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Research article

Thermal habitat fragmentation in stratified lakes induces resource waves that brook charr track across seasons

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The spatial configuration of thermal habitats constrains the thermoregulatory performance of ectotherms. Thermal landscapes also vary through time, which is particularly relevant in seasonal environments such as temperate lakes. Indeed, elevated temperatures in the epilimnion of dimictic lakes during summer could substantially reduce the use of this habitat by cold-stenothermic fish during the stratified period. The main objective of this study was to evaluate whether thermal habitat fragmentation in stratified lakes modulates accessibility to resources that brook charr, *Salvelinus fontinalis*, which is a mobile consumer, can track across seasons. More specifically, we hypothesize that reduced access to the littoral habitat during summer enhances foraging opportunities in this habitat during winter. We used an automatic acoustic telemetry system offering full coverage of the lake to continuously record brook charr locations across seasons, and we estimated zoobenthos abundances in the littoral habitat using image processing and semi-automatic classification. While brook charr concentrate in the metalimnion of the pelagic habitat in summer, most individuals in winter shift to a shallow bay that is unexploited in summer due to thermal constraints. In this habitat, zoobenthos abundance is more than twice as high at the end of the summer compared to littoral habitats close to the thermal refuge in the pelagic habitat. Surprisingly, brook charr showed strong within-lake site fidelity between two consecutive summers, which suggests that spatial memory could be a key driver of seasonal habitat use in this lacustrine population. Overall, our results suggest that thermal barriers create fragmentation between littoral and pelagic habitats that in turn produces resource opportunities that brook charr can track across seasons.

Keywords: acoustic telemetry, food resources, home range, macroinvertebrates, movement ecology, phenology, thermoregulation, winter ecology



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Introduction

The spatial configuration of thermal habitats constrains the thermoregulatory performance of ectotherms over space and time (Sears et al. 2016, Malishev et al. 2018, Kearney et al. 2021). Thermoregulatory performance can be defined as the absolute difference between the body temperature of an organism and its preferred temperature (Sears et al. 2016). Individual-based models of thermoregulatory behaviours in spatially explicit thermal landscapes showed that ectotherms thermoregulate more accurately when thermal resources are dispersed throughout space than when these resources are clumped (Sears et al. 2016). This issue could be particularly challenging for cold-stenothermic fish species living in dimictic lakes, where the metalimnion represents the thermal refuge during the stratified period and the epilimnion is the habitat where food resources, like benthic organisms, are usually most abundant (Vadeboncoeur et al. 2002, Vander Zanden and Vadeboncoeur 2002). Because the spatial configuration of thermal resources is clumped in these systems, we expect a decrease in the thermoregulatory performance of cold-stenothermic fish species when thermal constraints occur. In this context, lake morphology can also influence the availability of thermal habitats as well as accessibility to food resources, with potential consequences on littoral–pelagic habitat coupling (Dolson et al. 2009, Ridgway et al. 2023). Dolson et al. (2009) contrasted two ecological hypotheses on littoral–pelagic habitat coupling: the lake space hypothesis, which predicts that habitat coupling should increase as the amount of productive littoral space increases, and the accessibility hypothesis, which predicts that habitat coupling should increase when littoral production is close to thermal refuges. More specifically, it has been shown that in stratified lakes where stenothermic species dominate the fish community, lakes with more circular shapes have stronger littoral–pelagic coupling than lakes with more reticulate forms, where access to thermal refuges is more restricted (Dolson et al. 2009). Given the importance of habitat coupling in maintaining food-web stability by dampening oscillations in the abundances of both predators and prey (Post et al. 2000, Vadeboncoeur et al. 2005, Rooney et al. 2006), understanding factors controlling this coupling, like lake's spatial configuration, is of crucial importance. For instance, lake trout *Salvelinus namaycush* assimilated less littoral energy in thermally stressful years (i.e. shorter springs and longer summers) because of their reduced use of littoral habitat compared to deep pelagic waters, resulting in reduced growth and condition (Guzzo et al. 2017). The expected warming of lakes in response to climate change (Kraemer et al. 2015, O'Reilly et al. 2015, Bartosiewicz et al. 2019) and the potential for longer springs could amplify the problem of accessibility to food resources during summer, with consequences on energy pathways in lake food webs (Winder and Schindler 2004, Tunney et al. 2014, Guzzo et al. 2017).

These examples show that thermal landscapes not only vary through space and time, but have also potential consequences for habitat coupling and, in turn, food-web dynamics. This

is particularly relevant in seasonal environments such as temperate lakes. For instance, whereas future warming will impose greater thermal stress on lake trout during summer, longer springs could temper this negative effect (Guzzo and Blanchfield 2017). In lotic environments, fish can exploit the spatial heterogeneity in thermal and trophic resources on a daily or annual basis to improve their growth (Armstrong and Schindler 2013, Armstrong et al. 2013, Brewitt and Danner 2014). More generally, Armstrong et al. (2016) provided a conceptual framework to advance the study of phenological diversity. They showed that, for mobile consumers that can track the shifting mosaic of foraging opportunities (i.e. a form of habitat coupling), phenological diversity was often more important to consumer energy gain than was resource abundance per se. Their conceptual framework, which they termed 'resource waves,' was defined as an aggregate of trophic resources that 1) offers ephemeral foraging opportunities at fixed points in space, 2) exhibits spatial variation in phenology across landscapes and 3) protracts foraging opportunities for consumers that can track phenological variation across space, thus coupling different habitats or food chains, and time. However, barriers to animal movements could prevent accessibility to food resources, thus limiting the advantages provided by resource waves and potentially weakening habitat coupling. The permeability of physical barriers has been studied in both terrestrial and aquatic environments (Pépin et al. 2012, Beyer et al. 2016) under the general conceptual framework of habitat fragmentation (Eros and Campbell Grant 2015, Fahrig 2019). Temperature can also act as a barrier that results in variable permeability through space and time, thus temperature is now included in the conceptual framework of habitat fragmentation (Tuff et al. 2016). Therefore, combining the conceptual frameworks of resource waves and thermal habitat fragmentation or habitat coupling offers a stimulating research perspective to better understand fish habitat use and movements in temperate lakes.

In oligotrophic lakes of the Canadian Shield, littoral habitats provide rich-food resources for brook charr, *Salvelinus fontinalis* (Magnan 1988, Lacasse and Magnan 1992, Bourke et al. 1999), a species known to forage across littoral and pelagic habitats (Rainville et al. 2021, Stiling et al. 2023). Elevated temperatures in the epilimnion of dimictic lakes during summer could substantially reduce the use of these littoral areas by cold-stenothermic fish like brook charr. Decades of radiotelemetry studies have shown that large shallow areas are rarely used during summer, probably because elevated summer temperatures could act as thermal barriers, preventing brook charr from foraging in these areas (Bourke et al. 1996, Bertolo et al. 2011, Goyer et al. 2014, Pépin et al. 2015). The study of winter habitat use by cold-stenothermic fish species in ice-covered temperate lakes is challenging, but rapid advancements in acoustic telemetry technologies seek to fill this knowledge gap (Cote et al. 2020, McMeans et al. 2020, Marsden et al. 2021, Blanchfield et al. 2023). The main objective of our study was to evaluate whether seasonal thermal fragmentation in stratified lakes induces resource waves that brook charr, a mobile consumer, can track across

seasons. More specifically, we hypothesize that limited accessibility to the littoral habitat during summer would enhance foraging opportunities during winter because of reduced predation pressure on benthic organisms during summer. To this end, we used an automatic acoustic telemetry system to record brook charr positions for three consecutive years over the entire available habitat of this lacustrine population.

