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Internal seiches as drivers of fish depth use in lakes

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Abstract

Inland temperate lakes undergo various physical processes, such as thermal stratification, that dictate the spatial availability of suitable temperature and dissolved oxygen conditions. Here, we use intensive limnological monitoring and acoustic telemetry transmitters implanted in wild fish to document the magnitude and frequency of thermocline deflection events (i.e., wind driven internal seiches that lead to upwelling of hypoxic hypolimnetic water) and their influence on freshwater fish depth use in a coastal embayment of Lake Ontario. The embayment experienced around 100 internal seiche events during a 3-month period and tracking of walleye (*Stizostedion vitreus*) vertical positions in the water column showed clear trends of avoidance of low dissolved oxygen. Quantile regression showed a significant correlation between walleye vertical position and the depth of the 3, 4, and 5 mg L^{-1} oxyclines, with the 3 mg L^{-1} oxycline having the largest effect. Upwellings of the hypoxic hypolimnion forced walleye to use the water column above these fluctuating oxyclines (5th percentile, $p < 0.001$), with 94.2% of detections occurring at depths above the 3 mg L^{-1} oxycline. Understanding how fish respond to upwelling events (both temperature and oxygen) is important for fisheries assessment, management, and habitat restoration planning as there is clear avoidance of suboptimal oxygen conditions and sampling in the overcrowded fringes of these low-oxygen zones could artificially inflate population estimates.

Physical processes above and below the surface waters of an aquatic ecosystem influence how aquatic animals distribute themselves in space and time (Sexton et al. 2009). Thermal stratification, for example, is driven by the physical properties of water and occurs on a seasonal basis in both freshwater and marine environments. As surface waters increase in temperature, the density of that water decreases and therefore it remains above the cooler, denser subsurface water. This vertical separation in water temperature and density essentially creates two separate layers of water, that is, the surface epilimnion, and the deeper hypolimnion, separated by a thermocline, and sometimes a mesocline. Thermal stratification can alter the aquatic landscape for fish by vertically separating habitats that vary in physiological suitability (Tate et al. 2007; Aspillaga et al. 2017), prey types and abundance (Roberts et al. 2012), and predation risk (Manca and DeMott 2009). The spatial separation of habitat use by fish has been documented in various trophic levels using hydroacoustic surveys (Midwood et al. 2019), gillnet surveys (Järvalt et al. 2005; Vašek et al. 2009), and more recently, acoustic telemetry in both the marine (Aspillaga et al. 2017) and freshwater (Gorman et al. 2019) environments. Atmospheric processes, such as wind, can dictate the stability of thermal stratification and depth of the thermocline. For example, when a sustained wind blows over a body of water, surface water accumulates at the downwind area, depressing the thermocline, leading to a rise in the thermocline at the opposing, upwind area (Hlevca et al. 2015; Chowdhury et al. 2016). Depending on the fetch (distance across open water that the wind travels), strength of the wind, and stratification of the waterbody, this process can lead to a complete upwelling of hypolimnetic water to the surface (Coman and Wells 2012). A relaxing of wind forcing results in an oscillating thermocline depth and internal seiches (Bouffard and Boegman 2012). These internal seiches and upwelling events can lead to dramatic changes in water properties such as temperature, and oxygen in littoral habitats (Hlevca et al. 2015; Flood et al. 2021a).

During the summer, in many temperate freshwater lake systems, persistent thermal stratification prevents vertical mixing and re-aeration of the lower water column (Hutchinson 1957; Chowdhury et al. 2015). For eutrophic systems, any dissolved oxygen (DO) within the hypolimnion is eventually consumed

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Additional Supporting Information may be found in the online version of this article.

by biological respiration and sometimes chemical oxygen demand, creating hypolimnetic hypoxia (< 3 mg L^{-1}; Diaz and Breitburg 2009). Anthropogenic enhancement of nutrients via agricultural runoff or combined sewage overflows, for example, can further exacerbate the hypoxia issue (Diaz and Breitburg 2009; Kemp et al. 2009) and under extreme conditions can result in an anoxic environment (0 mg L^{-1}) that can influence the habitat use of many aquatic species (Breitburg 2002) and their potential mortality.

Fish respond to hypoxia in a variety of ways with a range of physiological, anatomical, and behavioral adaptations (reviewed in Chapman and Mckenzie 2009). Generally, remaining in hypoxic conditions is physiologically costly (Pollock et al. 2007) and so fish avoid these conditions in both laboratory (Wannamaker and Rice 2000) and field settings (Brandt et al. 2011; Brown et al. 2015). In a thermally stratified, eutrophic system with hypolimnetic hypoxia, wind-driven internal seiches have the potential to create a dynamic horizontal and vertical mosaic of suitable and unsuitable thermal and oxygenated habitats (Rowe et al. 2019; Tang et al. 2019; Flood et al. 2021a). The vertical fragmentation of the aquatic environment influences fish distributions on a species-specific level, dictated by their thermal preference, hypoxia tolerance, and their ability to move and locate optimal habitats (Levy et al. 1991; Breitburg et al. 2009).

Many temperate, freshwater fish species rely on coastal, littoral areas for spawning, nursery, and foraging habitats (Jude and Pappas 1992; Wei et al. 2004); including walleye (*Stizostedion vitreus*; Lyons 1987), a top predator that supports important traditional, recreational, and commercial fisheries. These littoral zones provide suitable physical (light, vegetation, and structure) and biological (prey) habitat for many fish species (Lyons 1987; Benson and Magnuson 1992) and are used on a seasonal basis by walleye (Brooks et al. 2019). In eutrophic systems that undergo thermal stratification and internal seiche activity, upwelling of less-oxygenated, hypolimnetic waters can lead to episodic hypoxia in the littoral zone (Rao et al. 2014; Kelly et al. 2018; Flood et al. 2021a). In extreme cases, a complete upwelling of these waters can lead to massive fish kills (e.g., Lake Erie; Rao et al. 2014). An open question is what is the response of fish to chronic partial upwellings in a stratified, eutrophic water body? Our objective was to determine if dynamic changes in DO driven by upwelling events influence the vertical positioning of walleye in the water column in a previously documented high-use area of the littoral zone.

