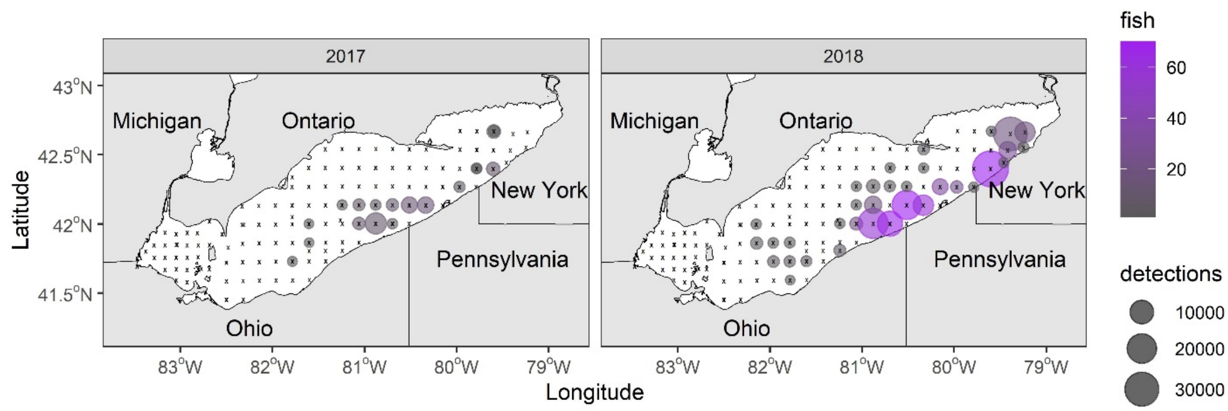

Figure 2. Maps of acoustic telemetry receiver stations in Lake Erie. Stations at which lake whitefish were detected during the months of July, August, and September are indicated by circles that are sized according to the total number of detections and shaded according to how many unique fish are represented by the detections. Receiver stations marked only with an x were locations for which hypoxia model results were predicted but no fish tags were detected.