Material and methods

Lake characteristics

The study was carried out in Lake Ledoux (46°38'N, 73°15'W), Mastigouche Wildlife Reserve, Québec, Canada, from 2016 to 2018. Lake Ledoux is a typical small oligotrophic temperate zone lake with respect to surface area (11.9 ha), mean depth (5.5 m), maximum depth (18.0 m), and general physicochemical characteristics (Magnan 1988, Gignac-Brassard et al. 2023). In summer 2018, dissolved

oxygen concentrations were monitored in the metalimnion with two probes (miniDOT logger; PME) located at 3 and 5 m of depth. No oxygen limitation was detected for brook charr (mean of dissolved oxygen concentration: 8.41 mg l⁻¹). We defined brook charr thermal refuges as > 6 m of depth, which roughly corresponds to the bottom of the metalimnion and where brook charr can easily adjust their body temperature by moving in the water column (Fig. 1). The euphotic zone depth, defined as the depth of 1% surface irradiance for photosynthetically active radiation (PAR), is estimated at 6.6 m and Secchi depth at 4.3 m (Gignac-Brassard et al. 2023). Most aquatic vegetation is found between 0 and 2 m of depth (Magnan unpubl.). We defined the littoral zone as being between 0 and 2 m depth from the shore because this is the area where prey preferred by brook charr are found. Studies on 30 lakes in the same geographical area have shown that allopatric brook charr populations feed mostly on benthic invertebrates (> 60% by weight; East and Magnan 1991, Tremblay and Magnan 1991, Lacasse and Magnan 1992, Rainville et al. 2021). Another study on three lakes showed

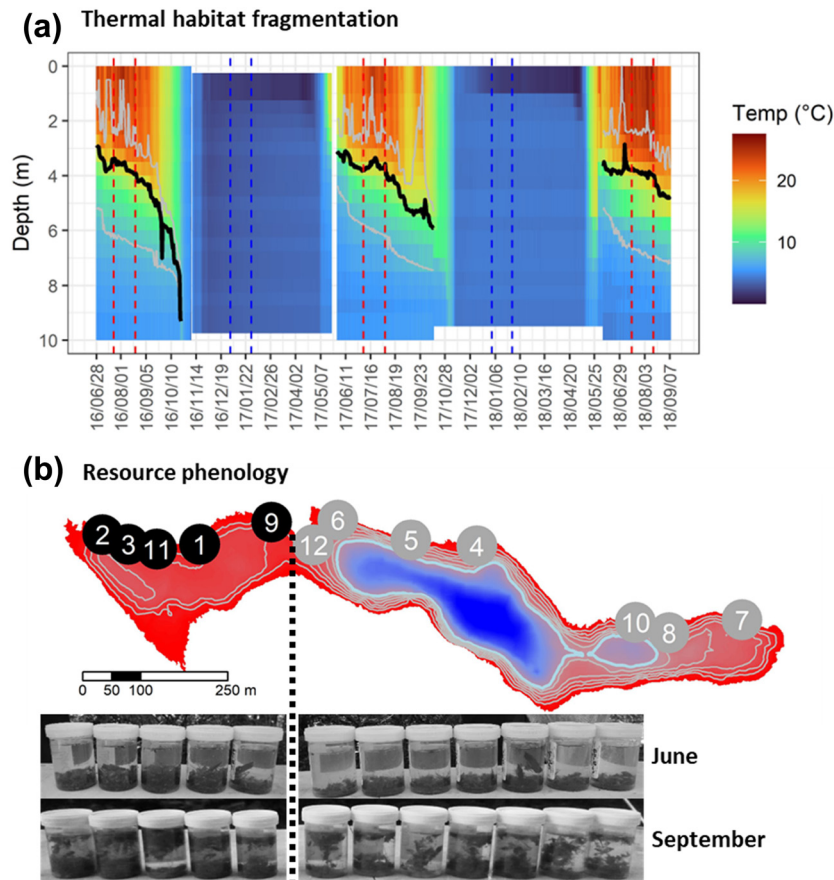


Figure 1. (a) Heat map of the temperature profile in Lake Ledoux from summer 2016 to fall 2018. The black line refers to the thermocline and the grey lines refer to the epilimnion (top) and the hypolimnion (bottom). Red and blue dashed vertical lines refer to the summer and winter periods covered in the present study, respectively. (b) Locations of zoobenthos sampling stations in Lake Ledoux. Circles indicate stations classified as accessible (grey) or inaccessible (black) to brook charr during summer (based on thermal constraints and spatial configuration of the lake; see details in text); numbers are station labels. Background colors show lake bathymetry from 0 m depth (red) to 18 m depth (blue). Light-blue line refers to the 6 m isopleth, the depth used to define the thermal refuge for brook charr. Grey lines refer to 1 m to 5 m isopleths. Photos show samples collected in June and September 2018, ordered from the western (left) to eastern (right) parts of the lake.

that the biomass of macrobenthos was on average 8.7 times higher in the littoral (< 2 m) than in the profundal (> 4 m) zone (Rodríguez and Magnan 1993). We also integrated other lake depth layers above the thermal refuge into our analyses of fish habitat use. Brook charr is the only fish species in this lake, and sport fishing is rigorously controlled by the Québec Government (Bourke et al. 1996). The lake was closed to fishing during the three years of the study, but illegal fishing was observed in Lake Ledoux (Pépin unpubl. details in the Supporting information).

Automatic acoustic telemetry system

We deployed acoustic telemetry positioning arrays to continuously follow brook charr movements and habitat use at fine spatiotemporal scales (< 1 min, < 5 m resolution) using two different VEMCO Positioning Systems (VPS). From 5 to 7 July 2016, we deployed 10 receivers (VR2Tx-069k-111-BAT; VEMCO Inc.) and two reference tags (V9TP-2x-069k-1-0034m; VEMCO Inc.). From 7 to 8 November 2016, four additional receivers were deployed to allow better coverage of the study lake during winter, especially in the shallow bay in the western section of the lake (Fig. 1, Supporting information). This VR2 positioning system was operational from 7 July 2016 until 22 May 2017, but full coverage of the lake was not accomplished until we added the four additional receivers in November 2016. Furthermore, the first VPS analyses revealed potential ‘collisions’ between tag signals, which occur when individuals are in proximity and create interference during signal transmission. In 2017, we changed to the HR2 VPS technology, which was specifically developed to circumvent this problem. This system consisted of 23 receivers (HR2-180k-100; VEMCO Inc.) and four reference tags (V9TP-2x-180k-34m; VEMCO Inc.). This HR2 VPS was operational from 21 June 2017 until 6 November 2018 and provided full coverage of the lake. Details of the VR2 and HR2 VPS as well as VPS performance are provided in the Supporting information.