Methods

Study site

This study was conducted in Hamilton Harbour between June and October 2016. The harbor is situated at the western end of Lake Ontario in the Laurentian Great Lakes (7 km long, 24.9 m maximum depth, 21 km^2 area; 43°17N, 79°49W; Fig. 1). Secchi disc data collected between 2002 and 2019 at the Center Station showed that turbidity of water in Hamilton Harbour was high during summer, with secchi depths being rather small and ranging between 0.24 and 7.00 m, with a mean of 1.79 m (median of 1.75 m) (Murray Charlton, Veronique Hiriart-Baer, and David Depew; ECCC Personal Communication).

Study species

Walleye were considered extirpated in Hamilton Harbour by the mid-20th century (Holmes and Whillans 1984) and were successfully reintroduced in 2012 into the harbor by the Ontario Ministry of Natural Resources and Forestry (Hoyle 2017). Walleye are a cool-water species, with optimal temperatures ranging between 20°C and 23°C (Christie and Regier 1988) and a documented DO tolerance range of 3–5 mg L^{-1} (reviewed in Barton 2011; Tang et al. 2019). They have the ability to see well in low light, are crepuscular, and often prefer feeding in more turbid waters at dusk (Ali and Anctil 1977; Lester et al. 2004). Walleye were caught by either trap nets or boat electrofishing and tagged during August and October of 2015 as part of a larger study to determine the spatial ecology of the reintroduced population (for full methods, *see* Brooks et al. 2019). Transmitters fitted with pressure sensors to determine depth (Vemco V13P-1x-069k-1-0034m, 13 mm diameter, dry mass 11 g, battery life 1386 d, depth accuracy ± 1.7 m, resolution 0.15 m) were inserted into the body cavity of 25 adult walleye (mean total length 524.8 mm, range 490–700 mm). Most of the individuals were thought to be 3 yr old based on a successful 2012 stocking event (Hoyle 2017). Fish handling and surgical procedures were approved and followed a Canadian Council on Animal Care protocol (#110723) administered by Carleton University.

Environmental monitoring

Fortnightly temperature and DO measurements were made at a central water quality monitoring station (Center Station 43.288N, 79.847W; Fig. 1; ECCC). Measurements were made at approximately every 1 m from the surface to a depth of 24 m using a YSI profiling buoy. The profiler was programmed to record DO, temperature, specific conductance, pH, and depth every 120 min (Gertzen et al. 2016).

Wind was measured at the ECCC-maintained, weather station at the Burlington Pier, 10 m above the water surface (Climate ID 6151061, WMO ID 71437 2021) from 01 July to 31 October 2016. Data showed a prevailing wind direction from the southwest in summer of 2016 (Fig. 1). Flood et al. (2021a) observed similar wind forcing in 2017 (i.e., predominantly diurnal and from the SW), which drove large-amplitude internal seiches with a dominant period of ~ 22–25 h. The thermal stratification in 2016 was very similar to 2017, and a detailed discussion of the spatial variability of internal seiches and DO levels is discussed in Flood et al. (2021a). Combined influences of basin morphometry and wind direction resulted in frequent upwelling events at