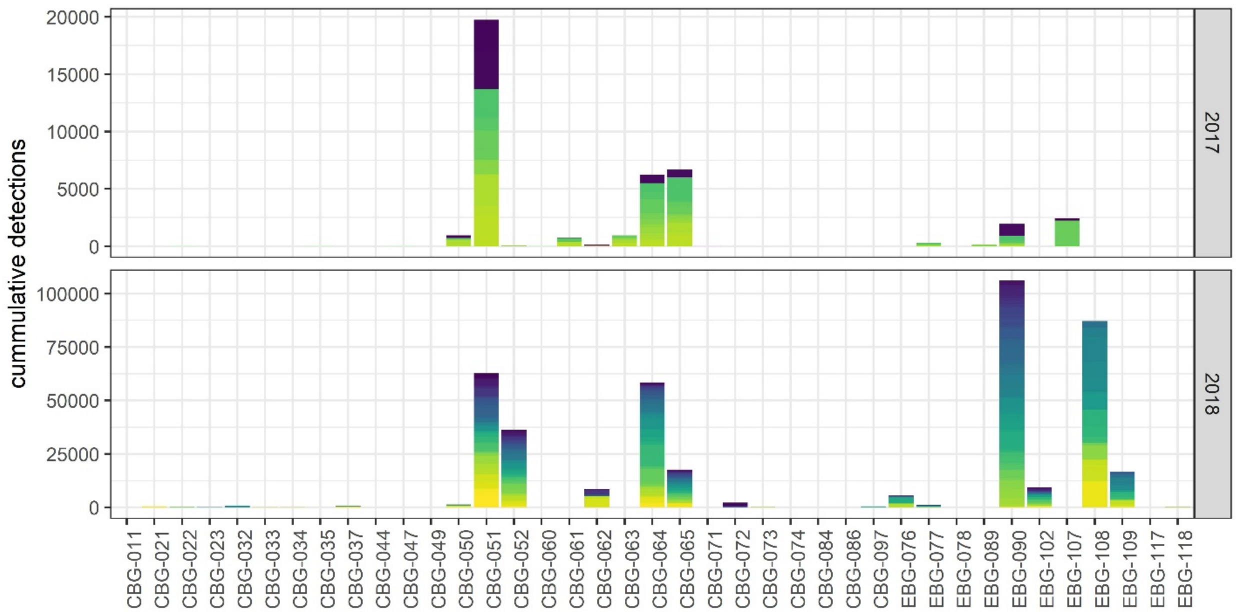

Figure 3. Acoustic telemetry receiver stations (horizontal axis) at which tagged lake whitefish were detected during months July, August, and September during 2017 and 2018. Total detections are indicated by the height of the bars, while the contribution of individual fish is indicated by each unique color (stacked). Note that vertical scaling is different between panels, and coding of stations provides an index to the data files associated with this manuscript.