Fish capture and tagging

Fish were caught using Alaska traps (1.0 × 1.8 m mouth opening, two 1 × 15 m wings, 1.27 cm mesh size; Fipec Industries) for three consecutive years (28 June–12 July 2016; 12–20 June 2017; 5–7 June 2018). After capture, brook charr were kept in an enclosure (3 × 4 × 6 m depth) and tagged on the same day. The tagging procedure was adapted from the methods described by Mellas and Haynes (1985), Adams et al. (1998), Bélanger and Rodriguez (2001), Bridger and Booth (2003) and Thiem et al. (2011), and it has been successfully used in previous studies (Goyer et al. 2014, Pepino et al. 2015). In 2016, 12 brook charr (mass: 282–438 g; fork length: 296–342 mm) were equipped with 6.2 g acoustic transmitters (V9TP-2x-069k-1-0034m; VEMCO Inc.). In 2017 (n = 30) and 2018 (n = 15), brook charr (mass: 226–600 g; fork length: 272–385 mm) were equipped with 4.0 g acoustic transmitters (V9TP-2x-180k-34m; VEMCO Inc.). The

transmitters had two sensors that alternately recorded water temperature and fish depth. Transmitter mass was always ≤ 2% of fish body mass, as recommended in previous studies (Mellas and Haynes 1985, Bridger and Booth 2003). After tagging, all fish released into the lake appeared to be in good condition and behaved normally, except the one fish found dead in the enclosure in 2016. Fish capture and tagging protocols are detailed in the Supporting information.

Thermal habitat fragmentation: lake stratification

Lake temperature profiles were made from the end of June 2016 until the beginning of September 2018 using thermographs (iButtons DS1922L in 2016 and 2017, iBCod DS1921G-F5 in 2018; Alpha Mac Inc.) moored at 0.5 m intervals from the surface to > 10 m. Thermograph lines were attached to a raft anchored at the lake’s deepest point. While iBCod are submersible, iButtons were encapsulated in aquarium silicone (clear SCS1200 silicone sealant) to protect them from prolonged water immersion. Temperatures were recorded at 4 h intervals. Lake Ledoux was generally stratified from mid-May to mid-October, and temperature dropped below 4°C from the beginning of November to the beginning of May, a period probably corresponding to ice cover (Fig. 1a). A simple moving average was used to calculate the mean surface water temperature for 30 consecutive days. Surface-water temperature was defined as the temperature from 0 to 2 m depth. This procedure helped us to define the warmest period for each year. The warmest 30 consecutive days of the water surface ranged from 22 July to 21 August in 2016, from 6 July to 5 August in 2017, and from 16 July to 15 August in 2018. These periods were used in statistical analyses to estimate home range and habitat use of brook charr during the warmest 30 consecutive days. Because of low temporal variations of water temperature during winter, we used monthly air temperature data from the Québec climate normal 1981–2010 at the Saint-Alexis meteorological station (46°28′00″N, 73°08′48″W) to define the coldest period (Data; accessed on 6 May 2022). Since January was the coldest month recorded at the meteorological station, brook charr data from 1 to 30 January were used in subsequent analyses to estimate home range and habitat use during the coldest 30 consecutive days. Characteristics of the lake’s thermal stratification were estimated with the ‘rLakeAnalyzer’ package (Winslow et al. 2019) in R (www.r-project.org).

Resource phenology: zoobenthos abundances

Zoobenthos abundances were assessed by a paired sampling design where the same 12 stations were sampled in late spring (13–14 June) and late summer (5–6 September) 2018. The stations were sampled parallel to the shore at depths of 60–65 cm, within 15 m from the shoreline. Benthic organisms were sampled by pushing a net (mesh size: 500 µm) along a 10 m straight line. At the end of the sampling, all living organisms were sorted and kept in 10% formaldehyde (Fig. 1b). In the laboratory, the 24 samples were rinsed with water and

identified with the Zooscan processing system (Gorsky et al. 2010). The minimum particle size for processing was set to 0.5 mm to avoid zooplankton and detritus noise. The maximum particle size was set to 100 mm to be sure to count large organisms like dragonfly larvae. All 30 934 images were imported into the EcoTaxa server to be semi-automatically classified at the lowest taxonomic level (Picheral et al. 2017). All identifications were checked visually. We retained the six most abundant taxonomic groups for further statistical analyses: Anisoptera, Chironomidae, Ephemeroptera, Gammaridae, Trichoptera and Zygoptera (the first five being common in the brook charr diet in this system; Tremblay and Magnan 1991, Magnan unpubl.). Taxonomic groups not included in the analyses represented less than 2.2% of total abundances and were, in order of decreasing abundance, Arachnidae, Culicidae, Mollusca, Cladocera, Notonectidae, Copepoda and Dystiscidae.

We used multivariate generalized linear mixed models (GLMM) with Poisson distribution to simultaneously analyze the abundance of the six taxonomic groups as a response variable according to the period of sampling (Month variable) and the accessibility to the station by brook charr during summer (Accessibility variable). To simplify statistical analyses, we used dummy coding for the Accessibility variable. Based on previous studies (Bertolo et al. 2011, Goyer et al. 2014), five stations in the shallow bay (western section of the lake) were classified as inaccessible to brook charr during summer and seven stations in the central and eastern parts of the lake were classified as accessible to brook charr because of thermal refuges (deep water) close to these stations (Fig. 1b). The mean distance to the thermal refuge (i.e. the 6 m isopleth) was 52 m (range: 26–158 m) and 287 m (range: 124–405 m) for accessible and inaccessible stations, respectively. Stations #7 and #9 were classified as accessible and inaccessible, respectively, because of the distances to the 4 m isopleth (37 m and 104 m, respectively), a depth where temperatures were still comfortable to brook charr (Fig. 1). This classification agrees with previous radiotelemetry studies on this lacustrine brook charr population (Bourke et al. 1996, Bertolo et al. 2011, Goyer et al. 2014) as well as results from the present study. The GLMM approach allows one to specify multivariate random effects for each station to estimate residuals correlations across taxa (Warton et al. 2015). We first compared three competing models varying in their fixed effects. Model 1 only includes the Month variable, model 2 includes both the Month and Accessibility variables, and model 3 includes both the Month and Accessibility variables as well as their interaction. Model 1 is the null model, which implies that there is no difference in brook charr accessibility to the station. Model 2 tests the hypothesis that differences in zoobenthos abundance are a function of brook charr accessibility to the station, but that these differences are constant through time. Model 3 tests the hypothesis that the difference in zoobenthos abundance according to station accessibility varies through time. We would expect that zoobenthos abundance would be higher at stations with low accessibility (model 2) and that these differences would tend to increase

throughout the summer (model 3) due to low predation by brook charr during summer, i.e. thermoregulatory costs would limit accessibility to littoral habitats far from thermal refuges (i.e. deeper part of the lake; Fig. 1b). All models include a multivariate random intercept at each station (i.e. random effect for the six taxonomic groups; Group variable). We also removed the overall intercept to obtain estimates for each taxonomic group and included the interaction between the Group variable and each of the fixed effects. GLMM models were performed with the *glmer* function of the 'lme4' package (Bates et al. 2015) in R (www.r-project.org).