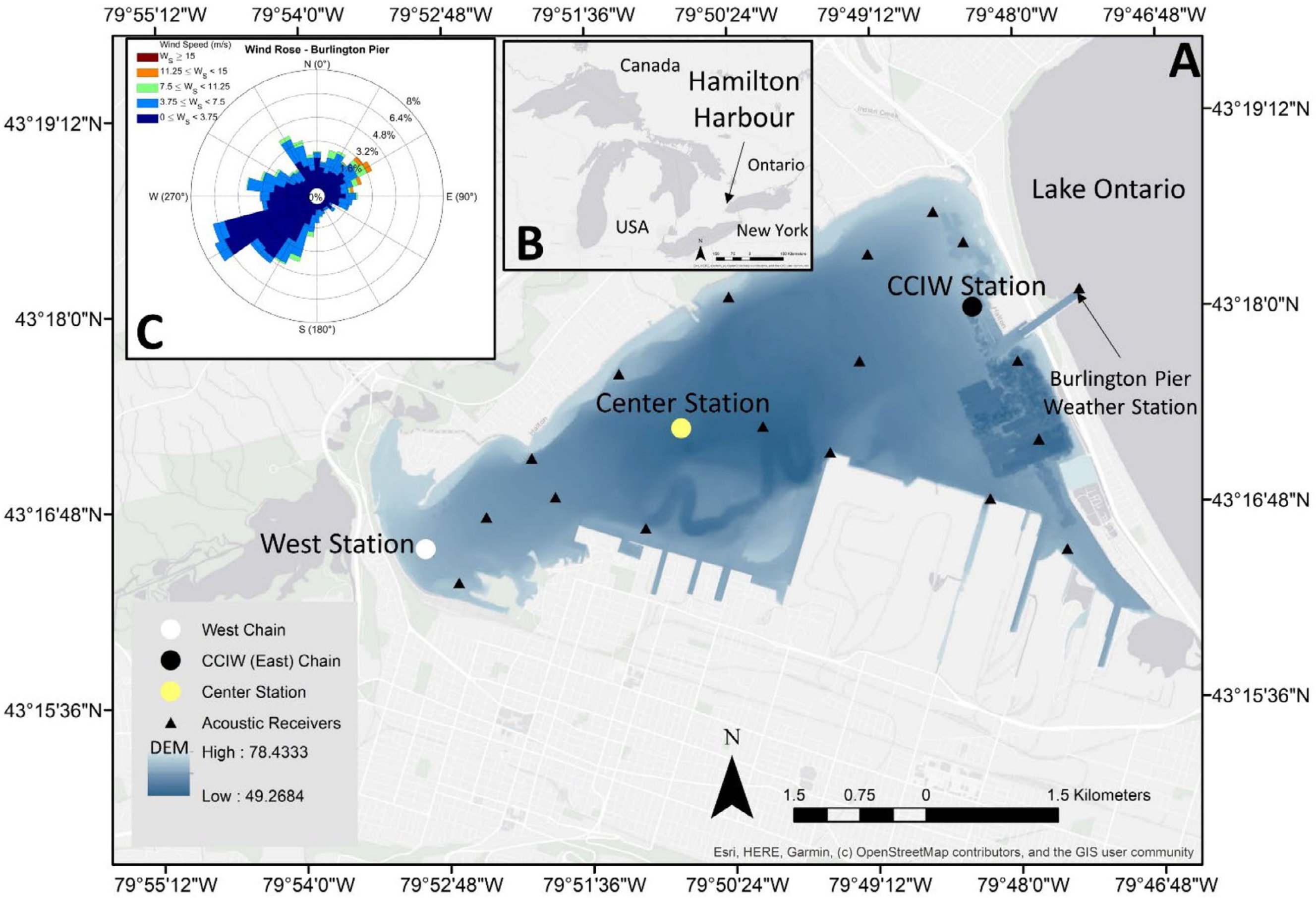

Fig. 1. (**A**) Hamilton Harbour is approximately 7 km long in the east–west direction, with an area of 21 km^2 and is situated at the western end of Lake Ontario (**B**). The location of acoustic telemetry receivers, temperature, and dissolved oxygen chains are marked at the west (West Station) and east (CCIW Station) ends, where the water depth was 7 m. Biweekly profiles of temperature and dissolved oxygen were taken at Center Station in 24 m of water (ECCC). (**C**) Wind data was obtained from ECCC-maintained weather station at the Burlington Pier.

the western and northeastern areas of Hamilton Harbour, repeatedly exposing the shallow, littoral zone to hypoxic, hypolimnetic waters (Flood et al. 2021a). Similarities in wind forcing and stratification between 2017 and 2016 suggest similar dynamics in 2016 (i.e., frequent upwelling of cool, hypoxic waters at the western and northeastern ends of the basin). In particular, Flood et al. (2021a) showed the period of free oscillation of internal wave (as calculated using Merian's formula) was calculated to be $T_1 = 18.7$ h. They also noted a spectral peak in wind forcing frequency of 23.8 h that indicated diurnal winds were likely the dominant forcing mechanism in Hamilton Harbour. Their spectral analysis of thermocline depth highlighted a corresponding peak centered around $T \sim 22.0–25.3$ h, while analyzing the spectral density of the mean epilimnetic and hypolimnetic velocities revealed similar peaks of 22.0–24.4 h. Thus, the periods were similar between forcing frequency, predicted basin internal seiche period, and response frequencies.

Precision Measurement Engineering™ Mini DOT loggers were attached at 1 m intervals to a vertical line from June to October 2016 at two sites in 7–8 m of water in the littoral zone of the harbor (west [43.276N, 79.883W] and east [43.300N, 79.806W]; Fig. 1). Thus, all three water quality monitoring locations were located along a straight line running southwest to northeast, in the same direction as the prevailing winds, and along the longest fetch of Hamilton Harbour.

Fish tracking

Fish detection data for this study were obtained from 2 of the 27 acoustic telemetry receivers (Vemco Amirix, VR2W 69 kHz, Bedford, Nova Scotia) deployed throughout Hamilton Harbour as part of a larger study (Brooks et al. 2019). These acoustic receivers were suspended from subsurface buoys and attached to the same anchor point as the temperature and DO logger chain deployed between April 2016 and October 2016.

Data preparation

Exported detection data from the full array of acoustic telemetry receivers were sorted and plotted by individual fish to visually check for mortality or expelled transmitters. Any detections recorded continually at a similar depth and on the same receiver(s) throughout the study period were removed from the database. False-positive detections can occur when multiple transmissions collide upon detection by a receiver, resulting in erroneous tag IDs being recorded (Pincock 2012). Detection data from the receivers were filtered for nonwalleye fish detections, random transmitter detections, and stationary transmitters (expelled tags or dead fish) using R Statistical Environment (R Core Team 2020). Several species from a wide range of hypoxia tolerance values were also detected; however, there were too few individuals per species to analyze and they were removed from further analysis. Preliminary plots of their depth vs. water quality showed that many individuals observed similar trends of avoidance to walleye (Supporting Information Fig. S1).

DO values from the logger deployed at 3 m at the West Station were removed due to heavy biofouling of the instrumentation's sensor that resulted in erratic values. Using the "stats" base package in R and the "approxfun" function, DO was interpolated linearly along the 1-m western string to determine the depths of 3, 4, and 5 $\mathrm{mg\,L^{-1}}$ oxyclines for every 10 min of the study period. These thresholds were selected as they covered the DO tolerance range for walleye identified in Barton (2011). When the entire water column was above these DO values, the oxycline depths were left blank as it was assumed that the oxycline was deeper than the study site. Each walleye detection was paired with a depth value for all three oxyclines, when available.