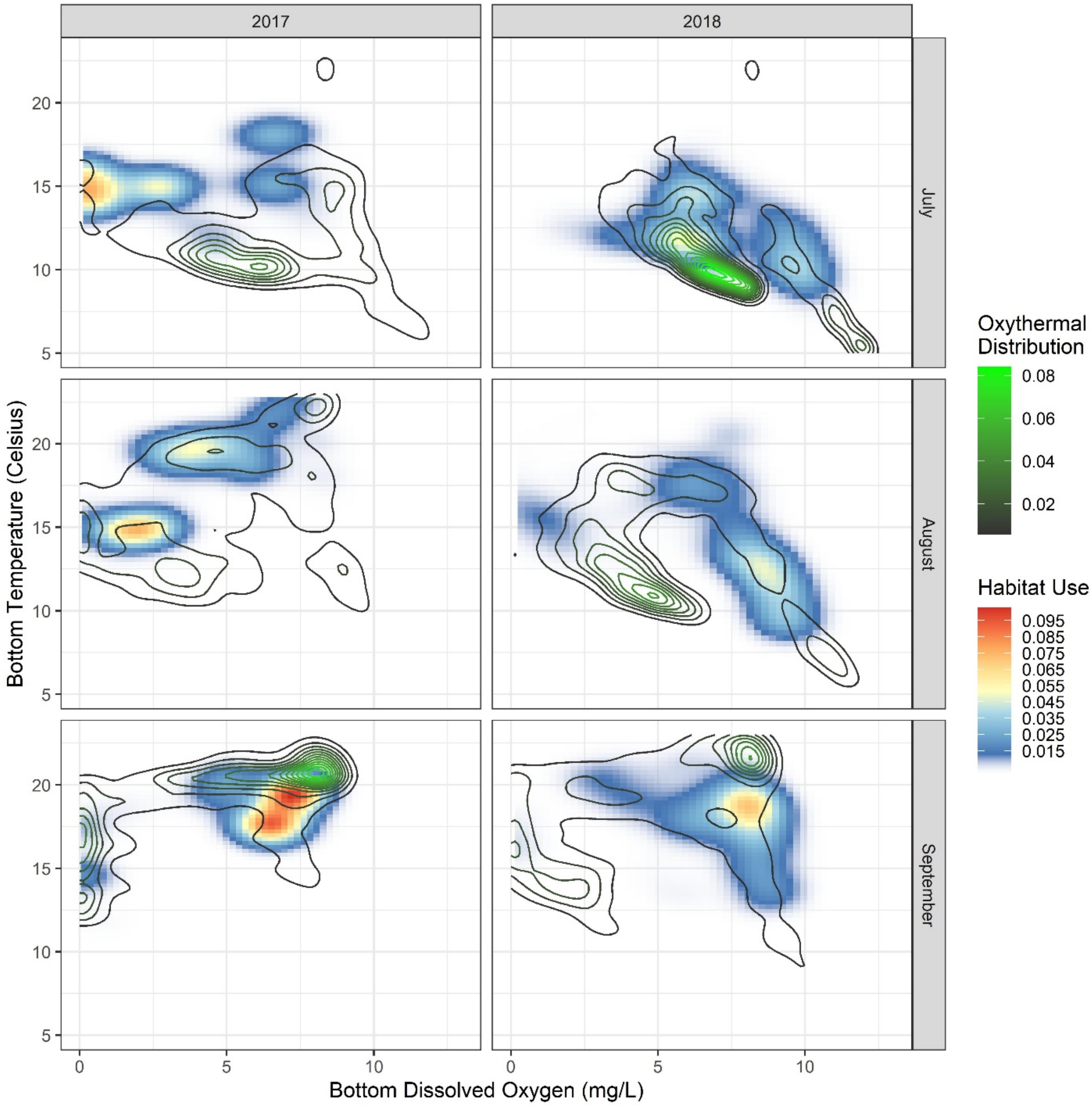

Figure 4. Bivariate kernel density distributions of hypolimnetic temperature and dissolved oxygen estimated hourly at acoustic telemetry receivers during months July, August, and September of 2017 and 2018. Oxythermal conditions are depicted as green shaded contour lines, representing all observed values for the acoustic telemetry stations. Habitat use is depicted as a color gradient map of low (blue) to high (red) proportions of total detections that were indexed to temperature and oxygen values in the hypolimnion.