Brook charr habitat use

The median number of positions per individual was 13 556 (range: 0–44 049) with the VR2 VPS and 439 459 (range: 4283–1 881 442) with the HR2 VPS. The number of daily individual positions was at least one order of magnitude higher with the HR2 VPS than with the VR2 VPS, corresponding to a median number of daily individual positions generally greater than 2000 positions day⁻¹ (see the Supporting information for details). Since the VR2 VPS did not provide full coverage of the lake during summer, fish habitat use and home-range analyses were performed on HR2 data only, although we also present the qualitative results of the VR2 data. Four variables were used to describe brook charr habitat use: fish depth (i.e. recorded by the sensor) and lake depth (i.e. derived from bathymetric map) where fish position was recorded (to show brook charr vertical distribution within the lake), and fish distance from the shoreline and fish distance from the thermal refuge (i.e. distance to the 6 m isopleth, to show brook charr horizontal distribution within the lake). We also calculated the proportion of positions at three lake depth layers (i.e. 0–2, 2–4, 4–6 m) outside the thermal refuge (i.e. > 6 m). Before conducting home-range analyses, position data were filtered to retain those having a horizontal position error (HPE) below 25 and a root-mean-squared error (RMSE) below 10. These thresholds allowed us to discard most of the positions that fell outside of the boundary of the lake but retain positions in the littoral habitat, where position accuracy was generally lower. However, because of the large amount of position data, changing the specific threshold values did not change the conclusions presented here.

For each fish having a full-year record of positions, we calculated the home range during the warmest 30 consecutive days in summer (i.e. 6 July–5 August 2017, 16 July–15 August 2018) and the coldest month in winter (i.e. 1–30 January of 2017 and 2018). These periods were chosen to maximize the differences in habitat use by brook charr between summer and winter, thus highlighting the thermal constraints imposed by lake stratification and avoiding spring and fall, when brook charr must cope with other biological needs (e.g. searching for spawning sites in fall). Since we suspected that sample size could have an influence on home-range estimates, positions were sampled randomly before calculating home range at three isopleth levels of the

utilization distribution (i.e. 0.5, 0.9 and 0.95). The isopleths, or contours of the utilization distribution, are typically defined at 50% for the core home-range estimate to 95% for the total home-range extent. We varied the number of positions used to calculate home range (i.e. sample size) from 100 random positions to the maximum number of positions for each fish and season (range: 42–408–149–416 positions). Home range was calculated 10 times for each fish, isopleth, and sample size using the kernel density method. We then calculated home-range overlaps between summer 2017 and winter 2018 or summer 2017 and summer 2018 for each fish based on 40 000 randomly selected positions for each fish during each season. Among the currently available methods to calculate home-range overlaps, we chose the utilization distribution overlap index (UDOI; Fieberg and Kochany 2005) for this study. UDOI measures the amount of overlap relative to two individuals using the same space uniformly and ranges from zero (two home ranges that do not overlap) to 1 (both home ranges are uniformly distributed and have a 100% overlap). UDOI is generally the most appropriate index for quantifying overlap in terms of space-use sharing (Fieberg and Kochany 2005). All analyses were performed in R (www.r-project.org). Fish positions were mapped with the 'tmap' package (Tennekes 2018). Brook charr habitat use was estimated by linear mixed models (fish and lake depths, distance to the shoreline, distance to the thermal refuge) or generalized mixed models (proportion of positions; binomial family) with season as fixed factor and fish as random effect using the 'glmmTMB' package (Brooks et al. 2017). Home range and home-range overlap were calculated using the *hr_kde()* and *hr_overlap()* functions of the 'amt' package (Signer et al. 2019), respectively.

Results

Lake thermal stratification

Lake thermal stratification was consistent across the three consecutive seasons for the warmest summer months (Table 1). On average, the metalimnion ranged from 2.3 m (epilimnion) to 6.4 m (hypolimnion) with a thermocline depth around 3.7 m (Fig. 1a). Surface temperatures were hottest in summers 2016 and 2018 and rose above 22.4°C – a temperature threshold above which brook charr avoid excursions into the epilimnion (Goyer et al. 2014) – on 27 days and 31 days

(i.e. the whole study period in summer 2018), respectively (Table 1). Although the mean surface temperature in summer 2017 was above the 22.4°C temperature threshold, it rose above this threshold only half of the time (i.e. 16/31 days; Table 1). Despite these small differences in surface temperature, thermal layers were comparable among summer seasons (Table 1).

Zoobenthos abundances

Model comparisons based on Akaike information criteria and log-likelihood ratio tests showed that model 3 outperformed the other two models (Supporting information). Taxonomic groups other than Gammaridae had higher abundances in less accessible habitats than in more accessible ones (Fig. 2, Supporting information). These differences increased at the end of the summer in two taxonomic groups (i.e. Trichoptera and Zygoptera), where abundances were 2.5 times higher in less accessible than in more accessible habitats in September (Supporting information). Abundances of Anisoptera and Ephemeroptera were approximately twice as high in less accessible compared to more accessible habitats, and these differences are stable through time. Finally, Chironomidae had the lowest abundances of the taxonomic groups, with abundances from 1.4 (i.e. September) to 2.1 (i.e. June) times higher in less accessible compared to more accessible habitats. Gammaridae was the most abundant taxonomic group; their abundances were stable throughout the lake and among seasons.

Brook charr habitat use

Among the 30 fish tagged in 2017, 29 had at least one season of positioning data, eight had at least two seasons, and seven had three complete seasons (Fig. 3). Of the 12 fish tagged in 2016, eight had at least one season of positions and five had two complete seasons (Supporting information). Fish mainly used the thermal refuge in the central part of the lake during summer and the shallow areas during winter, especially the large shallow basin in the western section of the lake (Fig. 3, Supporting information). Brook charr were mainly found in the metalimnion below the thermocline during summer and shifted to shallow areas during winter (Table 2, Fig. 3). Mean fish body temperatures were 12.34°C (range: 6.65–14.96°C) in summer 2017, 11.77°C (range: 8.96–14.23°C) in summer 2018, and 3.21°C (range: 2.28–3.91°C) in winter 2018.

Table 1. Characteristics of lake thermal stratification during the warmest summer month of each year. Mean (min–max) estimates are shown. Surface temperature refers to the mean daily temperature from 0 to 2 m of depth. $n_{22.4^{\circ}\text{C}}$ is the number of days when the surface temperature was above 22.4°C, a temperature threshold above which brook charr avoid excursions into the epilimnion (Goyer et al. 2014).