To investigate the relationship between fish depth and oxycline depth, we used quantile regression (QR). QR is a statistical method that allows analysis of an animal's relationship with a potentially limiting factor (Cade and Noon 2003). Linear regression (ordinary least squares) uses the conditional mean of a response and assumes a normal error distribution. However, statistical distributions of ecological data often have unequal variance due to animals responding to a complex interaction of environmental variables, and therefore, the mean response may not reflect the important ecological mechanisms (Cade and Noon 2003). For limiting factors as constraints on organisms, the edge of the distribution of responses (e.g., the 95th or 5th percentiles) is a more accurate representation of the ecological relationship. In addition, QR can estimate multiple rates of change (slopes at multiple quantiles) within a dataset to provide a more complete picture of how limiting factors can influence the distribution of animals within a habitat (Cade and Noon 2003). We used the "quantreg" R package (Koenker 2019) to estimate multiple relationships between the 50th (the median depth use) and 5th percentiles of walleye depth (the deeper range of depth use) vs. oxycline depth (3, 4, and 5 $\mathrm{mg\,L^{-1}}$ oxyclines). Although individual identity cannot be incorporated into QR which violates the assumption of independence, it allows us to focus the analysis on the lower depth use of walleye which is more biologically relevant to their average. We used a generalized linear mixed model with walleye tag ID as a random effect as a check to determine if walleye's vertical positions were driven by the position of the 3, 4, and 5 $\mathrm{mg\,L^{-1}}$ oxycline after accounting for individual variability and the lack of independence.

To explore any relationship with walleye's vertical position and time of day and potential diel vertical migration behavior, detections were categorized by day or night based on locational sunset and sunrise times using the "suncalc" R package and plotted. To determine the proportion of detections above the three oxyclines, the total number of detections above each oxycline was divided by the total number of detections.

Results

Environmental data

Temperature data obtained from the Center Station (Fig. 1) showed that thermal stratification started around 23 May 2016 (day of year [DOY] 144). At this time, surface temperature was 16.1°C and bottom temperature was 10.1°C. The largest range between surface and bottom temperature was on 07 August, when surface temperatures reached 24.6°C, compared to 13.3°C at the bottom. The thermocline was present between 5 and 7 m depth at the beginning of the summer and gradually deepened to around 8–10 m by the end of summer (Fig. 2A). As air temperatures decreased in the fall, surface waters cooled, and the surface layer deepened until the breakdown of the stratified layer, resulting in turnover of the water column on 16 October 2016 (DOY 290; Fig. 2A). Immediately following turnover, surface temperatures were 17.5°C and bottom temperatures were 14.9°C.

DO data obtained from the Center Station showed a clinograde profile, as would be expected for a stratified eutrophic lake, with the DO levels nearly saturated at the surface then sharply decreasing beneath the thermocline. The surface layer had DO levels between 8 and 12 $\mathrm{mg\,L^{-1}}$. In contrast, the hypolimnion was fully anoxic (0.52 $\mathrm{mg\,L^{-1}}$) by 11 August 2016 (DOY 224; Fig. 2B). Thus, during much of the summer, the sharp oxycline was located close to the thermocline. During fall turnover, the oxygenated surface waters mixed with the deep hypoxic waters, creating a homogenous DO profile again (Fig. 2B).

When wind forcing was strong enough, and long enough ($> 1/4$ period of the fundamental mode, corresponding to approximately 3–6 h for Hamilton Harbour as with other similarly sized large lakes/embayments), basin-scale, internal wave, complete upwelling can occur where the thermocline breaches the surface (Bouffard and Boegman 2012). The embayment experienced approximately 100 internal seiche events during the full summer 2016. Some of these movements of the thermocline came all the way to surface at upwind west end for example, on DOYs 184, 192, and 198 (*see* Fig. 3). At the upwind east end, the thermocline was out of phase with the