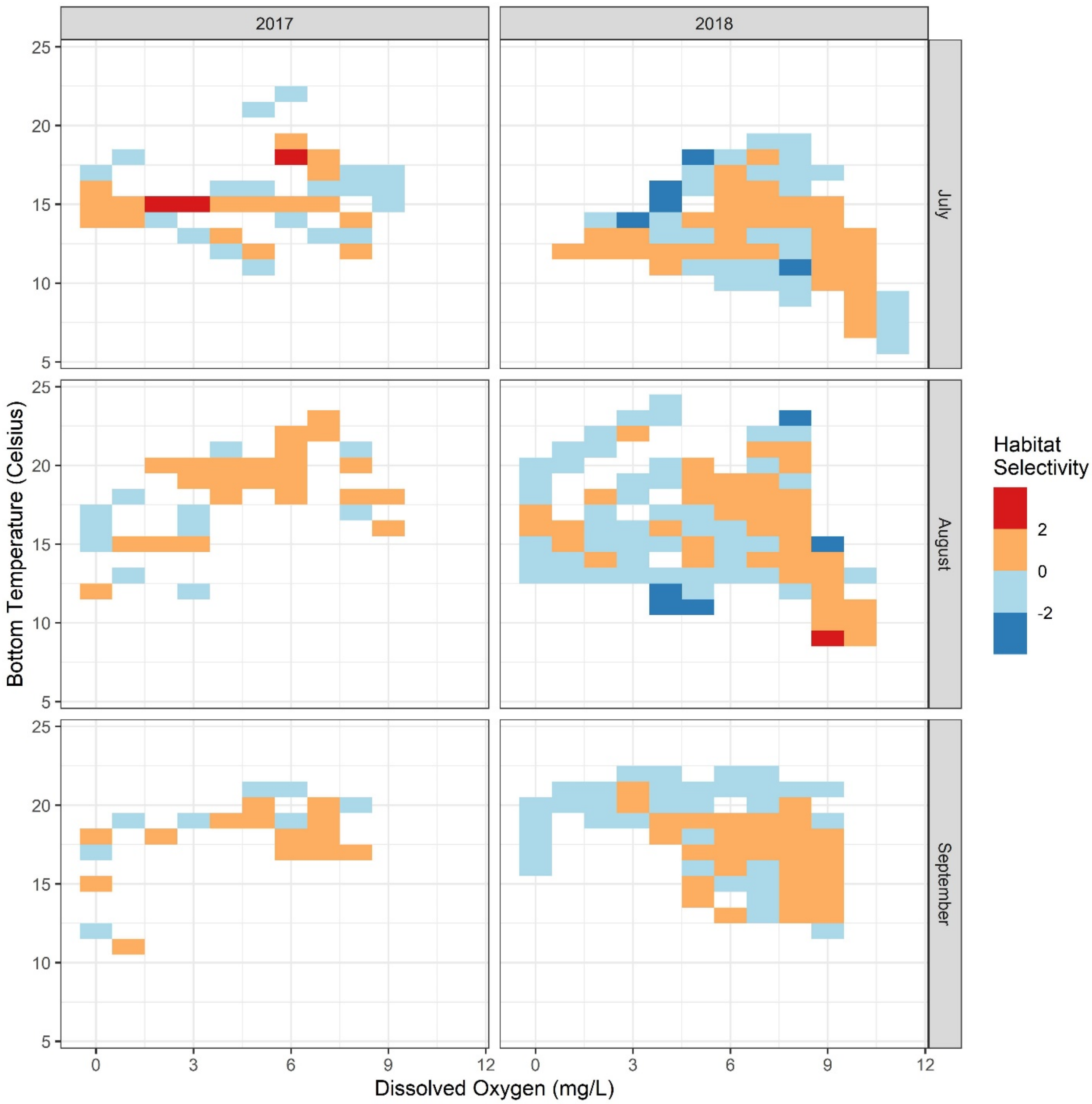

Figure 5. Habitat selectivity indices of hypolimnetic conditions based upon where tagged lake whitefish were detected on passive acoustic telemetry receivers during July, August, and September in Lake Erie. High positive values (red) indicated strong habitat selection, and low negative values (blue) indicate avoidance of conditions. Calculation of the index is explained in the text.

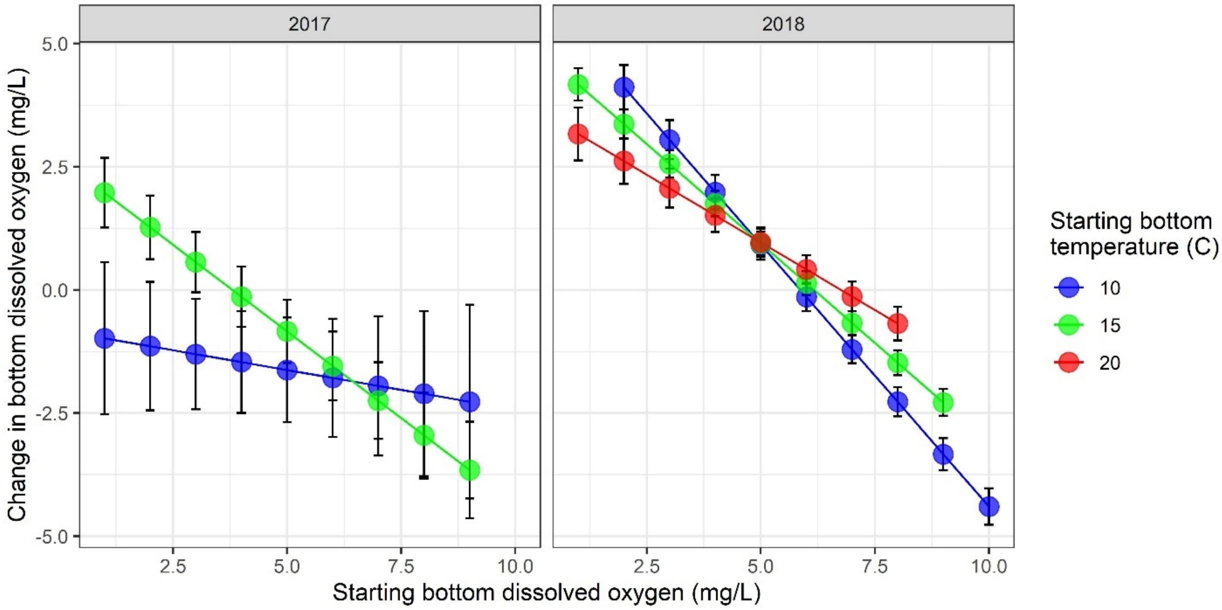

Figure 6. Movement of lake whitefish in Lake Erie expressed as change in hypolimnetic dissolved oxygen on successive detections of acoustic tags on different receivers. Data were modeled with a generalized linear mixed model as described in the text, and marginal means are plotted with 95% confidence intervals for three temperature values according to initial dissolved oxygen (covariate).