Season	Hypolimnion depth (m)	Thermocline depth (m)	Epilimnion depth (m)	Surface temperature (°C)	$n_{22.4^{\circ}\text{C}}$ (days)
Summer 2016	6.36 (6.16–6.57)	3.68 (3.37–3.94)	2.22 (0.50–2.94)	23.12 (22.18–24.74)	27
Summer 2017	6.01 (5.78–6.23)	3.62 (3.35–3.80)	2.13 (0.39–2.79)	22.56 (21.33–23.90)	16
Summer 2018	6.83 (6.64–7.03)	3.90 (3.74–4.09)	2.40 (1.64–3.08)	24.36 (23.50–25.58)	31

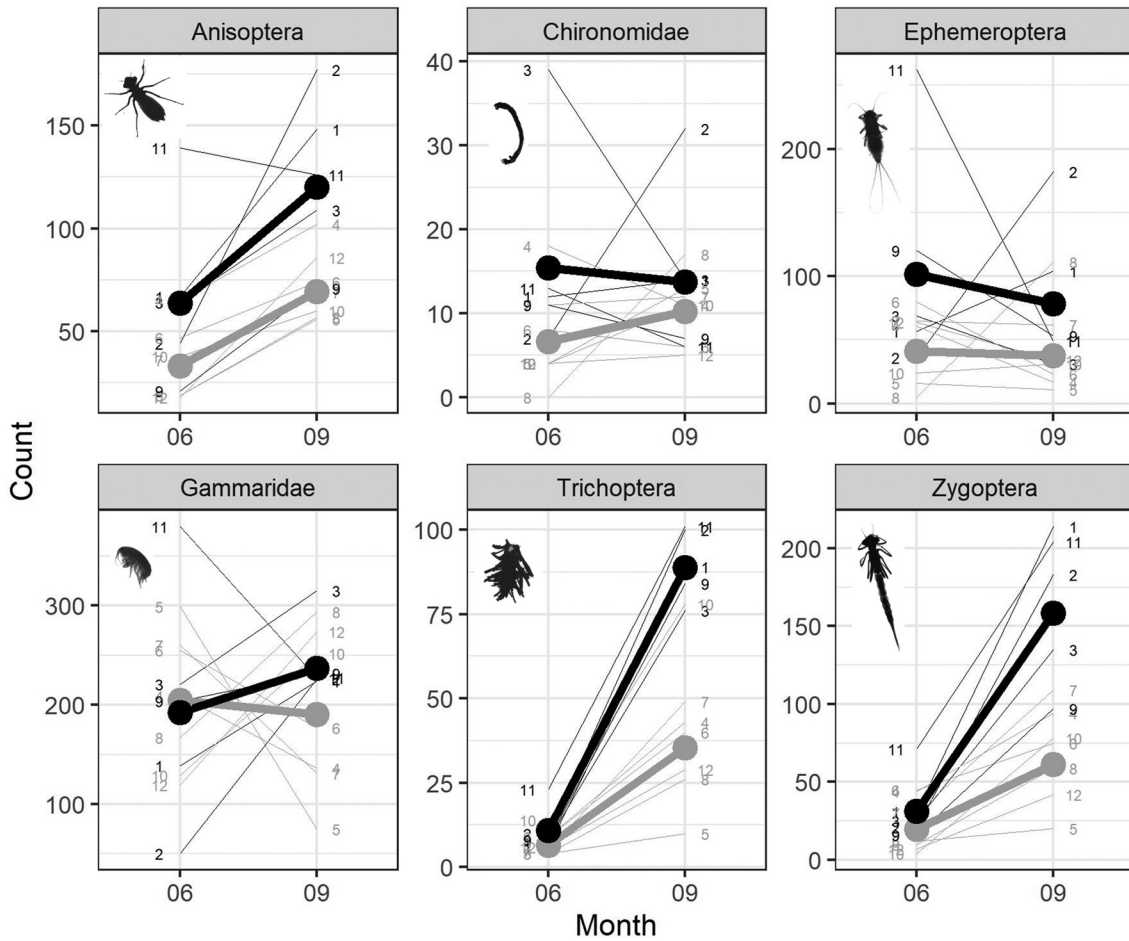


Figure 2. Observed and predicted zoobenthos abundances for each of the six main taxonomic groups in June (6) and September (9) 2018. Thin lines show abundance data at the station level (observed abundances). Heavy lines indicate the abundances predicted by the best overall model (i.e. model 3). Line colour indicates prey that were accessible (grey) or inaccessible (black) based on thermal constraints and spatial configuration of the lake; see details in text). Numbers (1–12) refer to station labels (map on Fig. 1 for details). Inset images were obtained by the Zooscan.

Although we found no evidence that distance to the shoreline changed among seasons, brook charr stayed close to the 6 m isopleth when positions were recorded outside the thermal refuge in summer, whereas the distance to the thermal refuge was one order of magnitude higher in winter (Table 2). The shift in brook charr habitat use between summer and winter was confirmed by examining the proportion of positions according to lake depth layers (Fig. 4). In summer, most brook charr positions were within the thermal refuge (i.e. > 6 m lake depth layer) followed by the 4–6 m lake depth layer. In winter, most brook charr positions were in the 2–4 m lake depth layer and brook charr were rarely found at deeper lake depths. The low proportion of positions in the 0–2 m lake depth layer could be an artifact of the VPS array’s performance (e.g. lower probability of detection nearshore; Roy et al. 2014), water level fluctuation or ice thickness during winter and should thus be interpreted with caution. For instance, natural water level fluctuation was around 20 cm in Lake Ledoux and ice thickness could reach 70 cm at the end of the winter season in nearby lakes (Pépinou unpubl.),

suggesting that some littoral areas could be inaccessible to brook charr during winter or when the water level is low. Dynamic bathymetric maps integrating water level fluctuation and ice thickness, as well as probability detection, could therefore provide better accuracy on lake depth layer occupied by brook charr.

Home-range estimates decreased as sample size increased, and variability in home-range estimates dropped considerably when we used ≥ 1000 random positions (Supporting information). With 40 000 random positions – the sample size used for home-range overlap calculation – no variation was observed in home-range estimates. Visualization of home-range areas confirmed the results from the position data (Supporting information). Home-range overlap showed that habitat use was different between summer and winter (i.e. no overlap; UDOI median: 0.000 ± 0.027 SD), but that there was strong site fidelity between two consecutive summers (i.e. high overlap; UDOI median: 0.549 ± 0.282 SD, Supporting information). Although all brook charr used the thermal refuge in the central part of the lake during summer,