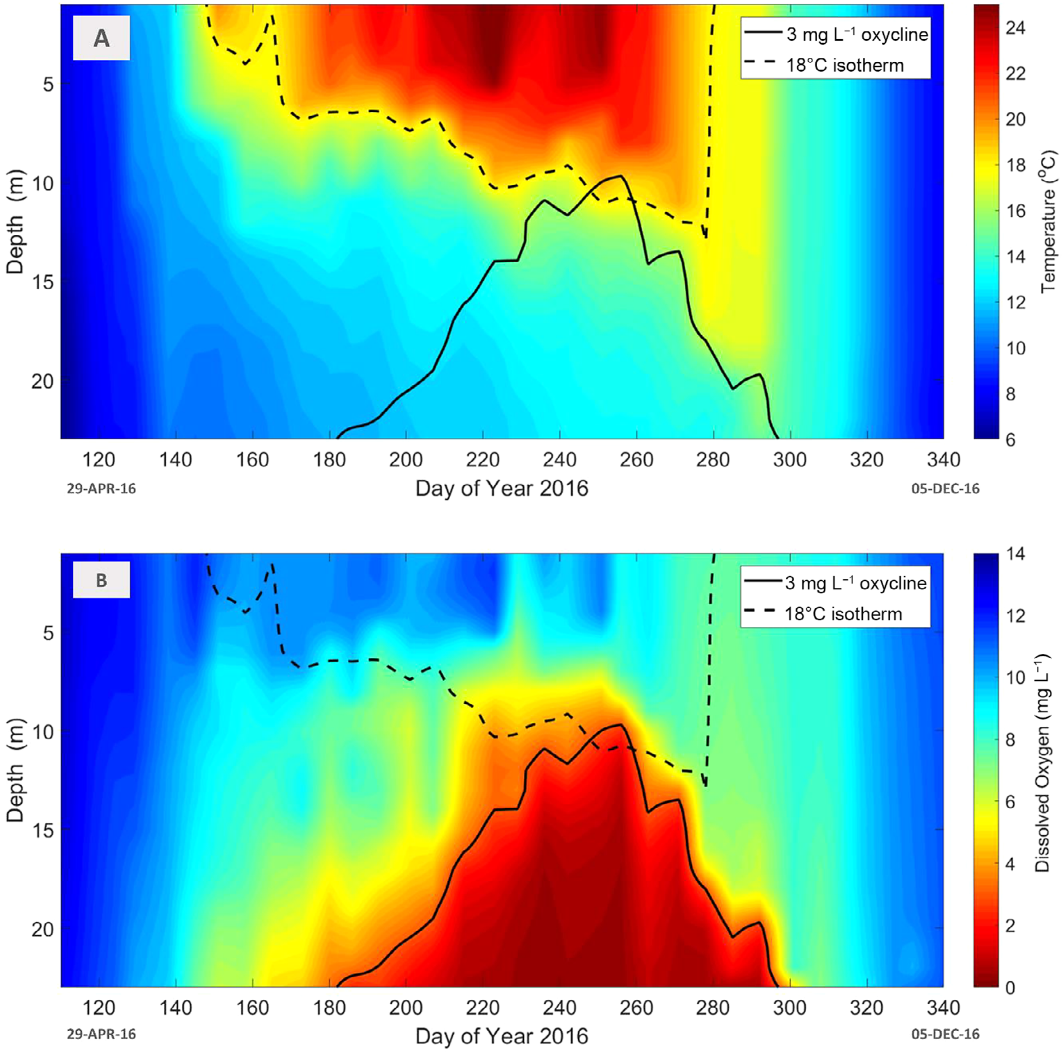

Fig. 2. (**A**) Temperature (°C) and (**B**) DO (mg L^{-1}) vs. depth (m) data from the center monitoring station. Thermal stratification began on DOY 144 (23 May 2016) and the breakdown of stratification, also known as turnover, occurred on DOY 290 (16 October 2016).

west end, seen most dramatically on DOY 184, 192, and 198 where warm surface waters were depressed to 7 m depth at east end, while cold water upwelled to surface at the west end (Fig. 3). Diurnal winds from the south-southwest in 2016, coupled with a long, internal seiche period easily excited internal seiches, with the largest amplitudes at the southwest and northeast coastal areas of the harbor (similar to 2017, *see* Flood et al. 2021a).

The profiles of temperatures and DO between 0 and 8 m depth fluctuated greatly as internal seiches oscillated at the West and East Station (Fig. 3); however, due to minimal fish detections at the East station, all further analyses focused on the West Station (*see* the Fish data section for further explanation). The water column at the West Station was largely homogenous without a vertical gradient, but conditions varied with internal upwelling activity. Bottom temperatures ranged from 12.4°C to 25.3°C (at 8 m) over the study period and DO ranged from 0.1 to 11.3 mg L^{-1} (Supplementary Table S1). Upwelling of hypoxic hypolimnetic waters was a ubiquitous feature in the upwind southwestern end of Hamilton Harbour (Fig. 4).

Fish data

The full telemetry array was downloaded and the plotting of fish depth by position determined the individuals that had not survived the tagging procedure or had expelled their tags. Live walleye depth values were then overlaid on interpolated DO values within the water column at both West and East stations. Supporting Information Fig. S1 shows a subset of a 3-week period in 2016 for walleye detections at both West and East stations. Although there were similar trends of avoidance at both sides of the Harbour, there were insufficient numbers of individual walleye detected at the East station ($n = 3$), and therefore the West Station was chosen for all further analyses.