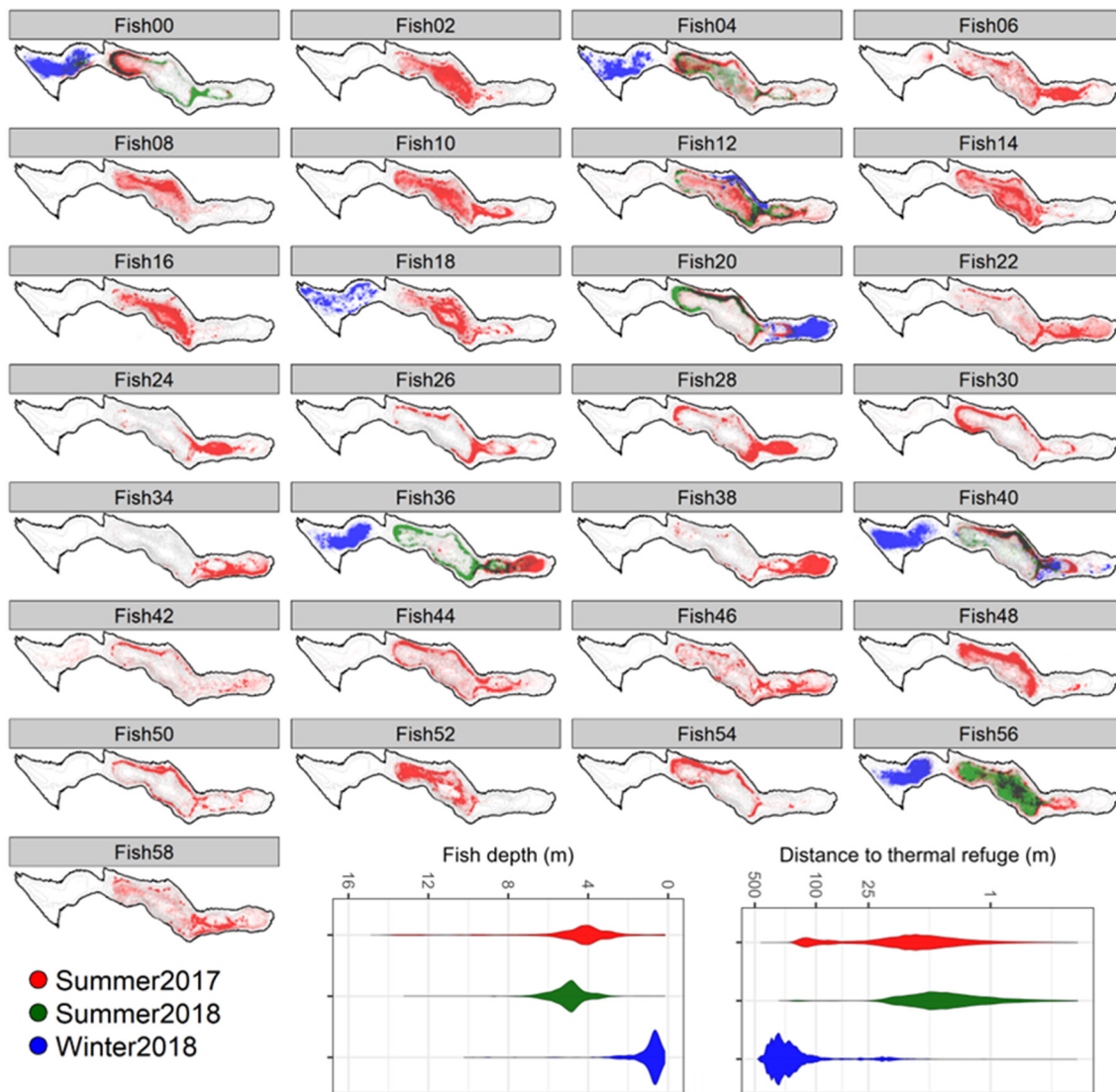


Figure 3. Fish positions for three consecutive seasons identified by colour. Only fish having at least one complete season are shown. Violin plots of fish depth and distance to the thermal refuge are shown as inset graphs (Table 2).

home-range overlap for individuals during two consecutive summers was globally higher than home-range overlap among individuals within the same season (Fig. 5). This result can be visualized with data on raw positions (Fig. 3), but it is particularly evident when comparing core home-range areas (i.e. 0.5 m isopleth level; Supporting information).

Discussion

Brook charr concentrated near the central part of the lake in summer, where they found thermal refuge in the pelagic habitat. The depletion of zoobenthos in littoral areas close to the pelagic habitat suggests that brook charr undertook

Table 2. Brook charr habitat use as represented by fish depth, lake depth (i.e. lake depth at which fish positions were recorded), distance to the shoreline, and distance to the thermal refuge (i.e. distance to the 6 m isopleth when fish were located between the shoreline and the 6 m isopleth). Estimates (95% confidence intervals) from the linear mixed model with season as fixed factor and fish as random effect are shown. Sample size refers to the number of brook charr positions.

Season	Sample size	Fish depth (m)	Lake depth at fish position (m)	Distance to shoreline (m)	Distance to thermal refuge (m)
Summer 2017	5 166 526	4.47 (3.76–5.17)	7.01 (6.22–7.80)	19.1 (17.7–20.5)	22.1 (11.71–32.4)
Summer 2018	1 491 870	5.40 (4.70–6.10)	7.41 (6.62–8.20)	20.0 (18.6–21.4)	15.8 (5.5–26.2)
Winter 2018	1 633 826	1.31 (0.61–2.01)	3.19 (2.40–3.99)	20.8 (19.4–22.2)	199.6 (189.3–210.0)

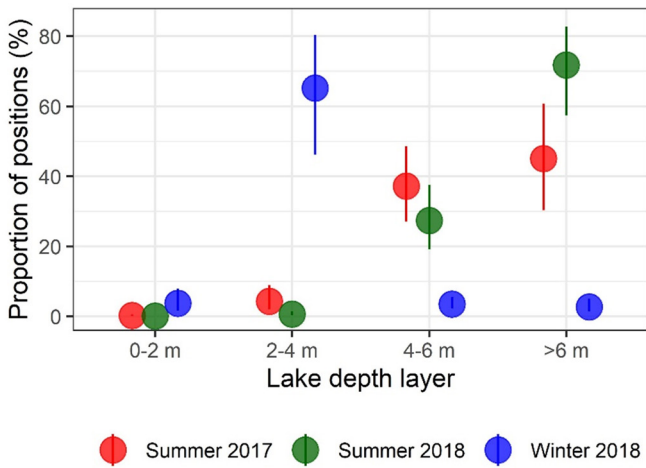


Figure 4. Proportion of brook charr positions according to four lake depth layers (0–2, 2–4, 4–6, > 6 m). Estimates (points) and 95% confidence intervals (bars) from the generalized linear mixed model (binomial family) with season as fixed factor and fish as random effect are shown for each lake depth layer.

short excursions to these littoral areas for feeding during summer. While other environmental factors (e.g. macrophyte cover, bathymetry) could affect benthic production in lakes (Mittelbach 1981, Hanson 1990, Rodríguez and Magnan 1993), the strong evidence that brook charr stayed close to thermal refuges in summer would certainly contribute to the

observed differences in benthos abundance, since benthic prey are preferred by brook charr (East and Magnan 1991, Lacasse and Magnan 1992, Rainville et al. 2021). Although the underlying mechanisms explaining benthos abundances are unknown – as are benthic abundances during winter because of logistic difficulties – brook charr habitat use in winter is highly consistent with benthos abundances at the end of the summer. Indeed, most individuals shifted to the shallow bay in the western section of the lake in winter, an area that was unexploited during summer and where zoobenthos abundances were more than two times higher than in littoral areas close to the thermal refuge at the end of the summer. To the best of our knowledge, this is the first study showing both within-lake site fidelity and migratory behaviours across seasons in a fish species living in a closed system. Overall, our study shows the complementarity of habitats across seasons and strong site fidelity during summer in a lacustrine brook charr population. Our results suggest that thermal barriers create resource waves (i.e. ephemeral foraging opportunities that change over space and time) that lacustrine brook charr can track across seasons.

Spatial configuration of thermal habitats

Our study agrees with the large body of literature showing that the thermal regime of stratified lakes restricts habitat use for cold-stenothermic fish species to deep water

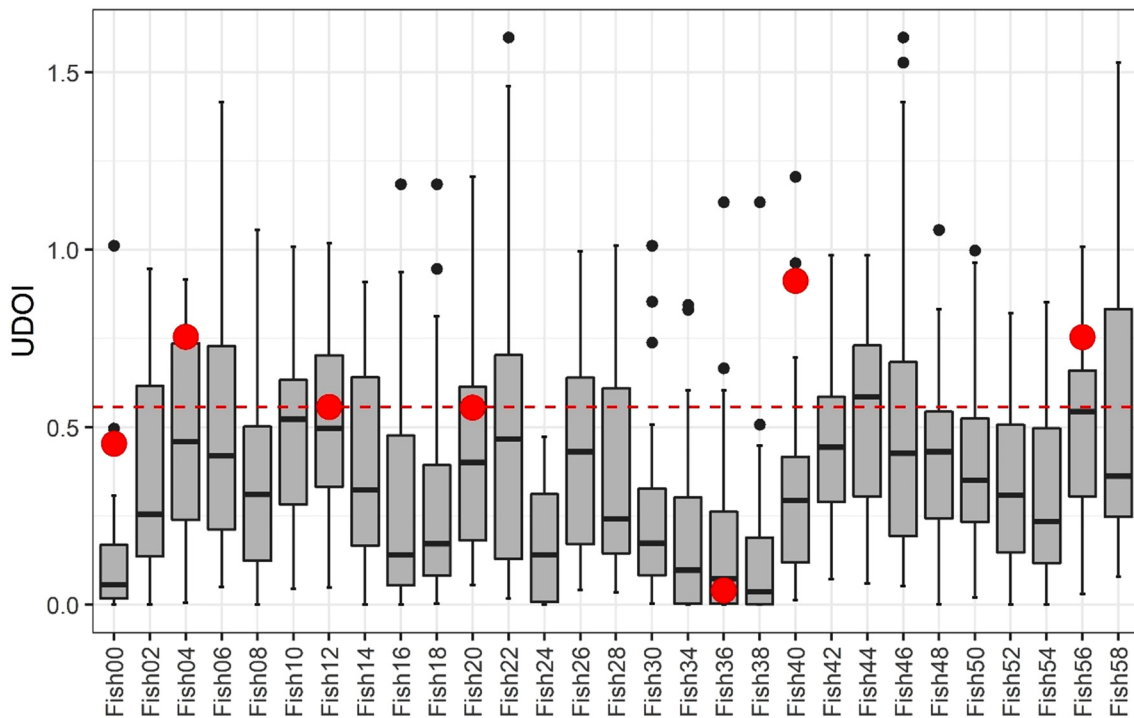


Figure 5. Boxplot of home-range overlap between individuals within the same season (i.e. summer 2017). The utilization distribution overlap index (UDO) is calculated at the 0.9 isopleth level. Each boxplot summarizes home-range overlap from one fish to all other fish. In this example, all positions are used to calculate home-range overlap. To facilitate comparison, red points (i.e. seven fish having both summer 2017 and summer 2018 positions; Fig. 3) and the horizontal dashed line (median of the seven individuals) represent the within-individual home-range overlap between summer 2017 and summer 2018. Black points are extreme data values that are more than 1.5 times the interquartile range from the box.

during summer (Blanchfield et al. 2009, Bertolo et al. 2011, Goyer et al. 2014, Guzzo et al. 2017, Cote et al. 2020). The exception to this general rule arises in lakes where the thermal constraint is relaxed (Dawidowicz and Maciej Gliwicz 1983), confirming that temperature is the primary driver of habitat use for cold-stenothermic fish species during summer. Indeed, brook charr stocked in an ultra-oligotrophic lake aggregated during summer in the epilimnion, which rarely exceeded 12°C, feeding mainly on terrestrial insects (Dawidowicz and Maciej Gliwicz 1983). Contrary to terrestrial ecosystems, where thermal refuges can be found in shelters close to food resources (Sears et al. 2016), thermal refuges are generally clumped and decoupled from food resources in aquatic ecosystems, imposing a stronger tradeoff between feeding and thermoregulatory needs (Brewitt and Danner 2014, Guzzo et al. 2017). Facing this tradeoff, fish could thus preserve energy by cooling down (Javard and Anderson 1967, van Dijk et al. 2002, Goyer et al. 2014) or shifting to alternative food resources in the pelagic habitat (Hayden et al. 2014, Tunney et al. 2014, Rainville et al. 2021). The roles of spatial heterogeneity for thermal and food resources in fish thermoregulatory behaviours have been reported in riverine networks (Armstrong and Schindler 2013, Brewitt and Danner 2014), but less attention has been given to lake ecosystems. Addressing this theoretical framework in lakes helps to improve our understanding of habitat coupling between littoral and pelagic habitats (Stiling et al. 2023). Our results agree with the accessibility hypothesis (sensu Dolson et al. 2009), which predicts stronger littoral–pelagic habitat coupling when littoral resources are more accessible due to the proximity of thermal refuges. Thus, littoral–pelagic coupling is expected to be relatively strong in our study system if only the central basin is considered (i.e. when the thermal refuge is close), but its strength varies dramatically if we consider among-basin coupling since average distance from the thermal refuge is larger.

Integrating the spatial configuration of littoral and pelagic habitats to the energy budgets of ectotherms will provide not only a better understanding of the habitats available to cold-stenothermic fish considering their ecological needs during summer (Plumb et al. 2014, Pépino et al. 2015, Malishev et al. 2018, Kearney et al. 2021), but also contribute to our understanding of habitat coupling in these systems. Our results suggest that brook charr is an ‘adaptive forager’ (sensu Post et al. 2000) that can change the proportion of time it feeds in different habitats depending on resources waves. It has been suggested that the existence of such prey switches – the mechanism allowing habitat coupling with prey from different habitats – can stabilize the dynamics of otherwise disconnected food webs (Post et al. 2000). In our case, food-web flexibility arises at least partly from changes in the physical environment that modulate predator behaviours. The consequences for food-web dynamics have yet to be assessed in natural systems, but theoretical work suggests that spatio-temporal variations in the strength of habitat coupling may dampen oscillations in predator–prey systems and are thus key to their stability (Post et al. 2000).