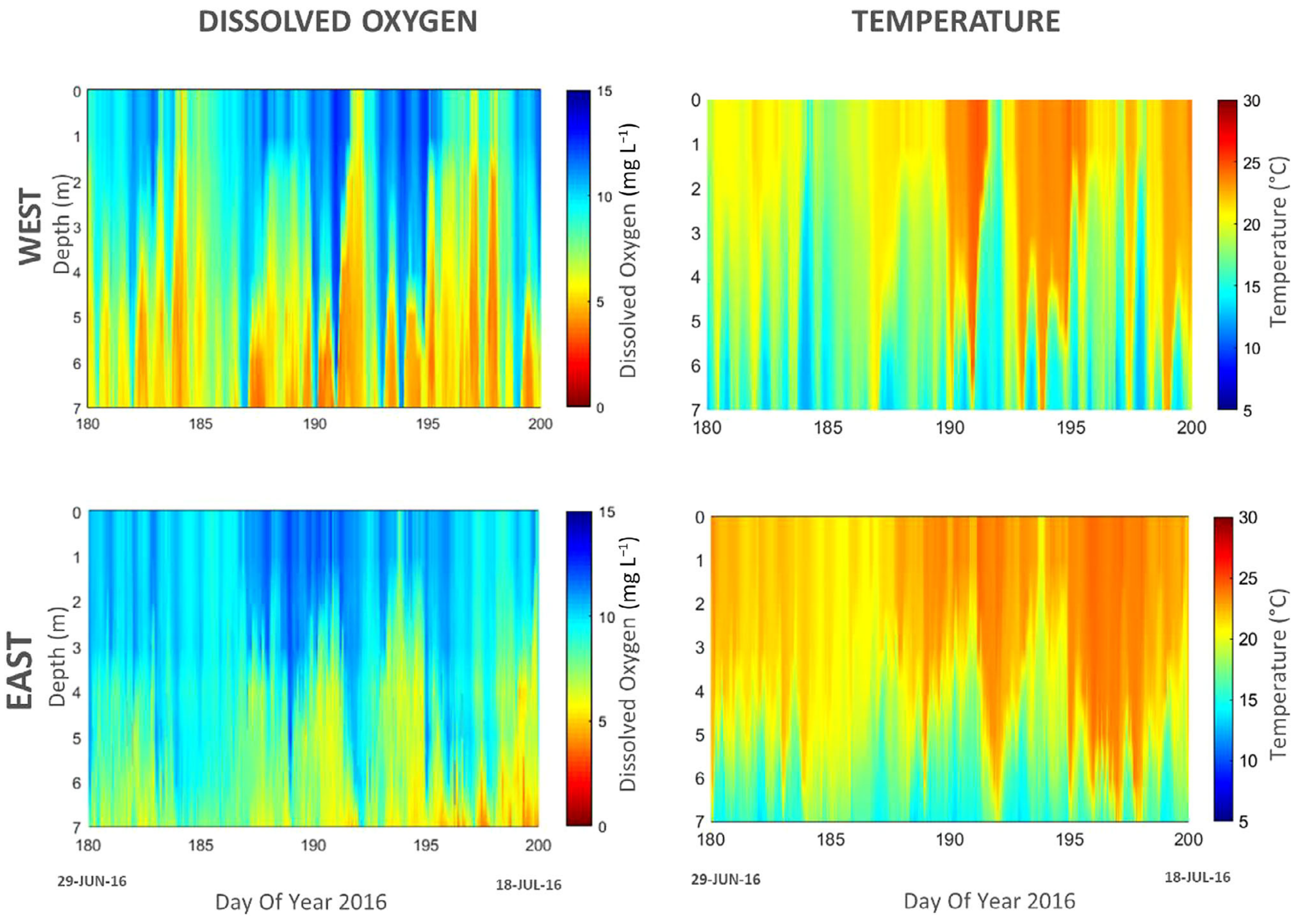

Fig. 3. Interpolated dissolved oxygen values (mg L^{-1}) and temperature (°C) at depth (m) at the West and East Station between DOY 180 and 200 of 2016 (29 June to 18 July 2016).

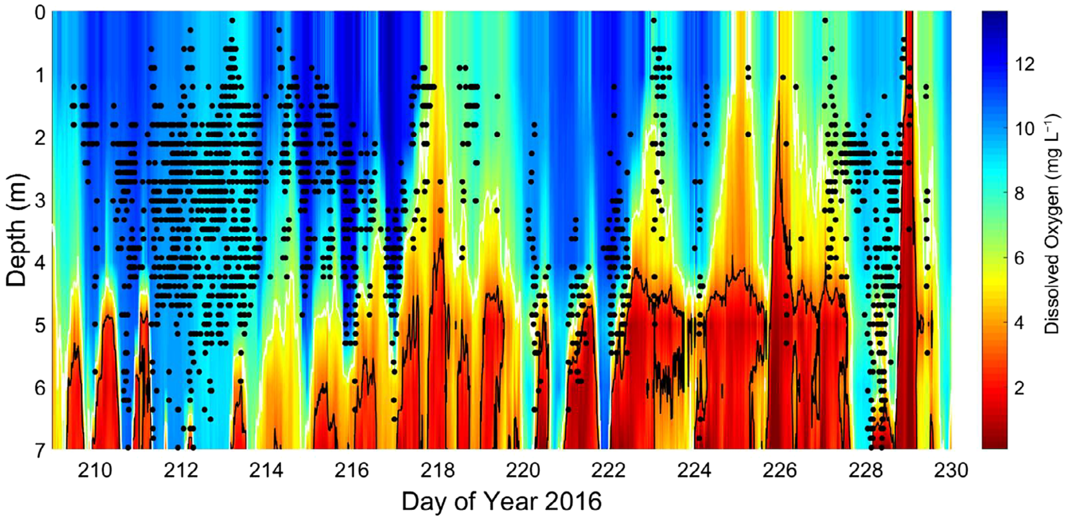

Fig. 4. Interpolated dissolved oxygen values (mg L^{-1}) at depth (m) at the West Station between DOY 208 and 230 of 2016 (26 July to 17 August 2016). Black points indicate individual walleye positions in the water column, detected on the west receiver at that time. The black line indicates the interpolated 3 mg L^{-1} oxycline position in the water and the white line indicated the interpolated 5 mg L^{-1} oxycline.

This aligns with previous fisheries sampling and telemetry data that have shown an increased abundance and residency of walleye in the western area of the Harbour (Boston unpubl. data; Brooks et al. 2019). Of the 25 walleye tagged, 8 walleye had not survived or had expelled their tags. Of the remaining 17 walleye, 10 individuals were detected on the West Station receiver throughout the study period with a total of 6876 detections (total fish lengths ranged from 490 to 570 mm, mean = 536 mm). Scatterplots of walleye depth vs. oxycline depth showed that most detections occurred to the left of the 1 : 1 fish depth to oxycline depth line, that is, walleye were using the water column above the oxycline (Fig. 5). An absence of detections below the 3 mg L^{-1} oxycline signified that walleye avoid hypoxic waters below 3 mg L^{-1}. Walleye were rarely detected in the top 1 m of the water column (2.7% of detections). The proportion of walleye detections above 3 mg L^{-1} was 94.2%, above 4 mg L^{-1} was 91.2%, and above 5 mg L^{-1} was 87.7%. There did not appear to be a strong relationship between walleye vertical positions during the day vs. night time; however, there was a slight difference in the mean depth that was less than the accuracy of the tag's depth measurements (Supporting Information Fig. S4).

Quantile regression

The ordinary least squares linear regression showed a positive relationship between walleye depth and oxycline depth, for all three oxycline values (Fig. 5 and Supporting Information Figs. S2, S3). Walleye depths were correlated with the oxycline depth; however, as predicted there was unequal variance in our dataset. Regression of various quantiles (5%, 10%, 50%, 75%, and 95%) showed that indeed, there were multiple slopes, and the 5th percentile showed the strongest correlation with a slope approaching 1.0 (Fig. 5; Supplementary Table S2). These results suggested that a strong limiting relationship exists between walleye and DO. Higher levels of oxygen (i.e., 4 and 5 mg L^{-1}) did not show as strong a relationship with walleye depth, and the slopes of these relationships did not approach 1.0 as closely as the 3 mg L^{-1} threshold (Supplementary Information Table S2; Figs. S2, S3), indicating that the 3 mg L^{-1} oxycline depth had the strongest influence on walleye depth distributions, as expected. The GLMM results showed a significant relationship between walleye depth and the depth of the 3, 4, and 5 mg L^{-1} oxyclines, after accounting for individual ID as a random factor. Outputs from the GLMM are found in Supplementary Information (Table S3)

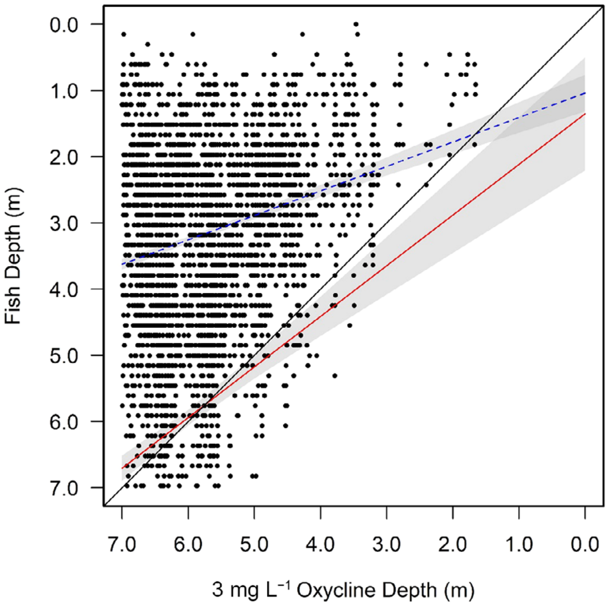

Fig. 5. Scatterplot of walleye depth (m) vs. depth of the 3 mg L^{-1} oxycline at West Station. Blue dashed line indicates ordinary least squares linear regression, red line indicates quantile regression using 0.05 quantile (the lower 5% of the walleye depths). Gray band shows the 95% confidence intervals around each line.

Discussion

We used a combination of intensive limnological monitoring and a comprehensive acoustic telemetry array to examine the subsequent effect of upwelling events on the depth use of an ecologically and economically important freshwater fish species. A littoral area known to be well used by walleye experienced almost daily upwelling events during the 3-month stratified period, with hypoxic water conditions reaching the surface on several occasions. Walleye demonstrated a preference for oxygenated waters and positioned themselves above the dynamic, ever-changing depths of the 3, 4, and 5 mg L^{-1} oxyclines.

Nearshore zones provide suitable habitat for all life stages of many freshwater fish species (Benson and Magnuson 1992). Our research, however, has shown that these areas overlap with the internal swash zone of internal seiche activity, and are subjected to greater fluctuations of temperature and DO than other areas of the lake proper (Flood et al. 2021a). Highly mobile fish such as walleye can elect to move away from suboptimal water quality conditions as our research has shown. However, this may not be without some energetic cost. Changes in behavior and spatial distribution due to avoiding hypoxic conditions likely have some bioenergetic and/or survival costs (Levy et al. 1991; Breitburg 2002; Pollock et al. 2007). Inhabiting suboptimal environments, for example, can lead to increased competition for space, prey, and refuge (Eby and Crowder 2002), less-preferred temperatures and light levels (Brandt et al. 2011), and increased risk to exposure to both piscivorous (Prince and Goodyear 2006) and avian predators (Kramer et al. 1983). Specifically, in Hamilton Harbour, crowding of prey fish in more highly oxygenated refuges has been documented using hydroacoustic surveys of the pelagic zone (Midwood et al. 2019). This crowding can result in density-dependent growth reductions (Eby and Crowder 2002), increased cannibalism (Aumann et al. 2006), feeding, and trophic interactions (Pihl 1994; Prince and Goodyear 2006; Ludsin et al. 2009; Stramma et al. 2012). As average secchi disk data in the Harbour shows the top ~ 2 m to be less turbid and therefore less ideal for walleye (preferred range is 2.0–4.9 m secchi depth; Ryder 1977; Einfalt et al. 2012). Further investigation into how these upwelling events might drive walleye to use less than ideal water clarity, temperature, and physical habitat conditions is required to test interactions and energetic costs in degraded environments.

Hypoxia has been shown to influence walleye habitat use in other systems (Lester et al. 2004; Gorman et al. 2019); however, bioenergetic studies have shown that, although the *quantity* of habitat available to walleye may have been reduced by hypoxia, it may not necessarily reduce the *quality* (Brandt et al. 2011). It is hypothesized that walleye are able to take advantage of these oxygenated refuges and foraging efficiency is increased because of prey compression (Brandt et al. 2011). Ameida (2016) found similar results for yellow perch (*Perca flavescens*) habitat use and bioenergetics and concluded that hypoxic conditions did not appear to have negative consequences on the quality of habitat. Individuals from both studies did not experience a net loss in body condition as a result of hypoxic conditions. It was suggested, however, that both species may typically seek to *increase* body condition in preparation for winter and therefore may be at a disadvantage when compared to populations in nonhypoxic conditions (Ameida 2016). While walleye in Hamilton Harbour can exit the system through a canal to Lake Ontario, previous studies have shown that residency during the summer/stratified period is relatively high (Brooks et al. 2019). With the documented prey compression above the thermocline (Midwood et al. 2019) and high residency, we would predict that walleye are also not experiencing issues with overall habitat quality during the stratified period.