Resource waves

Even though winter conditions impose strong ecological constraints on fish populations (Shuter et al. 2012, Hayden et al. 2015, Fernandes and McMeans 2019), the winter ecology of fish species has not often been investigated (Huusko et al. 2007), especially for ice-covered lake ecosystems (Blanchfield et al. 2009, Cote et al. 2020). However, recent advances in acoustic telemetry may be able fill this gap (Marsden et al. 2021, Blanchfield et al. 2023). Our study confirms that salmonid species preferentially use littoral habitats during winter (Amundsen et al. 2008, Bass et al. 2014), with non-overlapping home ranges between winter and summer seasons (Blanchfield et al. 2009, Cote et al. 2020). Brook charr were not uniformly distributed in littoral areas during winter, but they were mainly concentrated in shallow areas (i.e. the bay in the western section of the lake), where zoobenthos abundances were highest at the end of the summer. Since resource depletion and temperature could be important drivers for growth and survival during winter (Xu et al. 2010, Shuter et al. 2012, Hayden et al. 2015), littoral areas that are inaccessible to brook charr during summer could constitute rich food supplies during winter. This finding agrees with the idea that mobile consumers can track resource waves across seasons (Armstrong et al. 2016). However – and contrary to reported examples (e.g. bears synchronize their use of tributaries with the migration timing of salmon species; Armstrong et al. 2016) – our study suggests that the mobile consumer itself, here the brook charr, structures the spatial and temporal distribution of food resources across seasons: there is limited resource depletion in the most inaccessible areas of the littoral zone during summer due to the spatial configuration of the lake’s thermal habitat. Along with food resources, other environmental factors could affect brook charr habitat use during winter. Among them, light limitation and hypoxia are the most plausible (Blanchfield et al. 2009, Rodrigues et al. 2022, Perga et al. 2023). For instance, large shallow basins allow fish to forage on benthic resources away from the shoreline, which is often shaded due to the low angle of the sun in winter. Furthermore, lake Ledoux is a small and relatively shallow which is similar in size and morphology to a study lake where severe hypoxia has been documented (Rodrigues et al. 2022). Although we did not measure dissolved oxygen concentrations during winter or into the hypolimnion, the shift in habitat use to the shallow western basin before ice cover (Supporting information) suggests that the observed brook charr distribution in winter is highly consistent with the distribution of benthic resources. We think that this is the most parsimonious hypothesis for our system, but hypoxia should also be considered in future studies on winter habitat use by brook charr.

Spatial memory in animals

Although the study of spatial learning in fish ecology has gained interest in recent years, most studies on this phenomenon rely on captive fish in laboratory experiments, so future

studies on fish cognition in more natural settings are needed (Salena et al. 2021). Spatial memory – the retention of information acquired through spatial learning – is a central topic of research in movement ecology (Fagan et al. 2013) and is particularly relevant for revealing mechanisms explaining how mobile consumers can track resource waves. When environmental or seasonal predictability is high, memory-driven movements outperform other types of movements for finding the ‘right place to go’ (Mueller and Fagan 2008, Merkle et al. 2019, Riotte-Lambert and Matthiopoulos 2020). Although this theoretical framework has been validated for terrestrial species with long migrations, our results suggest that spatial memory could be a key driver of seasonal habitat use in brook charr populations – or stenothermic fish species in general – inhabiting stratified lakes in the temperate zone, where seasonal predictability is very high. We suggest that the general concept of animal migration could also be applied at smaller spatial scales for fish populations living in closed systems. However, contrary to other species that use route-based navigation to migrate over long distances (e.g. magnetic field, solar navigation), cognitive mapping or location-based navigation is likely the underlying process for retaining spatial information in closed systems (Fagan et al. 2013, Bett and Hinch 2016). The high temporal predictability and coarse spatial heterogeneity of resources could explain the emergence of such population-level home-range patterns across seasons (Mueller and Fagan 2008).

Only a few experimental studies have demonstrated spatial learning and memory in brook charr, especially in the context of individual differences, or personality, in animal behaviour (Cortez Ghio et al. 2016, White et al. 2017). The strong site fidelity observed at the individual level for two consecutive summers suggests that spatial learning and memory also occur in natural brook charr populations, as documented in lake trout inhabiting a small northern lake with distinct basins (Gallagher et al. 2021). This spatial pattern in habitat use was termed ‘sedentary ranges,’ with spatial memory hypothesized as the most effective individual-level movement mechanism (Mueller and Fagan 2008). The high temporal predictability and fine spatial heterogeneity of resources could explain the emergence of this population-level home-range pattern within the summer season (Mueller and Fagan 2008).

Impacts of non-native species on resource depletion during summer

In our model system of Lake Ledoux, brook charr live in allopatry. However, during the last century, bait fishers have introduced warm-tolerant fish species like creek chub *Semotilus atromaculatus* and white sucker *Catostomus commersonii* to many Canadian Shields lakes, which could reduce the relative abundance and biomass of brook charr by 30–70% (Magnan 1988, Tremblay and Magnan 1991, Lacasse and Magnan 1992). Intentional illegal introductions of warmwater species like smallmouth bass *Micropterus dolomieu* to establish a recreational fishery is another threat to native salmonid populations (Sharma et al. 2009). These warm-tolerant species

compete for food with brook charr in the littoral habitat. Their presence may contribute to resource depletion during summer, when brook charr seek thermal refuges, and thus deplete the ‘littoral winter pantry’ for brook charr. Given that summers should last longer in the future (Bartosiewicz et al. 2019), this could exacerbate the contrasting impacts of climate change on allopatric versus sympatric brook charr populations. Preventing future illegal introductions of warm-tolerant species should thus be a management priority, as has been suggested for other stenothermic fish species facing similar ecological threats (Morrissey-MacCaffey et al. 2019).

Speculations

Acoustic telemetry studies generate large amounts of data and raise more ecological questions than can be addressed in a single study. For instance, site fidelity was an unexpected result in our study, and we currently have no other explanation for this than spatial memory. Integrating memory into movement analyses (Van Moorter et al. 2009, Riotte-Lambert et al. 2017, Bracis et al. 2018) should thus refine the mechanisms behind fish habitat selection. Within the theoretical framework of behavioural thermoregulation and dynamic bioenergetic models (Plumb et al. 2014, Pépino et al. 2015), fine-scale movement analyses of fish forays to the epilimnion or the hypolimnion is another interesting avenue of study concerning the adaptation of fish behaviour to environmental constraints such as temperature or hypoxia (Roberts et al. 2012, Guzzo et al. 2017, Rodrigues et al. 2022). Finally, fall and spring, although short, can be very important foraging periods for fish, as demonstrated for lake trout (Guzzo et al. 2017, Blanchfield et al. 2023), but are unexplored in the present study. We hope that this study will stimulate future works to address these ecological questions.

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Author contributions

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Data availability statement

Thermal habitat fragmentation in stratified lakes induces resource waves that brook charr track across seasons. DOI: 10.5061/dryad.x69p8czr4.

Data can be uploaded using the following link: <https://datadryad.org/stash/share/jn2Hx1NOceezvCX4rrE-JLuGOXppiYnRMrThcCQwom0>

Data are available from the Dryad Digital Repository: <https://doi.org/10.5061/dryad.x69p8czr4> (Pépin et al. 2024).

Supporting information

The Supporting information associated with this article is available with the online version

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