The documented reduction in availability of suitable habitat due to hypoxia can lead to issues for fisheries managers when undertaking stock assessments and quantifying the amount and distribution of suitable habitat. Many assessment methods use capture techniques, such as netting or electrofishing, and sampling designs that do not incorporate extensive monitoring of the environmental conditions. As a result, biologists may be unknowingly sampling on the fringes of low-oxygen zones, that is, the overcrowded, compressed oxygen refugia, and therefore artificially inflating the stock estimates, eventually leading to higher catch allowances (Kraus et al. 2015). This has been documented in the marine environment with swordfish and sharks that tend to reside on the edges of oxygen minimum zones (Gilly et al. 2013; Vedor et al. 2021). Wind conditions often dictate the ability and location of fisheries sampling efforts from small boats. In coastal embayments such as Hamilton Harbour, transects or sampling sites that are in the "lee" of the wind direction are selected first for ease and safety of boat maneuverability and net setting. These areas of low exposure, however, could be undergoing internal upwelling events and therefore yielding catch rates not representative of "normal" or average conditions. Finally, fish responding to dynamic, daily vertical shifts in temperature and DO could potentially dampen or imitate diel vertical migration behavior. Fisheries biologists should therefore consider the environmental conditions surrounding their sampling locations to understand how they may influence the catch rates and resulting stock assessments. Habitat managers should also consider the dynamics of water quality conditions and potential swash zones when restoring or building new fish habitat.

Predicted increases in global temperatures can further exacerbate the impacts of hypoxia on aquatic ecosystems. Warmer temperatures are predicted to increase the length of periods of stratification in freshwater ecosystems (Zhang et al. 2020), the expansion of oxygen minimum zones (Stramma et al. 2012), and the intensity of upwelling events in the marine environment (Wang et al. 2015). Extreme weather events and precipitation levels are expected to increase (Michalak et al. 2013; Scavia et al. 2014), leading to increased surface runoff and eutrophication, in turn increasing the frequency and intensity of hypoxia events in inland aquatic ecosystems (Jones and Brett 2014; Jenny et al. 2016). For ectotherms such as fish, increased water temperatures lead to an increased metabolic rate (Brett and Groves 1979), and in turn, an increased demand for oxygen and prey (Deutsch et al. 2015; Rubalcaba et al. 2020). Understanding how fish respond to the fluctuations in temperature and oxygen availability is therefore important when predicting the impacts of climate change on aquatic ecosystems.

As with all broad-scale, acoustic telemetry studies, there are a few limitations in pinpointing to which environmental variables individual fish are responding. Previous detection efficiency studies in the Harbour have shown that the thermocline can influence the array's performance (Wells et al. 2021). A reduction of signal is greatest when a transmitter and receiver are on opposite sides of a thermocline, and as the thermocline moved above and below our receivers, and the walleye remained generally above the thermocline, there were likely some detection efficiency issues. The detection efficiency study demonstrated a reduction in range from approximately 500 to 350 m during the stratified period, therefore not a complete reduction in transmission across the thermocline (Wells et al. 2021). Our detections were also from one receiver, and it was assumed that the fish experienced the same environmental conditions as the loggers on the chain. However, with an approximate detection range of 350–500 m (Wells et al. 2021), the fish may have been positioned on the opposing side to the upwelling water, which could explain the presence of some detections below the 3–5 mg L^{-1} threshold during the upwelling periods (Fig. 4). This can also be seen in the multi species plot in Supporting Information Fig. S1, particularly with the Northern Pike (*Esox lucius*). Pike are known to be ambush predators (Casselman and Lewis 1996) and their depth use appears to be quite stationary at times, likely close to shore in the vegetation and away from the low DO, but without fine-scale positioning, we cannot know for sure what exact abiotic factors they are experiencing. The depth accuracy value of ± 1.7 m is less than ideal, especially when working in water depths as shallow as these. We argue that walleye are using the full water column and mostly staying above the highly variable oxycline depth, and therefore the visible trend of avoidance supports our statistical finding. Temperature and DO are inherently connected and we acknowledge that the internal seiche leads to a change in temperature and DO simultaneously, however we opted to concentrate our analyses on DO and documented a strong relationship with lower DO values. We also acknowledge the strength of wind is often correlated with time of day, and, although there did not appear to be any strong day vs. night shifts in vertical positioning, we recommend further investigations using a fine-scale positioning array to better tease apart the effects of changing temperature and DO and time of day on a fish's position in the water column in this dynamic system. This would also allow a better understanding of the avoidance behavior of fish when the conditions are very poor, that is, when the oxycline is at the surface and there are very few fish detections.

In summary, our results show that internal seiche events in lakes can drive the vertical positioning of fish. This observation builds upon other studies that also found fish in different thermally stratified systems also respond to internals waves (Levy et al. 1991; Pineda et al. 2020; Flood et al. 2021b). The compression of walleye into oxygen-rich and warm epilimnetic waters will increase their metabolic demand, therefore requiring an increase in prey biomass for sustenance. This habitat compression affects their vulnerability to fisheries capture, and potentially influencing agency-based population assessments for fisheries management, as well as habitat use. Given the predicted expansion and duration of hypoxia in aquatic environments (Altieri and Gedan 2015) under climate change even though nutrient management is improving, we suggest further research is required to extrapolate the impacts of hypoxia observed here on individuals to the population and on a system-wide basis. This information will help understand the consequences of these water quality impacts in the assessment, restoration, and management of the Laurentian Great Lakes fisheries, habitat management, and in other inland water bodies that are subject to similar conditions and yet are important for fisheries that support recreation, livelihoods, culture, and food security around the globe (Lynch et al. 2016).

Data Availability Statement

All data are available upon request to the corresponding author.

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Conflict of Interest

None declared.

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